

Microbiotic Crusts: A Review.

(Final Draft)

John Dana Williams  
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## **Purpose of report**

This report is a review of published microbiotic crust research. Researchers and naturalists have been espousing the multiple attributes of microbiotic crusts since early in the 1900's. These attributes include, but are not limited to: the ability to stabilize soil, influence nutrient cycling and vascular plant communities, serve as indicators of air pollution, and alter soil hydrologic processes. As a result, a growing number of researchers are examining how microbiotic crusts fit into arid and semiarid land ecosystems. Since 1988, eight reviews of microbiotic crust literature have been published (Harper and Marble 1988, Dunne 1989, Campbell et al. 1989, Isichei 1990, West 1990, Metting 1991, Johansen 1993, and Eldridge 1994e). In the last five years, three Doctoral dissertations have been completed (Belnap 1990a, Williams 1993, and Eldridge 1993c), a symposium held at the annual meeting of the American Bryological and Lichenological Society in San Antonio, Texas, and those proceedings published in *The Great Basin Naturalist* (Volume 53(1) 1993).

In this current review, I examined the information provided in previous reviews and make note of recent additional, confirming, or contrary evidence that has been presented in the last four years. I relied mainly on peer reviewed research reports published in scientific journals. However, I also relied on reports of recently completed research that are currently in review and cited in either currently published material or in symposia proceedings. I wrote this report in response to the stated desire of the Eastside Ecosystem Management Project to give full consideration to all potentially important ecosystem components in development of management plans for arid and semiarid land in the Northwestern U.S. This report is intended as a tool for deciding whether or not microbiotic crusts should be considered in the planning process.

### **Microbiotic Crusts: definition**

The term microbiotic soil crust (Belnap 1993) is synonymous with soil crust described as microfloral (Loope and Gifford 1972), cryptogamic (Kleiner and Harper 1972), biological (Danin 1978), organogenic (Evenari 1985), biocrusts or biogenic (Thomas and Tsoar 1990), microphytic (Cameron 1978), biotic (McCune 1992a), and cryptobiotic (Belnap 1993). Cryptogamic is the most commonly recognized term (St. Clair and Johansen 1993), but cryptogamic infers club mosses and ferns (Bold et al. 1987), life forms that do not contribute to arid or semiarid soil crusting (Cameron 1978, West 1990). "Crypto-" also infers hidden or secret and many of the crust organisms, although diminutive, are neither. Recently, microphytic has been used extensively because it differentiates between vascular plants and the life forms found in soil crust structure, and is interdisciplinary in that it is also used by aquatic ecologists (West 1990). However, both microflorae and microfaunae contribute to the crust development and structure. Microfaunae contribute to the crust structure by grazing microphytes and enhancing soil aggregation with their casts (Danin 1978, Gayel and Shtina 1974). Thus, microbiotic would seem the clearest and most accurate term (St. Clair and Johansen 1993, Williams 1993). All of these terms describe a suite of crusts developed through biological activity. More specific terms dependent on the most obvious crust components include: algal crust, lichen crust, algal-lichen crust, cyanobacterial-algal crusts, cyanobacterial-lichen crusts, lichen-moss crust. Recent arguments have been made for placing cyanobacteria in a separate taxonomic kingdom than algae. Given this differentiation, many of the algal crusts examined in the past would properly be identified as cyanobacterial crusts.

Microbiotic crusts develop in interspaces of open shrub and grass communities, from sagebrush steppe to salt brush steppe, and in woodlands of arid and semiarid environments (Harper and Marble 1988, West 1990, Beymer and

Klopatek 1992). They are distinguishable from crust and soil features formed by chemical or physical processes occurring soils of the Aridisol order (West 1990). Physico-chemico processes produce vesicular porosity, rain crusts, salt crusts, gypsum crusts, or silica crust, which often occur in association with microbiotic crusts. Microbiotic crusts are found globally (Bolyshhev 1964, Danin 1978, Gillette and Dobrowolski 1993, Rogers 1977, Rauh 1985, West 1990) and are common throughout the Great Basin, Colorado Plateau, and Columbia Basin in North America. Many of the organisms are ubiquitous around the world. Lichen spores, for instance, are carried aloft to upper atmosphere currents and subsequently fall globally (Rogers 1977). However, this means of dispersal has been questioned by During and van Tooren (1987).

The extensive occurrence of microbiotic crusts throughout the western United States has been associated with a lack of large herbivores before the Quaternary to the present (Mack and Thompson 1982). The shrub-steppe community structure is believed a response to interior-continental climate conditions created by the rise of the Cascade and Sierra Nevada mountain ranges and preserved by spatial displacement during glaciation periods through the Pleistocene (Mack and Thompson 1982). However, similar steppe exists from Ukraine through Tadzhik, an area populated by both ungulate herbivores and peoples to insure herd effect, yet microbiotic crust are present throughout, particularly in the more arid portions (Mack and Thompson 1982, Gillette and Dobrowolski 1993).

Combinations of mosses, lichens, algae (golden-brown, green), cyanobacteria, liverworts, fungi, diatoms, bacteria, and associated microfauna bind soil particles to develop a distinctive rough soil surface microtopography (West 1990). In areas undisturbed by large herbivores, humans or vehicles, the depth from pinnacle top to bottom can be as great as 10 cm in an area no larger than 100 cm<sup>2</sup>. Spatial coverage is often greater than that of vascular plants (Kleiner and Harper 1972, Harper and Marble 1988) and might

constitute 40-100% of the ground cover in arid and semiarid communities (St. Clair et al. 1993).

Cyanobacteria and algae are the major component of many microbiotic crusts. MacGregor and Johnson (1971) estimated that 4% of the Sonoran Desert contained algal crusts. Belnap (1990b) estimated algal crusts compose up to 70% of the living cover in arid and semiarid areas of the Colorado Plateau Biogeographical Province. Algal dominated crusts are a community of primary producers (algae) and decomposers (bacteria and microfungi) (Campbell 1977). Of these organisms, the cyanobacterium *Microcoleus vaginatus* is estimated to contribute 95% of the soil biomass in shrub and grass interspaces at sites in both Colorado Plateau and Great Basin Biogeographical Provinces (Anderson et al. 1982b, Campbell et al. 1989, Belnap 1993). These microbiotic crusts have developed in soils derived from sandstone, gypsum, limestone, shale, and lacustrine material (Belnap 1993). Often such crusts are in early stages of development or recovery from disturbance, are not readily obvious to the casual observer, and require a microscope to detect the presence of algae in what might otherwise be considered scaly soil. Such algal dominated crust are generally dark in color when dry. Lichens that contribute to microbiotic crusts are a variety of colors, predominately black but also red, white, or blue-green and are associated with rougher microtopography than an algal dominated crust.

Microphytes are able to exist in extreme environmental conditions, surviving through extended periods of desiccation and extreme high and low temperatures (Lange 1972, 1990). *Tortula ruralis*, a moss common to the Northwest, survives years in a desiccated state and become metabolically active within 8 to 10 hours when rewetted (Holden 1992). *Nostoc commune*, a terrestrial cyanophyte found in temperate grasslands, resumes nitrogenase activity with rehydration following desiccation and temperatures up to 65°C. Photosynthesis and respiration can be sustained or re-established in some

lichens by hydration from fog, dew, or simply high vapor pressure (Lange and Tenhunen 1982, Lange et al. 1990a, 1990b, Lange and Bádél 1993).

Algae in microbiotic crust are known for at least two unique properties: motility of filaments and swelling with water imbibition (Campbell 1977). Motility is a two part process triggered by light and water. First, dry *Microcoleus* filaments substantially expand in less than 15 seconds (Shields and Durrell 1964) and imbibe water 12-13 times that of sheath volume (Campbell 1977). The rapid water imbibition mechanically changes the shape of the outer sheath and propels the algae outward. Second, the sheath extends in a phototropic response. Factors that control trichome growth rates or determine trichome numbers per sheath are unknown, although there is an apparent relationship of gypsiferous-, limestone-, and undisturbed sandy-soils with large numbers of filaments per sheath (Belnap et al. 1994). Campbell (1977) considers the wetting and drying response as the critical factor for trichome survival (rejuvenation, release, and dispersal) in arid environments. Dry sheaths bundle trichomes, and protect them from evaporation thus extending conditions necessary for metabolic processes (Campbell 1977, Harper and Pendleton 1993). *Microcoleus* provide a substrate for other organisms that contribute to both microbiotic crust development and soil microbiological processes. As *Microcoleus* filaments migrate, substances essential for bacterial and yeast growth are exuded from the extending filament (Campbell 1977).

The study of organisms forming soil crusts in conjunction with associated vascular plant communities will provide a clearer picture of the functioning of ecosystems because of the difference in time scales relevant to microbiotic organisms and vascular plants (Rosentreter 1986). However, knowledge of both the autecology of microbiotic crust organisms and the synecology of the crusts is in its infant stage (West 1990). The preceding definition and explanation alone would suggest that there is much to be learned about microbiotic crusts.

Nearly all dissertations, reviews, and manuscripts published in the last six years have ended with the caveat that, although there is compelling evidence of the ecologic importance of microbiotic crust, there remains a great deal to be learned.

#### **Distribution (life forms and geographic locations)**

Microbiotic crust composition and development are influenced by a variety of environmental conditions. Some authors have primarily associated crust development with fine-textured soils (Anderson et al. 1982a, Danin 1983, Graetz and Tongway 1986), but crusts are also known to develop on sandy soils (Bond and Harris 1964, Marshall 1972). Measurable microbiotic growth requires a minimum of 4 - 5% clay and silt in the sandy Negev and Sinai deserts (Danin 1983: cited by West 1990). Bulk density has little apparent influence on microphytic growth (West 1990). West (1990) noted that microbiotic cover is smoother where associated with relatively high bulk densities, but attributes this characteristic to precipitation and temperature regimes.

