21 Influence of Biological Soil Crusts on Soil Environments and Vascular Plants

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21.1 Introduction

The presence of biological soil crusts can significantly change the physical and chemical soil environment. Such alterations can affect the germination, survival, and nutritional status of vascular plants. Some landscape surveys have found a negative relationship between biological soil crusts and vascular plant cover (West 1990; Johansen 1993; Eldridge 1993). Based on this, some authors have concluded that crust organisms limit vascular plant cover (Savory 1988). However, it is also possible that soil crusts merely occupy all soil surfaces not first covered by vascular plants. In support of this, numerous authors have reported that vascular plant cover either shows no correlation with crust cover (Anderson et al. 1982; Beymer and Klopatek 1992; Jeffries and Klopatek 1987; Kleiner and Harper 1972, 1977) or that there is a positive correlation between vascular plant and crust cover (Carleton 1990; Dadlich et al. 1969; Graetz and Tongway 1986; Ladyman and Muldavin 1994; Lesica and Shelley 1992; Mücher et al. 1988).

Many studies have addressed aspects of the relationship between crusts and vascular plants. These studies have been done at sites with different soil textures, physical and chemical crusting, soil surface roughness and stability, climate regimes, species composition of the biological crusts, and vascular plant species (each with different strategies for germination and survival). It is essential that all these differences be accounted for when generalizing about the relationship between soil crusts and vascular plants. In this chapter, we will discuss how crusts modify soils in ways that can affect vascular plants. We will then address the effects of biological soil crusts on seed dispersal and germination, and how crusts affect vascular plant survival and nutritional status in different climate regimes. Finally, we will discuss the overall effects of crusts on plant community structure.

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21.2 Modification of the Soil Environment by Biological Soil Crusts

The presence of biological soil crusts modifies soils in ways that can affect germination, emergence, and survival of vascular plants. Crust-caused soil alterations include changes in soil surface roughness, soil texture, thermal conditions, availability of nutrients, organic matter, and water. A large body of literature, cited below, shows that manipulation of each of these factors can influence vascular plants. As few experiments have directly linked crusts and vascular plant performance, it is hoped that the following discussion will help stimulate future research on this relationship.

21.2.1 Surface Roughness

Biological soil crusts influence the microtopography of soil surfaces (Chap. 1, Photos 30, 32, 48, 50; Chaps. 15, 16). In hot deserts that lack soil-freezing, changes in surface roughness are relatively small. Cyanobacterial crusts can smooth soil surfaces, while lichens and mosses growing above the soil surface increase roughness slightly. In contrast, soil surfaces in cool and cold deserts show large increases in soil-surface roughness due to frost-heaving and the differential erosion of crusted soils. Resulting soil pedicels can be up to 15 cm high (Belnap and Gardner 1993). These relatively large microtopographic features act to trap wind- and water-borne seeds, organic matter, soil fines, and water (Harper 1977; Harper and St. Clair 1985; Eckert et al. 1986; J. Belnap, unpubl. data).

21.2.2 Soil Texture and Chemistry

Crusted soil surfaces often have a greater silt/clay fraction than underlying soils, or adjacent uncrusted soil surfaces. Fine clay particles stick to the mucilaginous sheath material, especially when wet (Belnap and Gardner 1993; Verrecchia et al. 1995; see Chap.15). These negatively charged clay particles bind positively charged plant macronutrients, thus increasing soil fertility (Black 1968). The presence of biological crusts can significantly alter soil pH and the amounts and availability of plant-essential nutrients and organic matter. Studies in cool deserts and laboratory settings show that crusts enhance the content of most bioessential elements including N, K, Ca, Mg, P, Fe, Mn, Cl, and S (Harper and Pendleton 1993; Mitchell and Fullen 1994; Belnap and Harper 1995; Harper and Belnap 2000).

Nitrogen. Up to 70 % of the nitrogen fixed by cyanobacteria and cyanolichens is released immediately into the surrounding soil environment, and is available to associated organisms including vascular plants, mosses, fungi, and other microbes (see Chap. 16). This has specifically been shown for *Collema*, *Microcoleus*, and *Nostoc-Microcoleus* soil crusts from SE Utah (F. Garcia-Pichel and J. Belnap, unpubl. data). Multiple studies have reported that the presence of soil crusts increases surrounding soil N by up to 200 % (Shields and Durrell 1964; Rogers and Burns 1994; DeFalco 1995; Harper and Belnap 2000). In addition, stable isotopes show that soil crusts can be the dominant source of N for desert soils and plants (Evans and Ehleringer 1993; Evans and Belnap 1999; Chap. 19, 20).

