15 Comparative Structure of Physical and Biological Soil Crusts

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15.1 Introduction

The presence of physical and/or biological soil crusts alters many characteristics of the soil surface, and thus can play a defining role in many ecosystem functions (Greene and Ringrose-Voase 1994; Issa et al. 1999). The presence of a physical crust can seal and smooth surfaces, thus decreasing rainfall infiltration and increasing the volume and velocity of water runoff (Sumner and Stewart 1992). Physical crusts often inhibit vascular plant seedling establishment. Smooth biological crusts, like physical crusts, can also control local hydrology by smoothing and partially sealing soil surfaces (Kidron and Yair 1997). In contrast, soil surfaces roughened by biological soil crusts can increase rainfall infiltration, decrease water runoff volume and velocity, and retain seeds and organic matter (Loope and Gifford 1972; J. Belnap, unpubl.). Thus, understanding the factors that control the form of physical or biological soil crusts is essential in interpreting how the presence of these crusts may influence ecosystem functions (Mücher et al. 1988).

15.2 Physical (Inorganic) Soil Crusts

Nonbiotic soil-surface crusts, or physical crusts, are a major structural feature in many arid regions. The properties of physical crusts, and their manner of formation, have been studied for years, primarily because of the detrimental effect these crusts have on agriculture crops (Sumner and Stewart 1992). These crusts are transient soil-surface layers which range in thickness from less than 1 mm to a few cm, and which are structurally different from the material immediately beneath them (Fig. 15.1).

There are four main causes of physical crusts: the impact of raindrops, compressional forces such as animal trampling or vehicular traffic, evaporative processes (forming chemical crusts), and trapped gas bubbles (forming

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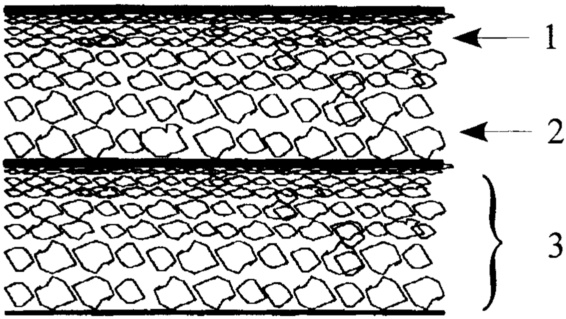

Fig. 15.1. Physical crusts are often layered as successive events break down larger soil aggregates into small particles. Water-ponding allows the small particles to rise to the surface and they then bind together to form a crust. This figure shows how breakdown of larger aggregates (*arrow 2*) by raindrops creates finer particles (*arrow 1*) that float to the soil surface, creating a physical crust. This can happen multiple times (*arrow 3*). Layers are generally a few mm thick. (After Sumner and Stewart 1992)

vesicular crusts). Physical crusts can also be created by any combination of these factors. Most physical crusts are formed by raindrop impact hitting unprotected soil surfaces. Raindrops break up soil aggregates and create smaller particles. These smaller particles can then wash into spaces between the remaining larger particles, clogging soil pores and reducing infiltration rates by as much as 90%. This can occur within the first few minutes of a rainstorm. As drying takes place, surface tension pulls the components together, forming a dense, strong layer (Sumner and Stewart 1992). Thackett and Pearson (1965) showed physical crusts that formed under simulated rainfall had a dense surface layer 1–3 mm thick that was coated with a thin layer of well-oriented clay. The physical crust was underlain by a more porous structure and the water permeability of the underlying material was about five times that of the surface 0–5 mm. Rain-formed crusts are thicker when raindrops are larger, as bigger drops have more energy and can "blast" deep into the soil, thus destroying the original structure to a greater depth. Most rain-formed crusts are less than 5 mm thick. Because large pores are absent in a physical crust, they usually have low saturated hydraulic conductivity and limited infiltration, thus increasing the velocity and amount of water runoff. This generally also increases soil loss.

