33 Structure and Functioning of Biological Soil Crusts: a Synthesis

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33.1 Introduction

Biological soil crusts play many important ecological roles worldwide, as amply demonstrated throughout this Volume. Given these roles, and the fact that soils in all semiarid and arid lands (representing over 30 % of the Earth's surface) have some degree of biological soil-crust development, these organisms are clearly a substantial force in shaping the structure and function of many ecosystems worldwide. Biological soil crusts are known to increase the stability of often easily eroded soils, influence local hydrological cycles in regions that receive limited precipitation, and increase soil fertility. Biological soil crusts occur in many diverse climates and soils. While some of the published information on soil crusts appears contradictory, chapters in this Volume show that most of the apparent controversy can be resolved by accounting for soil texture and climate (especially separating areas where soils do or do not freeze). Also, as can be seen in this Volume, new information has helped resolve what appeared to be contradictions in older studies.

33.2 Taxonomic Composition and Biogeography

Part I of this Volume showed that biological soil crusts occur in arid and semiarid regions throughout the world, as well as in locally suited sites in temperate, boreal, and arctic environments. While soil crusts exist in unconnected and seemingly dissimilar vegetation types and climates, they are taxonomically and structurally very similar. Most of the typical and often dominant cyanobacteria, lichen, and moss genera have a cosmopolitan distribution, even on the species level. Ecologically similar species, closely related taxa, and/or convergent life forms often replace each other both on neighboring sites and at sites separated by large distances (e.g., *Fulgensia fulgens* and *F. bracteata*; many species of vagrant lichens). On a regional basis, the

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relative dominance of the different species varies with climate and soils. However, many species maintain similar habitat preferences regardless of where they occur worldwide (e.g., the preferential occurrence of certain lichen taxa on stabilized calcareous soils, the salt tolerance of some *Microcoleus* species, the dominance of filamentous cyanobacteria in sandy soils, or the similar suite of phycolichens on most gypsiferous soils), which can also structure crust communities within a given site or region.

Our present understanding of floristics and phytogeography of biological soil crusts on a worldwide basis is still very limited. We are far from being able to construct statistically sound phytosociological groupings or to make detailed comparisons of soil-crust communities on anything except a local basis. It is apparent that we lack even rudimentary knowledge about distribution of biological soil crusts and of their species composition in many regions on most continents. Because species composition of a given soil crust strongly influences the role it plays in a specific ecosystem, additional surveys are needed to better understand the importance of soil crusts in a given area. Systematic work with taxonomically difficult and often scarcely studied groups of soil-crust organisms is urgently needed so comparisons of soil crusts can be made on a worldwide basis. Ecologists should be encouraged to view soil-crust components as part of the vegetation community, and not to restrict their studies to vascular plants. In addition, all groups of soil-crust components should be addressed in field studies, rather than the commonly observed tendency to restrict studies to one group (e.g., lichens, mosses, or cyanobacteria).

An exciting and important goal should be the systematic creation of a comprehensive, worldwide monographic treatment of the phytosociology and biogeography of biological soil crusts. Communities need to be classified with respect to the vegetation zones and higher plant formations in which they occur, ranging from the arid and semiarid lands in the Americas through the Eurasian and African continent to Australia, and from the Arctic, boreal, and temperate belts to Antarctica. This knowledge can then serve as a foundation for a solid assessment and appreciation of the ecological role that these soil crusts play worldwide. In addition, such an assessment will enable land managers to know what crust species should occur in a given ecosystem, and what functional roles these species might play in a given setting. This, then, can provide management and restoration goals for specific regions.

33.3 Heterotrophic Associates

As discussed in *Part II*, soil crusts consist not only of photosynthetic organisms, but also contain significant fungal, microbial, and invertebrate populations. Little is known about individual heterotrophic crustal components or interactions between them and the autotrophic crust components. Microfungi have been the most extensively studied, but these studies have been mostly descriptive and limited to a few geographical locations. Microfungi are known to colonize early after disturbance and to increase aggregation of soil particles, thus increasing soil stability. However, microfungi may also profoundly influence the physiological functioning of other crust species. For instance, both vesicular-arbuscular mycorrhizae and dark-septate microfungi are known to secrete acids that break the chemical bonds that keep phosphorus (P) unavailable to plants in high-pH soils. Microfungi may similarly enhance P acquisition by crust species, and thus differentially influence the relative success of cyanobacteria, lichens, or mosses on a given soil. Also, soil microbes are likely to utilize carbon provided by autotrophic components of the soil crusts. This source of carbon may be an important determinant of decomposition rates (and thus nutrient availability to vascular plants) in deserts, especially in the large interspaces that occur between plants.