Campbell et al. (1989) considered available inorganic nutrients, pH, high Eh (redox potential), temperature, aeration, and biotic interactions as determining factors of microbiotic crust development in the southwestern United States. Danin (1989) found that lifeform diversity was apparently influenced by salt concentrations in the Judean Desert, Israel. Observers note that some areas, such as the Saharan Central Plains, are devoid of lichens due to some combination of wind erosion and inadequate moisture (Llimona 1982). In south-east Australia, Downing and Selkirk (1993) reported that soil texture, pH, conductivity, nutrient status, vascular plant vegetation, light level, leaf litter, and fire frequency played a significant part in determining bryophyte distribution. Assemblages of bryophytes might be used for recognition of calcareous soils (Downing and Selkirk 1993).



Greater diversity in soil microphyte populations has been reported in undisturbed conditions in comparison to areas disturbed by fire, wind, livestock, or human activities (King and Ward 1977, Danin 1978, Zimmerman et al. 1980, Anderson et al. 1982a, Johansen et al. 1984, Andrew and Lange 1986a, Marble and Harper 1989, McCune and Rosentreter 1992). In Texas, a predominance of cyanobacteria over green algae was correlated to disturbed soils with increased pH (King and Ward 1977). Phosphorus availability is a limiting factor for algal growth in some areas (King and Ward 1977). Although the extent of microbiotic crust development is reduced by most soil surface disturbances, species diversity is not always immediately adversely effected. Johansen et al. (1982) and Johansen et al. (1993) reported similar species compositions following fires in Utah and Washington. In Washington, however, *Nostoc commune*'s contribution to soil flora was especially damaged (Johansen et al. 1993). Johansen et al. (1993) found important seasonal differences in soil microphyte taxa. Common filamentous cyanobacterial genera found in microbiotic crusts throughout the western United States are: *Microcoleus*, *Plectonema*, *Schizothrix*, *Nostoc*, *Tolypothrix*, and *Scytonema* (Johansen 1993).

As noted above, land use influences terrestrial algal and cyanobacterial diversity. Algae, cyanobacteria, and nutrients can be transported by overland flow to waterways. King and Ward (1977) hypothesized that cyanobacterial populations would increase in aquatic systems after a shift in edaphic species from green algae in disturbed soils.

Several investigators have examined the edaphic and vascular plant community characteristics that are associated with the presence or absence of moss, lichen, cyanobacterial, and algal species. Howarth (1983) examined perennial moss species in chenopod shrublands, South Australia; Cooke (1955) examined fungi, lichens and mosses on rocks, shrubs and soil in relation to vascular plant communities in eastern Washington and western Idaho; Rosentreter (1986) used ordination to examine relationships between lichens,

vascular plants, and edaphic conditions in rabbitbrush communities on the Boise Plateau. The latter author found a consistent relationship among the various microbiotic species and soil depth, salt concentration, and associated vascular plants. McCune (1992a) recently completed a comprehensive survey of lichens and their habitat in southwestern Idaho with special emphasis on present and past land use influences on microbiotic crusts.

Related to the ongoing study of microbiotic crusts is the identification of component moss, lichen, cyanobacterial, and algal species. Recently, four new mosses have been identified in the shrub-steppe of northwestern North America (Oregon, Washington, and British Columbia): *Crossidium rosei* Williams, *Phascum vlassovii* Lazar., *Pottia wilsonii* (Hook.) B.S.G., and *Pterygoneurum kozlovii* Lazar. (McIntosh 1989). Goward et al. (1994) identified 46 species of lichens and allied fungi heretofore unreported in British Columbia. Terricolous lichens, potential contributors to microbiotic crust development, identified in the semiarid interior of British Columbia (Goward et al. 1994) include: *Aspicilia reptans* (Looman) Wetm. [also reported in Idaho, Oregon, Utah, Wyoming], *Catapyrenium cinereum* (Pers.) Körber, *Catapyrenium squamulosum* (Ach.) O. Breuss, *Fulgensia desertorum* (Tomin) Poelt [also reported in Idaho, Arizona, Utah, Colorado], *Heppia lutosa* (Ach.) Nyl. [also reported in all western states except Idaho, Oregon, and Washington], *Leptogium schraderei* (Ach.) Nyl. [also reported in Utah], *Massalongia microphylliza* (Nyl. ex Hasse) Henssen [also reported in California], *Peltula euploca* (Ach.) Ozenda and Clauz [also reported in arid southwestern North America, Idaho, Washington], *Psora montana* Timbal [also reported in Colorado, Montana, Oregon, Utah, Washington, Wyoming], *Solorinella asteriscus* (Ahlner 1949) [also reported in undisturbed grasslands in Alberta], *Toninia candida* (Weber) Th. Fr. [also reported in Alberta, Arizona, Colorado, Montana, Nevada, New Mexico, South Dakota, Utah, and Wyoming], *Toninia tristis* (Th. Fr.) Th. Fr. [also reported as widespread in western North America including New Mexico

and Arizona], and *Xanthoparmelia planilobata* (Gyelnik) Hale. Many of these species are identified for the first time in British Columbia, but are species found elsewhere in the western United States. It would be a mistake to assume that lichen species found in Arizona or southern Utah microbiotic crusts do not also grow much farther north on the continent.

Recently, a lichen growing in microbiotic crusts of central Oregon, southern California, and southern Idaho has been considered for listing as an endangered species. McCune (1992b) and McCune and Rosentreter (1992) have identified and examined the ecology of *Texosporium sancti-jacobi*, a globally ranked (G2) lichen species. A species with G2 rank is very rare and considered a candidate for listing on the U.S. Fish and Wildlife Service Threatened and Endangered List. *Texosporium sancti-jacobi* currently is an Idaho BLM sensitive species. Microbiotic crusts with *Texosporium sancti-jacobi* have been identified in areas that are flat or nearly flat with noncalcareous, nonsaline, fine or coarse-textured soils developed on noncalcareous parent materials with little evidence of recent disturbance, and moderately sparse to sparse vascular plant vegetation with a dominance by native species (McCune 1992b, McCune and Rosentreter 1992). Microhabitat constraints include the presence of soil mixed with decomposing small mammal scat or organic matter (McCune 1992b, McCune and Rosentreter 1992). Of particular apparent importance is the presence of dead *Poa sandbergii* in stands of *Artemisia tridentata* ssp. *wyomingensis* (McCune 1992b, McCune and Rosentreter 1992). Loss of habitat is considered the major threat to this species. Efforts to limit disruption of microbiotic crust by livestock, plant community conversion to annual species with concomitant increase in fire frequency, and changes in land use from rangeland to agriculture and suburban developments are recommended by McCune (1992b) and McCune and Rosentreter (1992) on appropriate sites to reduce the threat to this species. Fire destroys *Texosporium sancti-jacobi* and recolonization apparently requires from

10 to 20 years. Evidence from disturbed sites in Idaho suggest a resilience if disturbance pressure is removed (McCune 1992b, McCune and Rosentreter 1992).

Persons trained in the identification of mosses, lichens, and algae are necessary if serious consideration is to be given the microphytic components of arid and semiarid ecosystem. Because microphyte response time to environmental changes is potentially shorter than for vascular plants, an understanding of the diversity of microphytes composing microbiotic crusts would be useful in recognizing early changes in arid and semiarid land plant communities (Rosentreter 1991).

### **Nutrient cycling**

Soils stabilized by cyanobacterial growth have been shown to have greater fractions of clay and silt than wind blown sites nearby (Fletcher and Martin 1948, Kleiner and Harper 1972, 1977a, 1977b, Harper and Pendleton 1993). The same relationship in soil texture was found in comparisons of the surface soil with a cyanobacterial-algal crust with the subtending soil horizon (Williams 1993). Clay particles are bound to, and incorporated into polysaccharide material exuded by the cyanobacterium *Microcoleus vaginatus* (Belnap and Gardner 1993). The sheath material and clay particles are negatively charged and thus potentially capable of binding positively charged macronutrients and are rich in organic acids, amino acids, and chelating agents (Lange 1974 & 1976, Belnap and Gardner 1993, Harper and Pendleton 1993). Greater concentrations of extractable phosphorus have been reported in microbiotic crust-influenced soils compared to nearby non-cruste soils (Kleiner and Harper 1972, 1977a). Microbiotic crusts with large concentrations of clay and silt correspond to greater concentrations of organic material, N, exchangeable Mn, Ca, K, Mg, and available P (Harper and Pendleton 1993). Harper and Pendleton (1993) attributed the greater concentrations of Mn, Ca, and P to

soil textural differences but organic matter and N were attributed to the presence of microbiota. Rozanov (1951) noted that microbiotic crust components are important to the breakdown of humus. Research conducted on Hawaiian lava flows suggests that lichen and associated microflora cause biological acceleration of chemical weathering as a result of respiratory CO<sub>2</sub> and the H<sup>+</sup> ions disassociating from organic acids, and reactions facilitated by organic complexing agents (Jackson and Keller 1970). Although pedogenesis is slow in arid land soils, the microphytes that make up microbiotic crusts might facilitate it somewhat (Kieft 1991). Thus, the micro-environment within a microbiotic crust is potentially rich in macronutrients in an otherwise nutrient poor system (Lange 1974 & 1976, Harper and Pendleton 1993).

