

Chapter 19

Interactions of Biological Soil Crusts with Vascular Plants

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19.1 Introduction

In most dryland ecosystems, biological soil crusts (biocrusts) coexist alongside herbaceous and woody vegetation, creating landscape mosaics of densely vegetated and biocrust-covered patches (Boeken and Shachak 1994; Belnap 2003; Cortina et al. 2010; Maestre et al. 2010). The patterns and dynamics of these patches are affected by multiple direct and indirect interactions between vascular plants and biocrusts and include negative and positive effects (Fig. 19.1).

In general, the influence of biocrusts on vascular vegetation is the result of interactions among biocrust type, vascular plant characteristics, and local climatic, environmental, and edaphic conditions. Differences in biocrust composition and substrate result in diverse morphological, physical, and chemical features that create unique microenvironments of temperature, nutrient and water availability, and trapping of organic matter and seeds. The manner in which biocrusts affect the capture and retention of plant seeds, the availability of water and nutrients, and the

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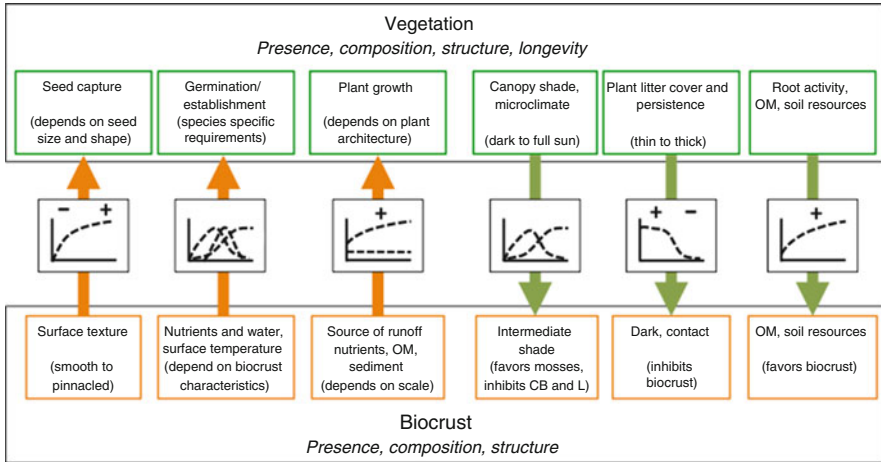


Fig. 19.1 Schematic diagram of the positive and negative mutual interactions between biocrust and vegetation and their dependence on various functions and properties of both (CB cyanobacteria, OM organic matter, M mosses, L lichens, Sp species)

temperature of the soil surface will ultimately determine whether crusts promote, inhibit, or have negligible effects on vascular plant communities. Furthermore, the effects of biocrusts on plants are not restricted to the crust-covered patches themselves, as they alter local hydrology (see Chap. 17 by Chamizo et al.) and nutrient cycles (see Chaps. 14 and 15 by Barger et al. and Sancho et al., respectively), thus influencing the availability of water and nutrients reaching nearby plants (Boeken and Orenstein 2001). The vascular plant communities, in turn, can affect biocrust presence, development, and composition through canopy shade, water relations, litterfall, and root activity, all of which vary depending on plant density, composition, and phenology.

19.2 Influences of Biocrusts on Colonization and Seedling Emergence of Vascular Plants

19.2.1 Seed Arrival, Retention, and Accumulation

Widespread seed dispersal is common in open habitats, where wind and water move seeds across the soil surface until they are trapped by depressions or barriers (Boeken and Shachak 1994; Jumpponen et al. 1999; Marteinsdottir et al. 2010). Biocrusts have diverse microtopographies (George et al. 2000; Davidson et al. 2002; Bowker et al. 2006; Langhans et al. 2009) that affect their ability to trap seeds, mainly depending on surface roughness in relation to secondary seed dispersal. In addition, external seed morphology, such as seed appendages, is

believed to influence germination via effects on water absorption (Harper 1977; Fenner and Thompson 2005; Baskin and Baskin 1998) 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) (Harper 1977; Fenner and Thompson 2005; Gros et al. 2006; Boeken and Shachak 1994). The appendages may also reduce the ability of seeds to fall through cracks in the biocrust. This may explain observations in the Gurbantunggut Desert (NW China), where seeds with appendages were virtually absent in the soil beneath moss and lichen biocrusts. Furthermore, plants having seeds with appendages were rarely found in these biocrusts. In contrast, plants having seeds with appendages were present in bare soil following biocrust disturbance or in cyanobacterial crusts (Zhang unpublished data).