33.4 Soil-Crust Structure

Water is everything to the poikilohydric organisms that dominate soil crusts. Thus, while the major determinant of crust structure can vary with the scale being examined, moisture availability is always an important factor in determining crust structure, which is discussed in *Part III*.

On a regional scale, the structure of a given biological soil crust is mostly controlled by climate. In very hot and hyperarid areas, soil crusts are smooth and dominated by cyanobacteria. As rainfall increases, the diversity and cover of mosses and lichens increases as well, and rugose crusts can be found. In regions where frost-heaving occurs, the pinnacled and rolling crusts are dominated by mosses and lichens.

On the landscape scale, the structure of soil crusts is heavily influenced by soil characteristics. Fine-textured soils generally support greater cover of a more diverse lichen and moss community than immediately adjacent coarse-textured soils. Soils with carbonates tend to support greater lichen diversity (especially phycolichens) than soils with low or no carbonates, while gypsiferous soils support the greatest lichen diversity of all. Excessive salt restricts crust species. Topographic position is important, as polar-facing slopes will support the greatest moss and lichen cover and diversity within a landscape, unless heavy vascular plant cover precludes their presence.

On the meter and centimeter scale, crust structure is influenced by microclimate factors. Greater lichen and moss cover and diversity are found in microhabitats where the combination of moisture, light, and temperature is the most favorable for photosynthesis. Soil chemistry may also be important in determining moss and lichen distributions on this scale.

On the millimeter (or smaller) scale, crust structure is mostly influenced by light: that is, by the balance between sufficient light for photosynthesis and protection from excessive light and excessive UV exposure. Species with no or low mobility (mosses, lichens, and small cyanobacteria) must reside at the soil surface in order to obtain sufficient light for photosynthesis. However, intense sun radiation (especially in the shorter wavelengths) at the soil surface requires these species to have protective mechanisms, such as heavy pigmentation. Species without such pigmentation (e.g., *Microcoleus*) must utilize behavioral adaptations to obtain sufficient light for photosynthesis while avoiding excessive light and UV radiation.

33.5 Carbon and Nitrogen Fixation

Semiarid and arid ecosystems have limited vascular plant productivity; thus, in these regions, the carbon contribution of soil crusts can be significant. In some desert regions (e.g., the coastal fog zone of Namibia), the area-related chlorophyll content of the soil crusts is in the range of C3 plant leaf. Thus, the seemingly bare desert surface is actually covered by photosynthetic machinery somewhat like a giant leaf. The maximal photosynthetic capacity of this "leaf" is similar to that of phanerogamous plants growing in the same area. However, metabolic activity of the poikilohydric autotrophs is restricted to the short periods of time when the crusts become hydrated by high humidity, fog, dew, or rain. Nevertheless, a substantial stream of carbon is delivered from the crust autotrophs to the ecosystem, contributing to soil and humus formation and becoming available to the soil heterotrophs.

Our knowledge of CO_2 exchange and photosynthetic production of soil crusts in the different ecosystems of the world is still very limited. The few data available are reported in *Part IV* of this Volume. However, most observations are extrapolations from measurements under controlled conditions and many address only a single organism (e.g., lichen thalli), rather than soil crust as a complex community. While allowing us to make general estimates, these laboratory studies cannot facilitate regional comparisons. Long-term monitoring of soil crust carbon fixation in nature is needed to establish carbon balances under different environmental conditions. In addition, specific ecophysiological work is needed to understand how soil organisms adapt to the extreme microclimate of the soil surface, and to explain metabolic performance of the soil-crust community. With such information, we will then be able to model and quantify carbon exchange in soil crusts of different ecosystems.

There is another important aspect to understanding the carbon exchange of soil crusts. As the dominant ground cover in arid and semiarid areas, soil crusts cover a substantial proportion of the Earth's surface. Thus, they may play a substantial role in the CO_2 fluxes between the ground and the atmosphere. Discussion about the causes of the present global increase in atmospheric CO_2 concentration, and possible mitigation measures, need to include the role of biological soil crusts during their different successional stages. Thus, future measurements and modeling work need to include large-scale estimates of how biological soil crusts contribute to the global carbon budget.

