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Biological Soil Crusts: An Organizing Principle in Drylands

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Evolution of biological soil crusts during thousands of millions of years of biosphere development of our planet (for detailed legend and explanations see Fig. 25.2);
drawing by B. Büdel and F. Spindler

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Editors

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Springer

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Preface

During the last decades, and probably at least partly triggered by the first Ecological Studies volume on this topic (volume 150), biological soil crusts (biocrusts) have quickly gained increasing interest from many audiences, with well above 100 publications per year published during the last few years. Thus, we found that there is now a wealth of new data covering a wide range of different topics on biocrusts and showing that biocrusts can act as “an organizing principle in drylands.” This observation inspired us to use this as the title of this second Ecological Studies volume. This book is divided into seven sections comprising a total of 25 different chapters.

When we selected the authors for the different chapters, we had two intentions in our mind. One was to include many scientists from as many regions of the world as possible, who also used different methodological approaches in order to get a thorough and comprehensive view on the different topics. Second, we also wanted to get a good mixture of younger and well-established researchers. With a total of 61 chapter authors and 28 of them being in the doctoral, postdoc, or associate professor stage, ~46 % of the book authors are in a nonfinal/early stage of their career.

This second book on biological soil crusts would not have been possible without the help of some people in particular, whom we would like to thank here: first of all, we would like to express our sincere thanks to Otto L. Lange, who gave us the opportunity to be editors of this book, who strongly supported us throughout the whole process of development, from the first ideas to the final editions, and who read and gave highly productive feedback to every single chapter of this book. Thank you so much! Second, we also would like to thank all the authors who contributed to the book. We are well aware of the fact that we sometimes asked for rather profound and time-consuming changes during the development of the book chapters. Despite this, all authors remained highly cooperative and motivated, a fact which cannot be taken for granted and which we deeply appreciate. Third, we would like to express our sincere thanks to Dr. Andrea Schlitzberger, who coordinated this biocrust book for Springer. She always was extremely patient and helped

us immediately upon all smaller and larger problems, and it really was a pleasure to work with her. Fourth, we want to thank our supervisors and colleagues, who allowed us to spend so much time and energy on this book and who believed that in the end, we would produce a worthwhile book that would advance this scientific field. Finally, we also would like to express our sincere thanks to our families and partners for their tolerance and support during the endeavor of this second biocrust book.

We sincerely hope this book will help many scientists, land managers, policy makers, and also the environmentally interested public, to receive an overall introduction into the fascinating world of biocrusts and that it will foster many new ideas and scientific projects. Our goal is reached if this book supports understanding of the overall role of biocrusts as an organizing principle in drylands.

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Part I

Introduction

Chapter 1

Biological Soil Crusts as an Organizing Principle in Drylands

Jayne Belnap, Bettina Weber, and Burkhard Büdel

1.1 Introduction

Biological soil crusts, including hypoliths (hereafter referred to as biocrusts), consist of microscopic (cyanobacteria, algae, fungi, and bacteria) and macroscopic (lichens, mosses, and microarthropods) poikilohydric organisms that occur on or within the top few centimeters of the soil surface. In regions where water availability limits vascular plant cover, these communities are especially notable, creating an almost continuous living skin that mediates most inputs, transfers, and losses across the soil surface boundary (Fig. 1.1). As these dryland regions constitute up to 40 % of the Earth's terrestrial surface, biocrusts are a major feature of Earth's surface (Fig. 1.2).

Taken together, the various biocrust types form one of the dominant community types on Earth. Despite this, their study has begun only very recently (Chap. 2 by Lange and Belnap). In addition to being among the most dominant community types, organisms similar to biocrust microbes are some of the earliest known terrestrial life-forms, with a possible appearance in the fossil record as early as 2.6 billion years ago (see Chap. 3 by Beraldí-Campesi and Retallack).

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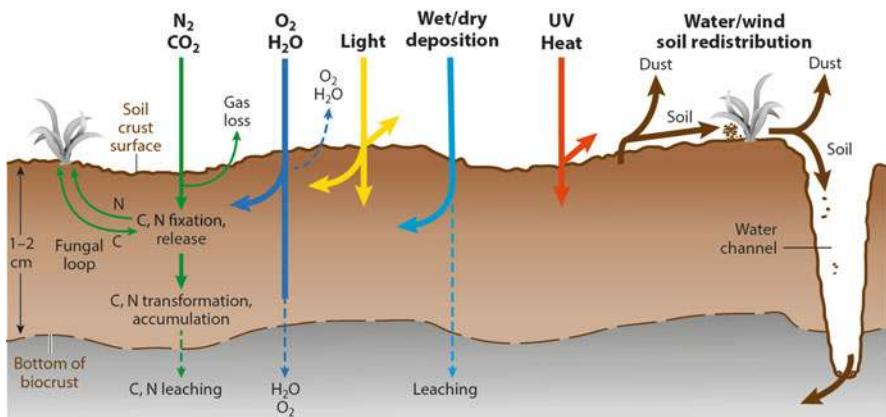


Fig. 1.1 A schematic diagram showing the many ecosystem processes affected by the presence of biocrusts

Cyanobacteria and algae (see Chap. 4 by Büdel et al.), bacteria, and microfungi (see Chap. 5 by Maier et al.) generally create the basic matrix of the biocrust, facilitating the colonization of bryophytes (see Chap. 6 by Seppelt et al.), lichens (Chap. 7 by Rosentreter et al.), and microfauna (see Chap. 8 by Darby and Neher).

At the global and regional scale, the composition and biomass of a given biocrust community depend mostly on climate: at the dry end of the potential evapotranspiration (PET) spectrum, biocrusts are dominated by a low biomass of cyanobacteria, bacteria, and microfungi, with no mosses or lichens present (see Chap. 10 by Bowker et al.). As PET decreases, cyanobacterial biomass increases and bryophytes and lichens appear. Whereas biocrusts are often classified by the type of photoautotrophs present and dominant (see Chap. 9 by Colesie et al.), bacteria, fungi, and micro-invertebrates are also very important components (see Chaps. 5 and 8). However, little is known about how the biomass, species composition, or ecological roles of these organisms change under different environmental conditions. Green algae are also present in biocrusts, but apparently of lower biomass, except in some settings (Chap. 4). Hypoliths dot desert soil surfaces and are colonized by a unique community of microbes, mosses, and lichens (see Chap. 11 by Pointing).

At the local scale, factors other than climate control the type of biocrusts present. Soils are extremely important, as biocrusts prefer soils derived from some parent materials over others, due to their nutrient content or soil texture (Chap. 10). Life at the soil surface in dryland regions exposes biocrusts to various abiotic stresses, including high temperatures, UV, salinity, pH, and low moisture, and thus micro-environments, such as shrub canopies, can also determine the type of biocrust present, as they can moderate these factors (see Chap. 19 by Zhang et al.). However, biocrusts are highly vulnerable to physical disturbance and alteration in climatic conditions, and severe disturbance will alter their species composition or cover, often setting them back to an early successional stage (see Chaps. 21 and 22 by

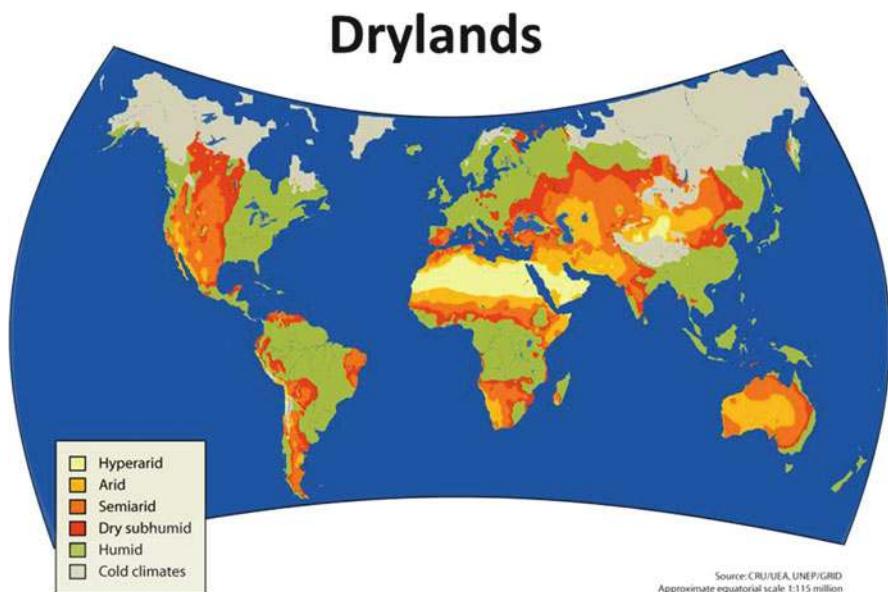


Fig. 1.2 Drylands of the Earth. Drylands cover ~40 % of the terrestrial land surface

Zaady et al. and Reed et al., respectively). Natural recovery from disturbance is often very slow; thus, techniques for enhancing this recovery are being explored and developed (see Chaps. 23 and 24 by Weber et al. and Zhao et al., respectively). Unfortunately, we have little information on long-term dynamics of recovering communities, either through natural or assisted processes (Chap. 25 by Weber et al.). Remote sensing offers an important tool to gain more detailed knowledge about recovery in the future (see Chap. 12 by Weber and Hill).

As studies on biocrusts continue, there is an ever-increasing understanding of the central role they play in the structure and function of dryland ecosystems. These organisms, such as cyanobacteria and lichens, enhance the weathering of soil from rock, and biocrusts stabilize the resultant soil particles and structure soils by creating soil aggregates (see Chaps. 13 and 16 by Garcia-Pichel et al. and Belnap and Büdel, respectively; Chap. 9). Because biocrusts often determine soil structure and the morphology of the soil surface, they influence hydrologic cycles (see Chap. 17 by Chamizo et al.) and the capture and retention of resources such as soil, organic matter, seeds, and nutrient-rich dust (Chaps. 16 and 19). Biocrusts further enhance soil fertility by fixing atmospheric carbon (C; see Chaps. 15 and 18 by Sancho et al. and Green and Proctor, respectively) and nitrogen (N; see Chap. 14 by Barger et al.) and secreting it to underlying soils, and these contributions appear to be globally significant (Elbert et al. 2012). Biocrusts may also alter the bioavailability of other nutrients such as phosphorus (P; Chap. 19). Combined, the presence of biocrusts enhances soil fertility at the surface relative to underlying or uncrusted soils, as documented in many studies [reviewed in Belnap et al. (2003)]. Because

biocrusts enhance soil fertility and influence local hydrologic cycles, studies show their presence affects the timing and spatial location of the germination and establishment of vascular plants, as well as their nutrition (Chap. 19). Indeed, there are indications that fungi in the biocrust layer create a direct nutrient and C link between biocrusts and vascular plants (Chap. 19). Because of their small size, ease of manipulation, multiple species composition, and multifunctionality, these communities are also now successfully being used as models to test basic ecology theory (see Chap. 20 by Maestre et al.).

1.2 Biocrusts as an Organizing Principle, and the Critical Zone, in Deserts

The *critical zone* concept is becoming commonly used by ecologists and others to explore the defining aspects of a given ecosystem. It is described as the “heterogeneous, near surface environment in which complex interactions involving rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources” (US National Research Council 2001). For mesic regions, this zone is generally measured in multiple meters above and below the soil surface, given the relatively tall plants and deep roots. In drylands, however, the situation is very different. Vegetation is generally sparse and short, with mostly shallow roots, and there is often a large amount of exposed bedrock. Given the criticality of biocrusts in these lands, as well as on Earth’s early land surface before the advent of vascular plants, we and others suggest the critical zone in drylands is now and, for most of Earth’s living history, at, on, or in the top few centimeters of rock or soil surfaces: that is, the zone characterized by the presence of biocrusts, endoliths, and hypoliths, not vascular plant roots (Pointing and Belnap 2012). This view is justified by the central role (discussed above and throughout this volume) that these surface layers play in most ecosystem processes in these landscapes, including (1) mediating almost all inputs and outputs (gases, nutrients, water) to and from the strata above and below the surface; (2) being the zone of high nutrient deposition, transformation, and availability; (3) structuring temporal, spatial, and compositional aspects of the vascular plant community; and (4) facilitating the direct delivery of C, nutrients, and water by biocrusts from the soil interspace to nearby vascular plants. Because of the centrality of biocrusts in these processes, we suggest that they are an organizing principle in dryland ecosystems.

The consideration of biocrusts as an organizing principle in drylands fundamentally alters how we view many ecosystem processes in these landscapes. Traditionally, the scientific community has allocated this structuring role almost exclusively to the more visible aspects of an ecosystem: vascular plants and the larger animals. However, as we will show throughout this volume, there is every reason to question this basic assumption, especially in drylands, and instead begin a careful consideration of the essential organizing role biocrusts can play.

1.3 Under-Examined Roles of Biocrusts in Dryland Ecosystems

There are many ways, which have yet to be fully examined, that biocrusts may influence structure and function of dryland ecosystems. Below, we present tantalizing evidence for several of these ideas, although there are certainly many more to be studied.

1.3.1 *Islands of Fertility or Oceans of Depletion?*

It has long been believed that dryland plants, especially shrubs, create fertile zones around their stems by capturing wind- and waterborne sediments, as well as mining surrounding soils with their roots and then depositing these nutrients via leaf drop, at their base. This results in nutrient levels often being higher under plant canopies than in the interspaces between the plants. On the other hand, it is well known that biocrusts contribute to soil fertility and that undisturbed biocrusts contribute to, and better sustain, fertility than disturbed ones (or bare soil). Biocrusts do this by enhancing soil stability (Chap. 16), by adding newly fixed atmospheric C and N to underlying soils (Chaps. 14, 15, and 18), and by harboring greater microbial and microfaunal populations (Chap. 8, Housman et al. 2007), thus likely increasing nutrient availability via higher decomposition rates. Combining these two sets of observations indicates the possibility of another story: that before wide-scale and high levels of utilization by human-associated activities, especially livestock grazing, well-developed biocrusts occurring in the plant interspace kept soil nutrients levels more or less equal to those under the shrubs. This has been observed in multiple studies comparing grazed and ungrazed areas [reviewed in Allington and Valone (2014); Belnap unpublished data] and the movement of large amounts of sediment, with associated nutrients, after livestock introduction into the Western United States has been documented (Neff et al. 2008). Therefore, human use may have converted much of these landscapes from fairly homogenous, relatively nutrient-rich “mainlands” into the situation found today: that is, generally characterized by highly heterogenous fertility islands surrounded by a sea of depleted soils.

1.3.2 *Biocrusts as the Transformative Zone*

Dust inputs can substantially increase the fertility of the soil surface, relative to underlying soils, in drylands (Reynolds et al. 2001). In addition, the surface zone of most dryland soils contains the highest levels of N, P, C, and other nutrients compared to underlying soils, due to biocrust (e.g., N and C fixation) and vascular

plant activity (e.g., leaf drop; Belnap et al. 2003). Most rainfall events in deserts are very small: for example, on the Colorado Plateau in Utah, USA, ~70 % of rainfall events are <5 mm and only 13 % exceed 10 mm (Bowling et al. 2011), and because the proportion of small events increases with aridity (Golluscio et al. 1998), many deserts see almost nothing but small events. Therefore, infiltration of most precipitation events in drylands is limited to the top few centimeters of soils, implying that water-driven input and transformative processes are activated almost exclusively in the biocrusts and far less frequently at depth. Thus, the dominant microbially driven nutrient transformations are decoupled in time and space from vascular plant production (Austin et al. 2004; Schwinning and Sala 2004; Collins et al. 2014). When large rain events do occur, nutrients at the surface are then available to be washed downwards into the plant root zone, especially as biocrusts most often enhance infiltration, at least at the hillslope scale (Chap. 17). Thus, the way in which the species composition of a biocrust influences the spatial and temporal aspects of nutrient input, transformation, and bioavailability may be critical in a more complex way than previously envisioned.

Another phenomenon concerning biocrusts and soil fertility is the mechanism by which the immobile lichens and bryophytes that lack roots obtain P from underlying soils. Phosphorus is an essential macronutrient, and relatively high levels are needed for organismal growth and function (e.g., for ATP production). However, most dryland soils are low in P and that which is present is often bound by carbonates or other elements, making it bio-unavailable. It is not known how lichens and bryophytes access sufficient P once they deplete the soils directly in contact with their tissue. Dust would provide some of this needed P, but is unlikely to provide sufficient amounts on an annual basis (Reynolds et al. 2001). Recent studies show that free-living fungi are likely conduits moving N from interspace soils to plants through the biocrusts in exchange for C from the plant (e.g., Green et al. 2008). Mycorrhizae are well known to deliver P to plants, likely in exchange for plant-derived C. It is well known that lichens secrete copious amounts of the C and N that they fix from atmospheric gases [reviewed in Belnap et al. (2003)]; this has always been somewhat mystifying, as these processes are expensive. This raises the intriguing possibility that either fungi may be delivering P to lichens and bryophytes in exchange for the secreted C (and N) or perhaps the fungi are secreting factors such as phosphatase, to make the P bioavailable to the lichen or bryophyte.

1.3.3 Biocrusts Structuring Vascular Plant Communities

Researchers have long observed that invasive plants, whose seeds have large appendages, are often prevented from germinating on a moss–lichen biocrust. A few recent studies have indicated that this may not only apply to invasive plants but to native plants as well (Chap. 19). These studies indicate that whereas all plant species in a given community can establish on bare soils, a few species, all with large appendaged seeds, are absent in soil seed banks and plant communities

covered with cyanobacteria. When soils are covered with lichens and/or bryophytes, many more species, all with large appendaged seeds, are missing from the seed bank and plant community. Thus, the species composition of biocrusts may have a profound impact on the structure of the associated vascular plant community. As biocrusts are often disturbed, there are still many places at the landscape scale where all species can establish, maintaining the larger species pool. The relationship between seed morphology and biocrust composition may set up an interesting spatial and temporal tension between the recovery of disturbed biocrusts that act to screen out more and more species as mosses and lichens colonize and the disturbance of biocrusts that creates bare soil patches where all species can establish. This hypothesis needs to be tested across many more deserts and vascular plant communities to establish how widespread and important this process is in determining the structure and function of dryland plant communities.

1.3.4 Biocrusts Creating Biodiversity Hotspots in Drylands

Biocrusts can significantly increase biodiversity for some ecosystems and can be especially important for biodiversity in regions where the numbers of vascular plants are low. This fact has been exemplified many decades ago with the lichen coefficient (Mattick 1953), i.e., the quotient of the number of lichens and vascular plants, which increases from tropical and temperate toward polar regions. But also in some drylands, as the Great Basin Desert, there are relatively few vascular plants, but a rich flora of lichens and mosses. In Idaho, USA, surveys of several different vegetation types show that biocrusts contribute significantly to biodiversity. In a *Chrysothamnus nauseosus*–*Poa sandbergii* community, there were 39 perennial species of nonvascular organisms (31 lichens, 6 mosses, and 2 liverworts), whereas there were only six perennial vascular plant species (Rosentreter 1984). At Orchard Training Grounds in Idaho, USA, the *Artemisia* community had 53 nonvascular biocrust species compared to only six vascular plant species; *Atriplex* community, 23 vs. 5 species; *Chrysothamnus nauseosus* community, 25 vs. 9 species; *Ceratoides lanata* community, 17 vs. 4 species; and *Poa sandbergii*, 25 vs. 4 species (R. Rosentreter, unpublished report, with herbarium vouchers of all the nonvascular biocrust species). In the Colorado Plateau Desert, UT, gypsiferous soils generally support less than five perennial vascular plant species, whereas there are up to 28 lichen and moss species (Bowker and Belnap 2008). Similarly, *Coleogyne ramosissima* communities in this region generally support only shrub and several forb and grass species, whereas there can be up to nine lichen and five moss species (Belnap et al. 2006). In these situations, the presence of well-developed biocrusts may convert biodiversity “cold spots,” based on the number of vascular plants, into biodiversity “hotspots” when biocrust species are included. Also, as we gain more information on lichen and moss species found in biocrusts from understudied regions, this phenomenon may become evermore commonly observed.

Lichens and mosses also significantly contribute to biodiversity in more northern latitudes, even though vascular plant numbers are high relative to drylands. For example, in Spitsbergen, Norway, 184 vascular plants and 1158 species of lichens and bryophytes, most of which were associated with biocrusts, were recorded at one site (Dahlberg et al. 2013). In Greenland, ~450 vascular plants and 1708 species of lichens and bryophytes were recorded; again, most of the lichens and mosses were biocrust species (Daniëls et al. 2013). It is not known if the increased biodiversity conferred by biocrust species results in greater resistance and resilience to disturbance, as has been posited for vascular plant communities (Naeem et al. 2000; Isbell et al. 2015), but this would be worthy of investigation.

1.3.5 Challenging the Definition of Lichen Individuals and the Boundary Between Being Heterotrophic and Autotrophic

It is generally believed that most lichen thalli in dryland regions represent individual, slow-growing organisms. However, there have been a handful of studies indicating this may not always be the case. First, a long-term study of lichen dynamics by Belnap et al. (2006) showed that cover values were very dynamic in the short and long term, with cover values changing by up to 10 % from fall to spring (increasing) and spring to fall (declining). Second, recovery from trampling disturbance is not always slow; it depends on the conditions during and following the disturbance (Chap. 23). For instance, several studies in both hot and cool deserts have shown that when biocrust material is removed from a surface, rather than trampled in place, recovery time is much slower (Belnap unpublished data; Chap. 21). Recovery from fires can be rapid in some sites, if fire intensity is low (Bowker et al. 2004, unpublished data).

These observations could be explained by the hypothesis that lichens, rather than being individuals, are connected by a common fungal mat, similar to many mushrooms. Thus, when conditions are unfavorable, the phycobionts of the lichen could sink down into the mat, becoming heterotrophic, and, when conditions become favorable, reform on the surface as phototrophs. Green algae and cyanobacteria are both capable of heterotrophic growth. Many studies have been done on heterotrophic cyanobacteria (e.g., Olson et al. 1999), although most have used marine species. However, Khoja (1973) found that 18 of 24 species tested were able to grow heterotrophically, and 13 of these were cultured from soil. Additionally, Yaeger et al. (unpublished data) found live *Nostoc commune* at 30-cm soil depth from the Colorado Plateau, Utah, USA, and Garcia-Pichel and Belnap (2003) found chlorophyll *a* at 30-cm depth. Far fewer studies have been done on green algae, but some of those tested can grow heterotrophically (e.g., Day and Tsavalos 1996; Ueno et al. 2005; Perez-Garcia et al. 2011). We also know that fungal threads (rhizines) can connect thalli and lichen prothalli (Letrouit-Galinou and Asta 1994).

The presence of a fungal mat connecting what has been considered individual lichen thalli would explain both the rapid appearance and disappearance of lichen thalli seen by Belnap et al. (2006) and the observation that under disturbance circumstances that leave fungal material in place (e.g., trampling, rapidly passing fire), recovery is much faster than when the fungal mat is removed.

1.4 Can Biocrusts Be Used as a Vital Sign of Ecosystem Health?

As discussed above and throughout this book, biocrusts influence many aspects of the ecosystems in which they occur. Therefore, they may be good bioindicators of the health of an ecosystem or of a specific ecosystem process. For instance, soil health is critical in sustaining ecosystem function. Because biocrusts influence so many aspects of soils, it may be that evaluation of their cover and composition can be used as an index of soil health, rather than requiring all the different aspects of soil health to be measured separately (Rosentreter and Eldridge 2003). Another example is that, as they are very responsive to temperature and water regimes, they may be excellent indicators of climate changes, regardless of the biocrust type being evaluated. As we are now developing ways to accurately assess biocrust cover and composition using remote sensing techniques (Chap. 12), development of such indices may give us the ability to easily monitor soil/ecosystem health and response to climate change at the regional scale.

1.5 Conclusion

As research into biocrusts continues, it is becoming increasingly evident that they perform such important functions in dryland settings that they are likely the critical zone in these settings. Biocrusts modify both the physical and biological environment, thus influencing soil stability, fertility, and hydrology. These changes to the environment then ramify throughout the ecosystem, affecting vascular plants and animals. As research continues on these communities, evermore exciting questions will continue to be raised. In addition, the answering of these questions will likely make it even more clear how central these communities are to the healthy and sustainable function of dryland ecosystems.

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Chapter 2

How Biological Soil Crusts Became Recognized as a Functional Unit: A Selective History

Otto L. Lange and Jayne Belnap

2.1 Introduction

It is surprising that despite the worldwide distribution and general importance of biological soil crusts (hereafter referred to as biocrusts), scientific recognition and functional analysis of these communities are a relatively young field of science. In this chapter, we sketch the historical lines that led to the recognition of biocrusts as a community with important ecosystem functions. For earlier treatments of relevant aspects of biocrust history, see Friedman and Galun (1974), Cameron and Blank (1966), and Belnap and Lange (2003).

Biocrusts have had multiple names through time. The term “cryptogamic crust” was first coined by Harper (Kleiner and Harper 1972). At that time, there were only two kingdoms, plants and animals, and the dominant organisms in the crust were all classified as nonflowering plants, or cryptogams. However, later taxonomic changes resulted in cyanobacteria and fungi, including lichens, being placed in different kingdoms. As a result, the name “cryptogamic crust” was no longer accurate, and other names were suggested, including microbial crusts (Loope and Gifford 1972), microphytic crusts (West 1990), microbiotic and cryptobiotic crusts (Belnap 1993), and finally, biological soil crusts (e.g., Lange et al. 1992; Belnap and Lange 2001). The name “biological soil crusts” or “biocrusts” has now become universally accepted, as it is taxonomically correct and inclusive of all organisms in the biocrusts, including microfauna. In addition, it clearly separates biological

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crusts from physical or chemical crusts, which is an important distinction, as biocrusts have very different influences on ecosystem properties than other crust types.

2.2 Two Lines that Lead to the Recognition of Biocrusts

The idea of biocrusts as a functional ecological community has come from two main scientific branches: botany and soil science. Botanists have long recognized that multiple organisms colonize the soil surface in the open and often dry areas occurring between vascular plants. Later, after the initial taxonomic and phytosociological descriptions were made, soil scientists and agronomists observed that these surface organisms interacted with soils in ways that changed the soil structure. Below, we trace these two lines from the distant past until 1990, when biocrusts became well-known to scientists and the public, at least in some parts of the world.

2.2.1 *The Floristic, Botanic Approach*

2.2.1.1 Lichens

Many lichens common to biocrusts worldwide were among those first described for scientific purposes, including *Psora decipiens*, *Toninia sedifolia*, and *Squamaria lentigera*. In most cases, these species were collected from European dryland habitats where they were found growing on top of the soil. Smith and Sowerby (1803) described *Lichen caeruleonigrans*, the “Black and Blue Lichen” (now *Toninia sedifolia*) (Fig. 2.1), as a lichen that “grows on the ground ... and consists of long branched tufted spongy roots, bearing tufted roundish clustered leaves”. Stahl, in 1877, depicted the long multibranched rhizinae of *Endocarpon pusillum* (Fig. 2.2). This biocrust lichen became an important milestone for lichenology when he performed the first laboratory synthesis of a green algal lichen with this species.

In the nineteenth century, there was the general impression that arid habitats were very poor in lichens (von Humboldt 1859; Zukal 1896), despite many early reports of desert soil lichens either from early explorers or specialized lichenologists. For example, Carl Per Thunberg (who named many South African plants) collected *Psora decipiens* in 1774 (see Doidge 1950), which he published as *Lichen incarnatus* (Thunberg 1823). Other early publications of soil crust lichens from desert and semidesert regions include Nylander (1878) and Steiner (1895) from the Sahara, Fink (1909) from Arizona, Tuckerman (1882, 1888) from North America, and Müller (1880) from Egypt.

The steppes, semideserts, and deserts of south Russia, with their rich soil lichen floras, appear to be one of the first areas to attract extensive studies of ground

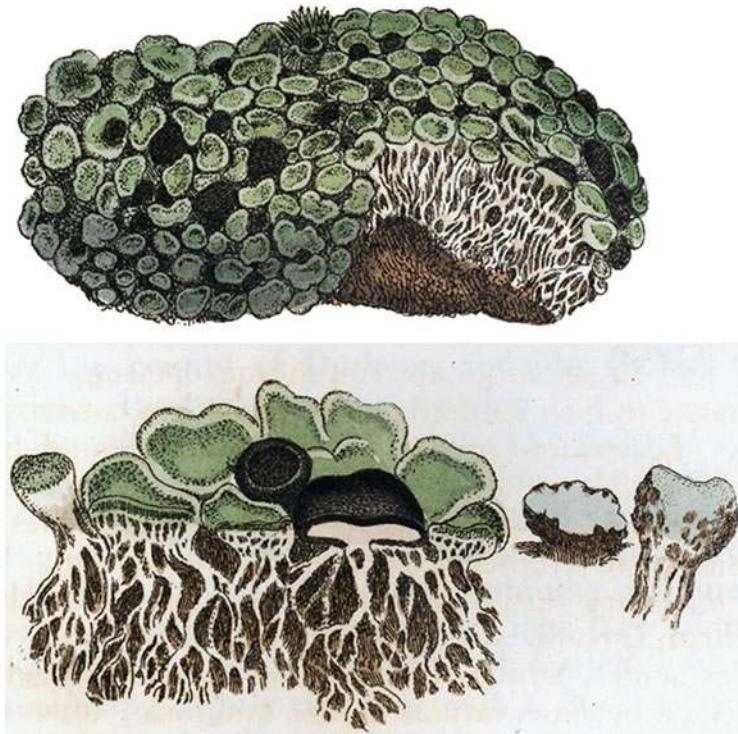


Fig. 2.1 “Black and Blue Lichen”, *Toninia sedifolia* [After Smith and Sowerby (1803)]

surface lichens. Peter Simon Pallas (1741–1811), a noted naturalist-explorer who traveled in service of Catherine II of Russia to explore the central Russian provinces, was possibly the first scientist to describe extensive soil lichen covers in the semiarid steppe formation of Kazakhstan (Pallas 1776). He reported that the loamy soil surface was covered by a whitish-gray crust (German “Rinde”) of “*Lichen tartareum*, *tinctorium*, *candidum*, *tuberculis*, *atris* Dillenius”, most probably a *Diploschistes* sp. He also observed the crust broke into pieces when dry and was growing together with *Tremella terrestris*, a *Collema* sp. These lichens formed a terrestrial community which, without a doubt, we would call a biocrust today. Much later, Tomin (1926) presented possibly the first key for 36 terrestrial lichen species found in the semideserts of southeast Russia. Most of these species had been collected by Keller (1930), who described several types of communities that we today call biocrusts. Keller also published photographs from this site, which was near Pallas’ site of 154 years earlier (Fig. 2.3), listing 44 soil lichen species or varieties (e.g., *Collema* sp., *Fulglesia fulgens*, *Psora decipiens*, *Squamaria lentigera*, *Toninia caeruleonigricans*, and *Diploschistes scruposus* var. *terrestris*, which probably is *Diploschistes muscorum* or *Diploschistes diacapsis*. His list also included cyanobacteria (*Microcoleus vaginatus*, *Scytonema ocellatum*, *Nostoc commune*) and a moss (*Tortula ruralis*). Keller mentions that growth of these

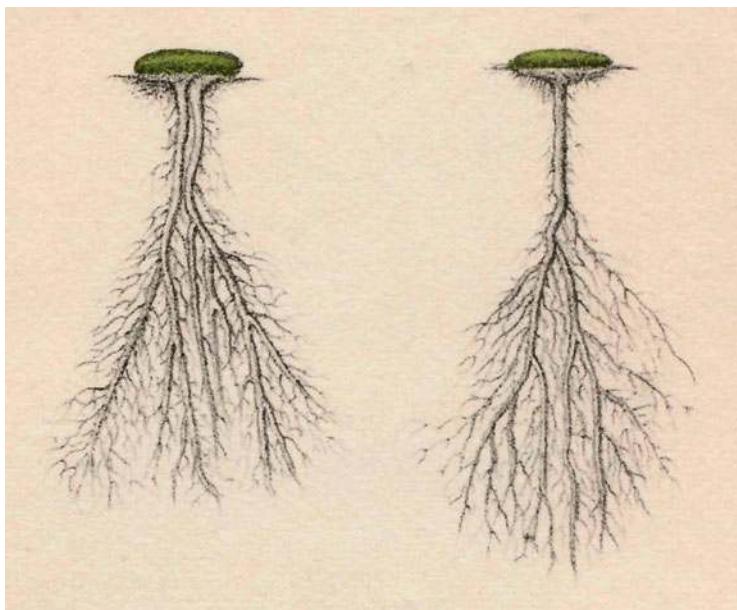


Fig. 2.2 *Endocarpon pusillum* [After Stahl (1877)]

organisms was supported by a dense layer of soil (“*dichte Schicht*”); however, he did not recognize that the organisms themselves were creating this dense layer. Thus, despite having described a true biocrust, Keller thought of this layer as the prerequisite to, rather than the result of, biological activity.

The common coexistence of a group of conspicuous and variously colored terrestrial lichens that included *Psora decipiens*, *Toninia sedifolia*, *Fulglesia* sp., and *Diploschistes* sp., together with *Cladonia* and *Collema* sp. on dry calcareous or gypsum soils, was also recognized early by lichenologists throughout Europe, including Arnold (1868–1897), Tirol; Kaiser (1926) and Gams (1938), Central Germany; and Du Rietz (1925), South Norway. After Braun-Blanquet (1928) had stimulated phytosociological classification of plant communities, lichenologists began defining lichen communities, and the grouping above was named “*Bunte Erdflechten-Gesellschaft*” (i.e., the “colored lichen community”; Reimers 1940, 1950). It is significant that this was one of the very first lichen communities to receive extensive study. For Central Europe, Klement (1955) proposed a general syn-taxonomy of the different types of lichen communities colonizing open soil mainly within local subarid steppe formations within the two main unions of “*Toninion coeruleonigricantis*” and “*Diploschistion terrestris*.” These lichen communities were often interpreted by him and by others as relicts from late and postglacial times. There continued to be a rich literature in which these or similar lichen communities were described throughout the world [e.g., Europe, Pause (1997); Australia, Rogers (1972); Israel, Galun (1963); Mongolia, Schubert and



Fig. 2.3 Soil vegetation of the lower Ural and Volga Rivers' area [After Keller (1930)]. Dominating “*Diploschistes scruposus* var. *terrestris*” (probably *Diploschistes muscorum* or *Diploschistes diacapsis*)

Klement (1971); Mesopotamia, Schubert (1973)]. Looman (1964) found a striking similarity between the soil lichen communities of the Great Plains in North America and Central Europe with 16 individual species in common.

2.2.1.2 Bryophytes

Similar to lichens, many bryophyte species typically found in biocrusts were taxonomically described in the eighteenth and nineteenth centuries. Several species were included in Linné's *Systema Vegetabilium* (1774), and there are several old reports of bryophytes from dry areas around the world. Examples include the *Conspectus Bryophytorum Orientalum et Arabicorum* by Frey and Kürschner (1991) and Griffith (1849) for Afghanistan, Geheeib (1902) for Syria, and Lorentz (1867) for Egypt and Sinai. Joseph Dalton Hooker collected four Antarctic moss species in 1843–1847 when he participated in James Clark Ross' expedition (Wilson and Hooker 1847), and Skottsberg (1905) was the first to describe moss-dominated tundra of the maritime Antarctic Peninsula.

By the first half of the twentieth century, there were many descriptions and vegetation analyses of habitats with coexisting soil lichens and bryophytes that today would be called biocrusts. In Europe, for example, this includes open patches in local steppe formations where the ground cover was described as communities of “colored soil lichens” growing together with mosses and liverworts on lime or gypsum soil (Du Rietz 1925; Kaiser 1930; Stodiek 1937; Reimers 1940; Bornkamm 1958; Marstaller 1971). There are even phytosociological units defined and named in which bryophytes and lichens are combined, as for instance the “*Caloplaca fulgens*–*Tortella inclinata* sinusia” (Zólyomi 1987). In the last decades, our knowledge of bryophytes of arid areas, including their distribution, sociology, and ecology, has considerably improved [e.g., Afghanistan (Frey and Kürschner 2009), Jordan (Frey and Kürschner 1995), and Saudi-Arabia (Frey and Kürschner 1987)]. In the Judean Desert, Frey et al. (1990) and Frey and Kürschner (1990) observed the close connection between bryophyte communities and the colored lichen communities; they also describe cyanobacteria in the loess soil.

Despite the very early taxonomic description of moss and liverwort communities on dry ground, the older literature does not mention these communities as being part of what we today call a biocrust community. There was also no demonstration or observation of these communities consolidating or protecting the soil surface. This may be because in many hot and temperate arid regions, bryophytes, mosses, and liverworts are generally sparse or even absent, whereas cyanobacteria and lichens conspicuously dominate the biocrusts. According to Scott (1982) and many other authors, the earliest stages of biocrust formation in drylands is the stabilization of the soil surface by filamentous cyanobacteria, followed by colonization of lichens and bryophytes. In contrast, cold-polar area biocrusts are often dominated by mosses that can even create continuous carpets. Temporarily wet areas in the continental Antarctic are typically covered by bryophyte flushes, as described by Rudolph (1963) for Cape Hallett in Victoria Land.

2.2.1.3 Cyanobacteria and Green Algae

Ehrenberg (1854) was one of the first to extensively analyze and depict microorganisms in different kinds of soil, and he identified many types of algae. At that time, the term “algae” included both blue–green (cyanobacteria) and green algae. The differentiation between these groups occurred early in the nineteenth century. In 1874, Sachs coined the term “Cyanophyceae” for blue–green algae, and in 1977, Stanier and Cohen-Bazire proposed the term “cyanobacteria” to be used to differentiate between these prokaryote organisms and the eukaryotic green algae. Despite the early separation of these two groups, older studies continued to refer to them collectively as “algae.” Whereas most later studies separate them, phycologists still accept the term “algae” when referring to both groups. Therefore, in our discussion below, we use the terms algae, green algae, blue–green algae, or cyanobacteria, depending on the term used in the study being cited.

The terrestrial species of the genus *Nostoc*, typically occurring in most biocrust communities worldwide, were most likely the first cyanobacteria to attract the interest of plant scientists, as well as the public. During the times of Paracelsus (1493–1541), a heavenly, divine, or devilish origin was ascribed to the frightening gelatinous “Nostoch” colonies that suddenly appeared on the surface of wet soil. These colonies were used for medical purposes (Schmid 1951, see monograph by Mollenhauer 1985–1986). More than 280 years ago, the Italian botanist Micheli depicted a *Nostoc* thallus (Fig. 2.4): “*Linckia terrestris, gelatinosa, membranacea, vulgarissima, ex pallida et virescente fulva*” in his 1729 publication. No one less than Johann Wolfgang von Goethe (1892) provided an early description of *Nostoc* growing on soil (see Schmid 1942). He reported in a handwritten journal entry that in 1785 he had found a large amount of gelatinous lobes (“*gallertartige Läppchen*”) on the ground in a sandy place after rain. He kept the material in water, and with a magnifying glass he recognized rows of spheres (“*Reihen von Kugeln*”), which he compared with Micheli’s *Linckia*. Common English names show the anxiety of people about these strange *Nostoc* colonies on soil, calling them fairies’ or witches’ butter, star-slime, star jelly, fallen stars, or will-o’-the-wisp. In Goethe’s tragedy Faust II (line 11741/42), Mephistopheles alludes to the captured will-o’-the-wisp (“*Irrlicht*”) as “disgusting gelatinous dirt” (“*ekler Gallert-Quark*”). Linné (“*Systema Vegetabilium*”, 1774) used the name *Tremella Nostoc* within his group “*Cryptogamia Algae*,” and Vaucher (1803) finally defined the genus name *Nostoc*. One hundred years after Micheli, a painting by Turpin (1838) depicts a *Nostoc* colony (Fig. 2.5).

In the article “On a substance known as ‘Australian Caoutchouc’”, Thiselton Dyer (1872) reports a strange material resembling elastic bitumen that was found on the ground of an open, sandy place in South Australia. It was thought to be the “mineral” coorongite or gamboge, a petroleum or asphalt-type product, some kind of gum, or a plant secretion of some type. However, microscopic analysis showed diatoms as well as cellular structures that were most probably derived from drying gelatinous algae, all intermingled with sand grains (see Fritsch 1907). Thus, this

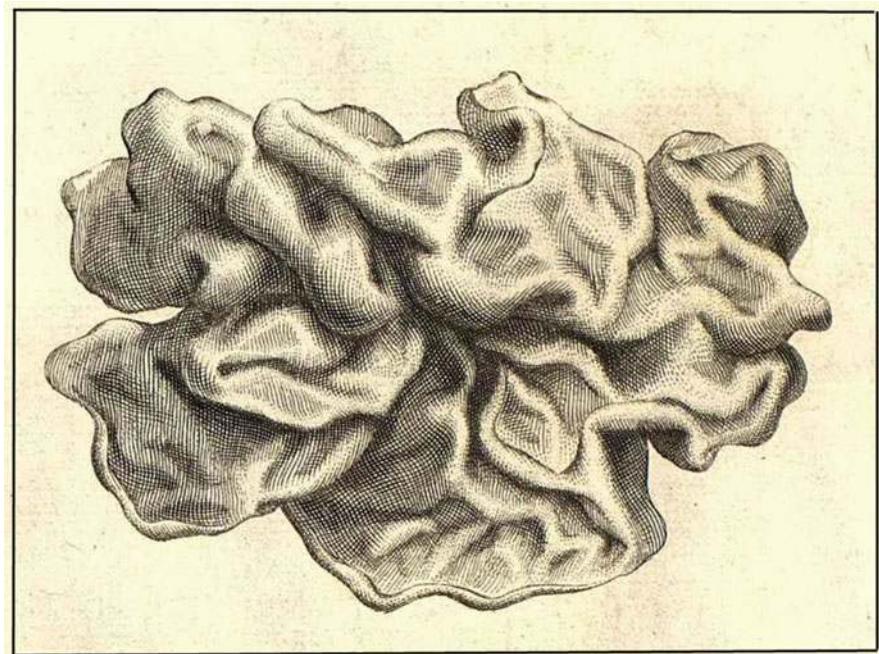


Fig. 2.4 “*Linckia terrestris*, *gelatinosa*, etc.”, *Nostoc* species [After Micheli (1729)]

would be an early recognition of a cyanobacterial soil crust according to our present terminology. Takyr soils were described for deserts and semideserts of Central Asia (Bolyshev and Yevdokimova 1944; Bolyshev 1952). These are formed in flat depressions which are filled with water during heavy rain and dry out during summer. These are often covered and consolidated by soil algae, mainly filamentous cyanobacteria.

There are many reports in the first half of the twentieth century regarding the diversity, life history, and habitat conditions of algae in different soils and locations. These include North America (e.g., Collins 1909; Martin 1939), England (Bristol Roach 1927), Australia (Phillipson 1935), the Sahara (Killian and Fehér 1939), the Negev (Friedmann et al. 1967), and many others. There is a general and extensive treatment “Soil Algae” (in Russian) by Gollerbach and Shtina (1969), in which more than 800 relevant publications are cited (see also Cameron 1974).

