BIOLOGICAL SOIL CRUSTS:
ECOLOGY AND MANAGEMENT

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Biological Soil Crusts: Ecology and Management

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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

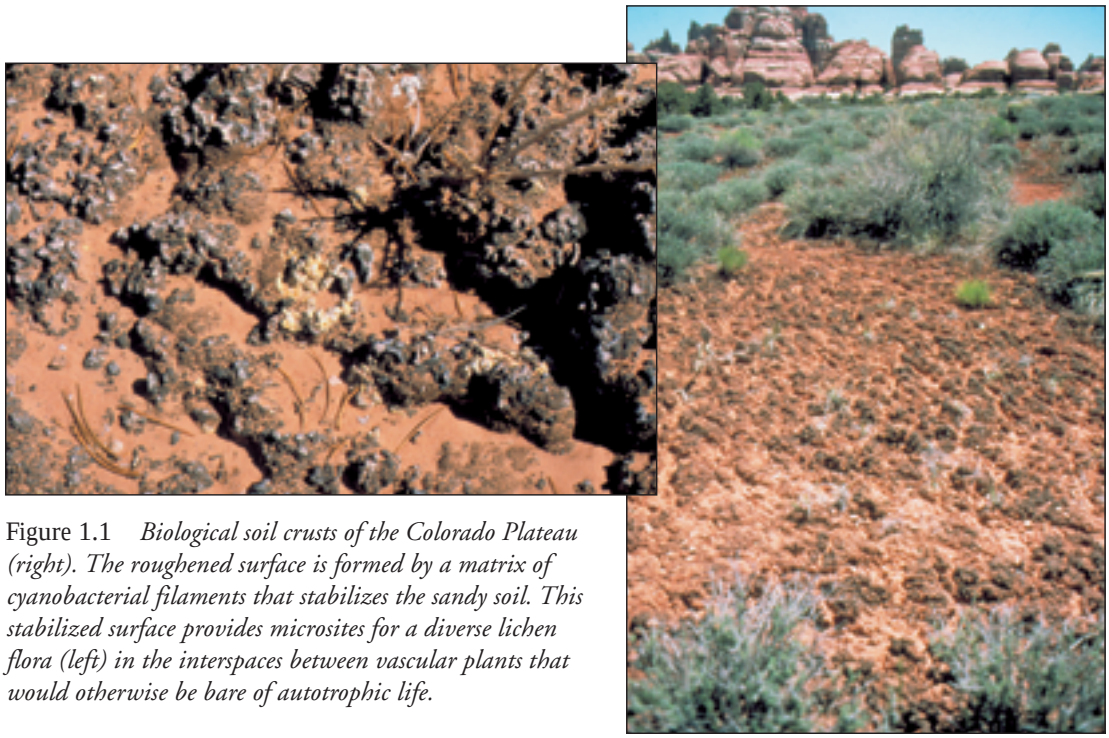

Figure 1.1 *Biological soil crusts of the Colorado Plateau (right). The roughened surface is formed by a matrix of cyanobacterial filaments that stabilizes the sandy soil. This stabilized surface provides microsites for a diverse lichen flora (left) in the interspaces between vascular plants that would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

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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-hetero-cystic (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.

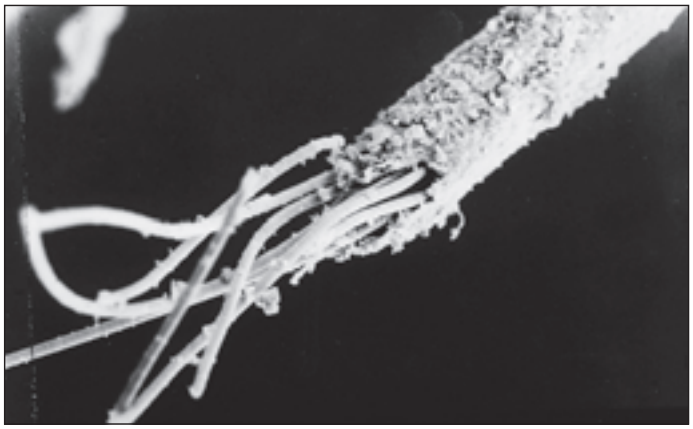

Figure 1.2 Microcoleus vaginatus*, one of the predominant cyanobacteria comprising biological soil crusts.* Microcoleus *exists as a cluster of filaments, surrounded by a gelatinous sheath (seen here with soil particles attached). The living filaments can migrate through the soil, leaving abandoned sheath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

Table 1.1 *Morphological groups for biological soil crust components with examples of common taxa or groups.*

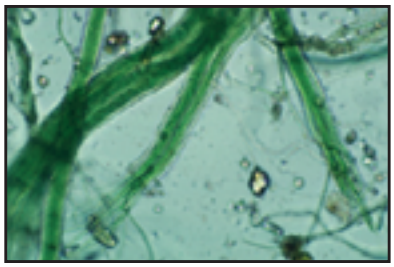
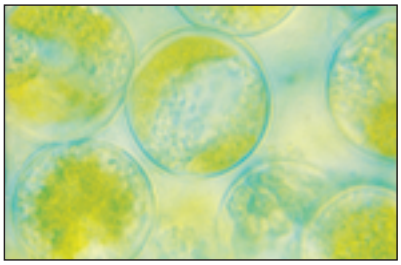
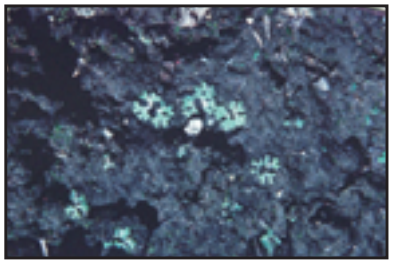
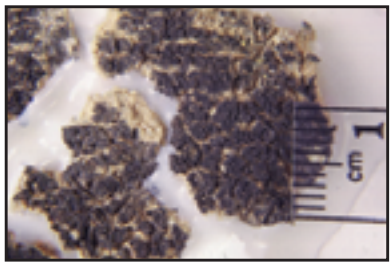
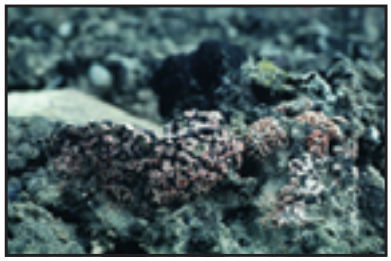
Morphological Group		Description and Representative Taxa
cyanobacteria		colonies are black to blue-green and visible primarily when moist *(Microcoleus vaginatus)*
algae		primarily occur as single-celled organisms; difficult to detect (coccoids)
BRYOPHYTES: short moss		mosses <10mm in height *(Bryum* spp.*, Ceratodon purpureus)*
tall moss		mosses >10mm in height *(Tortula ruralis)*
liverwort		flat, narrow ribbon or green-black dichotomously branching material on the soil surface *(Riccia)*

Table 1.1 (continued)

Morphological Group		Description and Representative Taxa
LICHENS:		
crustose lichen		crust-like growth tightly attached to the substrate *(Lecanora muralis)*
gelatinous lichen		blackish, jelly-like when moistened *(Collema coccophorum)*
squamulose lichen		discrete flakes that are round or ear-shaped, convex or concave, and often have lobed margins *(Psora decipiens)*
foliose lichen		"leafy," tending to be flattened with definite upper and lower surfaces *(Peltigera occidentalis)*
fruticose lichen		three-dimensional, ropey or branching, without definite upper and lower surfaces *(Aspicilia hispida)*

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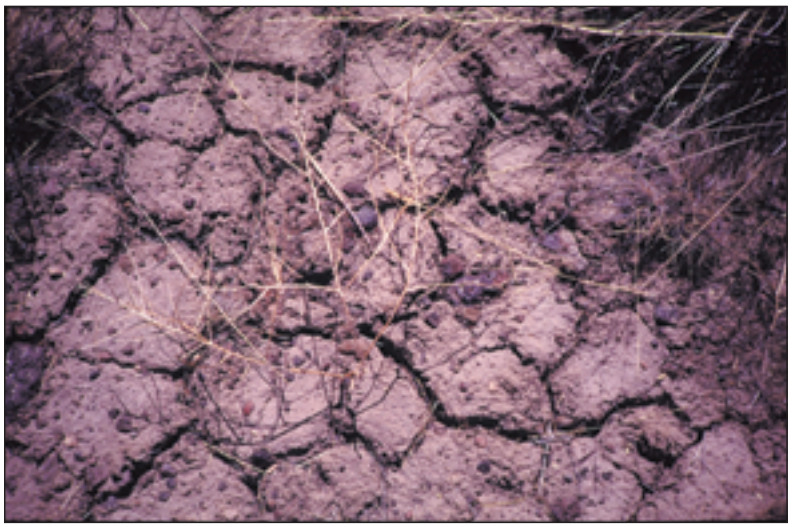

Figure 1.3 *Physical soil crusts. Vascular plant establishment is limited to cracks between polygons on physically crusted areas due to an impenetrable surface layer.*

aggregates by compacting them into a comparatively impermeable surface layer. 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.

Physical crusts may form on soil of almost any texture except coarse sandy soils containing very low silt and clay (Lemos and Lutz 1957). Soils especially susceptible to crusting are those with low organic matter and high silt, sodium, or calcium carbonate content. These characteristics are all related to soils with low structural and aggregate stability. Organic matter increases aggregate stability (through gluing of particles and moderation of forces that reduce aggregate stability), and places where plant residues are incorporated generally become planes of weakness, decreasing crust strength. Silts form strong bonds on drying, thus forming a hard crust. Silts also have low swelling and shrinking properties, so that the crust does not crack or disintegrate by itself.

Intensive grazing is often used to break up physical crusts. However, this result is short-lived, as the soil surface is resealed after the first minutes of an intense rainstorm. To effectively address a physical soil crusting problem, livestock grazing systems must promote greater soil aggregate stability (Thurow 1991). Therefore, management systems that promote soil surface protection (through plant and biological soil crust cover) and increase soil organic matter are the only lasting solution to physical soil crust reduction (Blackburn 1983).

CHAPTER 2

NOTES

DISTRIBUTION AND FACTORS INFLUENCING SPECIES COMPOSITION

2.1 Distribution

Biological soil crusts in North America are diverse and are most evident in arid and semi-arid ecoregions (Fig. 2.1, 2.2). They are also found on shallow lithic sites and in alpine habitats throughout the continent and in many early-successional vegetation types in moister ecoregions. Some crustal organisms are good indicators of a specific vegetation type or ecoregion. Others, including *Microcoleus*, *Nostoc*, *Collema*, *Psora decipiens*, *Cladonia* spp., and *Bryum* spp. are common to many different geographic, climatic, and vegetation types. For instance, the same soil lichens (*Collema*, *Placidium*, *Psora*) dominate crusts of both the Sonoran and Great Basin deserts, as well as areas of South Africa and Australia, although vascular plant species and climate vary greatly between these regions. While most algae, lichens, and bryophytes are cosmopolitan, a few are endemic and may be common on a local or regional level (Table 2.1). For example, several of the squamulose lichens, such as *Placidium squamulosum*, *Psora decipiens*, *Psora cerebriformis*, and *Psora tuckermanii*, have very broad geographic ranges. Others, including *Catepyrenium congestum* and *Psora montana*, are endemic to North America or have narrow geographic ranges within the continent. Squamulose lichens have more endemic species worldwide than any other lichen morphological group.

Similarities in species composition may occur due to similar environmental conditions during the active growth period for crustal organisms. For example, alpine biological crusts actively grow in summer under moisture and temperature conditions that are similar to winter environmental conditions in the Sonoran Desert. Most crust growth occurs during wet, cool periods. In most North American deserts, this is generally late fall to early spring.

The appearance of biological crusts is variable. Physical structure of biological crusts is very similar in the hot deserts of the world, such as the Atacama, Sonoran, Chihuahuan, and Australian deserts, while very different from the physical structure in cool and cold deserts, such as the Colorado Plateau, Great Basin, and the Arctic (Fig. 2.3). Pinnacled crusts are found in areas where crusts are dominated by cyanobacteria, freezing temperatures are common, and vascular plant roots are lacking. Winter freezing heaves the soil upward, forming pinnacle-type microtopography. Subsequent

Figure 2.1 *Arid and semi-arid ecoregions of western North America. Areas shaded in black are cool deserts, while grey-shaded areas are hot deserts.*

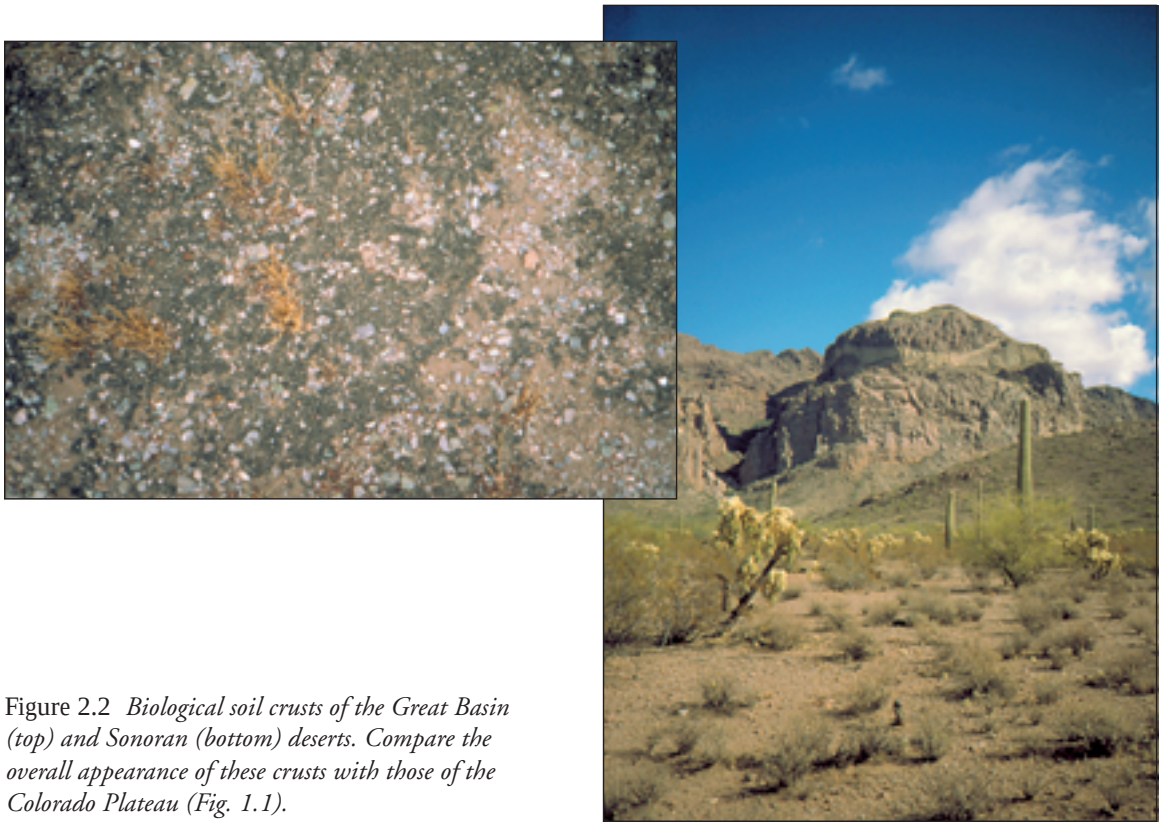

Figure 2.2 *Biological soil crusts of the Great Basin (top) and Sonoran (bottom) deserts. Compare the overall appearance of these crusts with those of the Colorado Plateau (Fig. 1.1).*

Table 2.1 *Soil crust lichens endemic to North America with both wide and limited distributions. Note that there are very few endemic species.*

Species	Distribution	Reference
Aspicilia californica	California Chaparral	Rosentreter 1998
Aspicilia filiformis	western North America	Rosentreter 1998
Aspicilia reptans	North America	Looman 1964
Catapyrenium congestum	Great Basin	Bruess and McCune 1994
Psora montana	western North America	Timdal 1986
Psora tuckermanii	Great Basin	Timdal 1986
Texosporium sancti-jacobi	western North America	McCune & Rosentreter 1992

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differential growth and erosion results in highly dissected pinnacles to 10 cm high (e.g., Colorado Plateau). Where freezing is common but soils are held in place with a heavy cover of lichens, mosses, and vascular plant roots, soil surfaces have a rolling rather than pinnacled topography (e.g., northern Great Basin). Where freezing is rare, crusts are flat when only cyanobacteria are present or rugose where lichens and/or mosses occur (e.g., the Sonoran Desert; Fig. 2.2, 2.3). In non-freezing regions, a layer of pebbles often covers cyanobacterial portions of the crust.

On the broad scale of western North America there are several different vegetation zones or ecoregions that contain biological soil crusts as major components (Fig. 2.1, Table 2.2, 2.3). The ecoregions used here are similar to those used by Bailey (1998). The most prevalent arid soils in North America are silt-loams and are more susceptible to physical disturbance than are clay-loams common to many other arid regions in the world, such as the red clay-loams of Australia.

2.2 Factors Influencing Distribution

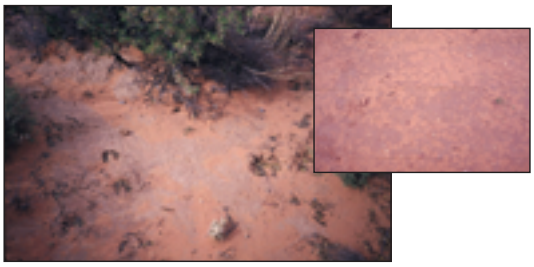
2.2.1 Elevation

Total crust cover is inversely related to vascular plant cover, as less plant cover results in more surface available for colonization and growth of crustal organisms (Fig. 2.4-A). Thus, when all crust types are combined (cyanobacterial, moss, lichen), cover is greatest at lower elevation inland sites (less than 1,000 m) compared to mid-elevation sites (1,000 to 2,500 m; Hansen et al. 1999; Fig. 2.4-B). However, relative lichen and moss cover increases with elevation and effective precipitation until vascular plant cover precludes their growth (Fig. 2.4-C). Crust organisms have reduced water and nutrient

Figure 2.3 *Biological soil crust forms based on temperature characteristics of the environment.*

HOT DESERTS

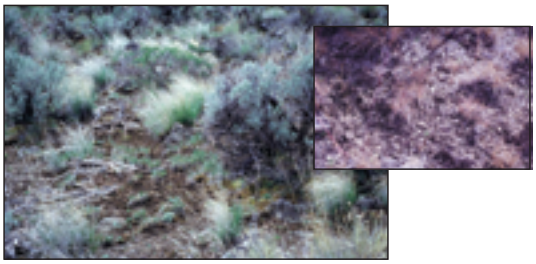
flat



rugose

COOL DESERTS

rolling



pinnacled

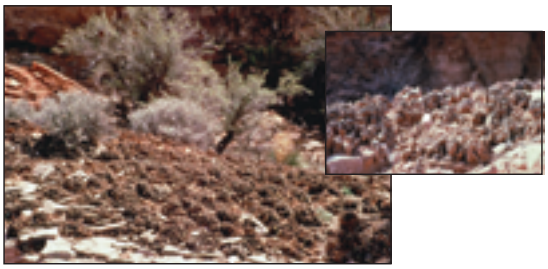


Table 2.2 *Soil, climatic, and vegetative characteristics for low and mid elevations in temperate North American arid and semi-arid ecoregions. Adapted from Bailey (*1995).

Ecoregion (Bailey's Ecoregion Province)	Dominant Soil Order	Soil Moisture/ Temperature	Average Annual Precipitation (mm)	Moisture Season/Form	Mean Annual Temperature Range (°C)	Predominant Evolutionary Disturbance	Vegetation Type
COOL DESERTS							
Columbia Basin (temperate semidesert)	mollisol	xeric/mesic	230-635	winter/rain spring/rain	4-14	drought	perennial grassland
Great Basin (temperate semidesert and desert)	aridisol	aridic/mesic to cryic	180-380	winter/snow spring/rain	4-13	drought	sagebrush steppe
Colorado Plateau (temperate semidesert and desert)	alfisol	xeric/thermic	205-510	winter/snow spring/rain summer/rain	4-13	drought	shrubland woodland
Great Plains (temperate steppe and dry steppe)	mollisol	ustic/mesic	485-735	winter/snow spring/rain summer/rain	8-15	fire, grazing	prairie
HOT DESERTS							
Mojave Desert (tropical/subtropical desert on sand)	aridisol	aridic/hyperthermic	100-150	winter/rain	13-29	drought	shrubland
Chihuahuan Desert (tropical/subtropical semidesert and desert on sand)	aridisol	aridic/thermic	205-325	summer/rain	10-18	drought	shrubland
Sonoran Desert (tropical/subtropical desert on sand)	aridisol	aridic/thermic	75-255	summer/rain fall/rain	10-24	drought	mixed thorn scrub
COASTAL CHAPARRAL							
California Chaparral (Mediterranean dry steppe)	mollisol	xeric/thermic	255-635	winter/rain	16-18	fire	chaparral

Table 2.3 *Dominant biological soil crust components and forms in North American arid and semi-arid ecoregions.*

Ecoregion	Dominant Biological Crust Components	Crust Morphology
Columbia Basin	tall mosses, green algae	rolling
Great Basin	moss, lichen	rolling
Colorado Plateau	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*	pinnacled
Great Plains	vagrant and foliose lichens	flat to rugose or rolling
Mojave Desert	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*, squamulose lichens, short mosses	flat to pinnacled
Chihuahuan Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, short moss	flat
Sonoran Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, gelatinous (nitroen-fixing) lichens (e.g., *Collema*), squamulose lichens, short mosses	flat
California Chaparral	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, lichens, liverworts	flat

needs compared to vascular plants and can withstand the harsh growing conditions found in plant interspaces (Anderson et al. 1982a).