Compressional forces, such as those generated by machinery or hooves of grazing animals, can also destroy soil aggregate structure and cause a physical soil crust (Lemos and Lutz 1957). Trampling compacts the soil aggregates into a comparatively impermeable surface layer, especially when soils are moist. These compacted surfaces have reduced infiltration rates and increased surface runoff. In this sense, they function hydrologically in a manner similar to raindrop-induced crusts. Chemical crusts are very common in more arid regions (Miller 1971). These crusts are often harder than those caused by raindrop or compressional impacts. As water evaporates, compounds such as salts, lime, and silica are deposited at the soil surface. Chemical crusts often form on top of raindrop or compressional crusts, which both decrease infiltration and cause water to pool on the surface. As this water evaporates, chemical crusts are formed. Vesicular crusts are common in arid soils that contain a high percentage of silt. They are characterized by numerous air pockets formed just under the soil surface, and can significantly impede water infiltration.

Physical crusts may form on soils of almost any texture except coarse sandy soils that contain very low silt and clay (Lemos and Lutz 1957). Soils especially susceptible to physical crusting are those with low structural and aggregate stability, including those with low organic matter, high silt, and/or high salt (e.g., sodium or calcium carbonates). Because organic matter increases aggregate stability (through cementation of particles and moderation of forces that reduce aggregate stability) and incorporated plant residues form planes of weakness within the soil, soils with high organic matter do not often form physical crusts. Sand particles do not form bonds between grains; many clays shrink and swell, breaking soil bonds. In contrast, silts form strong bonds on drying, and have low swelling and shrinking properties; thus, silty soils readily form physical crusts. High sodium or calcium carbonate contents can result in surface chemical crusts on any soil type.

Because physical crusts can reduce water infiltration and plant establishment, they are generally regarded as undesirable in a management situation (Sumner and Stewart 1992). However, once formed, they are very difficult to remove. Land managers are often told to use intensive grazing to break up physical crusts (Savory 1988). While livestock trampling does break the crust for a short time, the physical crust will reform after the first minutes of the next intense rainstorm. In addition, intense trampling further breaks and compacts the soil aggregates, leading to even greater long-term physical crusting. To effectively address a physical soil crusting problem, livestock grazing systems must promote greater soil aggregate stability (Thurow 1991). Therefore, management systems that increase soil surface protection and soil organic matter content through increased vascular plant and biological soil-crust cover are the only lasting solution to physical crust reduction (Blackburn 1983).

In contrast, there are situations where physical crusting can play an essential role in structuring ecosystems. In arid regions, plant interspaces are often covered by a combination of physical and biological soil crusts that reduce water infiltration. Runoff from these crusted plant interspaces can increase water to nearby vascular plants, thus providing water essential for their survival. Nearby areas that lack physical and biological crusting often also lack well-developed vegetation (Tongway and Ludwig 1990; Cornet et al. 1992; Zaady and Shachak 1994). Ancient peoples in the Middle East such as the Nabateans utilized these principles to support crops in arid regions. Studying remainders of ancient farm systems in the field, Evenari et al. (1982) reconstructed and reintroduced "runoff farming" in the Central Negev in Israel.

15.3 External Morphology and Internal Structure of Biological Soil Crusts

Both the external morphology and internal structure of biological soil crusts are very different from physical crusts. Thus, biological soil crusts generally have a very different influence on ecosystem processes. The following sections discuss the factors that influence the structure of biological soil crusts, including, climate, soil texture, soil chemistry, aeolian deposition, and disturbance history.

15.3.1 External Morphology: Major Types of Biological Soil Crusts

Biological soil crusts in different habitats can differ greatly in appearance, species composition and ecological function. Crust classification systems have been proposed for crusts in the western US (Johansen 1993) and Australia (Eldridge and Greene 1994). The classification presented below allows for worldwide comparisons and is based on the general literature and personal observations by J. Belnap and O.L. Lange. This classification is based on external crust morphology, as this aspect is easily distinguished visually, and also greatly affects many ecosystem functions. This classification also represents a potential evapotranspiration (PET) gradient. Four crust groups are recognized: smooth, rugose, rolling, and pinnacled (Table 15.1). Smooth crusts occur in hyperarid and arid hot deserts with the highest PET (Chap. 1, Photo 49); rugose crusts occur in hot, arid deserts with slightly lower PET (Photos 51, 53). Both crust types occur where soil freezing does not occur. In contrast, pinnacled crusts occur in arid to semiarid cool deserts (Photo 31), where soils freeze during cold winters and lower PET supports a higher biomass of mosses and lichens than the hot deserts. Rolling crusts occur in even colder semiarid cool and cold deserts (Photo 29), where soils freeze in winter and even lower PET supports a larger biomass of lichens, mosses, and vascular plants than found in less moist deserts. Exceptions to this distribution pattern are the rugose crusts which occur in temperate regions (with very