A potentially important component of mineral cycling occurs when desiccated lichens are rehydrated (Brown and Brown 1991). A number of nutrients, Ca, Cu, Na, and to a lesser extent Mg and Zn, are bonded to the exterior cell walls of lichens (Brown and Brown 1991). When the lichen is wetted, these nutrients are washed from lichen and become available to soil biota. However, care must be taken to quantify the ionic concentrations of rain or snowmelt before assigning contribution values to this process. Brown and Brown (1991) also report a release of soluble intracellular chemicals from dry lichens when wetted. However, insoluble chemicals might only be available to other organisms with the decomposition of the lichen.

Nitrogen is the most important limiting factor, after C, H, and O, to plant growth in arid and semiarid systems (West 1991). Symbiotic and heterotrophic nitrogen-fixing organisms are not common in the arid regions of the Intermountain West (West and SkujiÅš 1977, West 1981) and components of microbiotic crusts might be the most significant source of nitrogen for some (Evans and Ehleringer 1993 & 1994) if not all of these systems (Rychert and SkujiÅš 1974, West and SkujiÅš 1977, Rychert et al. 1978, Schlesinger 1991). Although atmospheric nitrogen fixed by many cyanobacterial, algal, and lichen species in microbiotic crusts has been well documented (Rozanov 1951,

MacGregor and Johnson 1971, West and Skujiš 1977, Skujiš and Klubek 1978a&b), there remain questions about its availability to vascular plants (West 1990). Growth chamber experiments using  $^{15}\text{N}_2$  enriched atmosphere have demonstrated that vascular plants can use nitrogen fixed by microbiotic crusts (Mayland et al. 1966, Mayland and McIntosh 1966, Snyder and Wullstein 1973). Millbank (1978) demonstrated that lichen thalli of *Peltigera canina* and *Lobaria pulmonaria*, mesic system terricolous and corticolous lichens, respectively, release nitrogen into the surrounding environment, when repeatedly wetted and dried. This release might also contribute nitrogen to vascular plants in arid and semiarid environments (Snyder and Wullstein 1973).

Nitrogen usable by vascular plants is made available through wet-fall, dry-fall or biotic fixation. Schlesinger (1991) calculated that atmospheric wet and dry fall nitrogen contributions are  $1.45 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  and  $1.54 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ , respectively. The availability of nitrogen deposited on soil and plant surfaces is debatable. Dry-fall requires moisture before it is dissolved and available, and arid and semiarid lands are source areas for dust storms from which there is a net loss of soil and nitrogen (West and Skujiš 1978, Goudie 1983). Heterotrophic bacteria potentially fix up to  $2 \text{ kg N ha}^{-1}\cdot\text{y}^{-1}$  (Rychert et al. 1978). Microbiotic crusts in the northeastern corner of the Great Basin are estimated to fix  $10\text{-}100 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  during optimal moisture and temperature conditions in fall and spring (Rychert and Skujiš 1974). West and Skujiš (1977) later reported  $25 \text{ kg N ha}^{-1}\cdot\text{y}^{-1}$  for the same area. Estimations for the Sonoran Desert were considerably lower as presented in a review by Rychert et al. (1978), ranging from 7 to  $18 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ . Annual nitrogen use by vascular plants in the Great Basin is estimated at  $\approx 12 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$  (West and Skujiš 1977). Jeffries et al. (1992) reported relatively low input estimates ( $0.7\text{-}3.6 \text{ kg N}_2 \text{ ha}^{-1}\cdot\text{y}^{-1}$  relic site,  $0.4 - 2.0 \text{ kg N}_2 \text{ ha}^{-1}\cdot\text{y}^{-1}$  lightly grazed site, and  $0.02\text{-}0.17 \text{ kg N}_2 \text{ ha}^{-1}\cdot\text{y}^{-1}$  in heavily grazed site) by cyanobacterial (*Microcoleus* and *Scytonema*)-dominated crusts in a blackbrush

community in southern Utah. Notably, Jeffries et al. (1992) questioned whether either cyanobacteria actually fixed nitrogen, attributing the available nitrogen in the crusts to heterotrophic bacteria. However, *Scytonema* has heterocysts, unnecessary except for nitrogen fixation, and the preponderance of evidence supports *Microcoleus* as a nitrogen fixer. Despite low nitrogen concentrations compared to other communities, Jeffries et al. (1992) note that any contribution would be important in this very sandy soil community that has intrinsically low sources of carbon and nitrogen. Bolton et al. (1993) reported that microbial biomass C and N, soil respiration, and soil dehydrogenase were 2-15 times greater in the upper 5 cm soil surface than the subtending 5-15 cm layer. Measurements were taken from beneath *Artemisia tridentata*, *Elytrigia spicata*, and associated microbiotic crusts, and *Bromus tectorum*. From these measurements, they concluded that loss of the surface soil would be detrimental to microbial-mediated nutrient cycling. However, when the above soil characteristics, including phosphatase activity, were compared between communities, they decreased in the following order: *B. tectorum* > *A. tridentata* = *E. spicata* > microbiotic crust. *B. tectorum* samples were from an annual grassland community converted from shrub-steppe in the 1940's whereas *A. tridentata*, *E. spicata*, and microbiotic crust samples were from an undisturbed perennial community.

Evans and Ehleringer (1993) measured  $^{15}\text{N}$  values in sites located in a Utah Juniper woodland (*Juniperus osteosperma*) interspersed with shrubs (*Artemisia tridentata*) without any nitrogen-fixing organisms other than those in microbiotic crusts and concluded that microbiotic crusts were the source of nitrogen for this ecosystem. Belnap (1994 et al., pers. comm.) found that compaction of microbiotic crusts by animals, vehicles (self-propelled howitzers, ORV's, mountain bikes) and disruption by raking all resulted in an immediate 80% reduction in nitrogen fixation. Schlesinger et al. (1990) and Evans and Ehleringer (1993) deductively concluded that disturbances to

microbiotic crusts' ability to fix nitrogen potentially affect changes in the overall plant community due to impaired plant growth and reproduction. The predicted shift is toward plants that are capable of nitrogen fixation and/or tolerant of low nitrogen availability. This model for community structure change is expounded upon by Evans and Ehleringer (1994), by examining <sup>15</sup>N ratios and the nutrient and water acquisition mechanisms of two shrubs, *Artemisia* and *Chrysothamnus*. *Artemisia* is shown to draw nitrogen primarily from just below the soil surface, whereas *Chrysothamnus* is able to draw on nitrogen reserves from soil water deeper in the profile. A shift is predicted to *Chrysothamnus* through a competitive advantage over *Artemisia* as nitrogen availability at the soil surface is disrupted by destruction of microbiotic crusts.

*Microcoleus vaginatus*, a major component of many microbiotic crusts as noted above, is also capable of fixing atmospheric nitrogen. It is unique in that it does not have heterocysts and thus must depend on other mechanisms for excluding oxygen. Evidence from morphologically similar species (*M. chthonoplastes*) suggests that anaerobic conditions are maintained within the polysaccharide sheath that bundles multiple *M. vaginatus* filaments (Belnap et al. 1994). When dry, these cyanobacterial filaments become brittle and little force is required to break them. Breakage thus destroys the integrity of the sheath and permitting oxygen contaminate the interior of the sheath.

Rychert and Skuji<sup>š</sup> (1974) proposed that a lack of organic carbon or inhibitors released from organisms in the algal-lichen crust in some arid and semiarid soils limits heterotrophic nitrogen fixation. Nitrogen fixation begins rapidly within five minutes after wetting cyanobacterial crust (Rychert and Skuji<sup>š</sup> 1974). Other factors that influence the time required for nitrogen fixing to begin are endogenous levels of ATP, ammonium (NH<sub>4</sub>) concentrations, or concentration of other reducing agents (Rychert and Skuji<sup>š</sup> 1974). Rychert and Skuji<sup>š</sup> (1974) reported that nitrogen fixation was lower



beneath shrubs, probably as a result of allelopathic substances from litter and mosses and temperature/moisture regimes. A window of opportunity, when optimal temperature (19° to 23° C°), soil moisture, and light, is needed for optimal cyanobacterial nitrogen-fixation to occur (Rychert and Skujiš 1974).

Cyanobacteria in Great Basin and Colorado Plateau soils are physiologically limited by low temperatures in the early spring and high temperatures during the summer when either snow melt or summer showers provide adequate moisture (Rychert and Skujiš 1974). However, low spring temperatures during snowmelt might be ameliorated by microbiotic black body effect (Harper and Marble 1988, West 1990, Harper and Pendleton 1993). Given that nitrogenase activity occurs rapidly when physical conditions are adequate, these brief periods of nitrogenase activity might make a small but significant contribution to the available nitrogen pool used by surface roots of vascular plant when denitrifier organisms are less active. Eskew and Ting (1978) believed previous research had overestimated nitrogen fixation and that cyanobacterial-algal-lichen crusts fixed relatively small amounts of nitrogen in Colorado Desert conditions. They did, however, recommend that sampling be conducted during periods of rehydration to more accurately assess the potential nitrogen contributions. In accordance with this recommendation, Coxson and Kershaw (1983a) examined nitrogenase activity of *Nostoc commune* during chinook snowmelt sequences. Such snowmelt sequences are diurnal and air and thallus temperatures fluctuate from -20 to +20°C. Although nitrogenase activity was influenced by the temperature, increasing from 0°C, seasonal inactivation did not occur. During summer months, lichens are potentially photosynthetically active for as much as 13 hours a day. They have no apparent mechanisms for water storage or detention but are capable of metabolic activity despite arid conditions because of the ability to imbibe water from dew, rain, or snow deposition (Kappen 1982, Kappen and Rogers 1982, Coxson and Kershaw 1983a). Coxson and Kershaw (1983b) examined the effects of

wetting and drying cycles on *Nostoc commune*. Maximum nitrogenase activity required 14 hours following rehydration at 14 and 21°C. Net photosynthetic compensation occurs within minutes and maximum photosynthetic rates are reached within 80 minutes at 21°C. However, at 7°C, nitrogenase activity is minimal and requires 48 hours after wetting and 6 hours for net photosynthesis. Illumination and temperature influence metabolic processes, specifically nitrogenase activity after sundown, suggesting that nitrogenase activity is dependent upon stored energy reserves. Drawing from these reserves, night nitrogenase activity of  $\approx 1 \text{ g N}\cdot\text{ha}^{-1}$  is possible (Coxson and Kershaw 1983b). Coxson and Kershaw (1983c) found that *Nostoc commune* nitrogenase activity responded rapidly to small rainfall events and dewfall. Maximum nitrogenase activity followed wetting on the previous evening.