The effects of biocrusts on seed retention and the soil seed banks are highly species specific and range from positive (Bliss and Gold 1999; Boudell et al. 2002) to minimal (Boeken et al. 2004; Megill et al. 2011) to negative (Boeken and Shachak 1994; Li et al. 2005; Clements et al. 2007). This variability is primarily related to the type of biocrust, as pinnacled and rolling crusts found in cool and cold deserts are able to trap seeds more effectively than smooth crusts common in hot deserts (Belnap 2003). For instance, two biocrusts with high surface roughness due to the presence of foliose lichens or mosses promoted both seed entrapment and seed bank accumulation in arid lands of Patagonia (Bertiller and Ares 2011) and Northern China (Su et al. 2007), respectively. However, increases in roughness due to biocrusts do not enhance seed entrapment in all cases (Olano et al. 2005; Clements et al. 2007). For example, Li et al (2005) found that a moss biocrust decreased seed entrapment and seed density in the soil seed bank despite the added roughness.

On undisturbed surfaces of smooth cyanobacterial crusts typical for hyperarid deserts, seeds are exposed to removal by wind, surface water runoff, and granivory (Boeken and Shachak 1994). Therefore, soils under this type of crust often have limited seed banks (Prasse and Bornkamm 2000; Boeken et al. 2004; Li et al. 2005). Some species overcome the physical barrier formed by flat, dense cyanobacterial crusts (and generally underlying physical crusts) by specific adaptations. For instance, the annual grass *Stipa capensis*, which dominates the smooth and dense cyanobacterial crusts in semiarid zones of North Africa and the Middle East, has specialized soil positioning and penetration mechanisms mediated by hygrocastic awn movement (Boeken and Shachak 1994, 2006). Seeds of the annual forb *Plantago coronopus*, which are dispersed from the dead parent plant during rainfall, adhere to cyanobacterial crusts by means of a mucilaginous seed coat and are thus relatively well protected against removal by water and granivores (Gutterman and Shem-Tov 1997).

19.2.2 Seed Germination and Seedling Emergence

Seed germination requires water imbibition under adequate temperature, which is followed by an increase in seed metabolic activity and subsequent radicle growth and emergence (Fenner and Thompson 2005; Finch-Savage and Leubner-Metzger 2006). Most studies on the effect of biocrusts on germination are not limited to the events leading to radicle emergence, but also include subsequent seedling growth and early survival. These stages are collectively the most precarious in the life cycle of most vascular plants, and the environmental conditions required for germination and establishment may determine the niche of many plant species (Grubb 1977).

According to Belnap et al. (2003), biocrusts generally enhance germination and emergence in cool deserts, but the response is more ambivalent in hot deserts. Recent studies summarized below support this analysis and furthermore demonstrate that the effect of biocrusts is both species specific and dependent on the biocrust type. Species-specific effects were, for example, reported by Godinez-Alvarez et al. (2012), who found positive effects of both a cyanobacterial biocrust and a mixed moss–cyanobacterial biocrust from a tropical desert in Mexico on the germination of *Agave marmorata*, but no effects on either *Prosopis laevigata* or *Neobuxbaumia tetetzo*. Similarly, positive but species-specific effects of biocrusts on seedling emergence were reported for herb species in a xeric Florida shrubland (Hawkes 2004) and for germination of arctic species in moss-covered patches as compared to bare gravel moraines in Svalbard (Muller et al. 2011). The subshrub *Atractylis serratuloides* (Asteraceae), also common to shrub- and grasslands in the same region, germinates well on cyanobacterial biocrusts (Elbaz 2012). This is partly because single seeds germinate within the intact *capitulum* after being stuck near small exposed rock fragments (Elbaz 2012). Most other annual and perennial dryland plants of North Africa and the Middle East lack mechanisms enabling germination on undisturbed biocrusts (Boeken and Shachak 1994; Boeken 2008). Unlike *Stipa capensis*, native grass species of the region, like *Bromus*, *Avena*, and *Schismus*, are therefore found more in disturbed, fragmented biocrust areas (Boeken and Shachak 1994; Boeken and Orenstein 2001; Zaady et al. 2003; Boeken 2008). In these grasses, seeds are dispersed within complete spikelets, ensuring efficient movement by wind across intact biocrusts and increased seed trapping in places with biocrust disturbance (Boeken and Shachak 1994). These mechanisms may play an important role in the invasiveness of Mediterranean annual *Bromus* and *Schismus* species (especially *Bromus tectorum*) in areas with extended biocrust disturbance in the western USA, South Africa, and Australia (Hernandez and Sandquist 2011; Peterson 2013; Belnap and Weber 2013; Milton 2004). Biocrust restoration may reduce these invasive species, but may enhance biocrust specialists such as *Stipa capensis*.