Cyanobacteria and cyanolichens are able to fix nitrogen (N), and soil crusts can be the dominant source of nitrogen in some desert ecosystems. Because only a few habitats have been investigated, it is not yet known how important these crusts are to worldwide N budgets. N fixation rates increase with temperature until a thermal limit of about 30 °C is reached. Thus, in deserts N inputs are greatest during cooler seasons, while in temperate and polar regions, N inputs are greatest in the warmest season. Absolute estimates of N inputs are currently not known for many ecosystems, as ^{15}N calibration of the commonly used acetylene-reduction method has not been done. The lack of conversion ratios for other environments, and year-round data on fixation rates, is a critical problem that needs to be addressed.

Much of the N fixed is immediately leaked to the surrounding soil. It is not known why this occurs: it may be that these simple organisms are unable to stop leakage, that they excrete N to prevent toxicity, or that they excrete N to attract beneficial organisms. The remainder of the N is incorporated in the ecosystem upon decaying of the cyanobacteria and cyanolichens.

Only a handful of studies have addressed N losses in deserts, especially in relation to biological soil crusts. There are many unanswered questions regarding how crusts affect volatilization and denitrification rates. While the crust environment may appear conducive to increased N losses, direct measures have unexpectedly shown very low rates of both volatilization and denitrification during most of the year. Losses appear greater in hot deserts than cool deserts, and higher in summer than at other times of the year. For sandy soils in southeastern Utah, N inputs and losses appear decoupled in time: when inputs are high during fall, winter, and spring, losses are neglible. In summer, the opposite is true, as inputs are low and losses are high. Further studies are needed in other environments that account for time of year, substrate availability, and differences in crustal components and soil characteristics (e.g., texture, nutrient status, and moisture content). With such information, we can then model N budgets for different soil-crust types (including different successional stages) in different ecosystems.

33.6 Interactions with Vascular Plants

Much controversy surrounds the effect of biological soil crusts on the germination and establishment of vascular plants. Some authors claim that crusts inhibit plant establishment and that crusts need to be broken or removed if greater vascular plant cover is desired, while others claim quite the opposite. As discussed in *Part IV* of this Volume, separating results of studies in regions where soils do not freeze from regions with soil freezing resolves most, if not all, this controversy. Regions that lack freezing generally have flat soil surfaces that are further smoothed by cyanobacteria. In such areas, water and wind easily move seeds, organic matter, and water off crusted surfaces to nearby obstacles (e.g., vascular plants or rocks), thus indirectly inhibiting plant establishment in plant interspaces. However, most desert soils have some inherent physical crusting, and the contribution of the biological versus the physical crusts to increased seed movement is not known. In regions where frost-heaving crusts create a roughened surface, the opposite is true: movement of seeds, organic matter, and water is inhibited across crusted surfaces, and the presence of crusts has been found to enhance seedling establishment in plant interspaces. Similarly, in cool regions, the presence of crusts either increases or does not affect seed germination, while in hot regions, germination of native plants shows a full range of responses (positive, negative, and no response).

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. There are many possible mechanisms to explain this finding: (1) crusts fix and secrete both N and C, and it has been shown that the fixed N is utilized by nearby plants; (2) C additions may stimulate microbial populations, increase decomposition rates of plant litter, and thus increase nutrient availability to living plants; (3) exopolymers secreted by crustal components bind metals on the polysaccharide surfaces, thus keeping them plant-available; (4) silts trapped by the sticky polysaccharide material hold positively charged plant macronutrients, keeping them from being leached downwards; (5) most crustal components secrete powerful metal chelators, keeping the metals in solution; (6) there is a strong positive correlation between the presence of crusts and plant mycorrhizal infections; such infections are known to enhance nutrient uptake of plants; and/or (7) the presence of biological soil crusts increases soil surface temperatures by up to 14 °C relative to adjacent uncrusted soils, thus greatly increasing rates of nutrient uptake by vascular plants.

33.7 Soil Stability and Hydrology

All studies reported in *Part V* show that soil crusts increase soil stability. However, as with vascular plants, there has been much disagreement in the literature about their effect on water infiltration. As summarized in Chapter 24, most differences in study results can be resolved if soil texture and site location are taken into account. Fine-textured soils, in regions both with and without frost-heaving, show an increase in water infiltration with the presence of biological soil crusts. Unfortunately, all studies on sandy soils have occurred in regions with no frost-heaving. Here, increased smoothing and sealing by cyanobacteria crusts decreases water infiltration. However, no studies have been done on frost-heaved sandy soils (e.g., Colorado Plateau, Great Basin, Asian steppes), where increased surface roughness from heaving is expected to increase water infiltration.

