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# The potential roles of biological soil crusts in dryland hydrologic cycles

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## Abstract:

Biological soil crusts (BSCs) are the dominant living cover in many drylands of the world. They possess many features that can influence different aspects of local hydrologic cycles, including soil porosity, absorptivity, roughness, aggregate stability, texture, pore formation, and water retention. The influence of biological soil crusts on these factors depends on their internal and external structure, which varies with climate, soil, and disturbance history. This paper presents the different types of biological soil crusts, discusses how crust type likely influences various aspects of the hydrologic cycle, and reviews what is known and not known about the influence of biological crusts on sediment production and water infiltration versus runoff in various drylands around the world. Most studies examining the effect of biological soil crusts on local hydrology are done by comparing undisturbed sites with those recently disturbed by the researchers. Unfortunately, this greatly complicates interpretation of the results. Applied disturbances alter many soil features such as soil texture, roughness, aggregate stability, physical crusting, porosity, and bulk density in ways that would not necessarily be the same if crusts were not naturally present. Combined, these studies show little agreement on how biological crusts affect water infiltration or runoff. However, when studies are separated by biological crust type and utilize naturally occurring differences among these types, results indicate that biological crusts in hyperarid regions reduce infiltration and increase runoff, have mixed effects in arid regions, and increase infiltration and reduce runoff in semiarid cool and cold drylands. However, more studies are needed before broad generalizations can be made on how biological crusts affect infiltration and runoff. We especially need studies that control for sub-surface soil features such as bulk density, micro- and macropores, and biological crust structure. Unlike the mixed effects of biological crusts on infiltration and runoff among regions, almost all studies show that biological crusts reduce sediment production, regardless of crust or dryland type. Published in 2006 by John Wiley & Sons, Ltd.

KEY WORDS arid; desert; infiltration; microbiotic crusts; runoff; semiarid; water cycles; water erosion

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## INTRODUCTION

It is well known that many soil factors influence local hydrologic regimes. The most often discussed variables controlling the dynamics of sediment production and runoff versus infiltration include factors such as soil texture, degree of soil aggregation, soil structure, plant and plant litter cover, rock cover, and physical crusting. Less understood and discussed is how the presence of biological soil crust (BSC) communities (consisting of soil surface-dwelling cyanobacteria, green algae, microfungi, bacteria, lichens, and bryophytes) influences local hydrologic dynamics. BSCs can profoundly influence many soil surface characteristics known to affect local hydrologic patterns (reviewed in Warren, 2003a,b), including soil texture, aggregation, cohesiveness, absorptivity, roughness, cracking, micro- and macropore formation, water retention, and patterns of infiltration, as well as the composition and architectural structure of vascular plant communities. Little is known about the relative importance of these features among themselves or relative to sub-surface soil characteristics, as

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few experiments have utilized the same equipment, measured the same variables across sites, or successfully distinguished the influence of crusts from other site variables.

This paper reviews what is known about how biological crusts influence soil surface features and local hydrologic processes and presents a conceptual model for how the modification of soil surface features likely influences local hydrologic patterns. It is hoped that this discussion and the conceptual framework presented will provide structure and stimulus for a more systematic investigation into how biological crusts affect local hydrologic cycles.

## AN OVERVIEW OF BIOLOGICAL SOIL CRUSTS

Biological soil crusts are created by an intimate association between soil particles and cyanobacteria, green algae, microfungi, bacteria, lichens, and bryophytes which live within, or immediately on top of, the uppermost millimetres of soil (Belnap and Gardner, 1993). These organisms, and the extracellular polysaccharide materials associated with them, connect soil particles together, creating a coherent living crust that covers the surface of many dryland regions. Biological soil crusts have had many names, including cryptogamic, cryptobiotic, microbiotic, and microphytic soil crusts.

### *Distribution of biological soil crusts*

Biological soil crusts organisms have a very wide distribution. They occur on most soil types and in almost all vegetative communities where sunlight can reach the soil surface. They have low moisture requirements and a high tolerance of extreme temperatures and light, thus enabling them to survive under conditions that limit vascular plant growth (Belnap *et al.*, 2003a). Because of these traits, they are often the dominant ground cover in low-productivity environments such as hyperarid, arid, semiarid, sub-humid, alpine, and polar regions, which constitute over 40% of the world's terrestrial land mass (Figure 1). Biological crusts also occur in localized areas in more mesic regions (e.g. pine barrens, serpentine soils, temperate steppe). Only the tropical evergreen rain forests appear to lack BSCs (Büdel and Lange, 2003).

Soils in dryland regions generally have a pH of 7 or greater. This factor, combined with the relatively high potential evapotranspiration (PET) found in these areas, results in the soil surface being mostly dominated by cyanobacteria, lichens, and mosses. Under these conditions, the biomass and cover of green algae, microfungi, and other bryophytes (e.g. liverworts) are quite limited. For this reason, we will only discuss cyanobacteria, lichens, and mosses in the following review. However, when considering the influence of biological crusts on hydrologic processes, the function of green algae and microfungi is similar to cyanobacteria, and the function of other bryophytes is similar to lichens, such as liverworts. Thus, it is not expected that the fundamental principles discussed below will show much change if the more common dryland species are replaced by those found in relatively more mesic areas.

### *Types of biological soil crusts among climatic regions*

The appearance, biomass, and species composition of BSCs vary widely among climatic regimes. These differences in external and internal structure result in distinct crust types, with each type having a different effect on ecological and hydrologic processes. Multiple classification schemes for crust types have been proposed (reviewed in Belnap *et al.*, 2003a). The classification system presented here is based on factors that influence runoff, infiltration, and sediment production and is therefore helpful in discussing how crusts may affect hydrologic function. This system defines four types of biological crust (Figure 2).

**Smooth crusts** occur in hyperarid hot drylands (e.g. Atacama, Sahara deserts) where soils never freeze and where PET is very high (Figure 2). The crust biota in smooth crusts is dominated by a thin layer of cyanobacteria and fungi that live on or just below the soil surface, with rare pockets of lichens and mosses in specialized microhabitats. Soils are generally young, coarse, and relatively unweathered. When the individual

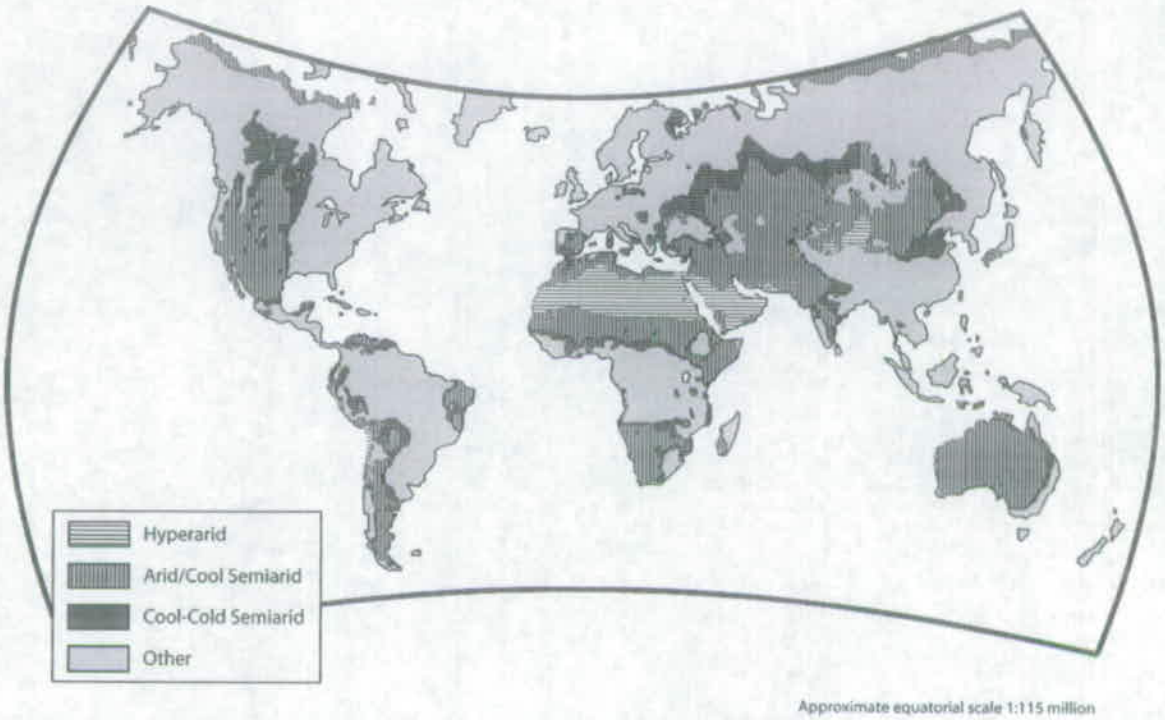


Figure 1. Patterned areas represent regions where biological soil crusts are likely to influence local hydrologic processes. Cumulatively, these lands represent 40% of the Earth's terrestrial surface

soil particles are bound together by the crust biota, the smoothness of the soil surface is increased. Very low moisture availability results in a low biomass and thus low absorptivity of crust organisms, with relatively high soil surface porosity and low surface roughness.