The inhibitory effects of biocrusts can be species specific, as reported by Zhang et al. (2010), who found not only dissimilar effects of biocrusts on the germination of desert species on semifixed sand dunes in China, but that the effect on different species varied depending on environmental conditions (dry or wet soil).

Germination experiments with three annual species on intact, crushed, or autoclaved cyanobacterial biocrust from a semiarid Negev shrubland (Zaady et al. 1997) also showed species-specific inhibition that was mechanical, related to the presence of cyanobacteria, or a combination of both. Seed size seems to be an important factor determining whether biocrusts inhibit germination. Briggs and Morgan (2011) found reduced germination of the large-seeded subshrub *Maireana excavata* in southeastern Australia on intact moss biocrusts, while three other species with smaller seeds had similar final germination success on intact and disturbed biocrusts. A number of other studies have demonstrated effects of biocrust type on germination and emergence of vascular plants. Higher seedling emergence has been reported in biocrusts dominated by mosses than algae (Su et al. 2007) or lichens (Deines et al. 2007; Serpe et al. 2006) and higher germination in a mixed biocrust with lichens and mosses than in a biocrust dominated by crustose lichens (Serpe et al. 2008). Greater seedling emergence was found after sowing on the foliose lichen *Squammarina cartilaginea* than on the crustose lichen *Diploschistes diacapsis* (Escudero et al. 2007). Furthermore, as biocrust characteristics may change with time, their effect on germination may vary with biocrust age as showed by Langhans et al. (2009), who found higher seedling emergence on older, stable biocrusts than on early successional biocrusts. On the other hand, Su et al. (2007) found no clear trend in germination with biocrust age.

19.3 Influence of Biocrusts on Seedling Establishment

19.3.1 Survival and Growth of Seedlings

Once vascular plant seedlings have emerged, biocrusts may provide favorable conditions for their survival and growth (Belnap et al. 2003; Boeken 2008). Such positive effects have been observed under greenhouse and field conditions (Danin and Nukrian 1991; Elmarsdottir et al. 2003; Godinez-Alvarez et al. 2012; Lesica and Shelly 1992; Seghieri et al. 1997; Zhang and Nie 2011). In a controlled environment, St. Clair et al. (1984) observed that the establishment of three grass species was higher in an undisturbed mixed biocrust than in a trampled one. On eroded areas in Iceland, higher seedling densities and reduced seedling mortality of several species were observed in microsites with biocrusts compared to sparsely biocrusted ones; these effects have been attributed to less soil erosion and frost heaving in the more biocrusted microsites (Aradottir and Arnalds 2001; Karlsdottir and Aradottir 2006). Biocrust effects on seedling survival and growth can also vary according to both biocrust type and plant species. In an algal-dominated biocrust from a temperate region (Cape Cod, USA), seedling survival of two plants, *Deschampsia flexuosa* and *Morella pensylvanica*, was higher than in a lichen–moss biocrust (Thiet et al. 2014). However, a moss-dominated biocrust increased

the survival of *Morella pensylvanica* as compared to the bare soil control, but did not influence *Deschampsia flexuosa* (Thiet et al. 2014).

In contrast to the above results, various studies have shown that disturbance or removal of biocrusts can cause an increase in survival and growth of seedlings (Beyschlag et al. 2008; Hernandez and Sandquist 2011; Langhans et al. 2010; Li et al. 2006). These studies included cyanobacterial, mixed, smooth, and rugose biocrusts. In some cases, the specific biocrust characteristics that were responsible for reduced establishment are unclear. Nevertheless, the results suggest that physical, chemical, and biological conditions created by intact biocrusts limit seedling establishment in many plant species. Disturbance can temporarily increase nutrient release from biocrust organisms, which may be particularly beneficial for seedling establishment in nutrient-poor soils (Beyschlag et al. 2008). In semiarid Negev ecosystems, seedling establishment in annuals benefits from biocrust disturbance and removal, perhaps because these events can increase water infiltration rate and reduce runoff (Eldridge et al. 2000, also see Chap. 17 by Chamizo et al.).

Most biocrusts are not considered a barrier to root penetration or root growth (Belnap and Gardner 1993). However, biocrust organisms may slow down these processes, extending the period when the seedlings are more vulnerable to environmental stresses (Escudero et al. 2007; Zamfir 2000). Even when seeds germinated, the establishment of two grasses on the crustose lichen *Diploschistes muscorum* was negligible because the roots were not able to penetrate the lichen thallus and many root tips became necrotic (Serpe et al. 2008).

