USDA

United States
Department of
Agriculture

Natural Resources
Conservation
Service

6200 Jefferson NE, Room 305
Albuquerque, New Mexico
87109-3734
Phone: (505) 761-4400
Fax: (505) 761-4462

June 29, 1998

NEW MEXICO RANGE TECHNICAL NOTE NO. 82

SUBJECT: INF – PUBLICATION, INTRODUCTION TO MICROBIOTIC CRUSTS BOOKLET

Filing Instructions: File in Range Technical Note Binder.

Explanation:

The enclosed publication, "Introduction to Microbiotic Crusts," was coproduced by the Soil Quality Institute and the Grazing Lands Technology Institute. This Publication provides the latest information to NRCS personnel and landowners on microbiotic crusts and how they impact soils, hydrology, and plant communities. The relative importance of these impacts is not currently understood. This new technology has not been widely recognized or characterized, yet needs to be understood by all people managing ecosystems where microbiotic crust is an important component. This publication should serve as an awareness builder for these organisms. Microbiotic crusts are commonly found throughout the world.

If you require additional information and/or assistance concerning this publication please contact State Rangeland Management Specialist George Chavez at (505)761-4421, E-mail: fchavez@nm.nrcs.usda.gov.

ROSENDO TREVIÑO III
State Conservationist

Enclosure

cc:
George Chavez, State Rangeland Management Specialist, Albuquerque, NM
Herman Garcia, Rangeland Management Specialist, Albuquerque, NM
Saundra Morris, Rangeland Management Specialist, Albuquerque FO
Garth Grizzle, Rangeland Management Specialist, Roswell, NM

United States
Department of
Agriculture

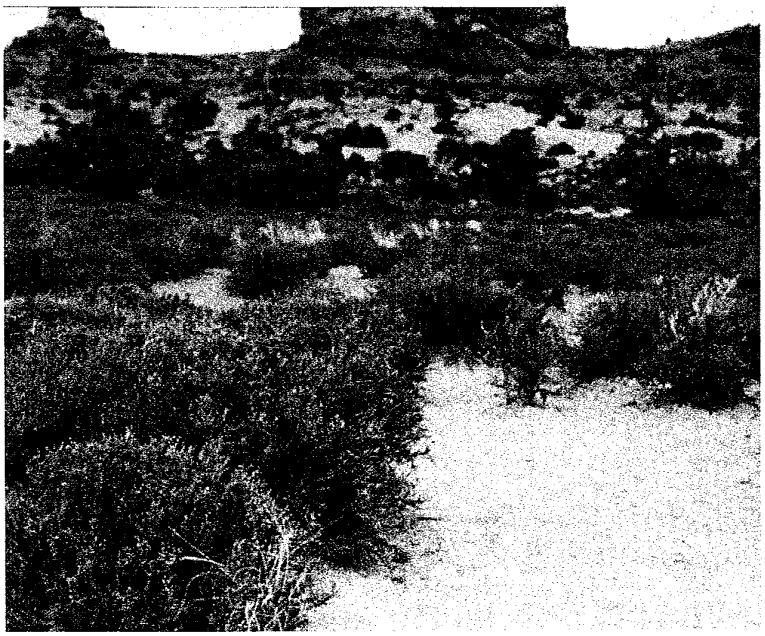
**Natural
Resources
Conservation
Service**

Soil Quality Institute

Grazing Lands
Technology
Institute

Introduction to Microbiotic Crusts

July 1997



Foreword

Introduction to Microbiotic Crusts provides information on a soil-associated component of many plant communities that has not been widely recognized or characterized. The majority of the research on these crusts is limited to the Great Basin and Colorado Plateau regions of the United States. There is validity in generalizing the basic functions of the crusts to wherever crusts are found, given that their gross compositions are similar (cyanobacteria, algae, mosses, lichens, etc.). However, it would not be valid to estimate the general importance of these functions in other regions because species composition does differ between crusts, particularly within the larger components (i.e., lichens, mosses) *(39)*. In addition, the plant composition and functions of associated plant communities where crusts occur differ between regions. Understanding the role of microbiotic crusts in total resource management is an ongoing challenge.