2.2.2 The Soil/Agronomy Scientific Approach

The presence of naturally occurring, nonbiological soil crusts has long been observed by soil scientists and others. In the 1820s in interior Australia, the occurrence of “hard bare soils along the Murrumbidgee River” was documented

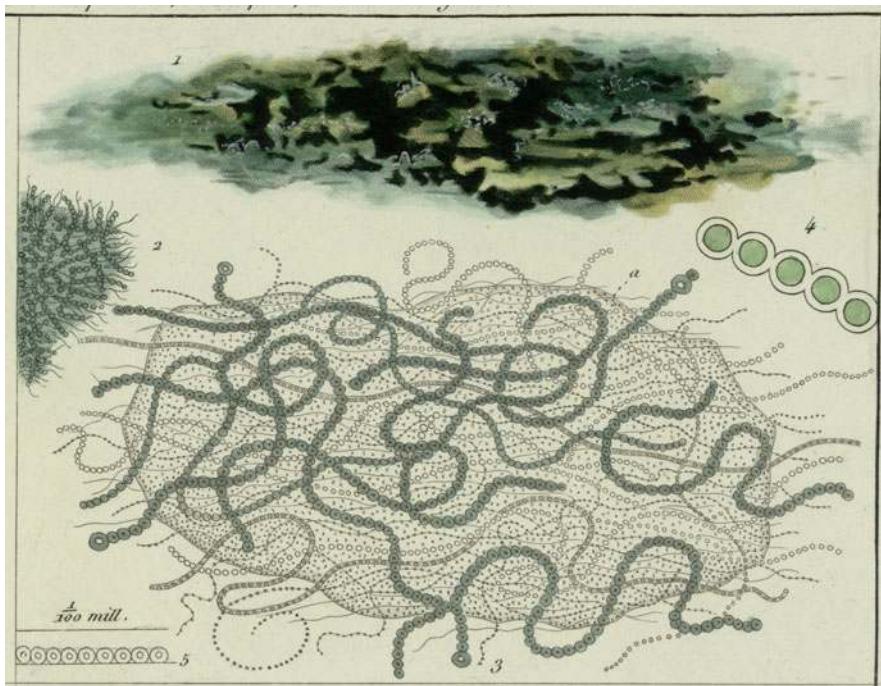
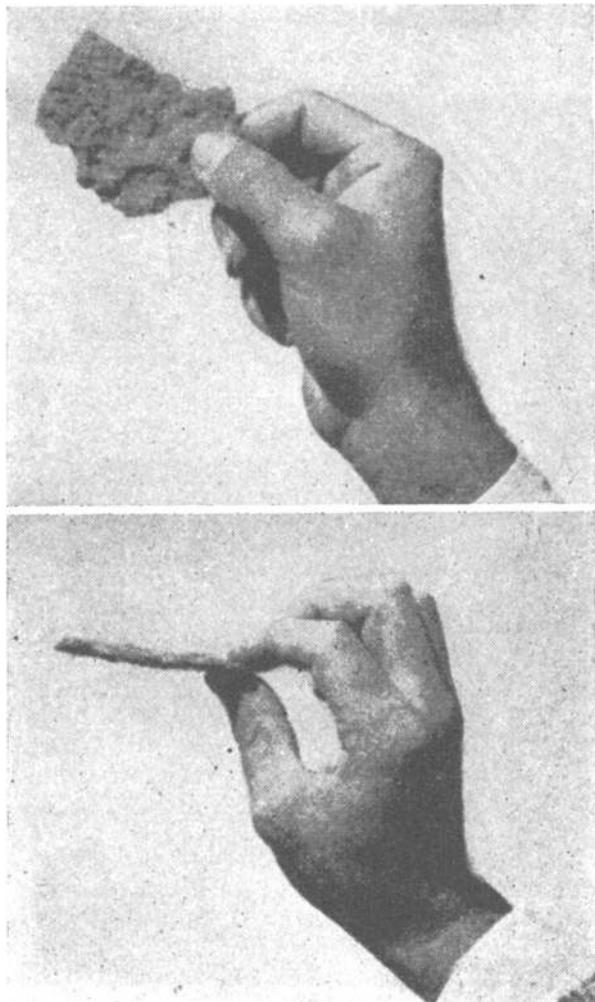


Fig. 2.5 *Nostoc thermalis* [After Turpin (1838)]

by Charles Sturt, an explorer [cited in Chartres (1992)]. Studies of these hardened surfaces in semiarid and arid landscapes began in earnest during the 1900s, and it was determined they were mostly physical and/or chemical crusts. Physical crusts are formed by the disruption of soil aggregates by raindrop or compressional forces (e.g., hoof action). When water pools on the soil surface, the fine soil particles are suspended and upon drying, adhere together to form a hard physical crust. Chemical crusts are formed by the deposition of salts or other compounds on the soil surface when soils dry (e.g., Blanck et al. 1926; Schiff and Yoder 1941). Both physical and chemical crusts increase runoff and erosion (Dudley and Kelly 1939). Early in the study of physical and chemical crusts, some soil scientists noted that algae often grew on top of, inside of, or in place of these nonbiological crusts (e.g., Booth 1941; Fletcher and Martin 1948). These authors noted that after rains, soil surfaces often turn green, which alerted them to the presence of the algae. Fletcher and Martin also observed that if one picked up a piece of these crusts (Fig. 2.6), the soil held together and the underside of “these algae-impregnated crusts had a fuzzy appearance with sand grains adhering to what proved to be fungus mycelium”. Both Booth (1941) and Fletcher and Martin (1948) went on to test how the presence of the algae affected local hydrology, and Fletcher and Martin also measured their influence on soil texture, organic matter, and nitrogen. In contrast to physical and chemical crusts, they found the algae decreased runoff and soil erosion and increased the silt,

Fig. 2.6 A piece of rain crust from the soil's surface, Arizona [After Fletcher and Martin (1948)]



clay, carbon, and nitrogen in the soil. This was, therefore, probably the first instance of soil scientists publishing on the presence of algal soil crusts and their influence on ecological processes.

Around the same time as the research into physical and chemical crusts began, agronomists noticed that soil algae could stimulate the growth of vascular plants by increasing soil N (therefore, it was actually cyanobacteria they were investigating). Breazeale (1929) was one of the first agronomists to intentionally introduce cyanobacteria onto the surface of a crop soil; in this case, he inoculated pots in which Valencia oranges were growing. He found this inoculation increased plant height, plant leaf length, and healthy plant color. Other early work showed the value

of cyanobacteria in stimulating rice production (De 1939) and other crops. Since this time, many studies have been conducted on this topic.

2.3 Biological Soil Crusts as a Functional Ecological Unit

Perhaps one of the earliest conceptualizations of the ability of biocrusts to consolidate soil was reported in 1861 by E.F. Klinsmann, a medical doctor. Earlier in this publication, he notes that in 1828, and again at later times, he observed a thick carpet of mixed lichen and algal threads on top and throughout the surface sands of dunes at the Baltic Sea near Gdansk, Poland. His material was sent to F.T. Kützing, who identified the dominant organism as an alga *Stereonema chthonoblastes* A. Br. (Kützing 1849), which was later determined to be a lichen (Kupffer 1924). Its name was changed to *Lecidea uliginosa* var. *chthonoblastes* (A. Braun) Erichsen and then again to *Placynthiella uliginosa* (Schrad.) Coppins & James. However, the description of threads being present in the samples of Klinsmann (1861) makes it likely that cyanobacteria and soil fungi were also present in the material collected. He noted this carpet stabilized blowing sand and facilitated the colonization of other species, starting first with the moss *Ceratodon purpureus* and other lichens and then later followed by vascular plants. The author even discussed the possibility of propagating and spreading this “alga” for dune stabilization, noting it was cheaper than planting grasses which was done at that time.

Subsequent early research showed soil algal growth was an important first step in increasing the fertility and stability of the soils, thus likely enhancing the recolonization of other organisms. One of the first places this was observed was following the volcanic eruption of Mount Krakatoa (Treub 1888), where the disturbed ground was first covered by a layer of blue-green algae before other species colonized the site. Fritsch (1907, 1922) developed an early conceptual model of terrestrial algae and their ecological relevance. He distinguished between subterranean and surface communities, describing the species composition and site morphology for different climatic regimes. His conclusion is very similar to a modern interpretation of algal soil crusts: “The . . . consideration will have shown that the terrestrial Alga possess an equipment which suits it admirably to be a coloniser of inhospitable substrates. Here its small moisture-requirements can probably often be better met than those of any other group of plants. As colonisers these Algae are of importance in three ways: they play a rôle in the erosion of exposed surfaces, by their decay they afford the first available supplies of humus, and especially the more mucilaginous forms afford a moisture-retaining substratum. . . On mobile substrata the filamentous forms are also often of great importance in binding the loose particles together” (Fritsch 1922, p. 232). In later publications (e.g., Fritsch and Haines 1923), the authors conducted field and laboratory experiments to examine the moisture relations of these organisms.

Use of lichens and mosses for sand stabilization was also reported later for several different areas of the world. Possibly one of the first examples of mosses

affecting soil function was noted by Moore (1931), when he observed them, along with lichens, consolidating moving sand on the British Isle of Man (Irish Sea) and preparing the way for the subsequent colonizers. Leach (1931) studied the ability of mosses like *Polytrichum piliferum* and *Polytrichum juniperinum* to act as pioneers on sand habitats in England, analyzing their soil-binding qualities with laboratory experiments. In the USA, Martin and Waksman (1940) showed that soil algae increased soil aggregation and decreased erosion.

In 1955, Vogel provided the decisive insight that the condensed layer at the soil surface, which he observed in South African deserts and which we today call biocrusts, was created by organisms such as lichens and algae. He published what was possibly the first vertical profile of a biocrust, describing it in German as “*Bodenkruste*” or soil crust (Fig. 2.7). In his illustration, a dust film is shown at the surface, below which lies a layer with *Schizothrix* sp. (cyanobacteria), followed by a layer of fungal hyphae mainly belonging to soil lichens. He provided a description of how these organisms are interwoven with the soil particles, gluing them together into compact layers. The text notes that when broken, fibers with soil particles can be seen dangling from the biocrust pieces. The nitrogen-fixing ability of the soil cyanobacteria is discussed as well. Vogel also posited that these “*Bodenkrusten*” are of geological importance by preventing soil erosion over the hundreds of square kilometers where he observed them. Thus, with this study, Vogel described 60 years ago most of the important ecological roles we ascribe to biocrusts today.

Studies of the ecological roles of biocrusts began intensifying in the late 1950s and 1960s. For instance, Shields et al. (1957), Tchan (1959), Shields and Durrell (1964), Bond and Harris (1964), Avnimelech and Nevo (1964), Rogers and Lange (1966), Mayland et al. (1966), and Granhall and Henriksson (1969) showed that biocrusts stabilize soils, affect hydrological cycles, and enhance soil nitrogen content. A very early photograph of typical biocrusts from Arizona Upland Desert (Fig. 2.8) was published by R. E. Cameron (1958) in his M.S. thesis. Prompted by finding ways to detect life in extraterrestrial environments, he and others conducted extensive investigations in the distribution and abundance of biocrusts in deserts throughout the world (e.g., Cameron and Blank 1966; Cameron 1969). Cameron and Devaney (1970) also described the successional sequence of soil surface organisms in the Antarctic dry valleys, starting with cyanobacteria and algae, followed by lichens and ending with mosses. Ugolini (1966) observed that initial soil formation exposed after the retreat of an Alaskan glacier occurred under a “mossy crust”. Worley (1973) found three types of “Black Crust” in the Upper Glacier Bay, Alaska, that covered and penetrated into the recently deglaciated soils, observing they protected the soil from erosion. These mats contained the leafy liverwort *Lophozia badensis*, mosses, lichens, and cyanobacteria in differing proportions.

A great deal of work was done on biocrusts in the western USA in the 1970s by scientists working independently or with the International Biome Program. They documented the controls on distribution and many ecological roles of biocrusts, including an influence on nitrogen cycling, soil aggregation, and soil moisture

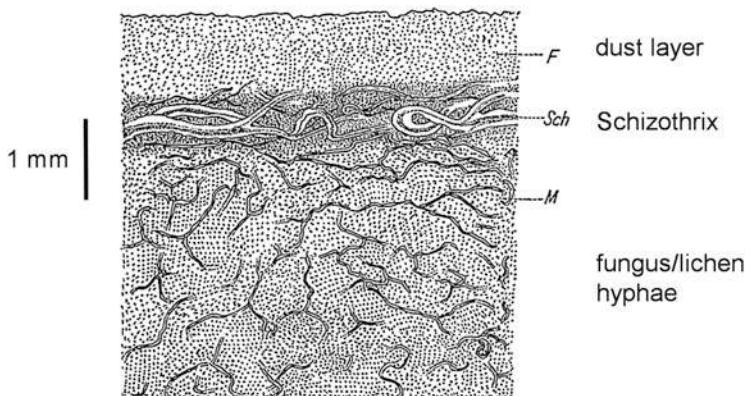


Fig. 2.7 Profile of the uppermost millimeters of soil crust, Knersvlakte, South Africa [After Vogel (1955)]



Fig. 2.8 Soil algal and lichen crusts, Arizona [After Cameron (1959), by courtesy of University of Arizona]. See also Cameron and Blank (1966)

(e.g., Faust 1971; Kleiner and Harper 1972, 1977; Bailey et al. 1973; Marathe 1972; Loope and Gifford 1972; West and Skujins 1977; Rychert et al. 1978).

The pace of studies increased even more rapidly during the 1980s and early 1990s, especially in Australia, Israel, and the western USA (e.g., Shachak and Steinberger 1980; Graetz and Tongway 1986; Rogers 1989). Research addressed all aspects of the ecological functions of biocrusts, ranging from their contributions to soil fertility, including carbon and nitrogen fixation, their ability to stabilize soils, their response to and recovery from fire and surface disturbance, and their effects on vascular plant establishment and growth. Sufficient research was done to produce at least six review articles within 6 years (Harper and Marble 1988; Dunne 1989;

Isichei 1990; West 1990a, b; Metting 1991; Johansen 1993). These efforts culminated in the first symposium on biocrusts held at the joint American Bryological and Lichenological and Ecological Society of America meetings in San Antonio, Texas, in 1991 (St. Clair and Johansen 1993). This marked a turning point in the acceptance by biologists and ecologists alike of the importance of the biocrust communities in the structure and function of dryland ecosystems. The first compendium volume on biocrust research, “Biological Soil Crusts: Structure, Function and Management,” was published in 2001 and reprinted in 2003 (Belnap and Lange 2001, 2003). Since then, there have been two international symposia on Biological Soil Crusts (in Germany and Spain), and the number of researchers involved in this field and the number of papers published have increased exponentially.

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Part II

Morphology, Composition, and

Distribution of Biological Soil Crusts at

Different Scales

Chapter 3

Terrestrial Ecosystems in the Precambrian

Hugo Bernaldi-Campesi and Gregory J. Retallack

3.1 Introduction

Three lines of evidence for ancient life on land are paleosols, microfossils, and MISS (microbially induced sedimentary structures). The three appear in the rock record as old as 3.5–2.7 Ga (Hallbauer and van Warmelo 1974; Rye and Holland 2000; Wacey et al. 2008; Johnson et al. 2010; Noffke et al. 2013). The primitive terrestrial biosphere is plausibly as old as the oldest marine biosphere (Schopf 1983; Schopf and Klein 1992), with both aquatic and terrestrial realms teeming with life 3.5 Ga ago. This result is unsurprising considering the modern ecological capabilities of microbes, which are comparable with fossil analogs and have profound effects in sediments and soils (Belnap and Lange 2001; Navarro-González et al. 2003; Bernaldi-Campesi and Garcia-Pichel 2011; Retallack 2012). Functional aquatic and terrestrial ecosystems may be even older than 3.5 Ga, but undisputable biosignatures before that time are ambiguous (Nutman et al. 2010; Papineau et al. 2010), and the timing when life first populated the Earth is still unresolved.

Direct evidence for ancient terrestrial communities comes from the fossil record, and the several limitations of such should be noted. First, it has many temporal gaps, which makes it difficult to appreciate the continuous history of life on Earth (Sadler 1981). Second, not all the rocks have been studied in detail, especially biosignatures preserved in it, so that recent and future discoveries may yield more tangible information about the history of the biosphere (Dutkiewicz et al. 2006). Third, microbial biological diversity of the Precambrian fossil record is

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fundamentally different and more challenging to study than Phanerozoic megafossils (Schopf et al. 2007), which unduly bias orthodox interpretations about the evolution of the biosphere.

3.2 Paleosols

The oldest geological unconformity in a sedimentary sequence, which is metamorphically recrystallized in a way that its sedimentary history is almost indecipherable, is ~ 3.4 Ga old (Fig. 3.1a; Buick et al. 1995). This surface beneath the Strelley Pool Formation has thick (4 m) clayey paleosols (Fig. 3.1b–d), which are deeply weathered, aluminous, and metamorphosed to apophyllite facies, implying high fluid fluxes, secondary mineralization, and an overall alteration after burial (Buick et al. 1995; Hoffman 1995; Ohmoto et al. 2007; Johnson et al. 2009, 2010). Such thick clayey paleosols are very common on basement unconformities of the Archean and Proterozoic record (Table 3.1). Well-developed paleosols as the Neoproterozoic Sheigra paleosol (Fig. 3.1e) are direct records of ancient landscapes, where microbial contribution can be sought. The development of relatively thick paleosols implies stable intracratonic settings where weathering and soil formation prevail and sediment transport is minimal. What stabilized these paleosols to allow such deep chemical weathering could have been life itself, considering evidence of elemental depletions, isotopic composition of carbon, and fossilized structures (Retallack 2001).

The master reaction for weathering in soils is hydrolysis, the incongruent dissolution of feldspars, or other minerals to form clays, by dilute solutions of carbonic acid from dissolution of soil CO₂ in pore waters (Retallack 2001). Such reactions have been demonstrated in many Precambrian paleosols, but could theoretically be created abiotically. However, life has accelerated weathering processes over geological time, and biotic effects are more obvious than abiotic effects. A series of experiments by Neaman et al. (2005) showed that organic ligands are necessary for any significant depletion of phosphorus in modern soils, and such depletions have been demonstrated in paleosols as old as 2.7 Ga (Driese et al. 2011), as well as for geologically younger paleosols (Retallack and Mindszenty 1994; Retallack et al. 2013a, b).

Carbon isotopic composition of biologically produced organic matter is depleted in ¹³C ($\delta^{13}\text{C}_{\text{org}} = -10\text{\textperthousand}$ to $-30\text{\textperthousand}$), and soil methanogens create extreme depletion ($\delta^{13}\text{C}_{\text{org}} = -30\text{\textperthousand}$ to $> -90\text{\textperthousand}$; Schidlowski 2001). Such low values have been reported from Precambrian paleosols as old as 2.7 Ga (Rye and Holland 2000), as well as for geologically younger paleosols (Retallack and Mindszenty 1994; Watanabe et al. 2000; Retallack et al. 2013a, b). Ironically, the carbon content of Precambrian paleosols is very low ($<< 1\text{ wt \%}$), about the same as for Phanerozoic paleosols (Tomescu et al. 2009). While low-carbon isotopic compositions reveal microbial primary producers in soils, low-carbon abundance also implies an active decomposition of organics by microbes on the land, which may imply well-

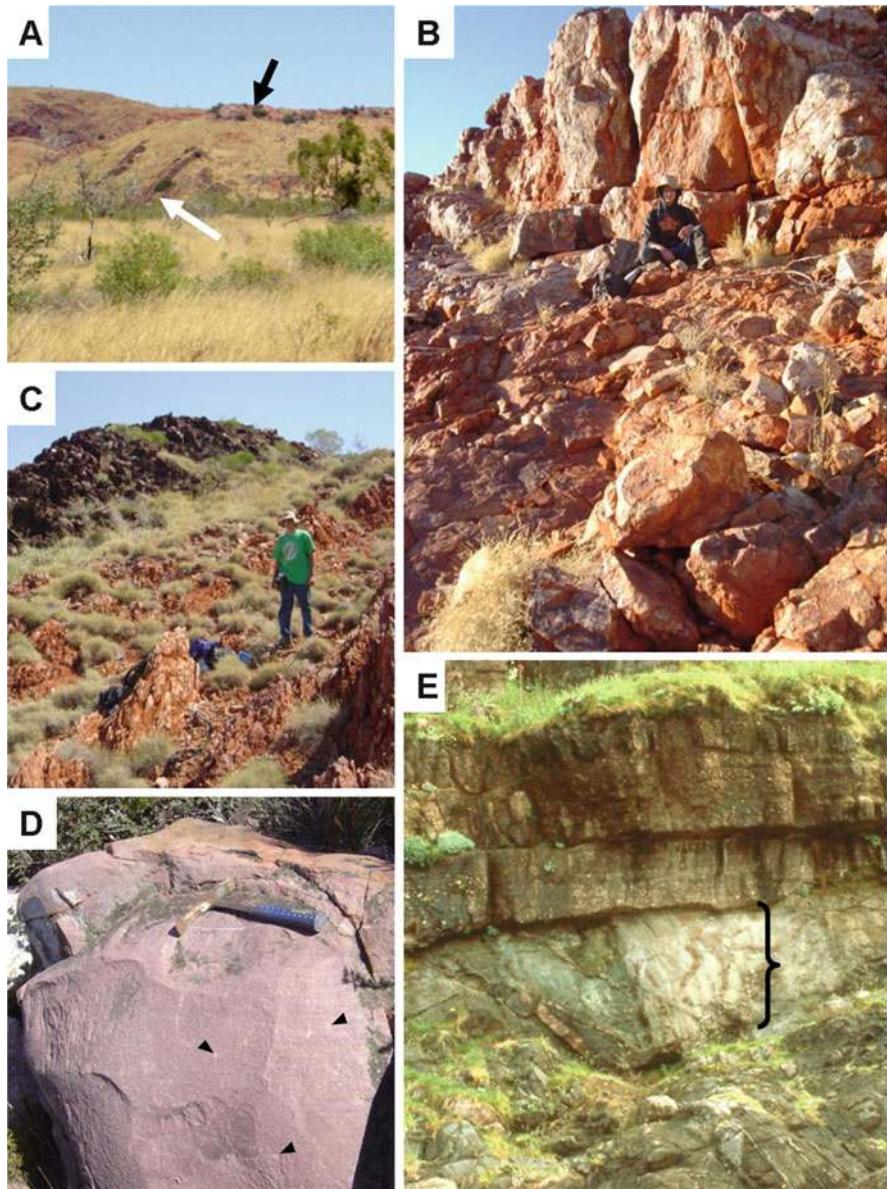


Fig. 3.1 Examples of Precambrian paleosols: (a) One of the oldest paleosols at the 3.42 Ga geological unconformity between the tabletop basalt (basalts dipping to left; white arrow) and Strelley Pool Formation (chert of ridge top; black arrow) 4 miles east of Strelley Pool, Pilbara region, Western Australia (Buick et al 1995); (b) Another section of the 3.42 Ga paleosol on Double Bar Formation basalts below basal cherty sandstones of the Strelley Pool Formation, Pilbara region, Western Australia (Van Kranendonk 2000; Altinok 2006); (c) Another section of the 3.42 Ga paleosol on Panorama Formation showing felsic tuffs that record ancient volcanism on Steer Ridge, Pilbara region, Western Australia (van Kranendonk 2000; Johnson et al. 2010); (d) A younger 1.8 Ga paleosol with elephant-skin texture (A horizon) above gypsum nodules (arrowheads) in Stirling Range Sandstone, Barnett Peak, Western Australia (Bengtson et al. 2007);

developed and complex communities, not only of photosynthesizers but heterotrophs as well.

The most common megascopic traces in Precambrian paleosols are irregular subvertical and macroscopic tubular structures, either picked out by drab haloes in red beds (Fig. 3.2a) or preferentially cemented compared with their matrix (Fig. 3.2b, c). These features are formed through pedogenic processes and may be biotically or abiotically mediated. As these macrostructures seem to be embedded within the paleosol profile, it is unlikely that photosynthetic microbes were involved in their formation. Nevertheless, similar alteration features have been observed in modern biocrusts (Retallack 2011). Fungi can also be envisioned as potential candidates for their formation. Examples include the honey mushroom, *Armillaria mellea* (Mihail and Bruhn 2005), or lichen rhizines like those of *Toninia sedifolia* (Poelt and Baumgärtner 1964). The drab-haloed tubular structures are a fossil form called *Prasinema gracile*, best known from Cambrian paleosols (Retallack 2011). The distinctive gray-green haloes of the fine tubules, preserved by burial gleization, are also comparable with drab-haloed root traces in paleosols (Retallack 2001). These tubular structures (Fig. 3.2b) also found analogs among calcareous and siliceous rhizoconcretions in paleosols (Esteban and Klappa 1983). However, unlike root traces in Phanerozoic paleosols, tubular structures in Precambrian paleosols are much smaller and lack several orders of branching and tapering downward.

Paleosols are important pieces of the record of continental evolution because they are widely distributed on all present continents and are represented in the rock record since 3.5 Ga. Most of them contain indirect evidence of biological weathering, biomass accumulation, and potential fossils and ichnofossils (Retallack 2001). Recognizing pedogenic processes is essential for better understanding depositional paleoenvironments and distinguishing those of marine from nonmarine origin. For instance, pedogenic processes recognized in association with Ediacaran fossils, such as *Dickinsonia costata* (Retallack 2013; Fig. 3.2d). Together with the evidence cited below, the long history of paleosols and their likely biotic features attest for well-established, nonmarine, and widespread terrestrial ecosystems by the Paleoarchean.

3.3 Microfossils

The oldest reported biosignatures occurring in shallow marine to nonmarine strata may be simple “ambient inclusion trails” from basal sandstones of the Strelley Pool Formation in Western Australia (Lowe 1983; Wacey et al. 2008). Higher within the

Fig. 3.1 (continued) (e) Cross section of the 1 Ga Sheigra paleosol on Lewisian gneiss (*bottom*) and Staca paleosol on amphibolite (*bracket*) beneath the Applecross Formation (fluvial facies) of the Torridonian Supergroup, west of Sheigra, northwest Scotland (Retallack and Mindszenty 1994)

Table 3.1 Examples of Archean and Proterozoic paleosols

References	Province	Country	Age
Johnson et al. (2010)	Warrawoona Group	Australia	3.4 Ga
Kimberley and Grandstaff (1986)	Dominion Reef Conglomerate	South Africa	3.1–2.8 Ga
Kimberley and Grandstaff (1986)	Pongola	South Africa	3.0–2.9 Ga
Grandstaff et al. (1986)	Dominion and Pongola Supergroups	South Africa	3.0–2.8 Ga
Reimer (1986)	Kaapvaal Craton	South Africa	3.0–2.5 Ga
Hallbauer and van Warmelo (1974)	Witwatersrand and Ventersdorp Supergroups	South Africa	2.9–2.7 Ga
Macfarlane et al. (1994)	Fortescue Group Mt Roe 1 and 2	Australia	2.7–2.6 Ga
Kimberley and Grandstaff (1986)	Timiskaming Group	Canada	2.7 Ga
Rye and Holland (2000)	Mt Roe 1 and 2	Australia	2.7 Ga
Martini (1994)	Paleosol on ultramafics in the eastern Transvaal	South Africa	2.6 Ga
Watanabe et al. (2000)	Transvaal Sequence	South Africa	2.6 Ga
Pandit et al. (2008)	Tulsi Namla section	India	2.5–2.1 Ga
Aspler and Donaldson (1986)	Nonacho Basin	Canada	2.5–2.0 Ga
Banerjee (1996)	Paleosols BGC–Aravalli boundary	India	2.5–1.9 Ga
Bandopadhyay et al. (2010)	Singhbhum–Orissa craton	India	2.5 Ga
Prasad and Roscoe (1996)	Lower and upper sub-Huronian paleosols	Canada	2.4–2.2 Ga
Kimberley and Grandstaff (1986)	Black Reef Quartzite	South Africa	2.4–2.0 Ga
Gay and Grandstaff (1980)	Huronian SpGp	Canada	2.3 Ga
Farrow and Mossman (1988)	Huronian SpGp	Canada	2.3 Ga
Yang and Holland (2003)	Hekpoort paleosol Pretoria Group	South Africa	2.23 Ga
Gutzmer and Beukes (1998)	Gamagara Fm	South Africa	2.2–2.0 Ga
Jackson (1967)	Gowganda Fm	Canada	2.2 Ga
Retallack (1986b)	Paleosol near Waterval Onder	South Africa	2.2 Ga
Holland and Zbinden (1988)	FlinFlon Paleosol	Canada	1.8 Ga
Driese et al. (1995)	Lochness formation	Australia	1.8 Ga
Gall (1994)	Proterozoic Thelon paleosol	Canada	1.7 Ga
Driese and Gordon-Medaris (2008)	Baraboo Range	USA	1.7 Ga
Zbinden et al. (1988)	Sturgeon Falls paleosol	USA	1.1 Ga
Retallack and Mindszenty (1994)	paleosols from northwest Scotland	UK	1.1 Ga

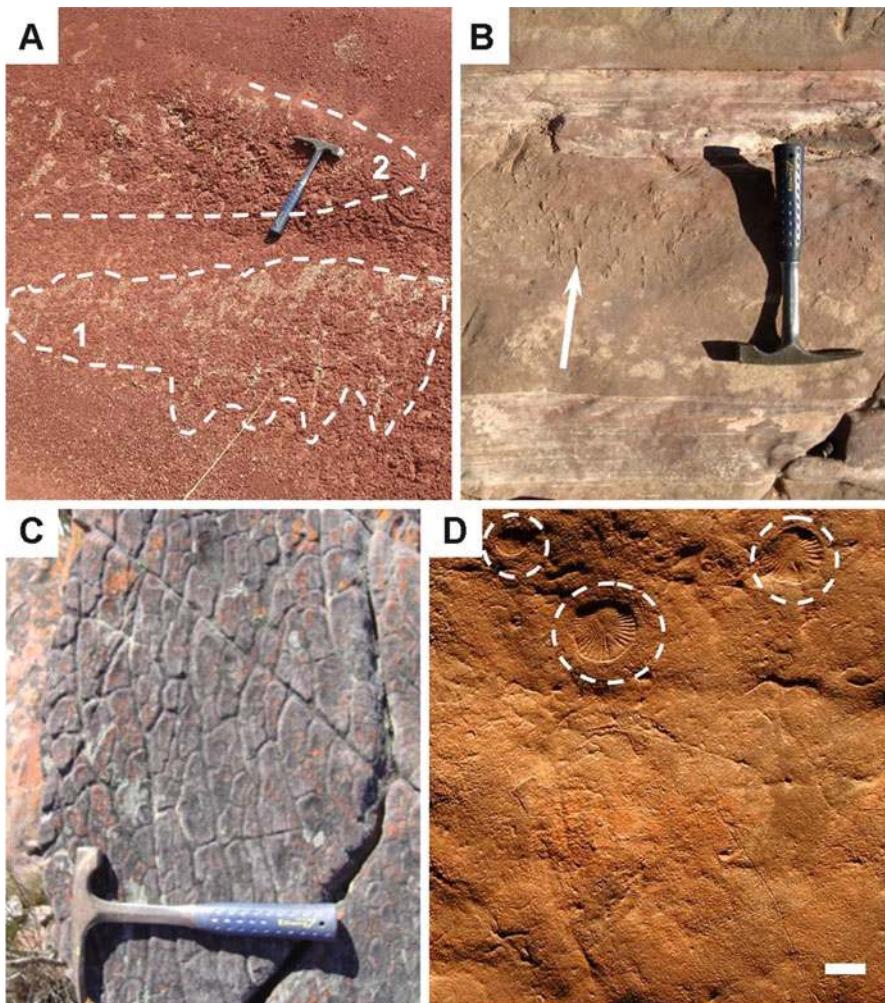


Fig. 3.2 Terrestrial sedimentary biostructures: (a) oblique cross section of drab-haloed tubular structures (dashed lines) from two successive paleosols (numbered 1 and 2, respectively) in redbeds of the 1.8 Ga Elgee Siltstone, 20 km south of Wyndham, Western Australia (Schmidt and Williams 2008); (b) cross section of a 2.7 Ga paleosol with silicified tubular structures (arrow), and bound by water-laid deposits. Carraman Formation in Nobles Nob mine, 14 km east of Tennant Creek, Northern Territory, Australia (Black 1984); (c) plan view of a sandstone surface of a cracked paleosol (A horizon) as if it were clayey, in the 1.8 Ga Stirling Range Sandstone, Barnett Peak, Western Australia (Bengtson et al. 2007); (d) sandstone surface with elephant-skin texture (*Rivularites repertus*) with three individual fossils of *Dickinsonia costata* (encircled) in the 550 Ma Ediacara Member of the Rawnsley Quartzite, from Crisp Gorge, South Australia (Retallack 2013); scale bar = 1 cm

Formation are shallow marine stromatolites, but the basal sandstones of the Formation unconformably overlay the clayey paleosol developed on basaltic basement (Fig. 3.1b, c), which has been interpreted as estuarine and littoral talus (Allwood et al. 2006). Possible taxonomic affinities of these trails are unknown other than they are small, simple, and very likely prokaryotic (Wacey et al. 2008). Small spheroidal microfossils found in the same formation (Sugitani et al. 2013) may have lived in shallow waters, although nonmarine environments, including fluvial and playa lake environments (Hickman 2008), were also present at the same time and space. In highly oxidized paleosols, where the primary organic matter may not be preserved, casts of putative microfossils may appear as ordered particles along “filamentous” structures that cut across bedding planes (Fig. 3.3a).

Thucomyces lichenoides is a striking fossil (Fig. 3.3b, c) forming palisades atop green paleosols in the carbon leader of the Central Rand basin of South Africa, and associated with filamentous (hyphae-like) microfossils (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977; Mossman et al. 2008). *Thucomyces* is now known to be as old as 2.8 Ga (Schaefer et al. 2010) and has been compared with lichens because it has clavate structures above the hyphae-like filamentous mesh and with the endocyanotic living glomeromycotan fungus *Geosiphon* (Schüller and Kluge 2000). However, there are complex radial and vertical partitions within *Thucomyces* (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977) unlike the central chamber of *Geosiphon*, where the latter hosts symbiotic *Nostoc* filaments. These folded structures are comparable with those in columnar biofilms of hot springs today (Hall-Stoodley et al. 2004). The enigmatic microfossil *Diskagma buttoni* from a 2.2 Ga paleosol in the Hekpoort Formation of South Africa (Fig. 3.3d, e) has also been compared with the living fungus *Geosiphon* given its ellipsoidal central chamber (Retallack et al. 2013b). Suggestive evidence of Archean and Paleoproterozoic filamentous Actinobacteria and fungi may explain the carbon-lean composition of many Precambrian paleosols and may imply the existence of mature biocrusts.

Microfossils recorded from the 2.7 Ga Mount Roe paleosol near Whim Creek, Western Australia, are associated with extremely light-carbon isotopic values suggestive of methanogens that now live in swamp-like environments (Rye and Holland 2000). In this case, the presence of organic matter and microfossils in the same suite of paleosols speaks for a wide distribution of microbial life in widely varied terrestrial environments.

Other Precambrian microfossils have been reported for nonmarine sedimentary paleoenvironments, including deposits of lakes of the ~1.1-Ga-old Torridonian Group in Scotland (Cloud and Germs 1971; Strother et al. 2011), and alluvial settings (Beraldí-Campesi et al. 2014) and paleokarst fill (McConnell 1974; Horodyski and Knauth 1994) of the ~1.2-Ga-old Apache Group in southwestern USA. These microfossils display coccoid and filamentous shapes and likely include both prokaryotic and eukaryotic components. From the sedimentary setting of these microfossils, they were more likely washed in from the surrounding land, rather than introduced from the sea. Aquatic terrestrial environments, such as lakes, also supported large organisms such as the 1.5-Ga-old *Horodyskia moniliformis*, which

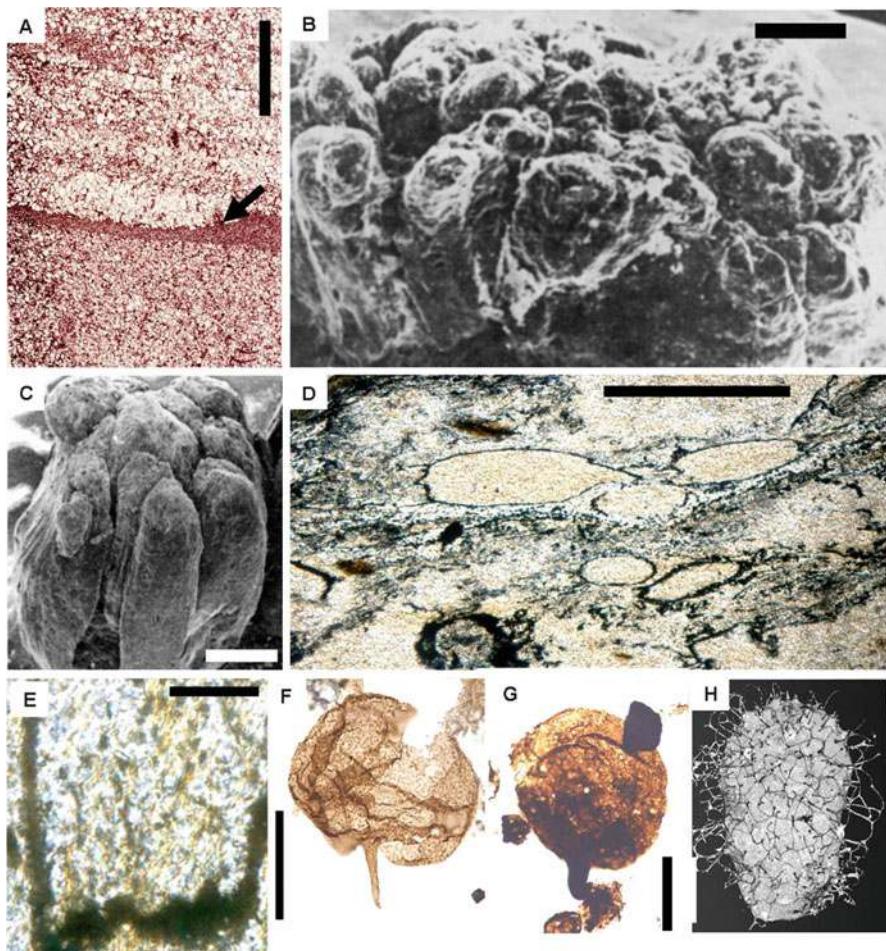


Fig. 3.3 Terrestrial microfossils: (a) petrographic thin section of oxidized filaments running across bedding planes (arrow) and more abundant in the lower paleosol than the overlying cross-bedded sandstone of the 1.8 Ga Stirling Range Sandstone on Barnett Peak, Western Australia (Bengtson et al. 2007); scale bar = 10 mm; (b, c) *Thucomyces lichenoides* from 2.8 Ga (Schaefer et al. 2010) Carbon Leader of the Central Rand Group near Carletonville, South Africa (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977); scale bars = 200 µm. (d, e) petrographic thin sections of *Diskagma buttoni* to reveal a thallus group (d) and details of the apical cup (e) from the 2.2 Ga Waterval Onder paleosol of the upper Hekpoort Formation, 2 km east of Waterval Onder, South Africa (Retallack et al. 2013a, b); scale bars = 500 µm and 50 µm, respectively; (f) acritarch with hyphal stalk (*Ceratosphaeridium mirabile*) from the 570 Ma Wilari Dolomite Member, Tanana Formation, Observatory Hill No. 1 well, northern South Australia (Grey 2005); scale bar = 50 µm; (g) *Germinosphaera* sp. indet. from 590 Ma ABC Range Quartzite, SCYW 1a bore, South Australia (Grey 2005); scale bar = 20 µm; (h) *Tappania* sp. from 820 Ma Wynniet Formation, on Victoria Island, Nunavut (Butterfield 2005); scale bar = 100 µm. Images (a) and (b) are courtesy of Kathleen Grey, (f) of Nick Butterfield and (g, h) of Dieter Hallbauer, all reproduced with permission

has been interpreted as prokaryotic colonies (Knoll et al. 2006), agglutinated foraminifers (Dong et al. 2008), brown algae (Grey and Williams 1990), sponge remains (Hofmann 2001), hydrozoan or bryozoan colonies (Fedonkin and Yochelson 2002), or metazoan fecal strings (Yang and Zheng 1985), but it could also be of fungal affinity (Retallack et al. 2013b). In any case, its presence in paleolake shores (Retallack et al. 2013b) indicates an ample distribution of nonmarine life in the Precambrian.

Another line of evidence for Precambrian life on land is the suggestion of Pirozynski (1976) and Butterfield (2005) that there is a Precambrian record of fungi among the enigmatic microfossil palynomorphs known as acritarchs (Grey 2005; Moczydłowska et al. 2011). Ediacaran (~580 Ma) acritarchs such as *Ceratosphaeridium* (Fig. 3.3f) and *Germinosphaera* (Fig. 3.3g), and Cryogenian-Mesoproterozoic (~850 Ma) fossils such as *Tappania* (Fig. 3.3h), are similar to Glomeromycotan chlamydospores and vesicles. Many of these fossils have attached aseptate hyphal structures, characteristic of Mucoromycotina and Glomeromycota fungi. These fungi today mainly represent saprobiontic and mycorrhizal growth forms, respectively, but it is unclear whether they avoided lake or marine habitats in the distant past. These fossils have not been considered anything but marine until recently, and reevaluation of the sedimentary facies and communities of these fossils is needed.

3.4 Sedimentary Biostructures

Although microbial mats developing on coastal carbonate facies (e.g., Demicco and Hardie 1995) can be included in the definition of “biological soil crust” (Belnap and Lange 2001), most modern biocrusts develop on sandy, subaerial, siliciclastic substrates. Many sedimentary deposits of this type, from the Archean onward, display sedimentary biostructures of presumed biotic origin and developed subaerially (Hupe 1952; Lannerbro 1954; Voigt 1972; Eriksson et al. 2000; Prave 2002; Noffke et al. 2013; Simpson et al. 2013; Beraldi-Campesi et al. 2014). These diverse sedimentary biostructures can also be found in modern terrestrial systems, such as supratidal, fluvial, and alluvial settings, and thus indicate that the mechanisms that operate today in forming those structures are similar to those operating billions of years ago. In this regard, it must be said that the main biotic components of this type of modern biostructures are cyanobacteria and particularly filamentous taxa. These bacteria are the primary producers that allow other organisms, such as heterotrophic bacteria and fungi (among others), to become part of the biocrust community and are also essential for the cohesive properties of terrestrial MISS (Garcia-Pichel and Wojciechowski 2009; Beraldi-Campesi and Garcia-Pichel 2011; Retallack 2012).

A striking indication of MISS from dry land was first indicated by Prave (2002), who pointed out that some Precambrian sandstone surfaces show a system of cracks morphologically similar to desiccation cracks in clay stones (Fig. 3.2c).

Comparable features are common in modern biocrusts (Retallack 2012), and comparable gypsic paleosols can be found under paleosols with such cracked surface sandy horizons (Fig. 3.1d). For all these examples, it is clear that clays do not play a dominant role in the formation of sedimentary biostructures (or MISS; Noffke 2010), as the cohesive behavior of a microbial cover does, in this case a biocrust-like community (Beraldi-Campesi and Garcia-Pichel 2011).

Both filamentous and EPS-producing taxa are necessary to form sedimentary biostructures. Filaments can build tight networks among clastic particles and support the biocrust framework, while EPS acts as a gluing agent that keeps particles together, especially if it is well hydrated (Noffke 2010). Aquatic and terrestrial and recent and ancient microbial communities can develop a variety of microscopic and macroscopic features that can be recognized in thin sections and in the field, as listed in Table 3.2.

Table 3.2 Examples of sedimentary biostructures (MISS) and features found in microbial mats and earths from siliciclastic environments

Feature	Observations	References
Cohesive behavior	Ductile rheological behavior of microbial mat layers before and after burial	Fagerstrom (1967), Schieber (1999), Eriksson et al. (2000) and Beraldi-Campesi and Garcia-Pichel (2011)
Collapsed gas domes	Desiccated gas domes that form hemispherical depressions	Beraldi-Campesi et al. (2014)
Desiccation roll-ups	Organo-mineral layers upturned and rolled by desiccation	Beraldi-Campesi and Garcia-Pichel (2011)
Erosional pockets	Formed after fragments of microbial earths or mats have been removed from site	Noffke (2010)
Fairy concentric rings	Formed by small-scale plume degassing or dewatering	Gerdes et al. (1993)
Gas domes and blisters	Formed by upcoming gas pressure underneath sealed microbial mats	Bose and Chafetz (2009) and Beraldi-Campesi et al. (2014)
Gravity or flow-mediated soft deformation	Creases, wrinkles, crinkles, crumples, kinks and furrows, of mm to cm scales	Beraldi-Campesi et al. (2014)
Irregular desiccation crack margins	Unlike pure clay cracks, these have irregular margins	Gerdes (2003)
Laminated leveling structure	“Leveling” of the microtopography due to growth and stabilization of the microbial mat	Gerdes et al. (2000)
Mat chips	Eroded mat fragments transported by flows	Fagerstrom (1967), Pfluger and Gresse (1996) and Schieber 2007
Mat-layer bound small grains and heavy minerals	Accumulation of heavy minerals and micas on bedding planes	Noffke (2009)

(continued)

Table 3.2 (continued)

Feature	Observations	References
Microsequences	mm- to cm-thick sedimentary layers, normally graded, often with organic matter vestiges	Noffke (2010)
Oriented grains	Elongated grains that have been oriented parallel to the bedding plane through microbial baffling	Noffke et al. (1997)
Petees	Ridged structures caused by dewatering along weak planes	Reineck et al. (1990)
Rolled up mats	Organo-mineral layers upturned and rolled by wind or water currents	Simonson and Carney (1999), Schieber (2004) and Eriksson et al. (2007)
Sand/sandstone cracks	Also called earth cracks, are formed by desiccation of microbial mats on sandy surfaces	Picard and High (1973), Sarkar et al. (2008) and Beraldí-Campesi et al (2014)
Sand folds	Organo-mineral layers folded by wind or water flow	Bouougri and Porada (2012)
Sand ridges	Similar to Petee structures but also caused by expansion of biocrust boundaries	Beraldí-Campesi et al. (2014)
Sinoidal structures	Preserved sinuous shapes on ripple marks stabilized by microbial mats	Noffke (2010)
Sponge pore fabrics and vesicular horizons	Gas-produced pores formed within or underneath microbial mats and earths	Noffke (2010) and Beraldí-Campesi et al. (2014)
Tufts, knobs and pinnacles	Protuberances, mm to cm tall, derived from microbial growth and behavior in microbial mats	Gerdès et al. (2000), Noffke et al. (2001), Rosentreter et al. (2007) and Noffke et al. (2008)
Wrinkle marks	Include a wide variety of rugose surface structures due to mechanical and behavioral traits	Hagadorn and Bottjer (1997), Hagadorn et al. (1999) and references therein, Gerdès et al. (2000), Porada and Bouougri (2007) and Shepard and Sumner (2010)

3.5 Conclusions

A great variety of terrestrial environments are known in the Precambrian, including soils, peats, ponds, lakes, streams, deserts, and dune fields (Rye and Holland 1998; Eriksson et al. 2004; Retallack et al. 2013a, b). Thus, environmental settings that could potentially become “terrestrial ecosystems” were already in place. Despite sustained uncertainties about these environments being populated or not (Shear 1991; Behrensmeyer et al. 1992; DiMichele and Hook 1992; Gray and Shear 1992; Gray and Boucot 1994; Bambach 1999; Blackwell 2000; Corcoran and Mueller 2004; Nesbitt and Young 2004; Gensel 2008), it is clear, through many lines of

evidence, that terrestrial ecosystems were indeed present, full of life, and functional since the Archean (Beraldí-Campesi 2013). The main lines of evidence are (a) paleosols with redoximorphic and concretionary features that are difficult to explain without the presence of microbial life, (b) microfossils found in rock deposits that represent “terrestrial” environments, and (c) sedimentary biostructures that are nonaqueous and microbially mediated. According to this evidence, the studied rock record shows that the period around the Mesoarchean to the Neoarchean (~3.2–2.5 Ga) was especially important for the development of terrestrial ecosystems, not because they could not exist before but because more plausible evidence is found in strata of that age. This “terrestrial” evolution was perhaps linked to supercontinent growth (Santosh 2010) and the associated emergence and diversification of potential new habitats and potential new biota.