The positive relationship between biological crust cover and available soil surfaces has been amply demonstrated (Rogers 1972; Harper and Marble 1988; West 1990; Eldridge 1993b; Johansen 1993). As harsh environmental conditions limit vascular plant cover, greater cover of crusts in lower elevation sites probably occurs in spite of, not because of, these conditions.

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2.2.2 Soils and Topography

Stable or embedded rocks near or at the soil surface can increase the percent crust cover by perching water and armoring the surface from physical disturbances (Fig. 2.4-D). Shallow soils often support a wide variety of cyanobacteria, lichens, and mosses, regardless of soil texture (Fig. 2.4-E).

Soil texture heavily influences the species composition of biological crust communities. The more stable, fine-textured soils (such as gypsum and silty loams) support greater cover and more varied populations of cyanobacteria, lichens, and mosses (Fig. 2.4-F)

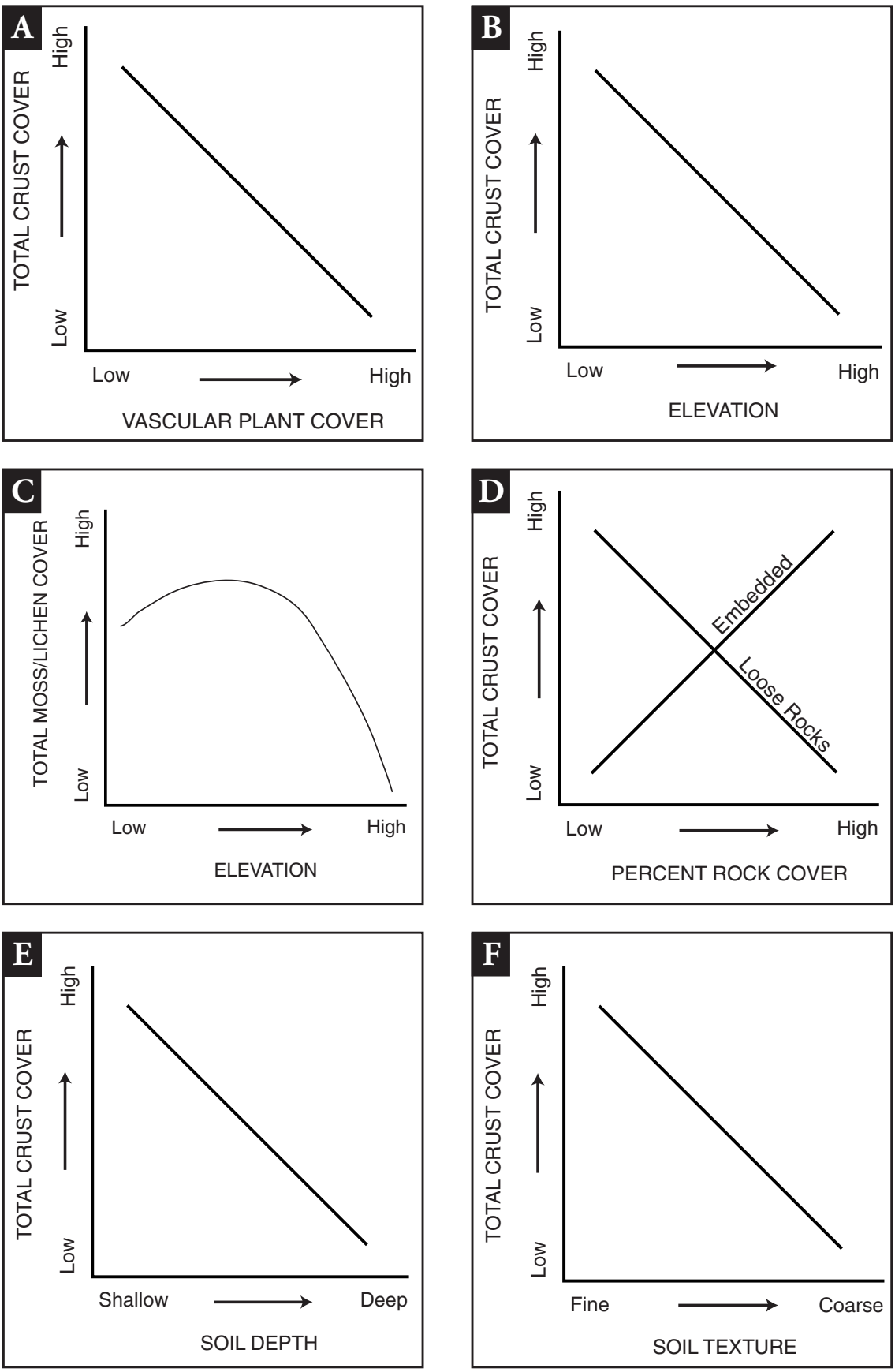

Figure 2.4 *General ecological relationships for biological soil crusts.*

than less stable, coarse-textured soils (Kleiner and Harper 1977b; Hansen et al. 1999). Coarse-textured soils may have only large filamentous cyanobacteria that are highly mobile (such as *Microcoleus*). However, once coarse-textured soils are sufficiently stabilized by larger cyanobacteria, other crustal organisms can then colonize, including smaller green algal and cyanobacterial taxa (such as *Scytonema* and *Nostoc*). Regardless of soil type, the first lichen to colonize is generally *Collema*, followed by *Placidium* (and *Caloplaca* in the northern Great Basin). In more unstable soils, lichens and mosses may be found only under vascular plants, where some protection from sediment burial is provided, or on north slopes, where greater moisture availability favors growth. Soil surface stability is influenced by texture (percent of sand, clay, silt), depth, and moisture content (wet, moist, dry). Sand and silt are more susceptible to surface disturbance when dry, while clay is highly stable (Fig. 2.5).

In later successional stages on stable surfaces, common lichen species include *Fulgensia bracteata*, *F. desertorum*, *Squamarina lentigera*, *Diploschistes muscorum*, and *Psora* spp. Common moss genera include *Tortula*, *Bryum*, and *Grimmia*. As soil stability increases, rich communities of cyanobacteria, lichens, and mosses become more widespread, covering all surfaces not occupied by vascular plants or rock.

Soil chemistry can also influence crust cover and composition. Calcareous and gypsiferous soils generally support high coverage of species-rich crust with some taxa being excellent indicators of soil chemistry (Table 2.4). Often physical crusts form stable surfaces that perch soil moisture, and given long periods without physical disturbance, will support both biological soil crusts and lichens or mosses normally found on rocks. Other abiotic factors that influence relative cover of microbiotic crusts are slope and aspect. Crustal organisms are only active when moist, and most active when warm. Therefore, north and east slopes generally favor crustal development in lower elevation desert regions. Slope angle does not generally affect crust cover or species richness, except where the slope or soils are unstable (Rosentreter 1986; Kaltenecker et al. 1997; Belnap and Bowker, unpublished data).

2.2.3 Disturbance

Intensity and type of soil surface disturbance, along with time since disturbance, influence the composition of biological crusts (see Chapter 4). The presence, absence, and abundance of early- or late-successional taxa can provide information regarding a site's disturbance history. This information, combined with data on vascular plant community composition, can assist the land manager in understanding a site's history, potential productivity, and ecological integrity.

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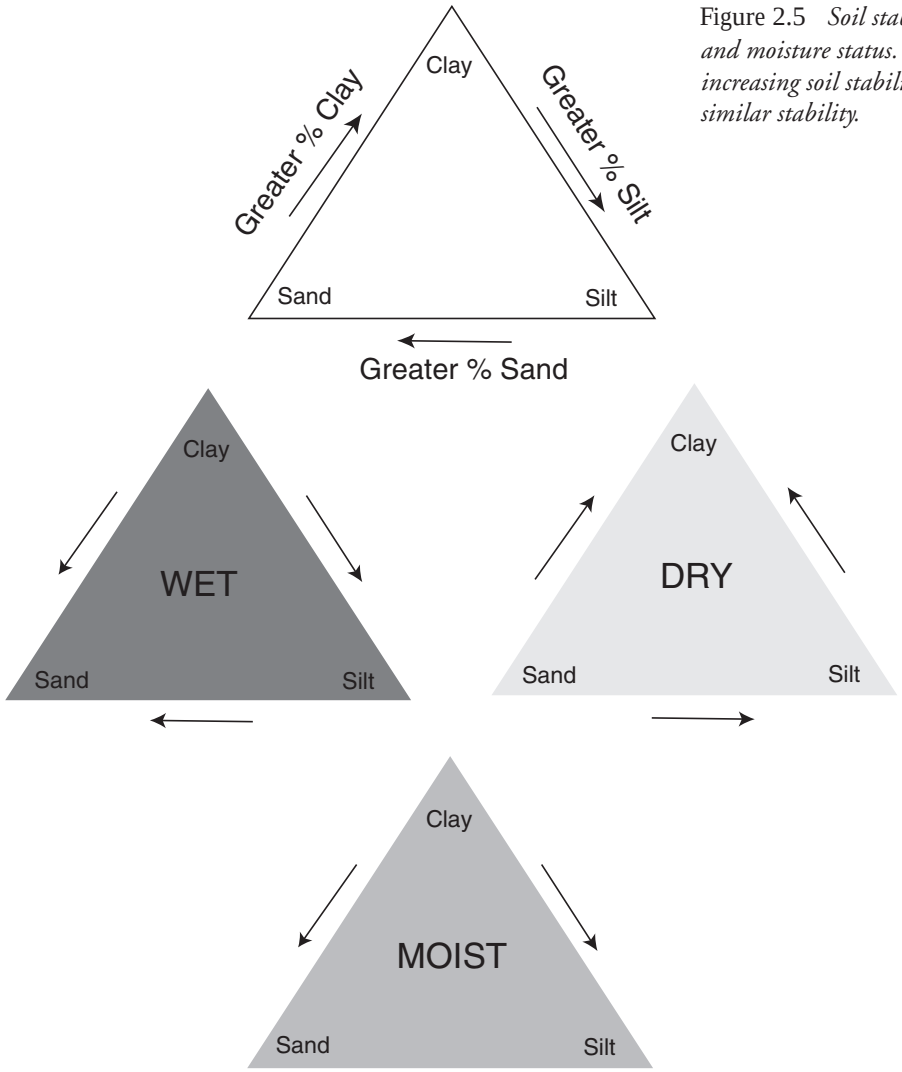

Figure 2.5 *Soil stability relative to texture and moisture status. Arrows indicate increasing soil stability. No arrow indicates similar stability.*

		Soil Texture		
		Sand	Clay	Silt
Soil Moisture Content	Frozen	High	High	High
	Wet	Medium-High	Low	Medium
	Moist	Medium	Low	Medium
	Dry	Low	High	Medium-Low

Table 2.4 *Soil crust lichens that are calcium carbonate indicators. Adapted from McCune and Rosentreter 1995.*

Low calcium carbonate	High calcium carbonate
Acarospora schleicheri	*Aspicilia fruticulosa*
Arthonia glebosa	*Aspicilia hispida*
Aspicilia reptans	*Buellia elegans*
Aspicilia filiforma	*Caloplaca tominii*
Cladonia borealis	*Collema tenax*
Diploschistes muscorum	*Fulgensia* spp.
Leptochidium albociliatum	*Heppia lutosa*
Megaspora verrucosa	*Phaeorrhiza nimbosa*
Ochrolechia upsaliensis	*Psora cerebriformis*
Placynthiella spp.	*Psora decipiens*
Psora nipponica	*Psora tuckermanii*
Xanthoparmelia wyomingica	*Toninia sedifolia*

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Intense disturbance results in bare soil. Severely, newly, or frequently disturbed soils are generally dominated by large filamentous cyanobacteria (Anderson and Rushforth 1976; Johansen et al. 1981, 1984; Johansen and Rushforth 1985; Harper and Marble 1988). When disturbance is less severe, less frequent, or some time has elapsed since the disturbance, crusts are generally in some mid-successional state, with some lichens and mosses present. Most of these species reproduce asexually, a life-history strategy that increases the probability of establishment (Rosentreter 1994). If disturbance continues, crusts will stay in early-successional stages (i.e., cyanobacteria only).

2.2.4 Timing of Precipitation

Dominance of biological crusts is highly influenced by seasonal precipitation patterns. Ecoregions that receive summer monsoons (e.g., the Sonoran Desert) tend to have a greater diversity of heterocystic cyanobacteria (such as *Lyngbya*, *Calothrix*, *Schizothrix*, and *Nostoc*) and lower lichen abundance. Lichens in these areas generally include the gelatinous genus *Collema* and squamulose genera *Placidium* and *Peltula* (Table 2.3). Large thalloid liverworts are more common in warm deserts than in the cool deserts of North America. In cool deserts, crusts are dominated by non-heterocystic cyanobacteria (such as *Microcoleus vaginatus*) and a diverse lichen flora, including *Acarospora schleicheri*, *Aspicilia* spp., *Candelariella*

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spp., *Collema* spp., *Diploschistes muscorum*, *Endocarpon pusillum*, *Placidium* spp., and *Psora* spp. These lichens physiologically prefer cool-season moisture and are adapted to lower light intensities common during winter months. The Columbia Basin, which receives more moisture and has more winter rain than the Great Basin, has a greater abundance of mosses than lichens (Ponzetti et al. 1998).

Biological soil crusts in regions influenced by fog, such as portions of the California Chaparral, support fruticose lichens that intercept moisture from the air (*Dendrographa* and *Schizopelte*). Biological crusts in many regions are best developed in interspaces between shrubs. In contrast, fog deserts show the best crust development under shrubs, due to the moisture intercepted by plant structure or by rock surfaces.

2.2.5 Vascular Plant Community Structure

The vertical and horizontal vascular plant structure of many arid and semi-arid vegetation communities optimizes growth of biological soil crusts. In cooler regions, greater structural diversity of vascular vegetation generally results in greater compositional diversity of biological crusts. Vascular plants create windbreaks and shade, influencing how much moisture and light reach the soil surface. They also trap leaf litter, keeping the interspaces free of substantial or persistent litter cover (Rosentreter and McCune 1992).

Invasive exotic plants generally decrease the structural diversity of native vascular plant communities by creating monocultures of densely spaced plants and by homogenizing litter distribution. They also lead to decreased biological crust cover and species richness in most ecosystems (Rosentreter 1994; Kaltenecker 1997). In addition, if moisture is retained under a litter layer for long periods while temperatures are warm, lichens can become parasitized by ubiquitous molds (Rosentreter 1984).

2.2.6 Ecological Gradients

Some lichens form natural replacement series along the same ecological gradients that influence vascular plants, although some lichen taxa are not good indicators of site conditions due to broad ecological amplitudes. For example, gelatinous lichens are most common in aridic calcareous sites and mesic non-calcareous sites (Fig. 2.6). Sites with frigid soil temperature regimes (mean annual temperature less than 8°C) lack significant cover of gelatinous lichens. The genus *Leptogium* might be present; however, *Peltigera* and *Massalongia* tend to be more common. Some species display a shift in substrate preference in different ecoregions. For example, *Leptochidium albociliatum* occurs on mosses in the Great Basin, while in the Columbia Basin it is more common and occurs on bare mineral soil (Rosentreter 1986; Ponzetti et al. 1998).

2.2.7 Microhabitats

Biological soil crusts can also create their own microstructure, which influences species distribution. Mosses create microsites that are very low in nutrients, low in calcium carbonate, and that retain moisture longer than bare mineral soil. This creates favorable sites for lichens that may benefit from the improved moisture regime and do not require many soil nutrients. Common examples include *Leptogium lichenoides*, *Massalongia carnosa*, and *Peltigera* spp. that grow only on mosses and are found in many sagebrush (*Artemisia*) steppe habitats.

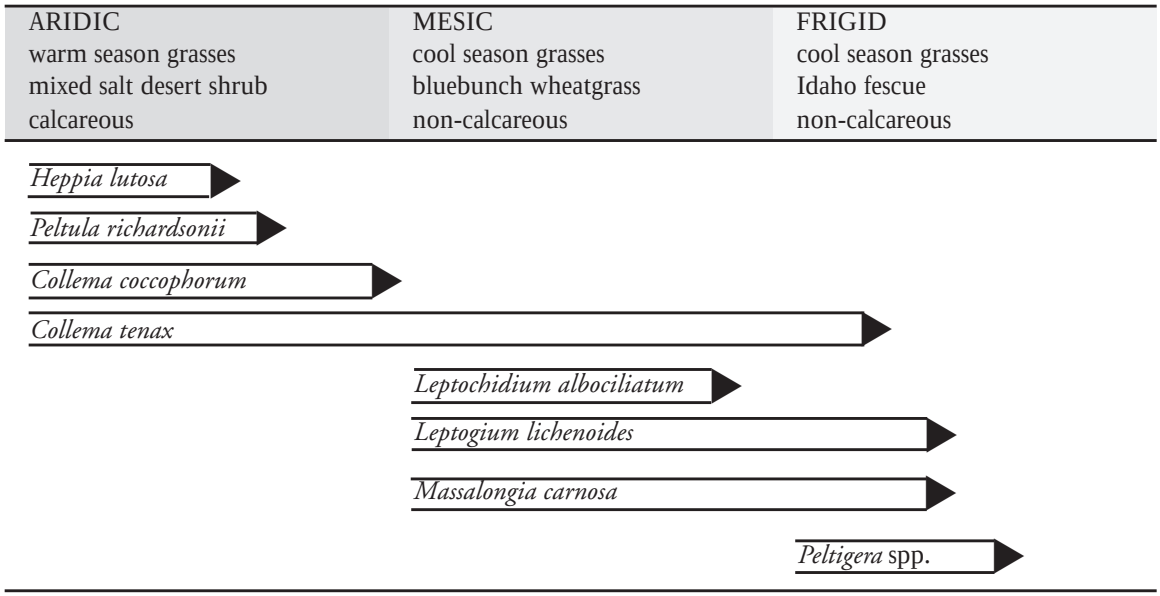
2.3 Unique Crustal Communities in North America

Special geologic features or soils create conditions that promote growth of biological soil crusts. Some of these sites support crusts containing uncommon associations or rare species. These unique crustal communities are not common across the landscape but are at times locally abundant. Some unique crustal communities are discussed below.

2.3.1 Gypsum

Gypsiferous outcrops are comprised of soils that are fine textured and have high concentrations of sulfate and calcium. Vascular plant cover at these sites is generally sparse with limited species diversity. Gypsiferous soils can support well-developed

Figure 2.6 *Gelatinous and other nitrogen-fixing lichens by relative soil temperature and calcareous influence.*



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biological crusts with a high lichen diversity (Anderson and Rushforth 1976; St. Clair et al. 1993), although sites in the hot deserts of the southwestern U.S. lack the species diversity of the cool deserts to the north. Common species include *Diploschistes diacapsis*, *Psora decipiens*, *Collema tenax*, *Placidium squamulosum*, *Buellia elegans*, and *Squamarina lentigera*. Several lichens are restricted to gypsiferous soils, including *Acarospora nodulosa* var. *nodulosa* (St. Clair and Warrick 1987), *Gypsoplaca macrophylla* (Timdal 1990), and *Lecanora gypsicola* (Rajvanshi et al. 1998). Gypsiferous sites are worthy of protection because of their high potential for cover and biological crust diversity. These sites are often threatened by mining activity due to the commercial value of gypsum.

2.3.2 Glades (Lithic and Shallow Soil Sites)

Glades are widespread across North America but are limited both locally and in overall area. Lithic and shallow soil sites are often colonized by biological crusts because these sites are extremely droughty and vascular plant growth is limited. In eastern forests, shallow disturbed or compacted soil (e.g., along roadsides) may be dominated by biological soil crusts, with *Baeomyces rufus* or *B. fungoides* often forming extensive crustal colonies. Pine barrens generally support extensive biological crusts. In western and more northern boreal forest openings, *Cladonia* spp., *Peltigera* spp., and occasionally *Multiclavula* spp. are dominant. These genera are also common on disturbed soil along roadways and cutbanks throughout the non-arid portions of the continent. Some lithic sites in wet climates are leached of soil nutrients and are often dominated by gelatinous lichens such as *Leptogium* or nitrogen-fixing cyanobacteria such as *Nostoc*.

2.3.3 Thermal Springs

Some parts of western North America contain extensive active or dormant thermal (hot) springs. Conditions in these areas are harsh, limiting vascular plant growth. Soil temperatures are often extremely high in summer and warm in winter. Soils containing thermal springs are often infertile, as warm water leaches many minerals, including calcium, magnesium, nitrogen, and phosphate. Toxic heavy metals can be present in the water and thus get deposited on the soil surface. These areas are covered with specialized thermic cyanobacteria when moist. When dry, they support either non-specialized biological crusts or crusts characteristic of gypsum.

2.3.4 Cold Desert Playas

Small ephemeral pools form in parts of the Pacific Northwest where summers are hot and dry and winters are cool and moist (Rosentreter and McCune 1992). These sites are located on poorly drained basalt or other rock types, often barren of vascular vegetation and usually surrounded by some species of sagebrush (*Artemisia*). Drainage may be impaired by rock type or frozen soils, causing water to pond seasonally in flat, exposed areas. In late winter and early spring these sites experience cool, yet above freezing, temperatures for portions of the day. These conditions allow for slow evaporation of standing water. Such sites are sometimes referred to as playettes, as they are similar to but smaller than large seasonal lakes called playas. Playas support either attached or vagrant forms of *Dermatocarpon miniatum* and *Nostoc*. *Nostoc commune* found in these sites includes the common filamentous form, the colonial-eggs form, and occasionally the long, hair-like unattached form (referred to as var. *flagellaris*). Small playettes covered with fine silts can be colonized by *Nostoc* and by crustose lichens more typically occurring on rocks, such as *Lecanora muralis* (Rosentreter 1986).

