An Overview of Cryptobiotic Soils in The American Southwest

By Casey D. Allen, Geographer, Ed.M

Introduction

What is cryptobiotic soil? How is it formed? What are its functions? Why is it important to the desert eco-systems? When first seen by most people, cryptobiotic or cryptogamic soils are not recognized as communities of living organisms. Cryptobiotic soils are the relatively dark-colored crust that covers nearly 70% of the soil in the desert regions of Arizona, California, New Mexico, and Utah (the American Southwest). (Belnap J., Gardner J.S., 1993) Although different stands of cryptobiotic soils have been studied for many years, the functions and benefits of cryptobiotic soils are understood by very few people.

Before the importance of cryptobiotic soils can be understood, a basic knowledge of how cryptobiotic soils function as a community of organisms is necessary. Mainly an understanding of the composition of cryptobiotic soils and how they grow, mature, and function.

Summary

Cryptobiotic soils are dominated by cyanobacteria (blue-green algae). Cyanobacteria were the first organisms to leave a fossil record dating back 3.5 billion years. Other members of the cryptobiotic soil community include green and brown algae, lichens, and mosses. These are the basic members of cryptobiotic soils. All of these organisms are autotrophic (make their own food) and need only sunlight, water, carbon dioxide, nitrogen, and a few other nutrients to survive. Working together, this community is able to colonize areas of soil and will aid with the creation of healthy soil so it can be occupied by new plant life. (Belnap J., Gardner J.S., 1993)

The Roles of Algae

Cryptobiotic soils contain the microorganism *Microcoleus vaginatus*, a member of the algae kingdom. *Microcoleus v.* is surrounded by a sticky polysaccharide sheath that swells and expands when wetted. During this process small, thread-like filaments extend throughout the soil. As *Microcoleus v.* absorbs more moisture, it produces additional filaments that form a sticky, net-like structure throughout the sandy desert soils. As *Microcoleus v.* and the soil dry, the now-intertwined filaments try to retract back into the sheath. By retracting, the filaments pull the net-like structures tight and bind large areas of soil together. Although these small, sticky net-like structures cover much of the soil's surface, roots of higher plants are still able to penetrate the soil between the sheaths of the *Microcoleus v.* (Belnap J., Gardner J.S., 1993)

To be self-sufficient, plants use a process known as photosynthesis. During photosynthesis plants take in oxygen, carbon dioxide, and mineral nutrients. Then, in the presence of sunlight, plants produce sugars, starches, and enough oxygen and carbon dioxide to be self-sufficient. Chlorophyll a, which is abundant in the algae of cryptobiotic soils, helps provide for the release of oxygen into the atmosphere. The algae works in conjunction with the mosses and lichens to produce organic matter that is distributed throughout the soil and allows higher plants to take root and grow. (MacGregor A.N., Johnson D.E., 1971)

The Roles of Lichens

Lichens are another important member of the cryptobiotic soil community. Plants need an abundance of nitrogen to develop roots and grow properly. Lichens provide a nitrogen-fixation process in desert soils. These organisms gather gaseous nitrogen molecules from the atmosphere and combine them into compounds that aid in the growth and development of higher desert plant life. Nitrogen fixation is a very important developmental process, but also very delicate. Lichens in cryptobiotic soil communities, can be easily damaged by a simple hoof-print of an animal or a foot step of a man. (Rychert R.C., Skujins, 1974) While cyanobacteria is readily reproduced in cryptobiotic soils, lichens that conduct the nitrogen fixation process are not. Lichens in communities of cryptobiotic soil can take 50 years or more to return to the stage of nitrogen fixation that was present before they were damaged.(Belnap J., et. al., 1994)

The Roles of Mosses

Mosses occur during the more advanced stages of growth in cryptobiotic soil communities and aid greatly in the stabilization and strength of the fragile desert soil. Like the filaments in the *Microcoleus v.* the roots of mosses also have the ability to bind and adhere particles of soil together. The small roots of the mosses easily penetrate the sheaths of *Microcoleus v.*, where they reinforce the strength of the already supportive filaments. Mosses also aid in water infiltration into the soil, and allow the other organisms in the community to collect and take-up water. Combined with the cyanobacteria, algae, and lichens, the mosses help create a roughened, microtopographic surface that decreases water run-off by creating "rain puddles". "Rain puddles" trap and disperse precipitation throughout the entire area where growth is occurring. While performing these functions, mosses aid in the prevention of erosion caused by water, wind, animals, or even people. (Belnap J., 1994)

Conclusion

Cryptobiotic soil communities are the essential first step in producing arable soils in a desert eco-system. These small, delicate organisms live a tenuous existence, subject to the uncertainties of weather and climate. Disturbances caused by humans and their animals are playing an increasing role in the damage and destruction of cryptobiotic soils. The small organisms in cryptobiotic soils are no match for the compression of a foot-print, walking stick, or vehicle tire -- especially during periods of drought. (Cole D.N., 1991)

If a disturbance occurs before or during a dry season, when cryptobiotic soils are dry, brittle, and easily broken-up, much of the area under the community will be destabilized. Cyanobacterial growth in cryptobiotic soils may begin in as little as six to twenty-four months and full, healthy growth may occur within a 5-6 year period if the soil is left undisturbed. Even though most disturbances do not kill the organisms directly, the fiber connections are broken, and in order to repair the damage, water must be available to the organisms.

Knowledge and awareness of cryptobiotic soils is important for the growth, management, and preservation of this small community of unobtrusive living organisms. Once they are damaged or destroyed cryptobiotic soil communities, which are the surface covering and agent to produce soil in many arid regions, will be long in recovering and returning to full productivity.

Bibliography

Belnap J. 1995. Soil surface disturbances: Their role in accelerating desertification. Environmental Monitor and Assessment, vol. 37.

Belnap J. 1994. Potential value of cyanobacterial inoculation in revegetation efforts. General Technical Report INT-GTR-313.

Belnap J., et al. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content, and chlorophyll degradation. Arid Lands and Resource Rehabilitation, vol. 8.

Belnap J. 1993. Recovery rates of cryptobiotic soil crusts: assessment of artificial inoculant and methods of evaluation. Great Basin Naturalist, vol. 53.

Belnap J., Gardner J.S. 1993. Soil microstructure of the Colorado Plateau: The role of the cyanobacterium *Micro coleus Vaginatus*. Great Basin Naturalist, vol. 53.

Cole D.N. 1991. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. Great Basin Naturalist, vol. 50.

Harper K.T., Pendleton R.L. 1993. Cyanobacterial and cyanolichens: Can they enhance availability of essential minerals for higher plants? Great Basin Naturalist, vol. 53.

MacGregor A.N., Johnson D.E. 1971. Capacity of desert algal crusts to fix atmospheric nitrogen. Soil Science Society American Proceedings, vol. 35.

Rychert R.C., Skujins J. 1974. Nitrogen fixation by blue-green algae-lichen crusts in the Great Basin desert. Soil Science Society American Proceedings, vol. 38.

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Soils and Cryptobiotic Crusts in Arid Lands

Cryptobiotic crusts (Fig. 1) are important features of arid and semiarid ecosystems throughout the Southwest, including pinyon-juniper woodlands and deserts. More data on the ecological role played by these crusts in the Southwest are needed, given the widespread (but unsubstantiated) belief among many range managers that the breaking up of such crusts by livestock hoof action may be beneficial (Belnap 1990; Ladyman and Muldavin 1996).

Fig. 1. Cryptobiotic crusts on the Colorado Plateau. Courtesy J. Belnap, USGS

Living soil crusts are found throughout the world, from the hottest deserts to the polar regions. In arid regions, these soil crusts are dominated by blue-green algae and also include soil lichens, mosses, green algae, microfungi, and bacteria (Belnap 1990; Johansen 1993; Ladyman and Muldavin 1996). In the cold deserts of the Colorado Plateau region (parts of Arizona, Colorado, New Mexico, and Utah), these crusts are extraordinarily well developed, often representing more than 70% of the living ground cover (Belnap 1990).

Blue-green algae occur as single cells or filaments; the most common form found in desert soils is the filamentous type. The cells or filaments are surrounded by sheaths that are extremely persistent in these soils. When moistened, the blue-green algal filaments become active, moving through the soils and leaving behind a trail of the sticky, mucilaginous sheath material, which sticks to surfaces such as rock or soil particles, forming an intricate webbing of fibers in the soil. In this way, loose soil particles are joined, and otherwise unstable and highly erosion-prone surfaces become resistant to wind and water erosion. The soil-binding action is not dependent on the presence of living filaments, however--layers of abandoned sheaths, built up over long periods, can still be found clinging tenaciously to soil particles at depths greater than 15 centimeters in sandy soils, thereby providing cohesion and stability in loose sandy soils (Belnap and Gardner 1993).