The general similarity of some ancient fossils with fungi (e.g., Hallbauer and van Warmelo 1974; Hallbauer et al. 1977; Mossman et al. 2008; Rye and Holland 2000; Retallack et al. 2013a, b) may be of great importance if these turn out to be phylogenetically related. Besides pushing back their antiquity, the existence of fungi in Proterozoic rocks would speak for a greater similarity between ancient and modern biocrusts. Also, the functioning of the ancient terrestrial ecosystems should be reexamined through new insights about the ecological role of fungi in biocrusts and their potential ability to distribute nutrients (or make them available) throughout extensive areas (Collins et al. 2008). It is necessary to continue studying the ancient record of exposed continental masses in order to provide a better appreciation of the impact of life on the development of Earth’s biosphere, especially that involving links between continents and oceans; however, by now, it should be well established in science that Precambrian landscapes were not barren.

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Chapter 4

Cyanobacteria and Algae of Biological Soil Crusts

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4.1 Introduction

Cyanobacteria are the oldest photoautotrophic component of biological soil crusts (biocrusts) known (see figure on front page). The oldest record of a fossil soil structure that may be interpreted as a biological soil crust is reported from as early as 2.6 billion years ago, and it presumably was composed of cyanobacteria

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(Watanabe et al. 2000; Beraldí-Campesi 2013, see also Chap. 3 by Beraldí-Campesi and Retallack). Fossil records suggest that eukaryotic algae first occurred on land 480–460 million years ago, while molecular clock estimates suggest an earlier colonization of about 600 million years ago. It is also hypothesized that this colonization of land by eukaryotes was facilitated by a partnership between a photosynthetic organism and a fungus (Heckman et al. 2001). Some of the early eukaryotic algae were able to form biocrusts (see Sect. 4.2.2). In this chapter, we will enumerate, as far as possible, cyanobacterial and eukaryotic algal species that are known so far to either form or occur in biocrusts. We will also discuss appropriate methods to assess their diversity and discuss ecological functions of the cyanobacterial and algal diversity.

4.2 Cyanobacterial and Eukaryotic Algal Diversity

4.2.1 Role and Diversity of Biocrust *Cyanobacteria*

From a functional point of view, cyanobacteria of biocrusts can be divided into three different groups: (1) Filamentous cyanobacteria, such as *Microcoleus*, that stabilize soils by gluing soil particles together and thus form soil aggregates due the presence of extracellular matrix (ECM; Figs. 4.1, 4.2, 4.3, and 4.4; see also Chap. 9 by Colesie et al. and Chap. 13 by Garcia-Pichel et al.). Those cyanobacteria are responsible for biocrust formation and are also the most abundant cyanobacteria species in the biocrusts. The formation of filaments in cyanobacteria is an essential feature that enables them to colonize physically unstable environments and to act as successful pioneers in the biostabilization process (Garcia-Pichel and Wojciechowski 2009). Due to the fact that the ECM remains over many years after the trichomes have either moved out of their sheath envelopes or died, the soil-stabilizing effect remains. (2) Cyanobacteria that prefer to live in the biocrust environment, enhancing the ecological role of biocrusts, e.g., through their contribution to C- and N-cycling. Examples are the unicellular *Chroococcidiopsis* (Fig. 4.5), the filamentous *Scytonema* (Fig. 4.4) and *Stigonema* (Figs. 4.6 and 4.7). (3) Cyanobacteria that only stochastically occur in biocrusts and may originate from other habitats, such as the aquatic environment or lichen symbiosis (e.g., *Chroococcus* Fig. 4.8, *Gleocapsa*, *Gloeocapsopsis*, *Cylindrospermum*, many *Phormidium* species, *Tolypothrix* Fig. 4.8).

In the first volume of the Ecological Studies series dealing with biocrusts (Belnap and Lange 2003), Büdel (2003) was not able to compare cyanobacteria at the species level at the scale of continents and subcontinents because only 35 cyanobacterial genera from biocrusts were known at that time. Since then, knowledge has increased considerably, and now more than 320 species in over 70 genera are known to occur in biocrusts worldwide. Many studies have included the cyanobacterial species diversity of biocrusts, identified either by morphological

Fig. 4.1 *Nostoc microscopicum*, biocrust of Southern Tunisia

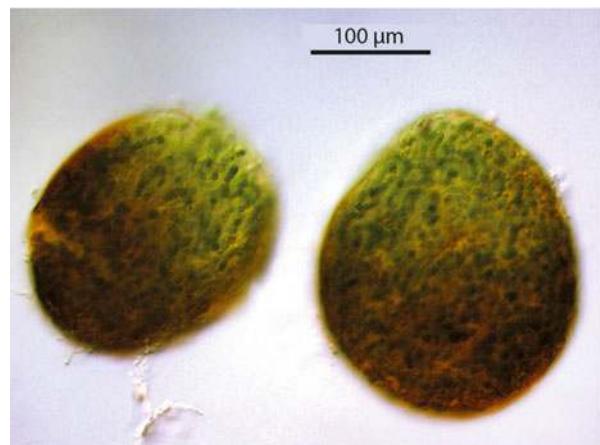


Fig. 4.2 *Nostoc commune*, trichomes inside a young colony, Negev Desert, Israel



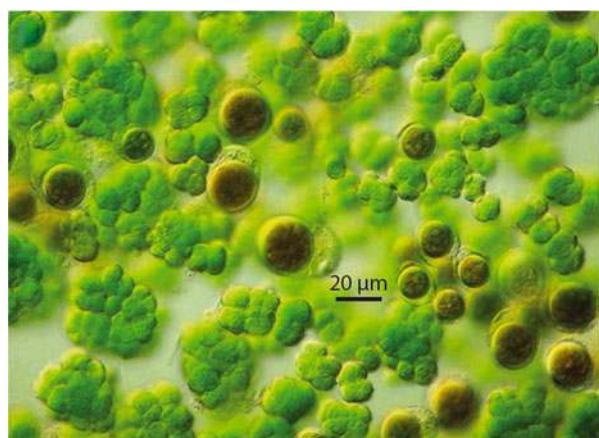
Fig. 4.3 *Microcoleus vaginatus*, biocrust of the Negev Desert, Israel



Fig. 4.4 *Scytonema* cf. *ocellatum*, biocrust of Israel



Fig. 4.5 *Chroococcidiopsis* sp., biocrust of Western Cape region, South Africa



(e.g., Langhans et al. 2009; Lewis and Flechtner 2002; Deb et al. 2013) or molecular methods (e.g., Gundlapally and Garcia-Pichel 2006) alone or, ideally, by both methods combined using the so-called “polyphasic approach” (e.g., Dojani et al. 2014). Of the 320 cyanobacteria species reported for biocrusts so far, only about 80 have been reported from at least two of the seven geographical regions distinguished here, while the majority (235 species) are listed only once (see Table 4.1 in the supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>). These numbers also include the hypolithic cyanobacterial diversity (see also Chap. 11 by S. Pointing et al.). On a continental scale, biocrust cyanobacteria are relatively well investigated with no major gaps (Fig. 4.9a). However, comparing the diversity of different continents, it immediately becomes obvious that the second smallest continent, Europe, has the highest species number, even though Asia and Africa are the two largest continents with considerably larger

Fig. 4.6 *Stigonema turfaceum*, biocrust of the high Arctic tundra, Canada

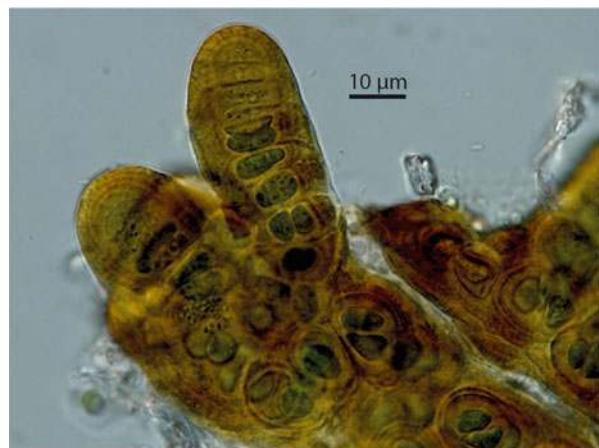


Fig. 4.7 Moss associated *Stigonema cf. hormoides*, Antarctic biocrust



amounts of arid and semiarid landscapes (Fig. 4.9b). This certainly does not reflect true biogeography but is rather an effect of the number of group-specialized scientists and the time they have worked on a certain continent. It is also obvious that there is a need for much more biodiversity assessments of biocrusts in the Americas. Knowledge about the actual distribution of cyanobacterial species and their abundance is of a great importance for understanding recent and ancient environmental dynamics. Cyanobacterial diversity influences ecosystem processes by changing the environment on a micro- and macroscale. Also the cyanobacterial diversity in biocrusts, as well as in any other environments, is regulated by many factors, including anthropogenic activities across temporal and spatial scales.

The two filamentous species, the heterocyst-bearing *Nostoc commune* (Fig. 4.2) and *Microcoleus vaginatus* (Fig. 4.3), have been reported for biocrusts of all continents. These may be the core ecosystem “engineers,” forming the early

Fig. 4.8 *Tolypothrix* sp. and *Chroococcus* sp., biocrust from loess sediment, Serbia



biocrusts and contributing the initial soil carbon and nitrogen inputs. Another two filamentous species found in biocrusts of all continents (except Antarctica) are *Coleofasciculus chthonoplastes* and *Trichocoleus sociatus*; both were formerly classified in the genus *Microcoleus*. Also the unicellular genus *Chroococcidiopsis* has been reported from biocrusts of all continents except Europe. Another three species are reported from biocrusts of five continents, i.e., *Nostoc microscopicum* (Fig. 4.1), *Schizothrix calcicola*, and *Scytonema myochrous*. The first two of them do not occur in the harsh climate of Antarctica. Ten species have been reported from biocrusts of four continents, i.e., *Aphanothecae saxicola*, *Aphanothecae muscicola*, *Calothrix parietina*, *Hassallia bysoidea*, *Microcoleus paludosus*, *Nostoc muscorum*, *Nostoc punctiforme*, *Scytonema hofmani*, and *Stigonema ocellatum* (Fig. 4.4). Twenty-four species have been reported from three continents and 48 species from two continents. A list of all biocrust cyanobacteria species worldwide, compiled from the literature, can be found in Table 4.1 of the online supplement of this book, which can be downloaded from <http://extras.springer.com/2016/978-3-319-30212-6>.

4.2.2 Role and Diversity of Eukaryotic Algae in Biocrusts

Based on their presumed role in biocrusts, the eukaryotic algae associated with biocrusts may be distinguished into four functional groups. (1) Crust-forming algae which may actively support the formation of crusts by entrapping soil particles due to their filamentous nature and/or secretion of mucilage, e.g., *Klebsormidium* (Fig. 4.10) and *Zygogonium*. Crust-forming algae occur in lower diversity, but may produce relatively high biomass. (2) Algae which are attached to soil particles and to the crust-forming algae. They are highly diverse and occur mostly in low abundances (Büdel et al. 2009), e.g., *Spongiochloris* (Fig. 4.11), *Neochlorosarcina*

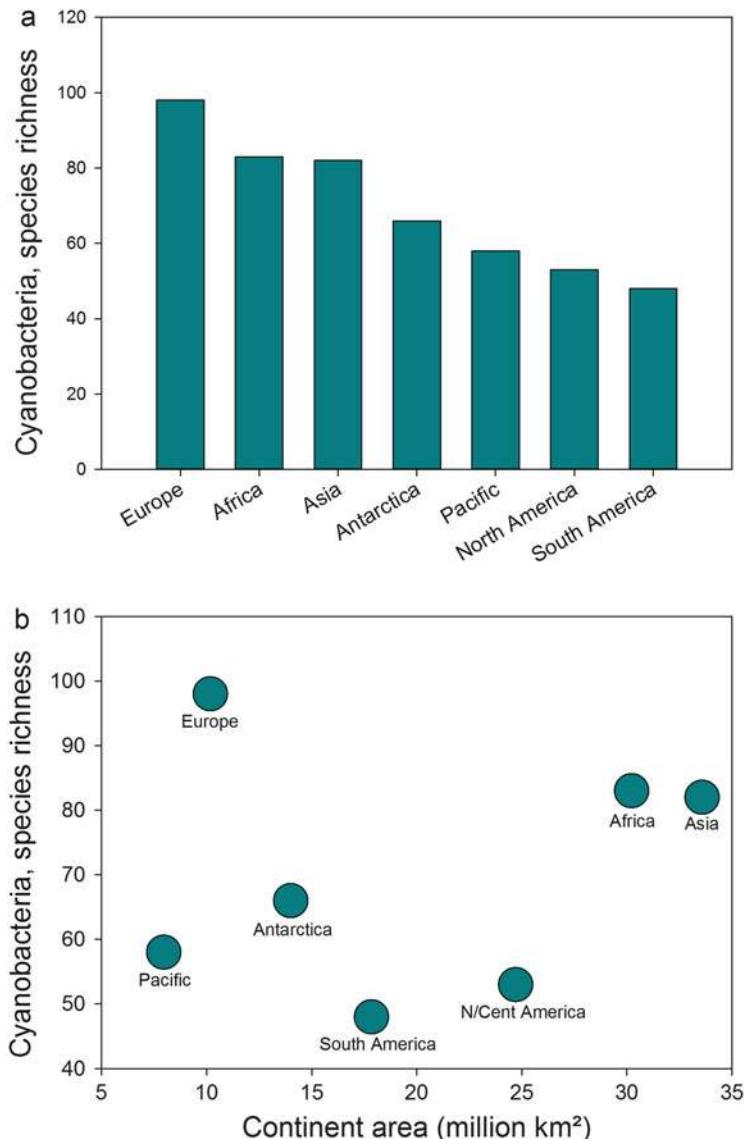


Fig. 4.9 Cyanobacterial species richness on a continental scale (a) and related to continental size (b); the region “Pacific” includes Australia and New Zealand

(Fig. 4.12), and most diatoms (Figs. 4.13, 4.14 and 4.15). (3) A smaller group of green algae that occurs within lichens as symbionts (photobionts), free living within the biocrusts, and/or living epiphytically on lichens, e.g., *Myrmecia* (Fig. 4.16) and *Stichococcus* (Fig. 4.17) (4) Freshwater algae which originate from aquatic habitats, but may occur in the soil, as it can be a “wet” habitat with many aqueous niches,

Fig. 4.10 *Klebsormidium flaccidum* (Kützing)
P.C. Silva, K.R. Mattox &
W.H. Blackwell

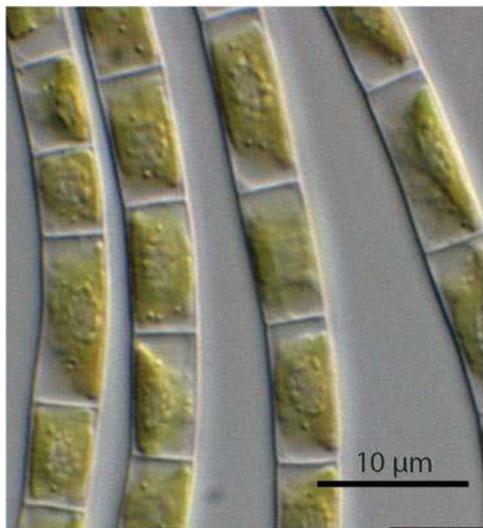


Fig. 4.11 *Spongiochloris minor* Chantanachat &
H.C. Bold



e.g., *Chlorococcum*, *Chlamydomonas* s.l., *Scenedesmus* s.l. and *Mychonastes* (Fig. 4.18). In biocrusts as well as desert soils, these algae may often be associated with bryophytes because of their higher water content, or they may be present as dormant resting stages.

There are no eukaryotic algae exclusively found in biocrusts; rather, they represent various algal lineages with different levels of ecological specialization. Eukaryotic algae are probably the least studied phototrophic component of biocrusts. The reasons may be that eukaryotic algae are rarely crust-forming species and they exhibit simple morphologies with distinguishing features only expressing

Fig. 4.12 *Neochlorosarcina negevensis* (Friedmann & Ocampo-Paus) S. Watanabe



Fig. 4.13 *Hantzschia amphioxys* (Ehrenberg) Grunow



in unialgal cultures. Using direct microscopy, algal forms other than the filamentous ones are hard to detect because they occur in low abundance or may be present as dormant resting stages, particularly in dry biocrusts. Also, early studies on eukaryotic biocrust algae were based on direct microscopy and, as they encountered many resting stages, may have recorded low algal diversity. Other sources of uncertainty in assessing the eukaryotic algal diversity of biocrusts may come from the fact that soil phycologists often do not pay attention whether the algae were found in “bare soil” or within biocrusts. In addition, molecular methods have

Fig. 4.14 *Luticola mutica* (Kützing) D.G. Mann

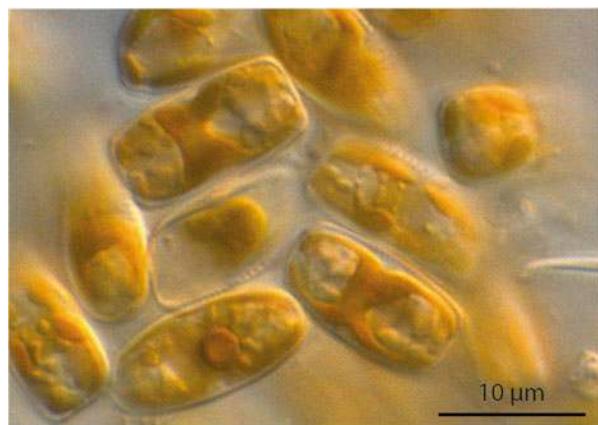


Fig. 4.15 *Pinnularia borealis* Ehrenberg



shown that many morpho-species and genera of soil algae are actually of different phylogenetic entities (species and genera), which makes their correct identification using microscopy even more difficult (e.g., Fucíková et al. 2011; Fucíková and Lewis 2012a, b).

The list of species (Table 4.2 in the supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>) represents the most current compilation of the literature on eukaryotic algae detected within, or clearly associated with, biocrusts. An overview of the eukaryotic algal diversity reported in this compilation is shown in Figs. 4.19 and 4.20. Eukaryotic algae that are reported from biocrusts were either green algae from both phyla, the Chlorophyta and Streptophyta, or members of one of three lineages of stramenopiles, i.e., the diatoms (Bacillariophyceae), xanthophytes (Xanthophyceae), or eustigmatophytes (Eustigmatophyceae). The identifications used in those studies have almost exclusively been based on morphological criteria observed by microscopy and from material in unicellular cultures. The geographical distribution of eukaryotic biocrust algae is only poorly understood, and there is still an ongoing debate whether microalgae exhibit biogeography or not. Due to their small size and desiccation resistance as well as other harsh environmental conditions, most terrestrial eukaryotic algae may

Fig. 4.16 *Myrmecia bisecta* Reisigl

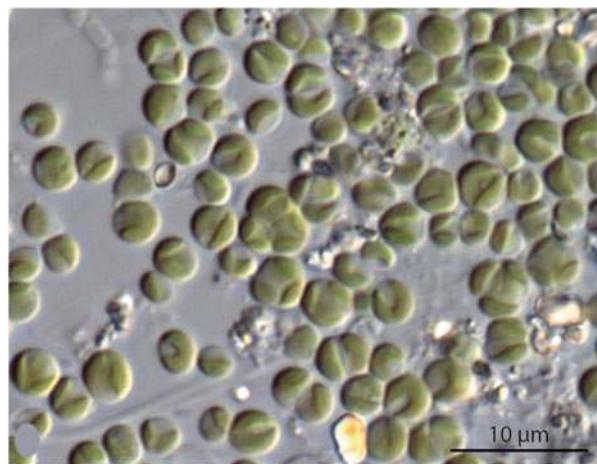


Fig. 4.17 *Stichococcus bacillaris* Nägeli



be easily distributed, e.g., by wind currents, and therefore one may anticipate an ubiquitous distribution for most species. In addition, when compared on a continental scale, the diversity of biocrust-associated eukaryotic algae as compiled from the literature is erratic (Figs. 4.19a, b and 4.20). This is probably reflecting the amount of work spent on samples from a certain continent rather than actual numbers of species diversity and geographic distribution. For example, the eukaryotic biocrust algal

Fig. 4.18 *Mychonastes homosphaera* (Skuja)
Kalina & Puncochárová



diversity appears much higher in Antarctica than in the Pacific region (Australia and New Zealand) or South America, as the latter two regions have been clearly neglected so far and require more attention (Fig. 4.19a).

Based on current compilations of literature, i.e., Table 4.2 in the supplementary online material (<http://extras.springer.com/2016/978-3-319-30212-6>) the filamentous species of *Klebsormidium* (Klebsormidiophyceae, Fig. 4.10) and *Zygogonium* (Zygnematophyceae), both from the Streptophyta, are most commonly encountered in biocrusts, especially in sandy soils. The unicellular zygnematophyte *Cylindrocystis* (Fig. 4.21) is the most common unicellular streptophyte green alga (Zygnematophyceae) in biocrusts, probably contributing to crust formation as it forms mucilage. Less frequent is the unicellular genus *Interfilum* (Fig. 4.22).

Biocrust Chlorophyta belong to three classes, the Chlorophyceae, Trebouxiophyceae, and Ulvophyceae; the systematics of the green algae as presented in this chapter follows Friedl and Rybalka (2012). Most biocrust green algae may not actively support biocrust formation but are associated with biocrust components in various ways (e.g., lichen photobionts).

The largest group of biocrust green algae are the Chlorophyceae (21 species, see Table 4.2 in supplementary online material at <http://extras.springer.com/2016/978-3-319-30212-6>). They are recorded from two or more geographic regions. All biocrust Chlorophyceae are unicellular but phylogenetically diverse within the class. They belong to several distinct phylogenetic lineages of the class, the orders Volvocales (syn. Chlamydomonadales) and Sphaeropleales (also called the “DO group”) and are even further distributed on various lineages within these orders. Several biocrust Volvocales form cell packages and may produce mucilage, thus somehow supporting crust formation, e.g., *Chlorosarcinopsis*, *Tetracystis*, *Neochlorosarcina* (Fig. 4.12), and *Borodinellopsis*. Other genera are either inconspicuous tiny coccoids (e.g., *Mychonastes*, Fig. 4.18) or form large unicells, e.g., *Macrochloris* and *Spongiochloris* (Fig. 4.11). Some coccoid members of Volvocales easily form flagellated stages (e.g., *Chlorococcum*); other Volvocales

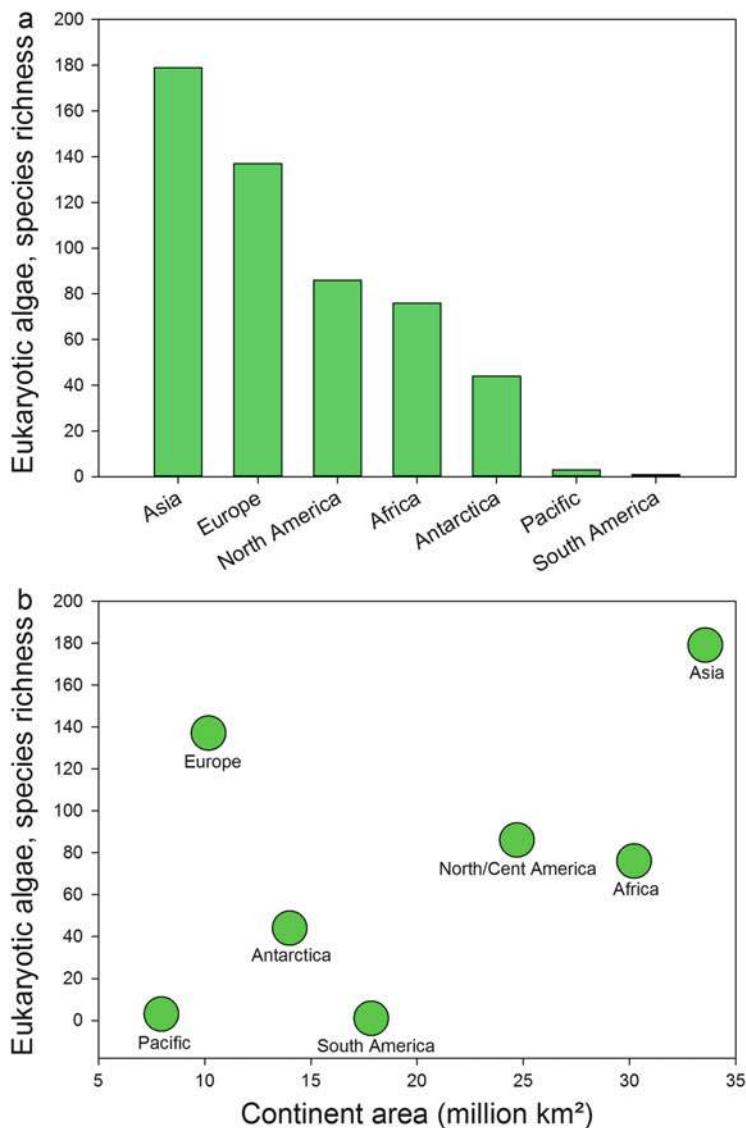


Fig. 4.19 Eukaryotic algal species richness on a continental scale (a) and related to continental size (b); the region “Pacific” includes Australia and New Zealand

are flagellates in their vegetative stages, e.g., *Chlamydomonas* and *Chloromonas*. The latter occur in immotile stages and are drought resistant by mucilage formation. Just a few members (five species) of the chlorophycean order Sphaeropleales, are common in biocrusts and are widely distributed. Unicellular coccoid *Bracteacoccus* species (Fig. 4.23) are most common in biocrusts, as well as representatives of the

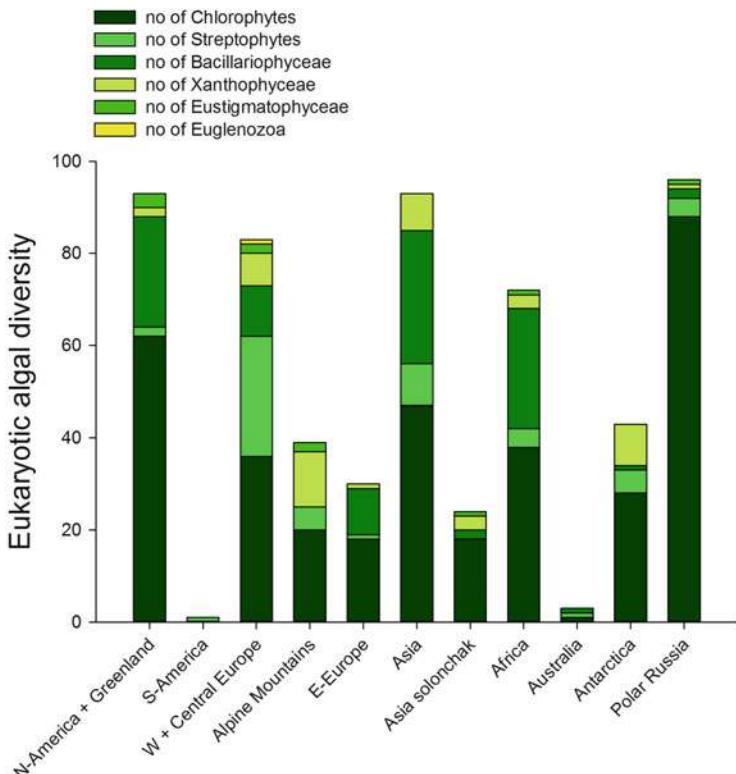


Fig. 4.20 Eukaryotic algal diversity related to class and higher taxonomic ranks and larger eco-regions

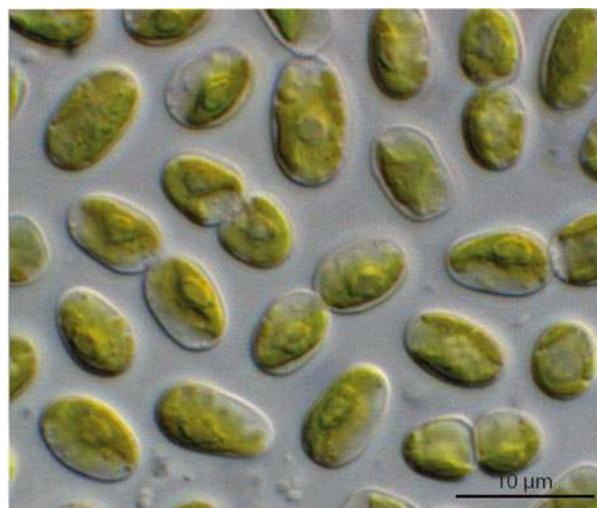
family of colony forming Scenedesmaceae, i.e., species of *Acutodesmus*, *Coelastrella*, and *Scenedesmus*.

Members of the Trebouxiophyceae form the second largest group of the Chlorophyta, i.e., 15 genera are reported and are widely distributed. Species of *Chloroidium*, *Coccomyxa* (incl. *Pseudococcomyxa*), *Muriella*, *Myrmecia* (Figs. 4.16 and 4.24), and *Chlorella*-like algae, including the “true” *Chlorella*, *Chlorella vulgaris* (Fig. 4.25), and *Elliptochloris* (Fig. 4.26) were found in almost every type of soil crust and from all geographic regions. However, *Chlorella* in its traditional taxonomic circumscription is of multiple origins and in fact represents several genera, separated from *Chlorella* s.str. only recently. The second most encountered trebouxiophytes are those which form cell packages, i.e., *Apatococcus*, *Desmococcus*, and *Diplosphaera* (Figs. 4.27 and 4.28). The filamentous trebouxiophyte *Prasiola* forms green turf and therefore may also contribute to crust formation in regions with maritime climate. However, it has been reported only from the Alps and Antarctica. Species of *Astrochloris*, *Chloroidium*

Fig. 4.21 *Cylindrocystis brebissonii* (Ralfs) De Bary



Fig. 4.22 *Interfilum terricola* (J.B.Petersen) Mikhailyuk, Sluiman, Massalski, Mudimu, Demchenko, Friedl, and Kondratyuk



(Fig. 4.29), and *Trebouxia* are frequently encountered as photobionts in lichens of biocrusts (Ruprecht et al. 2014).

The Ulvophyceae are the third green algal class commonly found in biocrusts, but just two inconspicuous unicellular or pseudofilamentous genera, *Planophilus* and *Pseudendocloniopsis*, were reported from more than just a single geographic

Fig. 4.23 *Bracteacoccus minor* (Chodat) Petrová



Fig. 4.24 *Myrmecia biatorellae* J.B. Petersen



region. The branched filamentous *Dilabifilum* is known as a crust-forming alga on different salty soils (solonchak or solonetz).

The second largest group of eukaryotic biocrust algae are the diatoms (e.g., Rumrich et al. 1989) with mostly pennate (elongated cells with bilateral symmetry) forms, i.e., the class Bacillariophyceae (Fig. 4.20). Inconspicuous species of the genera *Hantzschia* (Fig. 4.13), *Luticola* (Fig. 4.14), *Navicula* s.l. (incl. *Fistulifera*), *Nitzschia*, and *Pinnularia* (Fig. 4.15) were very common and may be found

Fig. 4.25 *Chlorella vulgaris* Beyerinck



Fig. 4.26 *Elliptochloris subsphaerica* (Reisigl) Ettl & Gärtner



associated with almost every soil crust type. Two groups of Stramenopiles algae are common in terrestrial habitats and soils but may also be found in soil crusts.

Members of the class Xanthophyceae are probably restricted to cooler geographic regions with the unicellular coccoid species of *Botrydiopsis* being the most common, but also some filamentous (*Tribonema*, *Xanthonema*) or branched filamentous forms (*Heterococcus*) are frequently found (Fig. 4.20). Rarely also the coenocytic *Botrydium* has been recorded. Eustigmatophyceae have been reported from biocrusts, with only four unicellular genera recovered, i.e., *Ellipsoidion*, *Eustigmatos*, *Gloeobotrys*, and *Vischeria*.

Fig. 4.27 *Diplosphaera chodatii* Bialosukniá

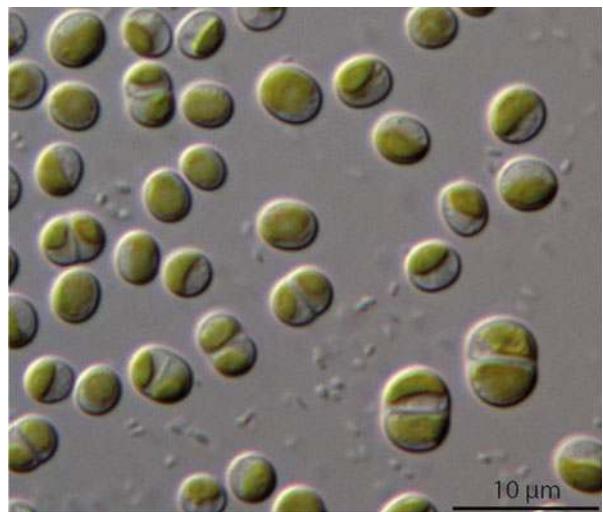


Fig. 4.28 *Desmococcus olivaceus* (Persoon ex Acharius) J.R. Laundon

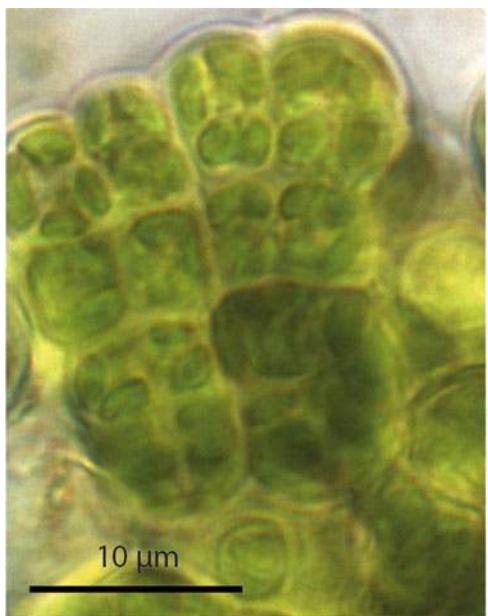


Fig. 4.29 *Chloroidium ellipsoideum* (Gerneck)
Darienko, Gustavs,
Mudimu, Menendez,
Schumann, Karsten, Friedl,
and Pröschold



4.3 Methodological Aspects

4.3.1 Sampling

For any assessment of the biodiversity of cyanobacteria and eukaryotic algae in biocrusts, the samples should be as fresh as possible. An appropriate method which leaves the crust mostly undisturbed and yields sufficient material at the same time has recently been described by Büdel et al. (2009). A lower lid of a 10-cm petri dish is lined with several layers of cellulose paper and pressed into the upper 2 cm of the soil crust after which a trowel is pushed below the lid, lifted together with the sample from the surrounding soil, and turned around to carefully remove surplus soil from the sample. For optimal biodiversity assessment, a number of smaller samples [e.g., a sufficient number of samples (test with a saturation curve of species numbers) of 2 cm × 2 cm × 1 cm in size with visible soil crusts] should be pooled (e.g., Gollerbach and Shtina 1969; Kostikov et al. 2001; Novakovskaya and Patova 2013). Wet samples need to be carefully dried (e.g., on cellulose paper) before lab work in order to avoid fungal growth, but on the other hand, drying may hamper the growth of certain algal groups (e.g., Xanthophyceae).

4.3.2 Identification, Cultures, and Morphological Approach

For identification of biocrust cyanobacteria in the crust samples by microscopy, small amounts of crust material are soaked in water and separated into two subsamples. Using a dissecting microscope, the first subsample is transferred to a microscope slide and examined under a light microscope. The second subsample is pre-cultured under wet and low light conditions for 3–4 days followed by a light microscopy examination. This will allow growth of cyanobacteria so that they can

be better recognized and identified. In order to start cultures, a small amount of biocrust material soaked in water is checked by microscopy using sterile slides and then transferred to both liquid and agarized media, e.g., BG-11 medium (Waterbury and Stanier 1978), which are known to be well suited for cyanobacteria. Subsequently, they are kept at a temperature of about 20 °C under low light (50–150 µmol photons m⁻² s⁻¹ photosynthetic active radiation) with a light-dark regime of 12:12 h. As soon as colonies are visible, they are checked by microscopy and then purified by transferring them several times onto fresh media. For developing cultures of biocrust cyanobacteria, many of the methods described below for eukaryotic algae can also be successfully employed. For identification of cyanobacteria using morphological criteria, the three volumes of the “Cyanoprokaryota” are recommended, i.e., Komárek and Anagnostidis (1998), Komárek and Anagnostidis (2005), and Komárek (2013).

For eukaryotic algae, direct microscopy of freshly collected soil samples can be useful for an initial survey of algal diversity. However, many eukaryotic algae in the crusts are present in untypical stages (e.g., resting cells), and feature characteristic for genus and species identification may only develop in culture. Therefore, a thorough microscopic investigation of eukaryotic biocrust algae involves several steps following microscopy of the sample, such as developing raw cultures using “wet chambers,” agarized enrichment cultures, and, finally, unicellular cultures (Gollerbach and Shtina 1969). The methods do not differ from those used for soil algae except that the biocrust samples need mechanical disruption before starting cultures so that the developing colonies can be better separated from each other. Many studies have used this procedure to determine the biodiversity of soil, e.g., Novichkova-Ivanova (1980), Vinogradova and Darienko (2008), Kostikov et al. (2001). However, employing cultures generally has the risk that those species which may be hard to culture using standard procedures (and they could even be dominant) may be left undiscovered, whereas those species not actively participating in the crust communities (e.g., present just as dormant stages) may be amplified simply because they grow well in culture.

To establish cultures of eukaryotic biocrust algae, some authors use only agarized enrichment cultures (e.g., Peer et al. 2010; Hoppert et al. 2004) or even just direct microscopy of the samples (Büdel et al. 1994; Colesie et al. 2014; Kanda et al. 2002), but mostly a combination of both are applied (e.g., Flechtner et al. 1998; Broady 1986; Broady and Weinstein 1998). Raw cultures using distilled water for wetting “wet chambers,” introduced by Fritsch and John (1942) for the observation of soil diatoms, facilitate the observation of biocrust algae and induce their growth without selecting certain algae too much. It is important to consider that the nutrient composition of culture media introduces a considerable bias, as certain nutrient compositions will accelerate growth of certain species while inhibiting others. The biocrust is placed in a sterilized petri dish at air humidity up to 80 %. After 2–3 weeks of exposure to a light-dark 12:12 h regime, biofilms will appear on the surface of the biocrust sample to which several cover slips are slightly pressed. The sample surface should be uneven to leave space between the biofilm and the glass cover slip—this will form small chambers in which favorable microclimatic

conditions for algal growth on the cover slip surfaces will occur. The cover slips can be used for microscopy after some time (2–3 weeks) of incubation on the sample surfaces and even allow observation of a succession of algae if the cover slips are used for microscopy after consecutive time intervals. Cover slips can also be put into liquid or on the surface of agarized culture media to start cultures of the algae from these surfaces. Alternatively, small fragments of the biocrust are placed on agarized culture media which should not be too rich in nutrients and devoid of vitamins or any organic compounds to avoid the growth of fungi and bacteria. After incubation for 2–3 weeks, the first small colonies, often formed by a variety of different algae, can already be used for an initial estimate of the algal diversity by microscopy and also for establishing unialgal cultures after several purification steps.

For liquid cultures, fragments of the biocrust are placed in liquid media, e.g., 1–2 g of a crust sample is added to a 50–80 ml sterile medium in 100–150 ml Erlenmeyer flasks. One disadvantage of this method is that algae (e.g., resting stages of freshwater algae), which were in an inactive state in the biocrust and do not belong to the active algal community of the biocrust, can then easily develop in those cultures.

4.3.3 Molecular Approaches

Molecular markers may be most promising for assessing biocrust cyanobacteria and eukaryotic algal biodiversity. For cyanobacteria, it was revealed that due to their high physiological plasticity, which allows for their rapid adaptation to various environmental conditions, new morpho- and ecotypes may be developed within short time. This makes the discrimination of species using morphological and ecophysiological characters rather difficult and calls for molecular studies to define species. DNA sequences allow an unambiguous characterization and the comparison with reference sequences (as available from public databases), providing reliable estimates of genetic distances to infer the phylogenetic positions of algae and cyanobacteria. The first cyanobacteria 16S (SSU) rRNA gene sequences have already been determined almost 30 years ago (Giovannoni et al. 1988), followed by corresponding sequences (18S rRNA) for eukaryotic algae, and since then their numbers have ever been increasing up to several thousands in publicly available databases (e.g., NCBI). Due to the large number of available reference sequences, the SSU rRNA genes became the “golden standard,” i.e., the molecular marker of choice for cyanobacteria as well as eukaryotic algae. There are many examples for studies on biocrust cyanobacteria which used 16S rRNA as molecular signatures (e.g., Abed et al. 2010; Zaady et al. 2010; Li et al. 2013; Dojani et al. 2014; Patzelt et al. 2014). However, SSU rRNA alone may not provide sufficient resolution for unambiguous distinction of species, and additional more variable markers (e.g., ITS rDNA) are required. For cyanobacteria, the 16S–23S spacer (ITS) has successfully been used, also because its secondary structure models bear valuable phylogenetic

information for species distinction (e.g., Boyer et al. 2002; Reháková et al. 2007; Siegesmund et al. 2008; Johansen et al. 2011). For eukaryotic algae, i.e., photobionts of lichens associated with soil crusts, the nuclear-encoded ITS rDNA in combination with the chloroplast-encoded intergenic spacer psbJ-L has recently been employed for species identification (Ruprecht et al. 2014).

There are two principal ways to apply molecular methods for assessing biocrust algal and cyanobacterial diversity: sequencing of cultured strains isolated from biocrusts and using DNA extracts directly from the biocrusts without culturing (culture-independent approach). For the latter approach, DNA is extracted directly from the fresh biocrust sample followed by PCR amplification, which will result in a mixture of PCR products from the various organisms present in the biocrust sample. They need to be separated by cloning before sequencing, and in order to assess the algal/cyanobacterial diversity most accurately, a larger number of clones need to be sequenced. The culture-independent approach requires PCR primers that selectively amplify certain groups of target organisms, e.g., PCR primers which preferentially amplify cyanobacteria (e.g., Nübel et al. 1997) or green algae (e.g., Hallmann et al. 2013), to enrich the clone libraries with sequences from the target organisms. Several recent studies used cyanobacteria-specific PCR primers for biocrust and/or soil cyanobacteria (Li et al. 2013; Dojani et al. 2014; Patzelt et al. 2014), whereas others studied biocrust cyanobacteria as part of the whole bacterial community using universal bacterial 16S rRNA PCR primers (Gundlapally and Garcia-Pichel 2006; Abed et al. 2010; Zaady et al. 2010; Zhang et al. 2012). Recently, next-generation DNA sequencing (NGS, e.g., using a Roche 454 FLX instrument with Titanium reagents, Steven et al. 2013a; Elliott et al. 2014) provided the ability to determine and read millions of DNA sequences in parallel, making them ideally suited for large-scale biodiversity analyses of environmental biocrust samples. There are already several studies which have analyzed biocrust cyanobacterial diversity based on 16S rRNA gene amplicons obtained with universal bacterial primers (Steven et al. 2013a, b; Elliott et al. 2014; Maier et al. 2014). For eukaryotic biocrust algae, almost all molecular studies have been based on unicellular cultured isolates established from biocrust samples; the culture-independent approach has been used not employing 18S rRNA but other conserved markers as plastid-encoded 16S or 23S rRNA genes (Maestre et al. 2006; Lin and Wu 2014).