2.3.5 Alpine Sod

Biological soil crusts are either dominant or common community components in many alpine and subalpine sites in North America. Alpine and subalpine sites contain some species common to the continent's arid regions. In contrast, a few lichens are characteristic of alpine crusts alone and include *Lecidoma demissum*, *Solorina* spp., *Lepraria neglecta*, *Ochrolechia frigida*, and *Thamnolia* spp. (DeBolt and McCune 1993). A genus that occurs on soil or rock in both alpine and arctic sites is *Stereocaulon*, which fixes nitrogen and is common worldwide in montane and alpine habitats (Lamb and Ward 1974). In the subalpine zone, biological crusts are often associated with areas where snowdrifts occur. Lichens characteristic of snow-patch sites are *Solorina crocea* and *Lepraria neglecta* (McCune 1998). Cyanobacterial crusts are also common in these areas and are generally dominated by *Nostoc* species (Reisiegl 1964).

2.3.6 Arctic Tundra

Alpine and tundra soils are often dominated by fruticose lichens (*Cladina* and *Cetraria*) and graminoids. Some areas are dominated by fruticose lichens that start out as crust communities in the early stages of succession. Tundra areas in North America have poor drainage due to frozen ground and are similar to other portions of the northern hemisphere, including Greenland. In some arctic regions there are also large areas of dry steppe-like vegetation, open

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Dryas heaths, and fell-fields with extensive coverage of biological crusts. Cyanobacterial crusts are commonly extensive and often dominated by *Nostoc* species (Hansen 1997).

2.4 Example: Biological Soil Crusts in Sagebrush Communities

Sagebrush species are common in western North America, particularly in the Great Basin and Columbia Plateau vegetation zones. Some of the same characteristics that influence sagebrush taxa distribution also influence biological crust development. Relative cover of biological crusts in various sagebrush vegetation types is presented in Table 2.5. Biological soil crusts tend to be lacking in sagebrush types that occur on seasonally flooded soils (silver, alkali, and fuzzy sagebrush; Winward 1980), as flooded soils create anaerobic conditions that are not well tolerated by lichens. Heavily saline soils also lack lichen cover, although moss is sometimes present if the salt concentration is not too great. Mountain, subalpine, and xeric big sagebrush types often lack significant biological crust cover due to dense vascular vegetation and accumulating plant litter. Other sagebrush types support higher biological crust cover unless soil surfaces are greatly disturbed or the current vegetation is in an early-successional stage.

Some lichens are good indicators of late-successional stages in sagebrush communities. The dual gradient theory proposed by McCune (1993) for lichen species succession in forested habitats applies well to arid and semi-arid regions in that species respond to time (age) and moisture in similar successional trajectories. Therefore, the length of time since the last major site disturbance or an increase in effective soil moisture will both provide suitable ecological conditions to support specific lichen species. This is why biological soil crust communities in different ecoregions recover at different rates (Table 2.2, Chapter 4).

Late-successional indicator species in sagebrush-steppe include *Acarospora schleicheri*, *Massalongia carnosa*, *Pannaria cyanolepra* (type b), *Trapeliopsis wallrothii*, *Trapeliopsis* sp. nov. (McCune, unpublished), and *Texosporium sancti-jacobi*. Some lichens are only present in late-successional communities because they grow upon other lichens or mosses. For example, *Acarospora schleicheri* grows upon *Diploshistes muscorum*, which in turn parasitizes the lichen genus *Cladonia*. Therefore, *Cladonia* can be considered a keystone organism influencing a site's diversity. *Massalongia carnosa* primarily grows on mosses and is not present until mosses become well established within a site. *Texosporium sancti-jacobi* is restricted to old-growth sagebrush communities and occurs only on decaying organic matter (McCune and Rosentreter 1992). Other lichens that commonly occur on decayed organic matter but are not restricted to old-growth sites include *Buellia papillata*, *B. punctata*, *Caloplaca* spp., *Lecanora* spp., *Megaspora verrucosa*, *Ochrolechia upsaliensis*, *Placynthiella* spp., and *Phaeophyscia decolor*.

Table 2.5 *Relative cover of biological soil crusts in sagebrush (Artemisia) vegetation types.*

HIGH biological crust cover	LOW biological crust cover
Tall Sagebrush	
Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*)	subalpine big sagebrush (*A. tridentata* ssp. *spiciformis*)
basin big sagebrush (*A. tridentata* ssp. *tridentata*)	xeric big sagebrush (*A. tridentata* ssp. *xericensis*)
mountain big sagebrush** (*A. tridentata* ssp. *vaseyana*)	mountain big sagebrush** (*A. tridentata* ssp. *vaseyana*)
	silver sagebrush (*A. cana*)
	three-tip sagebrush (*A. tripartita*)
Short Sagebrush	
low sagebrush (*A. arbuscula*)	alkali sagebrush (*A. longilobia*)
black sagebrush (*A. nova*)	fuzzy sagebrush (*A. papposa*)
stiff sagebrush (*A. rigida*)	
Bigelow sagebrush (*A. bigelowii*)	
fringed sage (*A. frigida*)	

**Biological crust cover high or low depending on site characteristics.

CHAPTER 3

ECOLOGICAL ROLES

In a given ecoregion, ecological roles of biological soil crusts can vary widely in their importance and will depend on crust composition and biomass, as well as characteristics of the specific ecosystem being considered.

3.1 Species Composition and Biomass

The relative importance of biological crusts and their different ecological roles within an ecosystem is highly dependent on relative cover of various crustal components. For example, carbon inputs are higher when mosses and lichens are present than when the crust is dominated by cyanobacteria. Nitrogen inputs are higher with greater cyanobacterial biomass and greater cyanolichen cover. Water infiltration and soil surface stability are related to cyanobacterial biomass as well as moss and lichen cover.

3.2 Carbon Fixation

Biological soil crusts can be an important source of fixed carbon on sparsely vegetated areas common throughout western North America (Beymer and Klopatek 1991). While vascular plants contribute organic matter to soils directly beneath them, large interspaces between plants receive little plant material input. Where biological soil crusts are present, carbon contributed by these organisms helps keep plant interspaces fertile, providing energy sources for soil microbial populations.

Crustal organisms are physiologically active only when wet, and metabolic functions begin almost immediately. Respiration begins less than 3 minutes after wetting, while photosynthesis reaches full activity after 30 minutes or more. Soil oxygen concentrations, a by-product of photosynthesis, reach steady states within 1 to 2 hours of wetting (Garcia-Pichel and Belnap 1996). Rain during hot months can place lichens in a state of carbon deficiency, as the lichens can dry out before photosynthesis has begun. Jeffries et al. (1993a, b) showed cyanobacterial crusts from the Colorado Plateau had positive carbon balances only during prolonged wet periods, such as winter and spring, and that short-term wet-dry cycles, which often occur in low-elevation inland sites during summer, resulted in net carbon loss for both *Microcoleus*- and *Scytonema*-dominated crusts (this would also be expected for *Collema* and other soil lichens). Consequently, timing

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and duration of precipitation may heavily influence carbon budgets in crustal organisms and thus influence the distribution of individual species.

Winter-rain deserts (e.g., Mojave and Great Basin) have a rich soil lichen flora, with the cyanobacterial flora heavily dominated by *Microcoleus*. In contrast, summer-rain deserts (e.g., Sonoran) have only a small subset of the lichens found in winter-rain deserts, while the cyanobacterial flora is a complex community co-dominated by up to 10 species. Different responses to timing and amount of precipitation and temperature may mean species composition will shift in response to predicted climate changes. Since many areas that are currently winter-rain dominated are predicted to receive increased summer rain, effects of climate change may be reflected in different soil crust composition than that currently found in the summer-rain versus the winter-rain deserts.

Soil lichens have several different strategies to optimize carbon gain (Lange et al. 1992, 1994, 1997). While photosynthesis is activated at low-water content for all species, each varies in response to higher water content. Cyanolichens, such as *Collema tenax*, showed dramatic drops in carbon fixation when water content exceeded 60 to 80%. Conversely, green algae generally showed little, if any, depression at high-water content. Water-holding capacity varies between lichens and will also influence time of carbon fixation for a given species.

Table 3.1 *Common nitrogen-fixing lichens and cyanobacteria in cool and hot deserts of the western U.S.*

Cool Deserts	Hot Deserts
Lichens	
Collema coccophorum	*Collema coccophorum*
Collema tenax	*Collema tenax*
Heppia	*Heppia*
Leptochidium albocilitatum	*Peltula*
Leptogium	
Massalongia carnosa	
Pannaria	
Peltigera	
Polychidium	
Cyanobacteria	
Microcoleus vaginatus (non-heterocystic)	*Schizothrix* (heterocystic)
Nostoc (heterocystic)	*Nostoc* (heterocystic)
Scytonema (heterocystic)	*Scytonema* (heterocystic)

Photosynthetic rates are also dependent on temperature (Rychert et al. 1978; Lange 1980; Nash et al. 1982; Nash and Moser 1982; Lange et al. 1997). Photosynthetic rates increase with increasing temperatures to about 28°C, above which rates decline dramatically. *Collema tenax* is an exception, with no such decline seen up to 36°C.

3.3 Nitrogen Fixation

Nitrogen concentrations are known to be low in desert soils compared to other ecosystems. Total atmospheric input over the past 10,000 years has been conservatively estimated at about 3 kg nitrogen/m^2, with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Extensive surveys in cool deserts have revealed only a few nitrogen-fixing plants (Farnsworth et al. 1976; Wullstein 1989). Since nitrogen can limit net primary productivity in many desert ecosystems (Ettershank et al. 1978; James and Jurinak 1978; Romney et al. 1978; Nobel et al. 1988), maintaining normal nitrogen cycles is critical to soil fertility and prevention of desertification (Dregne 1983).

Cyanobacteria and cyanolichens can be an important source of fixed nitrogen for plants and soils in desert ecosystems (Evans and Ehleringer 1993; Belnap 1995). Many biological soil crusts in western North America are dominated by nitrogen-fixing cyanobacteria and lichens (Table 3.1). These organisms are capable of both light and dark nitrogen fixation (Rychert and Skujins 1974; Pearson et al. 1981; Paerl 1990; Belnap 1994). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert et al. 1978; Belnap 1994). Fixation rates are highest after photosynthesis has replenished lichen carbon stores. For most lichen species, nitrogen-fixation rates increase with temperature to 25°C, given sufficient moisture. Since nitrogen-fixation rates depend on the cover of specific crust species, timing, extent, and type of past disturbance are also critical factors (Belnap 1995, 1996). Nitrogen-fixation rates in biological soil crusts have been estimated at 2 to 365 kg/ha annually (Mayland et al. 1966; MacGregor and Johnson 1971; Rychert and Skujins 1974; Eskew and Ting 1978; Jeffries et al. 1992), with recent studies indicating that higher rates are probably more accurate (Belnap, unpublished data). Still, rates are expected to vary greatly, depending on the species present and environmental conditions.

Five to 88% of nitrogen fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris 1954; Silvester et al. 1996; Belnap et al. 1997). Nitrogen released from crustal

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Figure 3.1 *Disturbance plots on the Colorado Plateau showing the difference in soil surface color between undisturbed (dark) and disturbed (light) plots. Note that the undisturbed plots have greater surface roughness than the disturbed plots.*

organisms is readily taken up by surrounding vascular plants, fungi, and bacteria (Mayland and MacIntosh 1966; Mayland et al. 1966; Stewart 1967; Jones and Stewart 1969). Vascular plants growing in biologically crusted soils show higher tissue concentrations of nitrogen than plants grown in uncrusted soils (Harper and Pendleton 1993; Belnap 1994, 1995; Belnap and Harper 1995). As with carbon, crusts contribute nitrogen to soils both under plants and in plant interspaces, thereby counteracting the tendency of these nutrients to concentrate around perennial plants.

3.4 Albedo

Soil albedo is a measure of the energy reflected off the soil surface. Dark surfaces absorb more energy, are warmer than light surfaces, and thus have lower albedo. Because soils with well-developed biological crusts are dark, they can be up to 23°F warmer than adjacent crusted surfaces (Fig. 3.1; Belnap 1995; Belnap, unpublished data). Disturbance of biological crusts increases albedo and therefore decreases soil temperatures. This affects many ecosystem processes. Metabolic processes, for example, including photosynthesis and nitrogen fixation, decrease at lower temperatures (see Sections 3.2 and 3.3; Nash 1996). Lower soil temperatures decrease microbial activity, plant nutrient uptake rates, and soil water evaporation rates; delay seed germination time; and decrease seedling growth rates. Timing of these events is often critical in deserts, and modifications can reduce species fitness and seedling establishment, which in turn may eventually affect plant community structure (Bush and Van Auken 1991). Changes in albedo can also affect animal populations. For instance, foraging times are often partitioned among ants, arthropods, and small mammals on the basis of soil surface temperature (Doyen and Tschinkel 1974; Wallwork 1982; Crawford

1991). In addition, many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth 1978). Consequently, altering surface temperatures can affect desert ecosystems at numerous levels.

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3.5 Effects on Vascular Plants

3.5.1 Seed Germination

Biological crusts can affect vascular plant germination. While small cracks and crannies on the soil surface are generally sufficient for small-seeded plants to lodge and germinate, most large-seeded plants need soil or plant litter cover to germinate. In deserts where plant litter is often limited in interspaces, large native seeds generally have self-burial mechanisms (such as hygroscopic awns) or are cached by rodents. Many exotic species, however, lack self-burial mechanisms. Because biological crusts stabilize soils, germination of such seeds can be inhibited in sites with well-developed crusts and low plant litter, as was recently demonstrated for the annual exotic grass, cheatgrass (*Bromus tectorum*), in both the field and laboratory (Larsen 1995; Kaltenecker et al. 1999a; Belnap, unpublished data). Though crusts can reduce germination of some seeds, seedling germination *per se* has not been shown to limit species density in desert plant communities. Rather, studies worldwide show vascular plant cover and structure are most often controlled by water and/or nutrient availability rather than other site factors (Mabbutt and Fanning 1987; Tongway and Ludwig 1990; Dunkerley and Brown 1995).

3.5.2 Plant Establishment and Cover

Biological soil crusts have not been shown to present a barrier to seedling root penetration once seeds germinate (Belnap, unpublished data; Pendleton and Meyer, unpublished data). This is in contrast to physical crusts, which often inhibit root penetration. Areas

Figure 3.2 *Sandberg bluegrass* (Poa secunda) *growing in well-developed biological soil crusts in the northern Great Basin.*

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that have been lightly trampled (to keep crusts from developing) over a 5-year period that included both wet and dry years show no additional plant establishment (Belnap, unpublished data; Fig. 3.1). Many authors have shown that seedling establishment of both forbs and grasses is either not affected or is increased by the presence of biological soil crusts, on both coarse- and fine-textured soils (Fig. 3.2; St. Clair et al. 1984; Harper and St. Clair 1985; Eckert et al. 1986; Harper and Marble 1988; Lesica and Shelley 1992; Belnap 1993).

Numerous authors have reported that biological crusts either do not compete with vascular plants (Kleiner and Harper 1972, 1977a, b; Anderson et al. 1982b; Jeffries and Klopatek 1987; Beymer and Klopatek 1992) or that vascular plant cover is enhanced by the presence of a biological crust (Dadlich et al. 1969; Graetz and Tongway 1986; Rosentreter 1986; Mucher et al. 1988; Carleton 1990; Ladyman and Muldavin 1994; Ladyman et al. 1994). This suggests that the presence of plants can aid the survival of crustal components, perhaps because of microclimate conditions associated with clumped perennial vegetation (such as decreased soil surface temperatures, increased surface moisture due to shading, and decreased wind speed on the soil surface). A few authors have speculated that there is a negative relationship between cover of biological crusts and vascular plants (Savory 1988 reviewed in West 1990). However, this view is not supported by the numerous studies that have directly addressed this issue. Rather, it appears more likely that biological crusts simply cover soils unoccupied by vascular plants.

3.5.3 Nutrient Levels in Vascular Plants

Plants growing in biologically-crusted soil often show higher concentrations and/or greater total accumulation of various essential nutrients than do plants growing in adjacent, uncrusted soils (Belnap and Harper 1995; Harper and Belnap in press). In one study, leaf tissue nitrogen was 9% higher in the perennial shrub *Coleogyne*, 31% higher in the perennial forb *Streptanthella*, and 13% higher in the annual grass *Festuca* (*Vulpia*), for plants growing in biologically-crusted soil compared to plants in adjacent uncrusted soil. Dry weight of *Festuca* plants in the crusted soil was twice that of plants in the uncrusted soil (Belnap 1995; Belnap and Harper 1995). Nitrogen concentrations in leaf tissue of the biennial *Mentzelia multiflora* was higher in plants growing in a biologically-crusted area relative to plants from an adjacent sand dune that lacked a crust. In greenhouse experiments, nitrogen levels in *Sorghum halepense* were higher when the plant was in pots with cyanobacteria than when in pots without cyanobacteria. Dry weight of plants in pots with cyanobacteria were up to four times greater than in pots without cyanobacteria (Harper

and Pendleton 1993). Other authors have obtained similar results with other species (Shields and Durrell 1964; Brotherson and Rushforth 1983; Pendleton and Warren 1995).

Several mechanisms may explain this enhanced effect on vascular plant growth and nutrient status. Material blowing across biological soil crusts can become trapped, either accumulating within low pockets in the microtopography or sticking by exudate to cyanobacterial sheaths. These sheaths are phototropic, and if not buried too deeply, will push through loose soil and organic matter, further trapping or entangling soil in the process (Fryberger et al. 1988; Campbell et al. 1989; Gillette and Dobrowolski 1993). Danin et al. (1989) proposed a positive feedback loop in which crusts trapping fine particles create nutrient-rich microsites, increasing germination and growth of vascular plants, which in turn reduces erosion potential and increases accumulation of washed or wind-blown soil.

In addition, cyanobacterial sheath material is often coated with negatively charged clay particles. These clay particles are more nutrient rich than sand (Black 1968), as they bind positively charged macronutrients and prevent them from leaching through the soil profile (Belnap and Gardner 1993). Lange (1974) demonstrated that compounds in the gelatinous sheath material of several cyanobacteria taxa were able to chelate iron, copper, molybdenum, zinc, cobalt, and manganese. Four of the five genera shown to possess this ability (*Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc*) are commonly represented in biological crusts of western North American deserts (Shields and Durrell 1964). It is also possible that the nutrient differences result from thermal effects, as crusted soils are darker and warmer than uncrusted soils; nutrient uptake by vascular plants would occur at a higher rate.

Herbivores and other consumers may benefit directly from the enhanced nutrient status of plants grown in healthy, biologically-crusted soils (Belnap and Harper 1995). Indirect effects include positive correlations between soil mycorrhizae and microarthropod populations with the presence of well-developed biological soil crusts (Harper and Pendleton 1993; Belnap, unpublished data).

3.6 Water Relations

The effect of biological soil crusts on soil-water relations is highly site dependent. Level of crustal development (e.g., cover and relative composition of cyanobacteria, lichen, moss), climatic regimes, the amount of surface roughness, time since destructive disturbance, soil texture, and soil structure can all heavily influence hydrologic cycles at a given site. Soil texture is especially important and can

override any effect of biological soil crusts. For instance, soils high in shrink-swell clays have relatively low infiltration rates, regardless of biological crust presence or absence.

Research conducted under a variety of soil and climate conditions around the world shows variable and interactive effects of biological crusts and soil properties. Biological crusts influence soil hydrology because they alter soil surfaces. Aggregate stability, soil structure, organic matter, and rough microtopography are all attributes associated with superior hydrologic properties, and biological soil crusts enhance these attributes in soil (Booth 1941; Fletcher and Martin 1948; Shields and Durrell 1964) on both micro- and macro-scales (Belnap and Gardner 1993; Belnap 1994).

Infiltration rates are controlled by the interaction of water-residence time on a soil surface and the permeability of that surface.

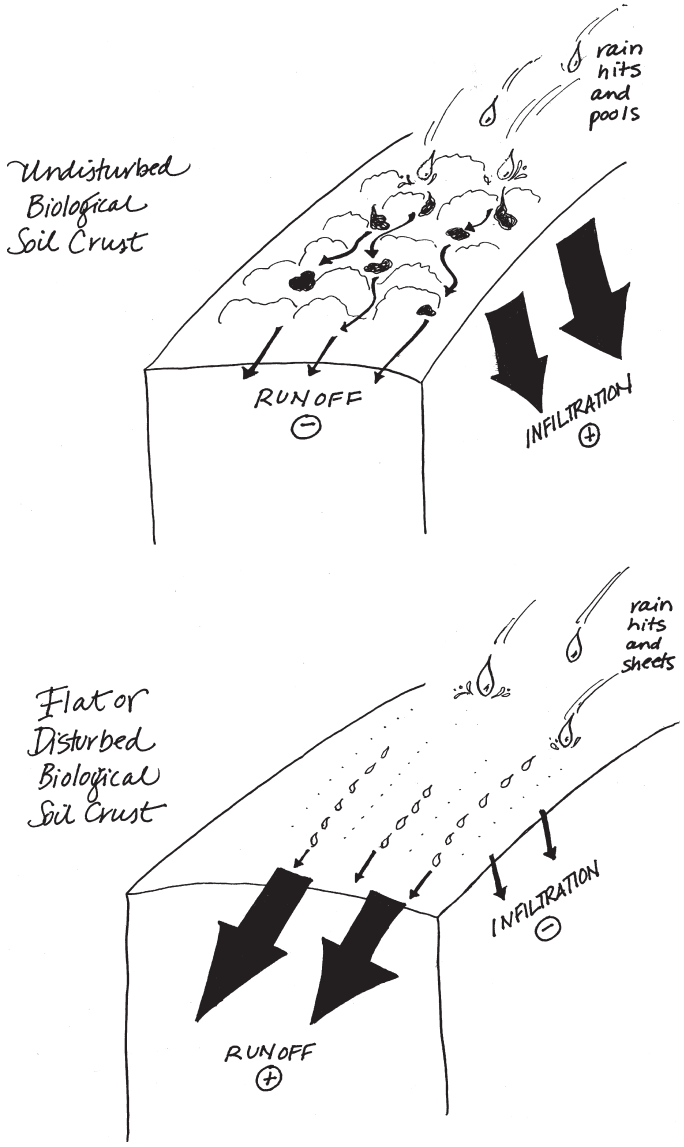

Figure 3.3 *Soil-water relationships with biological soil crusts. In the cool deserts (Colorado Plateau, Great Basin), roughened soil surfaces created by biological crusts act to impede overland water flow, resulting in increased infiltration. When biological soil crusts are removed, or with flat crusts in the hot deserts (Sonoran, Mojave, Chihuahuan), water runs over the soil surface unimpeded and infiltration is reduced.*

Biological crusts can produce a rough surface microtopography (less than 100 mm vertically) that acts as detention structures for water (Danin and Barbour 1982). This is especially pronounced in cool deserts (e.g., the Colorado Plateau), where frost-heaving is common and crusts are highly pedicelled. In these regions, biological crusts generally increase water infiltration (Fig. 3.3; Loope and Gifford 1972). In warm deserts, where frost-heaving is not present and biological soil crusts are flat, infiltration rates depend more on soil type and climatic regimes.