Nitrification and denitrification take place at the same time in the same place in microbiotic crusts (Skujiš and Klubek 1978a). The apparent energy source for denitrification is carbon supplied by photosynthesis of the microphytes in the crusts. Greatest nitrogenase activity occurred in the spring with rain, snowmelt or dew. Maximum carbon and nitrogen fixation rates occurred during midmorning coinciding with optimal temperature and moisture availability ( $5.2$  to  $10.0 \text{ g N}\cdot\text{ha}^{-1}\cdot\text{h}^{-1}$  at  $19^\circ$  to  $23^\circ\text{C}$ ). Nearly all of the nitrogen fixed in this period is denitrified within 10 weeks, 20% within one week and 80% within five weeks through volatilization. Skujiš and Klubek (1978a) discounted potential nitrogen availability to vascular plants. This loss is rapid and nearly 20% may be lost in a week, or as much as 80% in five weeks. Shields (1957) argued that fixed nitrogen was incorporated into the living tissue of algae and lichens. Once there, it was postulated that the nitrogen would become available to other organisms with the death of the algae and lichens (Shields 1957, Snyder and Wullstein 1973).

An accurate method to measure absolute quantities of biologically-fixed nitrogen does not exist (Weaver 1986). The acetylene reduction method in

particular has been criticized for over-estimating nitrogen fixation by microbiotic crusts (Weaver 1986, West 1990). The theoretical basis of the method states that  $\frac{1}{2}$  mole of nitrogen is fixed per mole of ethylene but this ratio might vary as much as a factor of four or greater. Because of this variation, estimates of microbiotic crust nitrogen contributions to arid and semiarid land ecosystems are unreliable and are not used in the most recent nitrogen cycle models (Peterjohn and Schlesinger 1990, Evans and Ehleringer 1993). The ethylene:N-fixed ratio must be evaluated for specific substrates if an absolute value is required. If comparisons with previously published research are necessary, the use of the 3:1 ratio must continue (e.g., Jeffries et al. 1992, West 1991). However, the argument has been made that the important issue is not how much nitrogen is fixed, but whether or not nitrogen is fixed and if it is available and/or necessary for vascular plants and community structure (Snyder and Wullstein 1973, Rychert et al. 1978, Harper and Pendleton 1993, Evans and Ehleringer 1994).

#### **Relationships to vascular plants**

Microbiotic crusts and vascular plants exist in a complex inter-relationship that is either competitive, mutualistic, or neutral, depending on the phenologic stage of the organisms, climate, edaphic resources, plant-animal interactions, and resource management. West (1990) discussed competition and successional interactions between vascular plants and the microbiotic crusts. Harper and Marble (1988) reviewed a wide range of experimental research and field survey literature examining microbiotic influence on seedling establishment, but reported that studies specific to arid and semiarid ecosystems were limited at that time.

West (1990) reviewed material that would indicate components of microbiotic crusts are in a 1:1 tradeoff relationship with vascular plants for space and nutrient resources. However, microbiotic crust development has been

positively correlated with floristic diversity in Australia (Graetz and Tongway 1986, Múcher et al. 1988), the Mojave Desert (Meyer 1986), and sites in Utah (Kleiner and Harper 1972 & 1977b), and Arizona (Beymer and Klopatek 1992). Increased seedling (shrubs, perennial and annual grasses) survivorship associated with microbiotic crusts has been demonstrated in greenhouse studies in Utah (St. Clair et al. 1984) and Arizona (Sylla 1987: cited by West 1990) and in field studies in Utah (Harper and Marble 1988), Nevada (Eckert et al. 1986). This positive relation between seedling establishment and diversity has been attributed to microbiotic crust structure providing safe sites and enhanced nutrient and water conditions necessary for plant growth (Mayland and McIntosh 1966, St. Clair et al. 1984, Eckert et al. 1986, Graetz and Tongway 1986, Lesica and Shelly 1992). Seedling establishment in experimental plantings on natural (control -- cyanobacterial-*Collema* dominated microbiotic crust) and scalped plots (Juab and Emery Counties) were evaluated and Utah County plots that had burned in 1978 were evaluated for microbiotic crust cover changes (Harper 1983). In both fine and coarsely textured soils, Harper (1983) found that seedling establishment was higher for both forbs and grasses in crusted areas when compared to areas where the crust had been removed. After one year, 2.8 times more seedlings of various species survived in plots with microbiotic crust in place than in plots where the crust had been scalped (Harper 1983). Species seeded included (Buckhorn reservoir) *Elymus junceus*, *Kochia prostrata*, *Lepidium montanum*, *Sphaeralcea coccinea*, (Tintic Junction) *Elymus junceus*, *Kochia prostrata*, *Linum perenne*, (BLM-USU pasture) *Ceratoides lanata*, *Oryzopsis hymenoides*, and *Sphaeralcea coccinea* (Harper 1983). Seedling survivorship of *Kochia prostrata*, *Lepidium montanum*, and *Sphaeralcea coccinea* was significantly greater in control plots (Harper 1983). *Elymus junceus* was apparently the only species to be positively influenced by the scalping treatment (Harper 1983). All five species growing in the undisturbed crust had survived in greater percentages after three years (Harper and Marble

1988). In a greenhouse study of plants grown in soils with and without cyanobacteria, plant production was four times greater in the cyanobacterial inoculated soil (Harper and Belnap - unpublished data). At four sites in southwestern Montana, juvenile (single sterile rosettes  $\leq$  20 mm diameter) and adult (single sterile rosettes  $\geq$  20 mm diameter, or multiple sterile rosettes) *Arabis fecunda* (Brassicaceae) plants were found in significantly greater numbers than expected in soils with microbiotic crusts (Lesica and Shelly 1992). In one of four sites sampled, greater numbers of juvenile plants were found in crusted soil (Lesica and Shelly 1992). No association of fecundity and presence of microbiotic crust was observed (Lesica and Shelly 1992).

West (1990) discussed the possible morphological adaptations seeds might have to establish in well developed microbiotic crusts. Seeds not adapted to penetrate undisturbed soil are not as likely to germinate and survive as seeds such as *Stipa* that has a hydroscopic awn and setae (West 1990). However, soil properties and degree of microbiotic crust development need to be considered (West 1990, Belnap pers. comm.). An examination of sandy soils with scanning electron microscopy (SEM) shows that adequate space exists for vascular plant root penetration into the soil (Belnap and Gardner 1993). Furthermore, Lesica and Shelly (1992) concluded that enhanced survival of juvenile and adult plants is more important than germination and establishment. Comparison studies of vascular plant cover and microbiotic crust development, in disturbed and protected sites, have ignored the possible differences resulting from the influence of invertebrates and microclimate (West 1990).

Alternatively, the argument has been made that microbiotic crusts are deleterious to vascular plant seedling establishment and community structure (Dulieu et al. 1977). Savory and Parson (1980) made a similar argument, but did not distinguish between microbiotic and non-biologic crusts. In Arizona, McIlvanie (1942) conducted a greenhouse study and found that *Eragrostis lechmanniana* and *Panicum antidotale* would successfully establish on soils from

a bare grazed area, but no seeds germinated on soils from a protected site with an algal-moss crust. However, seeds drilled into the protected soil produced more dry weight than plants grown in soil from the grazed site. Hacker (1986, 1987) reported low total nitrogen and organic carbon concentrations and a lack of suitable seed-bed conditions at sites dominated by microbiotic crusts in Western Australia. Eldridge (1993b) reported a negative correlation between microbiotic cover and plant and litter biomass in eastern Australia. In the Eocenic chalk hills of Israel, Noy-Meir (1990) speculated that production and species diversity of annual plants were limited by edaphic factors, competition from perennial plants, and fewer germination sites on the algal crust covering much of the surface in a livestock enclosure compared to adjacent broken and loose disturbed surfaces. Beymer and Klopatek (1992) stated that reduced microbiotic crust in an ecosystem will not necessarily lead to a change in vascular vegetation structure but they recommended using microbiotic crust as an indicator of ecosystem health because of significant correlations between microbiotic cover and associated vascular plants.

Recent research has focused on plant vigor (production and nutrient content) related to microbiotic crust development. Microbiotic crusts are characteristically dark colored and potentially act as black bodies (Harper and Marble 1988, West 1990, Harper and Pendleton 1993), increasing soil surface temperatures by as much as 15°C (Belnap unpubl. data). As such, there is a potential for elevated soil surface temperatures during periods of increased soil moisture associated with frost or snow melt. Under these conditions, elevated metabolic rates and uptake of nutrients by seedlings and mature plants could occur (Salisbury and Ross 1978, Harper and Pendleton 1993).