33.8 Disturbance to Biological Soil Crusts

Most arid and semiarid regions evolved with little soil-surface disturbance, as food and water limited the number and distribution of animals. These same ecosystems occur where biological soil crusts are most evident, and where human use is increasing rapidly. Extensive discussion in *Parts V, VI,* and *VII* shows that in most regions where biological crusts are a dominant feature, crusts are reduced or extirpated by intense or frequent soil-surface disturbances (e.g., grazing, recreation, and fire). This is especially true in soils with low aggregate stability such as sands. Disturbance to crusts generally results in reduced C and N inputs, and increased soil loss from wind and water erosion.

The effects of disturbance by livestock on soil crusts is currently controversial, as crusts can be found in both grazed and ungrazed regions. While most desert soil crusts show little resistance or resilience to grazing, there are some more temperate regions where soil crusts occur despite heavy use by hooved animals (e.g., the Serengeti Plain of east Africa, the Mongolian steppes, the Great Plains of the US, and Oman). While lichen and moss cover and diversity is generally lower in these areas compared to similar ungrazed areas, crusts still persist. Common features of these more resistant areas include (1) soils that are highly weathered, fine to loamy textured, and calcareous, with high water-holding capacity, high bulk density, and some physical crusting; (2) high water availability (due to relatively high rainfall, cold-season occurrence, and/or ponding on soil surface); (3) closely spaced plant material or rocks; (4) early-successional crust species (e.g., *Collema* and *Catapyrenium* species, surface *Nostoc commune*; and (5) intermittent animal use.

33.9 Recovery from Disturbance

Reported recovery rates of soil crusts after disturbance vary widely, as they depend on climate, soil type, and severity of disturbance. Factors that impede recovery include intense or frequent disturbance, large surface-volume ratios of disturbed areas, sandy soils, and high potential evapotranspiration (low rainfall and high temperatures). As the severity of one or more of these variables is lessened, recovery rates increase. Nevertheless, experiments and subsequent extrapolations show that a severely disturbed crust in most semiarid or arid landscapes usually requires many decades, or even centuries, for full recovery.

33.10 Crust Monitoring and Management

Because land uses can have such a profound impact on the structure and functioning of biological soil crusts, it is essential that the condition of soil crusts be monitored where anthropogenic activities are continually recurring. The principal aim of monitoring is to provide an objective basis for either changing or maintaining a current management practice. Thus, monitoring is intimately associated with management, providing information to the land manager and therefore the management process. During the past century, assessment of rangeland health has concentrated on perennial vascular plant attributes (e.g., cover, frequency). While many scientists acknowledge the close links between biological soil crusts and rangeland condition, soil-crust organisms have rarely been documented in field surveys. It is important that such measures be incorporated into rangeland health assessments, as the condition of soil crusts can tell the manager much about the stability and fertility of the site. Remote sensing is likely to be a critical tool in this assessment effort.

Studies show that concentration of use, both spatially and temporally, in desert landscapes is generally desirable. For recreational uses, this means (1) designated campsites and trails and (2) restricting roads to less sensitive areas, designing them to minimize erosion and sedimentation; and eliminating off-road travel. For grazing, protection of soil crusts requires that most low-elevation areas should be used only during wet periods, that livestock numbers be low, and grazing intermittent.

33.11 Summary

This Volume has shown that biological soil crusts occur in many ecosystems worldwide. Where they occur, soil crusts contribute to hydrological balance and erosion control, and are sources of nitrogen and carbon. Unlike vascular plant cover, crustal cover is not reduced in drought and, unlike rain crusts, these organic crusts are present year-round. They also contain extremely long-lived organisms. Consequently, biological soil crusts can offer ecosystem services continuously through time, in spite of conditions often limiting other soil-surface protectors. Unfortunately, the ever-increasing human population is demanding a greater land base for livelihood and recreation. As humans push further into the semiarid and arid lands previously considered unsuitable for such activity, the cover and diversity of crusts will be concomitantly reduced. Thus, it is a crucial task for present and future managers of these drier regions to find a balance between human needs and desires and sustainable use of these arid and semiarid landscapes.

We hope that this Volume, which summarizes our present knowledge on the structure, function, and management of biological soil crusts, will contribute to the appreciation and understanding of soil-crust ecosystems such that they become an object of concern and conservation for both the public and land managers. The well-being of our planet depends on maintaining the stability and fertility of our soils. With sufficient care, the small and inconspicuous soil-crust ecosystems that cover so much of our planet like a living skin will continue to provide this service long into the future.