Carbon, C:N Ratios, and Organic Matter. All crust components secrete extracellular carbon (C) within minutes to a few days of C acquisition. In cyanobacteria, these secretions can represent up to 50 % of total fixed carbon (Fogg 1966; Lewin 1956). As a result, presence of soil-crust organisms increases soil polysaccharides and total carbon by up to 300 % (Rao and Burns 1990; Rogers and Burns 1994), benefiting heterotrophic microbes, which are often carbon-limited. In addition, the presence of crusts can lower soil C:N ratios. This increases decomposition rates, making nutrients available faster to associated organisms (Kleiner and Harper 1972). Increases in soil organic matter are also well known to ameliorate compaction, reduce inorganic soil crusting, reduce nutrient leaching losses, and increase soil moisture retention (Tongway and Ludwig 1990; Evans and Young 1994).

Nutrient Binding. Microbial exopolymers not only add carbon to soils, they also modulate metal-ion concentrations at the microbial cell surface. The lipid, protein, and carbohydrate components combine to create a mosaic of many polyfunctional metal-binding sites that differ in affinity and specificity. Both cations and anions can be bound (Greene and Darnall 1990). Under natural conditions, most of the polymers act as polyanions that prevent excess quantities of highly charged molecules (such as heavy metals) from approaching the cell surface, while concentrating growth-promoting nutrients present at low concentrations in the surrounding environment (such as Na, K, Mg, Ca, Mn, Fe, Ni, Cu, and Zn) (Lange 1976; Geesey and Jang 1990). This binding occurs within minutes, and is largely a passive electrostatic interaction between cationic metals and anionic cell surface groups. Therefore, the organisms do not need to be alive or active (Gadd 1990a).

Binding capacity and affinity for one cation over another is determined by a variety of factors, including the microbial species, pH, temperature, cell densities, cell size, ion densities, and ion size. Different microbial species secrete polymers with different binding affinities, and selectivity coefficients may also be different depending on whether polysaccharides are in gel or solution. Small-celled organisms with larger surface areas adsorb more than large filamentous species with less surface area (Geesey and Jang 1990).

External soil factors also influence the binding properties of microbial exopolymers. In soils above pH 7 (e.g., most desert soils), cation exchange capacity increases significantly for all microbial species. Binding of metal ions cause polymers to condense into gels, altering cation binding affinities. Polysaccharide production is stimulated by Mg, K, and Ca, which then results in greater binding of these nutrients. Affinities also fluctuate depending on concentrations of other cations present. Initial binding may also be followed by inorganic deposition of an increased amount of metal. Particulate material can bind to crustal organisms (e.g., sulfides of copper, Zn, Pb, zinc dust, magnesic oxide, and ferric hydroxide; Lange 1974; Gadd 1990a,b; McLean and Beveridge 1990; Pirszel et al. 1995). Most adsorbed metals stay on or within the extracellular sheath, and are not absorbed by the cells, thus remaining available to plants (Geesey and Jang 1990).

Metal Chelation. Cyanobacteria (including the common soil genera *Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc*) green algae, fungi, lichens, and bacteria also secrete powerful metal chelators such as siderochromes (Lange 1974; McLean and Beveridge 1990; Schelske et al. 1962). Chelating agents are organic compounds that form complexes with ions of polyvalent metals. Their presence maintains metals that would otherwise be precipitated in solution. They are effective in sequestering essential trace metals at exceedingly low ambient concentrations (Paerl 1988). This is especially important in soils with high pH (such as found in many deserts), as some elements form insoluble oxides or hydroxides at or above pH 7. Cyanobacteria also secrete peptide nitrogen and riboflavin. Together with siderochromes, these substances form complexes with tricalcium phosphate, Cu, Zn, Ni, and ferric iron, keeping them plant-available. These secreted chelators are water-soluble, and capable of being translocated in soil and water. Consequently, chelated compounds are made available to associated, nonchelating plants or microbes. Binding and chelation may be especially important for nitrogen fixers, as they require high amounts of otherwise unavailable Fe (Bose et al. 1971; Lange 1974; Geesey and Jang 1990; Gadd 1990a).

Other Plant Nutrients and Plant Factors. Cyanobacteria also secrete other compounds that can influence vascular plant growth. Glycollate is a common extracellular product. Secretion of glycollate is increased at low cyanobacterial cell density (as in soils) and when cyanobacteria go from low to high light intensities, as on a partly cloudy day. Glycollate stimulates uptake of phosphate in cyanobacteria (Fogg 1966). Cyanobacteria also secrete various vitamins (e.g., B_{12}), auxin-like substances, and other substances that promote growth and cell division in plant and animal tissue (Fogg 1966; Venkataraman and Neelakantan 1967).