**Rugose crusts** occur in dryland regions where soils do not freeze, but with lower PET than hyperarid deserts (e.g. low-elevation Sonoran, Mojave, Australian deserts; Figure 2). Rugose crusts are dominated by a thin layer of cyanobacteria and fungi. In drier regions of these deserts, they contain sparse patches of lichens and mosses growing on the relatively even soil surface. As moisture increases within these regions, lichen and moss cover increases as well, although the soil surface still remains fairly flat. Overall low moisture results in moderately low crust biomass, soil surface roughness, and crust absorptivity, whereas soil surface porosity is moderately high.

**Pinnacled crusts** occur in mid-latitude cool desert regions (e.g. low-elevation Colorado Plateau, mid-latitude China deserts, high-elevation Sonoran and Mojave deserts) where soils freeze and PET is lower than in hot deserts (Figure 2). Pinnacled crusts are dominated by relatively thick layers of cyanobacteria with up to 40% lichen and moss cover. This crust type is characterized by strikingly pedicelled mounds formed as soils uplifted by frost heaving are differentially eroded by downward-cutting water. These castle-like mounds can be up to 15 cm high, with thin tips 4–10 mm across. Crust biomass, crust absorptivity, and soil surface roughness are high in this crust type, with relatively low soil surface porosity.

**Rolling crusts** occur in colder, lower PET regions (e.g. northern Great Basin, high-latitude deserts) than pinnacled crusts (Figure 2). Lichens and mosses heavily dominate these thick crusts. The upward frost heaving of the soil is counteracted by a cohesive, thickly encrusted mat of lichens and mosses. This mat presents an erosion-resistant surface that prevents differential downward cutting, creating a roughened, slightly rolling crust surface. The low PET in these regions allows for very high crust biomass and surface absorptivity, with low soil surface porosity and moderate soil surface roughness.

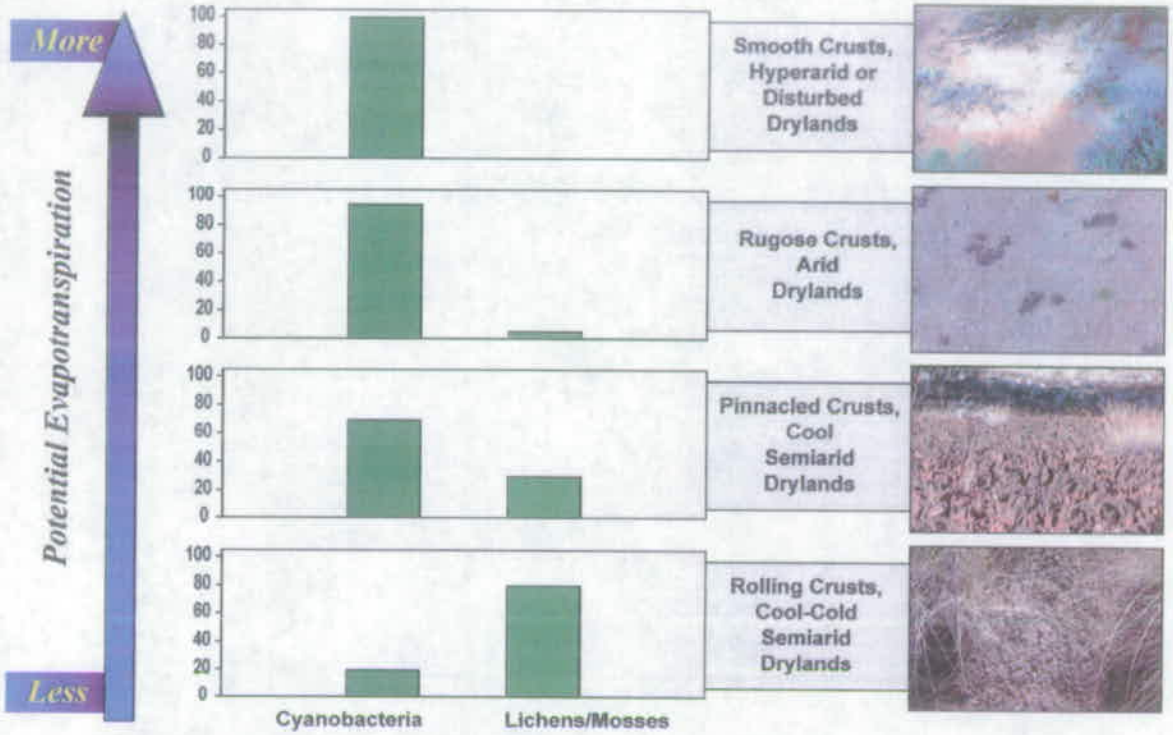


Figure 2. Classification of biological crust types based on flora and external morphology. The flora of BSCs change with rainfall timing and amount. In hyperarid deserts, biological crusts are dominated by cyanobacteria, whereas in dryland regions with lower PET, they are dominated by lichens and mosses. The external morphology of biological crusts also changes with climate. In hyperarid regions, biological crusts are flat. Decreasing PET and freezing soils increase the surface roughness of crusts

*Types of biological soil crusts within a given climatic region*

Within a given climatic zone, many factors can influence the external morphology of BSCs. Crusts with similar species and biomass are flatter when they occur on clay and silty soils compared to those on adjacent coarser soils. In soils with weak crystalline structures (e.g. soils derived from calcite and gypsum), extracellular polysaccharide materials combine with the dissolved minerals when soils are wet to create very strong microbial sheaths that are part organic and part inorganic materials. The internal strength of these soils resists winter frost heaving, and they do not form the highly dissected surfaces that may be found in adjacent sandy soils. Cyanobacteria generally dominate soils that are very sandy (>90%), very salty, or have a high content of shrink-swell clays, regardless of the climatic zone. Lichen cover generally increases with an increase in the amount of carbonate, gypsum, and/or silt in the soil (Büdel and Lange, 2003).

In soils with heavy physical crusting, the surface morphology of crusts is primarily controlled by soil physical and chemical characteristics, and the biological components have only a limited effect. If only cyanobacteria are present under these circumstances, the resultant crusts are smooth. If lichens and mosses colonize as well, the slight roughening of the soil surface creates a rugose or rolling crust. Pinnacled crusts seldom form in soils with a high degree of physical crusting.