This document was written by Roxanna Johnston, botanist, and includes the comments of numerous reviewers.

Cover
Top photo - mature crust in the Colorado Plateau
Bottom photo - Area without crust
Credits: Jayne Belnap / USGS-Biological Research Division
More information is needed about the functions that crusts perform and the effect of crust disturbance or elimination on the total plant community and production, the soil and the environment.

The United States Department of Agriculture (USDA) prohibits discrimination in its programs on the basis of race, color, national origin, sex, religion, age, disability, political beliefs and marital or familial status. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at 202-720-2600 (Voice and TDD).

To file a complaint, write the Secretary of Agriculture, U.S. Department of Agriculture, Washington, D.C. 20250 or call 1-800-245-6340 (Voice) or (202) 720-1127 (TDD). USDA is an equal employment opportunity employer.

Introduction to Microbiotic Crusts

Microbiotic crusts are commonly found in semiarid and arid environments throughout the world. Areas in the United States where crusts are a prominent feature of the landscape include the Great Basin, Colorado Plateau *(19),* Sonoran Desert *(12),* and the lower Columbia Basin *(23).* Crusts are also found in agricultural areas *(21),* native prairies *(36),* and sandy soils in Glacier Bay, Alaska *(42).* Outside the United States, crusts have been studied in the Antarctic *(13),* Australia *(33),* and Israel *(28),* among other locations. In fact, microbiotic crusts have been found on all continents and in most habitats, leaving few areas crust free *(39).*

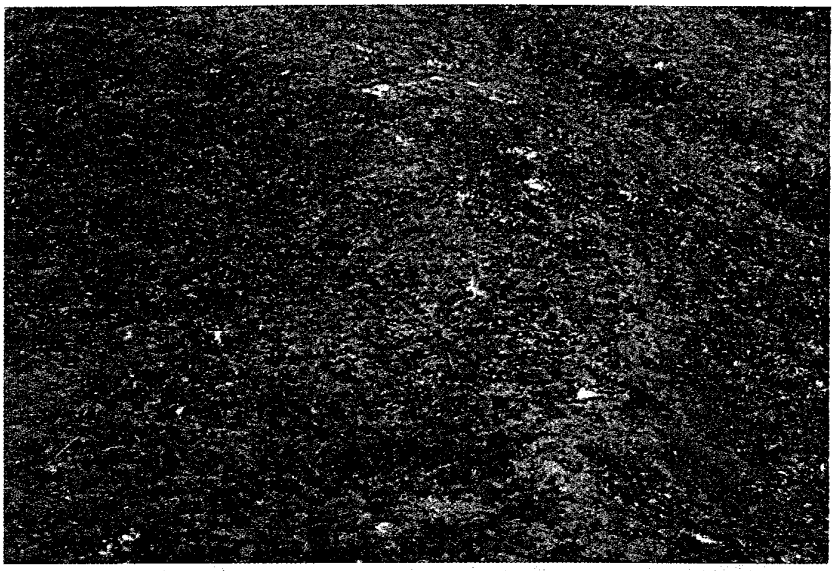
Microbiotic crusts are formed by living organisms and their by-products, creating a surface crust of soil particles bound together by organic materials.

Many names and many forms

Microbiotic crusts are also known as cryptogamic, cryptobiotic, and microphytic, leading to some confusion. The names are all meant to indicate common features of the organisms that compose the crusts. The most inclusive term is probably 'microbiotic' *(38),* referring to the small size of the organisms and not limiting crust components to plants. Whatever name used, there remains an important distinction between these formations and physical or chemical crusts.

Microbiotic crusts are formed by living organisms and their by-products, creating a crust of soil particles bound together by organic materials. Chemical and physical crusts are inorganic features, such as a salt crusts or platy surface crusts.

