CHAPTER 1

INTRODUCTION TO BIOLOGICAL SOIL CRUSTS

In arid and semi-arid lands throughout the world, vegetation cover is often sparse or absent. Nevertheless, in open spaces between the higher plants, the soil surface is generally not bare of autotrophic life, but covered by a community of highly specialized organisms (Fig. 1.1). These communities are referred to as biological soil crusts, or cryptogamic, cryptobiotic, microbiotic, or microphytic soil crusts (Harper and Marble 1988; West 1990). Biological soil crusts are a complex mosaic of cyanobacteria, green algae, lichens, mosses, microfungi, and other bacteria. Cyanobacterial and microfungal filaments weave through the top few millimeters of soil, gluing loose particles together and forming a matrix that stabilizes and protects soil surfaces from erosive forces (Cameron 1966; Friedmann and Galun 1974; Friedmann and Ocampo-Paus 1976; Belnap and Gardner 1993). These crusts occur in all hot, cool, and cold arid and semi-arid regions. They may constitute up to 70% of the living cover in some plant communities (Belnap 1994). However, biological soil crusts have only recently been recognized as having a major influence on terrestrial ecosystems.

Globally, this consortium of soil biota has many similarities in function, structure, and composition, in spite of their unconnected

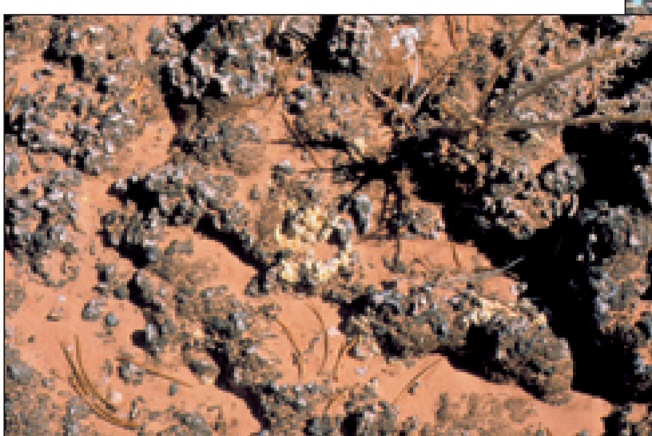

Figure 1.1 *Biological soil crusts of the Colorado Plateau (right). The roughened surface is formed by a matrix of cyanobacterial filaments that stabilizes the sandy soil. This stabilized surface provides microsites for a diverse lichen flora (left) in the interspaces between vascular plants that would otherwise be bare of autotrophic life.*

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and seemingly dissimilar environments. Crusts are found in an astonishing variety of habitats throughout the world:
in desert and semi-desert plant communities, ranging from shrub and succulent deserts to open woodlands; in steppe formations in both the northern and southern hemispheres; in the gaps between evergreen shrubs and in forests in the Mediterranean-type climate; and on open ground or between alpine or tundra vegetation. On a small scale, biological soil crust communities are found in open types of vegetation in temperate climatic regions; for example, they are frequently present in (and often restricted to) areas of a few square meters in xerothermic local steppe formations in central Europe and in the pine barrens of the eastern United States.

In rangelands, biological soil crusts can be viewed from functional, structural, and compositional perspectives. They function as living mulch by retaining soil moisture and discouraging annual weed growth. They reduce wind and water erosion, fix atmospheric nitrogen, and contribute to soil organic matter (Eldridge and Greene 1994). Structurally, biological crusts are a rough, uneven carpet or skin of low stature (1 to10 cm in height). Below ground, lichen and moss rhizines, fungal hyphae, and cyanobacterial filaments form a matrix that binds soil particles together (Belnap 1995). Horizontally, soil crusts occupy the nutrient-poor zones between vegetation clumps in many types of arid-land vegetation. Compositionally, biological soil crusts are diverse. In many arid and semi-arid communities there are often many more species associated with the biological soil crust at a given site than there are vascular plants (Rosentreter 1986; Ponzetti et al. 1998).