Table 15.1. Definitions of crust types

Topography	Surface Roughness	Organisms Involved	Region of Occurrence
Smooth no frost heaving	0–1 cm	Cyanobacteria, algae, etc. inside the soil. No lichens or mosses	Habitats without soil freezing, e.g., hyper-arid Australia, dunes in the Negev (partially fixed); physical and chemical encrustations may be involved (Photos 49, 50)
Rugose no frost heaving	1–3 cm	Scattered patches of lichens and mosses (in addition organisms inside the soil)	Habitats without soil freezing, e.g., Australia, Central Negev, Coastal Fog Zone of the Namib, Mediterranean area (Photos 48, 51, 52, 53) or as a successional stage in temperate regions (Photos 9, 55)
Rolling frost heaving	3–5 cm	Fairly continuous cover of lichens and mosses (in addition to organisms inside the soil)	Habitats with winter freezing, often in clay soil or with high moss-lichen cover, e.g. northern Great Basin, USA (Photos 29, 30)
Pinnacled frost heaving	5–15 cm	Cyanobacteria, algae, etc. inside the soil with or without lichens and mosses	Habitats with winter frost, e.g. Colorado Plateau, central Great Basin, USA, areas with low moss-lichen cover (Photos 31, 32, 33)

low PET, soil freezing) as a successional phase. This classification system is highly generalized, and the four different types represent a continuum; thus, intermediate crust types will be found between these four groups. These classifications are based on late successional stages of crusts; in frequently disturbed areas, smooth or rugose crusts can be seen in any geographic region.

Smooth Crusts. Smooth crusts consist mostly of endedaphic cyanobacteria, algae, and fungi. Soil surfaces are mostly mineral particles and extremely flat, as the cyanobacteria bind the sand grains together, creating an even smoother soil surface than where the cyanobacteria are absent (Photo 50). Smooth crusts occur in hyperarid and arid regions, where precipitation is very low, temperatures are very high, and soils never freeze (e.g., northwestern

Australia, the Arava Valley and Nizzana dunes in Israel, the Atacama Desert in Chile, and the central Sahara Desert). This type of crust can also be found in areas that are frequently disturbed in any region.

Rugose Crusts. Rugose crusts occur in arid and semiarid regions with lower PET than areas with smooth crust; however, both occur in regions that lack soil freezing. Like smooth crusts, rugose crusts are dominated by cyanobacteria, green algae and fungi, but, in addition, contain sparse patches of lichens and mosses growing on the more or less even soil surface (Photos 48, 52, 54). This type of crust occurs in areas such as the Sonoran and Mojave Deserts in the US, and the Central Negev in Israel. Rugose crusts also occur as a successional stage in temperate climates, where they can be dominated by mosses or by an epedaphic layer of filamentous algae (Photos 9, 55). Such crusts are found in mediterranean vegetation types, open woodlands (e.g., pine barrens of US, miombo woodlands of Africa), and steppe formations of Europe.

Pinnacled Crusts. Pinnacled crusts are dominated by endedaphic cyanobacteria (such as *Microcoleus* sp.), but can locally support up to 40% lichen and moss cover. These crusts are characterized by strikingly pedicelled mounds that are formed as the soils that are uplifted by frost-heaving are differentially eroded by downward-cutting water (Photos 32, 33). These castle-like mounds can be up to 15 cm high, and have delicate tips that are less than 4 mm across (J. Belnap, unpubl.). Lichens, mosses, small rocks, or concentrations of cyanobacteria often act as a cap for these tips, offering greater resistance to erosion than adjacent soil (Fig. 15.2a). Cyanobacteria occurring in the center of these tips still receive sufficient light for photosynthesis; thus, these mounds have a greatly increased surface area for colonization by crustal organisms. Pinnacled crusts occur in mid-latitude, cool deserts, such as the Colorado Plateau and mid-latitude China. This crust type is the most vulnerable to soil surface disturbance, as the frost-heaved surface is easily broken and churned, often burying crustal organisms (see Chap. 27).