As an alternative to the culture-independent DNA sequencing approach for the analysis of microbial biocrust communities, DNA fingerprinting based on PCR amplification has been used, i.e., DGGE (Gundlapally and Garcia-Pichel 2006; Zaady et al. 2010; Zhang et al. 2012), ARISA (Abed et al. 2012) and t-RFLP (Redfield et al. 2002), but so far only for cyanobacteria. DGGE profiling may be appropriate because the characteristic DGGE-banding patterns can easily be compared among many samples. If unique or different patterns are identified, a DGGE band representing a still unidentified species can also be sequenced and identified using sequence comparisons after excised from the gel, but this will yield only rather short sequences (Lin and Wu 2014; Maestre et al. 2006).

For species identifications, the molecular approach is often supplemented by microscopy of the cultures. The latter is still essential for correct identification when no sequences of closer relatives are available in public gene sequence databases (Lewis and Flechtner 2002, 2004; Büdel et al. 2009; Rindi et al. 2011; Flechtner et al. 2013). In general, in the culture-independent DNA sequencing approach, the PCR amplification step is crucial to the diversity assessment. The DNA of the most abundant or any other species may be preferentially amplified and mask the DNA of other less abundant or easy to amplify species and leave the latter species undiscovered. Shorter gene regions may be better amplified compared to longer ones—the lengths of amplicons depend on the type of PCR primers used or species present in the biocrust sample. In addition, biocrust samples may exhibit PCR-inhibiting compounds. It follows that also the culture-independent approach presents various biases. Culture-independent and culture-based approaches may therefore result in different diversities. Consequently, a combination of both approaches is required to assess the algal biodiversity as accurately as possible. In a recent example, results from the culture-dependent and culture-independent approaches were compared, and this pointed out the necessity of employing both techniques because several taxa could be recovered only via one or the other approach (Patzelt et al. 2014; Dojani et al. 2014).

4.4 Conclusion

Biocrust inhabiting cyanobacteria and eukaryotic algae are highly diverse, but only few of them are in fact responsible for crust formation. Most cyanobacteria and eukaryotic algae simply use the biocrust habitat but may enhance the biocrust functions by their presence. The main crust-forming cyanobacteria are *Microcoleus*, *Nostoc*, *Scytonema*, and *Stigonema*. In contrast, biocrusts formed by eukaryotic algae, i.e., *Klebsormidium* and *Zygogonium*, are relatively rare. Cyanobacteria from biocrusts are better studied compared to the corresponding eukaryotic algae. Data about the distribution of cyanobacteria and eukaryotic algae are fragmentary and strongly biased towards the intensity of work extended to samples from a certain continent. Also, there is an ongoing debate whether the cyanobacteria and eukaryotic algae exhibit biogeography at all. For microscopic identification of cyanobacteria and eukaryotic algae, it is recommended to develop cultures, but this has the risk that isolating procedures and culture conditions may lead to a strongly biased biodiversity. Therefore, the culture-independent molecular approach is recommended but so far has only been applied a few times, mostly for cyanobacteria. In order to assess the cyanobacterial/algal biodiversity as accurately as possible, the culture-independent and culture-based approaches need to be combined.

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Chapter 5

Bacteria and Non-lichenized Fungi Within Biological Soil Crusts

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5.1 Introduction

Microbial fungi and bacteria are ubiquitous, occurring in highly enriched concentrations in biological soil crusts (biocrusts), as compared to the surrounding uncrusted soil. Nevertheless, their diversity can hardly be estimated without molecular biology methods. Only the macroscopic phenotypes of lichen-forming fungal species, which may dominate the landscape in soil crust habitats, allow a more or less secure determination to species level even in the field. Lichens in biocrusts have therefore long been studied (see Chap. 1 by Lange and Belnap) and their diversity and ecosystem services specifically addressed in Chap. 7 by Rosentreter et al. Knowledge on the diversity of non-lichenized fungi in biocrusts is still quite limited, whereas investigation of bacterial communities has received global attention in the past decade. This chapter aims to review the current state of research on bacterial and fungal community composition in biocrusts.

Recent research on bacterial and fungal communities has been conducted in arid and semiarid regions, such as the Colorado Plateau, Chihuahuan Desert, and Sonoran Desert, USA (Garcia-Pichel et al. 2001; Yeager et al. 2004; Nagy et al. 2005; Yeager et al. 2007), the Sultanate of Oman (Abed et al. 2010), and the Gurbantunggut Desert in China (Zhang et al. 2011). In Europe, the bacterial communities of bryophyte and lichen-dominated biocrusts from southern Spain have been investigated (Castillo-Monroy et al. 2011; Moquin et al. 2012; Maier

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et al. 2014). This global assessment allows identification of common and distinguishing characteristics of the bacteria and fungi in biocrusts around the world. Although there are characteristics specific to geographic regions and land masses, many compositional characteristics are similar among the Earth's biocrusts and arid land surface soils.

The present research needs to be put into context with the technological advancements of recent years, which basically allow two approaches. Culture-based approaches have been applied (Garcia-Pichel et al. 2001, 2003; Gundlapally and Garcia-Pichel 2006; Abed et al. 2010; Zhang et al. 2011), providing isolates for in-depth study of biocrust organism genomes and physiology (Yeager et al. 2007; Starkenburg et al. 2011). However, as cultivation techniques only retrieve a small fraction of the total microbial diversity, culture-independent methods have been increasingly used. Community profiling techniques such as denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP) were initially used [for bacteria, see Garcia-Pichel et al. (2001), Kuske et al. (2002), Garcia-Pichel et al. (2003), Yeager et al. (2004), Nagy et al. (2005), Gundlapally and Garcia-Pichel (2006), and Castillo-Monroy et al. (2011); for fungi, see Bates and Garcia-Pichel (2009) and Bates et al. (2012)]. Furthermore, 16S ribosomal RNA (rRNA) gene clone libraries were applied [for bacteria, see Yeager et al. (2004), Gundlapally and Garcia-Pichel (2006), Yeager et al. (2007), Abed et al. (2010), and Moquin et al. (2012); for bacteria and fungi, see Steven et al. (2014)]. With the improvement of sequencing technologies such as high-throughput 16S rRNA gene sequence analyses and shotgun metagenome sequencing, there has been a resurgent interest in a wider characterization of the biocrust microbial communities (Steven et al. 2012a, b, 2013a, b, 2014; Angel and Conrad 2013; Davies et al. 2013; Büdel et al. 2014; Elliott et al. 2014; Steven et al. 2015). The complex physicochemical properties of biocrusts, dependence of DNA recovery on the soil type, and PCR bias should be kept in mind as prokaryotic diversity determined by high-throughput amplicon or metagenome sequencing is interpreted (Delmont et al. 2011; Lombard et al. 2011).

5.2 Bacterial Biomass and Community Composition

Since biocrusts typically colonize the top 1–2 cm of the soil surface, it is required to study small-scale variations in soil depth. Garcia-Pichel et al. (2003) assessed bacterial biomass and diversity of two stages in biocrust formation (early successional and well-developed late successional) from the Colorado Plateau at a millimeter resolution. According to their results, microbial biomass decreased with depth and increased with biocrust maturity, supporting the view that biocrusts represent “mantles of fertility” in arid regions (Garcia-Pichel et al. 2003).

Cyanobacteria, particularly species in the genus *Microcoleus*, are globally dominant biocrust-forming microorganisms in most arid lands (Garcia-Pichel et al. 2001; Boyer et al. 2002; Belnap and Lange 2003; Pointing and Belnap

2012; see Chap. 4 by Büdel et al.). The production of polysaccharide sheaths aids in formation of centimeter-long filament bundles, and these filamentous Cyanobacteria are thought to act as pioneers in the stabilization process of soils (Garcia-Pichel and Wojciechowski 2009). *Microcoleus steenstrupii* appeared to be the dominant filamentous cyanobacterium in Sonoran Desert biocrusts, but *Microcoleus vaginatus* as well as heterocystous groups (*Scytonema* and *Anabaenopsis*) and an unicellular cyanobacterium (*Synechococcus*) were also present. Yeager et al. (2004) revealed distinct differences in the diazotrophic communities between young and well-developed biocrusts from a cold desert in the Colorado Plateau and a warm desert in southern New Mexico, demonstrating a transition from a *Microcoleus vaginatus*-dominated poorly developed crust to mature crusts harboring a greater percentage of *Nostoc* and *Scytonema* spp. For a detailed account on Cyanobacteria, see Chap. 4 by Büdel et al. Interestingly, Cyanobacteria are not the sole prokaryotes in the biocrusts that harvest energy from light. Up to 6 % of the bacterial community cultured from Canadian biocrusts are aerobic anoxygenic phototrophs belonging to the genera *Belnapia*, *Muricoccus*, and *Sphingomonas* (Csotonyi et al. 2010).

Knowledge about bacteria is rapidly increasing with the convenience of culture-independent sequencing studies. Besides Cyanobacteria, the most common bacteria in the Sonoran Desert comprised members of Proteobacteria (mainly Betaproteobacteria), Actinobacteria, and Acidobacteria. These bacterial phyla are dominant and common in soils and sediments everywhere, in arid as well as wet landscapes (Fierer et al. 2012). All sequences of Betaproteobacteria were close to cultured members of the Oxalobacteraceae (Nagy et al. 2005). Samples from Colorado Plateau biocrusts were numerically dominated by the same top three phyla as found in the Sonoran Desert (Cyanobacteria, Actinobacteria, and Proteobacteria, largely Betaproteobacteria) (Gundlapally and Garcia-Pichel 2006). In particular, *Microcoleus vaginatus* and *Microcoleus steenstrupii* represented the dominant clades of Cyanobacteria (38.4 %). Actinobacteria (particularly the genera *Streptomyces*, *Sphaerobacter*, *Actinomadura*, *Rubrobacter*, and *Nonomuraea*) were common among non-phototrophs. Betaproteobacteria (genus *Massilia* and *Comamonas*) and Bacteroidetes (genera *Flexibacter*, *Spirosoma*, *Flavobacterium*, *Sphingobacterium*) contributed around 10 % each. Remarkably, mycelial genera of Actinobacteria were present (e.g., *Streptomyces*, *Actinoplanes*, *Pseudonocardia*), which are likely to be important during biocrust formation. Moreover, isolates of Proteobacteria and Bacteroidetes produced exopolysaccharides and thereby could also play a role in soil stabilization and biocrust formation (Gundlapally and Garcia-Pichel 2006). The predominance of Cyanobacteria was also demonstrated for the arid deserts of the Sultanate of Oman near Muscat and Adam. Again, *Microcoleus vaginatus* was the most abundant cyanobacterium. Using microscopy, the genera *Scytonema*, *Leptolyngbya*, and *Lyngbya* were also identified (Abed et al. 2010). Taken together, multiple genera of Cyanobacteria, both non-N-fixing genera such as *Microcoleus* and the N-fixing genera *Nostoc*, *Scytonema*, and *Spirilrestis*, constitute a major part of biocrust bacterial communities. In addition to the Cyanobacteria, many bacterial phyla that are common to soils are also

present. Similarly, microbial communities that form biofilms on the ventral surfaces and sides of translucent rocks termed hypoliths are dominated by Cyanobacteria and can also support heterotrophic bacteria. Actinobacteria, Acidobacteria, Alphaproteobacteria, and Gammaproteobacteria occur frequently in hypolithic communities (Chan et al. 2012; see Chap. 11 by Pointing et al.). Comparative analyses of the non-cyanobacterial communities at the genus and species level would define relationships among biocrusts from different regions; this has not been conducted but would be an interesting area to pursue. Some differences in microbial community structure of biocrusts have already been observed. In biocrusts from the Colorado Plateau and the Sonoran Desert, Actinobacteria were prevalent (Nagy et al. 2005; Gundlapally and Garcia-Pichel 2006; Steven et al. 2013a, b), whereas this group was absent in biocrusts from Oman (Abed et al. 2010). In contrast, Myxobacteria were detected in samples from Oman but not in those from the Colorado Plateau and Sonoran Desert (Abed et al. 2010). There is, however, no clear explanation for these differences so far.

Besides Cyanobacteria-rich biocrusts, several other subtypes of biocrusts have been recently studied. The bacterial phyla Proteobacteria, Actinobacteria, and Bacteroidetes comprised the majority of the community in lichen-dominated biocrusts from the Tabernas Desert, Spain. Unlike in the studies of Nagy et al. (2005) and Gundlapally and Garcia-Pichel (2006), Alphaproteobacteria represented the dominant class of Proteobacteria. Among the Alphaproteobacteria, the orders Sphingomonadales and Rhizobiales were predominantly observed. Furthermore, 45 genera of the class Actinobacteria were detected. The observation that Actinobacteria are very common and diverse within biocrusts is in line with studies conducted at the Colorado Plateau and in the Sonoran Desert. In lichen-dominated biocrusts from the Tabernas Desert as well as in samples from the Colorado Plateau, a low abundance of Bacteroidetes was found (Maier et al. 2014, Fig. 5.1). In contrast, a 16S rRNA gene library sequencing study of Moquin et al. (2012) on bacterial communities in bryophyte-rich biocrusts from the Sandia Mountains, USA, revealed the dominance of Bacteroidetes (primarily Chitinophagaceae and Cytophagaceae), Acidobacteria, and Proteobacteria (Oxalobacteraceae and Comamonadaceae). Using 16S rRNA gene pyrosequencing, Steven et al. (2013b) demonstrated that biocrust-associated bacterial communities of Arctic permafrost soils were as diverse as in temperate regions. Their samples were numerically dominated by Acidobacteria, Cyanobacteria, Proteobacteria, Planctomycetes, and Verrucomicrobia.

In general, biocrusts that colonize the top few centimeters of the soil from regions around the globe share similar bacterial composition at the phylum level. Comparisons between this biocrust stratum and the soil a few centimeters below the biocrust show less commonality, with distinct differences in biomass and bacterial composition. Steven et al. (2013a, b) demonstrated that community composition in soils with different parent material origin (sandstone, shale, gypsum) differed at small vertical scales of a few centimeters. Cyanobacteria and Proteobacteria had significantly higher relative abundance in biocrusts, whereas Chloroflexi and Archaea were significantly enriched in below-biocrust soils across the three soil

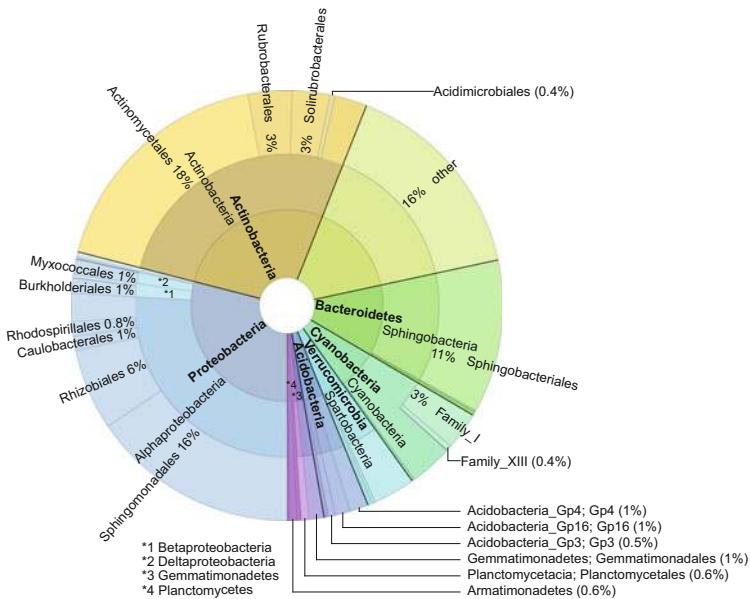


Fig. 5.1 Bacterial community structure of biocrusts from the Tabernas Desert, southeastern Spain. Based on 16S rRNA gene 454 pyrosequencing data; rarefaction with a depth of 1227 reads per sample. 16 % of the sequences could not be assigned to known bacterial taxa (Maier et al. 2014)

types (Steven et al. 2013a, b). As photic zones are generally limited to few millimeters beneath the soil surface, the distribution of Cyanobacteria is rather constrained in deeper layers (Garcia-Pichel et al. 2003). These differences were confirmed by Elliott et al. (2014) for biocrusts in the Kalahari Desert in Southern Africa. According to 16S rRNA gene 454 pyrosequencing, bacterial communities were distinct at the different soil depths, indicating niche partitioning of the microbial community between biocrusts and the subsurface soil. Again, Cyanobacteria (genus *Phormidium*) and Bacteroidetes were significantly more abundant in surface soils (0–1 cm depth), while in below-biocrust soils (1–2 cm depth) Acidobacteria, Actinobacteria, Chloroflexi, and Firmicutes were more frequently detected. This was broadly in line with observations made on samples of the Tabernas Desert, Spain (Maier et al. 2014). The surface soil communities differed from below-biocrust soil communities in having higher abundances of Cyanobacteria and at class level of Actinobacteria and Alphaproteobacteria. Acidobacteria and Verrucomicrobia, among others, as well as Crenarchaeota were overrepresented in the below-crust soil when compared to surface soil (Fig. 5.2).

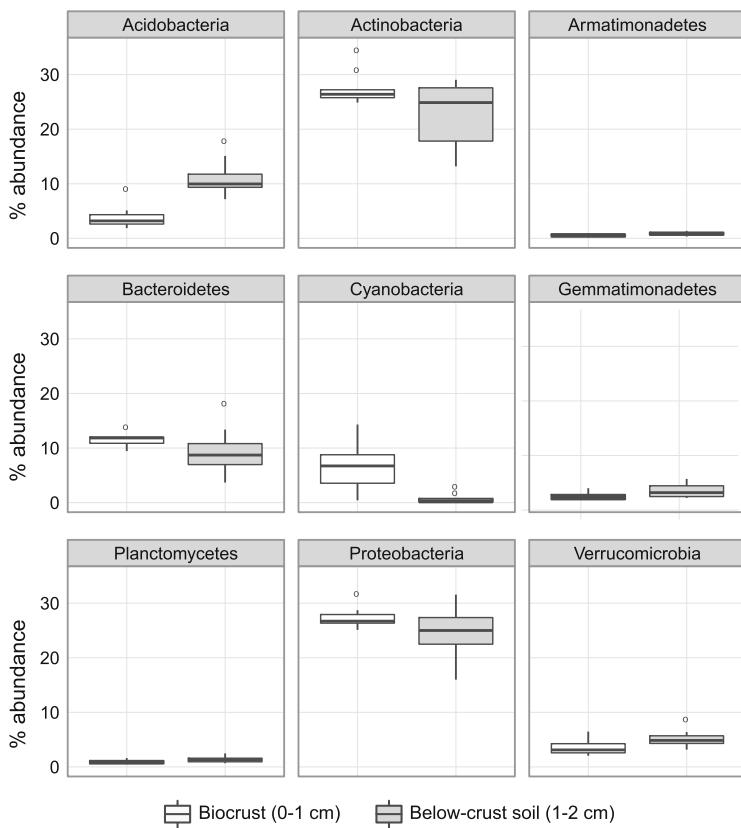


Fig. 5.2 Relative abundances of bacterial taxa in soil layers (biocrust, below-biocrust soil) from Tabernas Desert, southeastern Spain. Based on amplicon 16S rRNA gene 454 pyrosequencing data; rarefaction with a depth of 1227 reads per sample. Boxes represent the interquartile range; median values are shown as line and outliers as dots. $n=10$ per soil layer. Acidobacteria, Armatimonadetes, Cyanobacteria, Gemmatimonadetes, Planctomycetes, Verrucomicrobia ($P \leq 0.05$), Actinobacteria, Bacteroidetes, Proteobacteria (not significant), paired *t*-test or Wilcoxon signed rank test for paired samples if assumptions for parametric tests were not met

5.2.1 Impact of Biocrust Age, Soil, and Vegetation Type on Bacterial Community Structure

Variations in biocrust community composition related to differences in biocrust maturity (Garcia-Pichel et al. 2003), soil types (Steven et al. 2013a, b), and distance from plants and/or impact of intermittent water flow have been the focus of some studies. *Microcoleus vaginatus* in biocrusts from the Colorado Plateau was less abundant, and cyanobacterial diversity was lower in gypsum soils compared to biocrusts on sand, silt, and shale soils (Garcia-Pichel et al. 2001). Steven

et al. (2013a, b) showed that Actinobacteria and Proteobacteria were enriched and Cyanobacteria depleted on gypsum relative to sand and shale soils.

The widely spaced plants in arid lands influence the distribution of soil bacteria. The composition of the total bacterial community, particularly Acidobacteria, was significantly different between the plant rhizosphere habitat of bunchgrasses and the plant interspace surface soils colonized by cyanobacterial biocrusts (Kuske et al. 2002). Based on high-throughput 16S rRNA gene sequencing, Elliott et al. (2014) found that vegetation type (trees, shrubs, grasses) influenced bacterial communities of biocrusts in the Kalahari Desert of Southern Africa. In contrast, Nagy et al. (2005) detected no differences in biocrust microbial diversity or composition between biocrusts under plant canopies and those in plant interspaces of the Sonoran Desert using DGGE, indicating a biocrust independence from higher plant resources. Steven et al. (2014) employed rRNA gene sequencing and shotgun metagenomic sequencing to compare the microbial communities inhabiting the root zones of the creosote shrub *Larrea tridentata* and the plant interspace biocrusts in Mojave Desert. The numerically abundant bacterial operational taxonomic units (OTUs) were present in both the biocrusts and root zones, but the relative abundance of those OTUs differed between habitats. The biocrust bacterial rRNA gene libraries were dominated by Cyanobacteria, followed by Proteobacteria and Actinobacteria, whereas the root zones contained about twice as many Actinobacteria and Proteobacteria. Members of the Alphaproteobacteria orders Rhodospirillales and Sphingomonadales were more abundant in the root zones than in biocrusts (Steven et al. 2014).

Steven et al. (2013b) aimed to investigate the impact of naturally occurring intermittent water flow in water tracks, zones of enhanced soil moisture in polar permafrost regions, on bacterial community structure. Cyanobacteria, in particular Oscillatioriales, were more abundant inside the water tracks compared to samples from outside the water tracks. Moreover, Acidobacteria showed responses to wetting pulses in the water tracks.

5.2.2 Manipulation Experiments: Response of Microbial Communities to Disturbance and Differing Light or Soil Temperature Conditions

Recently, it has been demonstrated that biocrust bacterial community structures are altered by chronic physical disturbance (e.g., foot trampling) at sites on the Colorado Plateau. A decline in diazotrophic Cyanobacteria such as *Microcoleus vaginatus* in trampled plots was observed using 16S rRNA T-RFLP, whereas the proportion of members of Actinobacteria, Chloroflexi, and Bacteroidetes increased. Furthermore, T-RFLP profiles from trampled biocrusts showed higher variability among replicates indicating an unstable state after disturbance (Kuske et al. 2012).

The influence of light conditions on the establishment of soil surface communities was investigated on pasture soil in microcosm experiments using ribosomal marker gene analyses. The experimental setup included trays filled with pasture soil that were exposed to a 16:8 h light/dark cycle at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 20 °C for 80 days. Trays were covered either with a DS 226 light filter or an opaque filter to simulate dark conditions. At day 0, 20, 40, and 80 samples were taken using a steel sheet in order to separate the two soil layers, soil surface (upper 3 mm), and underlying bulk soil (3–12 mm). Similar phototrophic communities were found at the soil surface and in bulk soil in those microcosms exposed to light, indicating that light can influence phototroph community structure even in the below-biocrust bulk soil. The 454 pyrosequencing results revealed a significant selection for diazotrophic Cyanobacteria such as *Nostoc punctiforme* and *Anabaena* spp. and the green alga *Scenedesmus obliquus*. The soil surface also harbored different heterotrophic bacterial and fungal communities in the presence compared to the absence of light. In particular, a selection for the phylum Firmicutes was observed (Davies et al. 2013).

Angel and Conrad (2013) determined the metabolically active bacterial communities in biocrusts in the Negev Desert, Israel, by incubating samples under light-oxygenic and dark-anoxic conditions after simulated rainfall events. Using stable isotope probing of RNA and 454-pyrosequencing, they showed that the anaerobically growing bacterial communities were at first numerically dominated by members of the order Bacillales, which were later replaced by members of the order Clostridiales. Under aerobic conditions, Sphingobacteriales and Alphaproteobacteria (Rhizobiales, Rhodobacterales, Rhodospirillales and Rubrobacterales) were more abundant. In dry biocrusts, Actinomycetales were the dominant bacterial order. By the end of the incubation, however, Actinomycetales were rarely detected (<1 % of the community), indicating complex communities dynamics in biocrusts as these change from dormancy to an active state (Angel and Conrad 2013). Johnson et al. (2012) monitored impacts of increased soil temperature (2–3 °C) and altered precipitation patterns on biocrusts in the cold desert of the Colorado Plateau over 2 years. Increased soil temperature did not affect the cyanobacterial biocrust. However, they found significant declines in the surface soil biomass and chlorophyll *a* concentration in response to increased frequency of small precipitation treatments. Furthermore, a change of the bacterial community composition at phylum and family level was observed, with the proportion of Cyanobacteria being considerably reduced.

5.2.3 Novel Bacterial Species

Only few novel species of Bacteroidetes, Alphaproteobacteria, and Actinobacteria originating from biocrusts have been described so far, including *Dyadobacter crusticola* and *Hymenobacter arizonensis* (Bacteroidetes), *Sphingomonas mucosissima*, *Sphingomonas dessicabilis*, and *Belnapia moabensis*

(Alphaproteobacteria), *Modestobacter versicolor*, and *Patulibacter americanus* (Actinobacteria). All these species originated from Colorado Plateau sites (Reddy and Garcia-Pichel 2005, 2007, 2009, 2013, 2015; Reddy et al. 2006, 2007). Despite their high diversity, representation of biocrust bacteria in culture collections and curated sequence databases is still very limited. Owing to this limitation, most non-cyanobacterial sequences from DNA-based bacterial surveys cannot be reliably named or taxonomically defined. Studies to date have used primarily sequence-based species designations (e.g., operational taxonomic units, OTUs) and/or have binned their sequence data into higher-order taxa such as families and phyla. Discovery and characterization of these dryland-adapted bacterial species is a challenging area for future study.

5.3 Non-lichenized Fungi

Biocrusts are niches for specialized free-living fungi, which endure the conditions of desiccation stress. These fungi can play a key role in mediating nutrient exchange between biocrusts and plant vegetation in arid landscapes, an idea which has become known as the fungal loop hypothesis (Green et al. 2008; Collins et al. 2008, see also Chap. 19 by Zhang et al.). However, until now, the study of free-living fungi in biocrusts has been mostly descriptive, with the goal to assess biodiversity and discover the parameters influencing microbial species composition (Bates and Garcia-Pichel 2009, 2010, 2012; Steven et al. 2015).

Fungal communities in biocrusts vary among regions and soil types. Diverse fungal communities have been reported from arid soil lands in the Western USA (Ranzoni 1968) including the Sonoran Desert (States 1978), the cool desert of Arizona, and sagebrush-grassland in South Central Wyoming (Christensen, unpubl.). Greater diversity was reported for fungi than for Cyanobacteria in Colorado Plateau biocrusts (Bates and Garcia-Pichel 2009). Fungal diversity varies with biocrust age and type, and higher fungal diversity occurs in later successional stages than in younger patches (Bates et al. 2012). In addition, qualitative and quantitative changes in fungal assemblages have been reported to be associated with disturbance sites (States and Christensen 2001). Fungal community composition in biocrusts studied so far was dominated by Ascomycota and was highly variable across small spatial distances. Many of them have dark pigmented cell walls and are also known as dark-septate fungi. Consistently, these comprise lineages of the class Dothideomycetes, and in particular representatives of the Pleosporales (e.g., Green et al. 2008; Bates et al. 2010; Abed et al. 2013). Although they are ubiquitous, most of these fungi seem to lack sexual fruiting bodies in biocrusts.

Dark-septate fungi have melanin-rich cell walls, a pigment usually resulting from polymerization of phenolic compounds (e.g., di-hydroxy-naphthalene in many Ascomycetes). This pigment is thought to confer tolerance against multiple abiotic stress factors, including desiccation and UV irradiation (Gostincar et al. 2010).

Pleosporalean dark-septate fungi are also known to be part of fungal communities associated with plant roots in arid grassland. Their functional analogy to mycorrhizal fungi has been suggested (Jumpponen 2001; Mandyam and Jumpponen 2005), which is interesting as no arbuscular mycorrhizal (AM) fungi have been detected in biocrusts so far (Bates et al. 2010, and references therein). In addition, some arid land soil fungi have been shown to have a vital role as denitrifiers in the N cycle (Marusenko et al. 2013). These functions are well in line with the fungal loop hypothesis.

The hyphomycete genus *Alternaria* seems to be a very common and widely distributed representative in biocrusts (Bates et al. 2010). Coprophilous, moss-, and lichen-associated fungi, including the genera *Acremonium* or *Phoma*, also appear to be main biocrust components (Bates et al. 2012; Steven et al. 2015). In contrast, only few taxa of yeasts are known from biocrusts. Mesophilic yeasts hardly develop in deserts, as they prefer nutrient-rich habitats with high water availability, and only extremotolerant black yeast species present exceptions. The black yeast *Exophiala crusticola* was originally described from the Colorado Plateau and is also present in the Great Basin Desert, USA. Like many other black yeasts, the species can produce both yeastlike cells as well as torulose hyphae (Bates et al. 2006). More yeasts might be present in biocrusts of cool habitats, but this remains to be studied.

5.4 Lichens as Microbial “Hubs”

Lichen symbioses are life-forms of fungi that form composite organisms comprising the dominant fungus and a photosynthetic partner (green algae in about 90 % of lichen species, Cyanobacteria in >9 % of lichen species, and <1 % with both as partners). The photobiont is usually sheltered in tight fungal structures. The composite structure, the lichen thallus, is often highly resistant to environmental fluctuations and extremes of cold and heat. Lichens can be prominent components of many biocrusts in habitats with periodic drought and where mechanical perturbation is negligible. In such habitats, lichens often develop species-rich communities which display various life strategies and growth forms. Usually, lichen-dominated biocrusts do not only comprise crustose lichens, i.e., those that tightly seal the soil surface with their entire lower thallus surface. Many other species also develop squamulose phenotypes or forms which elevate their structures above the ground. As lichens are covered in Chap. 7 by Rosentreter et al., we restrict to some general remarks concerning lichens as a niche for other microorganisms.

Owing to their persistence and their morphological diversity, lichen thalli provide a rich diversity of small-scaled niches for microorganisms, in particular fungi and bacteria. While fungi associated with lichens have been studied for a long time, the common presence of bacteria received more attention only recently (Grube et al. 2009 and references therein). Metagenomic and metaproteomic data suggest that these bacteria are involved in complex interactions in the lichen as a “holobiont” (Grube et al. 2015), which may change the view of lichens as a two-tier

relationship between a mycobiont and a photobiont. Since bacteria attach primarily to the surfaces of lichen thalli, their larger morphological structures play a crucial role, also at the interface with soil.

The attachment of lichens to the soil is accomplished by characteristic structures, which have been studied by light and electron microscopy (Asta et al. 2001). Attachment structures range from mycelial felts of narrowly spaced hyphae (rhizohyphae) to rootlike rhizines that are composed of conglutinated hyphae (Poelt and Grube 1993). However, it still needs to be studied to what extent these structures influence the microbial colonization of the soil beneath. The diversity of chemical patterns and phenotypic shapes of upper surfaces of lichen thalli likewise contributes to variations in the microecological environment for associated microbes. Thalli, which detach from the soil surface with peripheric lobes or even develop leaflike or shrubby thalli, create additional habitats between thalli or between thalli and the soil for bacterial and fungal communities. Also, bacteria and fungi can colonize niches between areoles and squamules of crustose lichens. Some observations of these microhabitats are presented in more detail below. While bacteria mostly colonize coherent surfaces of lichens and only few of them may penetrate more deeply (Erlacher et al. 2015), lichenicolous fungi commonly invade the interior of their hosts with their filamentous hyphae to benefit from their symbiotic structures.

5.4.1 Life Strategies and Diversity of Lichenicolous Fungi

Lichenicolous fungi comprise all species living in or on lichens beside the thallus-forming fungus. This biological group has been studied extensively throughout the history of lichens. Approximately 1800 species of lichenicolous fungi have been described, but new species are still being discovered (e.g., Lawrey and Diederich 2011). A detailed report on the lichenicolous fungal diversity on soil lichens is beyond the scope here, but we would like to draw attention to some general features. Most lichenicolous fungi are highly specific regarding the hosts (i.e., the lichenized fungal species), which they colonize by means of localized mycelia that eventually develop sexual structures (these are traditionally important diagnostic characters, Fig. 5.3). Some species, however, are able to develop their own symbiotic thalli on their hosts and are then known as lichenicolous lichens. These are also known from soil-inhabiting lichens, where some of these species exploit their lichen host only in early phases of their life cycle, e.g., *Arthrorhapis citrinella* on *Baeomyces rufus* and *Diploschistes muscorum* on *Cladonia* species. In later stages, the thalli of these juvenile parasites become independent from their hosts. Interestingly, algal switching was observed at the onset of parasitic thallus reorganization by *Diploschistes muscorum* (Friedl 1987). Initially, this species lives with the algae of the infected hosts and may later continue thallus growth with another species of algae. This does not seem to be a completely fixed strategy, as we recently observed mature *Diploschistes muscorum* specimens maintaining the photobionts of the host

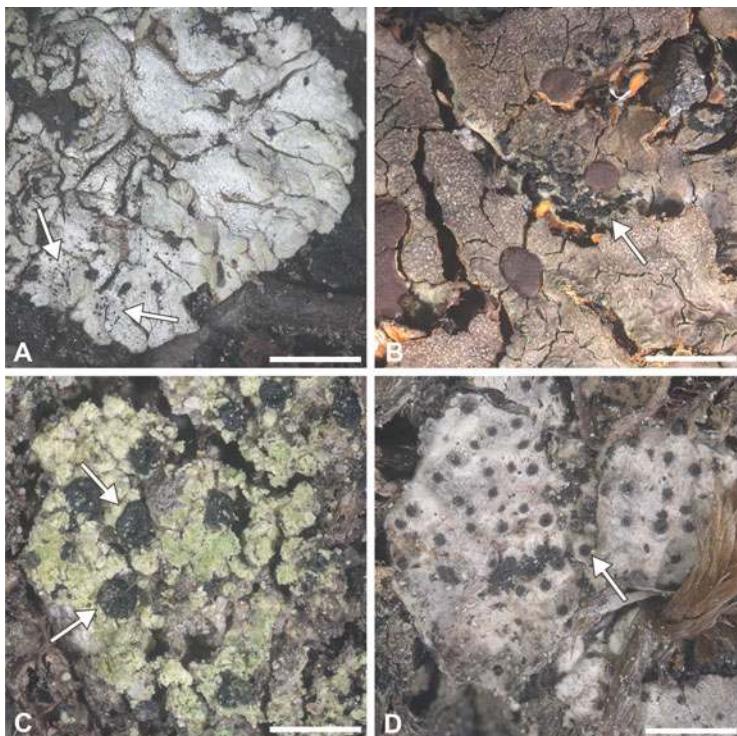


Fig. 5.3 Examples of lichens infected by different lichenicolous fungi: (a) placodioid lichen crust infected by *Dacampia hookeri*, which itself is infected by the lichenicolous fungus *Stigmidium schaeeri* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus); (b) foliose *Solorina crocea* infected by the lichenicolous fungus *Rhagadostoma lichenicola* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus); (c) sorediate crustose lichen infected by *Arthroraphis citronella* (arrows indicate the fruiting bodies, apothecia, of the lichenicolous fungus); (d) *Solorina octospora* infected by the lichenicolous fungus *Dacampia engeliana* (arrows indicate the fruiting bodies, perithecia, of the lichenicolous fungus). Scale bars: (a, b, d) 2 mm; (c) 1 mm

lichen, while others hosted multiple algal types (Wedin et al. 2015). Maintenance of the host's algae has been observed also in other lichenicolous lichens (de los Rios et al. 2002).

Even though lichenicolous species without a distinct thallus organization are usually called non-lichenized, the biology of some species is not entirely clear. The fungus *Tetramelas pulverulentus* (on moss inhabitant *Physconia muscigena*) slightly modifies the host morphology with externally recognizable infection symptoms. This species develops peculiar endokapylic (i.e., mycelia covered by strata of the host) lichenized thalli. Many other species spread infectious hyphae within their hosts and either do not produce any symptoms or become destructive for the host structures. Whether the hyphae of the lichenicolous species infect the algae and/or the fungi or remain without affinity for any of the host's biota is still unknown in

many cases. Infectious hyphal structures of mycobiont-parasitic species were described by de los Rios and Grube (2000). These structures comprise simple or complex haustoria with fingerlike projections into the host hyphae (observed in *Pyrenidium actinellum* infecting the soil-inhabiting *Peltigera venosa*). Even the growth of hyphae inside of host hyphae has been observed, as for *Dacampia engeliana* infecting the soil-inhabiting *Solorina* sp. Simple haustoria are also present, for example, in species that exploit the algae of their hosts such as known from the genus *Zwackhiomyces* (Grube and Hafellner 1990). Other algal exploiters establish contacts with the photobionts of their host lichens using appressoria (e.g., lichenicolous species in the genus *Arthonia*).

Even more complex cases of interactions, including the phenomenon of hyperparasitism are observed in various manifestations in soil crust lichens. Juvenile lichen-parasitic lichens, such as *Arthrorhaphis citrinella* (lichenicolous on *Baeomyces*, *Cladonia*-squamules, or decaying lichens), are occasionally infected by hyperparasitic non-lichenized fungi (*Stigmidium arthrorhaphidis*, *Cercidospora trypetheliza*, *Cercidospora soror*). Recently, hyperparasitism was also described among lichens: the lichenicolous lichen *Rhizocarpon diploschistidina* parasitizes the lichen *Diploschistes muscorum*, which itself grows as a juvenile parasite on *Cladonia* species (Lumbsch et al. 2011). These few examples demonstrate that the diversity of fungal interactions in soil crusts is a fascinating topic of biology. These specific interactions remain unsolved in pure sequencing studies, as their discovery still requires meticulous microscopic investigation.

5.4.2 *Bacterial Habitats in Soil Lichens*

Certain species of lichens regularly form interactions with Cyanobacteria, usually *Stigonema* spp., which are commonly present in biocrusts and perhaps more frequently in older successional stages of cyanobacterial crusts. This phenomenon is known since long as cyanotrophy (Poelt and Mayrhofer 1988), which indicates that certain cyanobacterial consortia facilitate the development of lichens. With the development of lichens, multiple new microhabitats now develop to host other bacteria. Using confocal laser scanning microscopy (CLSM), we demonstrated that bacteria associated with biocrust lichens are tightly connected with fungal structures and essentially represent fungal-bacterial interactions (Fig. 5.4). Maier et al. (2014) demonstrated that bacteria colonize the upper cortex in *Psora decipiens* and *Toninia sedifolia* (Fig. 5.4d). Using 16S rRNA gene-targeted fluorescence in situ hybridization (FISH) experiments, bacteria could be seen attached to the hyphal net at the thallus-soil interface of *Psora decipiens*. This pattern agrees with results of Muggia et al. (2013) for other biocrust lichens. In that study, bacterial cells were intermixed with photobiont cells in the lower parts of the lichen thalli and on the surface of the squamules of *Baeomyces placophyllus* and *Psora decipiens* (Muggia et al. 2013). In the inconspicuous thallus structures of *Arthrorhaphis citrinella*, *Baeomyces rufus*, *Icmadophila ericetorum*, and

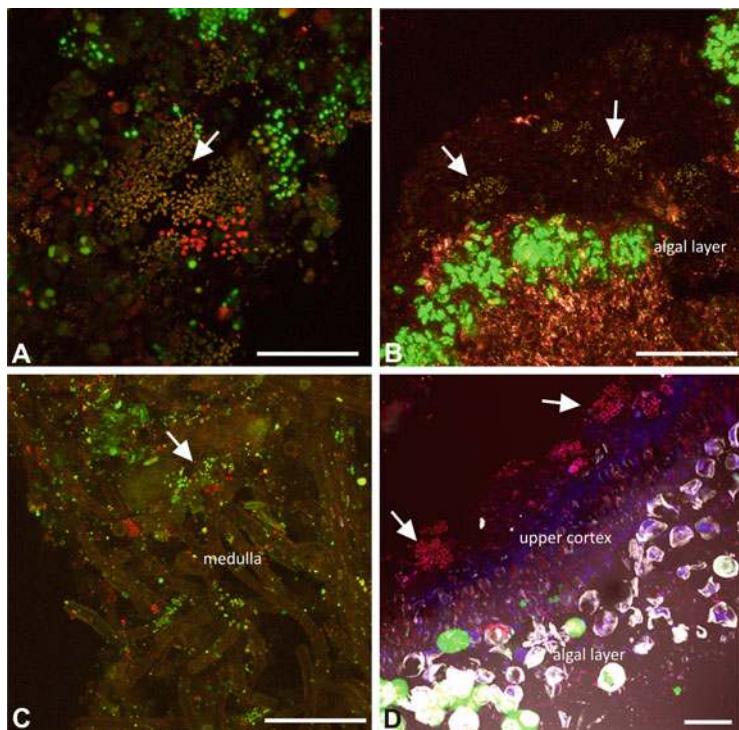


Fig. 5.4 Fluorescence in situ hybridization combined with confocal laser scanning microscopy to visualize bacteria in lichen biocrusts. **(a)** *Baeomyces rufus*; granulose thallus, which does not display a differentiation in algal layer and medulla, mixed with bacterial colonies. **(b)** *Icmadophila ericetorum*; leprose lichen, no internal organization with green algal layer, bacterial colonies on the upper surfaces shown in the left part. **(c)** *Psora decipiens*, part of medulla, with bacterial colonization. **(d)** Thallus cross section of *Toninia sedifolia*, richly developed bacterial colonies on the upper cortex. Merged 4-color images; the 16S rRNA targeted 5' end-labeled FItc oligonucleotide probe ALF968 was applied to visualize Alphaproteobacteria and Cy3-(indocarbocyanine)-labeled EU388mix to visualize Eubacteria. Calcofluor White was used to stain fungal structures. Colors: Eubacteria red, Alphaproteobacteria yellow in **(a–c)**, pink in **(d)**; autofluorescence of algae green; fungal structures gray. Arrows indicate bacterial cells. Scale bar: 30 µm. The settings for excitation were 405, 488, 532, and 635 nm. The ranges of wavelength set to detect the emission signal of the fluorophores were at 420–480 nm (CFW), 500–550 nm (FItc), 550–600 nm (Cy3), and 650–700 nm (Cy5)

Trapeliopsis granulosa, we also observed associations of bacteria with hyphae and algae, as well as bacteria on the outer surface of the mycobiont-photobiont aggregates (Fig. 5.4a, b). Due to the small-scale variation in ecological parameters in the stratified thallus and soil beneath, the composition of bacteria in lichens may likewise vary at very small scales. The host-specific enrichment of bacteria in lichens and in the subjacent layers of the substrate (the hypothallosphere) has also been demonstrated earlier for rock-inhabiting biocrust-forming lichens (Bjelland

et al. 2010). However, in order to interpret the specificity of bacteria in soil underneath lichens correctly, also the influence of possibly co-occurring non-lichenized fungi needs to be considered, since these free-living fungi could also influence bacterial diversity. Using microscopic observations, we commonly find hyphae of different types beneath soil biocrust lichens (Grube, unpublished data). Interestingly, we also observed that dark pigmented hyphae were poorly colonized by bacteria, whereas hyaline hyphae in biocrusts were frequently associated with small bacterial colonies.

One important factor for the small-scale spatial patterning of bacteria could be the accessibility of air and water within lichen thallus structures. Souza-Egipsy et al. (2002) studied the relative distribution of air- and water-filled spaces in the thallus and lichen-substrate interface using scanning electron microscopy and found correlations with the morphological features of the stratified thalli. According to their study, a water film covered the surface of *Diploschistes diacapsis* and *Squamaria lentigera* after hydration. Microscopic fissures between the areoles in the thalli of *Diploschistes diacapsis* facilitated seeping of water into the thallus without flooding the algal layer. The water then appeared to be retained in the lower part of the medulla. These differences certainly have an impact on the bacterial colonization, which needs to be further explored. In this context it is interesting to note that there are also differences of water conductance within lichen species depending on the geographic origin. According to own observations, the uptake of water is regularly faster in lichens of the Mediterranean provenience compared to those from alpine habitats (Grube, unpublished data).