*Internal structure of biological soil crusts*

The internal structure of soil crusts varies with the crust flora. Cyanobacteria and fungi, ubiquitous to all crust types, provide most of the cohesive quality of the BSCs. Bare soils are first colonized by large, mobile filamentous cyanobacteria (e.g. *Microcoleus vaginatus*; Figures 3(a), 4) that live 1–4 mm below the soil

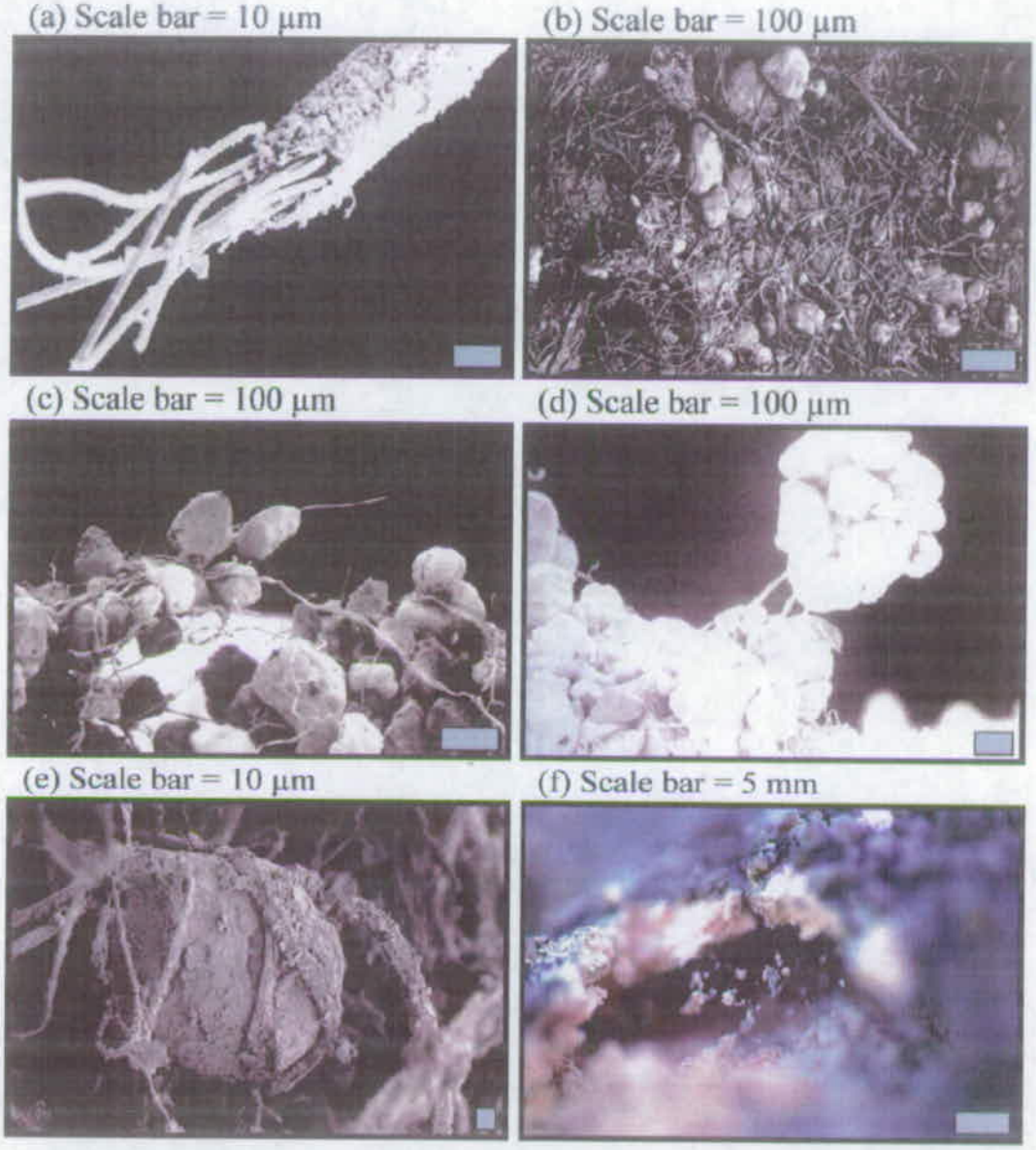


Figure 3. (a) *Microcoleus vaginatus* in sandy soils (bar = 10 μm). (b) When wetted (using freeze substitution), sheaths and filaments swell and cover the soil surface (bar = 100 μm). (c) Sheaths adhere firmly to the sand grain surfaces, binding the grains together (bar = 100 μm). (d) Soil aggregate formed by cyanobacterial sheaths (bar = 100 μm). (e) Multiple sheaths wrap around a sand grain, holding it firmly in place (bar = 10 μm). (f) Cyanobacterial sheaths hold together multiple soil aggregates (bar = 5 mm). Images (a) through (e) are scanning electron micrographs of BSCs. Image (f) is a photograph

surface. However, during wet periods, they can cover the soil surface (Figure 3(b)). Later, smaller and less mobile cyanobacteria colonize (e.g. *Nostoc, Scytonema*). These smaller species live on or just below the soil surface, creating layers of species in the soils (Garcia-Pichel and Belnap, 1996; Belnap, 2003a). The sticky, polysaccharide outer sheaths of the cyanobacteria wind throughout the uppermost soil layers (Figure 3(c)), linking soil particles together, forming soil aggregates (Figure 3(d)). These aggregates themselves are then further linked together by cyanobacterial strands (Figure 3(e), (f)).

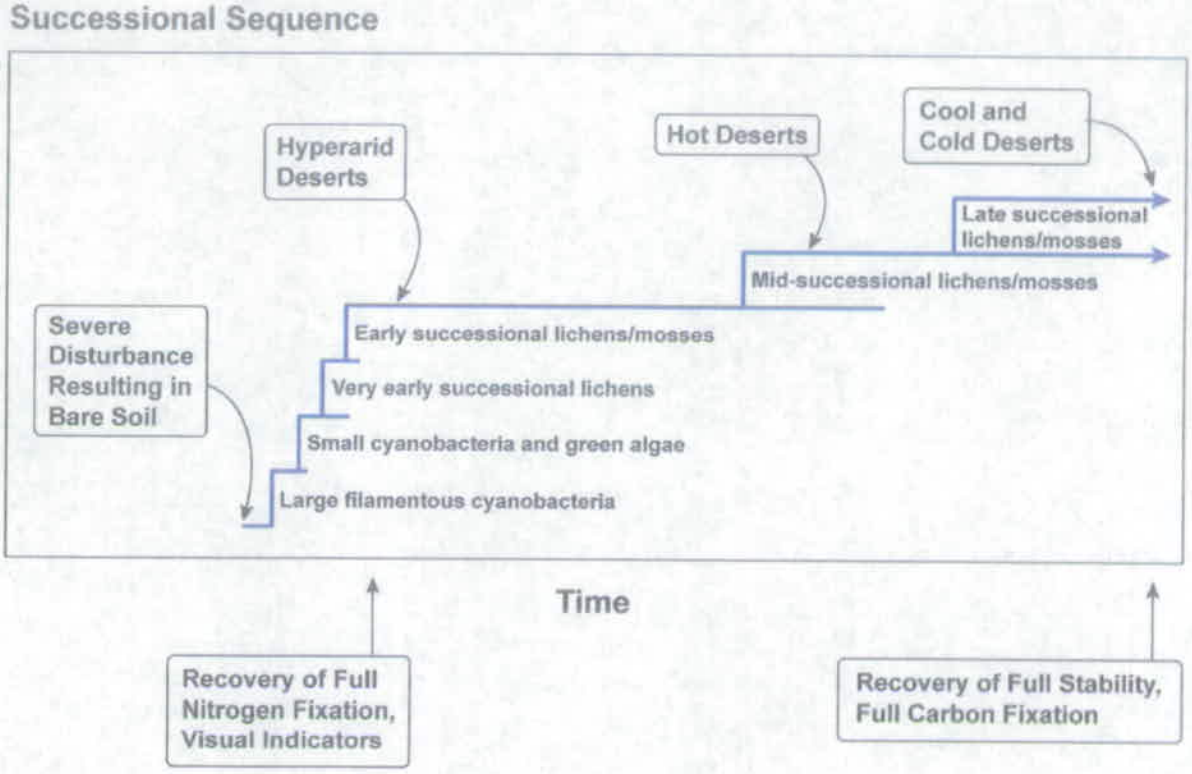


Figure 4. Colonization sequence for biological crust species. Arrows indicate colonization events; the length of the line indicates relative recovery time for each successional group. Species indicative of large filamentous cyanobacteria are *Microcoleus* spp.; for small cyanobacteria, *Nostoc* spp. and *Scytonema* spp.; very early successional lichens, *Collema* spp.; early successional lichens and mosses, *Placidium* spp. and *Pterygoneurum* spp.; mid successional lichens and mosses, *Psora* spp., *Fulgensia* spp., *Bryum* spp.; late successional lichens and mosses, *Acarospora* spp., *Panneria* spp

Once the soil surface is stabilized by cyanobacteria, lichens and mosses colonize if climate conditions permit (Figure 4). Unlike the soil cyanobacteria, which grow within the soil, lichens and bryophytes have most of their biomass above the soil surface (Figure 5), which protects underlying soils from raindrop impact and resists detachment of particles during overland flow events. Lichens and bryophytes also have anchoring structures (rhizoptae, rhizinae, and rhizomorphs; Poelt and Baumgärtner, 1964; Sanders, 1994) that penetrate down into the soil as deep as 14 mm (Belnap *et al.*, 2003a). In addition, multi-branched, subterranean moss protonemata are interspersed throughout the soil crust matrix. Combined, these structures form a dense, subterranean network of tissue that is intimately connected with soil particles and that strongly contributes to soil stability (Belnap and Gardner, 1993; Belnap, 2003a).