Apart from a mechanical effect, the extracellular components of crust organisms may affect root elongation by other mechanisms. Lichens in particular are known to produce compounds that affect the soil pH or have allelopathic properties (Concostrina-Zubiri et al. 2013; Frahm et al. 2000; Molnar and Farkas 2010). Some of these compounds have been shown to reduce seedling growth under laboratory conditions (Favero-Longo and Piervittori 2010; Tigre et al. 2012) although field tests of allelopathy are lacking. Moreover, biocrust types vary in their hydrophobicity (Drahorad et al. 2013; Kidron and Büdel 2014). A more hydrophobic environment will tend to be less favorable for water uptake by emerging roots (Blackwell 2000), thus reducing root growth and potentially decreasing survival. Presently, however, little is known about the significance of crust hydrophobicity on early seedling growth under field conditions.

It is worth noticing that negative effects of biocrusts on seedling establishment may be important for the functioning of arid and semiarid ecosystems as a whole. The inhibitory effect of biocrusts on vascular plant establishment appears to be more common for large-seeded weedy and exotic species than for native plants, which may increase habitat resistance to exotic plant invasions (Hernandez and Sandquist 2011; Li et al. 2006; Morgan 2006). Moreover and independent of species-specific effects, the decrease in seedling establishment can reduce biocrust fragmentation over the landscape, contributing to a patchy vegetation distribution. In arid environments, such mosaics can increase biodiversity, reduce fuel loads, and result in a better utilization of limited resources such as water and nutrients (Shachak et al. 1998; Boeken and Orenstein 2001; Eldridge et al. 2002; Peters

et al. 2006). For example, in arid regions, runoff of water and nutrients from biocrusted areas may be required to support downslope vegetation patches, whereas if biocrusts are broken, the resulting highly localized infiltration prevents sufficient water and nutrients from reaching downslope vegetation (Eldridge et al. 1999). This runoff also creates “islands of fertility” (Shachak et al. 1998; Boeken and Orenstein 2001) or bands of vegetation, which can be critical for plant survival and growth (Belnap 2006; Rodriguez-Caballero et al. 2013). Thus, limitations of vascular plant establishment on the biocrust *per se* may benefit plant growth at larger spatial scales (Bowker et al. 2010; Eldridge et al. 2002).

19.3.2 Biomass Accumulation and Allocation

Many studies have reported a positive effect of biocrusts on biomass and productivity of vascular plants (DeFalco et al. 2001; Pendleton et al. 2003; Langhans et al. 2009), although species-specific (Lan et al. 2014) or negative (Boeken and Shachak 1994; Thiet et al. 2014) effects have also been observed. The positive effects of biocrusts on biomass production are ascribed to enhanced soil conditions under biocrusts compared to bare soil, including greater content of soil organic matter and inorganic nitrogen (N; DeFalco et al. 2001; Pendleton et al. 2003).

Under natural conditions, the presence of biocrusts has been correlated with increases in plant biomass in different habitats (Langhans et al. 2009; Liu et al. 2013; Zhang and Nie 2011). In cold deserts of western North America, biomass of native plants was higher in biocrust-covered soils than adjacent bare areas (Belnap and Harper 1995; Brotherson and Rushforth 1983). Similarly, in the sandy Gurbantunggut Desert of northwestern China (Zhang and Nie 2011), the presence of biocrusts was associated with higher biomass of vascular plants, but only of herbaceous species. However, another study from the same area indicates that biocrusts can increase biomass accumulation of woody species as well. Liu et al. (2013) compared the growth of a clonal shrub, *Eremosparton songoricum*, on two microsites, one with naturally moving sand and one where the sand had been fixed by the straw checkerboard method. Sand fixation by well-developed biocrusts was correlated with higher plant biomass per unit area than in non-fixed sand. Similar observations of higher herbaceous and woody plant cover and biomass on biocrust-stabilized dunes were made in the sandy deserts of the Negev (Tsoar 2005), where biocrusts prevent plant burial and denudation and reduce deep infiltration (Kidron and Yair 1997). In contrast to sandy soil, absence or removal of biocrusts on heavier, loessial, or loamy soils increases plant biomass (Boeken and Shachak 1994; Eldridge et al. 2000). This may be partly due to higher water and seed capture.