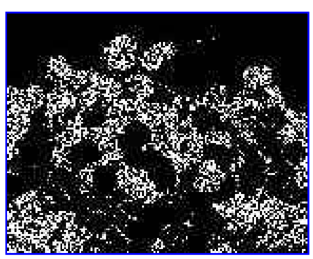

Fig. 2. Micrograph of filamentous cryptobiotic crust showing sheaths with attached clay particles.
Courtesy J. Belnap, USGS

The crusts are important in the interception of rainfall. When moistened, the sheaths absorb up to 10 times their volume of water. The roughened surface of the crusts slows precipitation runoff and increases water infiltration into the soil, which is especially important in arid areas with sporadic, heavy rainfall. Vascular plants growing in crusted areas have higher levels of many essential nutrients than plants growing in areas without crusts. Electron micrographs of sheaths (Fig. 2) show that they are covered with fine clay particles upon which essential nutrients cling, thereby keeping the nutrients from being leached out of the upper soil horizons or from being bound in a form unavailable to plants. In addition to stabilizing surfaces and increasing water harvesting, crustal organisms also contribute nitrogen and organic matter to ecosystems, functions that are especially important in desert ecosystems where nitrogen levels are low and often limit productivity.

Unfortunately, many human activities are incompatible with maintaining these blue-green algal crusts. The blue-green algal fibers that confer such tensile strength to these crusts are no match for the compressional stress placed on them by machinery or by being stepped on by cows or people, especially when the crusts are dry and brittle. Crushed crusts not only contribute less nitrogen and organic matter to the ecosystem, but the impacted soils are also highly susceptible to wind and water erosion. In addition, raindrop erosion increases and consequent overland water flows carry detached material away, a severe problem when the destruction has occurred in a continuous strip, as it does with vehicular or bicycle tracks. Such tracks are highly susceptible to water erosion and quickly form channels, especially on slopes. After such damage, wind blows away pieces of the pulverized crust and also blows around the underlying loose soil, covering nearby crusts. Since crustal organisms depend on photosynthesis, burial can mean death. When large sandy areas are impacted in dry periods, previously stable areas can become a series of moving sand dunes in only a few years.

Large areas that are disturbed may never recover. Under the best circumstances, a thin veneer may return in 5 to 7 years. When the crust is disturbed, nitrogen fixation stops and underlying sheath material is crushed. Damage done to the abandoned sheath material underneath the surface cannot be repaired because the living organisms occur only on the surface. Instead, sheaths must build up slowly after many years of blue-green algal growth.

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Changing Landscapes of the Middle Rio Grande

Before the fourteenth century, the Rio Grande between Cochiti and San Marcial, New Mexico, was a perennially flowing, sinuous, and braided river (Crawford et al. 1993). The river migrated freely over the floodplain, limited only by valley terraces and bedrock outcroppings; this shifting of the river created ephemeral mosaics of riparian vegetation (forests and shrublands) and wetlands (ponds, marshes, wet meadows) (Durkin et al. 1995). Water diversion for irrigated agriculture by Native Americans and later by European immigrants may have somewhat diminished river flows during growing seasons before 1900. Increased sediment loading, the result of climatic variations and agriculture, caused the river's channel to become broader and shallower, which increased the river's tendency to flood.

In the late 1800's, groundwater levels in the Rio Grande floodplain rose dramatically because of a rising riverbed, irrigation, and poor return of irrigation water. Salts, leached upward by the rising groundwater, created salinity problems. Levees, built in the 1920's and 1930's to cope with floods, tended to constrain the floodway and channel, thereby reducing the river's tendency to meander, which is critical for establishment of native bosque (cottonwood-willow) vegetation. In addition, the riverbed aggraded inside the levees so that by the 1950's it was higher than adjacent downtown Albuquerque. Upstream dams were built largely for flood and sediment control, as well as water storage, and drainage systems were established to lower water tables in the floodplain. These actions, combined with water diversion channels and increased groundwater pumping in Albuquerque, disrupted the connection between the river water and groundwater in the floodplain; thus, hydrological conditions in the riparian zones were no longer linked in a natural historical way (Crawford et al. 1993).

Cottonwood-willow forests have also been reduced by land clearing, tree harvesting, water diversion, and agricultural uses. About 90% of the Rio Grande's water is used for agriculture in the middle Rio Grande valley (Crawford et al. 1993). Livestock graze back new riparian vegetation (young cottonwood and willow), which contributes to watershed erosion and leads to increased sediment loading in the river. Groundwater drainage and the absence of periodic flooding caused most of the valley's wetlands to dry up. Plant and animal species dependent on such areas have disappeared or are confined to restricted habitats. Cottonwood and willow have been widely replaced by species that are not as reliant on spring flooding and inundation to reproduce--saltcedar in southern reaches and Russian-olive in northern ones (Figure).

Figure. Riparian vegetation. Mature cottonwood site (top) at Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico, showing the relatively open nature of such stands, and a stand of nonindigenous saltcedar (bottom) on the Rio Hondo, Chaves County, New Mexico, showing the almost impenetrable nature of invading stands. Courtesy J. N. Stuart, USGS

Roelle and Hagenbuck (1995), who documented surface cover changes in the Rio Grande floodplain from 1935 to 1989, found that five of eight wetland cover types declined by 17,000 hectares (45%) in that period; largest gains during the period were in urban and agricultural cover types. Only three wetland or riparian cover types increased: lake, wetland forest, and dead forest or scrub-shrub. The lake increase, though, was due to higher water levels in a large impoundment (Elephant Butte Reservoir), and wetland forest increase was primarily due to increasing forest cover between levees and the river channel, which has become narrower and straighter because of channel stabilization. Only 27% of the area forested in 1935 still supports forests. The flow regime of the river has been altered significantly, with lower peak flows, which means that cottonwood regeneration rarely occurs. Under current hydrological conditions, Russian-olive and saltcedar are likely to continue to replace cottonwood. Even though the middle Rio Grande valley in New Mexico supports the most extensive cottonwood gallery forest remaining in the entire Southwest (W. Howe, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, personal communication), human-induced changes in hydrology and land use are rapidly shrinking remaining forests.

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Rare Aquatic Snails

State Natural Heritage Programs in the Southwest have identified 30 species of rare aquatic snails (Figure a), most in the mollusk family Hydrobiidae. The Hydrobiidae are at risk throughout North America, with 16 endangered, threatened, or U.S. Fish and Wildlife Service Category 1 candidate species, and 90 species of concern (Mehlhop and Vaughn 1994).

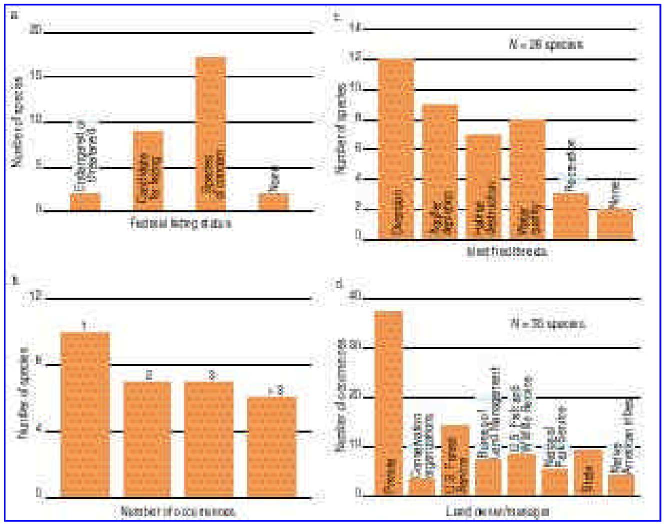

Figure. a) Federal status of rare or declining snails in the Southwest; b) number of known occurrences per species of rare aquatic snails; c) reported threats to rare aquatic snails in the Southwest; d) landowner or management agency of sites where aquatic snails in this study occur.

Several physiological and ecological aspects of rare southwestern snails render them vulnerable to extirpation. All are gill breathers and thus are intolerant of drying or anaerobic conditions. Individual snails tend to live about one year, making annual reproduction essential. Most snail species are geographically restricted to natural springs and nearby wetlands, with 83% of the species having a total range of less than 10 square kilometers. These mostly isolated habitats inhibit migration--of 30 snail species, most occur at only a single spring, and most of the others are found at only two or three springs (Figure b). Water-use activities that have altered the quantity or quality of many spring waters also threaten the snails (Figure c). Of 26 species for which threats have been assessed, only two were found to have no substantial identified threats.

Although the status of most of these rare aquatic snails is vulnerable (Mehlhop and Vaughn 1994), there are reasons for optimism. More than half (53%) of the snail habitats are in springs that are managed fully or in part by federal or state agencies or by private conservation organizations (Figure d). Also, although water-use activities appear to pose significant threats to the long-term viability of these species, these threats have existed for most of these species for decades, suggesting that such activities and snails may be able to coexist.

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This large patch of cryptobiotic soil is on top of No Man's Mesa, on BLM lands in the Paria-Hackberry roadless area near Grand Staircase-Escalante National Monument. A symbiotic web of lichen, algae, and fungus, this soil holds water and fixes nitrogen, but is rapidly destroyed by overgrazing and by human recreational use. Photo © 1999 Ray Wheeler.

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Cryptobiotic Soil Crusts

also called Microbiotic Crusts or Cryptogamic Soils

Mostly composed of cyanobacteria, lichens, mosses, and algae.
Might also have fungi or liverworts.
The exact species compositions of the crusts vary from place to place, as do the vascular plant communities that grow in the crusts.

Cryptobiotic crusts are very important ecosystems in arid and semi-arid regions. In the USA, these crusts have been studied in the Colorado Plateau, the Great Basin, and the Sonoran Desert. These areas include portions of NV, UT, CO, NM, and AZ.