*Effects of disturbance and climate change on external morphology and internal structure of crusts*

The intensity, type, and time since disturbance can control both the external and internal structure of biological soil crusts. Crustal components are brittle and easily crushed, especially when dry. Once buried, these photosynthetic organisms die. Damage to buried sheath material cannot be repaired, as living cyanobacteria are no longer present to secrete new sheath material. Most soil surface disturbances leave surfaces flattened relative to the previously roughened surface (Figure 2), and early re-colonization is exclusively by the large cyanobacterial species (Figures 3(a), 4). Recovery of both the external and internal structure of crusts occurs in the sequence outlined above, with the final developmental stage determined by climate (Figure 4). Biological soil crust organisms are also sensitive to other types of disturbance, including

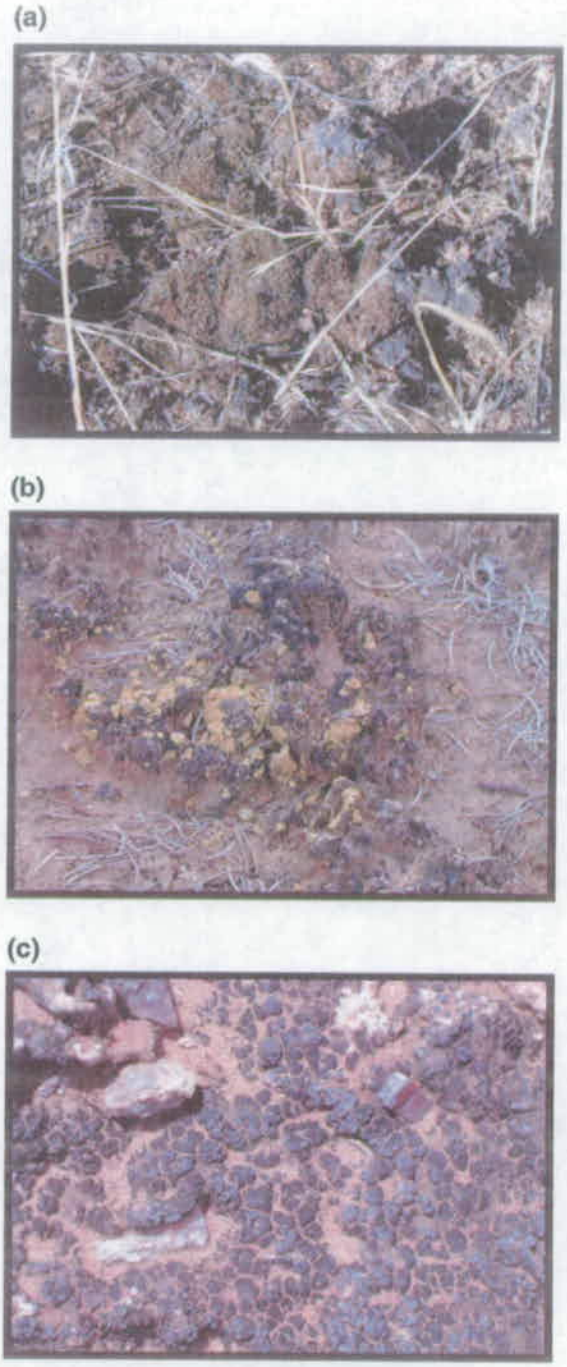


Figure 5. Photos of lichens and mosses on desert soil surfaces. Note that both lichens and mosses have substantial tissue above the surface that can completely cover soil pores. Cover can be continuous (a), discontinuously clumped (b), or more evenly, but still discontinuously (c) spread across the soil surface

air pollution, herbicides (Zaady *et al.*, 2004; Belnap *et al.*, 2003b), and climate change, including changes in precipitation (Belnap *et al.*, 2004) and increased air temperatures (Belnap *et al.*, 2006).

## BIOLOGICAL CRUSTS CAN INFLUENCE HYDROLOGIC PROCESSES

### *Soil texture*

Relatively unweathered, coarse-textured soils cover large amounts of global dryland surfaces. In these soils, particles deposited by aeolian processes can represent up to 60% of soil fines (Danin and Yaalon, 1982; Reynolds *et al.*, 2001). Airborne silts and clays are trapped by sticky cyanobacterial sheaths, by surface roughness created by biological crusts, and by protruding moss stems and lichen thalli. This results in a thin layer of silt and clay on the soil surface that is often lacking where biological crusts are absent (Verrecchia *et al.*, 1995). Silt and clay particles increase the absorptivity of the soil. However, they can also decrease soil porosity (Brady and Weil, 1996). It is predicted that dust-trapping efficiency will increase with increasing surface roughness, cyanobacterial biomass, and lichen-moss cover. Therefore, the dust-trapping ability of the soil surface is expected to increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6).

### *Absorptivity of biological crust organisms*

All BSC biota absorb water, but to varying degrees. Cyanobacteria absorb up to 10 times their volume of water and 8–12 times their dry weight (Campbell, 1979; Verrecchia *et al.*, 1995). Water absorption by lichens and mosses varies greatly among species. Gelatinous lichens and mosses can expand their cover and biomass by up to 13 times or more when wetted (Galun *et al.*, 1982), whereas crustose and squamulose lichens absorb smaller amounts of water (Blum, 1973). Mosses can absorb water directly, trap water in specialized leaf structures, and differentially channel water to their stems with special leaf arrangements (Catcheside, 1980).

Crust types vary widely in their thickness. Smooth and rugose crusts tend to be thin, whereas pinnacled and rolling crusts are much thicker, with occasional polysaccharide sheath material or moss anchoring structures found up to 10 cm below the soil surface. Biomass also increases as PET decreases. Therefore, the degree to which biological crusts affect soil absorptivity will depend on crust features as controlled by climatic factors. Unfortunately, crust absorptivity has not been quantified in any systematic way for either individual species or crusts as a mixed community. However, because cyanobacteria, mosses, and lichens all absorb water, it is expected that an increase in biomass and cover of these organisms will increase absorptivity of the crusts. Thus, absorptivity of different soil surface types is expected to increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6).

### *Soil surface porosity and the formation of micro- and macropores*

Biological crust organisms, by their very presence on the soil surface and by their ability to swell upon wetting, can clog soil pores and thus reduce soil porosity (Avnimelech and Nevo, 1964; Campbell, 1979; Eldridge and Greene, 1994; Verrecchia *et al.*, 1995; Kidron *et al.*, 1999). This is especially true when the crust organisms are concentrated on the soil surface (Figure 3(b)). However, cyanobacteria occur as strands, thus leaving spaces at the soil surface. Therefore, cyanobacteria are less likely to clog pores than lichens and mosses, which are large enough to cover soil pores completely (Figure 5(a)). However, the cover of any of these organisms is seldom continuous (Figure 5(b–c)). Because cyanobacteria occur on the soil surface, high intensity raindrop impact can break apart aggregates formed by the cyanobacterial filaments, allowing pores to clog (Faust, 1970). Unlike most cyanobacteria, lichen tissue and moss stems completely protect underlying soil aggregates. Data suggest that porosity at the soil surface decreases as cyanobacterial biomass and lichen/moss cover increase (Figure 6), especially once lichen and moss cover exceeds a critical threshold (Eldridge, 2003).