Allocation of biomass to roots is expected to decrease with increased soil fertility (Van Wijk 2011). Consequently, root–shoot ratios of plants growing on biocrusts may be lower than those of plants growing in uncrusted soils. In agreement with this hypothesis, Bliss and Gold (1999) and Pendleton et al. (2003)

reported lower root–shoot ratios of plants associated with biocrusts than 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. However, the presence of biocrusts is not always related to a decrease in the root–shoot ratio. For example, Liu et al. (2013) found higher root–shoot ratios on fixed than non-fixed sand, even though the fixed sand had a higher content of organic matter and N than the non-fixed one. Perhaps, under the dry conditions of desert sand with high infiltration rates, the low water status of the plants was a more important factor in determining the root–shoot ratio than soil fertility.

Overall, our literature review indicates that biocrusts tend to increase biomass of vascular plants. In addition, disturbance of biocrusts caused by trampling can transiently enhance biomass accumulation. At a small scale, these disturbances may be important for plant establishment in certain environments (Beyschlag et al. 2008; Zhang unpublished data). However, large-scale or frequent disturbance of biocrusts most likely reduces biomass accumulation by altering patterns of water infiltration and runoff and by preventing the buildup of organic matter and nutrients associated with the crust presence (Belnap 2006; Eldridge et al. 2002).

19.3.3 Phenology and Sexual Reproduction

Very little is known about the influence of biocrusts on the phenology of vascular plants. Nevertheless, some results suggest that biocrusts may promote early flowering and greater production of reproductive structures. In a study by Pendleton et al. (2003), an annual forb, a perennial grass, and a perennial forb flowered earlier and/or produced more reproductive biomass on crushed than intact biocrusts or sand. An effect of biocrusts on flowering time was also observed by Zhang and Nie (2011) in the field, where flowering and fruiting of annual forbs and grasses occurred sooner in biocrusted than uncrusted areas. Other studies have shown variable effects of biocrusts on flowering, fruiting, and/or seed production. For *Arabis fecunda* (Lesica and Shelly 1992), the number of inflorescences and fruits per plant was similar in biocrusted and uncrusted areas, while Bliss and Gold (1999) reported species-specific effects of biocrusts on the number of seeds per fruit and weight per seed.

19.4 Influences of Vascular Plants on Biocrusts

19.4.1 Canopy Shade

Although biocrust organisms are adapted to high light intensities (Harel et al. 2004), they often benefit from some shading by vegetation (Belnap 2003; Cortina et al. 2010; Singh et al. 2012), as the shade reduces light damage and desiccation. Some studies indicate that enhanced UVB radiation intensity causes significant reduction in photosynthetic function, destruction of chloroplast ultrastructure, and disordering of antioxidant enzyme systems in the moss *Bryum argenteum* (Hui et al. 2013), the lichen *Umbilicaria aprina* (Niemi et al. 2002), and the cyanobacterium *Microcoleus vaginatus* (Xie et al. 2009). On the other hand, complete canopy shade could also cause severe damage by light deprivation, but its occurrence is rare in dryland ecosystems due to the scattered distribution, open canopies, and low stature of the shrubs and trees and the short life span of the annuals.

In many dryland ecosystems, a woody plant canopy creates a gradient from deep shade near the stem to maximal irradiance outside the canopy, reflected in an uneven thickness of biocrusts and a radial distribution (zonation) of some biocrust organisms, particularly mosses (Eldridge et al. 2000; Martinez et al. 2006; Cole et al. 2010). Eldridge et al. (2000), for instance, found preference for shrub canopy shade in a number of moss species (*Aloina bifrons*, *Crossidium* sp., *Bryum* sp., and *Pterygoneurum subsessile*), particularly at sites with a northerly aspect. Cole et al. (2010) demonstrated that the Mojave Desert moss *Syntrichia caninervis* transplanted into exposed sites lost significantly more cover than those moved into shaded sites.

Shrub canopy shade also affected reproductive behavior in biocrust mosses, as it increased the density of sexual organs in male *Bryum dunense* in sandy deserts of the Negev (Herrnstadt and Kidron 2005), possibly caused in part by differential desiccation tolerance between the sexes (Benassi et al. 2011). In another study of two pleurocarpous mosses (*Rhytidiadelphus squarrosus* and *Calliergonella cuspidata*), lower irradiance beneath the shrub canopy decreased evaporation rates (Van der Hoeven et al. 1998). This prolonged photosynthesis compensated for the lower photosynthetic rates found under the shrub canopy. In addition, at low irradiance, the morphology of shoots of *Rhytidiadelphus squarrosus* changed, as the main axis lengthened and the branches shortened. In contrast, higher solar insolation in interspace habitats induced rapid drying and prolonged drought periods, limiting the metabolic activity of biocrusts (Hamerlynck et al. 2002). The combined stress of drying and heat-accelerated water loss in the biocrust moss *Syntrichia caninervis* was followed by a decrease of photosynthetic activity (Xu et al. 2009). In contrast to mosses, lichens were often promoted by higher light intensities (i.e., less shade) (Sedia and Ehrenfeld 2003).