FISH is an excellent tool to visualize the localization of specific bacteria in their histological and environmental context (Amann and Fuchs 2008). For the first time, Muggia et al. (2013) combined FISH with CLSM to visualize the lichen-soil interface in alpine lichen biocrusts. Their study also highlighted some technical challenges. While some lichen species have compact superficial thalli, the thallus of others is closely connected with the soil (Fig. 5.4a–c). Dry samples are very brittle and thus easily disintegrate into the different compounds during the preparatory work. Muggia et al. (2013) therefore suggested using blocks of thalli with attached soil (up to a few millimeters) for fixation and embedding prior to cutting 30 µm thick sections that are subsequently transferred to poly-L-Lysine-precoated microscope slides for further processing. Their study succeeded to visualize the predominance of Alphaproteobacteria and Acidobacteria in the studied soil crust lichens *Arthrorrhaphis citrinella*, *Baeomyces placophyllus*, *Baeomyces rufus*, *Icmadophila ericetorum*, *Psora decipiens*, and *Trapeliopsis granulosa*. Acidobacteria appeared to be particularly common in the lower part of and beneath the lichen thallus. This agrees with Grube et al. (2012), who studied the diversity of bacteria associated with the arctic-alpine soil lichen *Solorina crocea* using 16S rRNA pyrosequencing and found high abundances of Acidobacteria, Planctomycetes, and Proteobacteria. The presence of Acidobacteria in these habitats possibly correlates with the fluctuating water conditions and the acidic substrate. In addition to these initial studies focusing on alpine biocrust habitats, Maier et al. (2014) studied the bacterial communities of lichens from the Tabernas Badlands (Almería, Spain) in more

detail. Their results revealed the dominance of Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, and Cyanobacteria.

5.4.3 The Impact of Lichenicolous Fungi on the Lichen-Associated Bacterial Community

As the symbiotic integrity of lichens can be affected by the fungal parasites of lichens, a shift in the composition of the bacterial associates of these lichens might be the consequence. This hypothesis prompted Grube et al. (2012) to study the soil lichen *Solorina crocea*, which is commonly infected by a lichenicolous fungus known as *Rhagadostoma lichenicola* (Sordariomycetes). Forming black-colored perithecia on the living lichen host, *Rhagadostoma lichenicola* is a specialized biotrophic parasite of *Solorina crocea*. The grouped blackish ascomata emerge from the upper surface of the host thallus (Fig. 5.3b). Microscopy reveals a richly branched, dark mycelium beneath the parasite's fruiting bodies in the host plectenchyma. The mycelium extends locally into the internal layers of the nearby regions of the lichen thallus. No specific infection structures with algal or fungal host cells are observed. Apparently, these infections do not immediately impair the host's fruiting body formation nor do they kill the host. However, Grube et al. (2012) found evidence for a shift in the bacterial communities when data were analyzed at the strain level. Strain-specific abundance shifts occurred among Acidobacteria. The consequences for the bacterial community are clearly more pronounced in the course of the infection by lichenicolous lichens, which completely restructure the thallus of the host lichen. By analyses of different infection stages of *Diploschistes muscorum* on the host *Cladonia symphycarpa*, Wedin et al. (2015) found a decrease in relative abundance of Alphaproteobacteria. Also, Armatimonadia, Spartobacteria, and Acidobacteria were more abundant in *Cladonia*, but Betaproteobacteria increased gradually in relative abundance during the transition to mature *Diploschistes muscorum*. These results from few selected examples offer only a glimpse of the enormous complexity of fungal-bacterial interactions and the parameters regulating their diversity in biocrusts.

5.5 Conclusions

High diversity has sometimes been related to stability in ecosystems, and as we have seen here, biocrusts are definitely hotspots of fungal and bacterial diversity. However, as Ives and Carpenter (2007) point out, understanding the diversity-stability relationship needs an evaluation of the environmental drivers affecting both. For developing the complexity of fungal-bacterial life, the biocrust system depends largely on the stability of soil. Once the substrate is disturbed

mechanically, the biocrust community will progressively collapse with increasing physical stress (e.g., induced by wind and water). Thus, mechanical disturbance must be avoided not only to secure known ecosystem services provided by biocrusts (prevention of erosion and water runoff, carbon and nitrogen fixation, etc.) but also to save them as a precious microbial resource of yet unexplored biotechnological interest. Their further exploration requires integrating approaches. Continued and expanded culture-independent approaches still need to be coupled with physiological assessments of cultured isolates to improve our understanding of bacterial and fungal functions (da Rocha et al. 2015).

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Chapter 6

Bryophytes Within Biological Soil Crusts

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6.1 Introduction

Bryophytes (mosses, liverworts, and hornworts) can play an integral role in biocrust development, ecology, and diversity, yet the role of bryophytes in crusts has received comparatively little attention compared to the roles played by other organisms. In some ecosystems, bryophytes may be a conspicuous component of biocrusts, particularly in the later stages of crust development (Lange et al. 1997), where a diversity of morphological and physiological traits gives them a unique role in biocrust ecology.

Biocrust bryophytes contribute to soil surface stabilization through water entrainment and facilitation of water infiltration (Zhang et al. 2009), whereby reducing surface runoff (Zhao et al. 2014). They also promote soil formation through acceleration of chemical and physical weathering of soil and entrapment of mobile surface particulates (Danin and Gaynor 1991). Bryophytes also influence carbon and nutrient cycling through contributions of organic matter directly to the soil

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(Longton 1992; Melick and Seppelt 1992; Melick et al. 1994) and through indirect effects on soil nitrogen availability (Reed et al. 2012). Many crust bryophytes also provide habitats for invertebrates, algae, cyanobacteria, fungi and lichens (Davidson et al. 1990) and are useful in monitoring landscape health.

6.2 Bryophyte Diversity in Biocrusts

Global bryophyte diversity in biocrusts comprises at least 320 species, the majority of which is mosses (>250 sp.), followed by liverworts (>66 sp.). Biocrust bryophyte diversity has been examined most extensively in dryland ecosystems in North America and Australia, but records also exist from Europe, South America, Asia, and Antarctica.

6.2.1 Regional Diversity

Globally, the greatest biocrust bryophyte species richness has been recorded in the drylands of the Pacific region (Australia and New Zealand) and in Europe. In North and Central America, biocrust bryophytes are found throughout the Western USA and Northern Mexico in hot desert (Mojave, Sonoran, Chihuahuan) as well as cool desert ecosystems (Colorado Plateau, Great Basin; Fig. 6.1). Early accounts of hot desert bryoflora sampled at sites in the Mojave, Sonoran and Chihuahuan Deserts described species from the families Pottiaceae, Bryaceae, and Grimmiaceae and estimated total species numbers to be <25 (Nash et al. 1977). More recent estimates of the number of bryophyte taxa in hot and cool deserts in these regions, however, place bryophyte diversity above 300 species (two hornworts, 26 liverworts, 262 mosses), the majority being members of biocrust communities (Stark and Whittemore 2000; Brinda et al. 2007).

In Australia, the number of biocrust bryophyte taxa is estimated to be at least 130, including >30 liverworts and >100 mosses (Fig. 6.1). In a study of the distribution and floristics of bryophytes over a 500 000 km² area of Australian dryland crusts, Eldridge and Tozer (1996) reported 56 bryophyte taxa (41 mosses, 15 liverworts), dominated by the moss family Pottiaceae and the liverwort genus *Riccia* (Fig. 6.2a). While many bryophytes were ubiquitous in the study area, some were restricted to certain landform types due to the amount and seasonality of rainfall or calcium levels in the soil (Downing and Selkirk 1993).

Biocrust bryophytes are also common in drylands of Europe (90 species) and Asia (28 species), Africa (22 species), and South America (24 species), as well as ice-free soils on Antarctica (14 species, Fig. 6.1). In crusted soils of the Negev Desert, common genera include *Tortula*, *Bryum*, and *Brachymenium* (Lange et al. 1992; Kidron et al. 2002). In the Gurbantunggut Desert in Northwestern China, *Tortula*, *Bryum*, and *Crossidium* are the most common genera found in

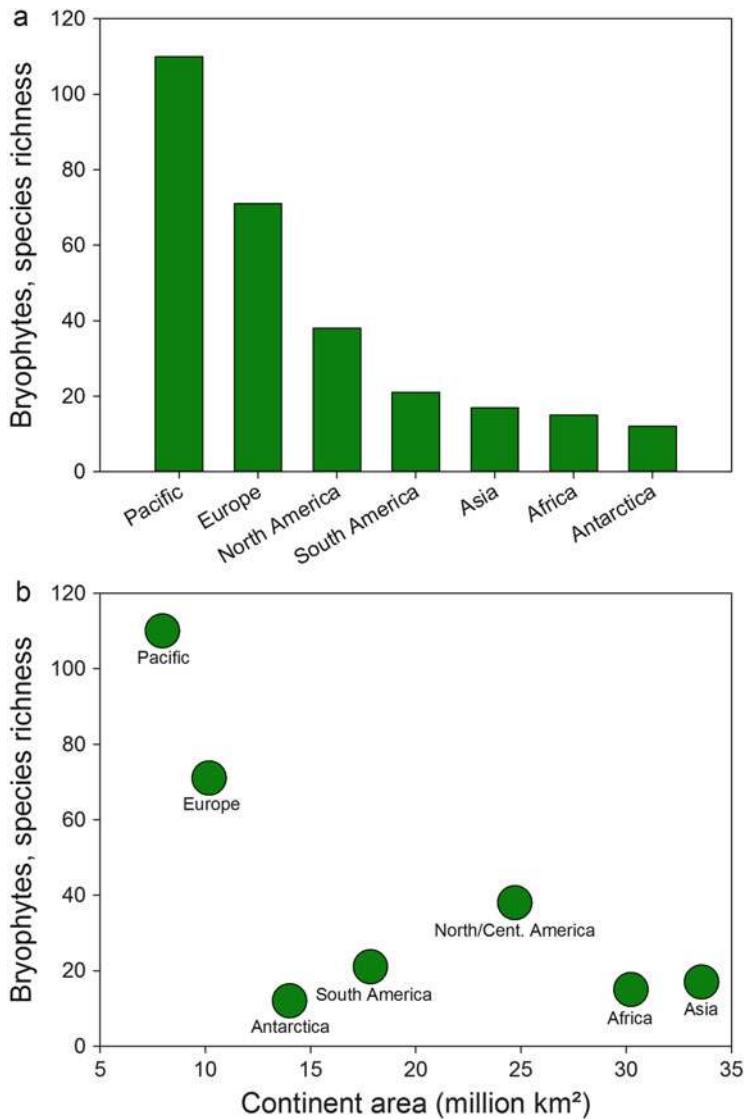


Fig. 6.1 Diversity of bryophytes on a continental scale (Graphic Burkhard Büdel)

biocrusts (Zhang et al. 2007; Wu et al. 2009), while on the Loess Plateau, the most dominant genus is *Didymodon* (Zhao et al. 2014). There are over 400 recorded bryophyte species on the Antarctic continent (Green and Broady 2003; Peat et al. 2007), yet only 15 have been reported as forming a component of biocrusts.

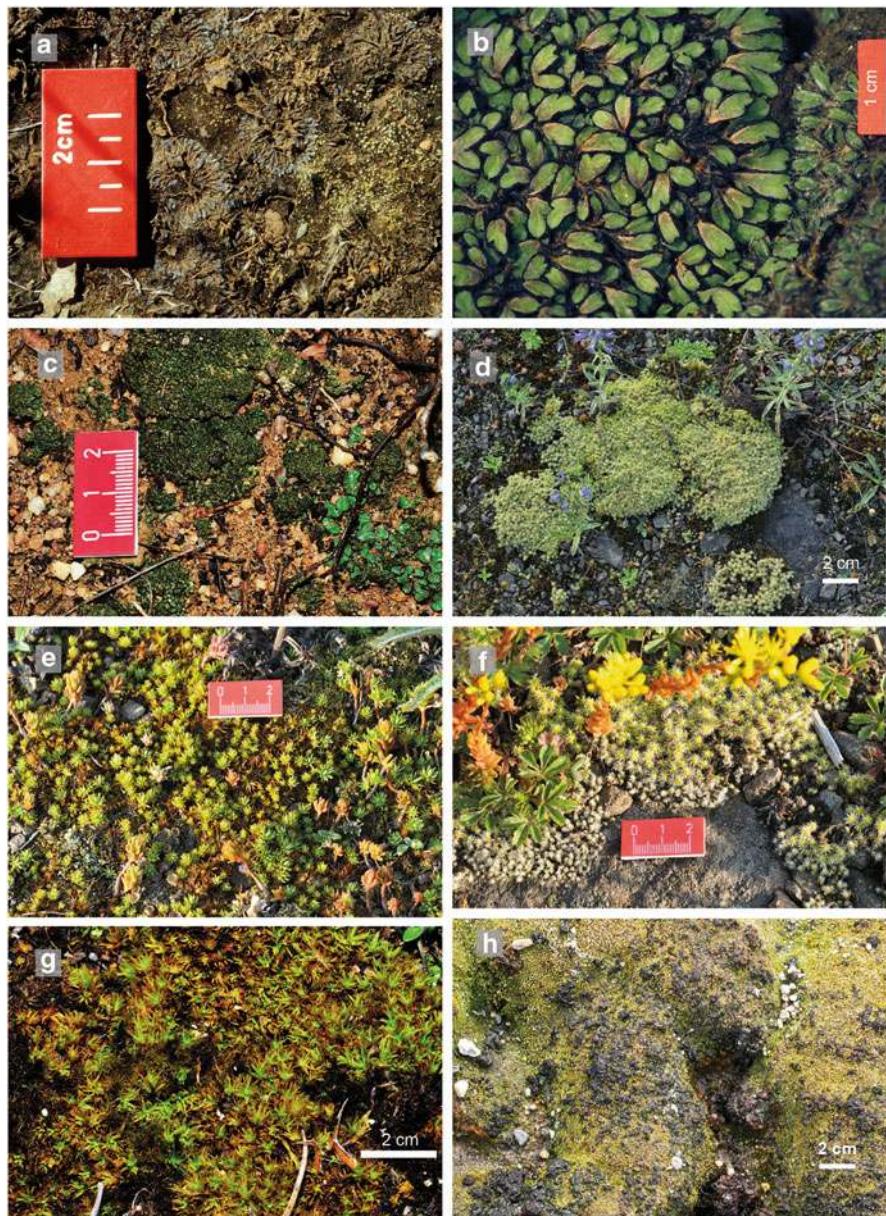


Fig. 6.2 (a) *Riccia* sp., a hairy species forming gray, circular thalli; located in the left to central part of the image. In the right hand part an unidentified moss. Biocrust after several months of drought; Queensland, Australia (Photo Burkhard Büdel). (b) *Riccia* spp.; species without hairs (left) and with hairs (right) next to each other; biocrust from Rehoboth, Namibia (Photo Burkhard Büdel). (c) *Riccia* sp. and a leafy liverwort forming part of a biocrust, Caatinga biome, Brasil (Photo Burkhard Büdel). (d) *Campylopus introflexus*, an invasive moss. (e) *Polytrichum piliferum*. (f) *Racomitrium canescens*. (g) *Trichostomum crispulum*, all in the biocrust of an abandoned stone quarry, Germany (Photo Burkhard Büdel). (h) *Bryum argenteum* dominated biocrusts, intermingled with blackish-brown colonies of the cyanobacterium *Nostoc commune*, melt water flush at Canada Glacier, Taylor Valley, Antarctica (Photo Burkhard Büdel)

6.2.2 Global Moss Diversity

In both North America and Australia, the moss family Pottiaceae dominates the bryoflora of soil crusts, with Bryaceae usually running a close second (Rosentreter et al. 2007). In Australia, annual and ephemeral species of Funariaceae (*Entosthodon* spp.) may also occur after rainfall events and together with *Fissidens megalotis* often play an important role as first colonizers of disturbed soils prior to the re-establishment of more characteristic soil crust assemblages (Downing and Selkirk 1993; Eldridge and Tozer 1997; Stoneburner et al. 1993). In biocrusts of southern Africa, *Ceratodon purpureus* is a dominant species (Weber et al. 2012), but also species of the genera *Bryum*, *Crossidium*, *Tortula*, and *Campylopus* occur (Büdel et al. 2009).

In Asia, 23 species of biocrust mosses have been reported, where *Barbula*, *Bryum* and *Tortula* are the most common genera. In the Gurbantunggut Desert of Northwestern China, moss crusts occur on calcareous semi-fixed dunes, usually in the swales or on windward faces of dunes. Dominating species in this area are *Syntrichia caninervis* and *Bryum argenteum*, and other commonly observed taxa include *Tortula muralis*, *Crossidium chloronotos* and *Bryum capillare* (Zhang et al. 2007). Of the 15 species of confirmed biocrust bryophytes in Antarctica, all are mosses, the most common genera being *Bryum* (four species) and *Grimmia* (three species).

6.2.3 Global Liverwort Diversity

Thallose liverworts, particularly *Riccia* (Fig. 6.2b and 6.2c) and *Asterella*, are abundant in biocrusts on calcareous substrates in the Australian arid and semiarid zones (Downing and Selkirk 1993; Eldridge and Tozer 1997), in some cases, producing crusts composed almost exclusively of liverwort thalli. *Fossombronia* is also an important component of biocrusts, but in southern Australia, it is restricted to higher rainfall ecosystems of temperate to semiarid forests and rangelands (Milner et al. 2011; Eldridge and Tozer 1997). *Riccia* is well known from dryland calcareous substrates but can also be a dominant component of crusts from non-calcareous substrates, e.g. shallow, siliceous soils over granitic inselbergs of Namibia (Bornefeld and Volk 2002) and sandy soils in Namibia and South Africa (Büdel et al. 2009). In North American biocrusts, common liverwort genera include *Cephaloziella*, *Athalamia*, and *Fossombronia* (Rosentreter et al. 2007). Few liverwort taxa have been documented in Asian biocrusts, but where they occur, *Riccia* is most commonly observed. Antarctica, while exhibiting a relatively species-rich liverwort flora of at least 50 species, currently does not exhibit any records of liverworts in crusted soils.

6.3 Bryophyte Establishment in Biocrusts

6.3.1 Establishment in Dryland Biocrusts

In contrast to temperate areas, where bryophytes may establish early in vegetation successional sequences following disturbance events (Fig. 6.2d-g), in dryland ecosystems, bryophyte biocrusts are generally accepted to be the third successional stage in crust development, after cyanobacterial- and lichen- dominated crusts. Bryophyte crusts are best developed on calcareous fine-textured silt and clay soils, where initial colonization of fungi, cyanobacteria, and microalgae facilitates bryophyte establishment by providing soil stability.

In recent years, research concentrating on the mechanisms that may assist in the restoration and recovery of biological soil crusts has helped elucidate colonization patterns during crust development. Photobionts (cyanobacteria, microalgae) were initially thought to be the first soil colonizers because of the lack of carbon for heterotrophic microbes. However, it is now widely accepted that oligotrophic bacteria and fungi precede colonization by cyanobacteria (Bamforth 2008; Pan et al. 2010; Wu et al. 2010). Filamentous cyanobacteria of cyanobacterial crusts, which follow soil stabilization by oligotrophic bacteria and fungi, exude polysaccharide sheaths which bind soil particles, enhance moisture uptake and increase soil fertility by N-fixation (Bailey et al. 1973; Belnap and Gardner 1993; Campbell et al. 1989; Rosentreter et al. 2007; Zhang et al. 2011a, b; see Chaps. 4 by Büdel et al., 17 by Chamizo et al., and 14 by Barger et al.). Over time, these collective processes act to facilitate bryophyte colonization and later dominance in biocrusts.

Bryophyte establishment on sand dune crusts is less common, as the substrate chemistry and disturbance regime typically favor green algal communities in the upper soil layers (Downing and Selkirk 1993; Rosentreter et al. 2007; Zhang et al. 2011a, b). However, bryophytes are common and abundant in biocrusts on dunes along the southern coast of Australia, where there is an abundance of CaCO₃ (Moore and Scott 1979). Bryophyte crusts are much less common on siliceous sands of the eastern coast of Australia, potentially because of the relative absence of a calcareous substrate.

6.3.2 Establishment in Polar, Alpine, and Antarctic Biocrusts

In polar and alpine regions, crusts may develop in rock interspaces, on exposed soil at the margins of ice fields, or following glacial recession (Fig. 6.2h). Compared to crusts in dryland ecosystems, there have been few studies of alpine or polar biocrusts (but see: Pérez 1997; Gold et al. 2001; Huber et al. 2007). However, in terms of patterns of bryophyte establishment in crusts, many commonalities exist.

In contrast to drylands, polar and alpine regions present particularly unstable surfaces for the formation of biocrusts. Nutrient levels may be low, free water may be

unavailable for plant growth during much of the year, and cryoturbation causes significant disruption of soil integrity. Pioneer colonists such as bacteria, cyanobacteria, algae, and fungi are crucial in stabilizing otherwise mobile surfaces (Wynn-Williams 1986, 1993; Elster 2002). These organisms initiate the basis of an organic- and nutrient-enriched medium on which more complex organisms or secondary colonizers (bryophytes, lichens and small herbs) may establish (Tearle 1986; Greenfield 1989). In alpine regions, species-rich assemblages of cyanobacteria and eukaryotic algae along with Aeolian deposits can contribute to initial pedogenesis in primary stages of crust formation (Peer et al. 2009). Later stages of development in many alpine regions are dominated by lichens, but abundant subsurface bryophyte protonema and rhizoids reveal that bryophytes, while not usually competitively dominant, can contribute to late stage crust diversity (Peer et al. 2010).

In continental Antarctica, where the extent of ice-free soil is a mere 0.8 %, development of biocrusts appears to be limited in extent and composed almost entirely of primary colonizers. There are extensive moss-dominated sites, e.g., Windmill Islands (66°S, 110°E), Botany Bay (77°S, 162°E), and Canada Glacier (78°S, 163°E; Fig. 6.2h), where there is an abundance of nutrients derived largely from former (Windmill Islands) or extant (Botany Bay) penguin or other seabird colonies and ample moisture during the late spring, summer and early autumn period. These areas represent biodiversity hotspots rather than localities with typical biocrust development. More typical biocrust development is rare and dominated by microbial primary colonizers, while secondary colonizers appear to be almost entirely lichens (Seppelt, personal observations).

In the Maritime Antarctic, at Jane Col on Signy Island, unvegetated soil contains a diverse and often abundant reservoir of bryophyte propagules. Similar to the continental Antarctic, this reveals the potential for bryophyte establishment under favorable conditions. Most of these bryophyte propagules originate locally, with a small proportion derived from external or remote sources (Lewis Smith 1993). Most propagules, however, are vegetative diaspores (detached leaves, deciduous stem apices, specialized gemmae, deciduous leaf apices, bulbils), and limited rates of sexual reproduction likely limit the abundance and establishment of crust bryophytes in these regions. In particular, species with spores that germinate under experimental conditions of favorable moisture have only sporadic occurrence in the field. Less than 20 % of the Signy Island bryoflora species regularly produce spores, and the dominant fell-field species produce recalcitrant spores with little germination (Webb 1973).

6.4 The Role of Substrate in Bryophyte Abundance and Diversity

Biocrusts can be found on a range of substrates, and substrate chemistry plays a key role in the abundance and diversity of crust bryophytes that occur. Much research has focused on comparisons between species assemblages growing on substrates

either high or low in calcium carbonate, as well as those growing on substrates characterized by high levels of gypsum and dolomite.

6.4.1 Calcareous Substrates

Distinctive calcium carbonate (CaCO_3) bryophyte floras have been described for many parts of the world, clearly demonstrating the dichotomy between bryophytes with an affinity for CaCO_3 (calciphiles or calcicoles) and those that grow only in the absence of CaCO_3 (calcifuges). This dichotomy is also apparent in bryophyte communities of biocrusts, where patterns of diversity and abundance are closely related to differences in substrate chemistry.

Bryophytes respond markedly to soil CaCO_3 , pH, and electrical conductivity (Anderson et al. 1982; Eldridge and Tozer 1997; Ponzetti and McCune 2001). CaCO_3 in particular contributes to abundance and diversity of bryophytes: biocrusts on calcareous substrates generally support a greater ground cover and species richness of bryophytes than those of non-calcareous substrates (Downing and Selkirk 1993; McCune and Rosentreter 2007). Soil CaCO_3 levels also influence the ratio of acrocarpous to pleurocarpous mosses, the ratio of thallose to leafy liverworts and the presence of certain bryophyte families, genera and species. In particular, acrocarpous mosses and thallose liverworts have been shown to increase in abundance compared to pleurocarps and leafy liverworts with increasing CaCO_3 (Downing 1992).

In spite of the differences between bryophyte assemblages on calcareous and non-calcareous soils, these patterns are not universal and may be context dependent. For example, Downing and Selkirk (1993) found that there was no clear dichotomy between calciphiles and calcifuges in Australian biocrusts. Rather, the bryoflora of calcareous substrates was composed of a few exclusively calciphilous species together with many opportunistic, non-substrate-specific species.

CaCO_3 can also interact with other factors such as soil pH to drive patterns of crust development and diversity. In shrub steppe in Oregon, USA, Ponzetti and McCune (2001) recorded considerable differences in dominant bryophyte species and total crust cover between sites with high levels of CaCO_3 and high pH, and those with lower levels and low pH, concluding that crusts were particularly sensitive to subtle changes in soil chemistry. In semiarid south-eastern Australia, Downing and Selkirk (1993) recorded the highest level of crust development in sites with the highest levels of CaCO_3 and highest pH. Similarly, in Idaho, North America, Anderson et al. (1982) recorded an increase in cover with increase in pH. However, the opposite has also been the case. Eldridge and Tozer (1997) recorded lower crust cover from sites with high pH and high CaCO_3 than sites with low pH and high CaCO_3 .

6.4.2 Dolomite and Gypsum Substrates

Dolomite [$\text{CaMg}(\text{CO}_3)_2$] and gypsum [$\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$] substrates often exhibit biocrust bryophyte assemblages that are distinct from CaCO_3 -dominated substrates. Biocrusts on gypsum substrates are typically rich in species number and have a high percentage of ground cover, and individual species can be useful indicators of soil chemistry (Belnap et al. 2001). In Australia, *Riccia albida* has been described by Scott (1982) as a species which grows in abundance on gypsum-rich soils of north-western Victoria, where it forms dense crusts of white, gypsum-encrusted thalli. In Spain, Guerra et al. (1995) identified 21 species of bryophytes from gypsiferous sites, which they suggest may provide refugia for many rare species. Here, Pottiaceae was the dominant moss family, accounting for 18 species, whereas only one thallose liverwort, *Riccia crustata*, was recorded. A study by Peer et al. (2009) of biocrusts in the mountains of Hohe Tauern (Austria) included one site with greywacke, dolomite and marble substrates, another with non-calcareous substrates including phyllites, mica schists, and quartzite. Ten mosses and four liverworts were recorded, all species with a wide altitudinal range and substrate tolerance, but in many of these sites, bryophytes were outcompeted by a dominant lichen flora.

6.4.3 Interactions Between Substrate Chemistry and Aridity

In general, the number of bryophyte species recorded from biocrusts on calcareous substrates decreases with increasing aridity. Such patterns can also be accompanied by a significant change in bryophyte assemblages, including ratios of acrocarps to pleurocarps and thallose to leafy liverworts. Eldridge and Tozer (1997) recorded 20 bryophytes (15 mosses in 12 genera, 5 liverworts in 2 genera) from semiarid areas of eastern Australia along a rainfall gradient decreasing from 500 mm per annum in the East to 220 mm per annum in the West. Species richness was directly correlated with annual rainfall and declined from East to West. These authors also determined that there was a significant negative correlation between annual rainfall and pH, indicating that with increased aridity, there was a corresponding increase in alkalinity and CaCO_3 content, both of which likely contribute to reductions in bryophyte diversity.

6.5 Adaptive Strategies of Biocrust Bryophytes

Bryophytes within biological soil crusts exhibit a diverse range of adaptations that permit them to tolerate and survive in unfavorable and often extreme environments. Many of these traits are related to performance, growth, and reproduction in

habitats where they must cope with desiccation, temperature extremes, and high radiation on short- or long-term timescales, all of which represent major obstacles to survival. Crust bryophyte phenotypes thus represent trade-offs among these competing processes. Plant habit, specialized leaves and leaf surfaces, hygroscopic leaf movements, physiological and biochemical adaptations, niche specificity, longevity and, for some species, short life spans are important to survival and colonization.

Crust bryophytes typically inhabit the soil-atmosphere interface region within the boundary layer of the ground surface, a microhabitat that functions to minimize water loss to the air through convective processes. Morphologically, they are plants of small stature (shoots typically < 15 mm height) that grow in a clonal habit. This dense growth form of tightly packed stems increases boundary layer resistance, maximizes transfer and absorption of water in the capillary spaces among and within shoots and minimizes water loss to the surrounding environment (Proctor 1982; Sveinbjornsson and Oechel 1992). In soil layers immediately below the moss, subsurface features (rhizomatous shoots, protonemal filaments, rhizoidal filaments, tubers) aid in asexual reproduction and colonization.

At the shoot level, most arid and semiarid biocrust species are small, with small leaves. Leaves may be tightly overlapping (e.g. *Bryum argenteum*) or exhibiting distinctive hygroscopic movements that maximize water absorption (e.g. *Syntrichia* spp., *Tortula* spp.). Specialized surface features such as hairpoints, incurved margins, surface papillae, glossy reflective costae, and surface filaments serve to trap and retain moisture as well as retard water loss (Wu et al. 2014; Zhang et al. 2009; Zhang et al. 2011a, b). Some thalloid liverworts, such as *Asterella*, *Plagiochasma*, and *Riccia*, enroll on drying, exposing the often darkly pigmented and protective scales on the under surface of the thalli (Scott 1982). High amounts of lipids stored in leaves and stems, together with anthocyanin and carotenoid pigments, may aid thermoregulation, freeze tolerance, and long-term survival.

In arid regions, persistent desiccation, limited temporal water availability, and skewed sex ratios in natural populations restrict reproductive frequency of crust bryophytes (Stark and Castetter 1987; Benassi et al. 2011; Stark et al. 1998; Bowker et al. 2000; see Sect. 6.6). Several adaptive strategies allow crust bryophytes to maintain reproductive outputs in spite of these limitations. First, propagule banks may exist in upper soil layers. Bryophyte propagule banks have been described from a variety of habitats from deserts (Smith 2013), temperate grasslands (During 1987), and temperate wetlands (Eckstein 2006) to polar (Lewis Smith 1987) and alpine regions (Peer et al. 2009). They are critical sources for colonization following natural (Furness and Hall 1981; Miles and Longton 1982) and anthropogenic disturbance (Bisang 1995; Hassel and Söderström 1998). Bryophyte soil propagule banks in arid and semiarid landscapes remain largely unstudied (see: During 1987; During and Moyo 1999; Smith 2013) but likely contribute to bryophyte diversity and abundance. In Australia, a number of arid zone mosses (Pottiaceae, Gigaspermaceae, Funariaceae) and hepaticas (*Riccia*, *Asterella*, *Fossombronia*) regularly produce spores that can form a component of propagule banks, while others produce rhizoidal tubers or perennating underground stems (*Gigaspermum*).

The relationship between propagule bank diversity and surface bryophyte diversity, however, may not be linear or simple to predict. Low elevation dryland propagule banks of high species richness have been shown to produce surface bryophyte communities of low species richness (Nash et al. 1977), illustrating that the mechanisms of maintaining diversity in subsurface soil banks may operate differently to that of surface communities (Smith 2013).

Adaptive life history strategies are another means by which biocrust bryophytes persist long-term in dry and unfavorable habitats. Although many biocrust bryophytes are long-lived, slow-growing perennials that rarely reproduce sexually, others exhibit very short life spans, a strategy which may function to increase annual reproductive output. Species with a short life span, the annual shuttle life strategy described by During (1992), may be extremely successful in producing few, but often very large, spores (up to 160 μm or more) with the potential to remain viable for many years.

6.6 Biocrust Bryophyte Physiological Ecology

6.6.1 Water and Temperature Relations

Crust bryophytes are poikilohydric organisms, for which internal water content is wholly dependent on water content of the surrounding environment. In general, they are adapted to capitalize on precipitation when it occurs (their only opportunities for growth) and remain in a state of suspended metabolism during all other times (Tuba et al. 1996; Proctor 2001). When precipitation events occur, shoots become hydrated and remain physiologically active for the duration of the precipitation event (Mishler and Oliver 2009; Coe et al. 2012a), after which tissues dry and enter a desiccated state.

The ability to withstand various degrees of drying duration and intensity, from which full physiological function can be recovered, is termed desiccation tolerance (DT). DT is a multifaceted suite of physiological and molecular traits that encompasses mechanisms of preserving tissues as they dry, maintaining tissues while desiccated and ensuring recovery of cellular functionality upon rehydration. As shoots dry, cellular components are packaged and protected by polysaccharides and proteins (Smirnoff 1992; Buitink et al. 2002; Oliver et al. 2005). While desiccated, biocrust mosses often lose virtually all cellular water and can dry to 5–10 % dry mass and water potentials of -100 MPa in the most desiccation-tolerant species (Proctor et al. 2007a, b). In this state, shoots can remain dry for periods of 190 days or more (Stark et al. 2005). Upon rehydration, membrane repair is initiated, and synthesis of proteins unique to the hydration process recovers within minutes (Oliver 1991). The genetic basis for DT has been shown to involve late embryogenesis abundant (LEA) proteins that protect cellular constituents while tissues are desiccated and as they rehydrate (Oliver et al. 2004). The mechanistic basis for gene expression during a wet-dry cycle likely includes polysomal retention of mRNA

transcripts during dehydration (Wood and Oliver 1999) and their rapid transcription into proteins upon rehydration (Oliver 1991).

Crust bryophyte species exhibit varying degrees of DT, and most are described as displaying either constitutive or inducible DT. In constitutive DT species (e.g. *Syntrichia caninervis*, *Syntrichia ruralis*), the cellular and molecular mechanisms that provide DT are present irrespective of environmental conditions, and plants will typically display the same degree of DT even if the surrounding environment causes different degrees of desiccation stress (Oliver et al. 2005). Conversely, species displaying inducible DT (e.g. *Physcomitrella patens*, *Pterygoneurum lamellatum*) fully activate DT processes only after conditions of desiccation stress are imposed. If the surrounding environment remains moist, plants ‘deharden’ and do not display DT phenotypes (Stark et al. 2013). Recent evidence suggests that in inducible DT species, the degree of DT displayed is directly related to the speed at which tissues dry: compared to shoots that dry rapidly (<3 h), shoots that dry slowly exhibit higher photosynthetic performance and rates of regeneration upon rehydration (Greenwood and Stark 2014). Speed of drying for crust bryophytes in dryland systems is related to temperature, degree of cloud cover following a precipitation event, microhabitat (under shrub vs. open interspace) or shoot density in a colony.

Crust bryophytes exhibit a large range of temperature tolerance but also can be very responsive to temperature changes while physiologically active. In dryland ecosystems, selective pressures to tolerate temperature extremes are high, and in the desiccated state, dryland crust mosses can withstand temperatures from –2.5 °C to 120 °C (Malek and Bewley 1978; Hearnshaw and Proctor 1982; Stark et al. 2009). While hydrated, however, moss tissues are far more vulnerable to both low and high temperatures. In hydrated crust mosses, optimal temperatures for photosynthesis range from 10 °C to 20 °C (Furness and Grime 1982; Alpert and Oechel 1987). At temperatures >30 °C, photosynthetic capacity becomes compromised (Grote et al. 2010; Coe et al. 2012b), and, depending on species, lethal damage to shoots occurs at temperatures between 42 °C and 51 °C (Meyer and Santarius 1998; Proctor and Pence 2002).

Tolerance of desiccation and extreme temperatures comes at the expense of growth and reproduction in crust bryophytes. Annual shoot growth increments can be 0.3 mm or less (Stark et al. 1998), inter- and intra-annual growth are both highly dependent on precipitation regime (Coe and Sparks 2014) and rates of sexual reproduction are typically very low.

6.6.2 Reproductive Ecology

Reproductive strategies and trade-offs in crust bryophytes often have been the subject of extensive study over the last decade. Nearly all crust bryophytes are dioecious, producing shoots that express either male (antheridia) or female (archegonia) sexual structures at maturity. Disparate sex ratios, where one sex is observed more frequently than the other, are widespread in dioecious bryophytes, and in

dryland ecosystems, bryophyte sex ratios are almost always skewed toward females. In fact, the crust moss *Syntrichia caninervis* exhibits the most disparate sex ratio (14 females to 1 male) among all land plants (Bowker et al. 2000; Stark et al. 2009). But sex expression and sexual reproduction are also both rare in dryland crust bryophytes. Several lines of evidence suggest these phenomena are related to differential costs of sexual structures in males and females as well as sex-based adaptations to disturbance regimes in dryland ecosystems.

For one, sex-expressing male shoots are often restricted to shade microsites with higher resource availability (e.g. under a shrub), whereas females are commonly observed in exposed plant interspaces (Stark et al. 2005). This results in a characteristic pattern of spatial segregation of the sexes and as a consequence, reduced sexual reproduction, as the transfer of liquid water between male and female gametophytes is required for fertilization. Using biomass as a metric, the cost of pre-fertilization reproductive effort expended by males is an order of magnitude higher than that of females (Stark et al. 2000), indicating it is energetically more expensive for a shoot to produce antheridia compared to archegonia. One explanation for male-expressing shoots to occur in such a low frequency thus relates to the relative abilities of mature shoots to produce either male or female gametangia. The “Shy Male Hypothesis” proposed by Stark et al. (2010) postulated that male and female shoots occur in equal frequency in nature, but males simply produce sex structures less frequently.

Disparate sex ratios and low sexual reproduction in crust bryophytes may also relate to the differential stress tolerance of male and female shoots. In *Syntrichia caninervis* exposed to drought conditions, female shoots appear to regenerate more rapidly and be less susceptible to microbial infection in controlled conditions, but these patterns do not necessarily manifest in the field (Stark et al. 2005). There is also evidence in *Tortula inermis* and *Grimmia orbicularis* for abortion of sporophytes from female shoots following episodes of desiccation stress (Stark 2001; Stark et al. 2007), which suggests these sexual structures may be particularly demanding for gametophytes to support unless environmental conditions are favorable. When subjected to high-temperature (120 °C) events, males from under shrub microsites displayed higher levels of thermotolerance compared to females from interspace regions (Stark et al. 2009). This has been thought of as evidence for selection to tolerate natural wildfires that burn hottest in shrub regions compared to plant interspaces (Stark et al. 2009). Environmental, developmental, and physiological factors all play a role in sexual segregation and patterns of sex expression in crust bryophytes, all of which lead to the disparate sex ratios and low rates of sexual reproduction ubiquitously observed in populations in nature.

6.6.3 Ecological Roles of Biocrust Bryophytes

Bryophytes within biological soil crusts play important ecological roles in many ecosystems. In drylands, they are dominant crust members in many high (>610 m)

and low desert habitats, where they can account for 30 % or more of cover within crusts (Thompson et al. 2005). Crust bryophytes influence soil stability through growth of fine rhizoids and protonemal mats during regeneration and contribute to soil formation through modification of the hydrologic and thermal environment of sandy soils as well as through capture and accretion of soil particles (Carter and Arocena 2000). Crust bryophytes also influence soil fertility by intercepting dust particles, whereby increasing dry atmospheric deposition of nutrients (Belnap 2003), and by facilitating development of microorganism communities that increase the nutrient status of crusts (Zhao et al. 2014). Dryland bryophyte nitrogen and phosphorus ratios often correlate with soil availability of these nutrients (Ball and Guevara 2015), and environmental stress in the form of alterations in precipitation regime has been shown to cause moss mortality, with consequences for changes in ecosystem nitrogen cycling (Reed et al. 2012).

Crust bryophytes influence carbon cycling in dryland ecosystems as well. Peak photosynthetic activity for many dryland crust mosses is in the winter months, due to favorable temperature and water status. These times of the year are when net ecosystem exchange can also be highest, even though (in the case of many North American drylands) dominant shrubs may be dormant. These observations suggest that crust bryophyte photosynthetic activity can control the overall carbon balance of some dryland ecosystems (Zaady et al. 2000; Jasoni et al. 2005).

As the global climate changes, dryland systems are among those that are likely to be most responsive to environmental change (Brown et al. 1997; Weltzin et al. 2003; Reed et al. 2012). Increased temperatures, elevated atmospheric CO₂, and changes in precipitation regime are all likely to impact the physiology, ecology, and distribution of dryland biocrust mosses. Increased temperatures, particularly high thermal stress events occurring during heat waves, are likely to reduce physiological performance in biocrust mosses and reduce viability, especially if they increase in frequency. However, the degree to which high-temperature events will be a large factor in future distributions depends on local hydrology, as they will only impose physiological stress if mosses are hydrated. In contrast, changes in precipitation are likely to cause rapid and potentially irreversible changes in moss viability and persistence in biocrusts. Even subtle changes in intra-annual precipitation have been shown to dramatically alter long-term C fixation and viability (Reed et al. 2012) with consequences for biocrust structure and function.

6.7 Concluding Remarks

Bryophytes are conspicuous components of biocrusts in the Northern and Southern Hemispheres, particularly in dryland systems, where they are represented by many species in relatively few families. Morphological and physiological attributes contribute to their adaptations to extreme environmental conditions in these habitats, where they take on an array of ecological roles. Much remains to be done to understand the basis of persistence and survival strategies in crust bryophytes, as

well as how functional plant traits influence ecosystem scale processes. From a diversity perspective, surveys of bryophyte propagules that may remain hidden in the soil for long periods may be critical to assessing potential biocrust biodiversity. Although rarely applied, molecular screening may assist biodiversity assessment, particularly with regard to ecosystem management of arid and semiarid lands. Finally, much could be gained by wide-ranging integrated collaborative studies examining interspecific interactions among crust and soil members that will enhance our understanding of biocrust ecology and soil biodiversity.

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Chapter 7

Structure, Composition, and Function

of Biocrust Lichen Communities

**Roger Rosentreter, David J. Eldridge, Martin Westberg, Laura Williams,
and Martin Grube**

7.1 Introduction

Lichens are symbiotic associations between a fungal partner (mycobiont) and one or more photosynthetic partners, either green algae or cyanobacteria (photobiont), living in a close physiological integration that forms a thallus. The mycobiont provides the basic lichen structure, and the alga provides the nutrition through photosynthesis. Like many other biological components of biological soil crusts (biocrusts), lichens are poikilohydric, meaning that they do not actively regulate water uptake or loss, but gain it from, and lose it to, the environment passively. When desiccated, their metabolic activity ceases and they undergo a transient cryptobiotic phase until metabolism can resume with changing environmental conditions. The particular characteristics of soil as a substrate may include high light intensities, poor water availability, and often an unstable surface to grow

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on. Such a poikilohydric strategy is perfectly suited for life within biocrusts where environmental conditions vary dramatically between the extremes of inundation and drought.

Lichens form a diverse and often colorful part of biocrusts in all parts of the world (see Fig. 7.1 and Chap. 10 by Bowker et al.) and can be the dominant

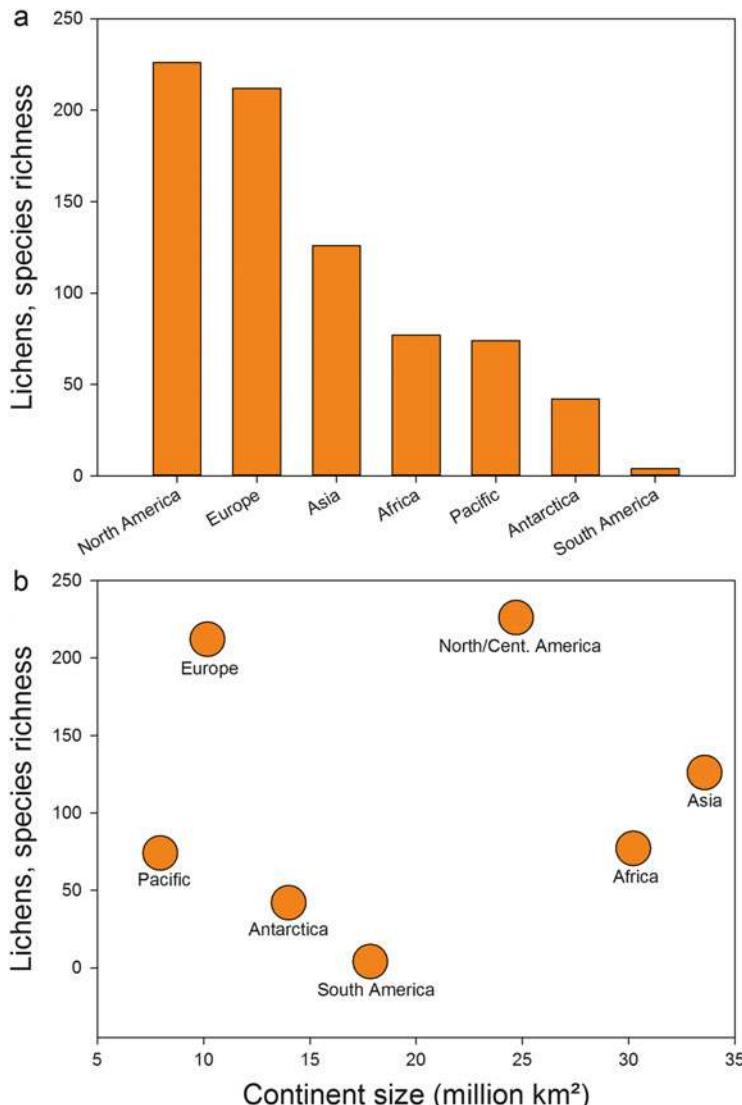


Fig. 7.1 Soil crust lichen richness (a) at the continent scale and (b) in relation to continental area. *S Amer* South America, *Pac* Pacific (Australia, New Zealand), *Ant* Antarctica, *Afr* Africa, *Eur* Europe, and *NC America* North and Central Americas and includes Greenland. Source: Büdel (unpublished data)

life-form in many soil surface communities. Their ability to tolerate severe abiotic stresses such as desiccation, extreme temperatures, and high light intensities makes them ideally suited for relatively resource-limited environments that support well-developed biocrust communities: polar regions, high mountains, arid and semiarid deserts, and xerothermic steppe. In temperate regions, lichens also form important biocrust communities. For example, in Europe, lichen-rich biocrust communities can occur where human activity has created or maintained environments and landscapes largely free of vascular plant vegetation through, for example, grazing by cattle or intense mining or military activity. Lichens can also be important as pioneer species in more ephemeral crusts establishing in areas with open soil created by either natural events such as rockslides or human activities such as road cuttings and forest clearings.