Rangeland managers in North America have historically used key indicator plants for determining the ecological trend and health of vegetation (USDA 1937; Stoddart et al. 1943). Biological soil crusts can also be used as indicators of ecological health. In addition, they act as indicators of abiotic factors, such as the presence of calcareous soils. Crustal organisms read environmental factors differently from and on separate time scales than do vascular plants (McCune and Antos 1982). Most crustal organisms are biologically active during the cool seasons when the soil surface is moist (Rosentreter 1986). In contrast, vascular plants are active in spring and summer when air temperatures are above freezing.

Unlike vascular plants, crustal organisms, particularly lichens, are not greatly influenced by short-term climatic conditions. This makes them ideal indicators of long-term environmental factors. Therefore, each community component can provide information that may complement, explain, or indicate something about a site's characteristics and disturbance history for rangeland management and evaluation. Just as plants increase or decrease with livestock grazing, many biological soil crust components are good indicators of physical disturbance, such as by livestock, human foot traffic, or motorized vehicles (Belnap 1995).

Land managers have been slow to use biological soil crusts in rangeland evaluations. Descriptions of vegetation or "habitat types" used by public land management agencies sometimes include biological soil crusts (e.g., Daubenmire 1970; Hironaka et al. 1983) but rarely present them as a dominant factor even when they are prevalent. This is partly because of perceived difficulties with identification (see Chapter 6). The problem of identification is exacerbated by the small size of these organisms, which often lack reproductive structures due to the harsh environments where they grow. However, identification problems can be substantially reduced by grouping organisms by function or general morphological characteristics (see sections 1.3 and 6.1.2).

1.1 Biological Soil Crust Components

Biological soil crusts are usually composed of multiple, unrelated organisms that occur together on the soil surface. The various types of organisms that comprise the crust share some interesting physiological traits. They are all capable of drying out and temporarily suspending respiration without negative effects, unlike vascular plants that either die or must regrow new tissue. These types of organisms are referred to as "poikilohydric." Most of them equilibrate their water content with the atmospheric humidity or soil surface moisture content. Poikilohydric organisms generally become photosynthetically active very quickly, producing carbohydrates or sugars minutes after wetting. However, most species still require high levels of hydration for optimal physiological functioning. The moisture content threshold for activity is species specific and helps determine the distribution of the various taxa that make up the biological crust. Many of these organisms perform under a variety of light intensities and prefer to dry out rapidly. Because they lack a waxy epidermis, crustal organisms also tend to leak nutrients into the surrounding soil upon wetting and drying.

Biological soil crusts have both macro- and microscopic components. Components that comprise these crusts are common in desert soils throughout the world. They will be discussed throughout this document in the context of their roles when they combine with other organisms as part of a biological soil crust. The term "total soil crust" will be used to refer to the combination of organisms. When visible cover (i.e., moss and/or lichen cover) alone is being discussed (thus excluding cyanobacteria), this will be specifically stated.

Bacteria are a diverse group of primitive, single-celled organisms. Bacteria can be either autotrophic (i.e., they synthesize

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carbon compounds from inorganic sources) or heterotrophic (i.e., they utilize carbon-containing substrates, such as organic matter in soil, for food). Some bacteria contribute to soil fertility by fixing nitrogen. Others are important in decomposition.

Microfungi occur either as free-living organisms or in mycorrhizal associations with plant roots. Free-living microfungi function as decomposers. They also contribute substantially to the living biomass in soils. Fungal filaments (hyphae) bind soil particles together, increasing soil water-holding capacity.

Cyanobacteria ("blue-green algae") are primitive filamentous or single-celled bacteria that can photosynthesize and, under anaerobic conditions, fix atmospheric nitrogen into a form that is available to higher plants (NH_4^+). Cyanobacteria can be heterocystic (i.e., they have special cells where nitrogen fixation takes place), or non-heterocystic (i.e., they lack these specialized cells). One of the most common cyanobacteria worldwide is the non-hetero-cystic, filamentous species *Microcoleus vaginatus. Microcoleus* can be seen with a 10x hand lens on the edge of a broken clump of soil. Under higher magnification, *Microcoleus* occurs as a cluster of filaments surrounded by a gelatinous sheath (Fig. 1.2). Single-celled cyanobacteria appear as small, blackish cells mixed with surface soil. When soils contain high amounts of cyanobacteria, they often have a slightly to highly roughened surface due to the organisms' binding of soil particles, coupled with processes like frost-heaving and erosion. For nitrogen fixation to occur in non-heterocystic cyanobacteria, the organisms need to be in an anaerobic environment, created by layering of cyanobacterial filaments just beneath the soil surface.