The crust that forms can be up to 10 cm thick, with the still living organisms in the upper few mm of the soil.

The cryptobiotic crust can account for >70% of the ground cover in arid and semi-arid environments, with vascular plants providing the remainder.
The organisms of the crust increase the stability of the soil, decreasing soil erosion.
The organisms increase the organic matter in soils.
Free-living cyanobacteria and cyanobacteria living as lichens with fungal partners increase the available nitrogen content of the soils by nitrogen fixation.
The availability of other soil minerals improves.
The amount of available water also improves.

Most of the cyanobacteria found in cryptobiotic crusts are filamentous. As they grow, they are covered by a sheath of mucous. As the cyanobacteria move through the soil, they leave a trail of the mucous as they go (think snail trail). The mucous acts like a glue to hold soil particles together. Clumps of soil resist wind and water erosion better than the small particles do. Even after the cyanobacteria die, the mucous is still in the soil, holding the particles together.

The filaments of green algae and the hyphae of the fungi also hold the soil particles in place, as do the rhizoids of the lichens, mosses, and liverworts.

Binding of the soil particles increases the amount of P available as this mineral is often high in soil fines.

The organic carbon put into the soils as the cryptobiotic organisms die improves the water and mineral holding capacity of the soil: fewer minerals are leached from the soil when it rains.

The nitrogen fixation is a very important contribution by the cyanobacteria. They serve as the primary source of nitrogen in the Colorado Plateau.

The crust organisms are very good at absorbing water from dew and water vapor; they are also good at retaining water even under very low relative humidity. Thus, they slow water evaporation from the soil surface, benefitting the vascular plants that grow in the crusts.

The crusts are highly susceptible damage when they are disturbed by hooves, feet, and vehicles (motorized or not). The damage is worse when the soils are dry because of the brittleness of the living organisms when they are dry. (The organisms in the crusts survive drying due to a mechanism called poikilohydry.)
The organisms are only active when wet. Therefore, in an arid environment, re-establishment of the crust is slow. In southern Utah, the estimated recovery time for lichens is 45 years and for mosses is 250 years.
Not only are the crust-free soils now subject to erosion, the soil particles now removed from these areas can cover adjacent crusts that were not disturbed.
The crusts can suffer substantial damage, even when there is no apparent damage to the vascular plant vegetation.

As a result of damage to the crusts:
runoff increases
soil loss increases
if runoff brings in N, the presence of that N will decrease natural nitrogen fixation
often, rangeland shrubs increase; some are allelopathic for nitrogen fixing bacteria

Review

In what types of habitats do you find cryptobiotic soil crusts? In which US states have they been most extensively studied?
What are the main types of organisms found in cryptobiotic soil crusts?
What specific advantages do the crust organisms provide to their ecosystem? What specific features of the organisms contribute to their ability to provide these advantages? (For example, what are the various factors provided by the cyanobacteria?)

What is poikilohydry? How does it contribute to the survival of organisms in soil crusts?

What are the possible consequences of damage to cryptobiotic soil crusts? What are estimated recovery times for damage to crusts in southern Utah?

The Microbial World

Cyanobacteria

Cyanobacteria and the "cryptobiotic crust"

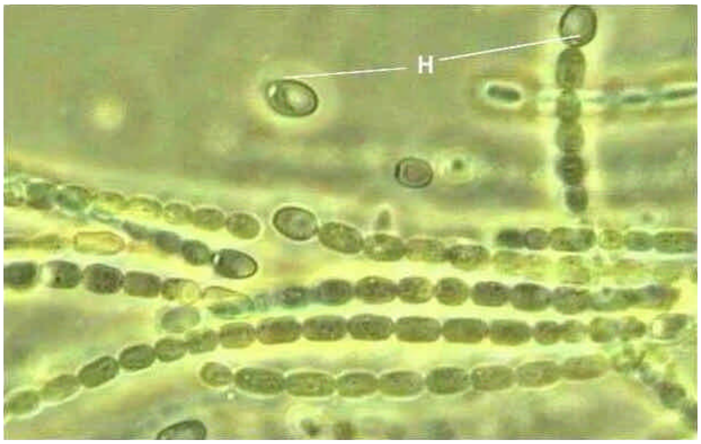
On the right is a sign in the Arches National Park, Utah, USA. Probably one of the few signs in the world that says, in effect:

Please don't walk on our microorganisms!

The image below shows a desert community in the canyonlands area of Utah, USA. This dryland community (top left; comprising saltbush, Pinyon pine, Utah juniper, Indian ricegrass) and all the animals it supports depend on the pioneer role of a microbial community termed the **cryptobiotic crust** (also known as **microbiotic** or **cryptogamic** crust). These microbial communities initially form an inconspicuous grey-brown covering of the sand surface (top right), consisting of fungi, cyanobacteria and lichens, but in later stages of development (after 50 years or more; centre right) the crusts form small "humps" on which mosses grow.

The growth of all these pioneer organisms contributes organic matter which aids water retention and paves the way for growth of higher plants. **Lichens** (see the micrograph, bottom right), which consist of a fungal tissue containing either green algae or cyanobacteria as the photosynthetic partner, play a vital role in colonisation of the bare sand (See Lichens). In this case the lichens contain **cyanobacteria** (bottom centre and bottom left) which fix atmospheric nitrogen (N_2) gas into amino acids and thus progressively enrich the soil with nitrogen for plant growth. The filamentous cyanobacteria also secrete a mucilaginous sheath which helps to bind sand particles together.

The image below shows a pure culture of the cyanobacterium *Nostoc*, a common photosynthetic partner of lichens. Nitrogen fixation occurs in special cells termed **heterocysts** or **heterocytes** (H) which occur at intervals along the cyanobacterial filaments. This separation of cellular functions is necessary because cyanobacteria have oxygen-evolving photosynthesis but the nitrogen-fixing enzyme, **nitrogenase**, is unstable in the presence of oxygen. This problem is overcome because the heterocysts contain only part of the photosynthetic apparatus, termed photosystem I, which can be used to generate energy (as ATP). But the heterocysts do not contain photosystem II, which is used to split water into hydrogen (for combination with CO_2 to produce organic products) and oxygen.



Cryptobiotic crusts are complex communities with many interrelationships that are only partly explored. As an example, we can consider a small part of the crust from the Chihuahuan Desert of Texas.

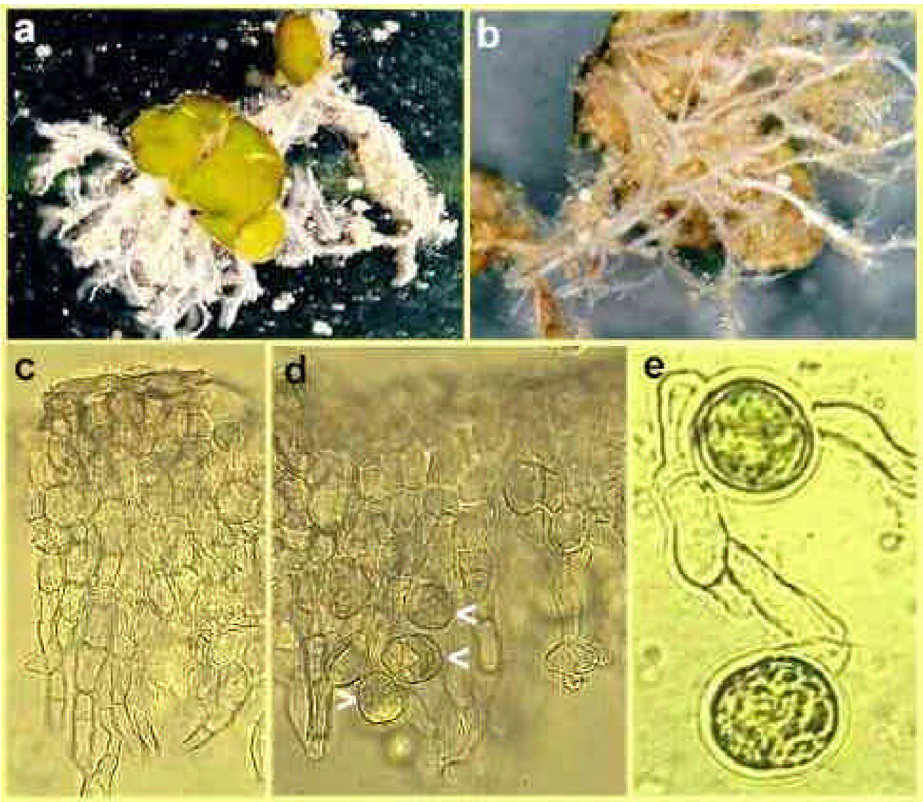
This crust is completely dry for most of the year, but when a fragment (marked by the white rectangle) was immersed in water the microbial community was reactivated and was found to have at least three components, shown in the image below:

1. a lichen (probably a species of *Peltula*) marked by the arrows;
2. a lichen with a dark, almost circular outline, marked by the square;
3. a carpet of cyanobacteria, part of which is shown in the circle.