Rolling Crusts. Rolling crusts occur in colder regions, such as the northern Great Basin in the US, the northern Mongolian steppes, and the Arctic, where low PET supports biological soil crusts that are heavily dominated by lichens, mosses, and/or thick mats of cyanobacteria. The upward frost-heaving of the soil is counteracted by the cohesive, thickly encrusted mats of lichens and mosses and the many surface roots of vascular plants; thus, rather than pinnacled surfaces, this combination creates a rough, rolling surface (R. Rosentreter, unpubl.; Photo 30). These types of crusts are sometimes easily detached from the soil surface, making them vulnerable to soil surface disturbance.

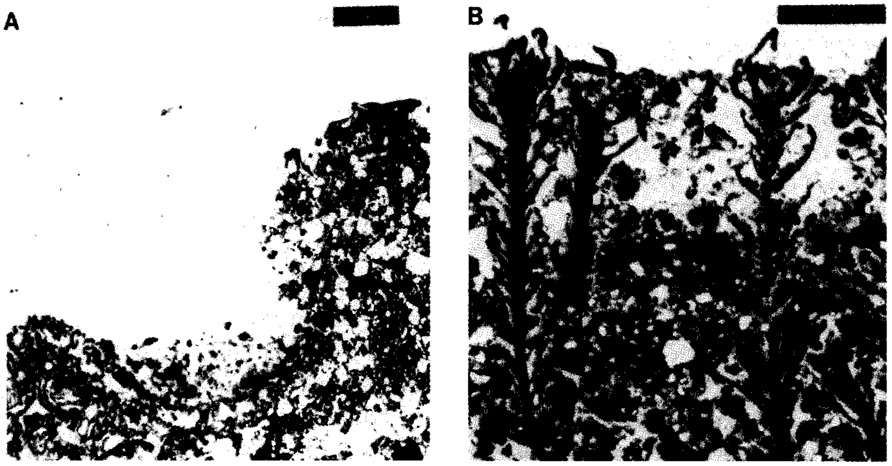

Fig. 15.2A,B Thin-sections of soil crusts from Australia. **A** Lichens can create pinnacled surfaces by protecting underlying soil from erosion. **B** Surface roughness created by lichens and mosses traps sediment. Unlike lichens, mosses can grow up through deposited sediment. *Bar* 1 mm. (Photos courtesy D. Eldridge)

15.3.2 Other Factors Influencing the External Morphology of Biological Soil Crusts

Soil Texture and Chemistry. Soil texture and chemical characteristics can partially or almost completely override the effects of frost-heaving or biological components in defining the external morphology of a soil crust. Crusts with similar species and climate on fine-textured soils are flatter than crusts on adjacent coarser soils, and on finer soils, cyanobacteria are concentrated closer to the surface, as light is quickly limited at depth (Garcia-Pichel and Belnap 1996; see Chap. 16). In soils with a weak crystalline structures (e.g., soils derived from calcite and gypsum), polysaccharide materials can combine with the dissolved minerals when soils are wet and, upon drying, sheaths are formed that are part organic and inorganic (Belnap and Gardner 1993; see Sect. 15.3.3). The internal strength of these soils resists winter frost-heaving and does not form the highly dissected surfaces that may be found in adjacent sandy soils. In addition, soils with a high carbonate content almost always support a higher lichen and moss cover (see Part I), and thus a rougher soil surface, than adjacent soils with lower carbonate levels (J. Belnap et al., unpubl.).

Soils with a high content of shrink-swell clays (e.g., bentonite) often create a very unstable soil surface. In deserts, biological crusts on these soils generally consist only of large filamentous cyanobacteria (e.g., *Microcoleus*), except in moist microhabitats where a limited cover of mosses or lichens can be found (J. Belnap, unpubl.). On these soils, surface morphology is controlled more by physical and chemical characteristics of the soil, with little contribution from the biological components. As with gypsiferous soils, soils with high clay content do not form highly pinnacled surfaces.

Physical crusts are often colonized by biological crusts. In soils with heavy physical crusting, the surface morphology of crusts is mostly controlled by soil physical and chemical characteristics, with the biological components having only a limited effect on external appearance of the crust (Mücher et al. 1988). If only cyanobacteria are present, the resultant crusts are smooth. If some lichens colonize as well, the slight roughening of the soil surface creates a rugose crust. Pinnacles can form in soils that have low to moderate physical crusting.