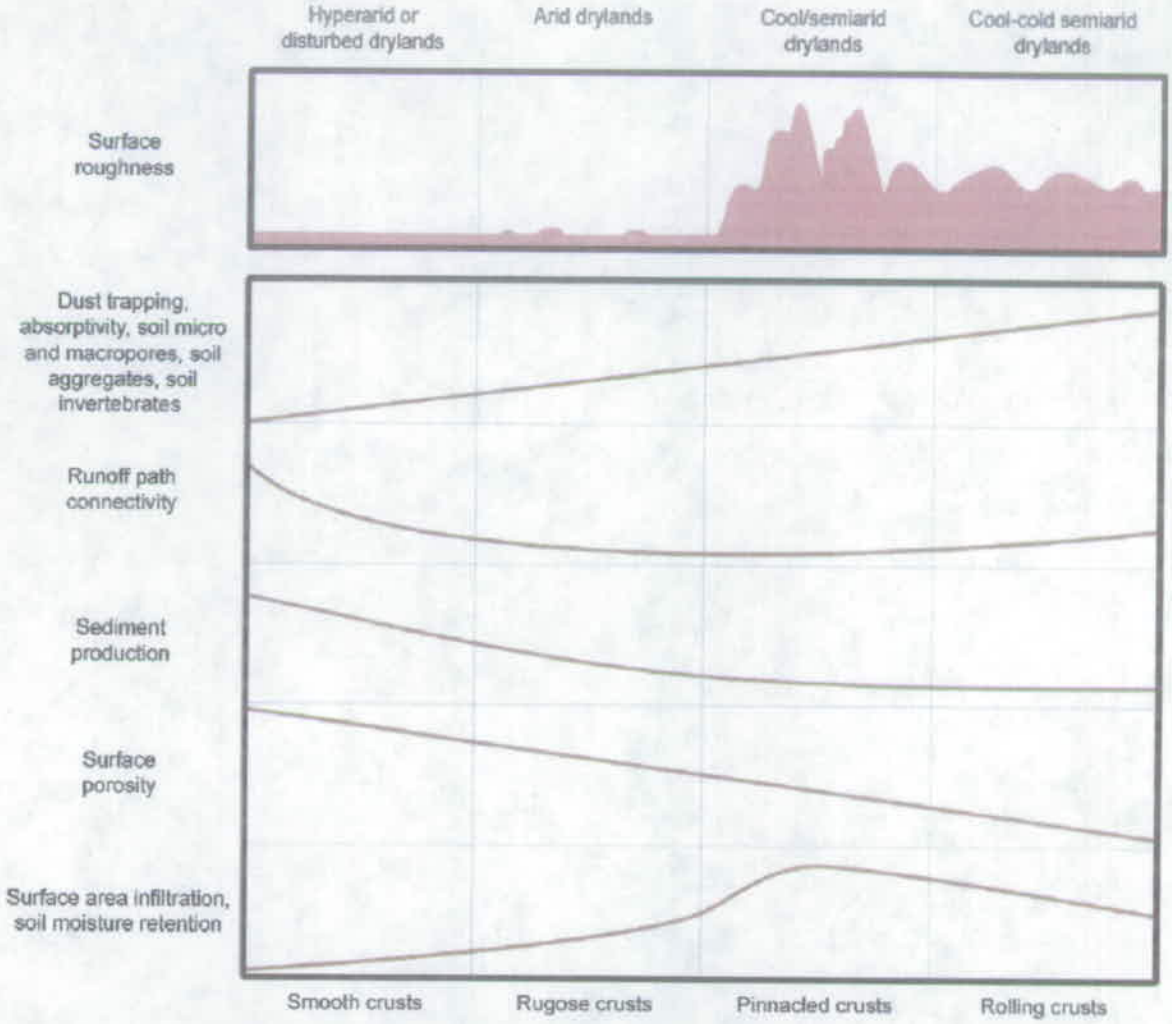


Figure 6. Conceptual diagram of the possible influence of different crust types on soil features that affect local hydrologic cycles

Counteracting the tendency to clog soil pores, biological crust organisms are known to increase aggregation via soil carbon additions. This creates micropore channels, which are known to increase water infiltration (Greene, 1992; Eldridge *et al.*, 2001). These micropore channels are also stabilized by crust organisms when soils are exposed to rainfall or overland flow (McIntyre, 1958; Bond and Harris, 1964; Rogers, 1989; Eldridge *et al.*, 2001; Eldridge, 2003). Therefore, as the numbers of cyanobacterial filaments and anchoring structures increase with decreasing PET and thus biological crust cover, the number of soil aggregates and micropores are expected to increase as well (Figure 6).

Soil micropores and macropores are also created by burrowing soil invertebrates, many of which feed on the cyanobacteria, lichens and mosses found in BSCs. These soil invertebrates include mites, collembolans, nematodes, rotifers, tardigrades, isopods, snails, mole crickets, tenebrionid beetles, protozoans, termites, and ants. Studies show that the diversity and abundance of soil invertebrates increase as lichen and moss cover increases (reviewed in Belnap, 2003b).

Because of larger numbers of filaments, lichen–moss anchoring structures, greater soil carbon, and burrowing invertebrates, an increase in micropore formation is expected with increased cyanobacterial biomass

and lichen/moss cover. Therefore, it is expected that pore formation on different soil surfaces will increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6). However, we have no reliable data on this. In addition, we have no data on the conditions under which pore clogging by crust organisms retards infiltration more or less than the formation and stabilization of pores increase infiltration.

*Differential infiltration patterns*

As discussed above, different soil biota can influence infiltration differently. Cyanobacteria generally occur just below the surface in strands with spaces between them (Figure 3(a)), while lichen and moss tissue can have low to high coverage of the soil surface (Figure 5(a–c)). Thus, water is expected to infiltrate more evenly in bare soil, a smooth cyanobacterial crust type, or in a continuous lichen–moss crust than in rugose and pinnacled crusts where lichens and mosses occur in patches. However, biomass within any crust type is also concentrated in patches, and differential infiltration patterns have been observed at a very small scale (e.g. Bond and Harris, 1964).

*Soil surface roughness*

The presence or lack of soil surface roughness can have a large influence on water retention times at a given site (Thurow, 1991). Smooth crusts flatten the soil surface and thus reduce water retention times relative to uncrusted surfaces (Yair, 1990). In contrast, retention time is greatly increased in crusts with high pedicels when compared to crusts having little pedicellation (Barger *et al.*, unpublished data; Belnap *et al.*, unpublished data). This is likely due to the large increase in path length experienced by water travelling over a pinnacled soil crust compared to a smooth crust (Figure 7, Belnap *et al.*, 2005). The only experiment assessing the effect of rugose crusts on retention time without the complication of disturbance (see Past Studies: How Crusts Affect Runoff and Infiltration below for further discussion on the undesired side effects of disturbance treatments) showed time to ponding was positively related to crust cover ($R^2 = 0{\cdot}35$), but there was no correlation with time to runoff (Eldridge *et al.*, 1997). There are no known measures for rolling crusts. If it can be assumed that surface roughness, and thus tortuosity, dominates retention time, then it is expected that retention time will change with the soil surface type, and increase in the following order: smooth crust < bare soil < rugose crust < rolling crust < pinnacled crust (Figure 6).

*Surface area for infiltration*

Because smooth and rugose crusts are relatively flat, they offer little increase in the amount of soil surface area available for water infiltration. Pinnacled crusts represent the other extreme, with an increase of 100% or more in surface area on the upslope side of a typical mound (Figure 2). Rolling crusts are expected to be intermediate between rugose and pinnacled crusts (Figure 6).

*Association with physical (mechanical, chemical, and vesicular) crusts*

Physical crusts are transient soil surface layers which range in thickness from less than 1 mm to a few centimetres and which are structurally different than the material immediately beneath them. Most physical crusts form due to one or a combination of the following factors: the impact of raindrops, compressional forces such as animal trampling or vehicular traffic, evaporative processes (forming chemical crusts), and trapped gas bubbles (forming vesicular crusts). Biological crusts are often associated with varying degrees of physical crusting, which is known to restrict infiltration and increase runoff (Romkens *et al.*, 1990; Eldridge, 2003; Warren, 2003a). However, very little is understood about the relationship between physical and biological crusts, and there is no known data on the threshold where the strength or thickness of the physical crust impedes infiltration relative to the various aspects of the biological crusts that may enhance (or impede, in the case of smooth crusts) infiltration. Strong physical crusting is more often associated with fine-textured