Components of microbiotic crusts potentially compete with vascular plants for nutrients. The previous sections discussed the evidence for increased nutrients in soil associated with microbiotic crusts. Examination of plant

tissue grown in microbiotic crust-influenced soils would indicate that the plants are able to make use of the available nutrients. Belnap (1994) reported N, P, K, Fe, Ca, and Mg in greater concentrations of *Festuca octoflora* tissue taken from plants grown in crusted areas protected from trampling for 10 years than in plants taken from a site where crusts (cyanobacterial-*Collema* lichen dominated) had been repeatedly trampled by humans for many years. The same relationship was found for N, Fe, Ca, Mg, and Mn in the native perennial for *Mentzelia multiflora* (Belnap 1994). Crusts associated with *M. multiflora* where either present or covered by wind blown soil. *Lepidium montanum*, taken from plots that three months previously had 1 cm of associated cyanobacterial crust removed, had lower concentrations of elemental nutrients than in plants taken from paired, crusted plots (Harper and Marble 1988). Belnap (pers. comm.) observed that diminutive plants, such as the annual *Festuca octoflora*, root in the soil surface zone of microbiotic influence (0-10 cm depth) and thus are morphologically suited to take advantage of increased nutrient reserves provided by microbiotic crust processes, whereas plants of intermediate stature and root development, such as *Mentzelia multiflora*, often develop mats of ephemeral fine root material just below the soil surface during periods of extended moisture in the spring. In greenhouse studies, *Sorghum halepense* tissue had significantly greater concentrations of N and Zn when grown in soils inoculated with cyanobacteria-*Collema* than non-inoculated soil of similar chemical composition (Harper and Pendleton 1993). However, Ca, P, Mn, and Na concentrations were greater in tissue from plants grown in cyanobacteria-*Collema*-free soil. Harper and Pendleton (1993) interpret these results to mean that (1) N or, perhaps, Zn are growth-limiting in the test soil and (2) *Sorghum* is competing with cyanobacteria for Ca, P, Mn, and Na. A relationship was also found between temperature in the rooting zone and nutrient uptake; N, Ca, Mg, Cu, and Na concentrations in *Sorghum* tissue were significantly greater in plants grown in

the cyanobacterial-*Collema* soil where soil rooting zone temperatures were 5°C warmer (Harper and Pendleton 1993). Competition for P, Fe, and Mn also appeared greater (Harper and Pendleton 1993). Evidence has been provided that cyanobacteria compete for P and Mn with seed plants (Belnap and Harper in review; cited by Harper and Pendleton 1993). Harper and Pendleton (1993) cogently argued that the apparent ability of microbiotic crust components to enhance nutrient uptake by vascular plants, particularly N, Ca, Mg, Na, and P might ultimately benefit herbivores, contributing to bone, eggshell and tooth development, increase protein availability, and decrease the likelihood of grass tetany in ruminants.

Microphytes can also be dependent upon the vascular vegetation present. Rosentreter (1992) states that conversion of shrub-steppe (*Artemisia*) to annual grasslands results in the loss of twisted moss (*Tortula ruralis*), which is found in the shade near the base of *Artemisia*. Cooper and Rudolph (1953) presented evidence that lichens are not necessary for the development of soils in rocky-barren sites for vascular plant establishment, thus bringing into question the classical role of lichens in soil formation and plant succession.

Vesicular arbuscular mycorrhizae (VAM) and microbial species might depend somewhat on the microenvironment provided by well developed microbiotic crusts. VAM infection of annual and perennial plants, collected in southern Utah, was greatest in plants grown in cyanobacterial-*Collema* crusted soils (Harper and Pendleton 1993). Microbial populations are suspected to influence available P for vascular plants (Lajtha and Schlesinger 1988). Phosphorous is important to the energetics of both microphyte and vascular plant growth. The apparently synergistic relationship between microbial species (generally not associated with microbiotic crusts), microbiotic crusts, and vascular plants deserves closer examination.



## **Microbiotic crust influence on soil stability**

Soil erosion is the detachment, entrainment and transport, and accumulation of soil particles at a site other than where the soil particles originated. The development of microbiotic crust in arid and semiarid lands is an accretionary phenomenon in an otherwise erosional setting (Campbell et al. 1989). Microbiotic crusts might act in at least one of two processes in the stabilization and accretion of soil. Danin and Barbour (1982) and Danin et al. (1989) proposed that vascular plants must first become established and trap enough clay and silt to provide an adequate environment for cyanobacterial growth. Once established, cyanobacteria would then contribute to the feedback process of further pedogenic development. Alternatively, Campbell et al. (1989) proposed that algal establishment and growth are necessary for sand stabilization by filament exudate prior to vascular plant community development. Although there is evidence that microbiotic crusts influence soil stabilization processes, it is unlikely that microbiotic crusts alone will halt geologic erosion (Rogers 1974).

A key factor in microbiotic crusts ability to enhance soil stability is their contribution to aggregate structure, and thus, stability. Well developed aggregate structure is a counter force to erosional force created by wind or water. Microbiotic crusts contribute to aggregate structure by binding soil particles within the physical structures of the microphytes and trapping soil particles in gelatinous exudate (Bond and Harris 1964, Marathe 1972, Anantani and 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). Microfaunae living within the crusts comminute detritus and thus indirectly contribute to decomposition of organic matter, thus enhancing soil aggregation and stabilization (Gayel and Shtina 1974, Danin 1978).

Microbiotic crusts might absorb the kinetic energy of rain drops (the force responsible for dislodgment of soil particles) in arid and semiarid environments much the same way as the sward in grasslands (Osborn 1952). Múcher et al. (1988) speculated that raincrusts in New South Wales, Australia, are quickly colonized by algae, which promote aggregate development and protection to mineral soil. Cyanobacterial crusts appeared to contribute to soil stability on micro-plots ( $\leq 2 \text{ m}^2$ ) at sites in Kansas, Oklahoma, and Texas (Booth 1941) and in Arizona (Brotherson and Rushforth 1983). Monoliths with surface areas from  $240 \text{ mm}^2$  to  $6,400 \text{ mm}^2$  and covered with various microbiotic life forms and degrees of development were removed from sites in Australia (Kinnell et al. 1990, Eldridge 1993d) and Utah (Tchoupopnou, 1989) and were subjected to simulated rainfall in laboratories. Soil stability increased with cover and with associated changes in the dominant microbiotic life form: bare soil < algal crust < lichen crust < moss-covered soils. Undisturbed microbiotic crusts are associated with increased soil surface roughness. Evidence from microscopic and microscale research of algal filaments contributing to soil stability has recently been supported at a somewhat larger scale ( $1 \text{ m}^2$  plots) in the Colorado Basin of southern Utah (Williams 1993).

Despite a preponderance of evidence that microbiotic crusts contribute to soil stability, there are exceptions. In the Colorado Basin of southern Utah, the complete destruction of a predominately lichen crust by chaining did not result in significantly increased raindrop erosion in the two years after chaining (Loope and Gifford 1972).

As the composition and diversity of microphyte life forms and species increase to include lichens and mosses, the microtopography becomes more complex, with a potential range of 15 mm (Danin and Barbour 1982) to 100 mm (Belnap pers. comm.) in surface elevation change. This surface roughness creates ponding during light rainstorms and reduces water velocities when overland flow occurs. Sediment deposition and accumulation occurs with

ponding and low water velocity (Brotherson and Rushforth 1983, Alexander and Calvo 1990). In addition to potentially slowing the rate of erosion from a site, this process has the potential for developing into a positive feedback loop (Danin et al. 1989) wherein sediment is collected, especially nutrient-rich silt and clay particles, thus creating microsites for vascular plant germination and growth.

Soil with well developed aggregate stability and a complex surface roughness, both attributes associated with microbiotic crust development, resists soil particle dislodgment by wind (Chepil and Woodruff 1963). Wind erosion has been implicated in the significant loss of nutrients found at the soil surface following disturbance of microbiotic crusts (Fletcher and Martin 1948, Andrew and Lange 1986a, Peterjohn and Schlesinger 1990). As soil particles are blown across the soil surface, particle winnowing and sorting occur. Microbiotic crusts might be responsible for a reduction of these processes (Bond and Harris 1964), however the crusts might enhance winnowing if they occur across a landscape in a patchy distribution wherein particles are trapped and concentrated after being blown from disturbed areas. Dune areas in the Negev Desert, Israel have larger concentrations of clay and silt in areas of developed microbiotic crusts than in mobile dunes (Danin 1978, Tsoar and Möller 1986). This statement is consistent with the contention by Fryberger et al. (1988) and Gillette and Dobrowolski (1993) that microphytes are a controlling factor in the development of accretionary sand sheets. Accretionary sheets develop when hydrated sheaths of algal filaments trap silt and clay size particles as they blow across the microbial mat (Campbell et al. 1989). The algal and cyanobacterial components of microbiotic crusts are phototropic and thus continue the process of upward growth and soil entrapment (Campbell et al. 1989). Algal crusts also reportedly reduce wind erosion on sandy soil in Australia (Bond and Harris 1964, Marshal 1972). In Australia, however, Andrew and Lange (1986a) were unable to show a relationship between increased microbiotic development, a decrease in sheep trampling, and measured

dustfall. Williams (1993) provided evidence from wind tunnel research that microbiotic crusts, both living and dead, enhance soil stability against the forces of wind. That dead algal crusts slow wind erosion is important in light of the finding that microbiotic crusts dominated by moss and algae have remained intact for 6-8 months after wildfire (Johansen et al. 1993).