While greater surface roughness can increase water pooling and residence time, the presence of mucilaginous cyanobacteria in soil crusts can also decrease soil permeability. These cyanobacterial components of biological soil crusts rapidly swell up to 13 times their dry volume (Shields and Durrell 1964; Campbell 1977), potentially closing flow pathways through the soil surface. Scanning electron microscopy shows sufficient openings in sandy loam soils for water flow (Belnap and Gardner 1993), but concentration of silt and clay particles in the crust, in combination with swelling, may restrict infiltration even in sandy soils when they are wet (Verrecchia et al. 1995). Some authors speculate that the hydrophobic nature of some crustal components contributes to soil surface sealing (Bond 1964; Dulieu et al. 1977; Walker 1979; Rutin 1983; Jungerius and van de Meulen 1988); however, others have shown crustal organisms at some sites are highly hydrophilic (Kidron et al. 1999).

Overall, infiltration rates appear to be increased in regions where crusts are pinnacled and decreased in regions where crusts are flat. This has been reported for sandy soils in Arizona (Brotherson and Rushforth 1983), Australia (Bond 1964; Rogers 1977; Stanley 1983; Graetz and Tongway 1986; Eldridge 1993a, b), and Israel (Yair 1990). In New South Wales, Australia, infiltration rates increased on a transect through a sandy-loam soil as grazing decreased and biological soil crust cover increased. However, compared with adjacent ungrazed soils with a continuous cover of lichens and mosses, the lightly grazed areas showed greater infiltration (Eldridge 1993b). Infiltration studies conducted on sandy soils in Oklahoma and Kansas (Booth 1941) and silt-loams and clayey silt loams in Arizona (Faust 1970, 1971) failed to find any influence of biological soil crusts on infiltration rates.

The influence of biological soil crusts on effective hydraulic conductivity (the rate at which water moves through the soil profile under field conditions) is also variable. Lichen-dominated crusts in Utah showed decreased hydraulic conductivity (Loope and Gifford 1972). Lichen and algal crusts in Australia were associated with high conductivity (Greene et al. 1990). Three-year-old algal crusts in Utah and non-disturbed crusts in Nevada showed no discernible influence on conductivity (Williams 1993; Dobrowolski 1994).

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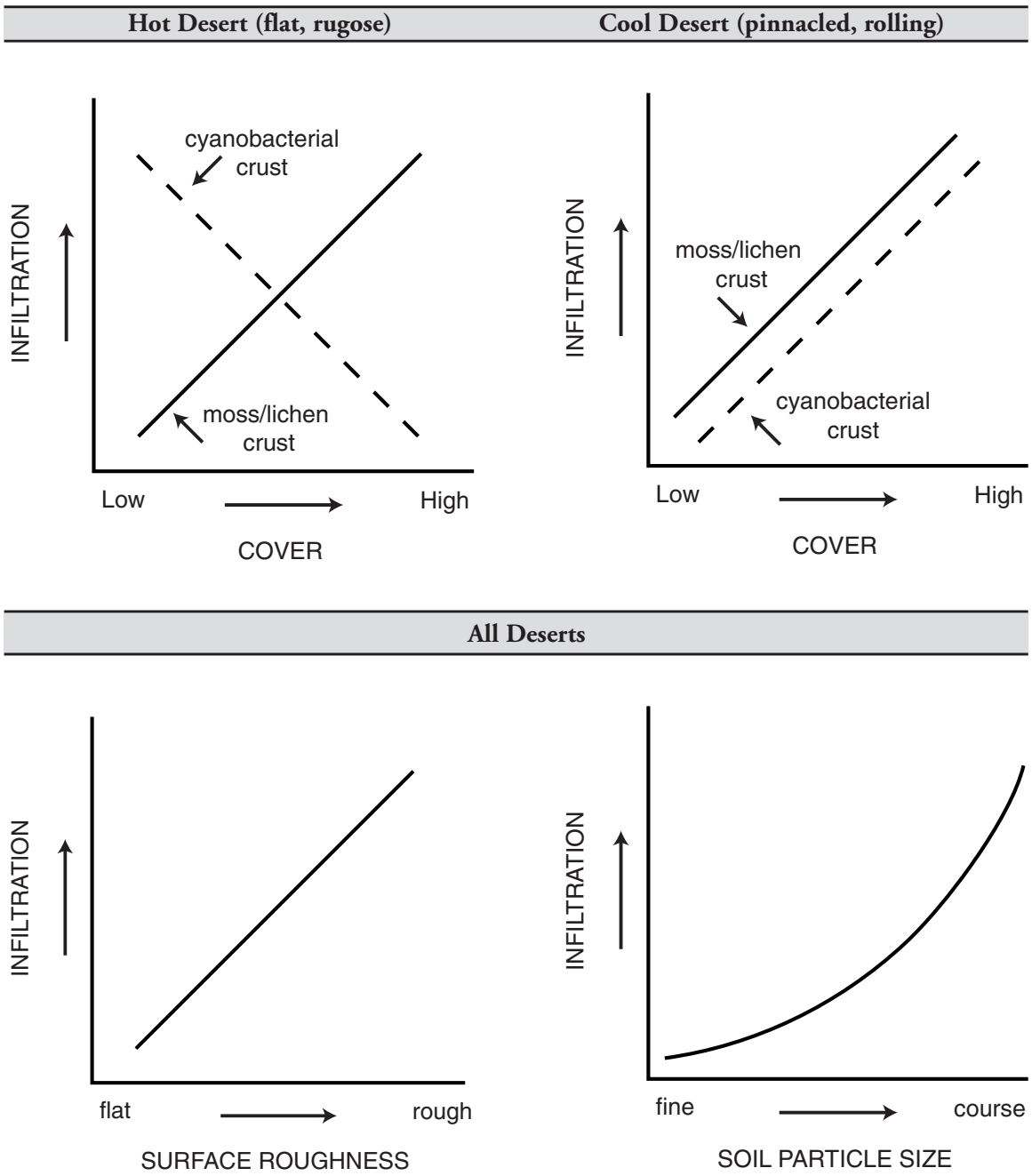
Biological soil crusts have varied effects on soil moisture at any given time. However, research results have been variable and again appear to depend on soil type and crust composition. The crust's ability to seal the soil surface and reduce evaporation because of its associated high clay and silt concentrations has been repeatedly proposed (Danin 1978; Brotherson and Rushforth 1983; Williams et al. 1995a). While some studies show soil moisture is greater under well-developed crusts (Harper and Marble 1988; Meyer and Garcia-Moya 1989; Verrecchia et al. 1995; Belnap et al. 1996), other studies have found decreased soil moisture under crusted surfaces (Harper and Marble 1988).

Though overall infiltration of precipitation is critical for plant growth, the location of water entering the soil can also be critical in maintaining plant community structure. Recent work has shown that the pattern of water infiltration and runoff is important in maintaining vegetative community structure, especially in hyper-arid zones where rainfall is too low to support homogenous distribution of vegetation. Instead of being distributed across the landscape, plants are concentrated in bands that occur perpendicular to the water flow. These bands or vegetation clumps capture water, nutrients, and fine soil particles. The bigger the bands, the more effective they are in resource capture; however, their overall size is limited by rainfall and nutrients. Biological soil crusts often cover interband soils. When these interband areas are disrupted, water infiltration can increase between vegetated areas; thus, less water is available for the vegetation, often deep-rooted, woody perennials (Eldridge et al. 2000). This decrease in water availability may lead to changes in plant community structure by enabling establishment of shallow-rooted species in the interband areas or by die-off of the perennial shrubs. Over time, changes in hydrology and plant community structure result in modification of site potential and ecological function. A similar situation applies to exotic plant invasions and their effects on site function. In the Great Basin, invasive exotic annual grasses modify the native community's patchy structure to a more homogenous structure (Kaltenecker 1997). The resultant increases in plant and litter density in interspaces previously occupied by biological crusts affect moisture infiltration, which may further facilitate changes in community structure because less moisture becomes available for deeply-rooted perennial plants.

As can be seen above, the impact of biological soil crusts on hydrologic cycles can be highly variable and can result from a combination of site, soil, and crust factors (Fig. 3.4). However, lack of standardized data collection methods and descriptions of soil, biological crust, and climatic characteristics at study sites makes comparison of research results difficult. These shortcomings have

Figure 3.4 *Biological soil crust and soil characteristics that influence infiltration.*



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undoubtedly contributed to much of the seemingly contradictory published information.

3.7 Soil Stabilization

Biological soil crusts are unambiguously effective in reducing wind and water erosion of soil surfaces (Belnap and Gillette 1997, 1998; McKenna-Neumann et al.1996). Wind can be a major erosive force in deserts, as sparse vegetation leaves large patches of soil unprotected by plant litter or vegetative cover (Goudie 1978). Interspace soils are most often stabilized by rocks or biological soil crusts. Biological crusts play an important role both in preventing soil loss and facilitating soil accretion. The degree to which different types of crusts protect the soil surface from both wind and water erosion is hierarchical in the following manner: bare soil < cyanobacterial/algal crust < lichen crust < moss crust (Tchoupopnou 1989; Kinnell et al. 1990; Eldridge and Greene 1994; Belnap and Gillette 1998). Polysaccharides exuded by cyanobacteria and green algae, in combination with lichen and moss rhizines, entrap and bind soil particles together, increasing the size of soil aggregates (Fig. 3.5). As soil aggregates enlarge, they become heavier, have a greater surface area, and are more difficult for wind or water to move. Biological soil crusts keep otherwise loose sandy soils in place on steep slopes; they also stabilize pockets of very shallow soil (Bond and Harris 1964; Marathe 1972; Gayel and Shtina 1974; Danin and Yaalon 1980; Schulten 1985; Graetz and Tongway 1986; Campbell et al. 1989; Danin et al. 1989; Belnap and Gardner 1993). Rough microtopography creates a still-air boundary layer that protects the soil surface from wind erosion. Detention dams pool and slow overland water flow, giving sediment time to settle out, reducing sediment loss (Fig. 3.3; Brotherson and Rushforth 1983; Alexander and Calvo 1990).

Fig. 3.5 *The sheath of* Microcoleus vaginatus *contains sticky polysaccharides that entrap soil particles and bind them together.*

CHAPTER 4

NOTES

RESPONSE TO NATURAL IMPACTS AND HUMAN ACTIONS

4.1 Evolutionary History of Natural Impacts

Euro-American settlement of western North America in the 19th and 20th centuries changed the type, timing, and intensity of natural disturbance. The following is a discussion of the nature of two processes—grazing and fire—in presettlement ecosystems.

4.1.1 Grazing Characteristics

Soil and plant characteristics of low- and mid-elevation arid and semi-arid ecosystems in North America west of the Rocky Mountains indicate that these ecosytems evolved with low levels of soil surface disturbance. This is suggested by these ecosystems' dependence on nitrogen provided by the biological soil crusts (Evans and Ehleringer 1993; Evans and Belnap 1999) and by dominant bunchgrasses' lack of adaptation (such as tillering, secondary compounds, or high tissue silica content) to grazing (Mack and Thompson 1982; Martin 1975; Stebbins 1981). Large mammal numbers would have been low due to limited surface water and sparse vegetation. Limited water availability would have restricted use of lower elevations to winter seasons, as is seen today (West 1988; Parmenter and Van Devender 1995). Dung beetles, present globally in other systems with large mammal herds, are also lacking in western North America (Fig. 4.1; Mack and Thompson 1982). Shallow soils can also limit distributions of burrowing vertebrates and invertebrates, further reducing soil surface disturbance. Current natural

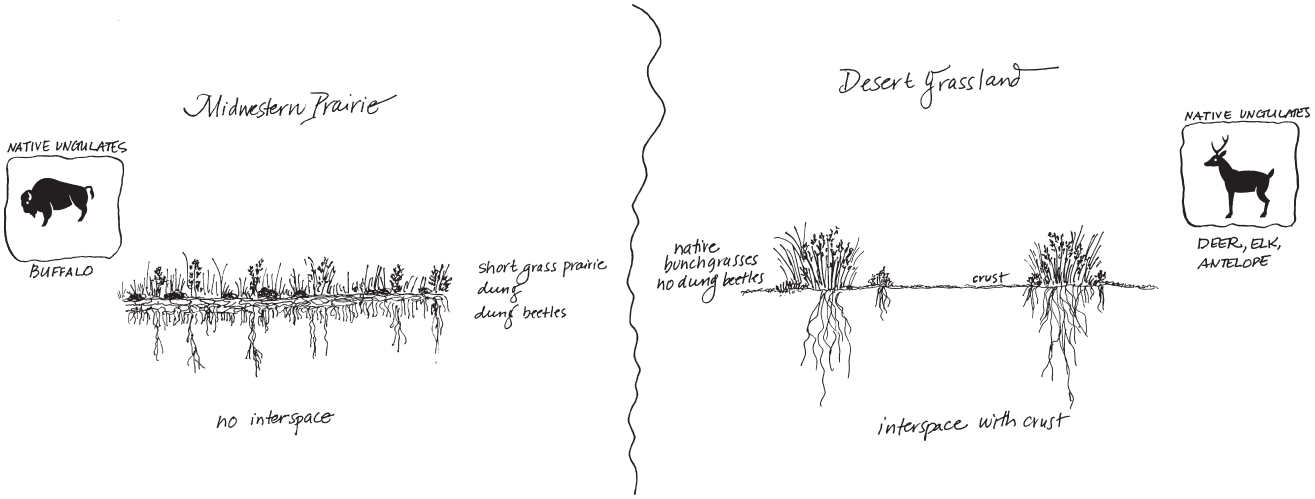

Figure 4.1 *Comparison of community structure in ecosystems that evolved with (midwestern prairie) and without (desert grassland) large herds of grazing mammals.*

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disturbance by large mammals and burrowing fauna in western North American deserts is greatest in the Sonoran and Chihuahuan Deserts, moderate in the Mojave Desert and Great Basin, and low in the Colorado Plateau. Because of their evolutionary history, these regions appear to be more negatively affected by soil surface disturbances than regions like the Great Plains that evolved with higher levels of surface disturbance (see section 4.2).

4.1.2 Fire

In arid and semi-arid native communities, plants have patchy distributions that result in discontinuous fuel and mosaics of various fire intensities (Whisenant 1990). Biological soil crusts provide little fuel to carry a fire through interspaces, thereby acting as "refugia" to slow the spread of fire and decrease its intensity (Rosentreter 1986). Unburned islands of vascular vegetation and biological soil crust provide propagules for reestablishment in burned areas (Fig. 4.2). Johansen et al. (1993) observed that the crust's structural matrix was left intact following low-intensity fire, indicating that a lightly burned crust still functions to maintain stability against erosive forces for both vascular plants and biological soil crusts during the recovery period.

Fire is a natural determinant of the sagebrush-steppe potential vegetation types. Historical fire patterns helped create mosaics of successional stages in both vascular plant and biological soil crust communities. More productive sites generally have fire-return intervals of less than 30 years (Burkhardt and Tisdale 1976; Arno and Gruell 1983; Fisher et al. 1987). Although this time period might constrain biological soil crust recovery, higher precipitation enhances regrowth (see section 4.3.3; McCune 1993). Fifty to 100 years has often been cited as the average return interval in shrub-steppe regions (Wright et al. 1979; Peters and Bunting 1994) and is adequate to restore biological soil crust components. However, there is no direct evidence for fire being a cyclic disturbance in lower elevation shrub-steppe. Here, shrub die-off from insect, disease, and winter kill is common and is probably responsible for most shrub turnover (McArthur et al. 1990). Historic fires were probably small, low intensity, patchy, and uncommon because of sparse and discontinous vegetation. Fire was not historically a common disturbance in most salt-desert shrub types (West 1994), except for the more productive types supporting Great Basin wildrye (*Elymus cinereus*). Likewise, sparsity of vegetation in the southwestern deserts resulted in long fire-return intervals and low-intensity fires (Allen 1998).

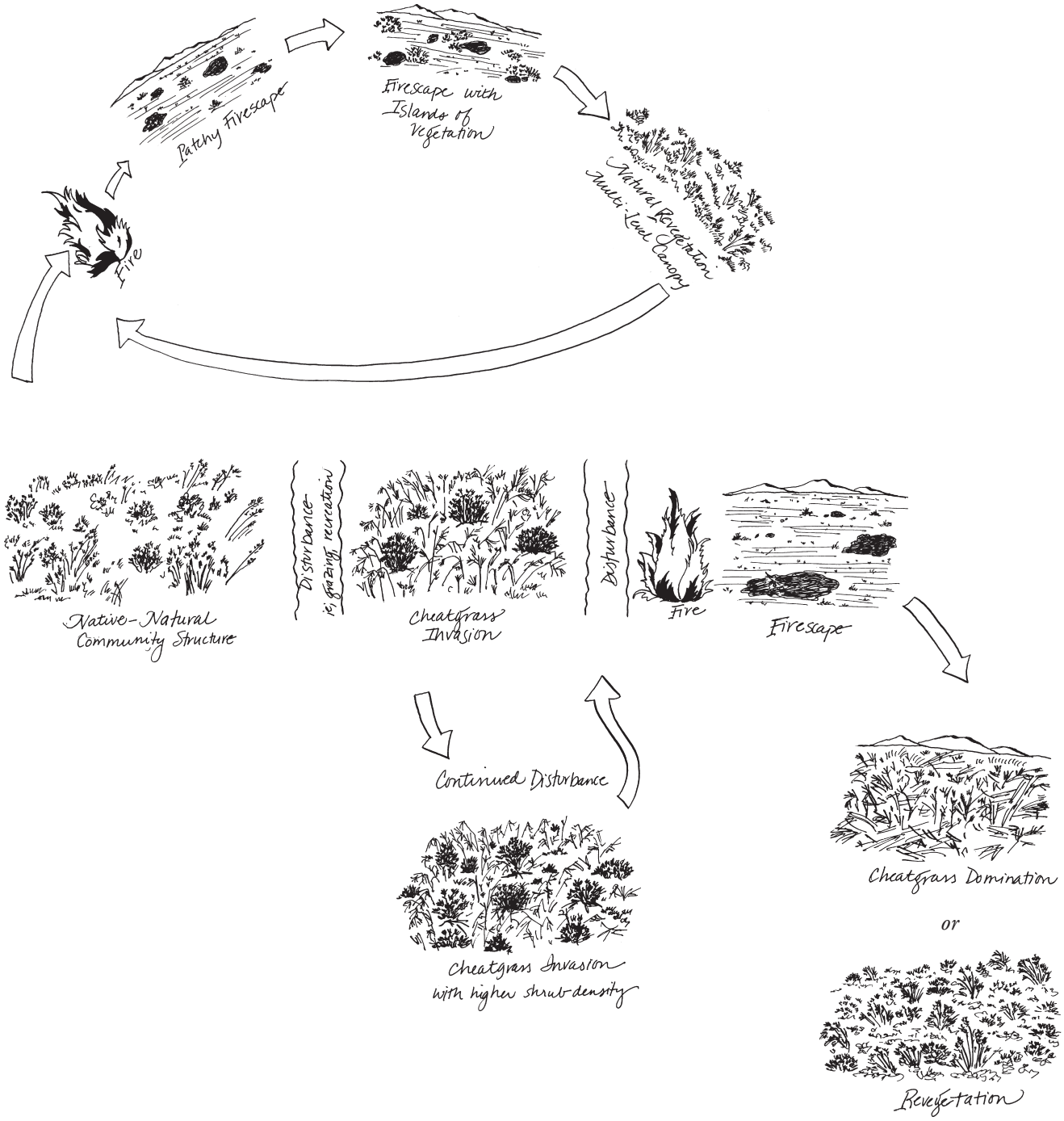

Figure 4.2 *Natural and altered fire cycles in sagebrush communities of the Great Basin. Fire at natural frequencies (50-100 year intervals or longer) occurred in a mosaic of intensities over the landscape due to discontinuity of fuel. This allowed natural regeneration of both the vascular plant and biological soil crust communities. Invasion of exotic species such as cheatgrass into these communities resulted in continuous fine fuels and larger, more intensive fires. Cheatgrass will often dominate the community following fire. Revegetation with perennial species can help reestablish a more natural community structure.*

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4.2 Disturbance Effects

Disturbance can directly and indirectly affect many aspects of the structure and function of biological crust communities, including cover, species composition, and carbon and nitrogen fixation. The impact of a given disturbance depends on its severity, frequency, timing, and type, as well as the climatic conditions during and after it.