Remoistened fragment of a Chihuahuan desert crust

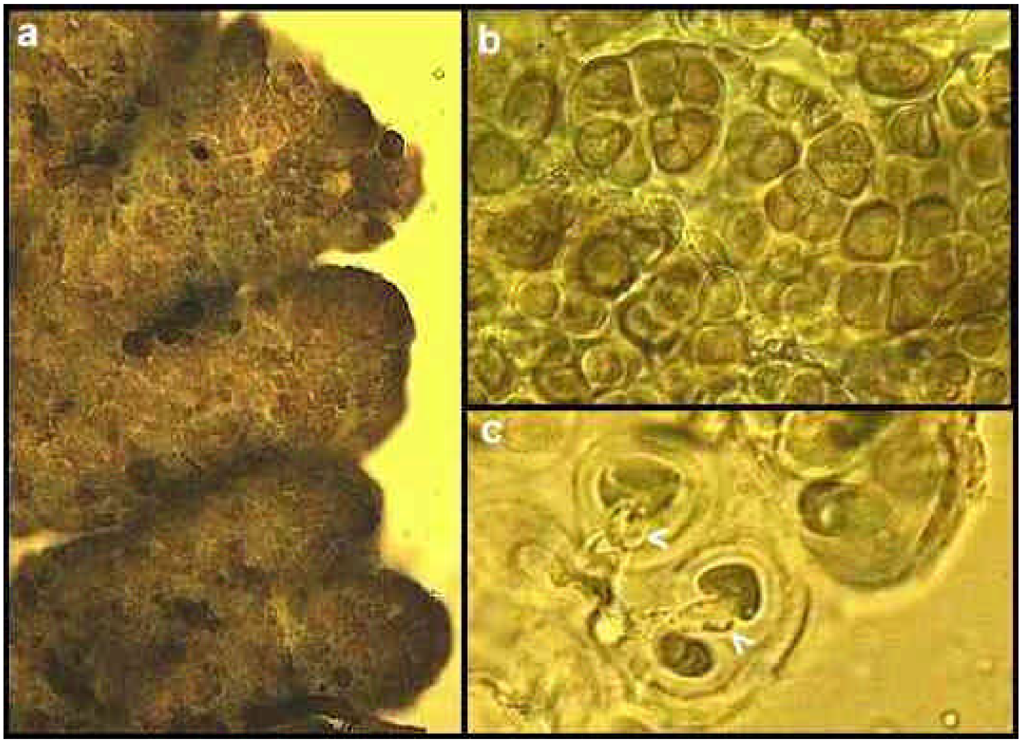
1. The lichen *Peltula*

Peltula is a rather unusual lichen consisting of separate lobes, termed squamules, that are connected to one another by a system of fungal hyphae. In (a) and (b) below, we see that these hyphae are aggregated into rope-like structures that lichenologists term "rhizines" (see Lichens) but mycologists call them **mycelial cords**. Their function is to transport nutrients. The mycelial cords were immersed in the carpet of cyanobacteria and penetrated into the underlying sand layers, perhaps obtaining nitrogen and other nutrients from the cyanobacteria. The cords have been dissected away from the sand particles in Figs **a** (top view) and **b** (underside). The green lobes of *Peltula* have a typical lichen structure. The top surface consists of a densely packed fungal tissue (the upper cortex), below which the hyphae have a more normal appearance (**c**). Cells of a green alga (probably *Trebouxia*) are found below the lichen surface (arrowheads, **d**) and are intimately associated with fungal hyphae (**e**) which gain carbohydrates from the algal cells.



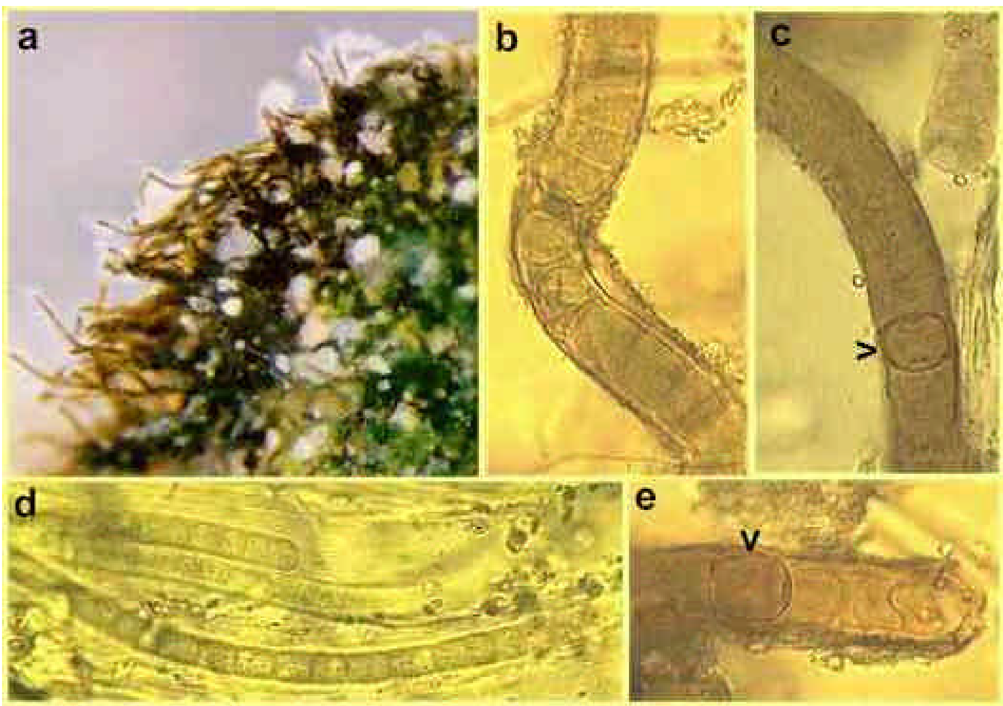
2. The dark-coloured lichen (unidentified)

This circular lichen has a lobed margin, seen in (**a**) below. There is no fungal cortex like that in *Peltula*. Instead, the upper surface of the lichen consists of clusters of dividing photosynthetic cells embedded in gelatinous sheaths (**b**). They appear to be cyanobacteria. A network of fungal hyphae extended into the sand from the base of the lichen. These hyphae branched repeatedly near the base of the lichen and the individual short branches (arrowheads in **c**, below) penetrated into the sheaths surrounding the cyanobacterial cells.



3. The cyanobacteria

The predominant cyanobacterium (possibly *Microcoleus vaginatus* - the most common cyanobacterium in desert crusts) is seen as a "fringe" of dark-coloured filaments in (**a**) below and at higher magnification in **b**, **c** and **e**. The filaments are encased in a sheath encrusted with mineral particles (**b**, **e**) and contain heterocysts (arrowheads in **c** and **e**). Narrower cyanobacterial filaments (**d**, below) grew from the greener regions of the crust when it was immersed in water for several days.



Other pioneer microbial activities

Several bacteria are involved in metal ion transformations in natural environments (see Winogradsky column) - they oxidise or reduce sulphur, manganese, iron, etc. to serve in energy-generating processes. These oxidation-reduction activities, whether microbially induced or merely chemical, can be very conspicuous in desert and other dryland regions, where they lead to rock coloration. A classic example is "**desert varnish**" (http://minerals.gps.caltech.edu/files/varnish/index.htm) (not on this server) which recently was shown to be at least partly caused by bacteria (http://ccf.arc.nasa.gov/dx/basket/storiesetc/97_32AR.html) (not on this server).

Further reading:

Journal articles:

DJ Eldridge & RSB Green (1994) Microbiotic soil crusts - a review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* **32**, 389-415.

RD Evans & JR Ehrlinger (1993) A break in the nitrogen cycle in aridlands? *Oecologia* **94**, 314-317.

Websites:

1. The "cyanosite"(not on this server)

2. **A site produced by a Soil Ecologist of the U.S. Geological Survey: Cryptobiotic soils: holding the place in place.**(not on this server)

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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.

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.

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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 Manage ment. 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 Man agement, 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 A*rabis 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 nitro gen-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.

Soil quality is the capacity of the soil to function. The symbol for soil quality represents all natural resources, their dependence on soil, and human dependence on the health of these resources.

Capitol Reef

National Park Official Information

. . . in DEPTH

CRYPTOBIOTIC SOIL

Introduction

Cryptobiotic soil is found throughout the world. In arid regions, these living soil crusts are dominated by cyanobacteria, and also include soil lichens, mosses, green algae, microfungi and bacteria. These crusts play an important role in the ecosystems in which they occur. In the high deserts of the Colorado Plateau (which includes parts of Utah, Arizona, Colorado and New Mexico), these knobby black crusts are extraordinarily well-developed, and may represent 70 to 80 percent of the living ground cover.

What Are Cyanobacteria?

Cyanobacteria, previously called blue-green algae, are one of the oldest known life forms. It is thought that these organisms were among the first land colonizers of the Earth's early land masses, and played an integral role in the formation and stabilization of early soils. The earliest cyanobacteria fossils found are called stromatolites, which date back more than 3.5 billion years. Extremely thick mats of these organisms converted the earth's original carbon dioxide rich atmosphere into one rich in oxygen and capable of sustaining life.

Cyanobacteria occur as single cells or as filaments. The most common form found in Colorado Plateau soils are the filamentous type, which are usually surrounded by sticky, mucilaginous sheaths.

When moistened, cyanobacteria become active, moving through the soil and leaving a trail of sticky material behind. The sheath material sticks to surfaces such as rock or soil particles, forming an intricate web of fibers throughout the soil. In this way, loose soil particles are joined together, and an otherwise unstable surface becomes very resistant to both wind and water erosion.