## **Hydrology**

### *Soil moisture regimes*

Microbiotic crusts potentially influence soil moisture by affecting depth of wetting as a result of infiltration and/or ponding, absorbing solar energy, thus increasing evaporation rates, or by imbibition.

Increased surface detention storage, often associated with well-developed microbiotic crusts, resulted in deeper water penetration in soils at Walnut Gulch Experimental Watershed near Tombstone, Arizona (Abrahams et al. 1988). Deep water penetration (Brotherson and Rushforth 1983), increased aggregate stability (Marathe 1972), and accumulations of silt associated with microbiotic cover (Danin 1978, Brotherson and Rushforth 1983, Williams 1993) are suggested as a mechanism for surface sealing following rainstorms and, thus, reduced evaporation rates and increased soil moisture availability to vascular plants (Danin 1978, Brotherson and Rushforth 1983, Graetz and Tongway 1986). Comparisons of measurements of moisture levels beneath predominately algal crusts and adjacent raincrusts before and after light rainstorms at sites in Kansas, Oklahoma, and Texas were inconclusive (Booth 1941). However, sample size was small ( $n = 3$ ).

Harper and Marble (1988) compared algal-lichen plots interspersed with scalped plots in central Utah and found consistently higher temperatures and significantly less soil moisture in the subtending soil profiles of the undisturbed plots. The differences were attributed to greater absorption of solar energy by the microphytes (Harper and Marble 1988). Meyer and García-

Moya (1989) measured greater microbiotic crust cover on ungrazed sites on semi-arid gypsum plains in northern San Luis Potosí, Mexico. They identified three site types: *Muhlenbergia purpusii*-dominant on exposed gypsum soils with indurated surface crusts, *Bouteloua chasei*-dominant on exposed gypsum soils with microbiotic surface crusts and shallow fine-calcareous alluvial surface soils with gypsum sub-soils dominated by desert shrubland species. All grazed sites had considerably less microbiotic crust (30.0:5.0%, 85.0:22.5%, and 47.5:7.5%, respectively). Soil moisture in the 50 - 100 mm depth range varied throughout the year in each of the identified areas and was greater in the grazed areas.

Various lichens are capable of rapidly absorbing from 1.5 to 13 times their dry weight in water, which can then be slowly used or released (Galun et al. 1982). Cyanobacterial and algal filament sheath material potentially will absorb eight times its weight in water, and thus is considered a critical factor in capture of summer rain (Brock 1975, Campbell 1979, Campbell et al. 1989).

#### *Effective Saturated Hydraulic Conductivity*

Limited and inconclusive research has been conducted to determine the influence of microbiotic crusts on effective saturated hydraulic conductivity ( $K_e$ ).  $K_e$  decreased as lichen-dominated microbiotic crust increased in soil cores collected from a variety of disturbed sites in southern Utah (Loope and Gifford 1972). Lee (1977) hypothesized that algal crusts reduce permeability in arid and semiarid soils of Australia, but did not present data to support his contention. In Australia,  $K_e$  increased fourfold following the removal of the lichen and algal microbiotic crust from a control plot (Greene et al. 1990). In a semiarid woodland in Australia, steady-state infiltration increased with microbiotic development at a grazed site and tended to decrease with microbiotic development at an ungrazed site (Eldridge 1993a), which was

attributed to differences in soil physical properties, e.g., the degree of macroporosity development. At a non-grazed site (35 y) in northern Nevada, vesicular horizons controlled  $K_e$ , not the presence of abundant microbiotic crusts (Dobrowolski 1994). An cyanobacterial-algal crust, protected from large mammalian trampling for three years and dominated by *Microcoleus vaginatus* in south-central Utah, had no apparent influence on  $K_e$  (Williams 1993).

### *Infiltration*

Microbiotic crust influence on infiltration has been reported positive, negative, and neutral. The lack of clear understanding about influence on infiltration is confounded by failure in early reports to discuss in detail the type of microphytes (algae, lichen, moss) in the crust, if the crusts are predominately the result of biological activity or inorganic components (West 1990), or the degree of microbiotic development or disturbance history (Belnap pers. comm.).

Microbiotic crusts might influence infiltration capacities through a number of mechanisms. In general, crust components contribute to aggregate stability and the physical structure, both positive infiltrability factors. Booth (1941), Fletcher and Martin (1948), and Shields and Durrell (1964) proposed that the components of microbiotic crusts reduce development of physico-chemico raincrusts in silt-loessal soils. Uneven microtopography effectively creates small detention dams that increase the tortuosity of overland flow and reduces the site gradient. As a result, flow velocity might be reduced sufficiently to increase the time water has to infiltrate before flowing from the site. The uneven microtopography associated with untrampled microbiotic crusts might either be the result of erosion around stabilized points or the uplifting and subsidence resulting from frost heaving with microphytes stabilizing certain points (Eckert et al. 1989).

Studies specifically designed to study microphyte-induced aggregation influence on infiltration have not supported this contention (Anantani and Marathe 1972, Marathe 1972) or only have inferred the possibility (Bailey et al. 1973, Gifford 1986, Schulten 1985).

Loope and Gifford (1972) reported low infiltration capacities in chained and windrowed pinyon-juniper woodlands compared to undisturbed sites in southern Utah. Greater infiltration in the undisturbed site was attributed to crustose lichen cover, however, permeability inexplicably decreased (Loope and Gifford 1972). At the Reynolds Creek Experimental Watershed in southwestern Idaho, Seyfried (1991) found greater infiltration capacity under sagebrush than in shrub interspaces. This pattern is similar to those found by others (Johnson and Gordon 1988, Johnson and Blackburn 1989) and was attributed to microbiotic mats under sagebrush (Johnson and Blackburn 1989). Increasing fire frequency did not influence unsaturated infiltration rates, but significantly and negatively influenced saturated infiltration rates in eucalypt woodlands of New South Wales, Australia (Greene et al. 1990). Eldridge (1993a) attributed the presence of microbiotic crusts to significantly greater infiltration capacity on some grazed sites but not to ungrazed sites in eastern Australia. Eldridge (1993b) argued that soil physical properties, porosity and aggregate stability are controlling infiltrability factors and that as these properties are damaged, the presence of microbiotic crust becomes more important.

A number of investigators reported no significant influence by microbiotic crusts on infiltration capacity. Booth (1941) found no significant differences in infiltration capacity in plots located in Kansas, Oklahoma, and Texas wherein algae dominated crusts were present or removed and sprayed with a high pressure hose. In Arizona, infiltration capacity was not different between paired growth-chamber plots, half inoculated with cyanobacteria, over a range of rainfall intensities after three months (Faust 1970, 1971). In a Utah field study, infiltration capacity was not different

in comparisons of scalped and control plots in a sandy-loam soil, protected from large mammalian trampling for three years following 90 years of trampling (Williams 1993). In the sagebrush-steppe of southwestern Idaho, microbiotic crusts were not significantly correlated with infiltration capacity within small plots (0.81 to 0.95 m<sup>2</sup>; Johnson and Gordon 1986). However, Johnson and Rosentreter (1988) re-interpreted Johnson and Gordon's (1986) data as showing effective soil loss prevention and increased infiltration capacity under sagebrush canopy in the early stages of rain storms.

A window of opportunity for enhanced infiltration capacity apparently exists between the development of algal-crusts and the length of time they dry between rainstorms. Fletcher (1960), working in the Sonoran Desert of Arizona, reported an increase in infiltration capacities during a brief period after drying and cracking, but a decrease after extended drying periods, apparently the result of the microphytes losing the ability to bind soil and maintain soil surface structure.

A number of investigators reported that microbiotic crusts negatively influence infiltration capacity (Bond 1964, Rogers 1977, Stanley 1983, Brotherson and Rushforth 1983, Graetz and Tongway 1986). Gifford (1972) suggested that "soil microorganism activity" contributed to decreased infiltration rates measured in southern Idaho. Desiccated microphytes imbibe water and swell to several times their dry size. Campbell (1979) described nearly instantaneous imbibition of water, which swelled dehydrated *Microcoleus* sheaths to several times their original size. Dry *Microcoleus* filaments have been observed to expand in less than 15 seconds (Shields and Durrell 1964) and imbibe water 12-13 times that of their sheath volume (Campbell 1977). Intuitively, turgid microphytes could fill soil pore space and create an impermeable seal, thus restricting the downward passage of water and the exchange of soil gasses (Rogers 1977, Graetz and Tongway 1986). Microbiotic crusts, when ground to powder and distributed over a sandy soil in the Caspian



lowlands near Sivash and Turgay, decreased the infiltration capacity by a factor of three (Bolyshhev 1964). Bolyshhev's (1964) findings might simply be the result of adding a large concentration of structureless fine soil material to a porous medium in which the pores are readily plugged. In sandy soils, SEM's show considerable space for passage of water in wetted *Microcoleus*-dominated crusts (Belnap and Gardner 1993).

The concept of a hydrophobic phase created by microbiotic crusts at the soil surface, resulting in decreased infiltration capacity, has received support from several investigators (Bond 1964, Dulieu et al. 1977, Walker 1979, Rutin 1983, Jungerius and van de Meulen 1988). Bond (1964) found a hydrophobic film formed around soil particles encased by basidiomycetes fungi. In dry soils of southeast South Australia, water first infiltrated under vascular plants and the zone of infiltration expanded laterally as the apparent hydrophobicity of fungi-encased soil particles was overcome (Bond 1964).