Methods of assessing impacts of, and recovery from, disturbance have been highly variable. Generally, measurements have been limited to visual estimates of crust cover. However, Belnap (1993) showed visual assessment can only accurately assess moss and lichen cover, and cannot be used to measure the degree of recovery of cyanobacterial biomass, soil stability, and/or physiological functioning of crustal organisms. In addition, some studies have only considered total crust cover but have not delimited the relative cover of cyanobacteria, mosses, and lichens. The relationship between total crust cover and disturbance impacts can be weak, as cyanobacterial cover generally increases, while moss and lichen cover decreases, after disturbance. This often makes total crust cover a poor measure of the dynamics of soil crust recovery. Differentiating between crustal components is also important because alteration of species composition can heavily influence the crust's ecological functioning (Eldridge 1998). Comparing recovery rates from different studies can be problematic, as factors known to control recovery rates (such as site stability and precipitation following disturbance) are often not reported. More importantly, disturbance severity is seldom quantified. Studies generally report disturbance levels as "light," "moderate," or "heavy" without any definition of these categories; thus, what is "moderate" in one study may be considered "heavy" in another. As studies cover a large range of climatic zones, soil types, and levels of disturbance, and as there has been no standard for measuring crust recovery, it is not surprising that in the literature recovery rates have ranged widely (2 to more than 3,800 years), and either appear to show no pattern or often appear contradictory (Anderson et al.1982a; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1990; Belnap 1995, 1996; Belnap and Warren 1998).

4.2.1 Disturbance Severity, Size, Frequency, and Timing

The impact of a disturbance is affected by its severity, size, frequency, and timing. While most compressional disturbances (such as from vehicles and trampling by people or animals) result in similar types of impacts, severity can vary widely depending on disturbance source. For instance, vehicles and trampling exert compressional and shear forces; however, these forces are much greater for vehicles than trampling. In addition, vehicles often turn soils over and bury crustal

organisms, while trampling tends to only compress the surface. Vehicle tracks often channel water off-site and thus slow or prevent recovery (Webb and Wilshire 1983). Intensifying physical impacts (such as high-intensity, short-duration grazing) is deleterious to biological soil crust cover and its species richness (Johansen 1993). Disturbance that removes or kills crustal organisms results in greater impact and slower recovery than disturbance that leaves crushed crust material in place. As lichens and mosses are less tolerant of disturbance than cyanobacteria, frequent disturbance can maintain the biological soil crust at a low-successional stage (e.g., dominated by cyanobacteria; Fig. 4.3, Harper and Marble 1988).

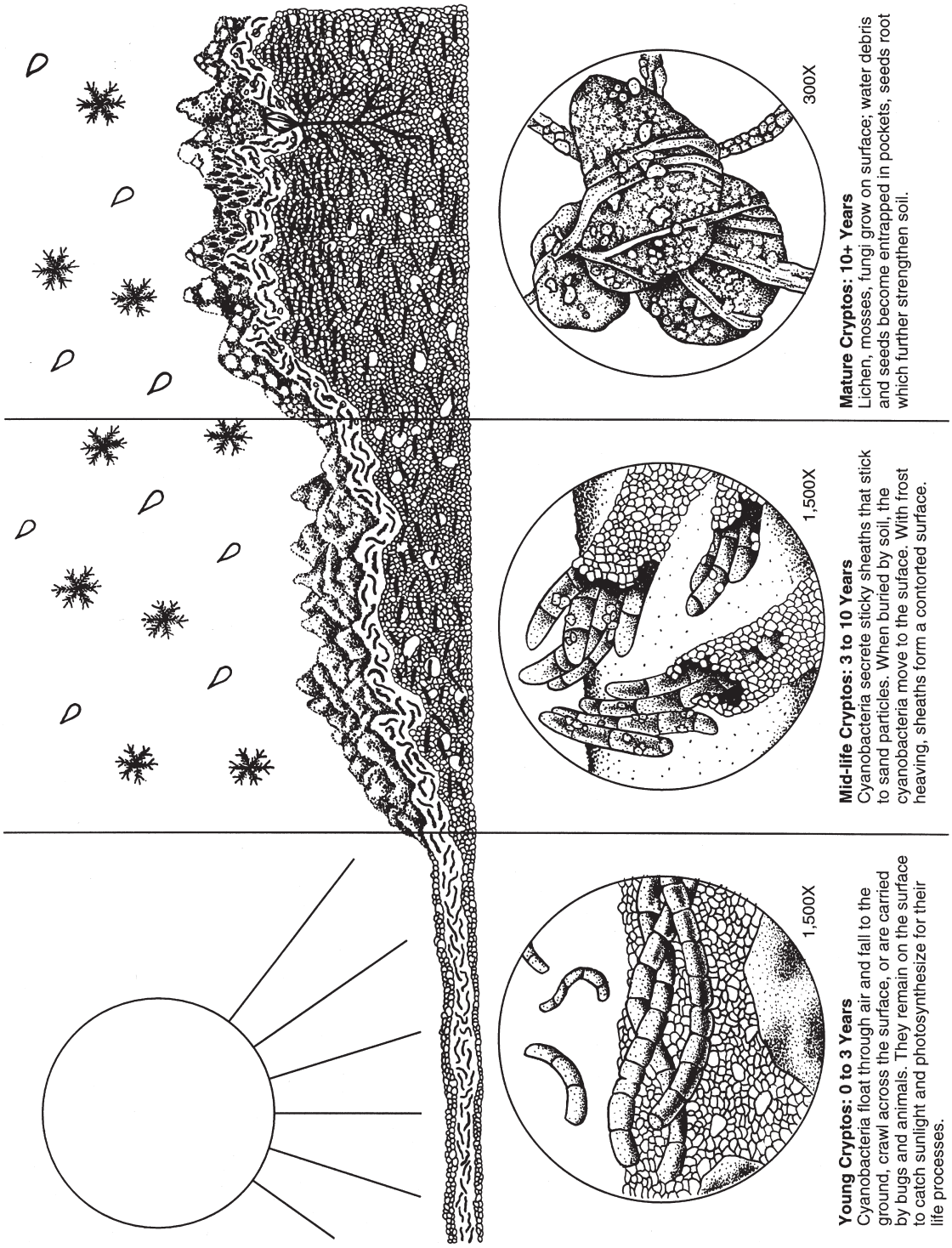
Disturbance timing can affect the degree to which the cover and species richness of a biological crust is reduced. Soils have different intrinsic soil strengths that vary with moisture content (see Fig. 2.5). Soils with little tendency to form aggregates, such as sands, are more susceptible to compressional stresses when dry. Fine-textured soils or those with inorganic crusts are more vulnerable to compressional disturbance when wet (Webb and Wilshire 1983). Crust components are brittle when dry, and the connections they make between soil particles are easily crushed. Thus, compressional disturbances can severely affect the crust's ability to stabilize soils, especially in dry sandy and silty soils. On silty soils of the Great Basin, early wet season (winter) use by livestock has been shown to have less impact on crust cover and species composition than late winter or spring use. As crustal species are only metabolically active when wet and are brittle when dry, disturbance in dry seasons is generally more destructive, and organisms are less able to recover, than when disturbed in wet seasons (Harper and Marble 1988; Marble and Harper 1989). Crusts on clay soils can be an exception, as they are often more vulnerable when wet (Fig. 2.5).

4.2.2 Disturbance Effects on Species Composition

Disturbance generally results in loss of species diversity, biomass, and surface cover of biological crust components. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the resulting crust community is generally greatly simplified from multiple species of cyanobacteria, lichens, and mosses to a community often dominated by one or a few species of cyanobacteria.

4.2.2.1 Air Pollution: A few studies have addressed the impact of air pollutants on soil lichens in desert environments. No differences have been found in species composition near pollution sources when compared to control sites. It is reasoned that lichens with thalli closely appressed to the soil surface, a condition common

Figure 4.3 *Successional sequence for biological soil crusts. This example is for* Microcoleus vaginatus*-dominated crusts on the Colorado Plateau. Sequences in other ecoregions are similar but may involve different taxa. (Illustration by Gloria Brown)*



to most desert soil crust lichens, are less susceptible to damage by air pollutants than lichens whose tissues are more exposed to air. In addition, most desert soils are very alkaline, and thus thought to buffer acidity from pollutants (Sheridan 1979; Nash and Sommerfeld 1981).

4.2.2.2 Oil Spills, Insecticides, and Herbicides: No known studies have directly addressed the effects of oil, oil dispersants, or insecticides on species composition of intact soil crusts. However, there has been a great deal of work on individual cyanobacteria, green algae, and mosses isolated from soil crusts. These experiments have shown that crustal species are differentially affected, depending on the compound and the species tested. Thus, exposure to these agents could potentially alter species composition of crusts (Metting 1981).

One study addressed herbicide effects on intact biological soil crusts. Direct application of two glyphosate herbicides (Roundup® and Accord®) on moss-dominated biological soil crusts had no short-term negative impact on bryophyte cover (Youtie et al. 1999). In fact, bryophyte cover decreased significantly in control plots due to litter buildup from exotic annual grasses that had invaded the site (see 4.2.2.3 below), while cover stayed the same or increased slightly in treated plots. However, repeated treatments are often required to effectively control weedy species. There is little information on the effects of repeated application or long-term effects of glyphosate and other herbicides. Therefore, caution should be used when applying these chemicals to remnant native areas supporting biological soil crusts (Youtie et al. 1989).

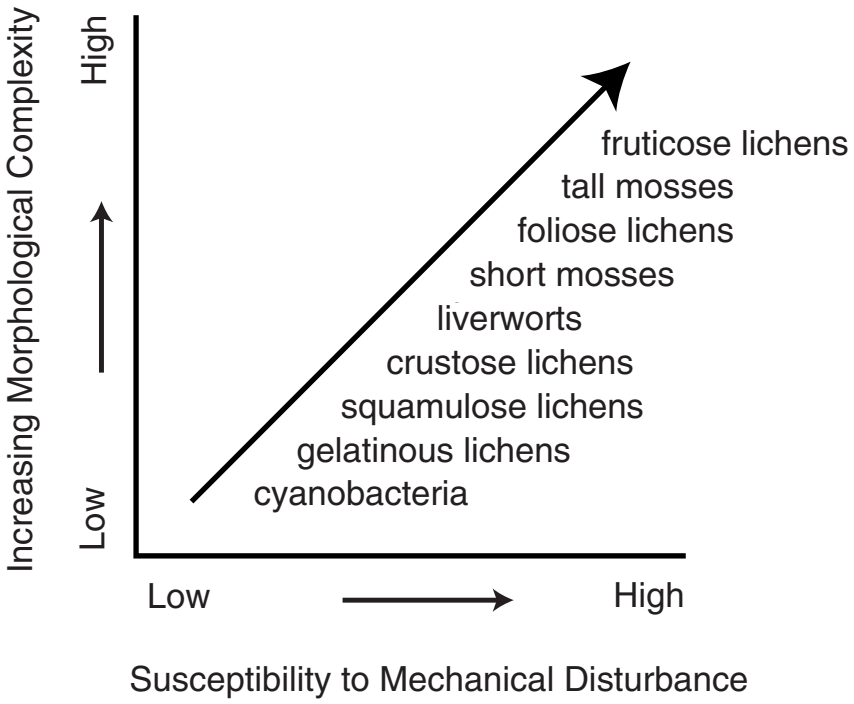
4.2.2.3 Annual Plant Invasion: Invasion of exotic annual plants into perennial plant communities can pose a long-term threat to biological soil crusts, as the crust-dominated interspace between perennial plants is often heavily invaded. Surveys in invaded communities show rich perennial moss/lichen communities are quickly replaced with only a few species of annual mosses and cyanobacteria (Kaltenecker 1997; Belnap and Phillips in press). The mechanism by which this shift occurs is not known, but probably results from a decrease in available soil surfaces (via increased cover of live plants and litter; Fig. 4.2, 4.4), higher cover of plant material shading the soil surface, and/or increased fire frequency (Kaltenecker 1997; Kaltenecker et al. 1999a; Youtie et al. 1999).

4.2.2.4 Fire: Biological crusts are generally killed by hot ground fires, resulting in loss of biomass and visible cover (Johansen et al. 1993). Frequent fires prevent recovery of lichens and

Figure 4.4 *Changes in the vascular plant community structure due to cheatgrass invasion.*

mosses, leaving only a few species of cyanobacteria (Whisenant 1990; Eldridge and Bradstock 1994). Damage to, and recovery of, biological crusts depend on the pre-fire composition and structure of the vascular plant community and on fuel distribution, fire intensity, and fire frequency. Historic fire regimes in semi-arid and arid landscapes generally left small-scale patches of unburned areas between perennial plants, and/or larger-scale patches of unburned shrubs across the landscape (Fig. 4.2). This resulted in a mosaic of successional stages of plants and biological crusts, with propagules readily available to replenish burned sites. Historic fires were also relatively infrequent, leaving time for later-successional crustal organisms to recolonize (Whisenant 1990; Peters and Bunting 1994). Many semi-arid areas are now invaded by annual weeds, and unnaturally frequent, large fires that preclude crustal species' recolonization or succession are common.

Figure 4.5 *Susceptibility of biological crusts to mechanical disturbance based on dominant morphological group.*



4.2.2.5 Mechanical Disturbance: Mechanical disturbance results from activities such as vehicle traffic (military and recreational), trampling by livestock and people, and land-clearing (such as mining). Such uses are increasing exponentially in arid and semi-arid areas of the world. Effects of mechanical disturbance are especially noticeable at sites with highly erodible soils and large topographic relief (Harper and Marble 1988).

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Over 30 studies on four continents document that livestock grazing, vehicle use (both recreational and military), and human trampling dramatically reduce lichen/moss cover and species richness of crusts. Resistance to disturbance generally decreases as the organisms become more morphologically complex (Fig. 4.5; Harper and Marble 1988; West 1990; Johansen 1993; Eldridge and Greene 1994; Ladyman and Muldavin 1996). Cyanobacteria, the most resistant to disturbance, are highly mobile and can recolonize disturbed surfaces rapidly. Lichens use a combination of adaptive thallus structures and pigments (Blum 1973; Galun et al.1982), water storage capacities, tolerance of frequent and/or prolonged inundation, and/or an ability to fix atmospheric nitrogen to increase resistance to disturbance. For example, Rogers and Lange (1971) showed that lichens *Collema coccophorum* and *Heppia lutosa* (*H. despreauxii*) were the least affected by sheep trampling around a watering point compared to other taxa. These lichens are able to fix atmospheric nitrogen and to store greater amounts of water than stratified green lichens (Galun et al. 1982). In a comparison of species inside and outside a grazing exclosure, vagrant foliose lichens *Chondropsis semiviridis* and *Xanthoparmelia convoluta*, crustose lichens *Diploschistes scruposus* and *Caloplaca* spp., and the squamulose lichens *Peltula imbricata* were associated with ungrazed sites (Table 4.1; Crisp 1975; Eldridge and Koen 1998). The gelatinous lichen *Collema coccophorum* was the most tolerant of livestock trampling (Rogers and Lange 1971; Eldridge 1996).

Most soil surface disturbance compacts soils. Compaction influences soil water and nutrient-holding capacity, which can lead to changes in soil crust community species composition. These subtle compositional changes often occur before cover changes are apparent (Eldridge 1996).

4.2.2.6 Burial: Crust disruption often destabilizes underlying soils, leaving adjacent crusts vulnerable to burial by wind- and water-moved sediments. When soils are moist, the large filamentous cyanobacteria can respond to burial by moving up to 5 mm every 24 hours. When dry, these organisms are not able to move. Burial kills non-mobile photosynthetic components of the crust, including mosses, lichens, green algae, and smaller cyano-bacteria (Campbell 1979). Therefore, burial generally results in a greatly simplified crustal community.

4.2.3 Disturbance Effects on Nutrient Inputs and Retention

4.2.3.1 Carbon Fixation: Cyanobacterial crusts near coal-fired power plants have greater chlorophyll *a* per unit soil surface area

Table 4.1 *Percent frequency of biological soil crust organisms on loamy and sandy soils inside and outside the exclosure at Koonamore Vegetation Reserve, South Australia, in May 1972. Adapted from Crisp (1975).*

		LOAMY SOIL		SANDY SOIL		
Species	Morphological Group	Exclosed	Grazed	Exclosed	Grazed	*p*
Lichens						
Acarospora smaragdula	crustose	2.4	0.5	7.6	2.2	n.s.
Aspicilia calcarea	crustose	39.4	20.6	26	26.2	*
Aspicilia calcarea	fruticose	13.6	1.1	18.2	2.4	*
Chondropsis semiviridis	foliose	0.08	0	0.1	0	n.s.
Collema coccophorum	gelatinous	81.4	63.6	21	0	*
Diploschistes scruposus	crustose	0.6	0	2.4	35.6	n.s.
Fulgensia subbracteata	crustose	20	5	25.2	14.2	*
Psora decipiens	squamulose	38.7	15.1	33.8	24.6	*
Psora crystallifera	squamulose	11.4	0.7	13.8	2	*
Toninia sedifolia	squamulose	13.1	3.8	13.8	7.6	*
Xanthoparmelia convulata	foliose	0.04	0	0.1	0	n.s.
Liverworts						
Riccia lamellosa	liverwort	4.2	0.4	8.2	1.2	*

** Indicates significant effect of exclosure at $p<0.10$; n.s. = effect of excosure was not significant.*

than crusts away from the plant, implying higher levels of carbon fixation. This is partially a result of fertilization by nitrogen and sulfur compounds from effluents (Sheridan 1979; Belnap 1991). Photosynthesis-inhibiting herbicides show significant impact on *Nostoc* growth and nitrogen fixation (Gadkari 1988). In general, herbicides inhibit growth and reproduction in culture (Metting 1981). However, effects appear to be more pronounced in the laboratory than the field, and may be transitory (Prasad et al. 1984).

Alteration in crust species composition will affect total carbon fixation, as lichens and mosses fix more carbon per unit soil surface area than cyanobacteria (Phillips and Belnap 1998). Because much of the carbon fixed by crustal organisms is released into the surrounding soils (Lewin 1956), crust cover reduction is expected to reduce soil carbon available for microbial populations that are often carbon limited. This, in turn, may affect decomposition rates of plant litter, and thus, levels of nutrients available to vascular plants (Paul and Clark 1996).

Table 4.2 *Reduction of nitrogenase activity for new and older disturbances on silty soils of the Dugway Proving Ground, Utah. All disturbance types resulted in material left on site except "Scalp," which removed the top 1 cm of crust.*

Age of Disturbance	Type of Disturbance	Percent Reduction in Nitrogenase Activity
New	Vehicle	68
New	Bike	79
New	Foot	62
6 months	Vehicle	100
9 months	Tank	83
9 months	Scalp	95
9 months	Rake	81

4.2.3.2 Nitrogen Inputs: Power plant effluents have been shown to decrease nitrogen fixation in *Collema* and *Microcoleus/Nostoc/Scytonema*-dominated crusts (Sheridan 1979; Belnap 1991). Atmospheric nitrogen deposition may offset reduced nitrogen inputs from crusts; alternatively, anthropogenic nitrogen deposition may aggravate nitrogen loss through increased ammonia volatilization and denitrification. In addition, biological soil crusts release ammonia in the soils, while anthropogenic nitrogen deposition contains large amounts of nitrate (Garcia-Pichel, unpublished data). Microbial and vascular plant species differentially use ammonia and nitrate; thus, deposition of additional nitrates may alter the dynamics of both soil and plant communities (Binkley et al. 1997).

Free-living or lichenized *Nostoc* show stimulation of nitrogen fixation at low concentrations of, or short exposure to, arsenic, nickel, lead, palladium, and zinc. However, longer-term exposure to cadmium, lead, and zinc inhibits fixation (Henriksson and DaSilva 1978). Exposure to crude oil and oil dispersants decreases nitrogen fixation in *Nostoc* (Marowitch et al. 1988). Nitrogen fixation is significantly inhibited in *Nostoc* by many insecticides, herbicides, and phenolic compounds tested (Bhunia et al. 1991; Megharaj et al. 1988).

Mechanical disturbance can result in large decreases in soil nitrogen through a combination of reduced input and elevated losses (Peterjohn and Schlesinger 1990; Evans and Belnap 1999). In all soils tested, disturbance by vehicles, human foot traffic, mountain bikes, and raking immediately reduces nitrogen input from crusts (25 to 40% on silty soils; 76 to 89% on sandy soils). Over time, nitrogenase activity can drop by 80 to 100% relative to controls, due to subsequent death of buried material (Table 4.2; Belnap et al. 1994; Belnap 1995,1996).

Species composition changes also affect nitrogen inputs, as cyanolichens (such as *Collema*) fix an order of magnitude more nitrogen than the equivalent soil surface area of cyanobacteria. Thus, the shift from a lichen crust to a cyanobacterial crust can result in less nitrogen entering the ecosystem, as has been shown in multiple studies. Jeffries et al. (1992) showed that heavy grazing reduced nitrogen fixation in sandy soils by 95%. In silty loam soil, Terry and Burns (1987) showed a 64% reduction of nitrogen fixation in burned areas, 85 to 94% reduction in grazed areas, and 99% reduction in a tilled area. *Collema* cover was reduced 50 to 80% in grazed areas relative to adjacent ungrazed areas (Brotherson et al. 1983; Johansen and St. Clair 1986). Expected nitrogen inputs would be reduced accordingly. Evans and Belnap (1999) showed nitrogen fixation in an area released from grazing 25 years was still 2.5 times less than an adjacent, never-grazed area due to reduction in *Collema* cover.

Decreased nitrogen inputs from crusts can have long-term impacts on soil nitrogen levels. Jeffries (1989) found 50% less nitrogen in grazed soils compared to adjacent ungrazed soils. Evans and Belnap (1999) found a 42% decrease in soil nitrogen and 34% decrease in plant tissue nitrogen when comparing a previously grazed (released 30 years previous to the study) site to an adjacent ungrazed area. In the same area, stable nitrogen isotopes showed that both soil and plants in the grazed area contained less newly fixed nitrogen than the ungrazed area, and nitrogen mineralization potential decreased almost 80% (Rimer and Evans 1997). This has large implications for ecosystems that are dependent on biological crusts for nitrogen inputs, such as those on the Colorado Plateau (Evans and Ehleringer 1993).