In many cases, variation in biocrust thickness, cover, and composition under woody plant canopies is correlated to other factors besides shade. For instance, Martinez et al. (2006) showed that the abundance of moss and lichen biocrusts

under canopies in Spain was also related to cover of litter, soil respiration, potassium content, and aggregate stability. Under the canopy of patch-forming dryland shrubs and in the exposed intershrub space, surface texture, surface cover, and soil properties tend to vary along with shade (Boeken and Orenstein 2001; Golodets and Boeken 2006).

19.4.2 Plant Litterfall

Litter deposition is probably the most important mechanism of biocrust disturbance by vegetation (Boeken and Orenstein 2001). Litter cover may affect the microenvironment of biocrusts in many ways: physical contact, soil properties, soil nutrient status, microbial composition and structure, and particularly light, temperature, and moisture (Belnap 2003; Jensen and Gutekunst 2003; Xiong and Nilsson 1999; Facelli and Pickett 1991). Biocrust burial by plant litter accumulated under woody plants can restrict its development under canopies (Boeken and Orenstein 2001; Berkeley et al. 2005) due to light reduction. In Negev shrublands, heavy and persistent litter cover kills the biocrust organisms (mainly the cyanobacterium *Microcoleus vaginatus*) and in many cases allows termites to remove the remaining physical crust structure (Boeken and Orenstein 2001).

Temporary or light litter cover can protect the biocrusts from photodamage (Serpe et al. 2013), reduce heat stress, and maintain suitable surface temperatures for photosynthesis (Lange 2003). Shade of moderate litter cover also creates favorable temperature and humidity conditions for increased microbial activity and litter decomposition, increasing soil organic matter and soil fertility (Zaady et al. 1997; Li et al. 2007). The changes in the microenvironment can ultimately lead to changes in the photosynthetic capacity of biocrusts (Serpe et al. 2013). Biocrust organisms are unequally affected by litter cover, due to the differences in metabolic requirements and the ability of mosses, and some lichens, to grow up through the litter (Lange 2003; Marschall and Proctor 2004). Briggs and Morgan (2008) found some moss species were competitively superior to lichens where litter cover was moderate.

Litter accumulation from invasive species may impede the recovery of biocrusts after fire (Hilty et al. 2004). Areas previously invaded showed reduced moss crust and lichen cover (Belnap et al. 2006). Some studies have shown that invasive species can hinder biocrust recovery in early successional stages, while mature biocrusts resist invasion (Dettweiler-Robinson et al. 2013). A rather dense litter cover (23.5 mg cm⁻² of biocrust) of the exotic annual grass *Bromus tectorum* reduced the chlorophyll content and the rate of gross photosynthesis and dark respiration of biocrusts dominated by either the moss *Bryum argenteum* or the lichen *Diploschistes muscorum* (Serpe et al. 2013).

19.4.3 Soil Properties

In addition to litter production affecting biocrusts and underlying soils, vegetation also alters subsurface soils by increasing soil organic matter, water holding capacity, and soil nutrient content (Maestre et al. 2010). However, little is known about the effects of vegetation-induced changes in the soil on biocrusts. Furthermore, in some instances, changes in soil conditions beneath vascular plants do not parallel those beneath biocrusts. For example in the northern Negev, the 0–20 cm soil under vegetation had higher moisture in the rainy than in the dry season, while soil covered by a cyanobacterial crust appeared unaffected (Golodets and Boeken 2006).

19.5 Nutrient Uptake by Vascular Plants as Influenced by Biocrusts

19.5.1 Availability and Uptake of Mineral Nutrients

In arid and semiarid environments, biocrusts can be the main source of available N (Evans and Belnap 1999; Elbert et al. 2012). The contribution of biocrusts to N availability tends to be higher for upper soil layers (Breen and Levesque 2008; Zhao et al. 2014). Gao et al. (2010) compared the organic content and total N in fixed and moving sand dunes. The biocrusts on fixed sand increased the organic matter and total N content of the soil, but only in the upper 5 cm. This unequal effect of biocrusts on N content may lead to differences in N uptake among plant species. Plants with shallow roots usually benefit more from the biocrust presence than deeper rooted plants (DeFalco et al. 2001; Yan 2009; Zhang and Nie 2011).