Disturbance History. Intensity, type, and time since soil surface disturbance can control the external morphology of biological soil crusts. Crustal components are brittle and easily crushed, especially when dry (Belnap and Gardner 1993). Damage to buried sheath material is nonrepairable, as living cyanobacteria are no longer present at depth to regenerate sheath materials (Harper and Marble 1988). When adjacent areas are disturbed, sediment can be blown or washed in on top of soil-crust organisms. The roughened soil surface often traps this material (Fig. 15.2b). While mosses can often grow up through this sediment (Fig. 15.2b), and the larger cyanobacteria can glide up to the surface of the new deposits, lichens and the smaller cyanobacteria are less mobile. Thus, if deposition rates are high, these latter organisms will die.

Intense disturbance results in bare soil. When colonized by large filamentous cyanobacteria, smooth crusts are formed (see Chap. 27). In regions with frost-heaving, some surface microtopography appears after the first winter, creating a rugose crust (Belnap 1995). As time passes, a combination of soil deposition, frost-heaving, differential erosion, and the colonization of lichens and mosses results in thicker crusts with greater surface microtopography (Belnap 1998; Photo 32). However, if disturbance continues, crusts will stay in early successional stages (i.e., a thin veneer of cyanobacteria only; see Chap 27).

15.3.3 Internal Structure of Biological Soil Crusts

In most desert soils, large filamentous cyanobacteria are most often the dominant species, providing the matrix in which other components of the biological crust are embedded. The scanning electron micrographs below present a detailed look at the internal structure of soil crusts and the role the dominant cyanobacterium *Microcoleus vaginatus* plays in soils from the Colorado Plateau (Belnap and Gardner 1993).

In Fig. 15.3a, the sheaths of *Microcoleus* can be seen winding among the sand particles, connecting the individual grains together, even though sheaths are dry. These sheaths act much like fibers in fiberglass, conferring great tensile strength to the soil. This high tensile strength can be seen in both the photo and the photo inset, where a single cyanobacterial strand can hold a sand grain aloft (Fig. 15.3a, inset). With moisture, the cyanobacterial sheath swells and becomes turgid, appearing like a fishing net on the soil surface (Fig 15.3b). This "net" holds soil particles firmly in place, reducing the possibility of soil loss by water or wind erosion.

Large filamentous cyanobacteria such as *Microcoleus* occur either as single filaments, or as a group of filaments, surrounded by a large polysaccharide sheath (Fig. 15.3c,d). The individual cells of the filaments can be clearly seen in Fig. 15.3d. When wetted, the polysaccharide sheaths swell and the filaments within are mechanically extruded from the sheath. As the soils dry, filaments retract into the sheath. The exposed portions of the filaments then secrete additional polysaccharide material. When dry, the cyanobacterial filaments are completely encased in the polysaccharide sheaths. Migrations to the surface, whether in response to rain or additions of sediment, result in sheath buildup underneath the soil surface. Visual examination of undisturbed soil crusts on sandy soils of the Colorado Plateau shows cyanobacterial sheath material to occur as deep as 10 cm below the surface of the soil (Belnap and Gardner 1993). Since most living biomass is in the top 4 mm of soil (Tchan and Whitehouse 1953; Garcia-Pichel and Belnap 1996), sheath material below that depth must represent remnants of cyanobacterial crusts once found near or at the soil surface and later buried by sediments. Though no longer associated with living filaments, such sheath material is still capable of binding soil particles together and still increases nutrient and moisture retention of associated soil.

Fig. 15.3A–E. (*see next page*) *Microcoleus vaginatus* in sandy soils: **A** Sheaths adhere firmly to sand grain surfaces, binding the grains together (note the intimate connection between the sheath and grain surfaces. *Bar* 100 μm. **B** Inset photo shows the strength of the sheath even when dry, as a single sheath holds a sand grain aloft. *Bar* 500 μm. **C** When wetted (using freeze substitution), sheaths and filaments swell and cover the soil surface. *Bar* 100 μm. **D** Note the large extracellular sheath surrounding the living filaments. *Bar* 10 μm. **E** Closeup of *M. vaginatus* sheath and filaments (note the cell walls). *Bar* 10 μm. (After Belnap and Gardner 1993)

Fig. 15.4. (*see next page*) **A** Multiple sheaths wrap around a sand grain, holding it firmly in place. *Bar* 50 μm. **B** Angular fine particles may be incorporated into sheath material. *Bar* 10 μm. **C** In fine-textured soils such as this limestone-derived substrate, many small particles adhere to the sheath material. *Bar* 10 μm. **D** In gypsiferous soils, sheaths can be made of both organic and inorganic material, and the sheaths are often coated with gypsum crystals. *Bar* 10 μm. (After Belnap and Gardner 1993)