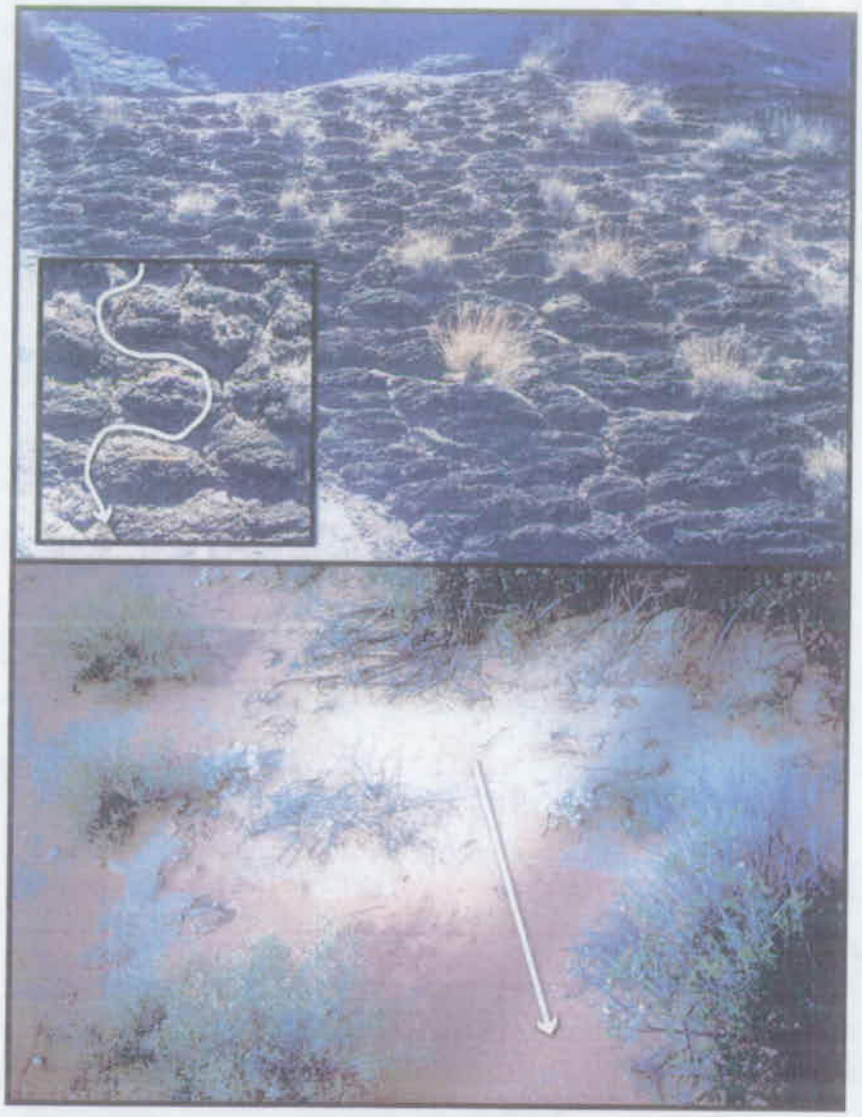

Figure 7. The path length of water leaving a site with smooth crusts is much shorter than the path length of water leaving a site with pinnacled crusts. Note that the mounds in a pinnacled crust are parallel to each other, affecting the direction of water flow

soils relative to more sandy soils. Therefore, it could be predicted that physical crusts are more likely than biological crusts to control infiltration rates on fine-textured soils. However, it has also been argued that the inherent lack of micropores in fine-textured or physically crusted soils (compared to coarse-textured soils) means that pore formation by biological crusts has a larger impact on infiltration rates of fine-textured soils than sandier soils (Warren, 2003b). Unfortunately, there is little known data to inform this debate.

*Soil surface cracking*

Polysaccharide secretions by crust organisms can increase the density of surface cracks on fine-textured soils (Danin *et al.*, 1998; Kidron *et al.*, 1999). In addition, the patchy nature of crust biomass concentrations can lead to differential drying between the upper and lower surfaces of the crust, resulting in upward curling of the polygon margins (e.g. Durrell and Shields, 1961; Danin *et al.*, 1998). This cracking and lifting upwards

of the soil surface can result in greater infiltration into a surface that is otherwise fairly impermeable (Kidron *et al.*, 1999). In addition, the roughness of the cracked surface lessens water velocity and allows more time for infiltration to occur. However, there is little information on the density of polysaccharides required to enhance cracking or uplifting of soil polygons, above that inherent to the soil alone.

*Patterns in biological soil crust mounds*

Mound formation in pinnacled crusts is initiated by ice needles pushing biologically crusted soils upwards (Belnap, 2003a). The crust organisms provide sufficient cohesion to stabilize the mounds, even after the ice needles melt. Once the surface is roughened, crust organisms preferentially colonize the east-northeast (ENE) aspects of the mounds in the northern hemisphere (George *et al.*, 2000; Bowker *et al.*, 2002), as it is the most favourable aspect for maximizing carbon gain in these organisms (Belnap, unpublished data). This greater biomass makes the ENE aspect less erodible than the other aspects, especially the west-southwest aspect. Continued greater growth and less erosion on the ENE result in mounds with their long axes facing ENE and running parallel to each other. If the mounds are at an angle to the slope, the path length of water leaving a site is greatly increased relative to a non-mounded slope (Figure 7) or to a slope where the mounds run parallel to the slope. The orientation of the mounds can also determine the path water takes as it leaves a site, thus influencing where it ultimately infiltrates into the soil. This patterning of soil crust mounds can mimic, on a microscale, the patterning of banded vegetation (d'Herbès *et al.*, 2001) and is expected to have a similar effect on the hydrology at the appropriate scale (Greene *et al.*, 2001). However, unlike banded vegetation, we do not understand the relationship between the length of the mounds or the distance between them and site characteristics likely to influence this patterning (e.g. slope degree, aspect, timing and intensity of precipitation, soil texture). Rugose and rolling crusts sometimes form small mounds, and in the northern hemisphere, these mounds are also oriented ENE. The formation process of these mounds has not been studied, although it is likely that differential growth also creates these phenomena.

*Vascular plant communities*

Biological crusts can influence many characteristics of vascular plant communities, including species composition, plant density, plant size, and community architecture. Plants, in turn, intercept, direct, and slow runoff water, thus influencing the location and amount of water retained on a site (Loik *et al.*, 2004; Ludwig *et al.*, 2005). The type and amount of influence biological crusts exert on vascular plant communities are determined by what crust type is present.

Smooth crusts increase the probability that seeds will be blown or washed from plant interspaces to nearby obstructions (e.g. plants, large rocks), as they act to flatten and smooth the soil surface (Prasse, 1999). Thus, seedlings are only infrequently found in interspaces on the smooth crust type. Instead, plants generally germinate under the canopy of nearby 'nurse' plants. Furthermore, smooth crusts are also the only crust type found to inhibit the germination of selected plant species (Boeken *et al.*, 1998), although very few species have been tested. Smooth crusts can significantly increase water runoff to downslope vegetation. In hyperarid areas, this runoff is critical to plant survival; when the crusts in the interband areas are removed, downslope plants die from lack of water and nutrients. As plants die, the banding effect of the vegetation is lost, as is the ability to retain water and nutrients at the local scale (Eldridge *et al.*, 2000; Eldridge *et al.*, 2001).

Pinnacled and rolling crusts affect vascular plants differently than smooth crusts as they retain seeds and other resources (e.g. water, organic matter) in plant interspaces, where the seeds can germinate and establish (Belnap *et al.*, 2003b). Wind tunnel experiments show, however, that when crust mounds are flattened, seeds skid off to nearby obstructions rather than staying in the plant interspace (Belnap, unpublished data). As mentioned above, the orientation of crust mounds can direct water toward, or away from, an individual plant, thus affecting survival of the plant. Seed germination and plant success are either enhanced or not affected by pinnacled and rolling crusts, with no known cases of native plants being suppressed (Belnap *et al.*, 2003b). Pinnacled and rolling crusts have a high cover of nitrogen-fixing species, which increases soil fertility, plant

density, and plant biomass in crusted soils when compared to uncrusted soils (Belnap *et al.*, 2003b). Pinnacled and rolling crusts also appear to increase the resistance of an ecosystem to invasion by exotic annual grasses (Larsen, 1995; Howell, 1998), thus conserving the hydrologic cycles associated with the native perennial plant communities. In wet years, the annual plants decrease water runoff and sediment production relative to the native perennial plants, but in drought years, the annuals often fail to germinate, leaving extensive areas of soils unprotected.