Figure 1—Utah
The general appearance of crusts in terms of color, surface topography and surficial coverage varies in different regions.(Jayne Belnap / USGS-Biological Research Division)



Characteristics and formation

Microbiotic crusts are formed by living organisms and their by-products, creating a surface crust of soil particles bound together by organic materials. Aboveground crust thickness can reach up to 10 cm *(39)*. The general appearance of the crusts in terms of color, surface topography, and surficial coverage varies (figs. 1-4). Mature crusts of the Great Basin and Colorado Plateau are usually darker than the surrounding soil. This color is due in part to the density of the organisms and to the often dark color of the cyanobacteria, lichens, and mosses. The presence or absence of a crust is partly determined by soil texture and conductivity, pH, moisture, and possibly temperature *(15, 21, 22)*. Crust coverage varies greatly, from less than 10 percent to nearly 100 percent *(39)*.

Figures 2, 3, and 4.
The general appearance of crusts in terms of color, surface topography and surficial coverage varies in different regions.
Fig. 2—Santa Barbara Island, California;
Fig. 3—southern Arizona;
Fig. 4—Salmon, Idaho)
(Figs 2 and 3: Jayne Belnap / USGS-Biological Research Division.
Fig 4: Julie Kaltenecker/USDI-BLM)

Some crusts are characterized by their marked increase in surface topography, often referred to as pinnacles or pedicles *(3)*. Other crusts are merely rough or smooth and flat *(22)*. The process of creating surface topography, or pinnacling, is due largely to the presence of filamentous cyanobacteria and green algae (fig. 5). These organisms swell when wet, migrating out of their sheaths. After each migration new sheath material is exuded, thus extending sheath length. Repeated swelling leaves a complex network of empty sheath material that maintains soil structure after the organisms have dehydrated and decreased in size *(7)*. A contributing mechanism is frost heaving and subsequent uneven erosion, leaving soil mounds bound by crust organisms. Lack of frost heaving has been used to explain the absence of pinnacles in warmer regions *(39)*.

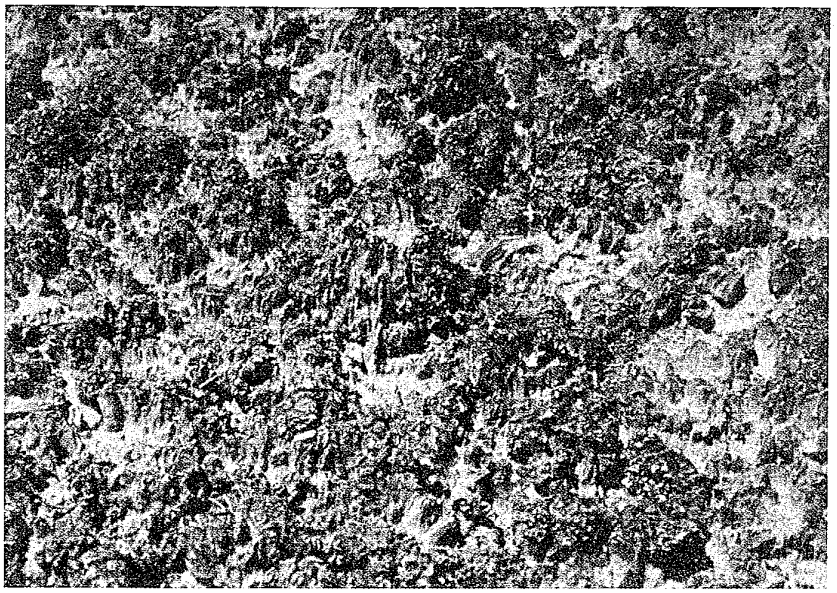


Figure 5
Pinnacles are formed by sheaths of cyanobacteria as they extend in length and bind soil particles together. Frost-heaving also causes sheath-bound particles to rise. (Jayne Belnap / USGS-Biological Research Division)

Glossary

algae	nonvascular photosynthetic plant-like organisms, they are informally divided into groups by their dominant pigments (i.e., green, brown, red, etc.).
bacteria	microscopic, single celled organisms.
cyanobacteria	photosynthetic bacteria formerly called blue-green algae, their growth forms tend to be filamentous.
fungi	nonphotosynthetic multicellular organisms that are either saprophytic or parasitic.
hyphae	single strands of a fungus.
lichen	a composite plant consisting of fungi living symbiotically with algae or cyanobacteria.
	liverworts and mosses – nonvascular plants of small stature, the two are similar with the exception of reproductive methods.
rhizines/rhizoids	root-like structures of lichens and mosses respectively, they are used for attachment.
sheaths	external coating formed by some filamentous cyanobacteria, those discussed in the article are formed from polysaccharides.