Green algae are light green to black, single-celled, photosynthetic organisms. Algae that occur on or just below the soil surface dry out in a vegetative condition and become physiologically functional when moistened. They do not rely on resting spores to regrow after dry periods, as do aquatic algae that inhabit ephemeral ponds or lakes. Therefore, they are well adapted to living and reproducing in dry desert environments. Algae are difficult to observe without a microscope (100x to 400x), but sometimes give the soil surface a green tint. Their growth period is often linked to cool, moist weather, and they may be difficult to detect when dry.

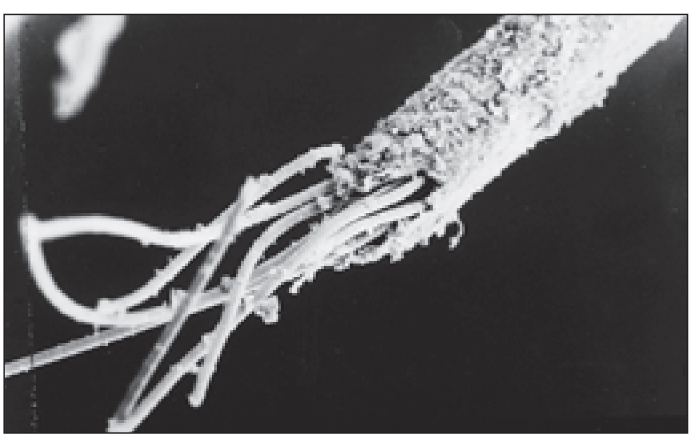

Figure 1.2 Microcoleus vaginatus*, one of the predominant cyanobacteria comprising biological soil crusts.* Microcoleus *exists as a cluster of filaments, surrounded by a gelatinous sheath (seen here with soil particles attached). The living filaments can migrate through the soil, leaving abandoned sheath material and a stabilized soil matrix behind. (2000x magnification)*

Bryophytes are tiny non-vascular plants. This group includes both mosses and liverworts. Having greenish leaves when moist, mosses are generally easy to identify. They reproduce by spore capsules that rise above the leaves. The spore capsules greatly simplify the identification of genera and species. However, in arid environments, mosses often lack reproductive structures and will reproduce asexually by simple or specialized fragmentation. Therefore, arid-land mosses are often difficult to identify in the field. Liverworts come in two general forms: thalloid or leafy. The thalloid form has a greenish-black thallus or flat, narrow ribbon of dichotomously branching material. Thalloid liverworts are adnate to the soil surface, and some can fold in half, almost disappearing from view (they look like thin black lines on the soil surface when dry). Leafy liverworts are rare in arid environments. They look like mosses but are smaller, and when dry the leaves are very black . Both types of liverworts reproduce by spores and by specialized asexual structures called “gemmae.” The spores are often produced in a structure within the upper surface of the liverwort and look like a black or smutty spot on a green background. The asexual gemmae are variable in size (1 to 3 mm), but are usually green, circular structures that easily break off the parent plant when mature.

Lichens are fungi that capture and cultivate algae or cyanobacteria, resulting in a new morphological entity. Lichens are typically used in ecology courses to illustrate the concept of symbiosis, as the algae or cyanobacteria provide the fungus with energy in the form of carbohydrates produced by photosynthesis, while the fungus provides protection from desiccation. Lichens come in a wide variety of shapes, sizes, and colors. They generally have an outer fungal layer, which, if cut in cross section, reveals a layer of algal cells. Lichens can cover the soil surface like a layer of skin or they can be three dimensional and leaf-like in appearance. Lichens occur in a variety of colors, including green, red, brown, white, and black. Sexual reproduction is limited to the fungal partner. Reproductive structures are generally round, dark-colored sessile disks on the lichen surface. Lichens can also reproduce asexually (as the combined organism) and have several types of specialized fragmentation structures to facilitate this type of dispersal. Lichens that reproduce asexually can colonize disturbed sites much more rapidly than those species that lack this ability.