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4.2.4 Disturbance and Vascular Plants

Crusts can affect vascular plant germination, survival, and nutrition. Lichen-moss crusts in areas with frost heaving (as in cool deserts) increase perennial vascular plant seed entrapment, germination, establishment, survival, biomass, and nutritional status (Belnap and Harper 1995). In these deserts, disturbance that flattens frost-heaved surfaces and/or eliminates mosses and lichens can have a negative effect on some or all of these characteristics. However, germination and survival of some exotic annual grasses can be enhanced with biological crust disturbance.

In hot deserts, seed entrapment, biomass, and fecundity of annual plants is generally increased when smooth cyanobacterial crusts are disturbed (Prasse 1999), although there are some exceptions (Gutterman 1994). Disturbance of smooth cyanobacterial crusts enhances germination of some annual species, while decreasing germination of others (Zaady et al. 1997). Rugose crusts in hot deserts have received little study, and no work has addressed the effects of disturbance on seed entrapment. Effects on germination in rugose crusts appear to be species dependent. In contrast to smooth crusts, disturbance to hot desert rugose crusts lessens survival and biomass of perennial plants (McIlvanie 1942; Crisp 1975).

Biological soil crusts have been shown to influence availability of many plant-essential nutrients. Crust loss can result in less plant-available magnesium, potassium, iron, calcium, phosphorus, manganese, and sulfur (Harper and Belnap in press). The spatial distribution of nutrients is also affected by disturbance, as disturbance will alter the relative distribution of biological crust components (i.e., lichens, mosses, cyanobacteria) across the landscape (Klopatek 1992).

4.2.5 Disturbance and Surface Albedo

Trampling of dark-crusted surfaces exposes underlying, lighter soils, thus increasing albedo (reflectance) by up to 50% at most wavelengths measured (Fig. 3.1). This increased albedo represents an energy loss from the soil surface of approximately 40 watts/m^2 and can reduce soil temperatures by up to 14°C (Belnap 1995). Such changes in reflectance are especially apparent using satellite imagery, as can be seen in the Negev Desert, along the U.S.-Mexico border, and in Australia. Much of this difference is attributed to loss of biological soil crusts (Graetz and Tongway 1986). Large-scale changes in surface albedo may contribute to changes in regional climate patterns (Sagan et al. 1979).

4.2.6 Disturbance and Soil Hydrology

The effect of biological soil crust disturbance on soil hydrology is very site specific. Water infiltration, runoff, and resultant soil moisture are influenced by soil surface roughness, soil texture, microtopography, surface albedo and temperature, vegetative cover (both vascular and non-vascular), and climatic conditions. All these factors can be altered when biological crusts are disturbed. In general, disturbance flattens pinnacled and rolling crusts, thus decreasing water infiltration and increasing runoff (Fig. 3.3). In hot deserts, disturbance to smooth and rugose lichen- or cyanobacterial-crusted surfaces can increase overall infiltration rates (Greene et al. 1990; Eldridge et al. 2000). However, this increase in infiltration may negatively affect nearby vascular plants that depend on interspace runoff for survival (see Section 3.6). Soil structure alteration as a result of soil compaction can also reduce infiltration rates. Available soil moisture results from a complex interaction of many soil and plant characteristics, including infiltration, soil moisture-holding capacity, albedo, plant root density, etc. Only two studies have addressed the combined effects of crusts on available soil moisture, with disparate results. One study found increased soil moisture under intact crusts, while the other found soil moisture increased under disturbed crusts (reviewed in Harper and Marble 1988).

4.2.7 Disturbance Relative to Water and Wind Erosion

Compressional disturbance damages soil-stabilizing cyanobacterial sheath material both at and below the soil surface. The damage below the surface is irreparable, as living cyanobacteria are not present to regenerate sheath material. As greater than 75% of photosynthetic biomass and productivity is from organisms living in the top 3 mm of soils, disturbance that results in even small soil losses can dramatically reduce site fertility and further reduce soil surface stability (Garcia-Pichel and Belnap 1996).

4.2.7.1 Water Erosion: Globally, all studies show crust cover loss significantly increases water erosion of both coarse- and fine-textured soils. Continuous tracks have a greater impact than non-connected disturbances (such as hoof prints) because of increased water flow volume and velocity along the tracks (Webb and Wilshire 1983). Crushing of cyanobacterial connections between particles results in smaller, isolated soil aggregates that are then more easily moved by water. In addition, surfaces flattened by compressional disturbances are less able to reduce water velocity, thereby allowing

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movement of larger soil particles and reducing opportunities for sediment to settle out.

4.2.7.2 Wind Erosion: All studies of wind erosion indicate that disturbed soils are more susceptible to wind erosion than undisturbed soils when dry (Fig. 4.6). When crusts are crushed or absent, soil particle movement is initiated at lower wind speeds, as resistance to wind erosion increases with better soil crust development. Well-developed crusts (with lichens and mosses) on both silt and sandy soils have 2 to 130 times greater resistance to soil erosion than less well-developed crusts or bare soil (Fig. 4.7; Williams et al. 1995b; McKenna-Neuman 1996; Belnap and Gillette 1997, 1998; Leys and Eldridge 1998). Vehicle tires result in greater damage than hooves on a given soil type (Belnap and Gillette 1998).

Decreased resistance of soils to wind erosion is directly associated with increased sediment movement. All experimental disturbances applied to crusts show increased sediment production—up to 35 times that of adjacent undisturbed crusts (Leys and Eldridge 1998; Williams et al. 1995b). Nearby soil crusts are often buried by blowing sediment, resulting in death of photosynthetic organisms.

4.3 Factors Influencing Natural Recovery Rates

Recovery rates are dependent on many factors, including disturbance type, severity, and extent; vascular plant community structure; adjoining substrate condition; inoculation material availability; and climate during and after disturbance. Comparing recovery rates reported in the literature is highly problematic, as studies range over a wide array of climatic zones, soil types, and levels of disturbance, and these factors are seldom quantified. Thus, most studies can only be used to define the general range of recovery rates. Some studies do report climate, soil, and/or disturbance data such that comparisons are possible (Anderson et al. 1982a; Jeffries and Klopatek 1987; Callison et al. 1985; Cole 1990; Belnap 1995, 1996; Eldridge 1996; Belnap and Warren 1998).

Examination of these studies indicates that general recovery times can be predicted for soil crusts in different environments. Most recovery time calculations for crust cover assume a linear recovery rate. On the Colorado Plateau, scalped plots were reassessed 2 to 5 and 10 to 14 years after disturbance. After 2 to 5 years, cyanobacterial cover was predicted to recover in 45 to 110 years, whereas it recovered within 14 to 34 years. Thus, linear assumptions greatly overestimated recovery time. Lack of moss recovery prevented useful estimates at two of the three sites at the earlier sampling time. At one site, early estimates were 400 years to recovery, while later estimates were 42

Figure 4.6 *Resistance of sandy loam soils to wind erosion following disturbance to a well-developed biological soil crust in four time classes. Threshold friction velocity is the force required to detach soil particles from the surface. Time classes indicate the length of time since disturbance to the control. Following determination of threshold friction velocities for controls, treatments were applied as follows: Foot = one pass wearing lug-soled boots; Tire, 1 Pass = one pass of a four-wheel drive vehicle with knobbed tires; Tire, 2 Pass = two passes of a four-wheel drive vehicle with knobbed tires. Within each time sequence, controls were significantly more resistant to wind erosion than treated surfaces. Adapted from Belnap and Gillette (1997).*

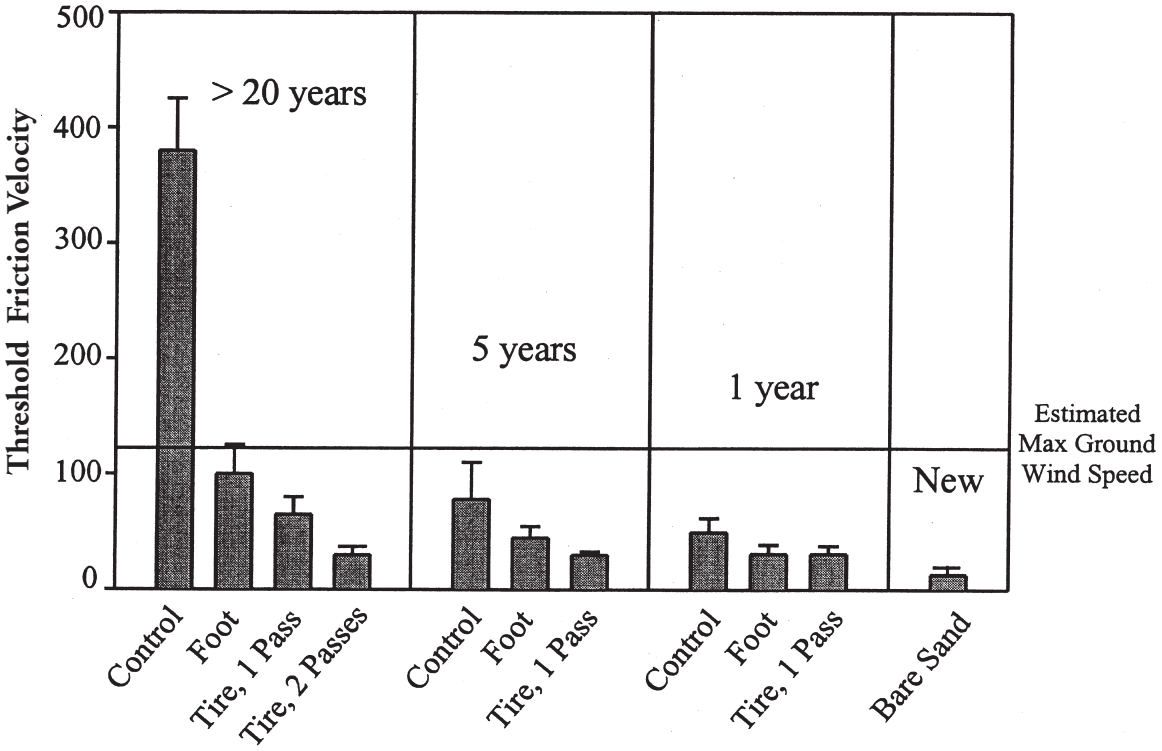
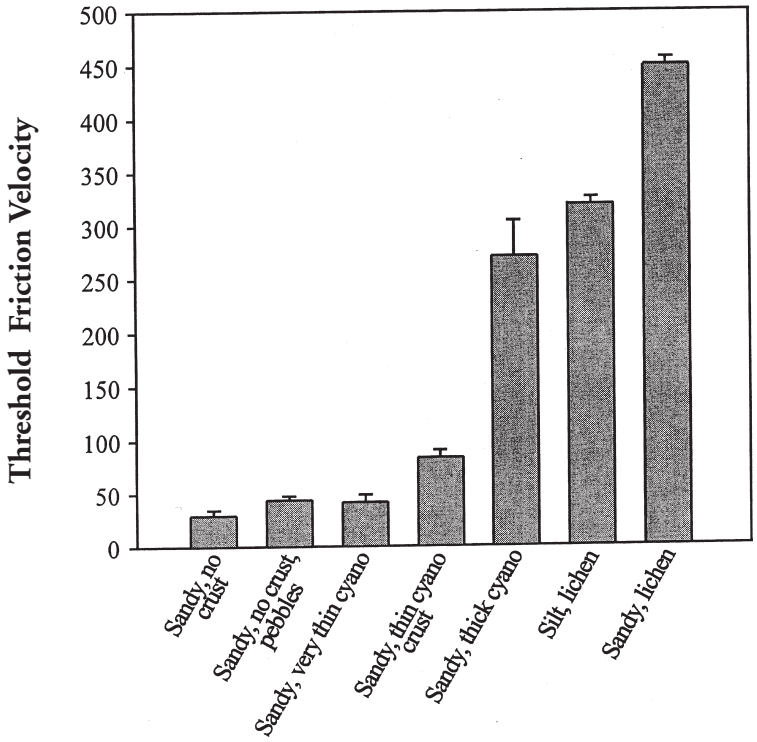


Figure 4.7 *Resistance of soil surfaces to wind erosion. Resistance increases with surface protection and development of the biological soil crust. The greatest amount of resistance is demonstrated by soils with well-developed biological crusts characterized by a diverse lichen flora. Adapted from Belnap and Gillette (1998).*



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years. As with cyanobacteria, linear extrapolations overestimated recovery time. In contrast, *Collema* recovery after 3 years was estimated at 85 years; after 14 years, the estimate for full recovery was 50 years, a fairly close match. *Collema* recovery at a second site was highly variable: after 2 years, recovery time was estimated at 487 years; after 11 years, estimates were site dependent, ranging from 40 to 766 years. Original estimates were therefore both under and over estimated, depending on individual site characteristics. Sites with more shade and less sandy soils were quicker to recover than original estimates predicted, while more exposed sites with sandier soils were less able to recover than originally estimated (Belnap, unpublished data).

4.3.1 Sequence of Species Appearance

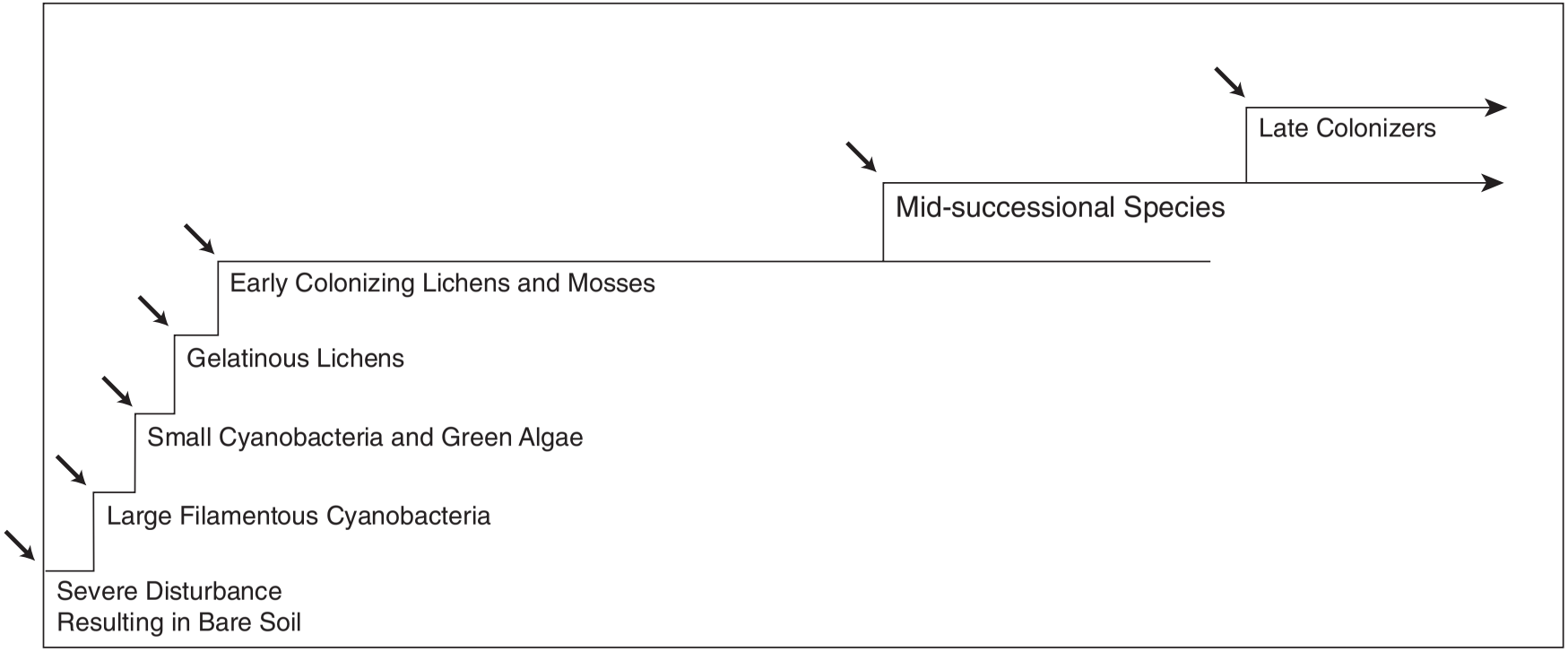
Cyanobacteria and green algae are generally the first photosynthetic species to appear on disturbed soils, probably because of their mobility across soil surfaces and their ability to colonize from the air (Schlichting 1969). Large filamentous cyanobacteria such as *Microcoleus* generally appear first (Fig. 4.3, 4.8), especially on unstable sandy soils (Ashley and Rushforth 1984; Belnap 1995). This species is then followed by smaller cyanobacteria and green algae. Occasionally, desert soils are slightly acidic, and here green algae can be the first to appear (Johansen 1993).

Lichens and mosses require stable soil surfaces for growth. This can be provided by a physical crust or by large, filamentous cyanobacteria. Once soils are stabilized, gelatinous nitrogen-fixing lichens (e.g., *Collema* spp.) are generally the first lichens to appear in disturbed areas, followed by other early-successional lichens and mosses (Table 4.3; Johansen et al. 1984; Belnap 1993). Early-colonizing lichens often disperse phytobiont-containing tissue (e.g., isidia, soredia, or algal-covered spores), as opposed to bare spores, thus precluding the need to find phytobionts on-site.

4.3.2 Soil Texture

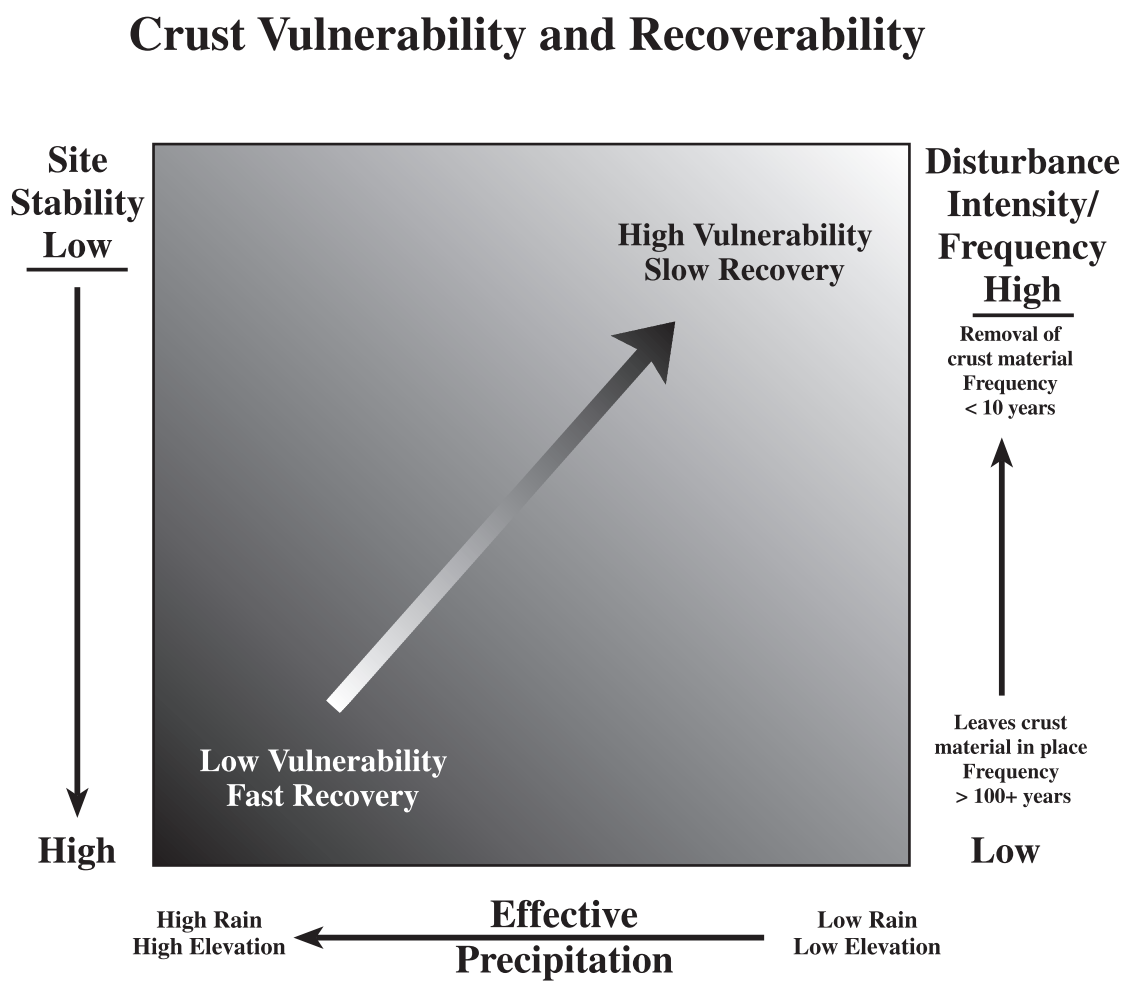
Soil texture influences crust recovery rates. Recovery of all crust components is faster in fine-textured soils than in coarse-textured soils, as fine-textured soils are often stabilized by chemical and rain crusts and retain soil surface moisture longer (Fig. 4.9; as reviewed in Harper and Marble 1988; Johansen 1993; Ladyman and Muldavin 1996). Recovery of the site's wind resistance is also more rapid in fine-textured soils, probably due to crust formation after rainfall. While silty and sandy soils show a similar reduction in wind resistance to vehicle disturbance (83% and 74%, respectively), silty soils show a 50% recovery of wind resistance after a single large rain

Figure 4.8 *Generalized recovery sequence for biological soil crusts. Successional stages are illustrated as steps on the diagram. Disturbance input (indicated by arrows) will cause the crust to revert to an earlier successional state, with severe disturbance resulting in complete destruction of the crust. Recovery time is dependent on environmental conditions, including effective precipitation (see Chapter 2). Note that recovery times, for mid- and late- successional species in areas with lower effective precipitation are unknown, as recovery times are so long no estimates are possible.*



Geographic Region (elevation, average annual precipitation)	**Estimated Years to Recovery**			
	Gelatinous Lichens	Early Colonizers	Mid Successional	Late Successional
Lower Mojave (<1500 m, 100 mm)	1,200	3,800	unknown	unknown
High Mojave (1500 m, 200 mm)	200	800	unknown	unknown
Colorado Plateau (1500 m, 200 mm)	50	500	unknown	unknown
Northern Great Basin (1000 m, 350 mm)	20	25	60	125

Figure 4.9 *Biological soil crust vulnerability and recoverability based on site stability, effective precipitation, and disturbance regime. Vulnerability decreases and recovery rates increase with increased site stability and effective precipitation, and infrequent disturbance.*



Factors Determining Site Stability

	Low Stability		High Stability
Soil Texture	Coarse	→	Fine
Rock/Gravel Cover	Unstable	→	Stable
Soil Depth	Deep	→	Shallow
Plant Spacing	Sparse	→	Dense

Table 4.3 *Characteristics of early-colonizing lichens.*

Species	Phytobiont	Reproductive Units
Caloplaca tominii	green algae	soredia
Cetraria islandica	green algae	isidia-like cilia
Cladonia chlorophea group	green algae	soredia
Collema spp.	cyanobacteria	isidia
Cornicularia normoerica	cyanobacteria	finger-like lobes
Endocarpon pusillum	cyanobacteria	algal-covered spores
Leprocaulon microscopum	green algae	soredia
Leptogium corniculatum	cyanobacteria	isidia
Peltigera didactyla	cyanobacteria / green algae	isidia
Peltigera rufescens	cyanobacteria	spores, unspecialized thallus fragmentation
Placidium squamulosum	green algae / cyanobacteria	algal-covered spores

event, while very sandy soils can take up to 10 years for similar recovery (Belnap and Gillette 1997; Belnap and Herrick, unpublished data).