Lichens perform many critically important ecological functions such as altering the physicochemical properties of soil, by, for example, enhancing soil stability and altering water infiltration and retention (Eldridge et al. 2010; Chamizo et al. 2012), increasing fertility through nitrogen fixation and carbon sequestration (Maestre et al. 2010; Elbert et al. 2012; Delgado-Baquerizo et al. 2013), and interactions with other organisms (e.g., hosts for parasitic fungi and food for various invertebrates such as snails, mites, and insects but also for larger animals such as reindeer Seaward 1988; Lalley et al. 2006; Li et al. 2006). While lichens are recognized as a key component in many biocrusts, there remain substantial gaps in our understanding of the taxonomy and diversity of the lichens. In this chapter we summarize some important aspects of lichens in biocrusts and highlight the need for taxonomic research on these organisms.

7.2 Structure and Morphology of Lichen Biocrusts

Biocrusts include the full range of lichen types including gelatinous, crustose, squamulose, foliose, and fruticose forms (Eldridge and Rosentreter 1999). The relative importance of these forms can change in relation to average annual rainfall and evaporation (aridity) and substrate type (see Büdel et al. 2009; Chap. 9 by Colesie et al.). A general introduction to the morphology and anatomy of the lichen thallus can be found in Büdel and Scheidegger (2008). Here we will focus on some aspects of lichen morphology that are relevant to their ability to form biocrust communities.

7.2.1 *The Importance of Fungal Hyphae*

Lichens attach themselves to the substrate by penetrating the soil with their fungal hyphae. These hyphae are generally assumed to be restricted to the surface of their substrate. However, the hyphae of saxicolous lichens have been shown to penetrate

the spaces between mineral particles to a depth of up to 12 mm (Bjelland and Ekman 2005; Chen et al. 2000), suggesting that fungal hyphae of biocrust lichens may be capable of deeper penetration into substrates that are substantially looser than rock. Observations of the dense aggregations of rootlike rhizines and rhizoids (e.g., Poelt and Baumgärtner 1964; see Chap. 3 (Fig. 3.3) by Beraldi-Campesi and Retallack), common in many biocrust communities such as those of the genera *Endocarpon*, *Catapyrenium*, and *Psora*, support this notion. This is also true for some Antarctic soil crust-forming species such as *Acarospora gwynii* (8 mm depth) and *Caloplaca citrina* and *Lecanora expectans* (24 mm depth; Colesie et al. 2013). Indeed, Belnap et al. (2001) demonstrated that hyphae of *Psora cerebriformis* can penetrate to depths of 14 mm. These dense clumps of deeply penetrating rhizines help to aggregate soil microaggregates into macroaggregates, increasing the resistance of biocrusts to wind and water and mechanical deformation (see Chap. 16 by Belnap). They also increase soil surface roughness, which may further improve resistance to wind and water erosion (Eldridge and Rosentreter 1999).

7.2.2 *The Role of the Lichen Photobiont*

Photosynthesis in lichens is performed by either green algae or blue-green algae (cyanobacteria). About 86 % of lichens have green algal photobionts (chlorobionts), creating chlorolichens, and about 10 % have cyanobacterial photobionts (cyanobionts), creating cyanolichens. In addition, about 3–4 % use both cyanobacteria and green algae as their photobionts (Honegger 1991). In the latter case, cyanobacteria are usually found in specific structures called cephalodia, where they are mainly responsible for nitrogen fixation and, consequently, have an elevated frequency of heterocysts (Hyvärinen et al. 2002). Despite the primacy of the photobiont, very little is known about the specificity of fungal–algal association in biocrust lichens. In general, green algae of the genus *Trebouxia* have been found to be the dominant photobiont of biocrust chlorolichens. Very little is known about physiological interactions between lichens and algal colonies outside the thallus structures. Chlorolichens are known to grow in close proximity to cyanobacterial colonies in a wide range of relationships, from facultative to obligate (cyanotrophy, sensu Poelt and Mayrhofer 1988).

Despite the diversity of algal species present in biocrusts, lichen mycobionts appear to be highly specific. For example, studies by Ahmadjian et al. (1980) and Ahmadjian and Jacobs (1981) showed that, although the biocrust lichen *Cladonia cristatella* and rock-dwelling *Rhizoplaca chrysoleuca* formed thalli when associated with several photobionts, at least in vitro, development was retarded when distantly related photobionts were used. Similarly, Schaper (2003) demonstrated the extremely photobiont-specific nature of certain lichenized fungi, with a proper lichen thallus developing only when associated with a specific partner. However, the degree of algal specificity of biocrust lichens does not contrast with those lichens growing on other substrates (Wirtz et al. 2003; Pérez-Ortega et al. 2012).

Interestingly, the soil lichen *Psora decipiens* has been shown to be associated with a wide range of chlorobiont species (Ruprecht et al. 2014). We assume that the ability to form associations with a wider range of locally available photobionts may be an important trait that increases the distribution and survival of biocrust lichens growing in environmentally extreme habitats, such as the Antarctic Peninsula (Romeike et al. 2002; Jones et al. 2013). This could account for its widespread global distribution and its ability to tolerate a wide range of environmental conditions ranging from alpine areas to deserts.

Photobiont pools may exist in areas that allow many species to take advantage of locally adapted species or haplotypes, and some species have even evolved to steal their photobionts from other lichen species. A noteworthy example of this is the soil lichen *Diploschistes muscorum*, which parasitizes different *Cladonia* species by developing apothecia in the *Cladonia* squamules and associating with its photobiont *Asterochloris irregularis*. Consequently the *Cladonia* structure breaks down, resulting in free-living *Diploschistes* thalli. In mature thalli of *Diploschistes*, the photobiont is exchanged for *Trebouxia showmanii* (Friedl 1987). *Toninia sedifolia* and *Fulglesia* species are often found growing together and appear to share the same photobiont pool of *Trebouxia* strains (Beck et al. 2002). Indeed, ascospores of *Fulglesia bracteata* have been found to germinate on the thallus of *Toninia sedifolia* and the invading hyphae gain access to the photobiont (Ott et al. 1995).

7.3 Composition of Biocrust Lichens

7.3.1 Distribution of Biocrust Lichens

Biocrust lichens are found on all continents (Fig. 7.2a), although richness seems to be largely independent of continent area (Fig. 7.2b). As with any other organism, the distribution of biocrust lichens ranges from highly localized to globally ubiquitous. Many biocrust species are ubiquitous and have a broad geographic distribution. Species such as *Psora decipiens*, *Toninia sedifolia*, and *Fulglesia bracteata* are often very common components of lichen-dominated biocrusts worldwide (Timdal 1986, 1987). However, morphological variation in *Toninia sedifolia* at different biocrust sites is difficult to interpret and may obscure the presence of different, closely related species. Similarly, *Psora decipiens*, thought to be taxonomically well defined (Schneider 1979; Timdal 1986), is now known to exhibit variation both in morphology and chemistry, and this variation has not been thoroughly studied using molecular techniques. It is likely, therefore, that the considerable variation within this particular lichen taxon could be sufficient to warrant the description of new species. Such variation is also apparent in many other biocrust lichen species and raises the question whether they are also associated with variation in ecophysiological traits of the species. In this context,

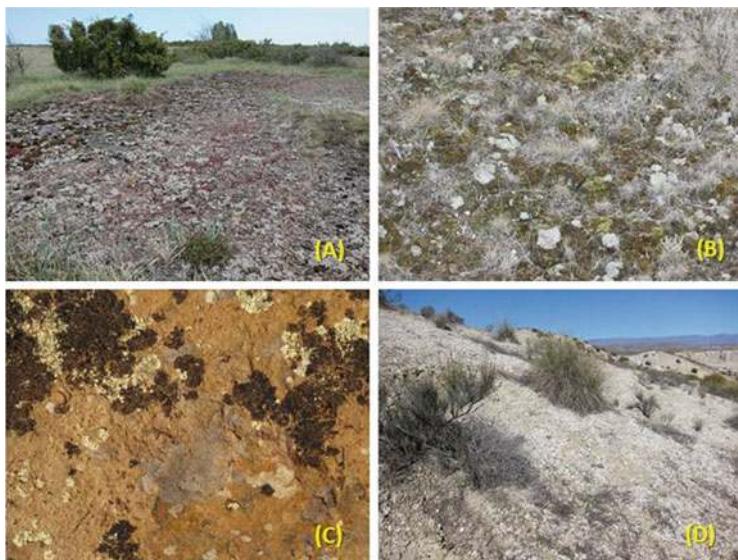


Fig. 7.2 Images of lichen-dominated biocrusts. **(a)** The Great Alvar on Öland, Sweden showing shallow soils on limestone pavement with, e.g., *Diploschistes muscorum*, *Toninia sedifolia*, *Toninia physaroides*, *Psora decipiens*, *Fulgensia bracteata*, and *Collema* spp. **(b)** *Artemisia* shrub-steppe near Boise, Idaho, USA, on deep loess soils with *Diploschistes muscorum*, *Fulgensia bracteata*, and *Psora montana*. **(c)** Crusted loamy soils near Deniliquin, NSW, Australia, with *Xanthoparmelia reptans*, *Neofuscelia pulla*, and *Lecidea ochroleuca*. **(d)** Tabernas badlands near Almeria, Spain, with well-developed biocrusts on gypsum-calcareous soil dominated by *Squamaria lentigera*, *Diploschistes diacapsis*, *Buellia zoharyii*, and *Acarospora nodulosa*

taxonomists often stress the concept of cryptic species (i.e., species that are not characterized by distinct phenotypic characteristics). This, however, may reflect merely an ignorance of subtle phenotypic traits that have been overlooked or inadequately studied.

The abundance of some biocrust taxa may exhibit skewed distributions across their geographic range due to differences in their ecological response to idiosyncratic environmental cues. One species with a skewed distribution is *Solorinella asteriscus*, a xerothermic continental species that typically occurs on loess soils. Its sporadic occurrence in continental valleys in Norway and dry valleys in the Canadian Alps and Italy does not reflect a global rareness, because it is relatively common in semiarid steppe grasslands in Asia, and also occurs in isolated pockets in moderate continental climates in urban and peri-urban environments in Europe (e.g., Bratislava, Slovakia). It is likely that populations of this species, which were isolated during the Late Glacial and Holocene periods, are also genetically distinct, although their scarcity in Central Europe may also be related to the loss of available habitats due to human activity (Farkas and Lököš 1994).

Other biocrust species have very limited geographic distributions and, to date, are known only from the locations where they were first described. For example, the

squamulose coralloid lichen *Protopannaria alcicornis* (Jorgensen 2001) is an endemic biocrust lichen known from only two specimens from the subantarctic Kerguelen Islands. It is difficult to establish the realized niche of this species because comparable habitats on other subantarctic islands are difficult to survey and therefore have been poorly sampled. The high number of currently endemic lichens worldwide probably reflects the poor state of floristic research rather than true endemism per se. For some species, local or regional endemism has been adequately established through substantial regional collections. For example, *Tephromela siphulodes* is a species with a distinct, three-dimensional growth form and has only been found on soils in high-altitude alpine areas in Nepal (Poelt and Grube 1993a). Similarly, *Lecanora himalayae* and *Lecanora chondroderma* are well-described species from the same area, but are absent from other alpine habitats (Poelt and Grube 1993b). In Mediterranean habitats, some white-colored *Buellia* species, known as the *Buellia epigaea* group, have a wide distribution in the Northern Hemisphere, but three species of the group (*Buellia dijiana*, *Buellia georgei*, and *Buellia lobata*) are only known from Australia (Trinkaus et al. 2001). The preceding discussion about lichen distribution and endemism indicates that considerable work is required to determine the true distribution of many of our biocrust-forming lichen taxa.

While many scientists acknowledge the close links between biocrusts and the condition or health of dryland ecosystems (Klopatek 1993; Rosentreter and Eldridge 2002), biocrusts and their component lichens and bryophytes are rarely recorded during field-based assessment (West 1990). In the mid- to late 1980s, Australian rangeland scientists pioneered a range of techniques to determine the health of landscapes that placed more emphasis on soil and landscape function rather than relying, as previously, on the status and condition of the vascular plant community (Tongway and Smith 1989). The resulting “soil surface classification system” used biocrust cover as an important measure of the capacity of the soil to carry out two functions: resist deformation and cycle nutrients.

7.3.2 Richness and Abundance of Biocrust Lichens

A global assessment of biocrust lichen richness is difficult to conduct. Part of the reason for this lies in the difficulties associated with the term “biocrust.” Although this term and its synonyms (biological soil crust, cryptogamic crust, cryptobiotic crust, microphytic crust) are widely used by ecologists, its application for a well-described group of lichens is problematic. Biocrusts have been defined as a community of organisms that are an intimate part of binding soil surface particles into a crust. However, fruticose (shrubby) lichens (e.g., *Chondropsis semiviridis*) do not form true crusts (Eldridge and Greene 1994), and it is doubtful whether vagrant (*syn.* vagrant) lichens (e.g., *Xanthoparmelia chlorochroa*), that are associated with soils and biocrusts, have a role in crust formation or whether the thallus itself represents a biocrust without the underlying soil. Here we avoid this ontological

issue by adopting a wider concept of biocrusts, which also includes lichen taxa that develop more complex thallus forms when growing on soils (i.e., terricolous lichens). A key of terricolous species in Italy includes 439 species (Nimis and Martellos 2004). Extrapolating globally, we expect that the worldwide number of species may be beyond 1000. Unpublished data on lichen richness (Büdel et al. 2014, pers. comm.) indicates a described lichen richness of about 550 taxa (Fig. 7.2a).

The composition of the lichen flora in biocrusts varies considerably with differences in soil physical and chemical properties, climate, and vegetation community (see Chap. 10 by Bowker et al.). Although lichens are often a prominent or even dominant component of biocrusts, it is often difficult to compare species richness between different areas because the taxonomic status of some ubiquitous species is under revision (e.g., *Buellia* spp., Trinkaus et al. 2001). Advances in the molecular taxonomic techniques and improved DNA sequencing could result in range extensions for some species or the splitting of globally distributed taxa into different species or subspecies.

In general, biocrust lichen richness tends to be higher in environments such as deserts, arctic, and alpine areas, where competition from vascular plants is low. Cool habitats, in particular, seem to support a large diversity and biomass of lichen taxa (Eversman 1995), possibly because the balance of photosynthesis and respiration between the symbiotic partners maximizes the opportunity to form complex thallus structures. Several studies have shown that large-seeded grass species, such as cheatgrass, *Bromus tectorum*, are inhibited by biocrusts (Serpe et al. 2006, 2008). In arid and semiarid environments, competition from vascular plants is generally low, either because the distribution of vascular plants is also low or lichen crusts inhibit vascular seed germination (Prasse and Bornkamm 2008; Serpe et al. 2006). In more mesic environments that support larger populations of herbivores, there is often positive feedback between increased soil moisture, fluctuations in vascular plant cover, and the response of biocrusts to these altered levels of bare soil (see Chap. 19 by Zhang et al.).

7.3.3 *Taxonomy and Identification of Biocrust Lichens*

Biocrust lichen taxonomy is still in its relative infancy compared with vascular plant taxonomy. For example, in a study of lichen species richness by a number of lichen experts at four sites in Europe (Austria, Germany, Spain, and Sweden, Büdel et al. 2014), about 9 % of all lichens collected remained unidentified at the species level even though these areas have previously been studied intensively. Given this uncertainty in identification, we would expect that even more remote and poorly studied biocrust communities would yield many new lichen species.

Similar to many other organisms associated with biocrusts, lichens are also often difficult to identify. In contrast to most prokaryotes and many other microscopic eukaryotes, however, lichens have macroscopic structures with characters that

allow the recognition of species or at least their classification to higher (taxonomic) ranks. Many terricolous macrolichens found in biocrusts are characterized by large, leaflike thalli. These biocrusts are easily recognizable but include “difficult” genera that are hard to identify at species level because they are morphologically variable and have few external characteristics. Genera typical of this group are found in the families of Aspiciliaceae, Acarosporaceae, Lichinaceae, and Verrucariaceae. In addition, the high substrate specificity typical for many lichens may not be strictly maintained on soil substrates. Some species normally found on rocks may occasionally be found on compacted or gypsiferous soils, and in alpine environments, corticolous (bark-inhabiting) species are sometimes found on soil (e.g., *Evernia divaricata*). The taxonomic significance of such substrate shifts is relatively unknown, but a reasonable hypothesis is that the variable composition of soils could facilitate the adaptation of species to alternative substrate types.

The accurate identification of biocrust lichens generally requires expert knowledge that goes beyond the information presented in formal lichen texts. Specific problems of identification arise when biocrust lichens lack reproductive structures needed for determination. Molecular techniques and DNA sequencing of individual thalli may help to improve the identification of species. Such a DNA bar-coding approach to the identification of lichenized fungi, however, will only be useful after basic data on the genetic variation of species have been collected (e.g., Del-Prado et al. 2010; Kelly et al. 2011; Pino-Bodas et al. 2013). Unfortunately, such information is virtually unknown for the majority of biocrust lichens. Moreover, microlichens often occur mixed together in a rich tapestry rather than occurring as discrete individuals. Without knowledge of the species, it is difficult to recognize which structures belong to separate species, and molecular approaches that do not consider these problems will undoubtedly lead to confusing results.

7.3.4 A Morphospecies Approach to Biocrust Lichen Identification

The notion that similar morphology reflects similar functions (or susceptibilities) in ecosystems could improve our understanding of biocrust function, leaving taxonomic intricacies aside. Ecological studies are often conducted by assessing “morphological groups” (sensu Eldridge and Rosentreter 1999), rather than fully resolving diversity at the species level. Morphological groups are groups of superficially similar species that are difficult to differentiate in the field, but which possess similar morphologies (e.g., “green leafy lichens” or “gelatinous lichens”) and often function similarly (Eldridge and Rosentreter 1999). In many cases, morphological groups are surrogates for functional groups (Pike 1978; Rosentreter 1995). For example, the gelatinous lichen genera *Collema*, *Leptogium*, and *Leptochidium* of shrub-steppe communities in the western USA all fix nitrogen

and provide a similar degree of protection from surface soil erosion (Anderson et al. 1982; Brotherson et al. 1983).

The concept of functional groups is well illustrated by the susceptibility of biocrusts to trampling, which is seen as a major factor threatening soil crust communities worldwide. Some lichen species appear more tolerant of trampling than others (Rogers and Lange 1971). This is probably due to differences in their morphologies, as foliose or fruticose forms seem to be more susceptible than crustose and squamulose forms (Eldridge and Rosentreter 1999). Morphological groups of lichens can also provide valuable insights into the health and recovery of ecosystems. For example, in a study across more than 0.6 million km² of eastern Australia, Eldridge and Koen (1998) found that the presence of the “yellow foliose” morphological group, which was comprised of foliose lichens of the genera *Heterodea*, *Xanthoparmelia*, and *Chondropsis*, was consistently correlated with stable, productive landscapes with little evidence of accelerated erosion.

Biocrust color has been shown to be a useful morphological trait to indicate the role of biocrusts in nitrogen cycling. For example, the later successional, dark cyanobacteria-dominated biocrust is known to be more closely involved in nitrification and denitrification than the earlier successional light forms (Barger et al. 2013; Rosentreter et al. 2007). While light cyanobacterial crusts are generally dominated by cyanobacteria of the genus *Microcoleus*, dark biocrusts contain nitrogen-fixing cyanobacteria (e.g., *Nostoc*, *Scytonema*) and often the nitrogen-fixing lichens *Collema tenax* and *Collema coccophorum*. Some lichen morphologies may be indicative of moisture type and inundation conditions. Gel-like cyanolichens (e.g., *Collema*) depend on liquid water for activity. Some chlorolichens may be activated by humidity alone. Thus, they are likely to be relatively intolerant of inundation and found therefore in exposed situations (Lange et al. 2001). Water vapor alone, however, is insufficient to activate some chlorolichens such as *Acarospora gwynii*. The ability of chlorolichens to be activated by water vapor may be an adaptation to very low liquid water availability (Colesie et al. 2014). Moderately cool habitats with high levels of humidity are often dominated by fruticose lichens. Their productivity under such conditions seems to be the result of high photosynthetic rates compared to respiration. The markedly different response of lichens to environmental conditions thus provides useful information on environmental quality.

7.4 Functional Roles of Biocrust Lichens

The important functional roles of biocrust lichens related to the physiological or chemical properties are already highlighted in several chapters of this book, including soil stabilization (see Chap. 16 by Belnap), weed abatement, lowering or raising of the albedo of the soil (see Chap. 12 by Weber and Hill, and Chap. 22 by Reed et al.), provision of microhabitats for invertebrates (see Chap. 8 by Darby and Neher), and nitrogen fixation (see Chap. 14 by Barger et al.). However, the

assignment of particular species or morphological groups to such categories is an important task if we are to be able to assess the ecosystem value of particular soil crust communities.

Different photobionts influence the capacity of biocrust lichens to undertake different functions. For example, cyanolichens fix nitrogen which makes them efficient pioneers on degraded soils (Eldridge 1998). They preferably grow at sites of lower potential radiation (Pinho et al. 2010) and tend to have a lower photosynthetic efficiency compared to chlorolichens (Wu et al. 2013). But the soil crust lichen *Collema tenax* has been shown to reach higher values than most soil crust chlorolichens and to be saturated at light intensities as high as $1500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Lange et al. 1998; Lange 2003). Soil biocrusts may also help to maintain resistance of ecosystems to invasion. In the western USA, lichen-dominated biocrust communities have been shown to reduce the invasibility of shrublands by large-seeded Eurasian weeds such as *Bromus tectorum* (Deines et al. 2007; Serpe et al. 2008; Reisner et al. 2013, see Chap. 19 by Zhang et al.). Before the introduction of European livestock, a combination of low levels of disturbance in dry times and the presence of a stable lichen-dominated biocrust have kept weedy flammable grass species at low levels. With an increase in human- and livestock-induced soil disturbance, European annual grasses have proliferated, increasing the extent and intensity of wildfire in areas which had not coevolved with frequent fire.

Recent research in the Orchard Combat Training Center south of Boise, Idaho, USA, has focused on the role of biocrust diversity on ecosystem functions, particularly the capacity of different biocrust taxa, including lichens, to withstand disturbance from livestock trampling and military vehicles (Table 7.1). Sites with a high richness of biocrust taxa have been shown to support only a sparse cover of flammable grasses whereas low-richness sites are dominated by flammable grasses (Rosentreter, unpublished report to the Idaho Army National Guard, Nov. 2014). Apart from their suppressive effect on large-seeded, annual plants, biocrusts may also facilitate the succession of other plant communities by, for example, fixing nitrogen, providing a niche for specialized microbes, or stabilizing the soil by trapping resources such as organic matter and water (Maestre et al. 2008). They also moderate the flow of water into the soil (see Chap. 17 by Chamizo et al.).

In order to convince land managers, practitioners, farmers, politicians, and the general public of the ecosystem role provided by biocrust lichens, it may be more useful to consider a functional group approach to lichen identification rather than one based on a traditional species approach. This emphasizes the extent to which they are critical for providing ecosystem goods and services rather than merely how many individual species they support. These roles and functions include, but are not limited to, erosion prevention and soil stabilization, which are of increasing concern in relation to environmental change and global warming (see Chap. 22 by Reed et al.). In some ecosystems, soil lichens form food for ungulates as well as invertebrates, and absorption of environmental pollutants by lichens can result in transfer into the food chain (Skuterud et al. 2005).

Table 7.1 Biological soil crust taxa recorded in the Orchard Training Center, Idaho, their life-form, functional role, and tolerance to disturbance

Species and authorities	Life-form	Functional role	Disturbance rating
<i>Bryum argenteum</i> Hedw.	Bryophyte	Soil stabilizer	H
<i>Bryum argenteum</i> Hedw. var. <i>lanatum</i> (P. Beauv.) Hampe	Bryophyte	Soil stabilizer	H
<i>Caloplaca cerina</i> (Ehrh. ex Hedwig) Th. Fr.	Bryophyte	Detritus binder	M
<i>Ceratodon purpureus</i> (Hedw.) Brid.	Bryophyte	Soil stabilizer	H
<i>Crossidium</i> sp.	Bryophyte	Soil stabilizer	H
<i>Didymodon vinealis</i> (Bridel) Zander	Bryophyte	Soil stabilizer	H
<i>Pterygoneurum ovatum</i> (Hedw.) Dix.	Bryophyte	Soil stabilizer	H
<i>Riccia frostii</i> Aust.	Bryophyte	Soil stabilizer	M
<i>Syntrichia caninervis</i> Mitten	Bryophyte	Soil stabilizer	H
<i>Syntrichia ruralis</i> (Hedwig) F. Weber & D. Mohr	Bryophyte	Soil stabilizer	H
<i>Microcoleus</i> sp.	Cyanobacterium	N fixer, soil stabilizer	H
<i>Acarospora schleicheri</i> (Ach.) A. Massal.	Lichen	Soil stabilizer	L
<i>Buellia punctata</i> (Hoffm.) Coppins & Scheid.	Lichen	Detritus binder	M
<i>Arthonia glebosa</i> Tuck.	Lichen	Soil stabilizer	M
<i>Aspicilia aspera</i> (Mereschk.) Tomin	Lichen	Soil stabilizer	L
<i>Aspicilia filiformis</i> Rosentreter	Lichen	Soil stabilizer	VL
<i>Aspicilia mansouri</i> Sohrabi	Lichen	Soil stabilizer	L
<i>Aspicilia</i> sp.	Lichen	Soil stabilizer	L
<i>Caloplaca jungermanniae</i> (Vahl) Th. Fr.	Lichen	Detritus binder	M
<i>Caloplaca tominii</i> Savicz.	Lichen	Soil stabilizer	H
<i>Caloplaca</i> sp.	Lichen	Detritus binder	M
<i>Candelariella aggregata</i> M. Westb.	Lichen	Detritus binder	M
<i>Candelariella rosulans</i> (Müll. Arg.) Zahlbr.	Lichen	Soil stabilizer	M
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.	Lichen	Soil stabilizer	M
<i>Candelariella</i> sp.	Lichen	Soil stabilizer	M
<i>Cladonia pocillum</i> (Ach.) Grognot	Lichen	Soil stabilizer	M
<i>Cladonia pyxidata</i> (L.) Hoffm.	Lichen	Soil stabilizer	M
<i>Collema tenax</i> (Sw.) Ach.	Lichen	N fixer	M
<i>Collema coccophorum</i> Tuck.	Lichen	N fixer	M
<i>Diploschistes muscorum</i> (Scop.) R. Sant.	Lichen	Soil stabilizer	L
<i>Endocarpon pusillum</i> Hedwig	Lichen	Soil stabilizer	H
<i>Lecanora flowersiana</i> H. Magn.	Lichen	Detritus binder	M
<i>Lecanora muralis</i> (Schreber) Rabenh.	Lichen	Soil stabilizer	M
<i>Lecidea laboriosa</i> Mull. Arg.	Lichen	Soil stabilizer	L
<i>Lepraria</i> sp.	Lichen	Soil stabilizer	H
<i>Leptochidium albociliatum</i> (Desm.) M. Choisy	Lichen	N fixer	L

(continued)

Table 7.1 (continued)

Species and authorities	Life-form	Functional role	Disturbance rating
<i>Massalongia carnosa</i> (Dickson) Körber	Lichen	N fixer, soil stabilizer	L
<i>Physconia enteroxantha</i> (Nyl.) Poelt	Lichen	Soil stabilizer	L
<i>Physconia muscigena</i> (Nyl.) Poelt	Lichen	Soil stabilizer	L
<i>Placidium squamulosum</i> (Ach.) Breuss	Lichen	Soil stabilizer	H
<i>Placynthiella icmalea</i> (Ach.) Coppins & P. James	Lichen	Detritus binder	H
<i>Psora montana</i> Timdal	Lichen	Soil stabilizer	M
<i>Psora tuckermanii</i> R. A. Anderson ex Timdal	Lichen	Soil stabilizer	L
<i>Texosporium sancti-jacobi</i> (Tuck.) Nadv.	Lichen	Soil stabilizer	L
<i>Thelenella muscorum</i> var. <i>octospora</i> (Nyl.) Coppins & Fryday	Lichen	Soil stabilizer	L
<i>Trapeliopsis bisorediata</i> McCune & Camacho	Lichen	Soil stabilizer	L
<i>Trapeliopsis steppica</i> McCune & Camacho	Lichen	Soil stabilizer	L
<i>Toninia ruginosa</i> (Tuck.) Herre	Lichen	Detritus binder	L

N fixer: fixes nitrogen; soil stabilizer: binds surface sediments using a range of mechanisms, generally hyphae or physical protection; detritus binder: stabilizes organic material. VL very low, L low, H high, and VH very high. Disturbance rating based on a soil crust index (Rosentreter and Eldridge 2004)

7.4.1 Sampling Biocrust Lichen Communities

Qualitative studies of lichen diversity often involve the collection of specimens in a somewhat haphazard sequence, over landscapes that are often of ill defined, or with no specific number, size, or extent of plots. The landscapes sampled are often of variable complexity and sampling is conducted with variable effort (Nash and Sigal 1981; Will-Wolf 1998). This opportunistic sampling, however, has resulted in the collection of data from ecologically interesting sites such as within ecotones, undisturbed areas excluded from grazing, or biodiversity hot spots (Wetmore 1985; Neitlich and McCune 1997). Consequently, there may appear to be some bias in the collection of these data (McCune et al. 2000).

Biocrust lichen research has advanced considerably in the past two decades with a greater attention to systematic sampling. Intensive sampling of different patch types within landscapes is now standard practice, with stratification of sampling sites in relation to vascular plant community composition, soils, and climate. For example, Root and McCune (2012) recorded 99 biocrust lichen species within fifty nine 0.4-ha plots. Of these, one-third were observed only once. The use of morphological, functional, or taxonomic group approaches has also improved field-based assessment of biocrust communities, allowing researchers to increase the consistency and statistical power by lumping taxa that are morphologically similar into groups (Ponzetti et al. 1998; Ponzetti and McCune 2001; Eldridge and

Rosentreter 1999). The use of morphological groups for biocrust lichens minimizes the errors associated with overlooking small or otherwise inconspicuous species or species which are frequently intertwined and decreases the sampling variance by increasing statistical power. It also increases the repeatability of cover or abundance estimates (Ponzetti et al. 1998). Using morphological groups in the field will, however, invariably underestimate true alpha diversity (Ponzetti and McCune 2001).

7.5 Lichens in Biocrusts: Concluding Remarks

A number of knowledge gaps compromise our ability to fully understand how lichens function and how they affect their environment. First, biocrust lichens are still poorly studied, resulting in an underestimation not only of their abundance and diversity, but a lack of understanding of how they interact with their environment and the extent to which they influence the provision of ecosystem goods and services. Some disciplines have developed lists of key indicator species that are useful for assessing the health of ecosystems (e.g., aquatic algae; McCormick and Cairns 1997). Extending this concept to biocrust lichen (and bryophyte) taxa would be a valuable contribution to the field of biocrust ecology. Second, any studies of biocrust lichens must take into account the physicochemical differences in substrates that are likely to affect their diversity and functionality. Third, a more comprehensive understanding of biocrust lichens must consider the degree to which they interact with associated microbiota. Only recently, for example, have bacterial communities associated with biocrust lichens been examined in detail using relatively modern techniques (see Chap. 5 by Maier et al.). Fourth, little is known about functional redundancy in biocrust lichen taxa and the physiological responses of different taxa to a range of perturbations. This can only be solved when taxonomic work has advanced to the stage where the majority of taxa are readily identified and can be studied in situ or where techniques are available for studying ex situ communities (e.g., Maestre et al. 2012). Finally, the study of biocrust lichens is hampered by the lack of consistent, rigorous methodologies, which are exacerbated due to the small size of the target organisms.

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Chapter 8

Microfauna Within Biological Soil Crusts

Brian J. Darby and Deborah A. Neher

8.1 Introduction

A variety of microfauna inhabit the biological soil crusts (biocrusts) of arid soils from all parts of the globe, including the southwestern USA (Bamforth 2004, 2008; Darby et al. 2006, 2007a, b; Neher et al. 2009), the Negev Desert of Israel (Jones and Shachak 1990; Pen-Mouratov et al. 2011), the Tengger Desert of northern China (Liu et al. 2011; Li et al. 2011), Australia (Robinson et al. 2002), and Antarctica (Bamforth et al. 2005; Sohlenius et al. 2004; Schwarz et al. 1993; Colesie et al. 2014). The objective of this chapter is to review the literature on microfauna associated with biocrusts and identify the major microfaunal groups that inhabit biocrusts, the functions they perform in the biocrust ecosystem, when they are most active, where they are located in the soil and biocrust profile, and how they are affected by surface disturbances and altered abiotic conditions. We conclude by proposing three research priorities that are most necessary to improving our understanding of the ecology of biocrust microfauna.

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8.2 Who Are the Microfaunal Inhabitants of Biocrusts?

8.2.1 Protozoa

Protozoa may be the least understood of the biological soil crust consumers because they are small and numerous, but difficult to quantify, observe, manipulate, and identify taxonomically. Most protozoans are generally considered bacterivorous, or predators of other protozoans and small invertebrates, but many species are known to feed on fungal spores and hyphae, and it is likely that many also feed on cyanobacteria in biocrust systems. Predation of cyanobacteria by protozoans is prevalent (Dryden and Wright 1987), but most reports are from aquatic species and it is not clear how many cyanobacteria-feeding species occur in biocrusts. Ghabbour et al. (1980) suggested that protozoans from desert soils (particularly a species of Acanthamoebae) consumed the cyanobacteria *Anabaena* spp. and *Nostoc* spp. in a liquid culture and contributed to the reduction of chlorophyll- α , but there was no definitive evidence that this was not due to grazing from the nematode microfauna also present. Protozoan predation of bacteria, spores, and other protozoans is generally by phagocytosis or engulfing of the whole cells, while predation of filamentous fungal hyphae and cyanobacteria can be either through phagocytosis of the cells/filaments or by a more specialized piercing mechanism. Filose pseudopods (in the case of certain amoebae), or specialized internal structures (in the case of some flagellates and ciliates), pierce fungal hyphae or cyanobacterial filaments to access the prey cells' cytoplasm. This method of feeding by piercing has been found in diverse protozoans, such as in the amoeboid genus *Vampyrella*, the flagellate family Viridiraptoridae, and the ciliate family Grossglockneridae, but it remains to be determined how many of these species are to be found in biocrust systems.

Much of the ecological research on biocrust protozoa distinguishes between mobility groups, which include “amoebae,” “flagellates,” and “ciliates.” These mobility groupings are not monophyletic groups, nor do they necessarily perform distinct functions, but this does not necessarily mean that mobility groupings are invalid methods of understanding the ecology of biocrust protozoa. Protozoa live within a network of water films and water-filled pore spaces, which constrains the size and number of organisms that can inhabit soil and organic matter. Presumably, small, amoeboid protozoa are able to occupy smaller pore sizes that are slow to dry out compared to larger, rigid-bodied protozoans like ciliates. If true, this would have significant implications for which species can be physiologically active in different levels of soil moisture. The difficulty that comes with counting, observing, and identifying protozoa also impedes our ability to distinguish specific niches or feeding habits of different protozoan species. Desert amoebae have been distinguished at finer mobility forms to differentiate between amoebae with (1) extended pseudopodia, (2) limax amoebae (see Fig. 8.1a, roughly cylindrical in shape, resembling a slug) with a single leading pseudopod and no subpseudopodia, (3) limax amoebae with eruptive cells, and (4) flattened, fan-shaped cells

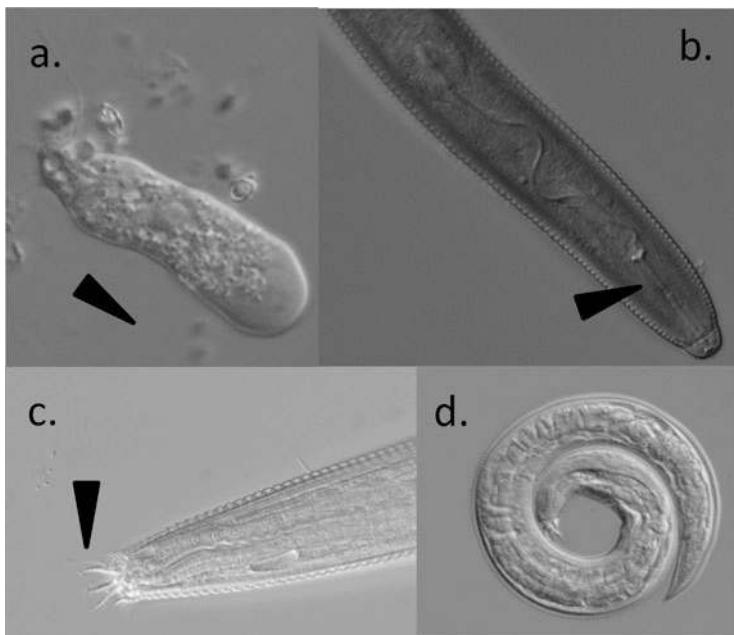


Fig. 8.1 Biological soil crust biota. (a) Limax (snail-like) amoebae (*arrow* points in the direction that the amoebae are moving). (b) Stylet-bearing fungivorous/omnivorous nematode of the genus *Tylenchus* (*arrow* points to needlelike stylet that is used to pierce fungal hyphae and filamentous cyanobacteria). (c) Bacterial-feeding nematode of the genus *Acrobales* in an active, hydrated form (*arrow* points to probolae). (d) Bacterial-feeding nematode of the genus *Acrobales* in a coiled, anhydrobiotic form. Images by B. Darby

(Rodríguez-Zaragoza et al. 2005; Zaragoza et al. 2007). Some studies have been able to further identify individual species belonging to some functional groups (Bamforth 1984, 2004, 2008; Bamforth and Bennett 1985; Bamforth et al. 2005; Robinson et al. 2002). The results of these meticulous studies at finer resolution have led to the observation that biocrusts contain numerous species of non-encysting protozoa (like Thecamoebae), which may suggest that biocrusts serve as microrefugia with pockets of adequately moist pores for some protozoa (Robinson et al. 2002).

8.2.2 Nematodes

Nematodes are not as abundant as protozoa in either numbers or biomass, nor are they as phylogenetically diverse as protozoa, but we have a greater understanding of nematode ecology in biocrust habitats, mostly because we can count, identify, and manipulate nematodes easier and with a finer level of taxonomic resolution. However, most of our understanding of feeding habits and life history traits of

specific nematode species is still based on generalizations made at the taxonomic level of family or genus. One of the outstanding questions of biocrust nematode ecology is whether the species that are found in biocrusts have similar or different feeding habits of comparable species of the same genus in non-biocrust habitats. Nearly every component of the biocrust food web has some potential nematode predator. For the purposes of estimating general trophic links in the nematode community, species of nematodes are typically grouped into one of several feeding types identified largely on the basis of the size and shape of feeding apparatus (Yeates et al. 1993). One of the most distinguishing factors is the presence or absence of a stylet (see Fig. 8.1b), a fine, needlelike piercing apparatus of organisms that pierce (rather than fully engulf) their prey. There are five types of nematodes: herbivores, fungivores, bacterivores, predators, and omnivores. Herbivores have a fine-apertured stylet with a length depending on whether the species tends to be an endo- or ectoparasite. Fungivores have a fine-apertured stylet that is typically short. Bacterivores do not have a stylet and instead have an open buccal cavity with various types of lips surrounding the anterior opening, from smooth and low-rounded to very elaborate, branched processes extending from the lips (called probolae, see Fig. 8.1c). Predators (order Mononchida) have a large, open stoma (oral opening), often with a prominent tooth or row of denticles (Fig. 8.2). There are two main types of omnivores that deserve to be acknowledged in biocrust systems. Nematodes in the orders Tylenchida and Aphelenchida have fine-apertured stomato-stylets and can potentially pierce filaments to feed on the cytoplasm of fungi, fine root hairs, moss rhizoids, and cyanobacteria (Fig. 8.3a). Nematodes in the order Dorylaimida have a broad-apertured odontostylet and can feed on fungi, cyanobacteria, and other microinvertebrates including nematodes, tardigrades, and rotifers. Previous outlines of nematode feeding habits advised against assigning the name of omnivore whenever possible, due to the ambiguity of the designation. However, they also acknowledged the significant “gaps in knowledge of feeding in the smaller tylenchids and many dorylaims” (Yeates et al. 1993). The nematodes that are most likely to consume cyanobacteria are those with a piercing/sucking stylet (such as those traditionally identified as fungivores or predator/omnivores) rather than those with an open buccal cavity (otherwise called bacterivores). This is supported by some of the earliest studies that documented nematode feeding habits as they demonstrated that feeding on algae (both green algae and cyanobacteria) was just as prevalent as feeding on fungal hyphae among the small Tylenchidae (Wood 1973a, b). Because cyanobacteria are such a significant portion of the biocrust soil food web, we consider it prudent to assume for now that many nematodes in genera thought to be primarily fungivorous in temperate ecosystems may also feed on cyanobacteria in biocrust systems (Fig. 8.3b).

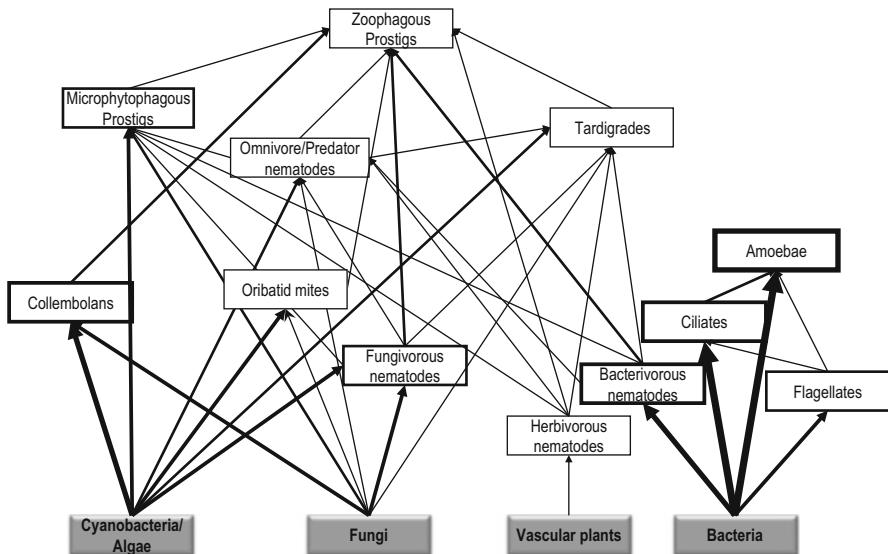


Fig. 8.2 Biocrust consumer food web. The consumer food web as based on the microfauna found in a Moab, Utah, biocrust system in southwestern USA (Darby et al. 2011; Neher et al. 2009). The width of the arrows linking prey to their consumer is proportional to the biomass nitrogen of that trophic link, and the width of the border around the consumer text box is proportional to the amount of inorganic nitrogen (N) being released from the consumer functional group [according to the results of the model as computed by Hunt et al. (1987) for the Moab, Utah, biocrust food web]. In contrast to a typical short-grass prairie soil food web: (1) has more N cycling through and from protozoans and (2) has more N cycling through and from the functional groups that are otherwise thought to be fungivorous (if, indeed, these functional groups are also capable of feeding on cyanobacteria, which is a reasonable but yet unconfirmed assumption)

8.2.3 Tardigrades and Rotifers

Tardigrades and rotifers are also among the microinvertebrates that one might find inhabiting the water films of a biocrust sample. Both tardigrades and rotifers are sometimes found exclusively on the surface of biocrusts as most species are extremely desiccation tolerant. Rotifers are filter feeders that primarily prey on small cells (e.g., bacteria, flagellates, and small unicellular algae), but probably not on filamentous cyanobacteria or large protist cells that are larger than their mouths. Tardigrades may be algivores, fungivores, cyanovores, or predators (on other microinvertebrates) depending on whether they have a piercing/sucking stylet or an open buccal tube. Compared to nematodes, there is less doubt that tardigrades feed on cyanobacteria (Fig. 8.3c), but it remains unclear which species of cyanobacteria are acceptable prey items and whether cyanobacteria are necessarily preferred over other potential foods (such as moss, fungi, or green algae).