Vesicular-Arbuscular Mycorrhizae. There is a strong positive correlation between mycorrhizal infections of some seed plants and crusted surfaces (Harper and Pendleton 1993; Pendleton and Warren 1995). In addition, consistent increases of biogenic mineral elements in crusted soils and associated plants that do not form complexes with chelating compounds suggest that the increased mycorrhizal fungi associated with crusts are also involved in increasing nutrient availability to plants (Harper and Pendleton 1993; Belnap and Harper 1995; Harper and Belnap 2000).

pH. The presence of photosynthetic crustal organisms significantly increases the pH of surrounding medium (see Chap. 16). Crustal organisms from SE Utah raise the soil pH from 8 to 10.5 (Garcia-Pichel and Belnap 1996). Endolithic cyanobacteria in Venezuela and South Africa raised the pH of surrounding solutions in rocks from about 8 to 10 as well (Büdel 2000). As seen above in the discussion on chelation, increases in pH decreases availability of some nutrients (e.g., P, Fe), CO_2 dissolution rates, carbonate formation rates, and solubilization of soil minerals (e.g., Si; Nobel 1991).

21.2.3 Thermal and Water Relations

The presence of biological soil crusts can increase soil surface temperatures by up to 14 °C relative to adjacent uncrusted soils in both temperate and polar deserts. This is expected to influence seed germination, plant growth, and nutrient uptake rates (Harper and Pendleton 1993; Belnap 1995; Gold and Bliss 1995).

Cyanobacteria and gelatinous lichens can absorb ten times or more their volume in water (Campbell 1979). While increased biomass of these organisms may increase the surface water-holding capacity of soils, this could be offset by increased loss of soil surface moisture due to higher surface temperatures in crusted than uncrusted soils (see Chap. 27). However, it has also been repeatedly observed in a cool desert setting that darker, more well-developed crusts retain surface moisture longer after rain events than bare sand or thin cyanobacterial crusts, regardless of air temperatures or insolation levels (J. Belnap, pers. obs.). While this may not affect germination of seeds lying on the crust surface, it may influence moisture status of seeds embedded in the crust. In hot deserts, surfaces dry very quickly when air temperatures are high; this increase in surface moisture may not influence seed germination during hot periods. It is not known what effect crusts have on subsurface soil moisture. Three studies have directly addressed this question. Two studies found that the presence of crusts increased soil moisture (Brotherson and Rushforth 1983; D. George et al., unpubl.); one study found that crusts reduced soil moisture (Harper and Marble 1988). D. George et al. noted that the type of soil crust (cyanobacterial vs. lichen crust) influenced study results.

The presence of crusts can also influence water distribution on a landscape scale. In hot deserts, plant interspaces are covered by smooth crusts that generally reduce water infiltration. The resultant increase in runoff from crusted plant interspaces potentially provides increased water availability for nearby vascular plants (Tongway and Ludwig 1990; Cornet et al. 1992; Zaady and Shachak 1994; Eldridge et al. 2000; Chap. 22). In cool and cold deserts, crusts enhance local water infiltration, thus reducing runoff on a landscape scale (Chap. 24).

21.3 Influence of Soil Crusts on Seed Dispersal and Germination

21.3.1 Seed Dispersal

Many factors influence movements of seeds once they are dispersed from the parent plant. As the establishment of perennial species is a fairly rare event, field studies concerning natural dispersal and emergence have generally addressed annual plant species. Regardless of seed size or shape, most seeds can be easily carried by wind or water across dry, smooth soil surfaces (Harper 1977). However, some seeds have mucilaginous coats or pappus hairs that can stick to wet soil surfaces, even when soil surfaces are smooth (Harper 1977; Gutterman 1994; Zaady et al. 1997). Smooth crust surfaces are most often found in hot deserts or soils recently colonized by cyanobacteria. Smooth surfaces are generally characterized by low plant litter, no frost-heaving, biological crusts heavily dominated by cyanobacteria, and some physical or chemical crusting. The effects of a smooth crustal surface on seed dispersal has been well illustrated by recent work at the Nizzana dunes in Israel. Using field experiments, Prasse (1999) showed that the probability of seed entrapment on these smooth cyanobacterial crusts is very low. Experimentally applied disturbances that roughened the smooth soil surface significantly increased seed entrapment. Seed-trapping was most effective when the disturbance was applied before main seed-dispersal times. Roughened plots that were covered to prevent seed input had no seedlings, indicating that no germinable seeds were available prior to surface roughening. This observation was supported by watering intact crusts in a greenhouse setting, where almost no germination was observed.