4.3.3 Climate Regimes

Crustal organisms are metabolically active only when wet; thus, recovery is faster in regions and microsites with greater effective precipitation (Fig. 4.8, 4.9; Johansen et al. 1993; Harper and Marble 1988). Crusts on north and east slopes, as well as at higher elevations, will recover more quickly than crusts on south and west slopes and at lower elevations. However, as discussed in Sections 2.2.1, 2.2.5, and 2.2.6, there are thresholds along ecological gradients where adequate precipitation results in development of a more diverse and dense vascular flora in lieu of the biological crust.

4.3.4 Disturbance Type, Frequency, Severity, and Size

No work has addressed recovery rates of lichens or cyanobacteria from air pollution. In general, crusts are highly susceptible to hot fires; thus, recovery will depend on the size and intensity of fires. As noted previously in “Disturbance Effects” (Section 4.2), most compressional disturbances have similar types of impacts. However, severity of mechanical disturbance can vary widely with disturbance type. Thus, on similar soils, vehicle tracks generally have longer recovery times than disturbances that do not churn the soil or make continuous tracks (Wilshire 1983; Belnap 1996).

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Repeated disturbance will generally keep crusts at an early-successional stage (e.g., cyanobacteria-dominated) by preventing lichen or moss colonization (Fig. 4.8; Belnap 1996).

Disturbance severity often controls recovery rates. In western North America, site recovery within a given soil and climate type is faster where disturbances are not severe enough to remove crustal material than it is at sites where crusts were removed. When crusts are completely removed, recovery can be excessively slow, especially in areas with low effective precipitation and/or sandy soils (Fig. 4.9; Eldridge 1996). In contrast, crusts crushed in place with vehicles, foot traffic, and horses recover much faster, especially on fine-textured soils.

Because recolonization of disturbed areas occurs mostly from adjacent, less-disturbed areas, the size and shape of disturbance can affect recovery rates. This is especially true for lichens. Desert soil lichens colonize only infrequently through spores; thus, recovery of lichen cover is mostly dependent on material washing or blowing in from adjoining areas (Eldridge and Ferris 1999). The rate of lichen recovery is much slower in areas with higher internal surface areas relative to perimeter area (Belnap, unpublished data).

4.3.5 Condition of Adjoining Substrate

In general, crust recovery is slower if soils adjacent to disturbed areas are destabilized. Detached sediment can both bury adjacent crusts, killing many crustal organisms, and/or provide material for sandblasting nearby surfaces, thus increasing wind erosion (Belnap 1995; McKenna-Neumann et al. 1996; Leys and Eldridge 1998).

4.3.6 Vascular Plant Community Structure

Crusts recover more quickly under shrub canopies than in adjacent plant interspaces. This is probably due to greater soil moisture and fertility under shrub canopies. In the Mojave Desert lichen recovery (after complete removal 50 years previously) was 36% under shrub canopies, compared with 4% in the shrub interspaces (Belnap and Warren 1998). A similar pattern was seen in plots established on the Colorado Plateau, where lichen recovery was 2 to 3 times faster under shrubs than adjacent interspaces (Belnap, unpublished data).

The growth of biological soil crusts and vascular plants can be an interactive process (Danin et al. 1989). Eldridge and Greene (1994) present a conceptual model in which crust development at sites is strongly linked to restoration of vital soil processes. As primary colonizers of recovering sites, biological soil crusts enhance microsite fertility and provide safe sites for seeds. In turn, established vascular

plants help stabilize soils, provide shade, and reduce wind speeds at the soil surface, providing conditions conducive to further development and diversification of the biological soil crusts (Wood et al.1982; Danin et al. 1989).

4.3.7 Nitrogen and Carbon Fixation

Overall, nitrogen and carbon fixation rates in biological soil crusts are dependent on its species composition, biomass, and physical structure. Thus, recovery is dependent on recovery rates of specific crustal components. Recovery of nitrogen fixation is dependent on recovery rates of cyanobacteria and cyanolichens. Nitrogen fixation in crusts can require anaerobic microzones in the soils, which may be dependent on buildup of cyanobacterial biomass (Belnap 1996). Carbon fixation increases when lichens and mosses colonize (Phillips and Belnap 1998). As recovery is faster with higher available moisture, both nitrogen and carbon fixation rates are expected to recover faster in cool deserts than in hot deserts, other factors being equal.

Lichen cover may not fully recover after disturbance. On the Colorado Plateau, soils previously occupied by cyanolichens were often occupied by mosses after release from grazing (Belnap, unpublished data). As long as cyanolichen recovery does not occur, reduced nitrogen inputs are expected, and soil and plant nitrogen levels may remain lower (Evans and Belnap 1999).

4.3.8 Surface Albedo

Restoration of normal surface albedos and temperatures will depend on the restoration of pre-disturbance cover of cyanobacteria, lichens, and mosses. While cyanobacteria do form a darkish matrix in which other components are embedded, mosses and lichens are much darker and can contribute 40% or more of the cover in an undisturbed crust (Belnap 1993). Consequently, surface albedo recovery will be controlled by factors that control lichen and moss recovery.

CHAPTER 5

NOTES

MANAGEMENT TECHNIQUES TO MAINTAIN OR IMPROVE EXISTING BIOLOGICAL SOIL CRUSTS

While total protection from disturbance is often the easiest way to maintain or improve biological soil crusts, this is not often possible or desirable. There are many factors to consider in the management of soil communities, including disturbance type, intensity, timing, frequency, duration, or extent. Research is needed to determine realistic biological soil crust objectives by soil type in most potential vegetation types, but initial estimates can be determined by using "healthy" reference areas as described by the National Research Council (1994). Protection of relic sites as rangeland reference areas is important, as these sites provide baseline comparisons for ecological potential and future scientific research.

5.1 Fire

Proactive management is needed to prevent unnaturally large and/or frequent fires in areas where fuel build-up or annual grass invasions have occurred. Such management actions may include altering grazing regimes to prevent annual plant invasions, prescribing fire to prevent fuel build-up, and/or restricting off-road vehicle use.

5.1.1 Prescribed Fire

Used cautiously, prescribed fire can be a useful tool in some situations for renewing community vigor. However, the site's ecology and evolutionary history need to be understood, as burning can result in conversion of some sites to exotic vegetation. Thus, even though a community evolved with fire, fire may no longer be desirable because of exotic plant invasions. Prescribed fire is not recommended for such sites unless post-fire restoration treatments are planned. Prescribed fire may be useful on more productive sites with low potential for exotic plant invasion to reduce high woody vegetation densities resulting from overgrazing. Other impacts (such as recreational or domestic livestock use) should be limited following treatment to allow full site recovery.

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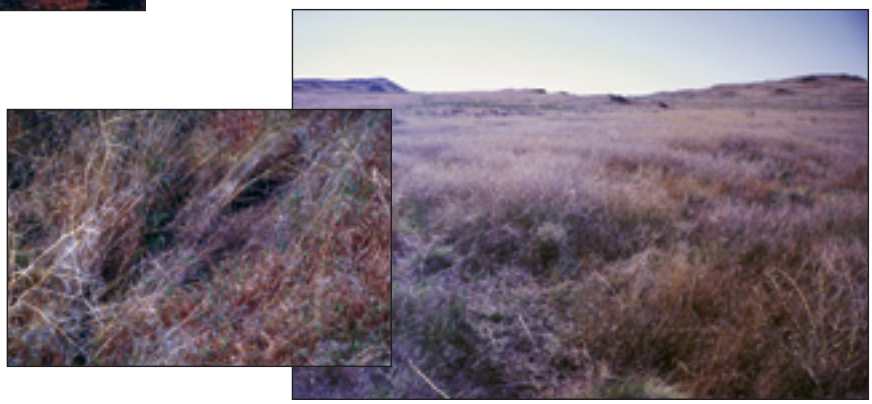
5.1.2 Post-fire Management

Once a site has burned, evaluation is needed to determine whether recovery will occur naturally or if revegetation is needed. Many burned sites, particularly those in the Great Basin and Intermountain regions, require revegetation to stop exotic plant invasion, and most techniques require some soil surface disturbance (Fig. 5.1). This may not appear consistent with recovery of biological crusts. However, failure to treat sites can result in irreversible dominance by annual species (such as cheatgrass), which prevents the return of well-developed biological soil crusts (Fig. 4.2, 4.5, 5.2; Kaltenecker 1997, Kaltenecker et al. 1999a). Once revegetated, protection from grazing and recreational use is often necessary for recovery of the biological soil crust and the vascular plant community. Recovery in these areas can be further facilitated by use of minimal-till or no-till drills or other seeding methods that minimize soil surface and compressional impacts. Emphasis should be placed on restoring the native plant community using local ecotypes, if available.

In the western U.S., revegetation of salt-desert shrub and lower-precipitation Wyoming big sagebrush communities presents some unique problems. West (1994) presents evidence that cheatgrass will remain and potentially increase in these types, as revegetation is difficult because of arid conditions and unpredictability of wet years. He suggests that without livestock consumption of cheatgrass, susceptibility to fire could increase. However, the effective use of livestock in long-term control of cheatgrass has not been demonstrated. In addition, such grazing would occur well into the growing season and thus to the potential detriment of biological crusts and native vascular plants.

Figure 5.1 *Soil surface disturbance associated with post-fire revegetation projects. This site was drill-seeded with a rangeland drill.*

Figure 5.2 *Biological crust development in a successful seeding in the northern Great Basin (above) and lack of development in an exotic annual grass community (below). Note the difference in plant density and the accumulation of litter on the soil surface that limits biological crust development in the exotic community.*



5.2 Livestock Grazing

Managing for healthy biological soil crusts requires that grazing occur when crusts are less vulnerable to shear and compressional forces. Timing for this is highly dependent on soil type and climatic regimes (see Chapter 4). Crusts on all soil types are least vulnerable to disturbance when soils are frozen or snow covered. Biological crusts on sandy soils are less susceptible to disturbance when moist or wet; on clay soils, when crusts are dry (Fig. 2.5; Marble and Harper 1989; Memmott et al. 1998). In general, light to moderate stocking in early- to mid-wet season is recommended. On low- to mid-elevation sites, winter use is advantageous to most vascular plants, including riparian communities, and substantially reduces supplemental feed costs associated with livestock production. Winter grazing also most closely replicates the grazing strategy of native herbivores, who use more productive, higher-elevation sites during summer and lower-elevation sites in winter (Fig. 5.3; Miller et al. 1994; Burkhardt 1996). It is important to remove livestock well

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before wet season's end to allow regrowth of crustal organisms before extended drought. Use when soil surfaces are very wet and muddy should also be avoided to prevent burying the crust (Kaltenecker and Wicklow-Howard 1994; Kaltenecker et al. 1999b). Implementation of rest-rotation strategies that minimize frequency of surface disturbance during dry seasons and maximize periods between disturbances will reduce impacts to biological soil crusts.

Dispersal of livestock throughout useable portions of pastures should also be emphasized. Disturbance of sensitive sites should be avoided or minimized when they are a small proportion of the overall pasture or landscape. Ways to disperse livestock include the following:

- Locating water and salt (or other supplements) on sites with low potential for biological soil crust development and in areas that discourage livestock from loitering. In many areas, sites with high rock cover are good options. Livestock trailing preferences need to be considered when evaluating locations.

- Using brush barriers or fence segments to divert trailing. Sites with high potential for biological soil crust development are often not preferred by livestock for forage; however, these same sites may be open and easy to walk across. Because of lack of forage, minimal barriers are usually sufficient to discourage access.

Figure 5.3 *Native grazers in the western U.S., such as pronghorn antelope and muledeer, tend to use higher, more productive sites during summer and move to lower elevation sites for winter forage. They may also move through areas, rather than staying in one area. This type of seasonality and intensity minimizes impacts to biological crusts by concentrating use when crusts are frozen or moist.*

Fig. 5.4 *Vehicular disturbance to biological soil crusts. Recreational disturbances are concentrated in open interspaces, where crusts are most abundant and vulnerable. The tracks in the top photo are approximately 10 years old.*

Stocking levels and season of use should be ascertained on an annual basis, jointly by managers and users, with optimal coverage of both vascular plants and biological soil crusts as the management goal (Kaltenecker and Wicklow-Howard 1994; Kaltenecker et al. 1999b). Optimal coverage should be based on site capability and rangeland health indicators of site stability and nutrient cycling. Livestock exclusion from reference areas and sites with highly erodible soils or low vascular plant cover is appropriate to protect biological crusts and site stability.

5.3 Recreational Use Management

Many recreational activities have impacts similar to those of livestock use. Therefore, principles relating to management of livestock disturbance intensity, timing, frequency, duration, or extent apply to recreational impacts as well. However, there are also major differences. People are often harder to control than livestock. People can carry food and water; thus, access to these essentials does not limit their activities. People tend to go where they want, even in the presence of barriers such as fences. People also have a greater affinity for open vegetation, as it is easier to walk or drive through; however, these same open sites are generally dependent on biological soil crusts for stability (Fig. 5.4). Education, legal restriction and/or use stipulations, and compliance activities may require proportionately

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higher management priorities and time requirements than for the control of livestock.

Concentration of recreational use is generally desirable. Designated campsite use reduces the impact of haphazard placement of sites by individuals. Trails minimize the amount of biological soil crust that is disrupted by trampling. Education can be used to teach people how to camp in areas without designated campsites (e.g., on hardened surfaces, such as rocks, or in areas with minimal crust potential) and how to travel cross-country in areas that lack trails (e.g., in washes, on rock, on fallen logs).

Recommended management practices include the following:

- Restrict road locations to less sensitive areas. Road drainage (culverts, water bars) should be designed so that erosion or sediment fill of adjacent off-site areas is minimized.

- Promote extensive, low-density uses, such as hiking and backpacking, during late fall and winter periods. Restrict access during dry seasons.

- Permit high-density, high-impact uses, such as Christmas tree and firewood cutting areas, for short durations during late fall and winter, preferably when soils are frozen. Areas should be rotated based on a total allowable disturbance threshold with long recovery periods (greater than 10 years minimum on moderate- to high-resiliency sites, such as in sagebrush communities [greater than 230 mm average annual rainfall] in the northern Great Basin) before redesignation for use. Exclude low-resiliency sites.

- Provide designated trails, and restrict use to trails in high-density recreational areas.

- Provide interpretive sites and literature on recognition and value of protecting biological soil crusts at major access points in areas of extensive or unique crust formation.

- Require an analysis of impacts to biological soil crusts and appropriate stipulations on all use applications, such as rights-of-way, oil and gas and other exploration permits, permits to drill, etc.

CHAPTER 6

MONITORING BIOLOGICAL SOIL CRUSTS

Monitoring is the collection and analysis of repeated observations so that trends can be assessed. Typically, monitoring is used to evaluate landscape condition changes over time, often in relation to defined management goals. A monitoring program's objectives will determine the position in the landscape at which measurements will be made and the period over which data will be collected and assessed. Monitoring is often designed so that measurements can be made by more than one observer, and the level of acceptable change is usually determined before monitoring commences.

Monitoring studies often differ from traditional research studies in that they are not designed to infer the cause of any observed changes. Monitoring studies usually lack replication and often have no controls. Plot sizes and measurement protocols may be similar in both monitoring and research studies, but the management objectives are often widely different. The following is a discussion of field-based monitoring strategies and procedures for biological crusts. Key attributes for each strategy are summarized in Table 6.1.

6.1 Monitoring Methods

During the past century, rangeland managers have grappled with methods to assess the health and trend of landscapes (Tueller 1988). Techniques have concentrated primarily on vascular plant attributes, such as cover, frequency, presence/absence, abundance, and biomass of various species, particularly perennial plants (Stoddart et al. 1975; Friedel and Bastin 1988; Friedel et al. 1988; Holechek et al. 1989; Milton et al. 1998). Recently, there has been more emphasis on soil surfaces, and monitoring techniques to assess soil surface condition have been developed (Tongway 1994; Pellant 1996; Whisenant and Tongway 1996; de Soyza et. al. 1997).

While many scientists acknowledge the close links between biological soil crusts and rangeland condition (Klopatek 1992), crusts and their component organisms have rarely been recorded during field-based assessment (West 1990). Early efforts to classify soil surfaces and include biological soil crusts were developed in the semi-arid woodlands of eastern Australia (Tongway and Smith 1989). This assessment showed differences in the stability, erosion, and nutrient status of soil surfaces, and provided a reliable estimate of potential productivity of the surface independent of vascular

Table 6.1 *Attributes of biological crust monitoring strategies. See the text for detailed discussion of each method.*

Recording Method: Individual Taxa vs. Morphological Groups	
Individual taxa	• Allows documentation of biodiversity. • More sensitive to change over time.
Morphological groups	• Quicker, easier identification. • Good evaluation of ecological function. • Less variability. • Less sampling time and intensity to get reliable estimates.
Sampling Methods	
Quadrats (using point or cover class estimates)	• Useful if clumps are <2 cm diameter or groups/taxa are highly interspersed. • Use if information on spatial relationships is not desired. • Provides cover estimate.
Line-point Intercept	• Useful if clumps are <2 cm diameter or groups/taxa are highly interspersed. • Provides information on spatial relationships. • Provides cover estimate.
Line Intercept	• Best if clumps are >2 cm diameter and groups/taxa are not highly interspersed. • Provides information on spatial relationships. • Provides actual measure of cover.

vegetation. The method used four classes for soil surfaces: Class 1 = stable, productive surfaces with high biological crust cover and species diversity; Class 2 = slightly unstable, moderately productive surfaces with broken biological crust cover and moderate species diversity; Class 3 = moderately unstable and unproductive surfaces with low biological crust cover and species diversity; and Class 4 = very unstable and unproductive surfaces where biological crusts are absent (Mucher et al. 1988).

This system was later refined and extended to other landscape types (Tongway and Hindley 1995) and other soil characteristics, such as the degree of cracking, surface coherence, microtopography, and biological crust cover. U.S. workers (Pellant 1996; USDI 1997) have also included biological crust cover as a component of federal land monitoring programs. In eastern Australia, the Department of Land and Water Conservation has been collecting data (including biological crust cover) on the condition and trend of rangelands since the mid-1980s (Green 1992). Monitoring staff in Canyonlands

National Park in southeastern Utah have been collecting cover estimates for biological crusts since 1987 (Belnap, unpublished data).

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6.1.1 Sampling Design and Procedures

Biological crusts are typically measured using standard or slightly modified rangeland assessment techniques. These are generally based on measurement of plant and soil attributes within permanent sampling units (quadrats), stratified within relevant vegetation or soil zones (Ludwig and Tongway 1992). Stratification may be necessary where the landscape is composed of a number of homogeneous land units. On degraded sites, nearby reference areas should be measured in order to determine the site's potential for biological crust development. Biological crusts are likely to be most pronounced in areas protected from trampling, such as under shrubs or adjacent to obstacles such as fallen trees and rocks. Shallow, rocky soils often provide "refugia" for crustal organisms that have been destroyed by livestock on more productive soils. However, reference areas should be as identical as possible to their paired disturbed sites with regards to soil characteristics (texture, chemistry, depth), placement on the landscape, and vegetation production potential.

6.1.2 Using Morphological Groups for Monitoring

Biological crust organisms are rarely recorded during routine rangeland monitoring despite increased acceptance over the past decade of their importance in ecosystem processes (Harper and Marble 1988; West 1990; Eldridge and Greene 1994; Ladyman and Muldavin 1996). West (1990) contends that this is due to difficulties in identifying the organisms *in situ*, lack of a standardized sampling procedure with often undue emphasis on laboratory culturing, lack of conspicuousness of some organisms (particularly when the soils are dry), and their patchiness in time and space. As identification is problematic, monitoring can be a daunting task to all but the most experienced (Eldridge and Rosentreter 1999).