The microbiotic life form (cyanobacteria, algae, lichen, moss) is another potentially important factor influencing infiltration capacities, as it is in influencing splash erosion (Tchoupopnou 1989). Moss impeded infiltration of ponded water into soils in the Navajo National Monument, Arizona (Brotherson and Rushforth 1983). When the moss was removed, infiltration capacity increased until a shallow subsurface layer of silt became saturated after which infiltration rates decreased. Moss-covered sites had greater infiltration capacity than algal- and lichen-crusts (Brotherson and Rushforth 1983). Graetz and Tongway (1986) reported a significant, threefold increase in infiltration capacity in sandy soils after the lichen crust had been removed in New South Wales, Australia. Yair (1990) has released preliminary results that indicate the removal of thin microbiotic crusts results in increased infiltration capacity and reduced erosion of clays and silts in the Negev, Israel.

Microbiotic crusts potentially influence infiltration capacity, but this influence appears to be secondary to soil attributes (structure and texture) in many cases, and is very likely dependent on the degree of microbiotic development after disturbance. Johnson and Rosentreter (1988) proposed that microbiotic crusts should be included in the USLE model for rangelands. Dobrowolski (pers. comm.) has proposed the same for the Watershed Erosion Prediction Project (WEPP). West (1990) recommended adding microbiotic crusts to monitoring programs to help improve the difficult task of quantifying erosion and land deterioration. Consideration must be given to methodology used to measure infiltration capacity. Many of the above studies, particularly those that showed negative influence by microbiotic crusts on infiltration capacities, were conducted using ponded water. Although this method is a measure of site infiltration capacity, it does not take into account important infiltration processes such as raindrop impact, soil sorting, and pore plugging that occur with natural rainstorms. The ultimate test, which unfortunately will be soil specific, has yet to be conducted. Also, although there is evidence from fence-line contrasts comparing microbiotic crusts that had developed for multiple years since disturbance with adjacent, disturbed sites, to date there has been no manipulative research conducted on such sites or pristine sites.

#### **Quantification and measurement**

Much of the task of quantification and measurement of microbiotic crusts has been accomplished through the efforts of taxonomists. Each life form, bacteria, fungi, algae, lichen, and moss is dealt with by members of different subdisciplines and rarely extends beyond identification and habitat. Recently discovered species have been identified in microbiotic crusts in the Intermountain Area of the western United States (St. Clair et al. 1993) and in southwestern Idaho (McCune 1992a). Thus, the flora is still incomplete.

The details of microbiotic crust development in the majority of studies have not been described in biologically meaningful detail (Belnap 1993). For example, Williams (1993) described cyanobacterial-algal crusts solely on visual observation of the soil surface covered or obviously influenced by microphytes, but did not describe depth or biomass development. Similarly, Cole (1990) observed recovery rates of microbiotic crusts trampled by humans in Grand Canyon National Park, but presented no quantitative discussion of the development, e.g., concentrations of organic matter or change in the depth of the microbiotic-modified layer. Johansen et al. (1993) recommended moistening the soil surface to determine seasonal floristic changes. Belnap (1993) examined the following methods of determining microbiotic crust development and recovery: (1) the use of chlorophyll a to quantify living cyanobacterial and algal components, (2) measured microtopography in microbiotic influenced soils, and (3) assessment of accumulated algal filament material. Visual assessment of moss and lichen cover might be acceptable, but is not satisfactory for determining chlorophyll a development or accumulation of abandoned sheath material in the soil profile or (Belnap 1993). Furthermore, as a result of cyanobacterial motility, empty polysaccharide sheaths give the surface the appearance of greater development than organism counts would support. Spectrophotometrical determination of chlorophyll a in surface soil is considered a time-efficient and reliable measure of crust recovery (Belnap 1993). The ability of microbiotic crusts to fix nitrogen should also be determined.

Although a microbiotic crust might appear continuous, the degree of species variability can be quite large. Grondin and Johansen (1993) reported that the patchiness of algal species can be significantly different on a scale of 0.013 m. Four scales of interest were identified: "(1) microscale patchiness, (2) small scale patchiness that reflects the type and extent of vascular plant cover, (3) a large-scale pattern that reflects differences in

disturbance levels due to grazing livestock, off-road vehicles, or fire, and (4) macroscale patterns due to differences in soil type, altitude, precipitation, annual temperature regimes, and type of vascular plant communities resulting from the sum of these factors" (Grondin and Johansen 1993). Grondin and Johansen (1993) recommended use of composite samples from 0.013 m<sup>2</sup> (based on minimal area calculations) for accurate identification of algal species. Seasonal differences in floristic composition have been observed after wildfire in Washington (Johansen et al. 1993) and in research conducted in central Utah (Johansen and Rushforth 1985). Seasonal changes are poorly understood and studies of microbiotic crust dynamics must take them into account (Johansen et al. 1993). Wheeler et al. (1993) demonstrated the complex heterogeneity of bacterial species population in microbiotic crusts and suggested taking multiple samples across a site, pooling them, and analyzing them for a description of bacterial populations.

West (1990) recommended the use of remote sensing to identify patterns of microbiotic crusts to help elucidate their role in plant community dynamics. O'Neill (1994) identified spectral wavelengths for two soil types with microbiotic cover and a range of moisture conditions in Australia. With this information, microbiotic crust and litter cover were identified during summer months in ungrazed areas. Reflectance was notably different between bare soils and crusted soils with the greatest differences occurring when the microbiotic crusts were wet. Karnieli and Tsoar (1994) reported satellite spectral reflectance differences at the Israel-Egypt border (Negev-Sinai deserts). Vascular vegetation, which is sparse (<30% cover), creates a low reflectance curve compared to microbiotic crusts, which have a darker spectral signature than active sand. Karnieli and Tsoar (1994) concluded that commonly accepted contrasts of the Negev and Sinai are the result of almost complete microbiotic crust cover on the Negev, not differences in vascular plant cover, and attributed the difference in cover to a lack of human and livestock activities in the Negev.

## **Environmental indicators**

Microphytes are potentially sensitive to pollutants because of anatomical structure and ability to rapidly imbibe water and nutrients (West 1990, Rosentreter 1991). Because of these qualities, microphytes, lichens in particular, have served as biological indicators and monitors for over a hundred years (Rosentreter 1991). They are especially useful because they are inexpensive, provide constant monitoring 24 hours a day, and integrate environmental effect over long periods (Rosentreter 1991). Rosentreter (1991) recommended using some or all of the following steps in using lichens to evaluate and monitor sites: (1) record presence or absence of key lichen species, (2) estimate percent coverage by lichens, (3) measure frequency of specific species, (4) record species richness, or (5) measure transplanted lichens for weight gain or loss. Lichens were proposed for use as biological markers by the US Forest Service in Class I Air Sheds as mandated by the Clean Air Act of 1977 (USFS 1987; cited by Rosentreter 1991). As a result of that proposal, a workshop was held (Stolte et al. 1993b) and the then current literature and techniques for using lichens to monitor air quality were discussed and examined. Lichenologists and ecologists familiar with the subject presented information on lichen floristics (Nash et al. 1993), characterization of monitoring sites (Stolte et al. 1993c), lichen species and communities (Smith et al. 1993), identification of lichen species sensitive to pollutants (Belnap et al. 1993), active monitoring with transplants (Pearson 1993), chemical analysis of lichens (Jackson et al. 1993), and case studies as examples of lichen biomonitoring scenarios (Stolte et al. 1993a).

Harper and Marble (1988) reviewed in detail fumigation effect on lichens using industrial pollutants:  $SO_2$ ,  $NO_2$ ,  $O_3$ , F,  $CO_2$ , Zn and Cd. The degree of metabolic responses was largely lichen species and chemical concentration dependent. Generally chlorophyll concentrations, respiration, nitrogenase

activity, and photosynthesis were inhibited with increasing concentrations and extended exposure (Harper and Marble 1988). Unnaturally high levels of SO<sub>2</sub> result in electrolyte loss from thalli, a process that is recommended for monitoring as an early warning of elevated pollution levels (Harper and Marble 1988). Nash and Nash (1974) found that moss reproduction was adversely affected by SO<sub>2</sub> fumigation and recommended monitoring moss regeneration downwind from SO<sub>2</sub> sources. West (1990) cautioned that microphyte response to low chronic levels of pollutants might be different than found in fumigation research.

The response of algal populations in microbiotic crusts is less well known. Metting and Rayburn (1979: cited by West 1990) examined herbicides commonly used on rangelands and found that algal populations are most affected by pre-emergent rather than post-emergent herbicides. The responses of all components of microbiotic crusts to herbicides, fertilizer, insecticides, and soil amendments require more examination (West 1990).

Field studies using microphytes as indicators of airborne pollutants are limited for arid and semiarid lands. Nash et al. (1981) recorded nonhomogeneous patterns of elevated B, Ba, Cu, F, Li, Mn, Mo and Se concentrations in lichens near the Four Corners power plant (Arizona - Utah) with maximum particulate concentrations 2 - 6 km distant. Belnap (1990a) reported patterns of chlorophyll a:phaeophytin ratio and reduced nitrogenase activity in lichens (*Collema tenax*) and elevated sulfur concentrations in cyanobacteria (*Microcoleus vaginatus*) that were apparently associated with the Navajo Generating Station.