In contrast to these smooth soil surfaces found in hot deserts, surfaces in cool and cold deserts are characterized by lichen-moss crusts, plant litter, frost-heaved soils, and limited physical or chemical crusting. Many studies have shown these rough surfaces trap seeds. In addition, these surfaces trap organic matter, water and soil fines, thus increasing microsite fertility (Harper and St. Clair 1985; Eckert et al. 1986; Harper and Marble 1988; Mücher et al. 1988; Chap. 14). Using a portable wind tunnel to generate winds of known speed, J. Belnap (unpubl. data) showed that smoothing of crusted surfaces by disturbance results in less trapping of seeds and organic matter at all commonly occurring wind speeds.

21.3.2 Vascular Plant Seed Germination and Establishment

Few studies have specifically addressed the effect of soil crusts on seed germination and plant establishment, and results have been variable. Most studies have used experimental sowing of selected species into crusted and uncrusted soils; thus, it should be kept in mind that seed placement may not mimic that of naturally dispersed seeds. Other studies have used comparisons of species composition and/or density of vascular plants in adjacent crusted and uncrusted soils. Interpreting results from these studies necessitates understanding the reasons for crust cover differences and the influence these differences may have on vascular plant germination and/or establishment.

Biological soil crusts do not present a physical barrier to root penetration for any plant species or soil type tested (Belnap and Gardner 1993; R.L. Pendleton, unpubl. data). In contrast, physical and chemical crusting often inhibits root penetration (see Chap. 15; Chartres 1992). Combinations of physical and biological crusts are expected to have intermediate effects on root penetration, depending on the level and type of crust development.

Biogeography. In cool deserts, crusts generally enhance germination and establishment of vascular plants. St. Clair et al. (1984) showed large increases in germination and establishment in the lab for the perennial grasses *Agropyron elongatum* (fivefold increase) and *Elymus junceus* (11-fold increase) on crusted southeastern Utah soils when compared to uncrusted soils. In the Great Basin, Eckert et al. (1986) showed that seedling germination was higher in crusts under shrub canopies and in adjacent crusted soils compared to the uncrusted plant interspace soils. Most seedlings were found at the base of crust pedicels. Schlatterer and Tisdale (1969) showed no effect of moss cover on the number of perennial grass seeds that germinated (*Stipa thurberiana, Sitanion hystrix, Agropyron spicatum*) when compared to artificial litter, although time to germination was slower. When compared to bare surfaces, germination was inhibited. However, seeds were placed under 2 cm of moss, rather than on top of the moss, as would occur in nature. In Idaho and southeastern Utah, Larsen (1995) and Howell (1998), respectively, showed that germination of native *Stipa* was not affected by biological soil crusts, while germination of the exotic annual grass *Bromus tectorum* was inhibited by intact crusts. *Bromus* germination was stimulated when crusts were broken but left in place. Thus, in cool deserts, seed germination is generally enhanced for perennial plants and decreased for exotic annual grasses.

In contrast with cool deserts, hot-desert species show a more ambivalent response to the presence of soil crusts. In Australia, Crisp (1975) found the same as Larsen (1995) did in cool deserts: germination and establishment of the native perennial grass *Stipa* was not inhibited on crusts, while germination and establishment of the annual exotic grass *Schismus* was inhibited. As with the annual *Bromus*, *Schismus* germination was stimulated when the crust was broken. In Arizona, McIlvanie (1942) found that two species of perennial warm-season grasses did not germinate on soils with 100% moss cover in southern Arizona. In the laboratory, Zaady et al. (1997) found that cyanobacterial crusts in Israel inhibited germination of the annual plants *Plantago* and *Reboudia*, while germination of the annual *Carrichtera* was enhanced. Hacker (1984) reported reduced germination on "crusted" soils for two shrubs in Australia; however, he makes no mention of biological crusts, and it is likely that these were physical crusts, as they increased with grazing. In 1987, Hacker found more adult plants, but fewer seedlings, of *Selenothamnus* (a chenopod shrub) on crusted soils. He speculated that crusts may reduce germination of this species; however, he did not directly test this hypothesis.