Composition

Microbiotic crusts are predominantly composed of cyanobacteria (formerly blue-green algae), green and brown algae, mosses, and lichens (figs. 6-8). Liverworts, fungi, and bacteria can also be important components. Cyanobacteria or green algae make up a large component of microbiotic crusts in semiarid and arid regions of the United States.

In the Great Basin and the Colorado Plateau, *Microcoleus vaginatus* (a cyanobacteria) composes the vast majority of the crust structure *(10, 3)*. Lichens of the genera *Collema spp.* and mosses from the genera *Tortula spp.* are also common *(3, 4, 26)*. In hot deserts, such as the Sonoran, *Schizothrix* species (another cyanobacteria) are more common *(12)*. Lower Columbia Basin crusts tend to be dominated by green algae *(23)*. Shifts between green algal and cyanobacterial dominance have been attributed to changes in pH, with decreasing alkalinity (pH) favoring green algae *(23, 27)*. Crusts from other regions can be dominated by lichens and/or mosses. The organism that dominates the crust is partly determined by microclimate and may also represent different successional stages *(39)*.

Figures 6, 7, and 8
Microbiotic crusts may include cyanobacteria, green and brown algae, mosses, and lichens.
(Figs 6, 7: Mike Pellant/USDI-BLM
Fig 8: Pat Shaver/NRCS)

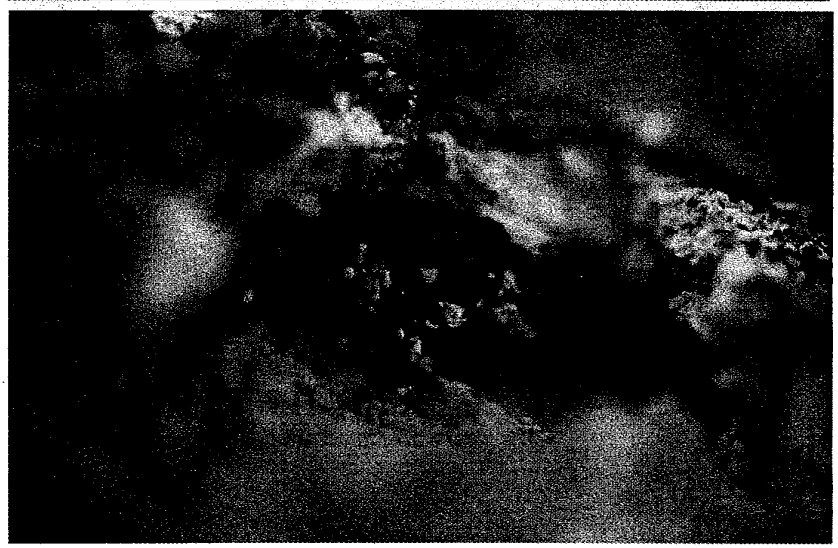


Figure 9
Polysaccharide sheaths of cynobacteria and green algae bind soil particles together. (Jayne Belnap / USGS-Biological Research Division)

Figure 10
Sheaths are at the soil surface. Soil particles are attached to the sheaths. (Jayne Belnap / USGS-Biological Research Division)

Functions

Crusts contribute to a number of functions in the environment. Because they are concentrated in the top 1 to 4 mm of soil, they primarily effect processes that occur at the land surface or soil-air interface. These include soil stability and erosion, atmospheric N-fixation, nutrient contributions to plants, soil-plant-water relations, infiltration, seedling germination, and plant growth.