### **Disturbance and recovery issues**

Evidence is accumulating that microbiotic crusts are easily damaged by mammalian trampling (livestock, wildlife, humans) and vehicular traffic (Harper and Marble 1988, West 1990). However, West (1990) pointed out many of

the studies cited were "snap-shot" experiments and questioned whether the damage recorded would be persistent, i.e., leading to the loss of microbiotic crusts from heavily trampled sites. Designed experiments, wherein pretreatment site characteristic data are collected and/or treatments are interspersed in time and space, have only recently been instituted. Andrew and Lange (1986a&b) examined piosphere development in Australia and determined that, within months, sheep grazing/trampling sharply depleted lichen frequencies. In central Utah, Belnap et al. (1994) examined microbiotic crusts for nitrogenase activity and chlorophyll content. Pretreatment plot characterization data was collected and treatments were applied, consisting of control (no disturbance) and a combination of disturbances involving a self-propelled howitzer, removal of the microbiotic crust by scalping, and disturbance of plot surfaces with a rake. Nine months after treatment application, no significant differences were found in chlorophyll measures in all but the scalped treatment, however nitrogenase activity was significantly greater (80-100%) in the control treatment than in any of the areas disturbed (Belnap et al. 1994). Although microbiotic components remain in place after compaction or other disturbance, their burial and subsequent death ( $\leq 6$  months) are one likely cause of reduced nitrogenase activity in disturbed soils (Belnap pers. comm.).

Recovery of trampled microbiotic crusts begins within one year with regrowth of cyanobacterial filaments in south-central Utah (personal observation). Belnap (1993) terms this primary recovery. In Arizona, microbiotic crusts visually exhibited little evidence, other than poorly developed microtopography, of disturbance five years after trampling by humans (Cole 1990). Belnap (1993) chronicled the recovery of scalped plots, some of which were then treated with microbiotic inoculum, at four sites in southeastern Utah for periods of three and five years. After one year, scalped plots were visually assessed at 100% cyanobacterial/green algal cover (Belnap 1993). In each of the four areas, the degree of cover and number of species

of lichens and mosses (where originally present) were significantly greater in the control plots than in plots that had been inoculated with microbiotic crusts material from the area, and inoculated plots had significantly greater measures of these attributes than plots that were not inoculated (Belnap 1993). The lichen *Collema tenax*, when present prior to disturbance, was the only lichen present on scalped plots one year following disturbance (Belnap 1993). Measures of chlorophyll a were 2-100% greater in control plots than in disturbed but subsequently inoculated plots and 22-400% greater than in plots disturbed and not inoculated (Belnap 1993). Microtopography measures indicated 41% recovery after five years on non-inoculated plots (Belnap 1993). Belnap (1993) estimated 30-40 years for sheath material replacement in the soil profile, 45-85 years for lichen diversity, and over 250 years for moss cover return. Inoculation of plots with a microbiotic crust slurry resulted in significantly larger population of cyanobacteria, but apparently did not enhance regrowth of green algae and diatoms six months after treatment (St. Clair et al. 1986).

Fire frequency appears to be increasing in the arid and semiarid lands of the western U.S. (West 1988). Microbiotic crusts are temporarily damaged by fire (Harper and Marble 1988, West 1990). The degree of damage and rate of recovery are dependent on pre-fire community structure, fire conditions and frequency, and climate and edaphic conditions. Greene et al. (1990) and Kinnell et al. (1990) reported increased fire frequency in a semiarid woodland of Australia decreased spatial distribution of microbiotic cover but that it recovered to levels found in unburned plots after four years. Johansen et al. (1982, 1984) examined response and recovery processes that followed wildfire (1984) in microbiotic crust dominated by moss and cyanobacteria on the Arid Lands Ecology (ALE) Reserve, Washington, where livestock, human, and off-road vehicles have been restricted since 1943. Patterns of greater algal abundance appeared in the winter following the fire and corresponded to patterns of fire



intensity and *Artemisia tridentata* distribution (Johansen et al. 1993). Species richness was not significantly different between burned and unburned sites, with 74 and 82 taxa, respectively (Johansen et al. 1993). The authors noted that the number of taxa identified were perhaps the greatest number identified at a single site and a result of the intensive sampling conducted for the study.

Recovery after the ALE Reserve burn was the most rapid reported at that time (Johansen et al. 1993). Recovery of similar magnitude has required considerably longer times, three to five years in shrub-steppe (Utah) (Johansen et al. 1982, 1984), and 30 years in blackbrush communities in southern Utah (Callison et al. 1985). The cooler-wetter climate in central Washington is potentially a major factor for the relatively rapid recovery (Johansen et al. 1984). Other differences that might have contributed to the rapid recovery are: soil pH (high in Utah and Arizona, low in Washington) and greater abundance of green algae in Washington (Johansen et al. 1993). Johansen et al. (1993) noted that algal numbers did not increase during the first 16 months following the Washington fire and proposed the following factors, in some combination, for this phenomenon: (1) hydrophobic conditions created by the fire and organic compounds associated with microphytes leading to less infiltration and less available soil moisture, and (2) the possibility that algae require a vascular plant canopy for development.

Recovery of microbiotic crusts is inextricably linked to issues of quantification previously discussed. Evidence presented suggests that the most important attributes of microbiotic crust occur below the soil surface. For instance, sheath material from cyanobacterium filaments contributes to soil organic matter and might play a role in nutrient (cations, water) availability for vascular plants and soil microbes. Sheath material has been found at significantly greater depths in the control plots than in scalped plots, in Utah (Belnap 1993). Finally, the physical integrity of *M. vaginatus*

sheaths, apparently necessary to fix nitrogen, is perhaps the most important aspect of the recovery question.

### Columbia Basin

Precious little research has been conducted on microbiotic crusts in the Columbia Basin (Harper and Marble 1988, Metting 1991, and West 1990). In this review, approximately 5% of the reviewed papers directly addressed microbiotic crusts or related issues in the Columbia Basin or portions of southern Oregon in the Great Basin (Table 1).

Research conducted in the Northwest has largely focused on identification, and relationships with vascular plants. Hydrologic and soil stability studies for this region have not focused on the role of microbiotic crusts, except in a speculative vein. Bioenergetics and nutrient cycling have not been addressed. Of particular interest is the small, but apparent

Table 1. Microbiotic Crust and Related Topics; Research and Papers from the Northwestern United States.

<u>Author</u>	<u>Year</u>	<u>Subject</u>
Cooke	1955	Microphyte and vascular plant relations
Fairchild and Willson	1967	Lichen floristics
Johansen et al.	1993	Recovery from fire
Johnson and Blackburn	1989	Infiltration/soil stability
Johnson and Gordon	1988	Infiltration/soil stability
Johnson and Rosentreter	1988	Infiltration/soil stability
Lesica and Shelly	1992	Microphyte and vascular plant
McCune	1992a	Lichen floristics
McCune	1992b	Lichen floristics
McCune and Rosentreter	1992	Lichen floristics
Metting and Rayburn	1983	Soil conditioner
Rayburn et al.	1982	Algal colonization
Rosentreter	1986	Microphyte and vascular plant
Rosentreter	1991	Lichens as bio-indicators
Rosentreter	1992	Microphyte and vascular plant
Seyfried	1991	Infiltration/soil stability
Zimmerman et al.	1980	Occurrence of cyanobacteria

differences in crust populations from other regions. Johansen et al. (1993) reported that algal flora of microbiotic crusts in central Washington are distinctly different than those found in the Great Basin, Colorado Plateau and Sonoran Desert, where the majority of studies have been conducted in the United States. Studies in the southwestern United States consistently report lower diversity of green algae and xanthophytes than found in central Washington (Johansen et al. 1993). Although a greater ratio of chlorophyte to cyanophyte species was reported for the central Washington soils than has been found in southwestern soils, considerably more cyanophyta taxa were found in the Washington soils (26) than the maximum number reported in studies in Great Basin or Colorado Plateau soils (17) (Johansen et al. 1993). These differences deserve further investigation to determine how they might influence nutrient cycling, recovery rates following disturbance, and soil hydrologic and stability properties.

Currently, three graduate research projects related to microbiotic crusts are in progress in the Northwest. At Boise State, Julie Kaltnecker is examining site rehabilitation following fire, and Kelly Larson is examining grass response in microbiotic crust influenced soils. A third student at Oregon State University is just beginning work with Dr. Bruce McCune and has yet to define a thesis problem.

## **Conclusion**

The literature reviewed supports the argument that microbiotic crusts are an important part of arid and semiarid ecosystems. West (1990) warned of shortcomings in some of the then current research and cautioned against over-generalization. A number of recently completed research projects were designed to avoid some of the shortcomings, such as spatial and temporal interspersions of treatments (e.g., Belnap et al. 1994, Williams 1993). However, the temptation to inappropriately extrapolate results remains,

particularly to the Northwest. As West (1990) points out, the reported influences of microbiotic crusts are not consistently advantageous to vascular plants or soil hydrologic processes. This knowledge alone, however, is not enough to justify ignoring microbiotic crusts in the development of management plans.

Microbiotic crusts were likely more extensive before initiation of current pastoral and agricultural practices in the Intermountain West and the Pacific Northwest. Although present throughout the region, most often microbiotic crusts are most readily observable in sites of low use, e.g., along roadside fencelines and areas inaccessible or uninteresting to livestock and humans (pers. obsv.). We can only speculate what impact their destruction or disturbance has had in larger community processes. West (1990) recommended increased efforts towards developing methods to quantify microbiotic crusts by broad taxonomic, structural or functional groups in order to facilitate research of functions at larger scales. This recommendation came with the warning that failure to begin research on microbiotic crusts' role in community dynamics carried with it the risk of losing some communities (West 1990). In the same vein, Belnap et al. (1994) recommended conservative management of microbiotic crusts until more is understood.

As noted previously, microbiotic crusts have not received much attention in the Northwest. Experimental research is needed to elucidate the influence of microbiotic crusts on nutrient cycling, vascular plant regeneration and vigor, soil hydrologic- and stability-properties, and plant community development and structure. Nutrient cycling and plant community dynamic issues warrant special attention given the conclusions of Jeffries et al. (1992) and Evans and Ehleringer (1993 & 1994).

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