The soil-binding action is not dependent on the presence of living filaments.

Layers of abandoned sheaths, built up over long periods of time, can still be found clinging tenaciously to soil particles, providing cohesion and stability in sandy soils at depths up to 10cm.

Nitrogen fixation is another significant capability of cyanobacteria. Vascular plants are unable to utilize nitrogen as it occurs in the atmosphere. Cyanobacteria are able to convert atmospheric nitrogen to a form plants can use. This is especially important in desert ecosystems, where nitrogen levels are low and often limiting to plant productivity.

The sheaths have other functions as well. When moistened, they swell up to ten times their dry size. This ability to intercept and store water benefits both the crustal organisms as well as vascular plants, especially in arid regions with sporadic rainfall.

Sheaths, and the organisms they surround, also contribute organic matter and help make essintial nutrients available to vascular plants. Negatively charged clay particles, often found clinging to the sheaths, bind positively charged nutrients, preventing them from being leached out of the upper soil horizons or becoming bound in a form unavailable to plants. Like soil stability, this function is not dependent on the presence of living filaments, but only the presence of sheath material.

Environmental Impacts

Unfortunately, many human activities are incompatible with the presence and well-being of cryptobiotic soils. The fibers that confer such tensile strength to these crusts are no match for the compressional stress placed on them by footprints or machinery, especially when the crusts are dry and brittle.

Air pollutants, both from urban areas and coal-fired power plants, also harm these crusts.

Tracks in continuous strips, such as those produced by vehicles or bicycles, are especially damaging, creating areas that are highly vulnerable to wind and water erosion. Rainfall carries away loose material, often creating channels along these tracks, especially when they occur on slopes.

Wind not only blows pieces of the pulverized crust away, thereby preventing reattachment to disturbed areas, but also disturbs the underlying loose soil, often covering nearby crusts. Since crustal organisms need light to photosynthesize, burial can mean death. When large sandy areas are impacted during dry periods, previously stable areas can become a series of shifting sand dunes in just a few years.

Impacted areas may never fully recover. Under the best circumstances, a thin veneer of cryptobiotic soil may return in five to seven years. Damage done to the sheath material, and the accompanying loss of soil nutrients, is repaired slowly during up to 50 years of cyanobacterial growth. Lichens and mosses may take even longer to recover.

Crypto Tips

- **Stay on existing trails.**
- **When you must go off trail, walk in wash bottoms or on slickrock.**
- **Camp on slickrock or in previously disturbed areas.**
- **Go out of your way, literally, to avoid cryptobiotic soil.**

More information

More information is available on the Internet at http://www.cnha.org/.

Reactivation of Stabilized Sand Dunes on the Colorado Plateau

by
Daniel R. Muhs and **Josh M. Been**
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Click on any graphic to view a larger version

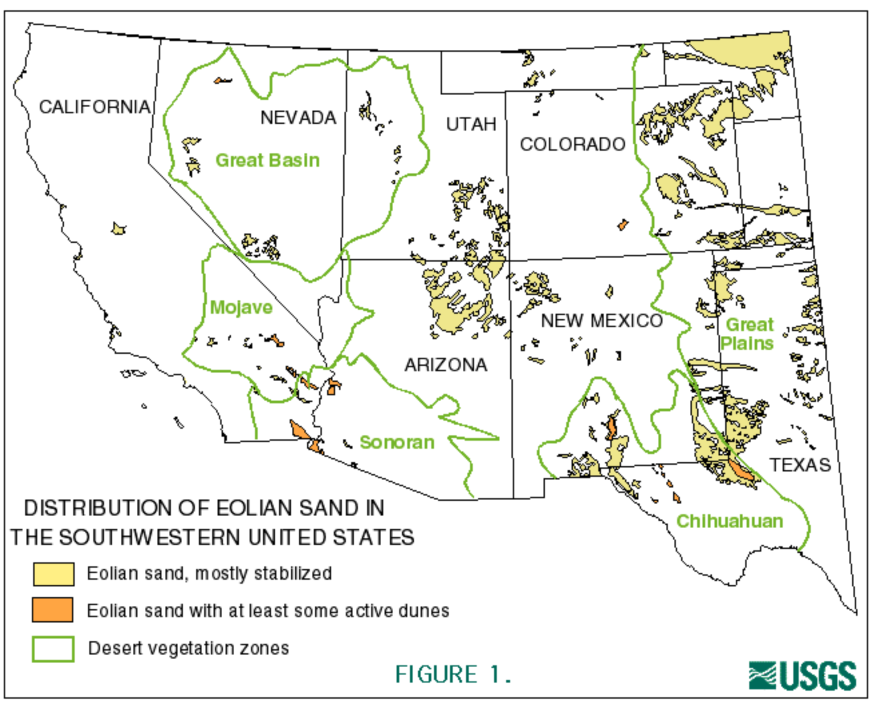
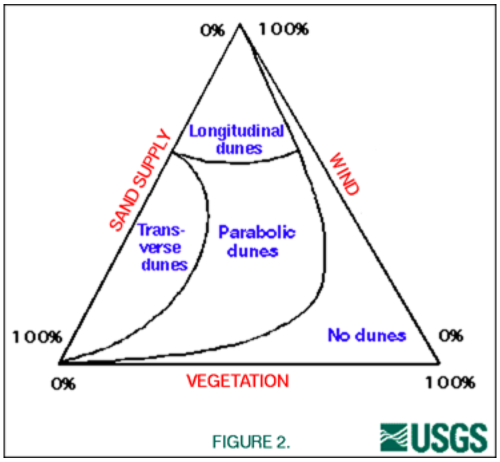


FIGURE 1.

Distribution of Eolian Sand in the Southwest

Sand dunes and *eolian* (wind-blown) sheet sands are widely distributed over the southwestern United States, particularly in the southern Great Plains and the southwestern deserts and high plateaus **(FIGURE 1)**. In the driest parts of the southwest, there are areas of active sand dunes, but most parts have dunes that are stabilized by vegetation and the sand is not moving at present.

References used to compile the eolian sand deposits map of the Southwestern U.S.



Factors Controlling Sand Mobility

For actively moving sand dunes, there are three requirements **(FIGURE 2)**: a source of sand, winds that are strong enough to move the sand, and a lack of stabilizing vegetation. Depending on the relative balance of these three variables, different dune types may result, including U-shaped dunes (*parabolic* dunes) with a moderate sand supply but abundant vegetation; linear or *longitudinal* dunes with a minimal sand supply but strong winds; and ridges with their long axes perpendicular to the wind (*transverse* dunes) where there is abundant sand and little or no vegetation. Dunes of all three types are found in the southwestern United States. If sand supply is minimal, winds are weak, and/or there is abundant vegetation, no dunes will form.

Sand Deposits and Wind

In the southwestern United States, the largest area of sand dunes is actually not in the deserts, but in the Colorado Plateau region, centered on the four corners area **(FIGURES 1 and 3)**. Sand supplies here are abundant from both sandstone bedrock and dry river channels. In this area winds capable of moving sand are dominantly from the southwest **(FIGURE 3)**. Compared to desert areas around the world where large sand seas are found, the Colorado Plateau has winds capable of moving sand (*drift potential*) that are very similar **(FIGURE 4)**.

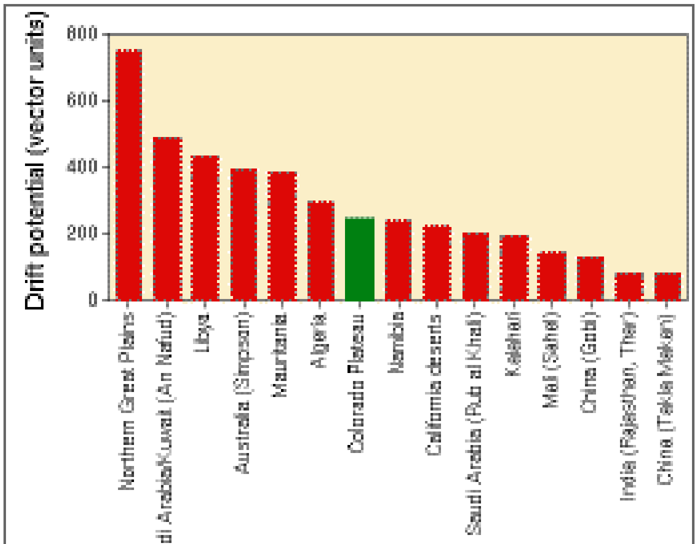


FIGURE 4.