Physical Influences on Seed Germination. Seeds require varying amounts of moisture to germinate. In the dry air of deserts, many species require some soil or plant cover to maintain sufficient moisture for germination. While the cracks and crannies in the soil surface are often sufficient for small seeds (Gutterman 1994; Chartres and Mücher 1989), most larger-seeded plants require additional cover by soil or litter (Evans and Young 1984). In deserts where litter is often limited, native seeds generally accomplish this by burial mechanisms such as hygrochasic awns or through rodent caching. However, some plant species lack specialized penetration structures (Boeken and Shachak 1994). These species are often annuals that evolved in regions where soil-surface disturbance is relatively high. Consequently, germination of these species is generally inhibited in areas where litter is sparse, soil crusts stabilize soils, and surface disturbance is low. This has been demonstrated for several annual *Bromus* species in the US and Israel (Evans and Young 1984; Larsen 1995; Howell 1998; Kaltenecker et al. 1999; Prasse 1999), *Schismus* in both Australia and Israel (Crisp 1975; Zaady et al. 1997), *Plantago* and *Reboudia* in Israel (Zaady et al. 1997) and *Salsola* in Australia and the US (West 1990). Increased spatial and temporal frequency of surface disturbance generally favors germination for these species. Unfortunately, this often results in exotic annual invasions of perennial plant-dominated cool desert communities (Larsen 1995). Increasing soil surface disturbance in ecosystems where annuals and disturbance are a significant component (e.g., Negev and Sonoran Deserts) leads to some increased plant productivity; however, seed availability and dispersal may quickly become limiting (Boeken et al. 1998).

Soil mobility is also an important control on seed germination. Seeds generally have optimal burial depths, and increased or decreased burial can prevent germination (Baskin and Baskin 1998). Because soil crusts enhance soil stability (see Part V), their presence or absence can differentially affect germination of seeds.

Nutrient and pH Influence on Seed Germination. Laboratory studies show that N additions can stimulate seed germination in some plant species (Baskin and Baskin 1998). Consequently, germination of some species may be stimulated with the presence of crusts; however, we are not aware of any experiments which directly test this hypothesis. Similarly, extreme soil pH affects seed germination (Baskin and Baskin 1998). Thus, the large increase in soil pH seen on crusted soil surfaces may influence seed germination of some plant species. Again, no experiments have been done to directly investigate this.

Influence of Soil Crusts on Soil Thermal and Water Relations. We found no work that specifically addresses how the thermal and moisture environments of soil crusts affect seed germination. Mücher et al. (1988) found higher seed germination on crusted surfaces in dry woodlands of Australia, and attributed this to the higher soil moisture found on crusted surfaces; however, this was not directly measured. Gold and Bliss (1995) speculated that increased seed germination and plant biomass on crusted surfaces was due to substantial increases in soil surface and subsurface temperatures, as well as subsurface moisture. Again, this was not directly tested.

21.4 Influence of Soil Crusts on Vascular Plant Survival, Biomass, Fecundity and Nutrition

21.4.1 Plant Survival

Cool and Cold Deserts. Studies from cool and cold deserts have spanned many plant species and life-forms, and have included both coarse- and fine-textured soils. All studies have found that biological soil crusts either increase or do not affect vascular plant biomass and survival. Harper and St. Clair (1985) seeded two perennial grasses, two perennial forbs, two annual forbs, and one shrub in crusted and uncrusted plots at three cool desert sites around Utah (USA). Soils ranged from 33 to 66 % sand. After 1 year, crusted plots had 2.8 times as many seedlings as scalped plots, with all species enhanced except the two perennial grasses, which were not affected. After 3 years, crusted plots had 1.6 times as many seedlings. All the species that survived on both the crusted and uncrusted plots had enhanced survival on the crusted plots. In a separate study, St. Clair et al. (1984) reported that survival of three perennial grasses was enhanced on crusted soils relative to adjacent uncrusted soils in both the field (1.3–4 times) and the greenhouse (1.6–12-fold).

Lesica and Shelley (1992) found that while crusts had no effect on the survival of small *Arabis fecunda* individuals (a perennial forb), the presence of crusts enhanced the long-term survival of medium and larger individuals in Montana. Eckert et al. (1986) reported that crust removal by trampling decreased survival of perennial grass seedlings (*Poa sandbergii, Sitanion hystrix*) while increasing the emergence of the shrub *Artemisia tridentata* and of annual forbs. However, after long-term protection, crusted areas supported more of both the perennial grasses and the shrub. DeFalco (1995) reported a greater number of individuals of five annual grasses and forbs on crusted soils relative to adjacent uncrusted soils. Jeffries and Klopatek (1987) and Kleiner and Harper (1977) report that vascular plant species richness and cover was positively correlated with crusted soils, while Anderson et al. (1982) found no significant correlation between crusts and vascular plant cover. Meyer (1986) reported a positive correlation between vascular plant species richness and crust development on gypsiferous soils.