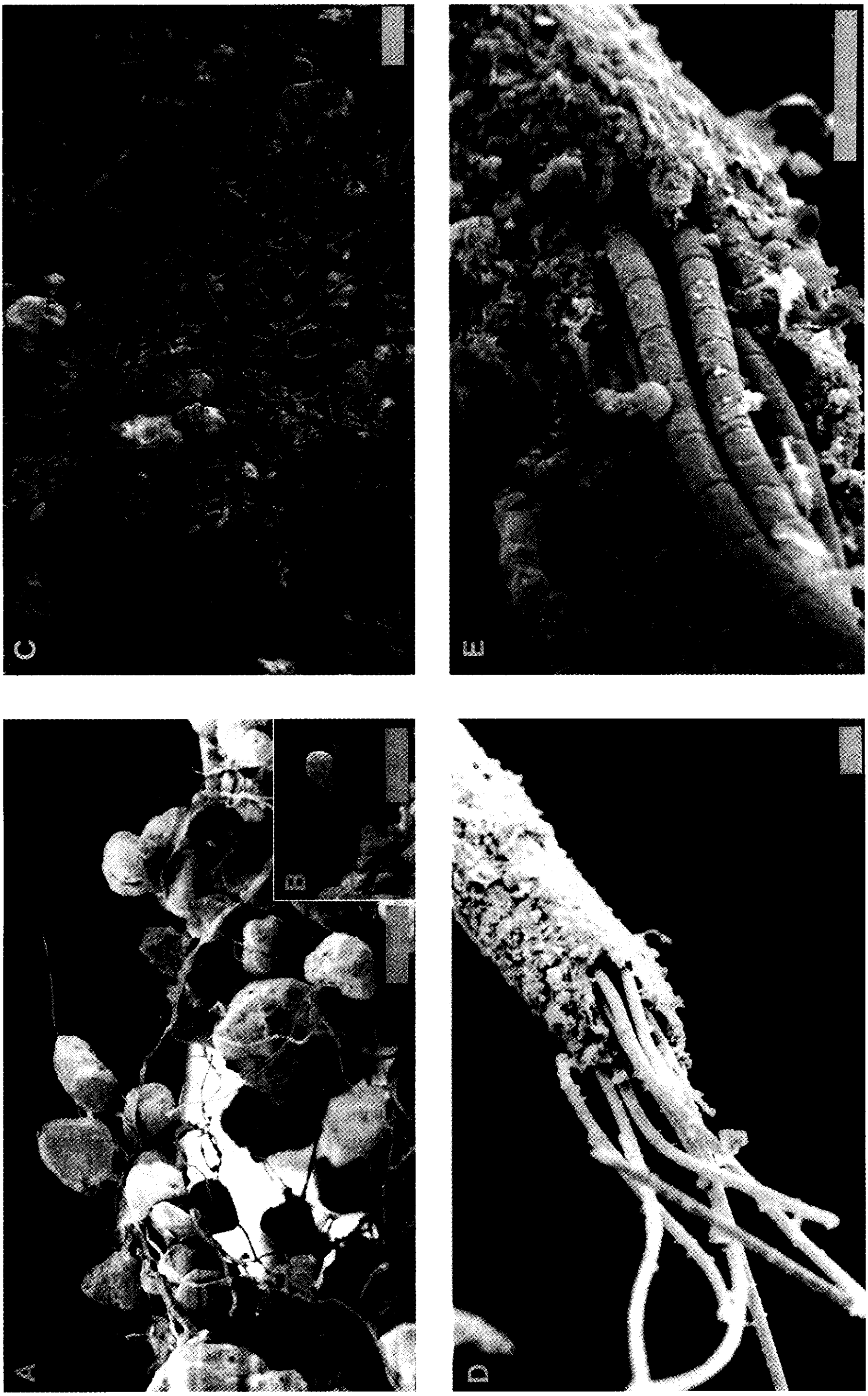

Fig. 15.3A–E

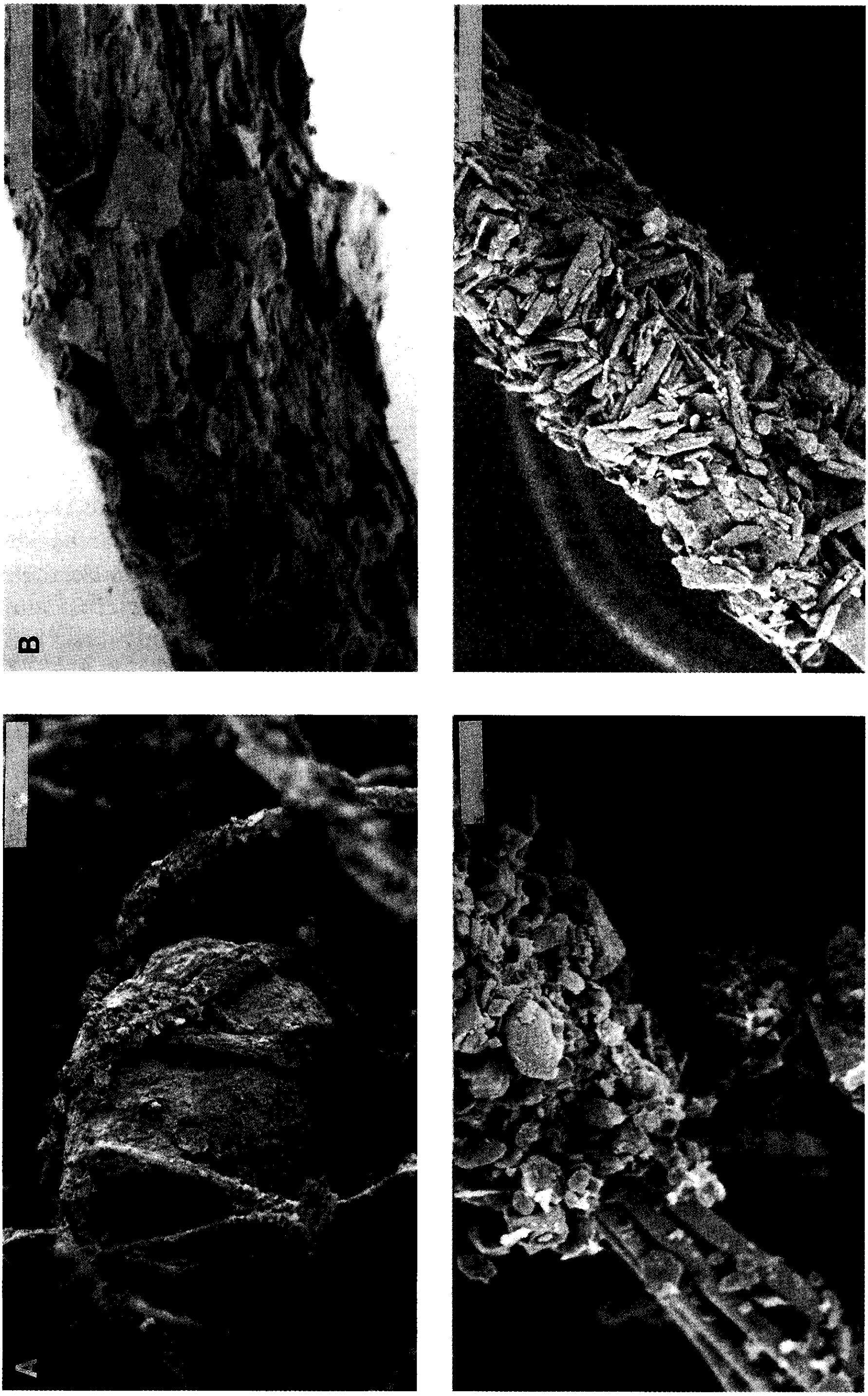

Fig. 15.4

In Fig. 15.4a, the extensive connections between sand grains by the sheath material can be seen, and multiple sheaths can often be seen attached to the same sand grain. Clay particles are also bound to, and incorporated into, the polysaccharide sheath material (Fig 15.4b). This may be a mechanism by which cyanobacteria increase mineral availability to themselves and vascular plants. Positively charged macronutrients are bound to both negatively charged clay particles and the sheath materials; thus, they are held in the upper soil horizons in a form readily available to vascular plants, instead of being leached away by water or bound in a chemically unavailable form (Belnap and Gardner 1993). In limestone (Fig. 15.4c), many fine particles are bound to the outside of the sheath. In gypsum (Fig. 15.4d), gypsum crystals often reprecipitate on the outside of the sheath. In many cases, the gypsum crystals combine with polysaccharide material, and take on a distinctive shape as a result.