Soil stability

Crust forming cyanobacteria and green algae have filamentous growth forms that bind soil particles (figs. 9-10). These filaments exude sticky polysaccharide sheaths around their cells that aid in soil aggregation by cementing particles together *(13, 7)*. Fungi, both free-living and as a part of lichens, contribute to soil stability by binding soil particles with hyphae *(1, 19, 36)*. Lichens and mosses assist in soil stability by binding particles with rhizines/rhizoids, increasing resistance to wind and water action *(2, 36)*. The increased surface topography of some crusts, along with increased aggregate stability, further improves resistance to wind and water erosion *(33, 40, 41)*.

Nutrient contributions

Microbiotic crusts can increase available nitrogen as well as other nutrients in the soil. This process is almost solely based on the cyanobacterial component of the crust, whether free-living or as part of lichens. It has been estimated that microbiotic crusts fix 2-41 kg N/ha/yr, though these numbers may be inflated due to the method of measurement *(39)*. Crusts can be the dominant source of fixed N in semiarid ecosystems *(37, 17)*, and this nitrogen appears to be available to higher plants *(32)*. Part of the increasing nutrient availability might be due to the ability of the cyanobacterial sheaths to directly bind positively charged molecules *(8)*. Phosphorus levels are also increased in soils with well developed crusts. This increase is accomplished by the binding of soil fines, which are relatively high in phosphorus content *(19)*.

Increased nutrient levels are most evident near the soil surface due to the dependence of the organisms on light. Maximum input of nitrogen and other minerals occurs when the organisms are most active. Photosynthesis and nitrogen fixation optimal temperatures are 75 to 86 degrees F and 51 to 61 degrees F respectively *(10, 34, 35)*. Photosynthesis in green algae has been shown to be particularly sensitive to high temperatures *(24)*. Moisture levels are also important. Photosynthesis maximizes when the soil surface is near saturation, and nitrogen fixation maximizes when the plant moisture level is between 60 and 80 percent *(19, 10, 15)*.

Water relations

Crust organisms are quickly able to utilize moisture from dews *(10)* and, in the case of green algae, water vapor *(37)*. An investigation of cyanobacteria and green algae in Death Valley determined that certain species of algae could retain water against an osmotic pull of 50 atmospheres (-50.7 bars) *(16)*. This ability to retain water under high tension might be beneficial to survival in dry habitats. Many crust organisms are extremely drought tolerant, but this does not ensure continuous growth and functioning. Crust samples from Idaho (predominantly *Microcoleus vaginatus*) were shown to be particularly sensitive to moisture levels. Photosynthesis and growth in cyanobacteria dominated crusts were inhibited at -18 bars and -7 bars respectively *(10)*. Lichens do not appear to be as sensitive to moisture levels *(19)*.

The water holding capacity of crust organisms has been proposed to benefit surrounding vegetation by slowing evaporation. It has also been proposed that this ability to hold water may be so strong as to prevent vegetation from accessing it, thereby decreasing available water. So far, a conclusion has not been reached on this issue.

Microbiotic crust functions include:

- -soil stability and erosion
- -atmospheric N-fixation
- -nutrient contributions to plants
- -soil-plant-water relations
- -infiltration
- -seedling germination
- -plant growth

Infiltration

Microbiotic crusts can alter infiltration. Some studies have shown increases in infiltration in the presence of crusts *(11, 30);* this is usually attributed to increased aggregate stability. Other studies found either decreases in infiltration or no effect *(18, 40).* Differences in findings seemed to be site specific and were often related to soil texture and chemical properties of the soil.

Effects on plant germination and growth

Studies investigating the role of crusts in plant germination have had varied results. Increased surface relief is presumed to provide safe sites for seeds while darker surface color increases soil temperatures to those required for germination earlier in the season, coinciding with spring water availability *(6, 19).* While the above conditions should favor seed germination, not all studies have supported this conclusion. Conflicting results might be reconciled by these considerations: 1) seeds that become worked into the crust will more likely be able to benefit from the crust environment than those that remain on the surface, and 2) seed size and degree of crust pinnacling may determine whether the crust environment is beneficial to germination and establishment *(29).*