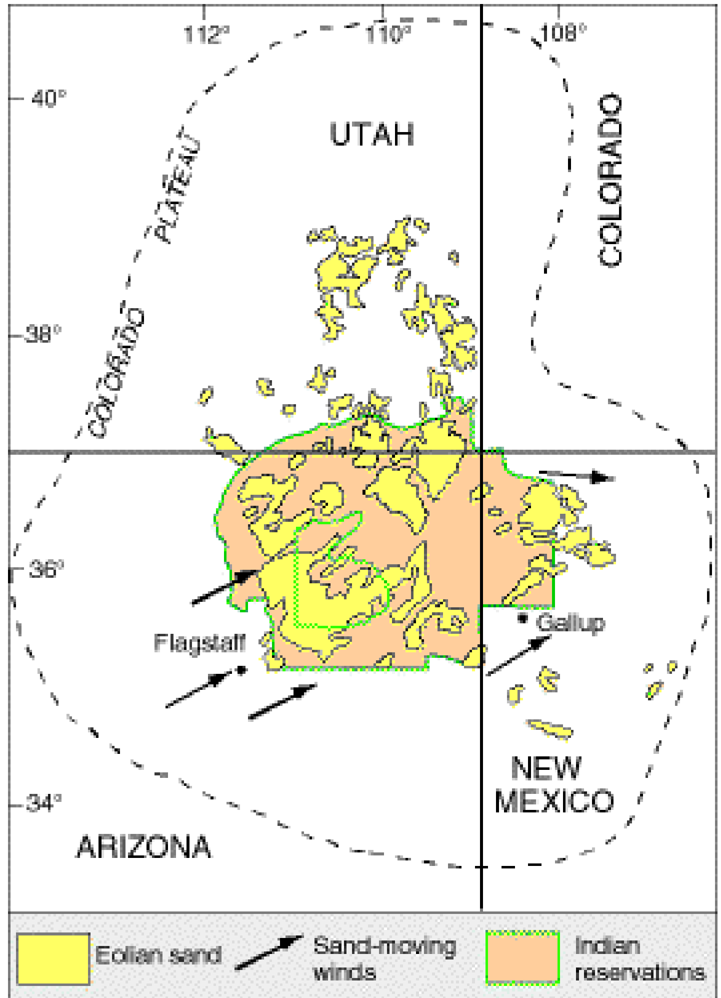


FIGURE 3.

Precipitation/Evapotranspiration Balance

Why aren't the sand dunes on the Colorado Plateau active even though sand supplies are available, and winds are strong enough to move the sand?

The answer is that the balance between precipitation **(P)** and potential evapotranspiration **(PE)** is such that vegetation can grow on the dunes and stabilize them. Although the Colorado Plateau has an overall moisture deficit (where the ratio of P to PE is less than 1.0), there is still enough moisture to support plants. In the areas where dunes occur, most P/PE values are around 0.3 to 0.5, which is high enough to support sagebrush and grasses at lower elevations and pinyon pine and juniper at higher elevations **(FIGURE 5)**. Therefore, the reason that dunes on the Colorado Plateau are stable is due to the P/PE balance and its support of stabilizing vegetation.

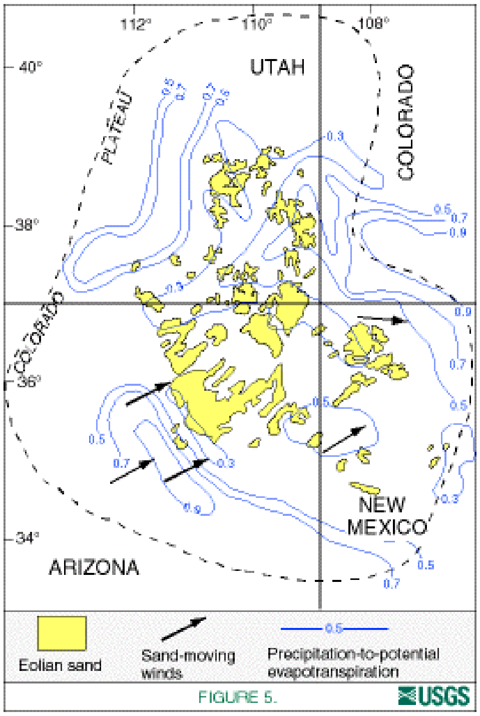


FIGURE 5.

Is it possible that future climate changes could change the P/PE balance and result in the removal of vegetation and reactivation of the dunes?

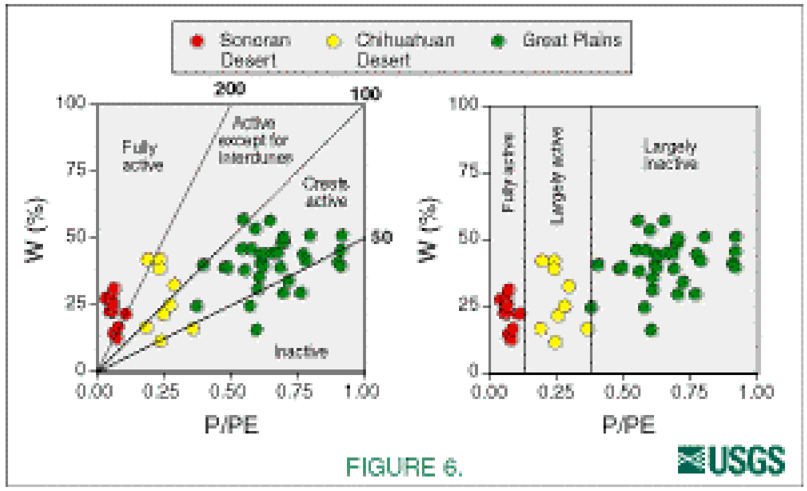


FIGURE 6.

This question can best be answered by examining the climatic characteristics of areas with active sand dunes. Studies of stabilized sand dunes in the Great Plains grasslands, mostly active dunes in the Chihuahuan Desert, and fully active dunes in the Sonoran Desert **(FIGURE 1)** show that there are definite trends toward greater dune activity in drier regions **(FIGURE 6)**. When the P/PE value is low and the percentage of time that wind is capable of moving sand **(W)** is high, dunes are fully active. The ratio of W to the P/PE value is referred to as the *dune mobility index*, and has been tested in many regions for its ability to describe the degree of dune activity as a function of climate variables. In fact, it appears that wind, as expressed by W, is actually not as critical as the P/PE value **(FIGURE 6)**. The moisture balance, through its effect on vegetation, seems to be the best indicator of dune activity. Therefore, with a decrease in the P/PE value, we could expect dunes to become more active in the future.

Climate Change and Sand Mobility

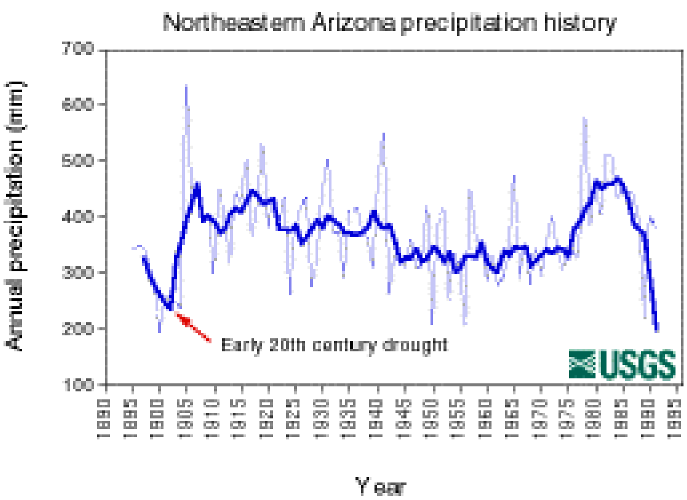


FIGURE 7.

Within recent history, has the climate ever been dry enough for dunes on the Colorado Plateau to be active?

Using the dune mobility index and the historic instrumental record, we can examine this possibility. In the past century, the worst drought, which was accompanied by higher-than-average temperatures, occurred in the years 1899-1904, which is shown on the rainfall graph as both a year-by-year and smoothed curve in **FIGURE 7**. If we calculate the dune mobility index values for W, P, and PE for the Colorado Plateau now (using average values for 1961-1990), we can see that dunes fall into the category of being partly active, but mostly stable, which is what we observe there today **(FIGURE 8)**. If we recalculate the dune mobility index values using data from the 1899-1904 drought, the values are shifted into the category of mostly active dunes. It is possible that some of the dune activity we see today on the Colorado Plateau is actually a remnant of greater activity during that drought, and really doesn't reflect modern conditions at all. In any case, greater dune activity could be expected in such a drought.

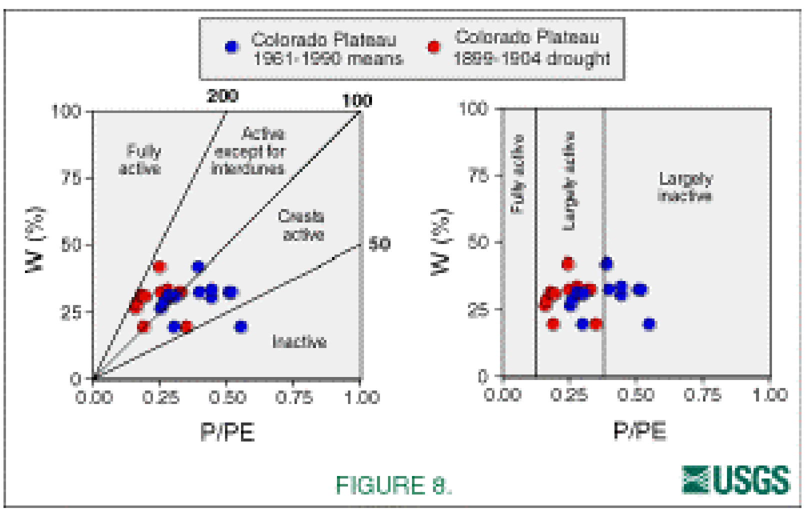


FIGURE 8.