However, strong relationships exist between form (morphology) of biological crust organisms and their ecological functioning in relation to landscape processes and disturbance (Eldridge and Rosentreter 1999). Morphology determines how crust organisms function ecologically (relative to erosion and water retention) and their tolerance to, and recovery from, physical disturbance. Morphological groups have been proposed as surrogates for species in biological crust monitoring (see Table 1.1; Kaltenecker 1997; Ponzetti et al. 1998; Eldridge and Rosentreter 1999).

Morphological groups are biologically and ecologically efficient and convey to non-specialists a better image of the

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organismal form and its likely impact on soils and landscapes. These relationships hold true in different regions and continents and eliminate the need for complex, often confusing changes in nomenclature. Other advantages of morphological groups for rangeland monitoring include ease of identification, which is independent of sexual reproductive structures, and the ability to monitor sites more quickly with less specialized staff (Eldridge and Rosentreter 1999). Cover and abundance measures of morphological groups can be obtained more rapidly than measuring each individual species. This allows use of the same size plot for varied sites and assessment of more sites per unit time.

Although morphological groups are appropriate for broad-scale or regional monitoring, their use may not allow the detection of individual species, particularly rare or uncommon taxa. Specific goals of individual studies (i.e., determination of total diversity vs. functional diversity vs. site stability) need to be determined prior to initiation of monitoring. This will determine whether morphological groups can be used or whether monitoring needs to occur at the generic/species level. In all cases, crustal organisms are best detected or identified when moist. When sampling during dry weather, the soil surface to be measured can be moistened with water mist prior to reading to make the organisms more visible.

6.1.3 Quadrat Methods

In communities where biological crusts are patchy, lichen and moss cover is sparse, and/or large areas are being assessed, crust monitoring is often done using quadrats. These can be located either randomly or along a line transect. Quadrats can be used to estimate both biological crust and vascular plant cover (Anderson et al.1982a, b; Brotherson et al. 1983), using either point-intercept or cover classes (Fig. 6.1, 6.2). While cover of the various strata within the community (i.e., biological crusts, herbaceous plants, and shrubs) can be determined, horizontal spatial relationships between groups of organisms cannot be defined using quadrat methods. Where biological crust cover is relatively dense or where personnel turnover is high, microplot sampling effectively estimates cover (McCune and Lesica 1992). Reduced quadrat size is also useful if a goal of the study is to observe greater detail in biological crust composition in relation to environmental variation within the site. For example, Rogers and Lange (1971) used 15 x 20-cm quadrats to examine changes in crust floristics related to stock watering points in semi-arid and subtropical Australia. Other Australian studies have employed 0.5 m^2 subplots within larger plots to assess cover and frequency of crustal organisms (Eldridge and Bradstock 1994; Eldridge 1996; Eldridge and Tozer

1996; Eldridge 1999). U.S. workers have adapted a 20 x 50-cm quadrat and cover classes traditionally used for vascular vegetation monitoring (see Daubenmire 1959) for estimating biological crust cover (Rosentreter 1986; Ponzetti et al. 1998).

Destructive sampling might be necessary if detailed documentation of biological crust species composition is desired. Eldridge and Semple (unpublished data) removed small cores (4 cm^2) from an area of high biological crust cover and diversity and used a dissecting microscope to record cover and abundance of crustal organisms. Use of a short-focus telescope is a similar, non-destructive method (Pickard and Seppelt 1984), but is less accurate.

Within a quadrat, cover and frequency are relatively quick to assess, can be recorded by taxa or morphological groups, and are often good indicators of the ecological and hydrological status of the landscape (Eldridge and Koen 1998). Frequency is determined as the number of times that an organism or group is recorded within a given number of sampling units (expressed as a percentage). This measure describes the abundance and distribution of species and is useful to detect changes in community composition over time. It is one of the easiest and fastest methods available for monitoring changes in vegetation (USDI 1996). Frequency methods are used extensively by federal land management agencies for monitoring changes in landscape condition or trend in relation to vascular plants, and can easily incorporate biological soil crusts.

6.1.4 Line-intercept Methods

Line-intercept has been used in the northern Great Basin in studies that characterized both the crust and vascular plant

Figure 6.1 *Quadrat frame used for point-cover estimation. This frame is 25 x 25 cm in size. Hits are determined by dropping a pin vertically from each intercept within the frame.*

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Figure 6.2 *Data form for point-intercept using a quadrat method (left) and example of data collection (right).*

Date:			**Personnel:**							**total = 20/stake**
Plot	**Stake**	**Cyano**	**Collema**	**Moss**	**Litter**	**Bare**	**Placidium**	**Psora**		

Date: 5-4-01 **Personnel:** JHK, RR **total = 20/stake**

Plot	Stake	Cyano	Collema	Moss	Litter	Bare	Placidium	Psora		
1	1	III	~~IIII~~	I	II	~~IIII~~	II	II		
1	2	~~IIII~~ I	III	II	~~IIII~~	IIII				

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communities (Kaltenecker 1997; Kaltenecker et al. 1999a, b; Kaltenecker, unpublished data). Using line-intercept (see Canfield 1944 for a description of the original methodology developed for vascular plant communities), taxa or morphological groups (Eldridge and Rosentreter 1999) are recorded every centimeter along a number of 10-m or 20-m line transects (Fig. 6.3, 6.4), with cover and floristics of the biological crust and vascular plant communities calculated as a percentage of the total line transect length (Rogers 1994). Each line forms a single, independent sampling unit.

Line-intercept is a rapid and efficient method of sampling when the vegetation community is strongly patterned and is therefore useful in many arid and semi-arid ecosystems. Line-intercept is easiest

Figure 6.3 *Use of line-intercept for measuring biological crust cover along with other community attributes (vascular plant cover, litter, bare mineral soil, rock). Note the placement of the transect line close to the soil surface. Cover of each entity is measured along the top edge of the tape. A misting of water makes crustal organisms more visible and therefore easier to measure.*

when organisms have a definitive boundary, and can be difficult to apply in sites with dense or intermingling vegetation. An advantage of line-intercept over quadrat methods is the ability to derive linear spatial relationships between organisms from the data.

Lines should be long enough to include most of the variability in both the vascular vegetation and biological crust. Optimum line length should be determined from pilot sampling. It is imperative that the line is placed in exactly the same location each time to prevent sampling error associated with repeated measure. Permanent markers, such as steel stakes or nails, may be located along the line to ensure correct placement. If vascular vegetation is measured at the same time, a longer transect might be required with intensive sampling of the biological crust along a shorter portion of the line (USDI 1997).

Figure 6.4 *Line intercept data form (this page) and example of data collection (next page).*

Site Name:				**Date:**			
Treatment:		**Transect #:**		**Reader:**		**Recorder:**	
Cover Type	**From (cm mark)**	**To (cm mark)**	**Under (Cover Type)**	**Cover Type**	**From (cm mark)**	**To (cm mark)**	**Under (Cover Type)**

Site Name: Kuna Butte				Date: 4-18-01			
Treatment: unburned		Transect #: 1		Reader: JHK		Recorder: EM	
Cover Type	From (cm mark)	To (cm mark)	Under (Cover Type)	Cover Type	From (cm mark)	To (cm mark)	Under (Cover Type)
Artrw	0	40					
tall moss	0	36	Artrw				
short moss	36	40	Artrw				
short moss	40	52					
crustose	52	55					
squamulose	55	62					
short moss	62	70					
Agsp	70	85					
short moss	70	74	Agsp				
short moss	83	85	Agsp				

6.1.5 Line-point Intercept Methods

The line-point intercept method is similar to line-intercept, but uses random or predefined points along a line rather than intercepts, and records only the entity or entities (if recording over- and understory) associated precisely with that point. Cover and floristics of the biological crust and vascular plant communities are then calculated as a percentage of the total number of points. Line-point intercept is useful for estimating cover in communities where the crust and vascular vegetation are not strongly patterned. As with line-intercept, linear spatial relationships can be assessed using this method.

6.1.6 The Issues of Scale

Size and shape of the sampling unit depends upon the vegetation type and spatial distribution. Ultimately, the size and number of quadrats will depend on a compromise between statistical considerations (see Section 6.1.8) and what is logistically possible. Generally, in sparsely vegetated landscapes, larger linear quadrats are useful in decreasing variability because of cover heterogeneity. Circular quadrats are often preferred to square because they reduce edge effects. The nature of the impact being investigated will also influence the monitoring method(s) used. For example, studies focusing on species composition will require microplot sampling, while compressional impacts (off-road vehicles, grazing) on biological soil crusts may be best examined by using repeated photo-points, remote sensing, or aerial photography interpretation on large plots of up to several hectares in area.

6.1.7 Voucher Specimens

Representative specimens of each crustal organism should be collected as vouchers for each site. Voucher specimens should include all the variation within a morphological group. A site's biodiversity can later be assessed by identification of voucher specimens by an expert and application of diversity indices.

Voucher specimens require specialized preparation to preserve them for long-term storage (Rosentreter et al. 1988). This often includes removal of excess soil, stabilization of the underlying substrate, and fixation of the specimen onto a stiff card to protect it from breakage. A collection of local or regionally occurring crustal organisms stored in a herbarium is useful for future identification of taxa and for describing a study area's floristics. This enables other researchers and land managers to evaluate differences in biological crust composition between regions.

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6.1.8 Statistical Considerations

Statistical considerations are important when designing any sampling procedure. It is important that the size and number of sampling units, their placement in relation to landscape heterogeneity, and their replication (if significance testing is required) do not compromise any future data analyses. The most efficient design is usually the one that yields the highest statistical precision (smallest standard error and narrowest confidence interval around the mean) for a given amount of effort or money. It is therefore crucial that a biometrician or a statistician with an ecological background be consulted prior to establishment of a monitoring program.

While the value of statistical analysis regarding changes in biological soil crust cover or floristics cannot be undervalued, rigorous statistical examination might not always be necessary or even desirable for a monitoring program (Eldridge and Rosentreter 1999). The danger, however, is that subsequent personnel may wish to look for statistically significant results using a monitoring protocol that was not established to allow rigorous examination. Monitoring sites are frequently unreplicated or pseudo-replicated, and analyses may therefore result in erroneous conclusions (Hurlbert 1984).

A pilot study may be necessary to determine optimal quadrat size, the shape or number to be used, or the transect length that will enable the operator to reduce Type I error (erroneously rejecting a true null hypothesis). For any site-by-time combination, a species-area curve (McCune 1992) can be calculated to give the optimal sampling intensity needed to estimate parameters for a given proportion of the population. For example, in semi-arid eastern Australia, Eldridge and Tozer (1995) found that between six and eight 0.5-m^2 quadrats were needed to adequately describe the biological crust in a woodland community, while only three quadrats were required to describe the crust in a grassland.

Species-area curves are likely to vary in relation to landscape heterogeneity, and the observers must ensure that all site measurements are made from a homogeneous sample. For example, in the patterned semi-arid woodlands in eastern Australia, where groves of trees located on the contour are separated by treeless inter-groves, the biological crust cover varies markedly between the two zones (Eldridge 1999; Tozer and Eldridge, unpublished data). Monitoring should occur within, rather than across, geomorphic zones; otherwise, species-area curves are meaningless and will fail to reveal the optimal number of units necessary to detect differences.

Despite the importance of statistical considerations, the sampling intensity may depend entirely on sampling efficiency. This is particularly important in studies where cores or samples are

collected for laboratory identification and analysis. As a broad generality, one day of collecting and recording crustal organisms in the field can generate up to 10 days of processing and identification in the laboratory. Sampling intensity, therefore, is often a compromise between what is statistically necessary and what is logistically feasible.

6.2 Other Monitoring Methods

As discussed in Chapter 4, changes in biological crust biomass and function often cannot be assessed by visible cover change (Belnap 1993). Obviously, monitoring of cover changes is the easiest and most practical method. However, if resources are available, additional methods should be used to more accurately track biological crust responses to disturbance or management change. The methods described below are examples of monitoring that provides information about biological crusts from a functional perspective.

Determination of cholorophyll *a* using spectrophotometric or high pressure liquid chromatography (HPLC) analysis is an efficient and reliable measure for monitoring changes in photosynthetic biomass, even when visible cover is difficult to detect (Belnap 1993). In areas dominated by cyanobacteria and cyanolichens, monitoring nitrogenase activity is an effective way to determine functional changes in the biological crust (Belnap et al. 1994; Belnap 1996). Both methods require destructive sampling, but can provide valuable information regarding stages in biological crust development.

The slake test is a simple method of determining soil surface stability under wet conditions. Small soil surface fragments (6 to 8 mm diameter) are immersed in rain-quality water, observed over a period of several minutes, and rated according to cohesion of fragments after soaking (Table 6.2). Biological crusts will maintain cohesion when soaked, while physical or chemical crusts will tend to slake or disperse (see Tongway and Hindley 1995 for detailed methods regarding this test). More complicated methods of determining stability include the use of wind tunnels and simulated rainfall.

6.3 Impacts of Monitoring

Care should be taken to establish rigorous protocols when sampling within quadrats and along lines. Because crustal organisms are susceptible to damage by humans, inadvertent trampling within the sampling units may create biased results. Studies on biological soil crusts require that voucher specimens be collected to provide a

Table 6.2 *Classification of results from the slake test. Adapted from Tongway (1995).*

Class	Stability Rating	Observed Behavior of Soil Fragment
1	Very unstable	Fragment collapses completely in <5 seconds into a shapeless mass. A myriad of air bubbles is often present.
2	Unstable	Fragment substantially collapses over about 5-10 seconds with only a thin surface crust remaining; >50% of the sub-crust material slumps to an amorphous mass.
3	Moderately stable	Surface crust remains intact; slumping of sub-crust material is <50%.
4	Stable	Entire fragment remains intact after 5 minutes. This level of stability can remain for many hours.

permanent record of the species found in an area. Removal of voucher specimens or destructive sampling modifies the community and should occur away from permanent plots.

CHAPTER 7

INTERNET RESOURCES FOR BIOLOGICAL SOIL CRUSTS

The Internet has a number of valuable resources for information on biological soil crusts or the organisms that comprise crusts (lichens, algae, etc.). Below we have listed several of the most useful web pages currently available.

Web Address	Author or Organization	Description
www.soilcrust.org	U.S. Geological Survey (Jayne Belnap) Bureau of Land Management National Park Service	Biological soil crust information, based in Canyonlands National Park. This web page contains a near exhaustive bibliography for all things crust-like and a recent version of this reference.
www.id.blm.gov/iso/soils/index.html	Bureau of Land Management, Idaho State Office	This site contains an introduction to soil biological communities, including soil crusts and subsurface micro-and macro-organisms.
www.ucmp.berkeley.edu/fungi/lichens/lichens.html	University of California, Berkeley, Museum of Paleontology	Introduction to lichens.
www.unomaha.edu/~abls/resources.html	American Bryological and Lichenological Society (ABLS)	Checklists and floras; links to institutions and individuals that are resources for information on nonvascular plants and lichens.
mgd.nasce.org/hyperSQL/lichenland	Department of Botany and Plant Pathology, Oregon State Univ.	One of the best introductions to lichens, complete with great color photos.
ucs.orst.edu/~mccuneb/	Bruce McCune Oregon State University	Bruce McCune is a leading ecologist in North America and specializes in lichen and moss ecology and taxonomy.

Web Address	Author or Organization	Description
www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm		
	Theadore Esslinger Department of Botany North Dakota State University	*Cumulative Checklist for the Lichen-forming, Lichenicolous and Allied Fungi of the Continental United States and Canada.*
www.fs.fed.us/land/ecosysmgmt/ecoreg1_home.html		
	USDA Forest Service Robert G. Bailey	Descriptions of Bailey's ecoregions of the U.S., including maps.
www.accessexcellence.org/BF/bf05/johansen/web.html		
	California Academy of Sciences Jeffrey Johansen	Text of a talk presented to high school teachers for the California Academy of Sciences. A layman's introduction to biological crust, focusing on algal and cyanobacterial components and research on inoculation to speed recovery following disturbance.
www.biblio.bio.purdue.edu/www-cyanosite		
	Department of Biology, Purdue University; Foundation for Microbiology	Web server for cyanobacterial research; includes a link to CyBib, a bibliographic database containing references on cyanobacteria.

GLOSSARY

adnate: Pressed closely against a surface.

aggregate stability: The degree to which a group of soil particles cohere so as to behave mechanically as one unit.

albedo: A measure of the energy reflected off a surface. Dark surfaces have a lower albedo than light surfaces; therefore, light surfaces absorb less energy than dark surfaces.

ammonia volatilization: The vaporization of ammonia into the atmosphere.

anaerobic: The absence of oxygen. Also refers to organisms able to live or grow in the absence of free oxygen.

appressed: Pressed closely against a surface.

autotroph: An organism whose growth and reproduction are independent of external sources of organic compounds. Carbon compounds are created by autotrophic organisms via the reduction of carbon dioxide (CO_2), with light energy driving the process.

bacteria: Members of a group of diverse and ubiquitous prokaryotic, single-celled organisms.

bryophytes: Tiny plants lacking vascular tissues. This group includes mosses and liverworts.

calcareous: Substrates rich in calcium carbonate, such as limestone or dolomite. Also refers to soils derived from or containing these substances.

cosmopolitan: Found worldwide.

crustose lichens: Lichens that form a crust-like growth form that is closely applied to the substrate.

cyanobacteria: "Blue-green" algae; prokaryotic, photosynthetic organisms that generally have a blue-green tint and lack chloroplasts.

cyanolichen: Lichen that contains a cyanobacterium as its phytobiont.

denitrification: The formation of gaseous nitrogen or gaseous nitrogen oxides from nitrate or nitrite by microorganisms.

desertification: Land degradation in arid, semi-arid, and dry subhumid regions of the world resulting from climatic and other natural stresses coupled with human activities. Processes that lead to desertification include soil loss through wind and water erosion; changes in soil quality due to salinization, waterlogging, and nutrient depletion; loss of vegetative biomass and cover; and compositional and structural changes in plant communities due to exotic plant invasion (Mouat et al. 1995).

foliose lichens: Lichens that are leaf-like in growth form, flattened with definite upper and lower surfaces, and usually loosely attached to the substrate.

fruticose lichens: Lichens with three-dimensional growth forms that are ropey or branching and do not have definite upper and lower surfaces.

gelatinous lichens: Lichens that are non-stratified (algal and fungal layers are not distinct) and that have a jelly-like appearance when moistened. All gelatinous lichens have cyanobacteria as their phytobiont.

gemmae: Structures produced by liverworts that function in vegetative reproduction.

green algae: Photosynthetic unicellular and multicellular organisms that lack true tissue differentiation.

heterocysts: Specialized cells occurring in some filamentous cyanobacteria that are the sites of nitrogen fixation.

heterotrophs: Organisms that require organic compounds for growth and reproduction.

***hydraulic conductivity (K_e)*:** The rate at which water moves through the soil profile under field conditions.

***hyphae*:** Fungal filaments.

***infiltration*:** The downward entry of water into the soil.

***interspace*:** The spaces in a plant community between shrubs or trees.

***lichen*:** A symbiotic relationship between a fungus and an algae or cyanobacterium.

***lithic*:** Pertaining to rock; rocky.

***liverwort*:** A small, non-vascular plant.

***microfungi*:** Fungi that occur free-living in the soil or in association with roots of vascular plants (mycorrhizae).

***mucilaginous*:** Having a sheath composed of sticky polysaccharides surrounding cyanobacterial, algal, or fungal filaments.

***mycorrhizae*:** A stable, symbiotic association between a fungus and the root of a plant.

***nitrification*:** The process in which ammonia is oxidized to nitrite and nitrite to nitrate.

***nitrogen fixation*:** The conversion of elemental nitrogen (N_2) to organic combinations or to forms readily usable in biological processes.

***nitrogenase*:** The enzyme that catalyzes biological nitrogen fixation.

***permeability*:** The ease with which gases, liquids, or plant roots penetrate or pass through the soil.

***photosynthesis*:** The process in which light energy is absorbed by specialized pigments of a cell and converted to chemical energy. The ultimate result of photosynthesis is the fixation of CO_2 and the production of carbon compounds (sugars).

***phytobiont*:** The photosynthetic partner in the lichen symbiosis, i.e., the algal or cyanobacterial component of a lichen.

***poikilohydric*:** Organisms that are capable of becoming physiologically dormant under dry conditions.

***prokaryotic*:** Cells that lack a nucleus.

***propagules*:** Material that results from either sexual or asexual reproduction by crustal organisms and disperses into areas where the biological soil crust has been removed by disturbance. This material "germinates" and grows to establish a new crust.

***resilience*:** The ability to recover following disturbance.

***resistance*:** The ability to withstand disturbance.

***respiration*:** The biological process whereby organisms oxidize carbon compounds to CO_2 and water as a source of energy.

***rhizines*:** Root-like structures of lichens and mosses that function to attach the organism to the substrate.

***saline soil*:** A soil containing sufficient soluble salts to impair its productivity.

***sessile*:** Attached to a surface without a stalk but not imbedded in the surface.

***squamulose lichens*:** Lichens that occur as discrete flakes or scales that are often round or ear-shaped. Squamulose lichens may be convex or concave and often have lobed margins.

***symbiosis*:** An obligatory, interactive association between two organisms, producing a stable condition in which they live together in close physical proximity to their mutual advantage.

***thallus*:** The vegetative body of a lichen or liverwort.

***xerothermic*:** Dry, hot conditions.

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13. ABSTRACT (Maximum 200 words)

This technical reference presents a review of current scientific knowledge on the ecology of biological soil crusts, then integrates this information into a discussion on monitoring and management of arid and semiarid lands in the western United States. The document begins with a discussion on the composition, structure, and distribution of biological crusts relative to environmental factors such as climate and soil characteristics. This information is then synthesized into guidelines on development of monitoring strategies as well as site-specific management prescriptions regarding livestock, recreation, and other multiple-use activities. The material is presented from a practical and applied management perspective and is summerized in numerous tables and figures.

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