Studies on plant health are more clear-cut. Many studies have shown increases in survival and/or nutrient content in crust covered environments as opposed to bare soil *(8, 19, 29),* though these results are not universal *(19).* Nutrients shown to increase in plant tissues grown in the presence of crusts are nitrogen, phosphorus, potassium, iron, calcium, magnesium, and manganese *(5, 8).* Some of the plants benefited by crust presence include *Festuca octoflora* (sixweeks fescue), *Mentzelia multiflora* (desert blazing star) *(5, 8), Arabis fecunda* (rock-cress) *(29), Kochia prostrata* (prostrate summercypress), *Linum perenne* (blue flax), *Lepidium montanum* (mountain peppergrass), and *Sphaeralcea coccinea* (scarlet globemallow) *(20).*

Response to disturbance

Microbiotic crusts are well adapted to severe growing conditions, but poorly adapted to compressional disturbances. Domestic livestock grazing, and more recently, tourist activities (hiking, biking, and ORV's) and military activities place a heavy toll on the integrity of the crusts (fig. 11). Disruption of the crusts brings decreased organism diversity, soil nutrients, and organic matter (9).

Direct damage to crusts usually comes in the form of trampling by humans and livestock. Trampling breaks up the sheaths and filaments holding the soil together and drastically reduces the capability of the soil organisms to function, particularly in nitrogen fixation *(9, 6, 17).* Changes in plant composition are often used as indicators of range health. This indicator may not be sensitive enough to warn of damage to microbiotic crusts *(31).* Studies looking at trampling disturbance have noted that losses of moss cover, lichen cover, and cyanobacterial presence can be severe (1/10, 1/3, and 1/2 respectively) *(2),* runoff can increase by half, and the rate of soil loss can increase six times *(20)* without apparent damage to vegetation. Adding nitrogen to the soil can retard natural nitrogen fixation by soil organisms *(19).*

Other disturbance impacts are indirect. Several native rangeland shrubs (*Artemisia tridentata*, *Atriplex confertifolia*, and *Ceratoides lanata*) may have allelopathic effects on the nitrogen fixing capabilities of crusts, potentially lowering nitrogen fixation by 80 percent *(35)*. Actions that increase the shrub component, such as excessive grazing, can have an unexpected impact on crust functioning.

Another indirect disturbance occurs through crust burial. When the integrity of the crust is broken through trampling or other means, the soil is more susceptible to wind and water erosion. This soil can be carried long distances, covering intact crusts. Crusts tolerate shallow burial by extending sheaths to the surface to begin photosynthesis again. Deeper burial by eroded sediment will kill crusts *(37)* (fig. 12).

Fire is a common component of many regions where microbiotic crusts grow. Investigations into the effects of fire on crusts show that fires can cause severe damage, but that recovery is possible *(25)*. The degree to which crusts are damaged by fires apparently depends on the intensity of the fire. Low intensity fires do not remove all the structure of the crust allowing for regrowth without significant soil loss (fig. 13). Shrub presence (particularly sagebrush) increases the intensity of the fire, decreasing the likelihood of early vegetative or crust recovery *(23)*.

Full recovery of microbiotic crusts from disturbances is a slow process, particularly for mosses and lichens *(4)*. There are means to facilitate recovery. Allowing the cyanobacterial and green algae component to recover will give the appearance of a healthy crust. This visual recovery can be complete (with the exception of lichens and mosses) in as little as 1 to 5 years given average climate conditions *(14, 4)*. Limiting the size of the disturbed area also increases the rate of recovery provided that there is a nearby source of inoculum *(4)*.

Figure 11
Crust disturbance along a trail breaks up the sheaths and filaments that bind the soil together. (Jayne Belnap / USGS-Biological Research Division)
Figure 12
Burial by wind blowing sand will kill crusts. (Jayne Belnap / USGS-Biological Research Division)

Future research

Information on microbiotic crusts is based on a small amount of research—most of which is from arid or semiarid regions. More studies are needed, especially those that expand into other ecological regions. Most pressing is the need to learn more about the functions of the crusts, such as soil stability, nutrient contributions, soil-plant-water relations, infiltration, seedling germination and plant growth. Information on the relative importance of these functions in different ecosystems is also needed. This understanding is necessary to determine the management strategies needed to protect or favor the development and functions of the crusts. Additional areas of research are 1) learning how crust composition and functions vary with climate, soil texture, soil chemical composition, and plant community, 2) how function correlates to differences in the composition and appearance of crusts, and 3) the effect of management practices on crusts.