What is the impact of active sand dunes on the Colorado Plateau?

The biggest impacts of active sand dunes in the region would be on the Navajo and Hopi people, whose reservation land is either on, or downwind of, the largest areas of sand dunes **(FIGURE 3)**. Many Navajo and Hopi homes are on or near sand dunes; reactivation of dunes would obviously have a negative effect on living conditions. Sheep and cattle are important to the economy of the Navajo and Hopi, and much of the vegetation required for grazing is dune vegetation. In addition, dry farming is practiced in much of the area, some of it on sand dunes. Thus, reactivation of sand dunes in the area would have serious impacts on living conditions, grazing, and farming.

For additional reading:

Breed, C.S., McCauley, J.F., Breed, W.J., McCauley, C.K., and Cotera, A.S., Jr. 1984. Eolian (wind-formed) landscapes. In: Smiley, T.L. et al. (eds.), Landscapes of Arizona--The Geological Story. New York, University Press of America, p. 359-413.

Hack, J.T. 1941. Dunes of the Navajo Country. Geographical Review, v. 31, p. 240-263.

Lancaster, N. 1988. Development of linear dunes in the southwestern Kalahari, southern Africa. Journal of Arid Environments, v. 14, p. 233-244. McKee, E.D. (ed.). 1979. A Study of Global Sand Seas. U.S. Geological Survey Professional Paper 1052, 429 p.

Muhs, D.R., and Holliday, V.T. 1995. Evidence of active dune sand on the Great Plains in the 19th century from accounts of early explorers. Quaternary Research, v. 43, p. 198-208.

Muhs, D.R., Bush, C.A., Cowherd, S.D., and Mahan, S. 1995. Geomorphic and geochemical evidence for the source of sand in the Algodones dunes, Colorado Desert, southeastern California. In Desert aeolian processes. Edited by V.P. Tchakerian. Chapman and Hall, London, p. 37-74.

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Cryptobiotic Soils: Holding the Place in Place

Jayne Belnap
Soil Ecologist
U.S. Geological Survey

Cryptobiotic soil crusts, consisting of soil cyanobacteria, lichens and mosses, play an important ecological roles in the arid Southwest. In the cold deserts of the Colorado Plateau region (parts of Utah, Arizona Colorado, and New Mexico), these crusts are extraordinarily well-developed, often representing over 70 percent of the living ground cover. Cryptobiotic crusts increase the stability of otherwise easily eroded soils, increase water infiltration in regions that receive little precipitation, and increase fertility in soils often limited in essential nutrients such as nitrogen and carbon (Harper and Marble, 1988; Johansen, 1993; Metting, 1991; Belnap and Gardner, 1993; Belnap, 1994; Williams et al., 1995).

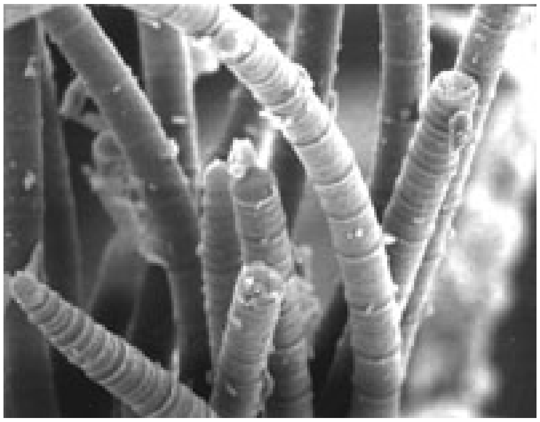

Figure 1. *Filaments of Microcoleus vaginatus (x 3000), the dominant organism in the crust. Individual cells abut each other to form the filaments. Click on image for full size.*

Cyanobacteria occur as single cells or as filaments. The most common type found in desert soils is the

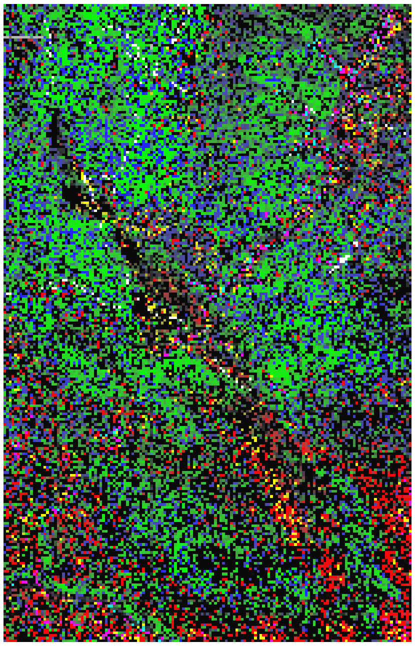

Figure 2. Arches Microbiotic Soils Map (Kokaly, Clark, and Swayze, 1993). Click on this image for full size and explanation.

filamentous type. The cells or filaments are surrounded by sheaths that are extremely persistent in these soils. When moistened, the cyanobacterial filaments become active, moving through the soils and leaving a trail of the sticky, mucilaginous sheath material behind. This sheath material sticks to surfaces such as rock or soil particles, forming an intricate webbing of fibers in the soil. In this way, loose soil particles are joined together, and otherwise unstable and highly erosion-prone surfaces become resistant to both wind and water erosion. The soil-binding action is not dependent on the presence of living filaments. Layers of abandoned sheaths, built up over long periods of time, can still be found clinging tenaciously to soil particles at depths greater than 15 cm in sandy soils. This provides cohesion and stability in these loose sandy soils even at depth.

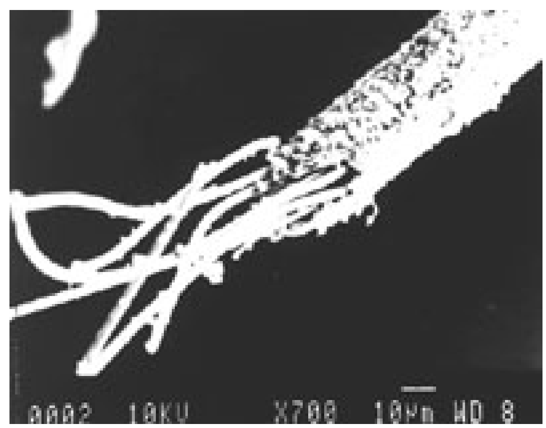

Figure 3. *Microcoleus filaments (lower left) emerging from mucilagenous sheath (upper right). Scale bar is 10 micrometers. Click on image for full size.*

Cyanobacteria and cyanolichen components of these soil crusts are important contributors of fixed nitrogen (Mayland and McIntosh, 1966; Rychert and Skujins, 1974). These crusts appear to be the dominant source of nitrogen in cold-desert pinyon-juniper and grassland ecosystems over much of the Colorado Plateau (Evans and Ehleringer, 1993; Evans and Belnap, unpub. data). Biological soil crusts are also important sources of fixed carbon on sparsely vegetated areas common throughout the arid West (Beymer and Klopatek, 1991). Plants growing on crusted soil often show higher concentrations and/or greater total accumulation of various essential nutrients when compared to plants growing in adjacent, uncrusted soils (Belnap and Harper, 1995; Harper and Pendleton, 1993).

Cryptobiotic soil crusts are highly susceptible to soil-surface disturbance such as trampling by hooves or feet, or driving of off-road vehicles, especially in soils with low aggregate stability such as areas of sand dunes and sheets in the Southwest, in particular over much of the Colorado Plateau (Belnap and Gardner, 1993; Gillette et al., 1980; Webb and Wilshire, 1983). When crusts in sandy areas are broken in dry periods, previously stable areas can become moving sand dunes in a matter of only a few years.

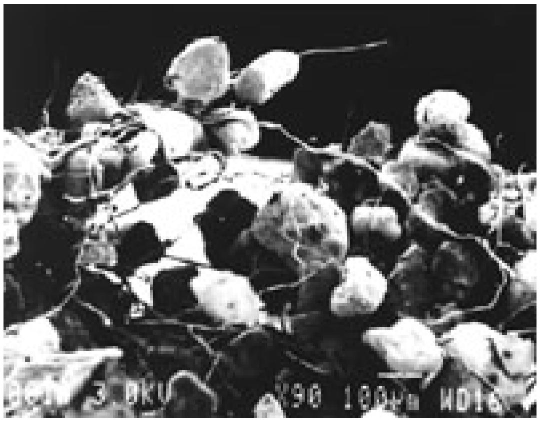

Figure 4. *Crust in sandy soils. The visible fibers are Microcoleus vaginatus. Note how Microcoleus connects the otherwise loose sand grains together, thus preventing wind and water erosion. Microcoleus is important in enhancing water and nutrient relations within the soil, as well. Scale bar is 100 micrometers. Click on image for full size.*

Cyanobacterial filaments, lichens, and mosses are brittle when dry, and crush easily when subjected to compressional or shear forces by activities such as trampling or vehicular traffic. Many soils in these areas are thin and are easily removed without crust protection. As most crustal biomass is concentrated in the top 3 mm of the soil, very little erosion can have profound consequences for ecosystem dynamics. Because crustal organisms are only metabolically active when wet, re-establishment time is slow in arid systems. While cyanobacteria are mobile, and can often move up through disturbed sediments to reach needed light levels for photosynthesis, lichens and mosses are incapable of such movement, and often die as a result. On newly disturbed surfaces, mosses and lichens often have extremely slow colonization and growth rates. Assuming adjoining soils are stable and rainfall is average, recovery rates for lichen cover in southern Utah have been most recently estimated at a minimum of 45 years, while recovery of moss cover was estimated at 250 years (Belnap, 1993).