Very little is known about the influence of rugose crusts on vascular plant communities. These communities generally contain a high biomass of nitrogen-fixing cyanobacteria. It has been shown that nitrogen fixed by biological crusts is utilized by associated vascular plants (reviewed in Belnap, 2003c), and thus it likely results in greater plant biomass. Rugose crusts have been found to exclude the invasion of annual grasses, as do pinnacled and rolling crusts (Crisp, 1975). Unfortunately, we have no information on how this crust type might structure perennial plant placement on the local landscape.

### *Soil moisture retention time*

Increases in crust biomass and lichen–moss cover darken soil surfaces, which increases soil temperatures (Belnap *et al.*, 2003b). Therefore, greater crust biomass may result in greater evaporative losses of soil moisture. Alternatively, decreases in soil porosity associated with increased crust cover and biomass may lessen evaporative losses. There have only been a few studies on this topic, with conflicting results. Booth (1941) found there was greater soil moisture under biologically crusted surfaces compared to bare surfaces 2 days after rainfall. Rushforth and Brotherson (1982) and George *et al.* (2003) also found soil moisture was higher under lichen crusted soils compared to bare soils. Harper and Marble (1988) found that when lichen and moss cover was less than 61%, there was no difference between crusted and uncrusted soils. However, soils with a lichen and moss cover exceeding 85% dried more quickly than bare soils. Given the wide range of climate, soil, and crust types, we need more data on the effect of biological crusts before any general conclusions can be drawn. On the basis of what data we have, it is expected that soil moisture retention will vary with crust type in the following order: smooth < rugose < rolling < pinnacled (Figure 6).

### *Possible feedbacks among water, crusts, and soil surface features*

There are many feedback loops among crust and soil features that can influence local hydrologic processes (Figure 8). For instance, the formation of mounds in pinnacled crusts slows water and increases surface roughness, thereby increasing soil infiltration. Greater soil moisture allows for greater crust carbon and nitrogen fixation, which results in greater crust biomass. Greater crust biomass increases soil surface absorptivity, soil aggregates, soil micropore formation and stability and, up to a point, may also increase soil moisture retention. The loop is closed as these factors in turn lead to greater mounding and crust biomass. Eventually, as soil biota increase soil fertility, vascular vegetation structure and biomass are increased, which further facilitates water infiltration. This model also applies to smooth crusts. However, as smooth crusts reduce surface roughness and surface porosity, their presence will also reduce water infiltration. In hyperarid areas where smooth crusts naturally occur, the reduction of water infiltration at the microscale will still enhance vascular plant biomass at the local scale (see discussion above). If smooth crusts are a result of disturbance, the reduction of water infiltration will reduce vascular plant biomass. In either case, the other relationships described in the model still hold.

## BIOLOGICAL CRUSTS AND SOIL LOSS

### *Water velocity*

The effect of BSCs on water velocity has been found to be the same as the effect of crusts on water retention time. Smooth crusts connect sand grains together, flattening and smoothing the soil surface. This

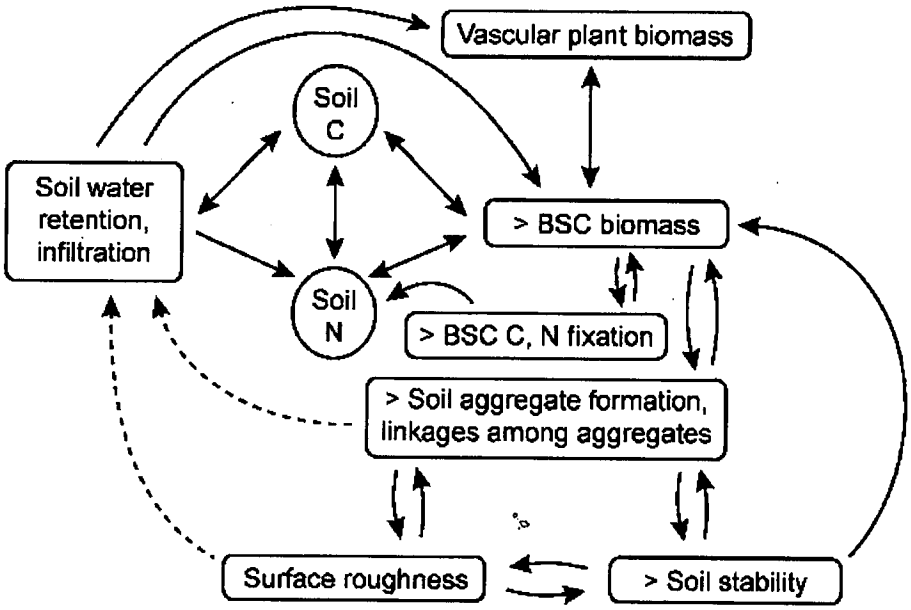


Figure 8. A conceptual model of the feedback loops in deserts connecting biological soil crusts (BSC), water and nutrient cycles, and vascular plants. The solid lines represent linkages that have been explicitly studied; the dotted lines represent hypothesized connections. It is important to note that the effect of smooth biological crusts on water infiltration and surface roughness is the opposite of other crust types (see text), and thus the type and direction of linkages noted in this model can vary with crust type

facilitates an increase in the velocity of water leaving a site (Yair, 1990). In contrast, the extreme soil surface roughness created by pinnacled crusts greatly slows time to runoff (Barger *et al.*, unpublished data; Belnap *et al.*, 2005). As discussed above, rugose crusts appear to influence time to ponding but not time to runoff (Eldridge *et al.*, 1997). There is no known information on how rolling crusts affect water velocity. Given that their surfaces are highly absorptive and of intermediate roughness between rugose and pinnacled crusts, they are expected to slow water velocity more than rugose crusts but less than pinnacled crusts.

*Soil aggregation and linkages between particles*

As discussed in several sections above, soils colonized by BSCs are filled with a network of cyanobacteria and microfungal filaments, as well as the anchoring structures of mosses and lichens (Figure 3(a–f)). This provides these soils with a tremendous resistance to movement by water (e.g. Durrell and Shields, 1961; Bond and Harris, 1964; Schulten, 1985; Belnap and Gardner, 1993; Rogers and Burns, 1994; Mazor *et al.*, 1996). Biological soil crusts also contribute significant amounts of organic carbon to arid soils via carbon fixation (Beymer and Klopatek, 1991) and decaying organic matter (Danin and Ganor, 1991), which also contributes to aggregate formation and thus stability. In fact, the organic mass of algal crusts can exceed that of vascular plants in some deserts (Rodin and Bazilevich, 1967). The ability of biological crusts to stabilize soils can exceed that of physical crusts (McCalla, 1946; Eldridge and Kinnell, 1997). As the number of cyanobacterial filaments and lichen and moss anchoring structures increases (Figure 4), the ability of these organisms to stabilize the soils is also increased (reviewed in Warren, 2003a, b).

Because lichen tissue and moss tissue actually protrude above and cover the soil surface, these organisms can offer complete protection to underlying soils from raindrop impacts. Cyanobacterial crusts, on the other hand, offer less protection to the soil surface, as the bulk of the cyanobacteria reside just under the surface. Although they weave a protective web throughout the soil that often connects to soil particles at the surface, raindrops still directly impact these soil particles. The type of cyanobacterial species present also affects the protective ability of cyanobacterial crusts. For instance, the filamentous *Scytonema* is more effective at

stabilizing surfaces than the unicellular *Nostoc* (Kidron *et al.*, 1999). Therefore, as cyanobacterial biomass and lichen–moss cover increase, it is likely that resistance to soil erosion from raindrop impact and overland flow increases and sediment production declines. Therefore, erosion resistance is least in smooth crusts, more in rugose crust, even more in pinnacled crusts and the highest in rolling crusts (Figure 6).

*Surface cracking*

As discussed above, cyanobacterial crusts can increase surface cracking of fine-textured soils, and differential drying of the upper and lower layers of the crust can result in an upward curling of the polygon margins (Durrell and Shields, 1961; Danin *et al.*, 1998). This upward lifting decreases velocity of runoff water, reducing its erosive force (Kidron *et al.*, 1999).