Biocrusts secrete phosphatase, and higher phosphorus (P) availability beneath biocrusts is associated with higher concentrations of P in plant tissue. For example, in southeastern Utah foliar levels of P in *Festuca octoflora* were 78 % higher in plants growing in biocrust covered as compared to uncrusted soil (Belnap 2011). Positive effects of biocrusts on plant P uptake were also observed in the Kubuqi and Gurbantunggut 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; Zhang and Nie 2011).

Cyanobacterial biocrusts can synthesize anionic polysaccharides that bind cations (Reddy et al. 1996; Chen et al. 2003; Parker et al. 1996). Moreover, the increase in organic content of the soil caused by the biocrust presence increases the cation exchange capacity of the soil (Breen and Levesque 2008; Guo et al. 2008; Zhao et al. 2014). Notwithstanding this increase in cation retention, the effects of biocrusts on plant uptake of cations have ranged from negative to positive (Harper and Belnap 2001; Pendleton et al. 2003). This range of responses may be attributed to other effects of biocrusts on the soil such as moisture or pH, which influence the

availability of cations and other nutrients (Concostrina-Zubiri et al. 2013; Wu et al. 2013; Zhao et al. 2014). In addition, competition for nutrients with microbes in biocrusts might cause lower concentrations of available cations in the soil and thus in plant tissue. 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; Zhang and Nie 2011). In contrast, plant Fe uptake appears to be lower in soil covered with biocrusts. For other cations, such as Ca, Mn, and Na, positive, minimal, and negative effects of biocrusts on plant uptake have been reported (Harper and Belnap 2001; Pendleton et al. 2003). Similar to P and N, differences in cation uptake among plant species reflect, in part, differences in root architecture. The increase in soil cations caused by the biocrust is mainly limited to the upper soil layers. Consequently, ephemerals rooted primarily within the surface soil benefited more from the biocrust presence than more deeply rooted shrubs (Harper and Belnap 2001; Yan 2009; Zhang and Nie 2011).

19.5.2 Fungal Linkages Between Biocrusts and Vascular Plants

The nutrients released from biocrusts to the soil and those that become available following mineralization are generally thought to enter plants via direct absorption by the roots or through arbuscular mycorrhizae (AM) that form symbiotic associations with the roots. In dryland ecosystems, fungi rather than bacteria likely dominate the nutrient cycles, given their ability to function at much lower soil water potentials (Allen 2007; Porras-Alfaro et al. 2011). Biocrusts are heavily dominated by dark septate endophytes (DSE), although they also contain AM (Allen 2007; Bates et al. 2012; Porras-Alfaro et al. 2011). Except for liverworts, AM are not known to form associations with organisms present in biocrusts, and AM lack any significant saprophytic capability (Hodge 2014; Ligrone et al. 2007). Nevertheless, the higher levels of organic matter and nutrients beneath biocrusts relative to bare soil may promote hyphal proliferation and growth, increasing the potential for transferring nutrients to plants (Gryndler et al. 2005; Joner and Jakobsen 1995). The role of AM on enhancing P uptake from deeper soils is well established (Smith et al. 2011), but P transfer mechanisms from biocrusts to plants are not known. Several lines of evidence indicate that AM may contribute to N transfer (Tu et al. 2006). Pioneer work by Hawkes (2003) showed that the $\delta^{15}\text{N}$ values of a cyanobacterial–algal crust were similar to those of mycorrhiza-associated plants and lower than the $\delta^{15}\text{N}$ values of non-mycorrhizal plants. Further work is needed to determine the forms of N transferred from biocrusts to plants via AM since these fungi can transfer NO_3^- , NH_4^+ , as well as several amino acids to roots (Jin et al. 2005; Ngwene et al. 2013; Whiteside et al. 2012). Similarly, it would

be valuable to determine the carbon cost to the plant associated with N transport since both symbionts have large demands for N (Johnson 2010).