The land where crusts occur is used for a wide range of purposes—from grazing and recreation to military uses, and in some places, crops. Ultimately, land managers want to know how the functions of crusts change under different practices. Where the functions of crusts are impaired or eliminated because of land use practices, and are essential to the health of the ecosystem, land managers need guidelines to adapt their practices to protect or restore the functions of crusts.

Where the functions of crusts are impaired or eliminated because of land use practices, and are essential to the health of the ecosystem, land managers need guidelines to adapt their practices to protect or restore the functions of crusts.

Figure 13
Microbiotic crust in a 1983 seeding (crested wheatgrass, Siberian wheatgrass and bluebunch wheatgrass) following a 1996 fire. The crust remained intact between the burned bunchgrass clumps. (Julie Kaltenecker/USDI-BLM)

For further reading see the References section and:

Harper, K.T., and J.R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands *in* Vegetational Science Applications for Rangeland Analysis and Management. P.T. Tueller (ed.). Kluwer Academic Publishers. Dordrecht, Netherlands. Articles in the Great Basin Naturalist, volume 53, 1993.

Johansen, J.R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. Journal of Phycology 29:140-147.

References:

1. Anderson, D.C., K.T. Harper, and R.C. Holmgren. 1982a. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management 35(2):180-185.
2. Anderson, D.C., K.T. Harper, and S.R. Rushforth. 1982b. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Journal of Range Management 35(3):355-359.
3. Anderson, D.C., and S.R. Rushforth. 1977. The cryptogam flora of desert soil crusts in southern Utah, U.S.A. Nova Hedwigia 28(4):691-729.
4. Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. Great Basin Naturalist 53(1):89-95.
5. Belnap, J. 1994. Potential role of cryptobiotic soil crusts in semiarid rangelands. USDA, Forest Service, Intermountain Forest and Range Experiment Station. General Technical Report. INT 313:179-85.
6. Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. Environmental Monitoring and Assessment 37:39-57.
7. Belnap, J., and J.S. Gardner. 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53:40-47.
8. Belnap, J., and K.T. Harper. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Research and Rehabilitation 9:107-115.
9. Belnap, J., K.T. Harper, and S.D. Warren. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content, and chlorophyll degradation. Arid Soil Research and Reha bilitation 8:1-8.
10. Brock, T.D. 1975. Effect of water potential on a *Microcoleus* (cyanophyceae) from a desert crust. Journal of Phycology 11:316-320.
11. Brotherson, J.D., and S.R. Rushforth. 1983. Influence of cryptogamic crusts on moisture relation ships of soils in Navajo National Monument, Arizona. Great Basin Naturalist 43(1):73078.
12. Cameron, R.E. 1960. Communities of soil algae occurring in the Sonoran Desert in Arizona. Journal of Arizona Academy of Science 1(85-88).
13. Cameron, R.E., and J. R. Devaney. 1970. Antarctic soil algal crusts: scanning electron and optical microscope study. Transactions of the American Microscopical Society 89(2):264-273.
14. Cole, D.N. 1990. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. Great Basin Naturalist 50(4):321-325.
15. Dunne, J. 1989. Cryptogamic soil crusts in arid ecosystems. Rangelands 11(4):180-182.
16. Durrell, L.W. 1962. Algae of Death Valley. Transactions of the American Microscopical Society 81:267-273.