## PAST STUDIES: HOW CRUSTS AFFECT RUNOFF AND INFILTRATION

There has long been a debate in the literature on how the presence of BSCs influences water infiltration and runoff. A considerable literature reports that the presence of crusts increases infiltration and decreases runoff (e.g. Booth, 1941; Fletcher and Martin, 1948; Osborn, 1952; Faust, 1970; Loope and Gifford, 1972; Blackburn, 1975; Brotherson *et al.*, 1983; Harper and St. Clair, 1985; Greene and Tongway, 1989; Eldridge, 1993; Perez, 1997; Seghieri *et al.*, 1997); or reduces infiltration and increases runoff (e.g. Bond and Harris, 1964; Roberts and Carson, 1971; Dulieu *et al.*, 1977; Brotherson *et al.*, 1983; Graetz and Tongway, 1986; Dekker and Jungerius, 1990; Greene *et al.*, 1990; Abaturov, 1993; Bisdom *et al.*, 1993; Danin, 1996; Mazor *et al.*, 1996; Kidron and Yair, 1997; Eldridge *et al.*, 2000). However, other studies show no effect on either process (e.g. Faust, 1970; Dobrowolski and Williams, 1994; Eldridge *et al.*, 1997; Williams *et al.*, 1999). When summarizing all these studies, Warren (2003a) suggested that overall, biological crusts decreased water infiltration in sandy soils (>66% sand) and increased infiltration where clays exceeded 15%. However, almost all the studies discussed were in hot deserts, where there was no surface roughening by soil crusts. In addition, there was a great deal of variability within the studies on those finer-textured soils. Of the 13 studies presented, 7 showed that the presence of biological crusts increased infiltration, 4 showed no effect, and 2 showed biological crusts decreased infiltration.

Most studies examining the effect of biological crusts on hydrologic cycles compare crusted soils that have not been disturbed to soils where the researchers removed the crusts by various methods (e.g. trampling by humans or livestock, scalping the surface soil, driving over with vehicles or tanks, fire). Unfortunately, in addition to the removal of biological crusts, such applied disturbances result in many changes to the structure of surface and sub-surface soils (Eldridge, 2003; Warren, 2003a). Disturbance to the soil surface breaks soil aggregates, crushes macropores, disrupts physical and chemical crusts, and compacts soils. Removal of the crusts necessitates removing the top few millimetres to centimetres of soil. Therefore, subsequent experiments encounter a surface with altered soil texture, structure, and physical crusting relative to the original surface.

Using fire to kill BSCs can create hydrophobic soils, seal surfaces, and alter soil chemistry. Killing the crusts chemically still leaves polysaccharide materials in place, which are able to stabilize the soils. Thus, the complications created by applied disturbance make it extremely difficult to reach any conclusion about how crusts affect infiltration and runoff. Instead, these studies tell us how disturbance affects previously crusted soils. In addition, the role of biological crusts on infiltration and runoff may be greatly influenced by site conditions existing before the disturbance is applied. For instance, Eldridge *et al.* (1997) suggested that biological crusts increase infiltration on degraded sites, but do not affect infiltration on sites in good condition.

Another factor that makes it difficult to draw conclusions from previous studies (even comparing among undisturbed controls of the various experiments) is the lack of reported information on soil features known to influence water infiltration and runoff such as (but not limited to) the relative cover of the crust biota by species, cyanobacterial biomass, soil surface roughness, soil texture, bulk density, the degree of other types of crusting (physical, vesicular, or chemical), surface and sub-surface soil aggregate stability, percentage of

shrink-swell clays, calcrete formation, depth to bedrock, and the number of macropores. Without this type of information, it is impossible to separate the effect of biological crusts from other soil factors, as there are many that could easily override any influence of the biological crusts (e.g. a high percentage of heavy shrink-swell clays, the presence of thick vesicular crusts, a high number of macropores; Blackburn, 1975; Dobrowolski and Williams, 1994; Warren, 2003a). Results from previous studies are also difficult to compare because most studies used different instruments, methods, and even measured different variables. Many studies also utilized methods or plots too small to allow all factors, especially soil surface roughness, to influence the results. Lastly, most studies were done in hot deserts, with little data from cool or cold deserts.

Of the 41 published studies reviewed for this paper, only 8 used a gradient of existing crust types to avoid at least some of the confounding variables introduced when surfaces are disturbed to remove crusts. Of these 8, only 5 studies utilized rainfall simulators on plots large enough to integrate most or all of the factors influencing infiltration and runoff. Four of these were conducted on smooth cyanobacterial crust (Faust, 1970; Verrecchia *et al.*, 1995; Kidron and Yair, 1997; Eldridge *et al.*, 2000) and one on rugose crusts (Eldridge *et al.*, 1997). There are also two unpublished studies on pinnacled crusts (Barger *et al.*, unpublished data; Belnap *et al.*, unpublished data). Whereas all these studies reported sufficient detail on the crusts and some reported vital information on soil structure, none of these studies quantitatively measured factors such as physical crusting or soil macropores. This makes it difficult to assess if the results obtained were the influence of crusts or other soil features.

However, there were consistent results among the studies within a particular crust type. All four studies on smooth crusts found that the presence of algal crusts reduced infiltration and increased runoff. The two unpublished studies on pinnacled crusts both found that as crust development increased (as measured by species richness, biomass, and surface roughness of the biological crust), so did total infiltration. The one study on rugose crusts in Australia showed no effect of soil crusts on runoff. Despite this consistency among crust types, we still need far more data before any generalizations are made about the influence of BSCs on infiltration and runoff.

To address the above issues, we need studies designed to explicitly address how biological crusts influence infiltration and runoff relative to other soil factors, without influencing these factors by applying disturbance. Such experiments need to use standardized equipment and measures on sample areas that (1) are large enough to integrate all the ways crusts may influence infiltration and runoff or (2) have specific characteristics that allow separation of individual factors influencing infiltration and runoff (e.g. the relative effect of clogging vs creating micropores). In addition, such studies need to avoid disturbance that may impact other surface and sub-surface soil characteristics. One approach would be to measure infiltration and runoff on a range of naturally occurring crust covers (*sensu* Eldridge *et al.*, 1997). Another would be to inoculate soils with similar surface and sub-surface characteristics with crust organisms (*sensu* Faust, 1970), with experiments performed after the crusts are formed. However, all studies need to control for underlying soil factors if we are to truly elucidate the role of biological crusts. We also need new, creative ways to approach this question. For instance, Ladyman *et al.* (1993) reasoned that greater infiltration would transfer more calcium carbonate to depth in calcareous desert soils. They then used pH changes between the surface and sub-surface soils to investigate relative infiltration among soil crust types.

## PAST STUDIES: HOW CRUSTS INFLUENCE SEDIMENT PRODUCTION

In contrast to the conflicting results on how biological crusts affect infiltration and runoff, there is a general consensus among studies in all regions that biological crusts significantly reduce sediment production from experimental sites (e.g. Booth, 1941; Fletcher and Martin, 1948; Osborn, 1952; Faust, 1970, 1971; Mücher *et al.*, 1988; Chartres and Mücher, 1989; Tchoupopnou, 1989; Greene *et al.*, 1990; Kinnell *et al.*, 1990; Eldridge, 1993; Eldridge and Greene, 1994; Eldridge and Kinnell, 1997). There are a few exceptions, but they are rare and appear restricted to smooth crusts on sand dunes (Warren, 2003b). As with the research

on infiltration and runoff, most of these studies compare undisturbed crusts with those disturbed by the researcher, making it difficult to draw definitive conclusions. However, because almost all studies obtained the same result, information on sediment production appears more reliable than that on infiltration and runoff. In addition, the studies that did not rely on disturbance treatments (e.g. Tchoupopnou, 1989; Yair, 1990; Eldridge and Greene, 1994; Eldridge and Kinnell, 1997) all found soil stability increased as crust biomass, cover, and development increased.

## CONCLUSIONS

Although previous studies have highlighted many aspects of BSCs that can, or are likely to, influence local hydrologic patterns, the role of these organisms in upland hydrologic patterns is far from well understood. The most fundamental question that remains unanswered is the relative contribution of different crust types to infiltration and runoff relative to other soil factors such as texture and sub-surface structure. Answering this question will require carefully executed studies, creative thinking, and perhaps a change in the scale of studies.

Future changes in land use and climate are likely to have a negative effect on the presence and development of BSCs. Increased human use of drylands is expected to convert many lichen–moss crusts to cyanobacterial crusts and to flatten many currently roughened surfaces. In addition, increasing air temperature is likely to decrease lichen cover in many crusts. Therefore, it is probable that the current influence of BSCs on infiltration, runoff, and sediment production will be greatly altered in the future.

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