A recent intriguing hypothesis is that a fungal bridge may largely control nutrient transformation and translocation between biocrusts and vascular plants (Green et al. 2008; He and Xu 2009; Zhuang et al. 2014). As DSE dominate the biocrusts, it is believed they play an important role in this nutrient transformation and transport. Dark septate fungi can increase the pool of nutrients available to plants through solubilization of P complexes and mineralization of proteins, peptides, and amino acids (Barrow and Osuna 2002; Newsham 2011). The DSE may stimulate mineralization by facilitating breakdown of organic matter derived from biocrusts. They may also contribute to exchange of nutrients between biocrusts and plants. Spot application of $^{15}\text{N}\text{-NO}_3$ and $^{13}\text{C}_5, ^{15}\text{N}$ -glutamic acid to biocrusts demonstrated that ^{15}N compounds can be transferred to plants 1 m away in 24 h through root-free soils, presumably via DSE, which were the dominant fungi in the soil and on the roots (Green et al. 2008; Zhuang et al. 2014). Because DSE can enter plants through plant tissue (Barrow and Osuna 2002), it is possible this translocation is bypassing roots. In addition, spot application of ^{13}C from $^{13}\text{C}_5, ^{15}\text{N}$ -glutamic acid to plant leaves showed a transfer of C to biocrusts, again through root-free soils, which suggests that plants may provide metabolic support to biocrusts during active periods (Green et al. 2008).

Combined, these studies indicate that exchange of nutrients between biocrusts and vascular plants can occur through different pathways. Knowledge in this area is still very limited. Mesocosm studies are needed to determine the specific organisms that mediate nutrient transfer between biocrusts and plants and to quantify how important fungal transfers are to plant nutrition.

19.6 Conclusions

Biocrusts can have positive and negative effects on vascular plants, depending on species, development, and life cycle stage. During seed dispersal, biocrusts with high surface roughness tend to increase seed entrapment, while entrapment is low in biocrusts with smooth surfaces. Following entrapment, the proportion of seeds reaching microsites favorable for water imbibition and germination varies with biocrust microtopography and seed morphology. Similarly, root growth during seedling establishment may be affected by biocrust characteristics such as pH and hydrophobicity, as well as biocrust effects on nutrients and water. Given these various factors and differential responses of seedlings to a particular environment, generalizations about the effect of biocrusts on seed germination and seedling establishment are presently difficult to make. Modeling approaches that evaluate the contribution of different factors and interactions may help to identify those that are particularly important. In addition, further work is needed to determine whether certain biocrust types are overall more conducive to seed germination or seedling establishment than others. A meta-analysis of the meanwhile rather numerous

studies on biocrust effects on seeds and seedlings may reveal general trends that are not obvious from the various and often contrasting results found in the literature.

Following establishment, the effects of biocrusts on plant growth are for the most part positive. It is also likely that biocrusts increase plant reproductive output; however, more studies will help to verify this. Promotion of plant growth by biocrusts has been attributed to changes in the distribution of water and in the levels of organic matter and nutrients. Effects on plant growth may also reflect biocrust-induced changes in the soil biota. Such changes have been studied in relation to nutrient mineralization and, to a lesser extent, nutrient acquisition. It is plausible that biocrusts mediate other changes such as the abundance of microorganisms, which promote growth via alterations in plant hormone concentrations or decreases in pathogens (Wardle et al. 2004). Studies on this topic and on the specific and overall responses of plant communities to biocrusts are needed, as overall responses are often unknown or unreported (Boeken and Shachak 1994; Boeken and Orenstein 2001).

Canopy shade tends to benefit biocrust development, and effects of litter on biocrusts can range from positive to negative depending on litter thickness and persistence. The cover provided by canopy and light litter alters the duration of hydrated periods and the rates of photosynthesis, changing the biocrust carbon balance and ultimately influencing its taxonomic composition and functioning. Invariably, a thick, persistent litter layer seems to inhibit or eliminate biocrusts, likely as a combination of a negative carbon balance in the dark and physical contact. The precise litter levels that begin to cause damage to biocrusts are unknown, warranting further analysis.

The positive and negative interactions between biocrusts and vascular plants play a role in determining their coexistence. An interesting hypothesis claims that the types of interactions that promote coexistence vary with the degree of aridity. Under high aridity, plant growth is predominantly restricted by lack of water, and negative effects of biocrust on establishment and growth of vascular plants are minimal. Under this scenario, biocrust effects would be predominately beneficial, resulting from reduced soil erosion and increased availability of nutrients and water. Similar conditions occur in dry arctic environments, where frost and erosion severely limit plant growth. This hypothesis, that evolution has led to biocrusts with distinct effects on vascular plants based on differences in aridity or prolonged frost, requires further investigation. It would be worthwhile to test this notion in a global study on the spatial interactions between biocrusts and vegetation in relation to aridity and other environmental stressors. Within this framework, detailed positive and negative biocrust–vegetation interactions, including those on entire communities, can be compared and modeled. Of particular interest would be to identify patch-forming ecosystem engineer species and distinguish between transient and more persistent interactions between plants and biocrusts and between the scales at which they operate.

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