1.2 Microstructure

The dominant components of biological soil crusts are photo-synthetic and therefore require sunlight. When soils are dry, the bulk of the cyanobacterial biomass is 0.2 to 0.5 mm below the soil surface,

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where sufficient light for net carbon gain is available but UV exposure is reduced. *Microcoleus vaginatus*, which lacks UV-screening pigments, migrates to the surface for short time periods when soils are moistened and returns to subsurface zones as they dry (Fig. 1.2). Populations of *Scytonema* and *Nostoc*, cyanobacteria containing UV-screening pigments, are more commonly found directly on the soil surface.

1.3 Morphological Groups

Morphological groups consist of organisms that are similar in shape and general appearance. The crust morphology largely determines its ecological function relative to water infiltration, erosion, water retention, and resistance and resiliency to disturbance (Eldridge and Rosentreter 1999). Morphological groups also convey an image of a particular organism. Table 1.1 outlines the major morphological groups for biological crusts. Ecological function and management implications relative to morphological groups will be discussed in detail in later chapters.

1.4 Differentiating Types of Biological Soil Crusts in the Field

Biological soil crusts are usually composed of various organisms and morphological groups, unless the crust is in an early-successional stage. However, one or two morphological groups will normally dominate the crust. The following are examples of morphological groupings:

- *Cyanobacterial crusts* are dark colored or black. When moist, the organisms may be visible as black filaments on and near the soil surface.
- *Green algal crusts* are not always visible, but might appear as a green cast on the soil surface when it is moist.
- *Moss crusts* are easily observed as a furry carpet with patches of green, gold, brown, and/or black.
- *Liverworts* are difficult to detect and usually occur in a mosaic with other dominant organisms. Close examination with a hand lens will reveal tiny black ribbons that become more obvious with moistening.
- *Lichen crusts* can be identified by their diversity of shapes and colors. The lichen morphological groups form an anatomical gradient from a low, simple morphology to taller and three-dimensional growth forms.
    - *Crustose lichens* are flat and fused to the substrate.
    - *Gelatinous lichens* are usually black and may appear flat or three-dimensional. They become jelly-like in texture when

moistened and will swell to several times their size when wet. This is an important group to identify from a functional perspective because they have cyanobacteria as their phytobiont and therefore fix atmospheric nitrogen.

- *Squamulose lichens* occur as small individual flakes or scales that often grow in colonies or clusters.
- *Foliose lichens* are leaf-like and loosely appressed to the substrate. In dry habitats, foliose lichens inhabit the relatively moist microsites under plant canopies and on north aspects.
- *Fruticose lichens* are three dimensional and are often upright, branched, or thread-like.

1.5 What Biological Soil Crusts are Not: Physical Soil Crusts

Non-biotic soil surface crusts are a major structural feature in many arid regions. Their properties and manner of formation have been studied for many years, primarily because of their detrimental effects on agricultural crops. These crusts are transient soil-surface layers (ranging in thickness from less than 1 mm to a few cm) that are structurally different from the material immediately beneath them. Physical crusts reduce water infiltration and can prevent the emergence of vascular plant seedlings (Fig. 1.3).

The most important process in the formation of non-biotic crusts is generally raindrop impact, which breaks up soil aggregates on unprotected surfaces. Smaller particles wash into spaces between 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 soil components together, forming a dense, strong layer. Thackett and Pearson (1965) showed that physical crusts formed under simulated rainfall had a dense surface layer 1 to 3 mm thick, coated with a thin layer of well-oriented clay. The 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 to 5 mm. Rain-formed crusts are thicker when the raindrops are larger because these larger drops have more energy and "blast" deeper holes, destroying the original structure to a greater depth. In general, rain-formed crusts are less than 5 mm thick. This layer is often harder than the rest of the soil because compounds such as salts, lime, and silica are deposited at the surface as water evaporates. Because large pores are absent, the crust usually has low saturated hydraulic conductivity and limits infiltration. This increases water runoff and soil erosion.

Soil aggregate structure is also destroyed by machinery or the hooves of grazing animals. Trampling moist soils destroys existing soil