As with germination, Larsen (1995) showed that seedling density of native *Stipa* was not affected by biological soil crusts relative to uncrusted soils. However, in contrast to native annuals, density of the exotic annual grass *Bromus tectorum* was lower on intact crusts. *Bromus* density was greater on crusts that were broken, but left in place. Greater seedling success in crusted soils, when compared to uncrusted soils, has also been reported by Fritsch (1922), Booth (1941), Fletcher and Martin (1948), and Shields and Durrell (1964). The presence of a well-developed lichen-moss crust in arctic cold deserts supported a higher diversity of vascular plants. This was attributed to reduced cryoturbation and increased nutrient availability, organic matter, and soil temperature associated with the presence of soil crusts (Gold and Bliss 1995).

Hot Deserts. Eldridge and Greene (1994) found no relationship between Australian *Atriplex* shrub seedling establishment and crust cover. Graetz and Tongway (1986) found the cover of chenopod shrubs was positively correlated with crust cover, citing increased moisture and nutrients in the upper 10 cm as responsible. Survival of the native grass *Stipa* in Australia was not affected by the presence of soil crusts, while survival of the exotic *Schismus* was reduced on crusted sufaces (Crisp (1975). The annual grasses *Bromus* and *Schismus* have been found to have higher densities on broken crust in the cool deserts of the US and hot deserts of Australia and Israel (Crisp 1975; Larsen 1995; Prasse 1999). Prasse (1999) also found higher densities of all annuals on crusts that were broken. He also noted no effect of crusts on plant mortality. Studies in Israel showed that vascular plant densities correlated with surface stability (Danin 1978; Kadmon and Leschner 1995; Tielbörger 1997), although a direct connection with biological soil crusts has not been established.

21.4.2 Plant Biomass

Cool Deserts. Pendleton and Warren (1995) reported that one annual grass (*Bromus tectorum*), one perennial grass (*Sitanion hystrix*), two perennial forbs (*Gaillardia pulchella*, *Sphaeralcea munroana*) and one shrub (*Coleogyne ramosissima*) all showed greater shoot and total plant weight in crusted soils than adjacent uncrusted surfaces. All species except *Coleogyne* had greater root weight. All species showed smaller root/shoot ratio in crusted soils, indicating greater soil nutrients were available in the crusted soils. Schlatterer and Tisdale (1969) showed that the height and biomass of *Sitanion hystrix* were significantly increased, and biomass and height of *Stipa thurberiana* and *Agropyron spicatum* were not affected by moss cover when compared to artificial litter. Generally, height and biomass were greater with moss cover than no litter for all three species.

DeFalco (1995) reported greater biomass in individuals of five annual grasses and forbs on crusted soils relative to adjacent uncrusted soils. In another study, biomass of the native annual grass *Festuca octoflora* was twice that on crusted soils compared to uncrusted soils (Belnap 1995). Similar results were obtained by other authors (Brotherson and Rushforth 1983; Shields and Durrell 1964). In the Arctic, crusted sites had higher plant diversity and biomass. These sites also had increased soil nutrients, organic matter, and temperature, as well as reduced soil cryoturbation, due to the presence of crusts (Gold and Bliss 1995).

Hot deserts. In southern Arizona, McIlvanie (1942) found the biomass of four species increased 45–300% when grown on crusted surfaces relative to uncrusted surfaces. However, it should be noted that he was also comparing grazed and protected soils. In Israel, vascular plant biomass was correlated with surface stability (Danin 1978; Kadmon and Leschner 1995; Tielbörger

1997). However, the role of biological soil crusts in these findings has not been directly tested.

21.4.3 Vascular Plant Fecundity

Only two studies examined the effect of crusts on plant fecundity. Lesica and Shelley (1992) found that crusted soils had no effect on the fecundity of any size class of the perennial *Arabis fecunda* in Montana. In a hot desert (Israel) on a smooth cyanobacterial crust, Prasse (1999) found the annuals *Ifloga spicata* and *Senecio glaucus* had the same or higher capitules/plant where crusts were broken or removed compared to where crusts were left intact. Enhanced plant fecundity was attributed to greater water interception in areas where the crusts were broken.

21.4.4 Vascular Plant Nutrition

Alteration of soil-surface chemistry by biological soil crusts is significantly correlated with changes in the content of bioessential elements in the tissue of associated seed plants (Harper and Marble 1988; Belnap and Harper 1995; Harper and Pendleton 1993; Pendleton and Warren 1995; Harper and Belnap 2000). Findings from these studies are summarized for ten plant-essential elements in Table 21.1. All studies occurred with *Microcoleus-Nostoc-Collema* soil crusts on sandy, calcareous soils. Soil crusts enhanced N content of associated seed plants in all trials. In contrast, P in plant tissue from crusted areas was increased as often as reduced. The presence of soil crusts generally enhanced plant uptake of Mg, K, Cu, and Zn, while generally reducing Fe uptake. Ca and Mn in tissue of seed plants grown in crusted soils show no consistent differences from control plants.