Because of such slow recolonization of soil surfaces by the different crustal components, underlying soils are left vulnerable to both wind and water erosion for at least 20 years after disturbance (Belnap and Gillette, 1997). Because soils take 5,000 to 10,000 years to form in arid areas such as in southern Utah (Webb, 1983), accelerated soil loss may be considered an irreversible loss. Loss of soil also means loss of site fertility through loss of organic matter, fine soil particles, nutrients, and microbial populations in soils (Harper and Marble, 1988; Schimel et al., 1985). Moving sediments further destabilize adjoining areas by burying adjacent crusts, leading to their death, or by providing material for "sandblasting" nearby surfaces, thus increasing wind erosion rates (Belnap, 1995; McKenna-Neumann et al., 1996).

Soil erosion in arid lands is a global problem. Beasley et al. (1984) estimated that in rangeland of the United States alone, 3.6 million ha has undergone some degree of accelerated wind erosion. Relatively undisturbed biological soil crusts can contribute a great deal of stability to otherwise highly erodible soils. Unlike vascular plant cover, crustal cover is not reduced in drought, and unlike rain crusts, these organic crusts are present year-round. Consequently, they offer stability over time and under adverse conditions that is often lacking in other soil surface protectors. However, disturbed crusts now cover vast areas in the western United States as a result of ever-increasing recreational and commercial uses of these semi-arid and arid areas. Based on the results of several studies (McKenna-Neumann et al., 1996; Williams et al., 1995; Belnap and Gillette, 1997), the tremendous land area currently affected by human activity may lead to significant increases in regional and global wind erosion rates.

LITERATURE CITED

Beasley, R.P., M. Gregory, and T.R. McCarty, 1984, Erosion and Sediment Pollution Control, 2nd edition: Iowa State University Press.

Belnap, J., 1994, Potential value of cyanobacterial inoculation in revegetation efforts, *in* S.B. Monsen and S G. Kitchen, eds., Proceedings-Ecology and Management of Annual Rangelands: U.S. Department of Agriculture, Forest Service, Technical Report INT-GTR-313, Ogden, Utah, p. 179-185.

Belnap, J., 1993, Recovery rates of cryptobiotic crusts: Inoculant use and assessment methods: Great Basin Naturalist, v. 53, p. 89-95.

Belnap, J., 1995, Surface disturbances: their role in accelerating desertification: Environmental Monitoring and Assessment, v. 37, p. 39-57.

Belnap, J., and J.S. Gardner, 1993, Soils microstructure in soils of the Colorado Plateau: the role of the cyanobacterium Microcoleus vaginatus: Great Basin Naturalist, v. 53, p. 40-47.

Belnap, J., and D.A. Gillette, 1997, Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in SE Utah, USA: Land Degradation and Development. In Press.

Belnap, J., and K.T. Harper, 1995, The influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants: Arid Soil Research and Rehabilitation, v. 9, p. 107-115.

Beymer, R. J., and J.M. Klopatek, 1991, Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands: Arid Soil Research and Rehabilitation v. 5, p. 187-198.

Evans, R. D., and J. R. Ehleringer, 1993, Broken nitrogen cycles in arid lands: Evidence from 15N of soils: Oecologia v. 94, p. 314-317.

Gillette, D.A., J. Adams, A. Endo, D. Smith, and R. Kihl, 1980, Threshold velocities for input of soil particles into the air by desert soils: Journal of Geophysical Research, v. 85, p. 5621-5630.

Harper, K. T., and J. R. Marble, 1988, A role for nonvascular plants in management of arid and semiarid rangelands, *in* P. T. Tueller, ed., Vegetation Science Applications for Rangeland Analysis and Management: Dordrecht, Germany, Kluwer Academic Publisher, p. 135-169.

Harper, K. T., and R. L. Pendleton, 1993, Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants?: Great Basin Naturalist, v. 53, p. 89-95.

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

Mayland, H. F., and T. H. McIntosh, 1966, Availability of biologically fixed atmosphere nitrogen-15 to higher plants: Nature, v. 209, p. 421-422.

McKenna-Neumann et al., C.D. Maxwell, and J.W. Bolton, 1996, Wind transport of sand surface with photoautotrophic microorganisms: Catena, v. 27, p. 229-247.

Metting, B., 1991, Biological surface features of semiarid lands and deserts, *in* J. Skujins, ed., Semiarid Lands and Deserts: Soil Resource and Reclamation: New York, Marcel Dekker, Inc., p. 257-293.

Rychert, R. C., and J. Skujins, 1974, Nitrogen fixation by blue-green algae-lichens crusts in the Great Basin desert: Soil Science Society of America Proceedings, v. 38, p. 768-771.

Schimel, D. S., E. F. Kelly, C. Yonker, R. Aguilar, and R. D. Heil, 1985, Effects of erosional processes on nutrient cycling in semiarid landscapes, *in* D. E. Caldwell, J. A. Brierley, and C. L. Brierley, eds. Planetary Ecology: New York, Van Nostrand Reinhold, p. 571-580.

Webb, R. H., 1983, Compaction of desert soils by off-road vehicles, *in* R. H. Webb and H. G. Wilshire, eds., Environmental Effects of Off-road Vehicles: Impacts and Management in Arid Regions. New York, Springer-Verlag,, p. 31-80.

Webb, R. H., and H. G. Wilshire, 1983, Environmental Effects of Off-road Vehicles: Impacts and Management in Arid Regions. New York, Springer-Verlag.

Williams, J. D., J. P. Dobrowolski, N. E. West, and D. A. Gillette, 1995, Microphytic crust influences on wind erosion: Transactions of the American Society of Agricultural Engineers, v. 38, p. 131-137.

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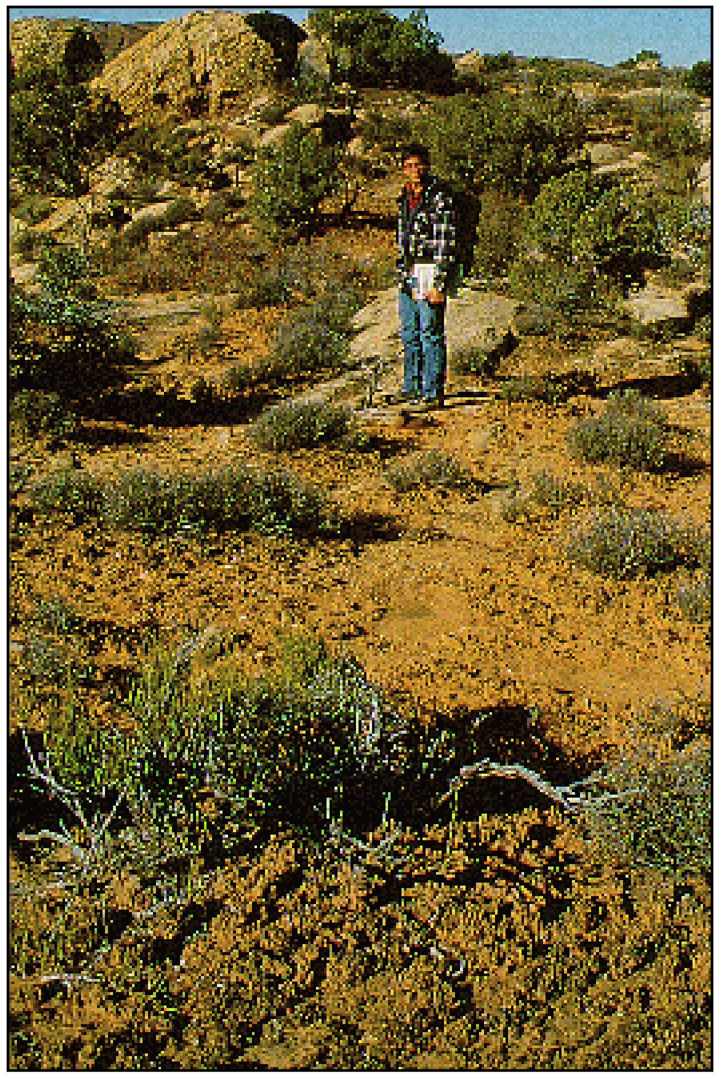

Cryptobiotic soils, also called cryptogammic soils, cryptogammic crusts or microbiotic soils, primarily consist of cyanobacteria, along with lichens, mosses, fungi, and bacteria. These soils or crusts are vital to the desert ecosystem. On the Colorado Plateau, thay may make up 70-80 percent of the living ground cover in some areas. The crusts are living autotrophic organisms.

Cryptobiotic soils occur in arid and semi-arid regions throughout the world. We have even seen them around the Mammoth Hot Springs in Yellowstone National Park.

The image here shows well-devloped cryptobiotic soils in Arches National Park. Ray Kokaly, USGS is in the background. Photo by Roger Clark (public domain image).

More detailed image of Cryptobiotic soils, 332 K GIF.

Papers

Vegetation and Cryptobiotic Soils Mapping in Arid Regions

Phone, email and regular mail addresses of spectroscopy lab personnel for further information.

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