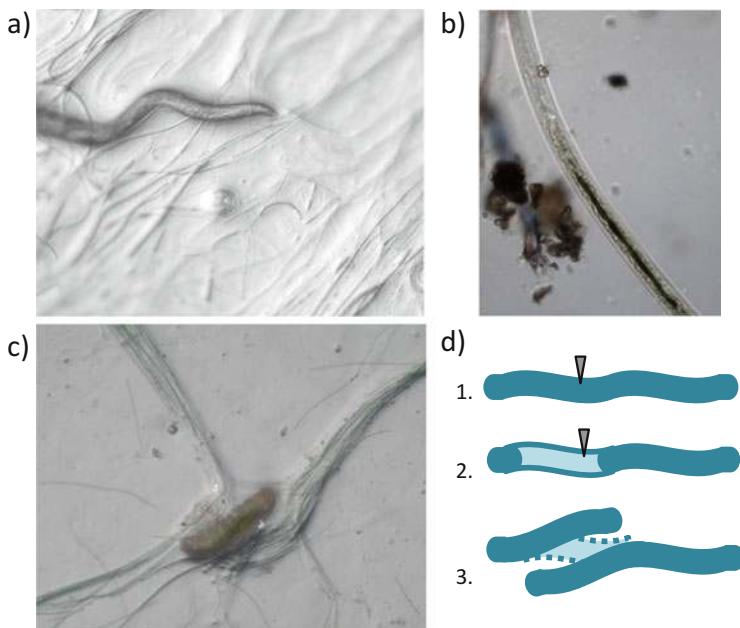


Fig. 8.3 Feeding on cyanobacteria. Digital images of microfauna feeding on cyanobacteria. (a) *Aphelenchoïdes* sp. feeding on *Microcoleus vaginatus* in monoxenic culture, (b) dark green/cyan pigmentation in the intestines of an Aporcelaimidae extracted from soil, (c) tardigrade *Haplomacrobiotus utahensis* feeding on *Microcoleus vaginatus*, (d) schematic of the regrowth of evacuated cyanobacterial filaments after being fed on by a piercing and sucking stylet-bearing nematode or tardigrade. First, the stylet-bearing nematode or tardigrade pierces the cyanobacterial filament with its piercing stylet (represented by the triangle). Second, the organism sucks out the cytoplasm of the segments adjacent to the initial stylet piercing. Finally, the ends of the filaments regrow into and out of evacuated segments, effectively creating two new ends from which the cyanobacteria grows

8.2.4 Microarthropods

A variety of animals that do not require thin films of water, including arthropods and mollusks, also inhabit biocrusts around the world (Shepherd et al. 2002; Colesie et al. 2014; Shachak and Steinberger 1980). Microarthropods such as mites and collembolans inhabit primarily air-filled pore spaces (unlike the water-film fauna that include protozoans, nematodes, tardigrades, and rotifers) and are typically more mobile than water-film fauna (both vertically and horizontally) across larger spatial scales (Shepherd et al. 2002). Like nematodes, the feeding habits of most microarthropods are predicted based on observations of closely related taxa and on the morphology of feeding structures. Most biocrust collembolans are microphytophages, feeding on cyanobacteria, fungi, and detritus, but some are also facultatively predaceous on smaller microinvertebrates such as nematodes. However, biocrust mites can feed on diverse food items such as cyanobacteria, fungi,

nematodes, detritus, mammals, carrion, arthropods, lichens, pollen, and plants (Neher et al. 2009). Larger invertebrates, including mollusks such as snails and macro-arthropods such as ants and pseudoscorpions, can also be significant components of some biocrusts (Li et al. 2011). Unlike microfauna, which are thought to have minimal impact on the physical structure of soil and biocrusts, arthropods like ants have been shown to alter the physical architecture of soil and biocrust hydrology (Chen and Li 2012; Li et al. 2014). Predators of microarthropods form the link between the soil microinvertebrate fauna and the aboveground insectivores. Snails graze lichens, cyanobacteria, and mosses of rocky surfaces (Jones and Shachak 1990; Shachak and Steinberger 1980).

8.3 What Microfauna Do in Soil Crust Ecosystems

Microfauna in biocrusts perform many of the same functions that microfauna perform in grassland or forest systems. This includes regulating their microbial prey populations, cycling nutrients by stimulating microbial growth and excreting waste nutrients as soluble inorganic or low molecular weight organic form, dispersing spores or vegetative microbial cells that are viable and not fully crushed during digestion, and serving as prey for macrofauna at higher trophic levels in the soil food web (Neher 2001; Freckman 1988). However, the relationship between microfauna and autotrophic (and in some cases diazotrophic) cyanobacteria in the soil food web is one of the primary questions that remains regarding the role of microfauna in biocrust systems: that is, how many microfauna consume cyanobacteria, and what is the significance of this trophic link for the biocrust food web? The nutrients that microinvertebrates mobilize are thought to depend on the elemental ratio of their prey (Hunt et al. 1987). For example, a nematode that feeds on fungi with a relatively high carbon(C)/nitrogen(N) ratio is thought to be N limited and therefore will mineralize more C by respiration than N by waste release. Additionally, the ecosystem function that would be affected by grazing would be the decomposition performed by fungal extracellular enzyme activity. However, if this same nematode species can also prey on N-fixing cyanobacteria with a low C:N in a biocrust system, then we would expect the nematode to be relatively C limited and would instead mineralize more N as a waste product instead of C by respiration. Additionally, the ecosystem function that would be affected by grazing would be photosynthesis and N-fixation from the cyanobacteria. These possibilities have not been demonstrated experimentally with nematodes, but they have been shown for protozoa feeding on *Azotobacter chroococcum* (Nasir 1923; Cutler and Bal 1926) and Collembola feeding on arctic cyanobacterial mats (Birkemoe and Liengen 2000). In both cases, the experimenters found that N-fixation increased with intermediate levels of grazing from their microfaunal predator.

To demonstrate the potential effect of biocrust fauna on nutrient cycling, N cycling through the biocrust food web was estimated for a field site in a cool desert location in the southwestern USA (Darby et al. 2011; Yeager et al. 2012; Zelikova

et al. 2012), based on the approach of Hunt et al. (1987) and de Ruiter et al. (1993). The desert food web was constructed based on best estimates of feeding habits known for the organisms found at this site and accounted for the findings of grazing on cyanobacteria by stylet-bearing nematodes and tardigrades, as well as microphytophagous mites and collembolans. Biomass of micro- and mesofauna at this site was obtained from 2-year mean abundances of all functional groups previously measured at Colorado Plateau (Darby et al 2011). To facilitate comparison, and conform to published conventions, biomass per gram of dry soil was converted to biomass per area (to 10 cm depth) assuming a bulk density of 1.0 g cm^{-3} (Belnap 1995), and biomass N was estimated as 5 % of total dry biomass. Feeding preferences and physiological parameters were assigned according to Hunt et al. (1987) with the following exceptions. First, the generation time of omnivore nematodes in the order Dorylaimida was set to 50 days per year, representative of the slower-growing omnivore-predators in the desert such as *Aporcelaimellus* and *Qudsianematidae* (Wood 1973a, b). Second, the generation time of all protozoa was decreased from 6.67 days to 2 days, which is a conservative estimate of the maximum growth rate (0.5 per day) of these desert protozoa (Darby et al. 2006). Finally, microphytophagous prostigmatid and oribatid mites, collembolans, tardigrades, and tylench- and dorylaim-type omnivores were assumed to prey on cyanobacteria with the same preferences as on saprophytic fungi (Neher et al 2009; Wood 1973a; Yeates et al 1993). Microarthropods were assumed to be active and growing for 365 days per year because they are thought to be active even in dry, air-filled pores. Nematodes and protozoa were assumed to be active and growing for 40 days per year (Hunt et al. 1987). This model predicted that belowground soil fauna produce $311 \text{ mg N m}^{-2} \text{ year}^{-1}$ inorganic N and $97 \text{ mg N m}^{-2} \text{ year}^{-1}$ organic N from feces (Table 8.1) or $3.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$ inorganic N and $1.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$ organic N from feces. Like in temperate grassland systems, most of the inorganic N comes from protozoa and bacterivorous nematodes grazing on bacteria (Fig. 8.3). However, what is unique in this system is that a large portion of biologically fixed N from cyanobacteria would be mobilized by microfauna under the assumption that fungivorous functional groups also prey on cyanobacteria. This is a reasonable but unconfirmed assumption, which is why detailing the actual feeding habits of desert microfauna is so important to understanding overall ecosystem function.

Another significant function of microbe-feeding microinvertebrates is the dispersal of viable microbial spores and cells to new locations. In the case of biocrusts, this would include fungal spores and bacterial cells that are not crushed or enzymatically degraded by a predator that feeds by engulfing its prey. However, this would not include filamentous prey items (such as fungal hyphae and filamentous cyanobacteria) that are consumed by predators that feed by piercing their prey (Fig. 8.3). Even though piercing-type predators of filamentous cyanobacteria, such as nematodes or tardigrades, would not disperse vegetative cells, it may still be possible that these predators may nonetheless alter the distribution of filamentous cyanobacteria in biocrusts. As predators such as tardigrades pierce a cyanobacteria filament and suck out the cytoplasm, they leave a gap of evacuated cytoplasm. As

Table 8.1 Faunal contributions to nitrogen cycling

Functional Group	Biomass (mg N m^{-2})	Inorganic ($\text{mg N m}^{-2} \text{ year}^{-1}$)	Feces ($\text{mg N m}^{-2} \text{ year}^{-1}$)	Death ($\text{mg N m}^{-2} \text{ year}^{-1}$)
Zoophagous	35.6	0.76	0.90	0.60
Microphytophagous	88.4	1.99	3.56	1.57
Oribatid	33.1	0.50	0.89	0.39
Collembolans	1070.7	24.14	43.10	18.97
Tardigrades	9.6	0.03	0.06	0.03
Dorylaim omnivore nemas	88.6	0.19	0.30	0.11
Tylenchid omnivore nemas	541.6	2.21	5.71	1.30
Herbivore nemas	2.7	0.007	0.03	0.004
Bacterivore nemas	1861.8	33.25	26.08	5.87
Amoebae	2406.7	161.14	11.01	(48.13)
Ciliates	1185.1	79.95	5.47	(23.88)
Flagellates	98.6	6.90	0.47	(2.06)
Total (mg N m^{-2})	7422.5	311.08	97.61	102.91

Nitrogen (N) cycling results from soil food web model [adapted from Hunt et al. (1987)], including standing biomass and nitrogen contributions to inorganic substrates and organic substrates through feces and death. Death of amoebae, ciliates, and flagellates was computed as for other organisms (inverse of generation time) but is presented in parentheses because they are thought to not die naturally but rather continue to divide. Thus, contributions to substrate from death may be much less than modeled and limited to environmentally induced mortality rather than natural turnover

the adjacent cells grow and extend into the gap, they sometimes extend past the opposing end, which results in lateral branching, creating twice as many ends from which the cyanobacteria can grow (Fig. 8.3d). This phenomenon was observed in laboratory cultures on flat agar surfaces, but it is unclear if it occurs similarly in a more complex natural environment.

8.4 When Are Microfauna Active?

The water-film fauna that are restricted to water-filled pores are often constrained to brief windows of activity in biocrusts. Most biocrust microfauna have diverse cryptobiotic (“hidden life,” Crowe and Cooper 1971) capabilities that allow them to enter temporary dormant stages such as anhydrobiosis (to survive life without water, Crowe and Crowe 2000), cryobiosis (to survive freezing), and anoxybiosis (to survive life without oxygen, although this is less common in surface biocrusts). As soils dry, microinvertebrates enter anhydrobiosis by converting storage carbohydrates into low molecular weight cellular protecting sugars, such as trehalose (Crowe 2002; Madin and Crowe 1975). Specimens that have entered anhydrobiosis are often seen in a coiled, anhydrobiotic state (Fig. 8.1d). Entering and exiting

anhydrobiosis is metabolically costly (Crowe et al. 1977; Madin et al. 1985), and the frequency and duration with which microinvertebrates must endure hydration cycles is thought to affect their fitness in a biocrust habitat. The microinvertebrate species that exist in surface biocrusts must be able to tolerate frequent wetting/drying cycles, brief periods of activity following hydration events, prolonged periods of drought, and extreme temperatures while anhydrobiotic. The surrounding soil conditions, such as texture, depth, and cover, can influence the severity of the abiotic stresses. Soil pores dry out more quickly at the surface than at depth, in coarse relative to fine soils, and in soils with very low organic or vegetative cover than soils with higher cover. As a result, the biocrust microinvertebrate community composition differs somewhat between soils of different depth, texture, and cover (Darby et al. 2010), as does the mobility of microfauna after rain events (Whitford et al. 1981; Parker et al. 1984).

8.5 Where Are Microfauna Found in Biological Soil Crusts?

Perhaps the best characterized aspect of biocrust microfaunal ecology, more so than their feeding habits or life history traits, is the overall abundance and distribution of organisms relative to soil depth, cover type, successional stage, and proximity to vascular plants. Microfauna can generally exist wherever sufficient microbial prey exists, and this usually matches the distribution of plant biomass or organic matter. This means that microfauna are associated with diverse types of biocrusts even in relatively extreme environments or with little moisture, such as sand savannas (Neher et al. 2003), desert biocrusts (Belnap and Phillips 2001; Shepherd et al. 2002), tropical inselbergs (Vaculik et al. 2004), and Antarctic soils, glaciers, and hypoliths (Sohlenius et al. 2004; Schwarz et al. 1993; see Chap. 11 by Pointing). In arid systems, nematodes can be found as deep as 11–12 m (Freckman and Virginia 1989), but the peak abundance of microfauna in soils covered by biocrusts is usually within the top 10–20 cm. In most soils, protozoa, nematodes, and microarthropods are more abundant in the surface 0–10 cm than in the next 10–20 cm or 20–30 cm (Darby et al. 2006, 2007a, b, 2010; Housman et al. 2007; Neher et al. 2009). However, the proportion of microfauna that are anhydrobiotically inactive is inversely proportional to soil moisture or relative humidity, and relative humidity in soils below 10 cm is generally greater than in surface 0–10 cm soils. Thus, the abundance of active, hydrated water-film fauna may actually be greater below 10 cm than above 10 cm depth because even though microfauna are generally more abundant above 10 cm than they are below 10 cm, most of them are inactive at the surface (Darby et al. unpublished results). This is potentially significant because if the autotrophic biocrust components are most active at the surface during brief periods after rain events, but the heterotrophic consumers are most active at depth in between rain events, then this means that

productivity and consumption is potentially decoupled in both space and time. The full implications of this spatial and temporal decoupling have not been explored experimentally.

The second most determining factor of the abundance and distribution of microfauna is the distribution of vascular plants. Microfauna are generally more abundant and taxonomically diverse close to plant rhizospheres than in the inter-space between plants (Darby et al. 2010; Housman et al. 2007). This is generally true for all ecosystems, but it is easier to quantify in arid systems with more sparsely distributed vascular plants. Furthermore, microfauna are more abundant and taxonomically diverse beneath and associated with late-successional stage “dark” lichen and moss biocrusts than when associated with early-successional stage “light” cyanobacteria biocrusts (Darby et al. 2006, 2007a, b, 2010). This can reasonably be explained, as greater productivity and microbial prey biomass is found in lichen and moss biocrusts than in cyanobacteria crusts. It has also been observed that nematode communities are more “ecologically mature” in late-successional stage biocrusts than early-successional stage crusts (Darby et al. 2007a, b). A greater proportion of the individuals associated with late-successional stage crusts are “K-strategists” (*sensu* Pianka) that are late to develop and have low reproductive output, slow generation times, and longer life spans (Bongers 1990). However, the persistor-type “K-strategist” nematodes that are associated with late-successional stage crusts also tend to be higher trophic levels (such as predators and omnivores). We cannot necessarily distinguish whether predatory K-strategist nematodes are associated with late-successional stage biocrusts due to increased biomass and autotrophic productivity going into the soil food web, or because late-successional stage biocrusts tend to ameliorate temperature and moisture fluctuations that promote persistor-type nematode species. Similarly, physical trampling of surface crusts reduces the biomass and architectural complexity of the lichen, cyanobacteria, and moss cover. This is associated with reduced abundance and species richness of nematodes relative to that of non-trampled biocrusts (Darby et al. 2010). However, we are not yet able to determine whether the effect of physical trampling on reducing nematode abundance and richness is due to the reduced biomass of microfloral prey items or because of the altered hydrology and reduced architectural complexity and pore size distribution of the trampled biocrust surface.

8.6 How Are Microfauna Affected by Surface Disturbance and Altered Climate?

The effect of altered climate on crust microfauna is a complex interaction of temperature, moisture, and the seasonality of these changes. Most microfauna can tolerate relatively high temperatures ($>40\text{--}50^{\circ}\text{C}$) if they gradually enter their anhydrobiotic state, but cannot tolerate being hydrated at high temperatures.

Similarly, many microfauna can tolerate frequent wetting and drying cycles in moderate temperatures, but they incur significant mortality if these wetting and drying cycles are at high temperatures ($>35\text{--}40$ °C). Thus, we predict that neither increased temperature during drought nor decreased moisture during warm seasons is necessarily going to alter microfaunal communities if they are already dormant. Instead, the combination of altered temperature and moisture is likely to be more influential than either alone. However, empirical evidence of the effect of altered temperature and precipitation on microfaunal communities is likely to come only after long-term experimentation (Darby et al. 2011). The primary literature does not have sufficient empirical evidence of the influence of altered climate on desert soil fauna community composition and their role in soil ecosystem functioning, so instead we rely on model predictions. Hunt and Wall (2002) addressed this challenge in temperate food webs by asking the question “how many species does it take to maintain ecosystem function?” They compared food web dynamics run to steady state after deleting each of the 15 functional groups, one at a time. They found that only two functional group deletions (i.e., bacteria and saprophytic fungi) resulted in the extinction of other groups, and only three functional group deletions (i.e., bacteria, saprophytic fungi, and herbivorous nematodes) resulted in a 10 % alteration in some index of ecosystem function (i.e., nitrogen mineralization or primary production). They concluded that “the results suggest that ecosystems could sustain the loss of some functional groups with little decline in ecosystem services, because of compensatory changes in the abundance of surviving groups.” However, we suggest that the wholesale loss of entire functional groups is an unlikely scenario from climate change predictions. Instead, the more likely changes appear to be subtle and sometimes idiosyncratic shifts in the relative proportions (or species composition) of existing functional groups (Sohlenius and Bostrom 1999; Todd et al. 1999; Convey and Wynn-Williams 2002). Intolerant species that are lost from a functional group are often replaced by what appears to be redundant species of a similar functional group (Todd et al. 1999; Bakonyi and Nagy 2000). Thus, rather than addressing the question “how many species does it take to maintain ecosystem function,” it would be more prudent to ask, “what happens to ecosystem function after a directional shift in species and functional group composition?”

To address the question “what happens to ecosystem function after a directional shift in species and functional group composition?” we first have to identify a likely directional shift in community composition and the functional significance of that change. In the case of biocrusts, we have observed that nematodes are affected more negatively by these abiotic stresses than amoebae (Darby et al. 2011). Because nematode body size is an order of magnitude greater than amoebae, they are expected to respire less per unit of biomass than amoebae (West et al. 1997, 1999; Ryszkowski 1975). Thus, nematodes contribute proportionately more to nitrogen cycling through dissolved organics (Wright 1975a, b), while amoebae contribute more to nitrogen cycling through excretion of inorganic nitrogen (Hunt et al. 1987). In sum, climate changes of increased temperature and summer precipitation could decrease the abundance of nematodes more than that of amoebae and shift the balance of nitrogen cycling by reducing the relative contributions of

dissolved organics and increasing the relative contributions of labile inorganics. This is significant because ammonium, the form of inorganic nitrogenous wastes by nematodes and protozoa, can be oxidized rapidly in this system (Johnson et al. 2005) and exported through leaching of nitrate (Johnson et al. 2007). Future research should be careful to compare the balance of organic and inorganic nitrogen in desert soils and determine whether changes in soil microfauna affect these substrate pools (Belnap et al. 2005).

8.7 Future Directions and Research Priorities

In the last decade we have learned much about the microfauna in biocrusts, including who are the main taxa and functional groups, what important functions they perform, when they are most active, where they exist in relation to depth and vegetative cover, and how they are affected by physical disturbance and abiotic stresses. We have identified three areas of research that we believe will be most beneficial in leading us toward a more complete understanding of the importance of microfauna in biocrust systems: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

8.7.1 Feeding Behavior

For most families and genera in biocrusts, we have a reasonable idea of what potential prey items they *could* consume (largely based on the size and shape of feeding structures), and what some of their sister species *likely* consume (largely based on published reports of feeding trials or tissue analysis), but we most likely do not know what the biocrust species *actually* consume. The two main pieces of information that need to be distinguished for each species are (1) the full breadth of *acceptable* prey items and (2) the subset of *preferred* prey items. Accomplishing this goal will require multiple different empirical approaches, such as culturing assays with feeding trials (Wood 1973a, b), molecular gut content probing (Treonis et al. 2010), stable isotopes (Darby and Neher 2012), and phospholipid fatty acid signatures (Buse et al. 2013; Ruess et al. 2005). This is important information because even though each functional group of biocrust fauna is represented by multiple species, we have no way to confirm whether or not these species are truly functionally redundant as we do not know if there are actually more subtle feeding preferences. This is especially true for taxa that are broadly considered omnivorous (e.g., stylet-bearing nematodes of Dorylaimida and some Tylenchidae). In many of these cases, we do not know whether omnivorous genera represent many species who themselves are all omnivorous, or if they represent many species who

themselves are all specialists but on different trophic levels, so that the genus as a whole appears omnivorous.

8.7.2 Increased Taxonomic Resolution

Most studies of biocrust microfauna are performed at the taxonomic resolution of family or genus. This provides enough information on the broad feeding or functional groups that are present but does not provide enough information to distinguish between biocrust and underlying soil species, nor does it allow comparison of species composition across studies in geographically distinct locations. We still do not know whether the species of a particular genus inhabiting biocrusts of one site are the same species of that genus inhabiting the soil beneath the biocrust or even if they are the same species of that genus inhabiting biocrusts at a different site. There is a clear possibility that many of the species found in biocrusts have yet to be described (as in Pilato and Beasley 2005). To further our understanding of the ecology of biocrust food webs, there is a need for future ecological studies to aim for species-level taxonomic resolution in their enumeration of biocrust microfauna. This is challenging, but molecular techniques such as high-throughput amplicon sequencing (Bik et al. 2012; Darby et al. 2013; Steven et al. 2014) are making high-resolution enumerations rapid, accessible, and informative. Various methods of specimen preservation are available to allow for the recovery of both molecular and morphological information (Yoder et al. 2006). Thus, species-level taxonomic resolution can be obtained by combining, from the same specimen, both molecular sequence data and virtual morphological vouchers by digital multifocal imaging (De Ley and Bert 2002). The cumulative benefit of increasing taxonomic resolution to the species level will be to allow more reliable comparison of species composition between communities of different study sites or of different habitats (e.g., biocrust versus underlying soil) within a site.

8.7.3 Ecological Genomics

The effects of abiotic stresses on biocrust microfaunal communities have been studied mostly by the application of acute short-term experimental treatment (such as heat, desiccation, and UV radiation). However, the chronic, long-term implications of abiotic stresses on biocrust microfauna community composition have not been well studied, nor have we been able to quantify the consequences of changes in community composition on ecosystem processes. We believe this is largely because our understanding of the genetic and genomic adaptations of biotic and abiotic stress on biocrust microfauna lags behind that of the research on biocrust microflora (Zelikova et al. 2012; Steven et al. 2014). This is a significant research need, because the role of microfauna in ecosystem-wide functioning is

linked to the physiological traits that allow biocrust microfauna to survive in this unique habitat. If we can understand how biocrust microfauna are adapted to the biocrust habitat at a genetic and genomic level, then we may be better able to predict the ecosystem implications of changes in species composition. For example, the relative composition of waste nutrients that are mobilized by microfauna is thought to be related to the stoichiometry of the biomolecules that are used and extracted by the organism (Sterner and Elser 2002). Sugars and simple carbohydrates are high C-containing biomolecules, proteins are rich in N, and nucleic acids are one of the molecules that contain a large proportion of phosphorous. Thus, the biomolecules that microfauna use and synthesize in response to biotic and abiotic stress are biased in their chemical stoichiometry (Elser et al. 2000), and we can use ecological genomics approaches to understand how microfauna are adaptations to environmental stress and how these adaptations will influence the environmental cycling of key nutrients. Fortunately, advances in high-throughput sequencing technologies allow for more advanced genomic analysis of non-model organisms from ecological systems (Ungerer et al. 2008). Ecological genomics approaches can be used to identify the adaptively significant genomic variation that may lead to our understanding of how changes in community composition affect the functioning of biocrust microfauna.

8.8 Conclusion

In conclusion, biocrusts serve as unique habitat for a broad range of microfauna, including protozoa, nematodes, tardigrades, rotifers, mites, collembolans, and even larger arthropods and mollusks. These microfauna feed on the bacteria, cyanobacteria, algae, fungi, bryophytes, and plant roots that are found in the biocrusts. Consumer food web as a whole performs several important functions, such as cycling nutrients, dispersing propagules, and moderating their microbial prey populations. Many species of biocrust microfauna tolerate periods of drought in an anhydrobiotic dormant state, so they are typically active only during brief windows of time. Most microfaunal groups tend to be more abundant, species rich, and diverse in mature, late-successional stage biocrusts that are dominated by diverse microflora (such as lichens, bryophytes, fungi, and cyanobacteria) than in early-successional stage biocrusts that are dominated by less diverse microflora (such as cyanobacteria alone). Biocrust microfauna are susceptible to the same surface disturbances that affect biocrust microflora, such as physical trampling or altered temperature and summer precipitation, but the specific ecosystem consequences of altered community composition due to surface disturbances are still largely unknown. To fully understand the ecosystem consequences of biocrust microfauna, we propose that the three main research needs in the future are to: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify

the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

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Chapter 9

Composition and Macrostructure of Biological Soil Crusts

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9.1 Introduction

Surface crusting, even at small spatial scales, has a strong impact on many soil properties, which ultimately determine various ecosystem functions (Assouline 2004). Being a physical discontinuity in the soil profile (Coppola et al. 2011), a soil crust changes the soil structure and morphology of the soil surface, therefore changing soil properties such as infiltration, runoff, and erosion. It is crucial to understand and to describe the spatial structure of biological soil crusts (here referred to as “biocrust” because this term has been recently gaining favor as it is short and understandable, although less precise) and to classify different surface structure types in order to understand the influence of biocrust structure on those soil properties. The structure of biocrusts itself is affected by numerous physical, biological, and chemical characteristics, all of which may as well interact with each other, making a classification and general statements challenging.

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9.2 Abiotic Crust Structure

Abiotic crusts can be either physical or chemical. Chemical crusts occur wherever mineral-bearing water evaporates, leaving behind precipitating soluble salts, gypsum, carbonates, or silica, or when the soil above an illuvial horizon (enriched in minerals) is eroded. Chemical crusts (also termed duricrust; Woolnough 1927; Khalifa et al. 2009) reduce the hydraulic conductivity of the soil. Physical soil crusts are either formed by raindrop impact that destroys soil aggregates (resulting in soil compaction) or by direct soil compaction provoked by livestock trampling or vehicles, which again causes a reduction of hydraulic conductivity (Assouline 2004). There are three types of physical crusts: (1) structural crusts, formed by rearrangement of soil particles without lateral movement; (2) depositional crusts that develop as a consequence of lateral movement of sediment (Chen et al. 1980); and (3) erosional crusts, which are comprised of only one thin, smooth surface layer that is enriched in fine soil particles and which results from the erosion of a structural crust (Valentin and Bresson 1992). While chemical crusts are restricted to areas with high evaporation, physical crusts can occur in various environments and in almost all textures, except on very coarse sandy soils (Lemos and Lutz 1957).

9.3 Biocrust Structure: Biotic Influences

In nature, soils are never sterile, so it is difficult to draw the line between an abiotic and initial biocrust. Here, we define a soil crust as “biotic” when the organisms play any ecological role, such as altering fertility, stability, or soil structure. Soil structure, topography, and morphology, here in the range of millimeters to only a few centimeters, are strongly determined by the size and the shape of the occurring organisms themselves.

Filamentous pro- and eukaryotic algae form the matrix of biocrusts and grow in the uppermost millimeters. There, they are important for initial soil particle aggregation that leads to enhanced soil stability. Pócs (2009) describes two main cyanobacterial crusts: (1) the epiterraneum type, having all photosynthesizing components above the soil surface and therefore needing UV-protective pigments, and (2) the subterraneum type, which has at least one active, photosynthesizing layer below the soil surface. In the subterraneum type the uppermost layer of soil or rock protects the organisms from fast desiccation. The resulting crusts are horizontally structured (Fig. 9.1a), and in sandy soils layering may be observed. With higher cyanobacterial abundance in flat crusts, the physical status of the soil changes, for example, by having finer grain sizes, lower infiltration rates, lower soil moisture contents, and an almost four times higher breaking pressure (Zaady et al. 2014). On the other hand, cracks in cyanobacterial crusts, that either derive from frost or biogenic (Fig. 9.3), can increase infiltration and therefore soil moisture. Cyanobacteria influence soil cohesion and resistance to erosion. The filamentous

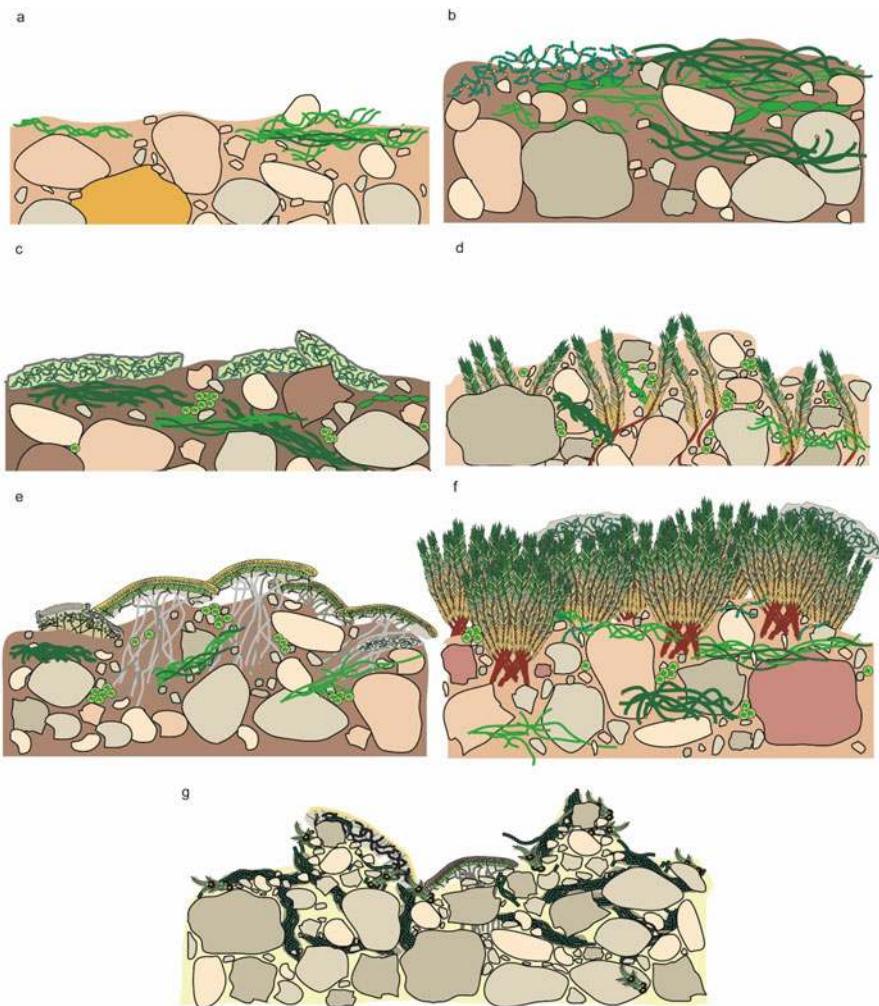


Fig. 9.1 Schemes of typical biocrust types. (a) Light or thin cyanobacterial crust. Filamentous cyanobacteria (*Microcoleus* sp.) dominate this crust, which is only a few millimeters thick. Patches of bare soil are visible. (b) Dark or thick cyanobacterial crust. Besides the filamentous species of *Microcoleus*, also coccoid species (*Nostoc* colonies) and other filamentous cyanobacteria (*Phormidium*) form this up to 5 mm thick biocrust. (c) Crustose “rugose” cyanolichen biocrust. Different *Collema* species or other cyanolichens dominate this crust type, but free-living cyanobacteria and green algae occur as well. (d) Rugose moss crust. Moss stems grow mainly embedded within the uppermost centimeters of soil. Only the uppermost leaves or the fruiting bodies rise over the soil surface. (e) Rolling chlorolichen crust. Mainly crustose and squamulose chlorolichens on top of the soil with rhizines penetrating deep into the soil dominate this crust type. Other components like cyanobacteria or green algae are also free living in this biocrust. (f) Rolling “thick” moss crust. Up to 5 cm thick moss carpets and cushions with cyanobacteria and green algae living on top of or in between the stems. (g) Pinnacled crust. Turret-like structures are elevated over the ground surface where organisms prevent soil erosion

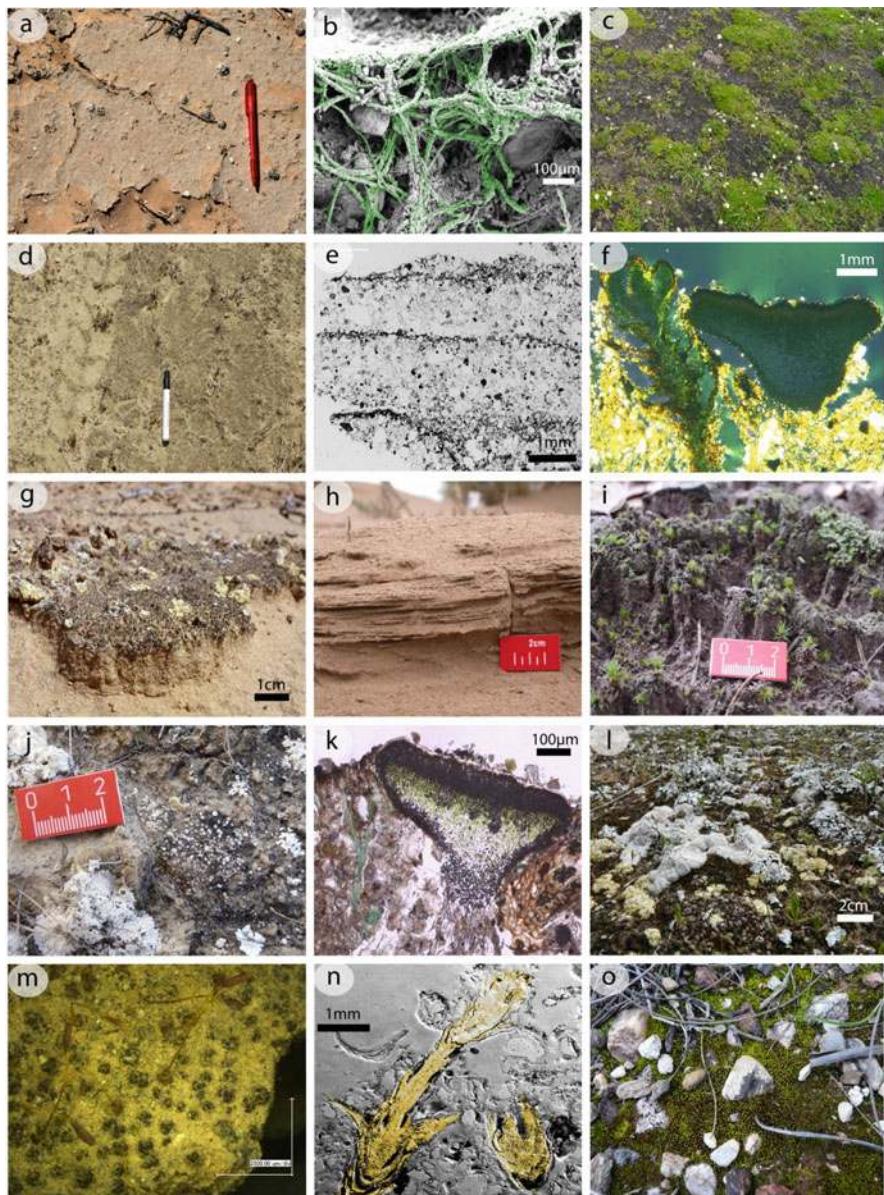


Fig. 9.2 Soil crust forming organisms and their structure. **(a)** Cyanobacterial crust with patches of bare ground visible. **(b)** Cross section through a green algae (*Zygoonium*)-dominated biocrust; the filaments are smoothly aggregated at the surface but also penetrate into the soil and aggregating soil particles. **(c)** Dark cyanobacterial crust including green algae. Picture from the wet and humid orobione in the high Austrian Alps. **(d)** Dark cyanobacterial crust showing the influence of mechanical disturbance. **(e)** The effect of oversanding and the layering of cyanocrusts. **(f)** Chlorolicichen thalli growing in close association with moss stems. **(g)** Crustose cyanolichen crust. Lichens grow closely associated with the soil and form a more or less hard layer. **(h)** Burial by sand of several layers of biocrusts, Tengger Desert, China. **(i)** Pinnacled soil crust. Turret-like structures are elevated over the ground surface, where organisms prevent soil erosion. **(j)**

microorganisms trap sand particles and finer particles stick on the filament surfaces (Fig. 9.2b). Soil porosity is also increased by the microbial cover, with additional pores delineated by filaments on the surfaces of crusts and porous organic bodies derived from microbial remains at depth (Malam Issa et al. 1999). Biocrusts consisting of green algae are equivalent to cyanocrusts in being horizontally structured (Lan et al. 2012). Initial algal crusts show an inorganic surface layer with no or few algae from 0 to 0.02 mm, followed by a dense algal layer at a depth of 0.02 to 1 mm and a sparse algal layer underneath that at a depth of 1 to 5 mm (Lan et al. 2012). In the temperate zone, these crusts cover the soil surface more or less completely forming a smooth green carpet that can be easily removed from the soil surface when dry (Belnap et al. 2003).

Unlike soil cyanobacteria and algae, lichens and bryophytes with their complex thalli have almost all of their photosynthetic tissue on or above the soil surface. The above-surface thalli create roughness of the biocrusts' surface. In addition, capping of the soil surface provides protection from raindrop erosion (Fig. 9.2i). The size and type of biotic structures (i.e., organism morphology) can control the amount of dust captured, which ultimately defines the resulting sedimentary features. For example, the leaf structure of mosses controls the size of trapped grains (Fig. 9.2n), and the high shrink–swell potential of gelatinous lichens and incremental dust accretion cause the formation of sharp surface topographies (Fig. 9.2g). Thallus parts below the surface, such as rhizines of lichens or rhizoids and protonemata of bryophytes, create soil aggregates and extend the stabilized soil structure deeper into the soil (Figs. 9.1c–e and 9.2f, k). In contrast to the filamentous pro- and eukaryotic algae, these thalloid organisms add a vertically growing component to the biocrust and allow three-dimensional expansion (Fig. 9.2 l). Lan et al. (2012) describe lichen crusts as showing a thallus layer up to 1 mm above the soil surface, a rhizoid layer from 0.1 to 3 mm, and a sub-rhizoid layer from 3 to 7 mm depth. Depending on the lichen species, the above-ground layer thickness (as a proxy for surface roughness) can be even higher (Fig. 9.2j, l). For example, a crustose lichen-dominated biocrust from Antarctica was found to be 4.5 mm thick (Colesie et al. 2014a), whereas for fruticose or foliose lichen-dominated biocrusts, this may be in the range of several centimeters (Fig. 9.1e). Lan et al. (2012) describe typical moss-dominated biocrusts characterized by a stem–leaf layer, which stands 2 mm above the soil surface, a rhizoid layer from 0.2 to 6 mm depth, and a sub-rhizoid layer at depths of 6–15 mm from Chinese deserts. Generally, in dry habitats thin moss crusts with the stems being deeply embedded into the soil

◀
Fig. 9.2 (continued) Chlorolichen crust. *Psora decipiens* growing crustose on the soil surface (Photo by L. Williams). (k) Chlorolichen thallus and cyanobacterial filaments embedded tightly into the soil in a crustose chlorolichen crust (Photo by M. Cardinale). (l) Natural appearance of chlorolichen-dominated crusts, in this case the Bunte Erdflechten Gesellschaft (colored lichen community). (m) Moss-dominated crust. Individual moss stems are mainly embedded into the soil, and only the upper parts are visible on the surface. View from above. (n) Moss stems in moss-dominated crusts are embedded into the soil. Moss tips catching sand grains. (o) Natural appearance of the thick moss-dominated crust

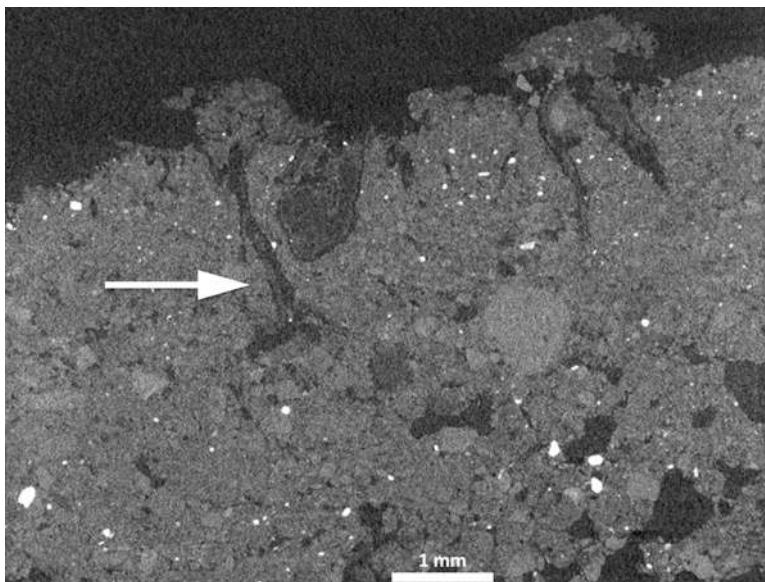


Fig. 9.3 CT scan of a cross section through a dark cyanobacteria/lichen crust from the Karoo, South Africa. Biogenic macropore (arrow) besides buried lichen (CT scans by courtesy of Stephan Peth and Rainer Horn, soil sample by courtesy of Bettina Weber)

(Figs. 9.1d and 9.2m) are frequent, but short and tall mosses occur there as well. In wetter habitats the moss layer gets thicker (Figs 9.1f and 9.2o).

9.4 Biocrust Structure: Abiotic Influences

9.4.1 *Macroclimatic Influences*

On a continental scale, only a few studies exist that correlate macroclimatic influences to biocrust occurrence and diversity. These studies include Büdel et al. (2009), Green et al. (2011), and Colesie et al. (2014b) and were conducted in southwestern Africa and the ice-free Drylands of Antarctica. They present descriptions of the cryptogamic composition and diversity of biocrusts extending over several degrees of latitude being correlated to the overall macroclimate. Interestingly, the studies show that (1) water availability has the strongest influence on biocrust occurrence and composition (therefore structure), and (2) biocrust occurrence is much more the result of the natural scenery and water availability than of regional macroclimate. In Fig. 9.4 we indicate macroclimatic regions in different colors and include recent findings and descriptions of different biocrust types into the same map (marked as different symbols). It becomes obvious that

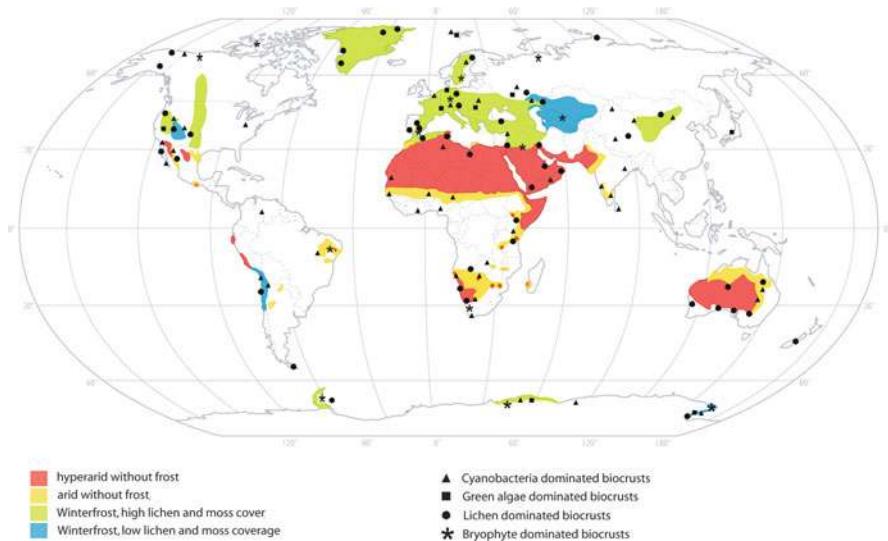


Fig. 9.4 Distribution of biocrusts on Earth. Macroclimatic regions are color-coded. Symbols indicate individual locations of diverse crust types dominated by different organism groups (their distribution may be much more extended). Each of the four color-coded macroclimatic regions include all types of different crust types (different symbols), either defined by topography or taxonomic composition. Data based on Büdel (2003), Orlovsky et al. (2004), and personal observations of authors until recently

macroclimate cannot be correlated to biocrust type on a global scale. Each of the four color-coded macroclimatic regions include all types of different crust types (different symbols), either defined by topography or taxonomic composition. This finding can be interpreted in the concept of zonal vs. azonal vegetation that was first applied by Walter in 1985. He distinguishes between zonal vegetation, the vegetation/plant occurring typically in a certain climatic zone, and the azonal vegetation/plant, occurring inside another climatic zone but, due to the local meso-/microclimate, resembling the climate of its origin. Single biocrust communities can be considered as functional types, and besides the zonal biocrust type, other types occur azonal according to the local variation of the meso-/microclimate.