Other researchers have found similar results. Schlatterer and Tisdale (1969) observed that N was higher in *Stipa thurberiana* (18 %), *Sitanion hystrix* (10 %), and *Agropyron spicatum* (19 %) under moss litter when compared to artificial litter. With no litter, only *Agropyron* had higher N (18 %). They found no difference in P among the treatments. DeFalco (1995) measured N and P in five annual forbs. Individual plants in crusted soils had lower concentrations of N; however, plant biomass was much higher on crusted soils. When plant concentrations were calculated on a m^2 basis, total N and P was much higher in combined plant tissue on the crusted soils. Individually, two of the species showed no difference between crusted and uncrusted soils (*Cryptantha pterocarya*, *Eriophyllum wallacei*). *Bromus rubens* and *Erodium cicutarium* showed higher N on crusted soils (sixfold and tenfold, respectively) and P (ninefold and tenfold, respectively). *Descurainia pinnata*, on the

Table 21.1. Elemental content of vascular plant tissue. (Harper and Belnap 2000)

Element	Substrate	Shrub		Forb				Grass
		CORA seedlings	*CORA* adults	*BRRA* adults	*LEMOJO* adults	*LEMOMO* adults	*STLO* adults	*STHY* adults
Ca, %	No Crust	0.88	3.13	2.98	0.62	1.17	1.16	1.42
	Crust	0.86	3.19	2.44*	0.64	1.41	1.80**	1.00**
K, %	No Crust	1.19	0.80	1.72	2.19	3.03	1.49	1.50
	Crust	0.86**	0.78	1.43**	2.26*	4.15*	2.06**	2.01*
Mg, %	No Crust	0.49	0.41	0.45	0.29	0.34	0.20	0.14
	Crust	0.46	0.43	0.34**	0.26*	0.43	0.25**	0.14
N, %	No Crust	5.60	0.98	NM	1.29	1.42	1.44	1.99
	Crust	5.83	1.07	1.24	1.41*	1.58	2.09**	2.30**
P, %	No Crust	0.55	0.11	0.35	0.07	0.25	0.28	0.24
	Crust	0.69*	0.11	0.23**	0.08*	0.28	0.27	0.13**
Cu, ppm	No Crust	13.80	4.00	4.80	8.60	3.08	5.80	8.60
	Crust	15.00*	4.00	3.80	8.80	6.33*	7.20*	9.10
Fe, ppm	No Crust	765.40	138.60	66.60	29.70	474.10	419.20	130.40
	Crust	646.90	84.60**	60.50	27.60	772.70	222.40*	117.90
Mn, ppm	No Crust	0.49	0.41	119.10	49.50	52.50.	28.80	24.20
	Crust	0.46	0.43	163.90**	47.10*	102.50	25.00	71.90**
Na, ppm	No Crust	61.50	8.40	28.50	51.30	161.00	NM	NM
	Crust	69.80	9.20	22.50	50.70	281.00*	NM	NM
Zn, ppm	No Crust	51.10	13.00	829.70	24.80	12.20	20.20	7.70
	Crust	74.10**	11.20	917.10	23.90	15.20	19.80	12.60*

CORA=Coleogyne ramosissima, BRRA=Brassica rapa, LEMOJO=Lepidium montanum var. jonesii, LEMOMO=L. montanum var. *montanum, STLO=Streptanthella longirostris, STHY=Stipa hymenoides.*
For adult *Coleogyne*, leaves and current year twigs were analyzed.
For *LEMOJO* and *STHY*, leaves were analyzed.
For *BRRA, LEMOMA,* and *STLO*, roots, stems and leaves were analyzed.
Crusted and uncrusted soils were separated by more than a 4.0 m linear distance. Sites were similar in soil type, aspect and vascular plant cover.
$^{*}=P<0.05$, $^{**}=P<0.01$. NM=not measured.

other hand, had lower N and P (3× and 10×, respectively). Cyanobacterial inoculations have long been known to increase N in rice plants (Venkataraman and Neelakantan 1967) and vegetable crops (Dadlich et al. 1969).