17. Evans and Ehleringer. 1993. Broken nitrogen cycles in arid lands: evidence from N15 of soils. Oecologia 94:314-317.
18. Graetz, R.E., and D.J. Tongway. 1986. Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semiarid chenopod shrubland.Australian Journal of Ecology 11:347-360.
19. Harper, K.T., and J.R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands *in* Vegetational Science Applications for Rangeland Analysis and Management. P.T. Tueller (ed.). Kluwer academic publishers. Dordrecht, Netherlands.
20. Harper, K.T., and L.L. St. Clair. 1985. Cryptogamic soil crusts on arid and semiarid rangelands in Utah: effects on seedling establishment and soil stability. Final report Bureau of Land Management, Utah State Office, Salt Lake City.
21. Hilton, R.L., and F.R. Trainor. 1963. Short communication: algae from a Connecticut soil. Plant and Soil 19:396-399.
22. Johansen, J.R. 1993. Crytogamic crusts of semiarid and arid lands of North America. Journal of Phycology 29:140-147.
23 Johansen, J.R., J. Ashley, and W.R. Rayburn. 1993. Effects of rangefire on soil algal crusts in semiarid shrub-steppe of the lower Columbia Basin and their subsequent recovery. Great Basin Naturalist 53(1):73-88.
24. Johansen, J.R., and S.R. Rushforth. 1985. Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah. Great Basin Naturalist 45(1):14-21.
25. Johansen, J.R., and L.L. St. Clair. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. The Bryologist 87(3):238-243.
26. Johansen, J.R., and L.L. St. Clair. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. Great Basin Naturalist 46(4):632-640.
27. King, J.M., and C.H. Ward. 1977. Distribution of edaphic algae as related to land usage. Phycologia 16(1):23-30.
28. Lange, O.L., G.J. Kedion, B. Budel, A. Meyer, E. Kilian, and A. Abeliovich. 1992. Taxonomic composition and photosynthetic characteristics of the 'biological soil crusts' covering sand dunes in the western Negev Desert. Functional Ecology 6(5):519-527.
29. Lesica, P., and J.S. Shelly. 1992. Effects of cryptogamic soil crust on the population dynamics of *Arabis fecunda* (Brassicaceae). American Midland Naturalist 128:53-60.
30. Loope, W.L., and G.F. Gifford. 1972. Influence of a soil microfloral crust on select properties of soils under Pinyon-Juniper in southeastern Utah. Journal of Soil and Water Conservation 27:164-167.
31. Marble, J.R., and K.T. Harper. 1989. Effect of timing of grazing on soil-surface cryptogamic communities in a Great Basin low-shrub desert: a preliminary report. Great Basin Naturalist 49(1):104-107.
32. Mayland, H.F., and T.H. McIntosh. 1966. Availability of biologically fixed atmosphere nitrogen-15 to higher plants. Nature 209:421-422.
33. Mucher, H.J., C.J. Chartres, D.J. Tongway, and R.S.B. Greene. 1988. Micromorphology and significance of the surface crusts of soils in rangelands near Cobar, Australia. Geoderma 42:227-244.
34. Pentecost, A. 1985. Relationships between light, temperature and photosynthesis in a temperate *Microcoleus* (cyanobacterium) mat. Microbios 43:141-148.
35. Rychert, R.C., and J. Skujins. 1974. Nitrogen fixation by blue-green algae-lichen crusts in the Great Basin Desert. Soil Science Society of America Proceedings 38:768-771.
36. Schulten, J.A. 1985. Soil aggregation by cryptogams of a sand prairie. American Journal of Botany 72(1):1657-1661.

37. Shields, L.M., C. Mitchell, and F.Drouet. 1957. Alga- and lichen-stabilized surface crusts as soil nitrogen sources. American Journal of Botany 44:489-498.
38. St. Clair, L.L., and J.R. Johansen. 1993. Introduction to the symposia on soil crust communities. Great Basin Naturalist 53(1):1-4.
39. West, N.E. 1990. Structure and Function of soil microphytic crusts in wildland ecosystems of arid and semiarid regions. Advances in Ecological Research 20:179-223.
40. Williams, J.D., J.P. Dobrowolski, and N.E. West. 1995a. Microphytic crust influence on interrill erosion and infiltration capacity. Transactions of the American Society of Agricultural Engineers 38:139-146.
41. Williams, J.D., J.P. Dobrowolski, N.E. West, and D.A. Gillette. 1995b. Microphytic crust influence on wind erosion. Transactions of the American Society of Agricultural Engineers 38(1):131-137.
42. Worley, I.A. 1973. The "black crust" phenomenon in upper Glacier Bay, Alaska. Northwest Science 47(1):20-29.