Once soils are stabilized by the large, filamentous cyanobacteria, the number of smaller cyanobacteria and green algae increases (Dor and Danin 1996). Cyanobacteria, green algae, and fungi all secrete polysaccharide material that sticks to soil particles. Once lichens and mosses colonize, their rhizines and rhizoids also contribute internal structure to the crust and increase soil stability (Fig 15.2). Unlike lichens, cyanobacteria and mosses can grow upwards through deposited sediment. However, this ability is limited, especially in areas with low precipitation, and the crustal organisms can easily be buried and die (Chap. 27).

15.3.4 Other Factors Influencing the Internal Structure of Biological Soil Crusts

Cyanobacterial Layering. Well-developed crusts show a vertical layering of cyanobacterial species (Davey and Clarke 1992; J. Belnap, unpubl.; see Chap. 3). Smaller, less mobile organisms (e.g., *Nostoc*, *Scytonema*, *Chroococcidiopsis*) are most often found at the soil surface, and contain specialized pigments for UV-protection. The larger cyanobacteria (e.g., *Microcoleus, Phormidium*) are found below the soil surface when soils are dry. When soils are wetted, these large cyanobacteria partially leave their sheaths and glide up to the soil surface. As soils dry, they retreat back into their sheaths below the soil surface (Tchan and Whitehouse 1953; Dor and Danin 1996). These species generally lack UV-protective pigments. A similar layering of species is found in intertidal cyanobacterial mats (Cohen and Rosenberg 1989).

Aeolian Deposition. Aeolian deposition is often the dominant source of fine soil particles in desert soils (Danin and Yaalon 1982; Reynolds et al. 1998). Many authors report that airborne silt and clay are trapped by sticky

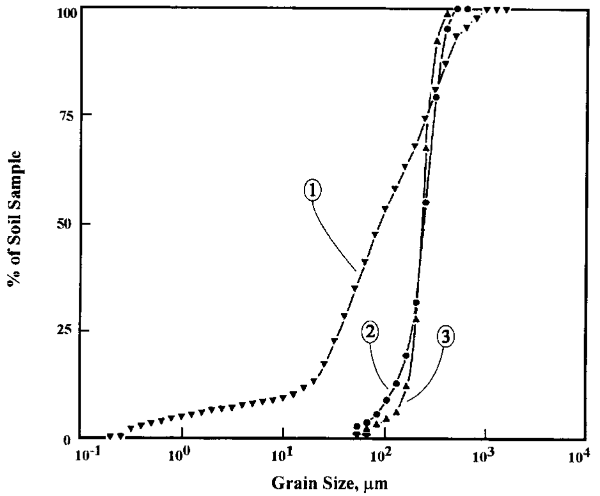

Fig. 15.5. Cumulative size distribution curves for soil particles in three dune samples. Note the greater amount of silt and clay particles in the crusted soil (*curve 1*) relative to the sand directly underneath the crust (*curve 2*) or from a nearby active dune (*curve 3*). (After Verrecchia et al. 1995)

cyanobacterial sheaths, by frost-heaved surfaces, and by the protruding moss stems and lichen thalli. This results in a thin layer of silt and clay on the crust surface (Figs. 15.2 and 15.5). Silt particles increase soil fertility and water-holding capacity (Nieboer and Richardson 1981; Puckett 1985; Danin and Ganor 1991; Davey and Clarke 1992; Verrecchia et al. 1995; although see Littman 1997).

15.4 Conclusions

The external morphology of biological soil crusts is determined by multiple factors. Of these, climate and disturbance history are probably the most important, followed by soil texture and chemistry. The morphology of the soil crust determines how susceptible the crust is to soil-surface disturbance, as frost-heaved soils are easily compacted and churned, thus burying crust organisms. Morphology also determines how soil crusts influence ecosystem functions such as hydrology, vascular plant relations, and water and wind erosion.

Much of the internal structure of crusts in most deserts is provided by large filamentous cyanobacteria. They aggregate soils and provide great tensile strength. Other contributors to internal structure are microfungi, and anchoring structures of mosses and lichens. Silt is often increased on crusted surfaces, increasing site fertility.

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