The negative effects of crusts on plant P and Fe may be related to competition between the soil-crust organisms and the roots of seed plants for bioessential elements. P and plant-available Fe are often in short supply in the calcareous, sandy soils common to many deserts (Black 1968). Thus, crustal microorganisms may compete with vascular plant roots for these elements. This competitive effect is expected to be most severe for small, short-lived (especially annual) plants that root heavily at the soil surface, which is the area most influenced by the biological soil-crust organisms. We have observed that many plants, including shrubs, produce hair-like feeder roots in the surface 2 cm of soil, especially in seasons of unusually abundant rainfall (Belnap and Harper 1995; Harper and Belnap 2000). Such roots could scarcely escape competition for bioessential elements with organisms of the microbiotic surface crusts.

Biological crusts can exert positive influence on uptake of essential elements in a variety of ways. Crusted soils are enriched by cyanobacterially-fixed N, and uptake of this N by associated organisms has been documented (see Sect. 21.2.2 above; Chap. 19). Soil content of K, Mn, Ca, Mg, and P are consistently shown to be greater where biological crusts occur. Although Fe and Zn soil concentrations are generally lower in crusted areas, plant tissue concentrations of Zn and, occasionally, Fe are elevated (Belnap and Harper 1995; Harper and Belnap 2000; Harper and Pendleton 1993). Thus, the biological crusts appear to somehow render those elements more available to plant roots. It is well known that both Zn and Fe, along with other elements such as Cu, Co, Mn, and Mo, can form stable complexes with chelating compounds (see Sect. 21.2.2).

Studies examining mycorrhizal infection rates show plants growing on biologically crusted surfaces consistently have higher infection rates than the same species growing on adjacent, uncrusted surfaces. This association may also partially explain higher nutrient concentrations in leaf tissue. Differences may also be partially ascribable to a thermal effect. Dark crusts are warmer than lighter uncrusted soils; therefore, uptake of nutrients would occur at a higher rate (Harper and Pendleton 1993).

Herbivores and other consumers may benefit indirectly from the enhanced nutrient status of these ecosystems (Belnap and Harper 1995). Populations of microarthropods are also correlated with the presence of well-developed soil crusts (see Chap. 14). Subsequent enhancement of decomposition rates may also contribute to greater availability of nutrients to associated vascular plants. Secreted subsurface carbon compounds may also influence water availability to vascular plant seedlings.

21.5 Conclusions

The effect of soil crusts on final seed placement once seeds are dispersed from the parent plant is fairly well understood. Seed entrapment is low in areas where soil surfaces are smooth (cyanobacterial crusts in hot deserts or soils with significant physical or chemical crusting that lack frost heaving), while entrapment is high in regions where crusts significantly increase surface roughness (well-developed crusts and frost-heaving).

The effect of biological soil crusts on seed germination is more complex. Germination of annuals and seeds that lack burial mechanisms appear most affected by biological soil crusts, especially in areas with smooth soil surfaces or for plant seeds that lack structures that facilitate soil-seed contact. Consequently, crusts may significantly affect plant germination and initial establishment in ecosystems where annuals or plants without burial mechanisms contribute a significant amount of the primary productivity, and where soil surfaces are smooth. This combination of characteristics is most often found in hot deserts. In contrast, crusts probably have much less influence on plant germination and initial establishment in communities dominated by perennial plants and/or seeds with burial mechanisms, and in areas with roughened soil surfaces that facilitate seed-soil contact. These characteristics are most often found in cool and cold deserts. However, it should be kept in mind that the ultimate determinant of perennial vascular plant density or biomass in any desert is seldom seed dispersal or germination per se. Instead, water and nutrients are generally the limiting factors (Mabbutt and Fanning 1987; Tongway and Ludwig 1990; Dunkerley and Brown 1995). Introduced annual grasses that lack burial mechanisms have shown inhibited germination on all intact crust types in both hot and cold deserts. This may result from their evolution in livestock-disturbed areas.

Once plants have become established, the effect of biological soil crusts on survival and biomass appears universally positive or without effect in cool and cold deserts. No study has documented a negative relationship between plant survival or biomass and the presence of crusted soils in these habitats. In hot deserts, studies are much more limited, and thus few generalizations can be made. Biomass of the four perennial plants tested in one study showed biomass was higher, or not affected, by the presence of crusts. However, studies of annual plants show a highly variable response.

To fully understand the relationship between soil crusts and vascular plants, we need studies that specifically address the influence of biological soil crusts as separate from the influences of inorganic crusts, soil types, and climate regimes. We need data on how variation in crustal species composition affects seed dispersal and germination, as the influence of cyanobacterial crusts on soil factors may be very different from moss-lichen crusts

(West 1990). And lastly, we need a better understanding of how crust-caused modifications of the soil environment affect vascular plant communities.

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