On a regional scale, the general temperature regime of a biocrust habitat can have a formative influence on its structure mainly by controlling the species composition. Also frost heaving, freezing events, and the rainfall regime of an area are relevant for biocrust formation and structure. There are a few general trends for biocrust structure being influenced by regional climate:

- Cyanobacterial biocrusts (smooth, rugose, or pinnacled) mainly occur in geographical regions with an at least temporarily expressed arid element (tropical, subtropical, mediterranean, dry continental but also the arctic-alpine climatic (higher altitudes) zones; Figs. 9.1a, b and 9.2a, c, d).

- Green algal biocrusts (smooth, rugose, or pinnacled) preferentially occur in temperate but also arctic–alpine (lower altitudes) climatic zones (Fig. 9.2b, c).
- Lichens and bryophytes add to the primary crusts (rolling crusts) in habitats with higher water availability (Fig. 9.2l, o).
- The difference between the occurrence of cyanobacterial lichens or green algal lichens as a dominant component of the biocrusts depends on the type of water source. If rainfall is the predominant water source, cyanobacterial lichens become an important element of biocrusts, whereas if dew and/or high air humidity are prevailing, green algal lichens dominate the climax state of local biocrusts.
- Bryophyte presence depends on the total amount of water per annum and the frequency of wet–dry cycles (e.g., Hoppert et al. 2004; Büdel et al. 2009; Reed et al. 2012).

9.4.2 Mechanical Disturbance

Different kinds of mechanical disturbance, such as human influences (trampling, vehicular traffic), and burial by soil particles (see also Chap. 21 by Zaady et al.) affect biocrust structure. Soil disturbance by humans, livestock, or vehicles flattens the biocrust. Since the structure of biocrust changes greatly with succession (Williams et al. 2012), a mechanical disturbance sets this succession and attendant structure back to an earlier level (Kuske et al. 2011, Fig. 9.2d). Although only very few studies explicitly investigated the impact of disturbance on soil microstructure, it is well known that biocrust disturbance drastically increases the soil susceptibility to both, wind (Belnap and Gillette 1998; Zhang et al. 2006) and water erosion (Eldridge 1998; Herrick et al. 2010), which always results in a depletion of fine soil particles, thus changing the structure to a more coarse-grained one (Belnap et al. 2007). Further, the reduction of soil carbon and nitrogen after disturbance (Kuske et al. 2011) will cause a breakdown of organo-mineral complexes and ultimately decrease aggregate stability of micro- and macroaggregates (Amézketa 1999), resulting in higher compaction and a partial breakdown of the secondary pore system (Horn und Peth 2012).

To our knowledge, the only available study that explicitly investigated the influence of mechanical disturbance on internal biocrust structure was conducted by Menon et al. (2011). Using 3D computed tomography techniques and the Lattice Boltzmann method on a disturbed Kalahari Desert cyanobacterial crust, they detected a significant reduction of the modeled water flow through the crust after disturbance, which they also attribute to the loss of secondary pores and paths of preferential infiltration.

Burial by soil is a special kind of disturbance for two reasons. First, it does not actively destroy the biocrust structure; rather it significantly reduces light and water availability in the microenvironment (Rao et al. 2012). Second it can, to a certain degree, induce or promote a structuring process (Fig. 9.2e, h). A study on the impact

of burial in the Hopq desert, China, found that if the thickness of burial by sand does not exceed a threshold of 1 cm, it can actually promote a structuring process by applying selective stress on the biocrust organisms that favors mobile genera (e.g., *Microcoleus*) (Rao et al. 2012), which can move upward to the new surface, thereby creating new surface layers (Feldé et al. 2014). However, if the sand burial height exceeds this threshold, the biocrust is severely damaged (Rao et al. 2012) and may not be able to recover. Here, it should be considered that burial by quartz sand may be tolerated to a larger depth compared to silt or clay, as the former has better light-transmissive qualities (Ciani et al. 2005).

9.4.3 Pedogenic Influences

In contrast to many studies that focus on the influence of biocrusts on soil properties, very little is known about the influence of soil properties on biocrust structure. This is an important field of research, as biocrusts may not establish or structure soils equally on different soil types. The main processes of the formation of biocrust structure and topography as described by Williams et al. (2012) for the hot Mojave Desert, USA, are (1) mineral precipitation and stabilization, (2) wetting–drying with resultant expansion–contraction of soil, (3) dust capture, (4) microscale mass-wasting, and (5) biologically mediated vesicular horizon formation. For biocrusts in the Mojave Desert, these processes lead to the formation of two layers at the macroscale, called the bio-rich and bio-poor zone of the crust. At the microscale, they describe nine distinct morphological features: (1) filament sheets, (2) filament knobs, (3) upturned or curled features, (4) rafts, (5) pedestals, (6) towers, (7) micro-hoodoos and sharp protrusions, (8) curved features, and (9) biosediment bridges. The unique characteristics of each of these nine features are tied to associated biota and vary with crust type.

Some other trends for pedogenic influences on biocrust structure are suggested by Belnap (2006). Biocrusts with similar species and biomass are flatter when they occur on clay and silty soils compared to those on adjacent coarser soils. In soils with weak crystalline structures (e.g., soils derived from calcite and gypsum), extracellular polysaccharide materials combine with the dissolved minerals when soils are wet to create very strong microbial sheaths that consist partly of organic and partly of inorganic materials. The internal strength of these soils resists winter frost heaving, and thus they do not form the highly dissected surfaces that may be found in adjacent sandy soils. Cyanobacteria generally dominate soils that are very sandy (>90 %), very salty, or have a high content of shrink–swell clays, regardless of the climatic zone. Lichen cover generally increases with an increase in the amount of carbonate, gypsum, and/or silt in the soil (Belnap et al. 2003). The importance of the silt content for vesicle formation is highlighted by Dietze et al. (2012), who showed that vesicular horizons can be found in a large variety of texture classes under natural conditions, which, however, always have a high silt content. In soils with heavy physical crusting, the surface morphology of biocrusts

is primarily controlled by soil physical and chemical characteristics, and the biological components have only a limited effect. If only cyanobacteria are present under these circumstances, the resultant biocrusts are smooth. If lichens and mosses colonize as well, the slight roughening of the soil surface creates a rugose or rolling crust. Pinnacled crusts seldom form in soils with a high degree of physical crusting.

9.5 Classification of Biocrusts

There are multiple ways to classify biocrusts. Classification can be based on species composition, functional groups, or a combination of surface appearance and functional groups (Table 9.1 and Fig. 9.2). All approaches have advantages and disadvantages.

Composition Approach This is the most desired but most expensive approach, as it provides information on biocrust morphology as well as species composition. The advantage of an approach based on taxonomic composition is that knowledge on the species composition also comprises information on the ecological roles of that biocrust. The drawbacks are that it is time-consuming, and expertise on field identification of lichens, mosses, and other biocrusts components is needed.

Functional Group Approach Eldridge and Rosentreter (1999) first provided a framework to classify biocrusts on the level of morphological groups (see also Chap. 7 by Rosentreter et al.). The advantage of using such an approach is that less expertise is needed to identify organisms on a species level. Büdel et al. (2009) utilized this approach along a 2000 km long transect through South Africa and southern Namibia, using a classification of biocrusts based on the dominating organism group. The authors distinguish seven general crust types: light

Table 9.1 Suggested classification of different biocrust types

Surface texture	Biocrust appearance	Dominant organism group	Thickness	Characteristic localities (examples)
Smooth	Light	Cyanobacteria, green algae	0–2 mm	Negev Desert
	Dark	Cyanobacteria, green algae		Austrian Alps, Alaska, Australia, Central Europe, Karoo, savannas
Rugose		Cyanobacteria	2–4 mm	Sonoran Desert, Tengger Desert, Gobi Desert, Central Europe
Rolling	Thin	Lichens	5–50 mm	Namibia, Greenland, Columbia Plateau, Tabernas badlands, Russian steppe
	Thick	Mosses		Iceland, Columbia Plateau, maritime Antarctica
Pinnacled		Cyanobacteria, lichens, mosses	6–150 mm	Colorado Plateau, NE Australia, Central Europe

cyanobacterial crust, cyanobacterial crust, cyanobacterial crust with cyanolichens, cyanobacterial crust with cyanolichens and/or green algal lichens, crust with bryophytes, hypolithic crust, and the unique Namib Desert lichen fields.

In addition, the functional groups used can be defined relative to the questions of interest. For example, if nitrogen inputs are of interest, then having two categories for lichens, those that fix nitrogen and those that do not, would be necessary. If soil stability is of interest, separating lichen types best at stabilization (e.g., foliose) from those less good (e.g., crustose) can be useful.

Combined Approaches There have been two main combined approaches suggested over time. Belnap (2003) developed four categories that combine surface morphology and functional groups: (1) Smooth crusts that consist mostly of endedaphic cyanobacteria, algae, and fungi. The soil surface consists mainly of mineral particles and has a very low surface roughness. We suggest subdividing this category into two subtypes, light smooth crusts (Fig. 9.1a) and dark smooth crusts (Fig. 9.1b). The light subtype is almost exclusively composed of endedaphic cyanobacteria and extremely flat (Fig. 9.2a). The dark subtype may rise a few millimeters upon the surface, has a higher abundance of organisms, and appears like a smooth carpet covering the ground (Fig. 9.2c). Smooth biocrusts represent the initial stage of crust development and are also very common in areas with frequent disturbance. (2) Rugose crusts that are also dominated by cyanobacteria and fungi. They have a low surface roughness (up to approx. 3 cm), originating from scattered lichen and/or moss clumps (Fig. 9.1c, d). (3) Pinnacled crusts that are generally dominated by cyanobacteria but can have up to 40 % lichen/moss cover. They exhibit a micro-topography of up to 15 cm, resulting from frost heaving and subsequent differential water erosion (Figs. 9.1g and 9.2i). (4) Rolling crusts that are dominated by a lichen/moss cover, creating a gently rolling surface (Fig. 9.1e, f). The heavy lichen and moss cover restricts pinnacle formation during frost heaving to a height of approx. 5 cm, due to the strong cohesion of the lichens and mosses.

The second type of a combined approach utilizes the overall appearance or dominant genera of the biocrust. Belnap et al. (2008) suggested a classification using surface coloration, roughness, and presence of different biocrust components as an indicator for the level of development (LOD) of biocrusts. For the SE Utah crusts that were studied by the authors, they developed six categories with the lightest type of cyanobacterially dominated biocrusts designated as LOD Class 1, and the darkest type dominated by cyanobacteria, but also containing mosses and lichens designated as LOD Class 6. The authors noted that this index could be extended to higher numbers for biocrusts dominated by lichens and mosses. This approach has the advantage of a quick and easy classification for experts and nonexperts alike and allows an easy classification of biocrust types, facilitating a worldwide comparison of biocrusts. The disadvantage is a highly generalized scheme of crusts and complications with a categorization of lichen- and moss-dominated crusts.

9.6 Conclusions

Classification of biocrusts can be based on macroscopic structures, taxonomic composition, and overall appearance (including color) or combined by overall morphology and taxonomic composition. However, a universal classification system in more detail than given here is disputable. First, the composing organisms and the various proportions of them have significant influence on the macrostructure of a biocrust. Second, physical parameters such as climate and physical and chemical soil properties impact biocrust macrostructure, to various extents.

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Chapter 10

Controls on Distribution Patterns of Biological Soil Crusts at Micro- to Global Scales

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10.1 Introduction

Like all biological phenomena, biological soil crusts (biocrusts) are spatially variable. Considerable research has been devoted to determining what drivers generate this heterogeneity. The earliest investigations, to our knowledge, are

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those of Rod Rogers in Australia in the early 1970s (Rogers 1972, 1973). He developed a continental scale conceptual model depicting biocrust type and abundance as a function of amount and seasonality of rainfall (Rogers 1973). In the 1990s, additional work in Australia further delineated the types of biocrusts occupying a system of landscape types (Eldridge and Tozer 1997). In the early 2000s, Belnap and Lange (2003) synthesized in several chapters what was known about the composition and characteristics of biocrusts within different continents and regions, and two chapters addressed the specific drivers of biocrust distribution at multiple scales and their quantitative relationships with biocrusts or particular biocrust components (Garcia-Pichel and Belnap 2003; Ullmann and Büdel 2003). At the time the latter two chapters were written, the amount of literature to be reviewed was sparse, and the collective knowledge was that there were a few key soil properties (alkalinity, calcareousness, gypsum concentration, texture) and climate-related factors (continentality, annual precipitation, thermal regime) known to commonly influence biocrust abundance or composition (Eldridge and Tozer 1997; Rogers 1972). Also in Belnap and Lange (2003), Büdel (2003) provided the first global study of the biogeography of biocrust genera. As our science has progressed, literature on this topic has accumulated, and the geographic scope of our regional knowledge of biocrust distributions has expanded in North America (e.g., Bowker et al. 2005; Ponzetti and McCune 2001; Rivera-Aguilar et al. 2006; Root et al. 2011), Asia (e.g., Rosentreter et al. 2014; Tirkey and Adhikary 2005; Zhang et al. 2007; Zhang et al. 2011), Africa (e.g., Büdel et al. 2009; Lalley et al. 2006; Zedda et al. 2011), the Middle East (e.g., Abed et al. 2010, 2013), and Europe (e.g., Concostrina-Zubiri et al. 2013; Martínez et al. 2006). Our synthesis presented here does not encompass the distribution of hypoliths (see Chap. 11 by Pointing).

10.1.1 Nomenclature for Scale

Because biocrust distribution patterns may differ based on the spatial scale of observation (Bowker et al. 2006a; Concostrina-Zubiri et al. 2013), we adopt the following nomenclature to denote scale. Microscopic and submillimeter scales (Garcia-Pichel and Belnap 2003) are discussed in another chapter (see Chap. 13 by Garcia-Pichel et al.) and are thus omitted here.

Global scale—Pertaining to variability across all habitats in the world (e.g., Büdel 2003)

Intracontinental scale—Pertaining to variability across a continent or major land mass [e.g., Australia (Eldridge 2003), North America (Rivera-Aguilar et al. 2006)]

Ecoregional scale—Pertaining to variability across an ecologically defined (based on environmental conditions, major vegetation associations, etc.) portion of a major land mass [e.g., Gurbantunggut Desert (Zhang et al. 2007)]

Local scale—Pertaining to variability within a collection of nearby sites [e.g., a local altitudinal-climatic gradient (Hernandez and Knudsen 2012) or a comparison among soil types (Bowker et al. 2006a)]

Intra-site scale—Pertaining to variability within a “typical” (as defined by most literature) sample unit which may range from multiple 10s of m² to 1 ha (Bowker et al. 2005, 2006b; Büdel et al. 2009; Concostrina-Zubiri et al. 2013; Eldridge and Tozer 1997), such as distance gradients from shrub canopies (Thomas and Dougill 2007) or small-scale soil gradients (Martínez et al. 2006)

Microscale—Pertaining to variability within a few square meters or less [e.g., soil chemistry or texture gradients within interspaces (Bowker et al. 2006a) or micro-aspect effects (George et al. 2000)]

10.2 Determinants of Biocrust Distribution at Different Spatial Scales

The forces underlying the distribution of biocrusts in space can be described as biogeographic, climatic, edaphic, topographic, and biotic (Fig. 10.1). These forces are distinct but partially dependent upon one another. The influence of these forces abruptly shifts from primarily biogeographic at the largest scales, to primarily climatic at intermediate scales, to primarily edaphic, topographic, and biotic at smaller scales. Biogeographic influences are those that act on the dispersal capabilities of the biocrust organisms themselves. For example, distance or degree of isolation is a barrier for biocrust propagule (e.g., spores, cells, thalli) dispersal over long distances (Marshall and Chalmers 1997). We may hypothesize that land masses that are isolated from one another by large distances or lacking connection via major wind patterns will tend to support less similar biocrusts; the temporal duration of this isolation will also act to promote distinction.

Biocrust variation within the dryland biome is primarily climatic. Climatic forces change among geographic areas, with latitude and altitude shaping thermal regimes and rain shadows and continentality further shaping the amount, type, and timing of precipitation received. For example, several different, yet contiguous, dryland regions are present in western North America and are distinguished by climate (e.g., Chihuahuan desert, hot/arid to semiarid, dominated by summer rainfall; Great Basin, cool/semitropical, dominated by winter rain/snow).

At ecoregional and smaller scales, biocrust variation is dictated increasingly by edaphic, topographic, and biotic forces. The physical and chemical properties of soils are determined by the parent materials and the degree of weathering that these parent materials have undergone. Most ecoregions are a mosaic of different soils, and substantial heterogeneity exists within a given soil, even at the very smallest scales. At smaller scales, topographic influences generate deviations from larger-scale climate patterns. The erosional-depositional setting generates geomorphological features that can be important across ecoregional to microscales. Biotic forces,

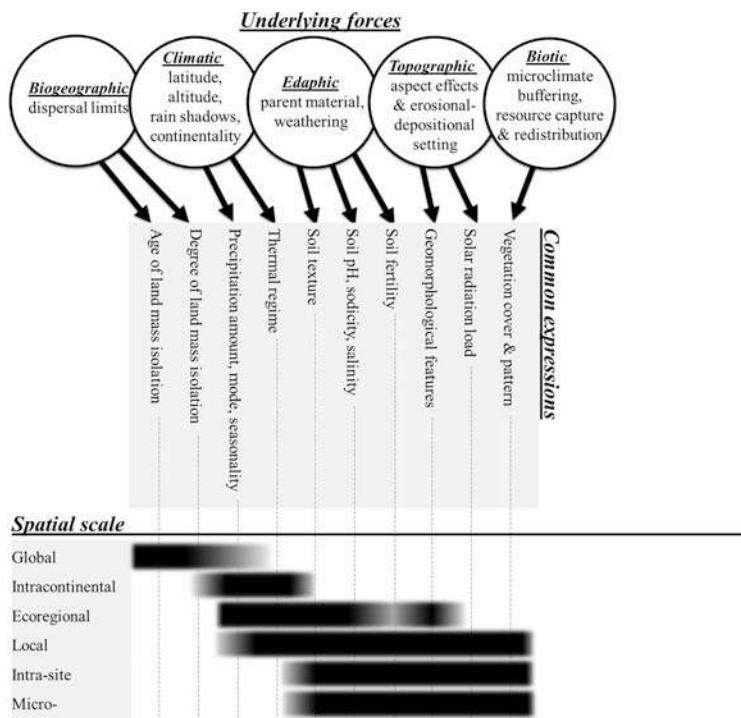


Fig. 10.1 Scale dependency of forces underlying biocrust distribution

especially the type and arrangement of vascular plants, are additional modifiers by providing shade and capturing or redirecting the flow of resources (e.g., water, nutrients, litter, and/or soil) at local or smaller scales.

10.2.1 Biogeographic Factors

Since the first description in the late eighteenth century by Pallas (1776), the presence of biocrusts has been reported in hot and cold deserts around the world, as well as having some presence in other biomes. However, little is known about the main determinants of their composition, distribution, and abundance at the biogeographic scale (Steven et al. 2013). Despite this situation, some intracontinental studies suggest biogeographic patterning of biocrusts. In a 2000 km transect in southern Africa, the six different dryland ecosystems surveyed had distinct biocrusts (Büdel et al. 2009). Similarly, arid to subhumid regions supporting biocrusts differ strongly in community composition within North America (Rivera-Aguilar et al. 2006).

Table 10.1 Number of species in biocrusts reported for different organism groups on different continents worldwide

	Europe	N. America + Greenland	S. America	Africa	Australia	Asia	Antarctica	Global
Cyanobacteria	98	53	40	83	58	82	66	320
Eukaryotic algae	137	86	1	76	3	179	44	353
Mosses + liverworts	90	45	22	22	131	28	14	320
Lichens	212	226	4	77	72	126	42	551
Total	537	410	67	258	264	415	166	1544

Compiled from: Büdel et al. (2009), Dojani et al. (2014), Haarmeyer et al. (2010), Zhao et al. (2008), Belnap and Lange (2003), Pichirtova et al. (2013), Eldridge and Tozer (1997), Rogers (2006), McCune and Rosenzweig (2007), De los Rios et al. (2011), Nagy et al. (2005), Pushkareva and Elster (2013), Pócs (2009), Frey et al. (1990), Fritsch (1916), Hu et al. (2003), Eldridge and Koen (1996), Eldridge and Koen (1998), Pointing et al. (2009), Stewart et al. (2011), Detweiler-Robinson et al. (2013b), Tirkey and Adhikary (2005), Phillipson (1998), Flechtner et al. (2008), Flechtner et al. (1998), Flechtner (2007), Hawkes and Flechtner (2002), Lewis and Flechtner (2002), Montoya et al. (1998), Novichkova-Ivanova (1972), Novichkova-Ivanova (1980), Azúa-Bustos et al. (2009), Azúa-Bustos et al. (2011), Forest and Weston (1966), Williams and Büdel (2012)

A meta-analysis of species composition and richness of biocrusts compiled from the literature revealed a total of 1544 cyanobacteria, algae, bryophyte, and lichen species worldwide. When compared on a biogeographic scale, lichen species numerically dominate the European and North American floras, whereas bryophyte and liverwort species prevail in Australian biocrusts (Table 10.1). Europe and Asia stand out as having the highest species numbers of cyanobacteria and eukaryotic algae (Table 10.1). These patterns may indicate a geographic imbalance of biocrust species diversity data and/or possibly of taxonomic expertise.

We conducted a floristic similarity analysis using the Sørensen coefficient (Q_s) that weights matches in taxon composition of biocrusts between two samples. As a consequence of the uneven species richness data from continents and sub-continents, this analysis can only be regarded as a first approach to the real conditions.

Cyanobacteria are the most ancient group of biocrust organisms, appearing up to 2.6 billion years ago on land, and as might be expected, they are also the most homogenous when compared among land masses. Even for the most isolated continent, Antarctica, the similarity with all other continents is >10 % (Fig. 10.2a). This pattern may reflect either a common community prior to the breakup of Pangaea or possibly a very effective intercontinental dispersal via the atmosphere. With the exception of South America, lichens are quite well investigated in terms of diversity. The high similarity coefficient between Europe and North America (Fig. 10.2c) might be explained by the long connection between these continents in geological history, but may also be an artifact of more extensive sampling in these regions and therefore a greater degree of detection of the species present. Bryophytes and eukaryotic algae have not been investigated as thoroughly as lichens, and species numbers are much lower, making reliable comparisons possible only for restricted geographic regions (Fig. 10.2b, c). One clear pattern that emerges is the distinctness of the bryophyte flora of Australia from other land masses, possibly reflecting its long-term isolation. While cyanobacteria occur in biocrusts across the globe, eukaryotic algae are more common on continents with a higher proportion of temperate regions (Tables 10.2 and 10.3).

From this preliminary diversity analysis of biocrusts, we can conclude that biocrusts contribute considerably to the biodiversity of the ecosystems to which they belong (also see Chap. 1 by Belnap et al.), despite the species assessment of biocrusts being far from sufficiently known. As most of the data presented here are based on classical determinations and only a few on molecular studies, we would like to emphasize that it is of great importance to relate operational taxonomic units generated by molecular data to described taxa. Only with those analyses can we thoroughly test biogeographic hypotheses.

Fig. 10.2 Sørensen floristic similarity coefficient (Q_s) at the species level between continents for (a) cyanobacteria, (b) eukaryotic algae, (c) bryophytes including liverworts, and (d) lichens. Values below a Q_s of 10 % are not shown; species numbers are given in red numbers at each continent; Q_s in black numbers at each connecting line between continents; bold lines indicate Q_s values of 30–39 %; semi-bold lines between 20 and 29 %, and thin lines between 10 and 19 %

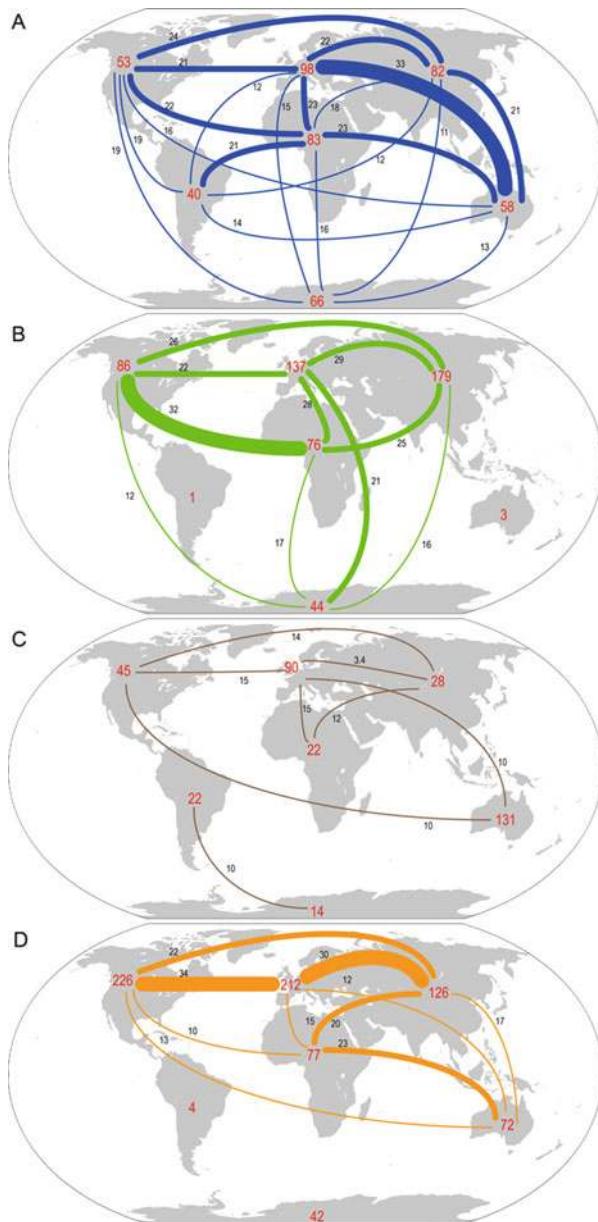


Table 10.2 Distribution of algae with a 43 % frequency (three out of seven continents)

	Europe	N-America + Greenland	S-America	Africa	Australia	Asia	Antarctica
<i>Bracteacoccus minor</i> (g)			insufficiently investigated				
<i>Pinnularia borealis</i> (d)							
<i>Klebsormidium montanum</i> (g)							
<i>Stichococcus bacillaris</i> (g)							
<i>Hantzschia amphioxys</i> (d)							
<i>Desmococcus olivaceus</i> (g)							
<i>Klebsormidium flaccidum</i> (g)							
<i>Klebsormidium crenulatum</i> (g)							

d = diatom, g = green alga

10.2.2 Moisture Availability

That moisture influences biocrust distribution at multiple scales has been amply demonstrated on multiple continents (Belnap and Lange 2003). In general, where space between plants is large, biocrust abundance and level of development increase with moisture availability (Bowker et al. 2006a; Büdel et al. 2009; Kidron et al. 2010). However, as vascular plant and plant litter cover becomes more continuous, there is less available habitat for biocrusts (Bowker et al. 2005) and less light reaching the soil surface (Belnap et al. 2003). In the most hyperarid regions (Aridity Index < 0.05; Pointing and Belnap 2012; e.g., Atacama, Sahara, Negev, Colorado deserts), biocrusts contain only a low biomass of microbial components (e.g., endedaphic cyanobacteria, bacteria, and fungi). Arid zones often support primarily cyanobacterial biocrusts with subdominant mosses and lichens (Kidron et al. 2010; Pietrasik et al. 2011a). As aridity further decreases, cyanolichens become more prevalent, followed by chlorolichens (Galun et al. 1982). Mosses and liverworts are generally only found in wetter microhabitats (e.g., under shrubs, on polar exposures), due to their higher moisture requirements than lichens and cyanobacteria. In cooler semiarid deserts and grasslands (e.g., Colorado Plateau, Columbia Basin, and Great Basin, USA; Gurbantunggut Desert, China), soil moisture is much more abundant, and the cover and biomass of biocrusts, especially bryophytes and lichens, increase until they often fully cover soil surfaces (Ponzetti and McCune 2001; Marsh et al. 2006; Zhao et al. 2014).

Table 10.3 Most frequent species

	Aus-tralia	Africa	S-Amer-ica	Antarc-tica	Asia	N-Amer-ica + Greenland	Europe
<i>Nostoc commune</i> (c)							
<i>Microcoleus vaginatus</i> (c)							
<i>Coleofasciculus chthonoplastes</i> (c)							
<i>Trichocoleus sociatus</i> (c)							
<i>Chlorella vulgaris</i> (g)							
<i>Bryum argenteum</i> (b)							
<i>Schizothrix calcicola</i> (c)							
<i>Nostoc microscopicum</i> (c)							
<i>Diploschistes diacapsis</i> (l)							
<i>Diploschistes muscorum</i> (l)							
<i>Heppia despreauxii</i> (l)							
<i>Placidium lacinulatum</i> (l)							
<i>Placidium squamulosum</i> (l)							
<i>Psora decipiens</i> (l)							
<i>Toninia sedifolia</i> (l)							
<i>Fulgensia fulgens</i> (l)							
<i>Tolyphothrix byssoides</i> (c)							
<i>Collema tenax</i> (l)							
<i>Klebsormidium flaccidum</i> (g)							
<i>Peltula patellata</i> (l)							
<i>Collema coccophorum</i> (l)							
<i>Heppia lutescens</i> (l)							
<i>Bryum caespititium</i> (b)							
<i>Placidium pilosellum</i> (l)							
<i>Microcoleus paludosus</i> (c)							
<i>Nostoc muscorum</i> (c)							
<i>Ceratodon purpureus</i> (b)							
<i>Calothrix parietina</i> (c)							
<i>Nostoc punctiforme</i> (c)							
<i>Aphanothecce saxicola</i> (c)							
<i>Stigonema ocellatum</i> (c)							
<i>Chroococcidiopsis</i> spp. (c)							

c = cyanobacterium, g = eukaryotic alga, b = bryophyte or liverwort, l = lichen, black = in all areas (100 %), dark gray = 6 of 7 continents/subcontinents (86 %), gray = 5 of 7 continents/subcontinents (71 %), light gray = 4 of 7 continents/subcontinents (57 %)

10.2.3 Moisture Mode, Seasonality, and Temperature Effects

In addition to the total amount of precipitation received, the timing, frequency, and size of precipitation events are critical in determining the species composition of biocrusts. Summer monsoonal events can be large but are often short and intense, with little water infiltrating into the soils. Soil temperatures after summer events can rise quickly, and rapid evaporation rates result in short activity times for biocrusts. Small rain events, especially combined with the high temperatures of summer, also

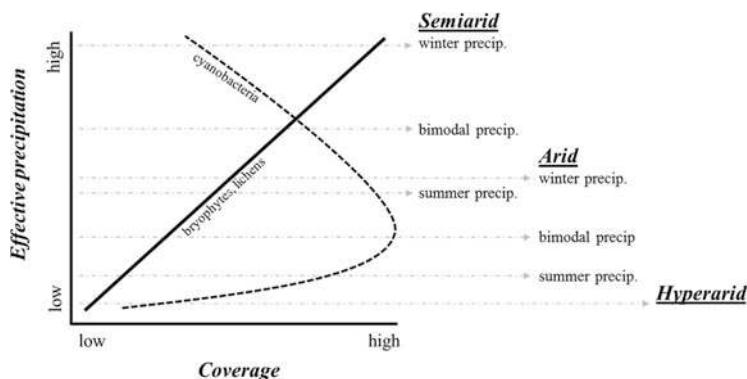


Fig. 10.3 Conceptual model depicting the general interplay of amount and timing of precipitation and its influence on community composition in biocrusts. The model applies to cool to hot semiarid and drier zones, excluding polar and alpine regions, fog deserts, and unique or unusual edaphic environments such as gypsiferous soil

result in short activity times. When wetted, all biocrust organisms respire carbon, but the replacement rate of this carbon is species specific; thus, only some species are able to handle short wetting times (e.g., Lange 2003). Other species will die: experimentally repeated frequent small rain events resulted in moss mortality within only a few months on the Colorado Plateau, USA (Reed et al. 2012). Garcia-Pichel et al. (2013) recently showed that the cyanobacterium *Microcoleus vaginatus* dominates cool desert soils dominated by winter precipitation, whereas *Microcoleus steenstrupii* dominates hot arid to semiarid deserts with summer precipitation. Thus frequency of rain events may also influence biocrust composition at a given locality.

The lichen composition of biocrusts has been observed to also vary where rainfall timing is different (i.e., winter versus summer dominated) in North America (Rosentreter and Belnap 2003), Africa (Büdel et al. 2009), Australia (Eldridge 2003), and Asia (Mongolia to Uzbekistan; Belnap pers obs). Figure 10.3 illustrates in a general sense how amount and seasonality of precipitation codetermine absolute and relative abundance of different groups of biocrust species in these drylands.

The type of precipitation is also important in determining the composition of biocrusts. Cyanobacteria, and therefore also cyanolichens, require liquid water for photosynthesis, whereas green algae and chlorolichens can also utilize water vapor (Lange 2003). Thus, in deserts where most moisture is derived from fog and dew (e.g., Namib, Atacama, central Negev), the lichen flora is dominated by chlorolichens, and cyanolichens are generally absent. In addition, fog and dew are more effectively captured by species with a three-dimensional growth form (e.g., foliose lichens) compared to those appressed (e.g., crustose lichens) to the surface.

10.2.4 Soil Properties

Biocrust cover, richness, and composition are strongly influenced by differences in soil properties at ecoregional to microscales. The extent to which the biocrusts themselves have an effect on underlying soil properties by forming a stable, nutrient-rich, near-surface layer is described elsewhere (see Chap. 1 by Belnap et al., Chap. 13 by Garcia-Pichel et al., and Chap. 23 by Weber et al.).

At ecoregional and local scales, parent material influences substrate quality and degree of weathering, directly affecting soil water-holding capacity (Noy-Meir 1973) and thus indirectly controlling the distribution and composition of biocrusts. Biocrust organisms have been shown to vary in abundance and richness among soils derived from different parent material (e.g., sandstone and shale bedrock-derived soils on the Colorado Plateau in the western USA, Bowker et al. 2006a; on igneous, sedimentary, and metamorphic bedrock-derived soils in the Mojave Desert, Belnap et al. 2014) or in soils subjected to different levels of weathering (e.g., fluvisols, regosols, and calcisols in the Tehuacan Desert, Mexico; Rivera-Aguilar et al. 2006). For example, filamentous cyanobacteria can flourish in sandy, poorly aggregated soils, which are less likely to support highly developed lichen and moss communities (Root and McCune 2012), whereas mosses and lichens are more likely to reach their strongest development on calcareous or gypsiferous soils (Bowker et al. 2006b; Bowker and Belnap 2008; Martínez et al. 2006).

Globally, the most significant soil properties influencing the ecoregional-scale cover and richness of biocrusts in dryland environments are soil texture, pH, and to a lesser extent, soil calcareousness (e.g., Rogers 1972; Eldridge and Tozer 1997; Ponzetti and McCune 2001; Eldridge 1996; Lalley et al. 2006; Lobel et al. 2006; Bowker and Belnap 2008; Root et al. 2011; Ochoa-Hueso et al. 2011). At smaller local, intra-site, or microscales, however, biocrust distribution and cover are tightly coupled to a relatively narrow range of soil physical and chemical properties, often in idiosyncratic ways. Biocrusts are likely to respond to small gradients in nutrients, such that small-scale changes in microrelief, temperature, and/or soil characteristics such as texture, salinity, structure, porosity, and oxidation can potentially play an important part in determining patterns of fine-scale distribution (Bowker et al. 2006a).

The concentrations of macro- (C, N, P, Ca, K, Mg) and micro- (Cu, Fe, Mn, Zn) nutrients are also important in influencing biocrust distribution and composition. Lichens are often associated with high levels of soil N, C, and P (e.g., Read et al. 2008) or K (Martínez et al. 2006), but the extent to which these nutrients are the drivers or the result of a well-developed crust is unknown. Lichen and moss biocrusts have been shown to be positively correlated with Mn, Zn, K, and Mg, but can also be negatively correlated with P across a range of spatial scales (Bowker et al. 2005; Bowker et al. 2006a). Similarly, Fe, Mg, and Ca have been shown to be positively associated with lichen cover, while Mn and sometimes Zn have been negatively associated with lichen diversity (Ochoa-Hueso et al. 2011). Other minerals such as Cd, Li, Cu, Mo, and Sr are known to negatively affect either

abundance or diversity of algae (Starks and Shubert 1979). Read et al. (2011) identified the Th/K ratio as a chemical signature that can be a remotely sensed proxy for soil texture and thus predict biocrust distribution (see Chap. 12 by Weber and Hill).

10.2.5 Solar Radiation Load

Most biocrust organisms exhibit the photosynthetic characteristics of “sun” plants (reviewed in Lange 2003). Despite this, the production, abundance, and diversity of biocrusts are often negatively correlated with high radiation at local and smaller scales. This is because high-light habitats are also drier due to shorter residence time of moisture and receive detrimental ultraviolet radiation loads. Polar-facing aspects receive lower radiation loads, resulting in greater biocrust abundance at the local or subhectare scale, on both hillslopes (Nash et al. 1977) and dune slopes (Veste et al. 2001), although not all authors have observed this effect (Dettweiler-Robinson et al. 2013b). Radiation load may also be reduced by shade-providing vascular plant canopies or rocks, favoring greater biocrust abundance at intra-site scales (Bowker et al. 2006a; Li et al. 2010; Maestre 2003), although in the case of plant canopies, burial by litter or dew interception by the plant canopy may counterbalance this positive effect (Hernstadt and Kidron 2005; Thompson et al. 2005). Protruding rocks provide favorable microhabitats and the capture of resources (e.g., nutrient-rich dust and water, spores, biocrust fragments) which, in turn, facilitates biocrust development, especially moss and lichen propagation (Pietrasik et al. 2011b, 2014; Williams et al. 2012, 2013). Even at microscales, different faces of 10 cm biocrust pinnacles (Bowker et al. 2006a; George et al. 2000) or depressions such as hoof prints (Csotonyi and Addicott 2004) may generate different micro-aspects supporting differing levels of biocrust cover or different communities.

10.2.6 Vegetation Cover and Spatial Patterns

At intra-site- and microscales, biocrust communities often differ among habitats when comparing beneath plant canopies and plant interspaces. The influence of plant canopies on soil stability, fertility, and moisture is complex. Plants create shade, increase or decrease dew and moisture inputs to soils depending on their architecture, and collect wind- and waterborne sediments and plant materials at their base, increasing soil fertility. Furthermore, plants facilitate or discourage animal digging and trampling. Often, biocrust absolute cover and richness are greater in microsites with a sparse cover of vascular plants (e.g., Eldridge et al. 2002, 2005; Pintado et al. 2005; Langhans et al. 2010; Zaady et al. 2013) and litter (e.g., Briggs and Morgan 2008; Serpe et al. 2013; Zhang et al. 2013).

However, enhanced biocrust cover and/or richness in habitats nearby or under plant canopies is also reported (Maestre 2003; Bowker et al. 2005; Li et al. 2010) because vascular plants buffer environmental stress by generating distinct microhabitats. Different effects of plants on biocrusts can be mediated by differences in soil type (Eldridge et al. 2005), vegetation community type, plant successional stage (Dettweiler-Robinson et al. 2013a), or intensity of grazing (Root and McCune 2012). For example, when erosion or grazing impacts are high, biocrusts may refuge near shrubs (Zhao et al. 2010, 2011). Effects of plants will also vary according to the distributional pattern of vascular plants (Maestre and Cortina 2002) or the composition of the biocrust community. For example, positive plant-biocrust correlations in space are common for bryophytes, but not necessarily for other biocrust organisms (Pharo and Beattie 1997).

Banded and other patterned landscapes have distinctive distributional patterns of plants and biocrusts. Banded landscapes are usually found on gentle uniform slopes in arid and semiarid climate around the world (Malam Issa et al 1999). Biocrusts play a substantial role in the flow of water, seed, and sediment to the downslope run-on zones that are usually dominated by perennial vegetation (Tongway and Ludwig 1994; Malam Issa et al 1999; Belnap et al. 2005). These source-sink relationships, which operate across at mostly local and intra-site scales, arise largely through the redistribution of water, which exerts tight controls on landscape function, productivity, and diversity (Ludwig et al. 1997). Sources and sinks may sometimes support fundamentally different biocrust communities. For example, sinks tend to be dominated by biocrust morphological types that trap resources (e.g., tall mosses, fruticose lichens), while those in the runoff zones tend to be resource-shedding types (e.g., squamulose and crustose lichens or cyanobacteria; Dunkerley and Brown 1995).

10.2.7 Geomorphological Features

The distribution of dryland biocrusts is shaped by both eolian (Li et al. 2010; Veste et al. 2001) and alluvial geomorphologies (Briggs and Morgan 2008) at ecoregional, local, and intra-site scales. For example, the distribution of biocrusts on the dune fields of the Negev Desert in Israel has been described in detail by several authors [reviewed in Veste et al. (2001)]. Dune crests lack biocrusts, while lower slopes are stabilized by biocrusts and interdune spaces are characterized by higher vegetative cover and biocrusts. Aspect effects may be expressed on dune slopes with mosses becoming more common on north slopes. Zhang et al. (2007) and Li et al. (2010) describe a similar segregation of different organisms on dune crests, hollows, leeward, and windward slopes in the deserts of China. At ecoregional or local scales, different depositional-erosional processes can lead to distinct alluvial geomorphological surfaces, such as outwash slopes, sand plains, or riverine plains, which support distinctive vegetation and biocrust communities (Briggs and Morgan 2008; Eldridge 1996). Similar effects can be observed at

intra-site scales. For example, in the badland clay domes of Tuscany, Italy, biocrust cover increases from the eroded slope to the edge of the eroding surface, but eventually decreases in portions of domes with greater plant cover (Loppi et al. 2004). More recently, a detailed understanding of the ecoregional influence of alluvial geomorphology on biocrusts has been developed for the Mojave Desert (Sect. 10.3).

10.3 The Emerging Understanding of Ecoregional Biocrust Distribution in Three Case Studies

Studies of the controls on biocrust distribution at the ecoregional scale are becoming less descriptive, more predictive, and more often being expressed in the form of maps or conceptual models than in the past. Three case studies including the Sahel region of Africa and both the Colorado Plateau and Mojave Deserts of North America allow some generalizations to be made. First, they support the generalization in Fig. 10.1 that, at ecoregional scales, biocrust distribution is controlled by climatic gradients and edaphic gradients, both of which may be dictated by geomorphological gradients. Second, the specific climatic, edaphic, or geomorphic driver that is most informative differs by ecoregion. Third, heterogeneity in biocrust distribution patterns is largely driven by the degree of edaphic heterogeneity. In an area with a low degree of edaphic complexity (e.g., the Sahel Region), biocrust distribution will be primarily based on (usually) gradual climate gradients. In an edaphically complex region with young soils (e.g., the Colorado Plateau), distinctions among parent materials may be among the best predictors of biocrust distribution. Finally, in edaphically complex regions with older, more weathered soils and complex ancient and modern alluvial features (e.g., the Mojave Desert), geomorphological age may emerge as the most informative parameter.

10.3.1 Case Study: Ecoregional Patterns in the Sahel (Africa)

The Sahel is normally defined as the north to south zone that corresponds to the 200–600 mm mean annual precipitation gradient. It is located between the Sahara in the North and the Sudanian zone in the south and between the Atlantic Ocean in the west and the Red Sea in the east. Previous studies demonstrated that biocrusts (mostly cyanobacterial) are present over a large proportion of the Sahel, mostly in the form of filamentous cyanobacteria (Malam Issa et al. 1999; Valentin et al. 2004). Later, a north-south transect to document biocrusts along a latitudinal rainfall gradient concluded that biocrust fractional soil cover was strongly positively correlated with average annual rainfall, with very little biocrust cover where

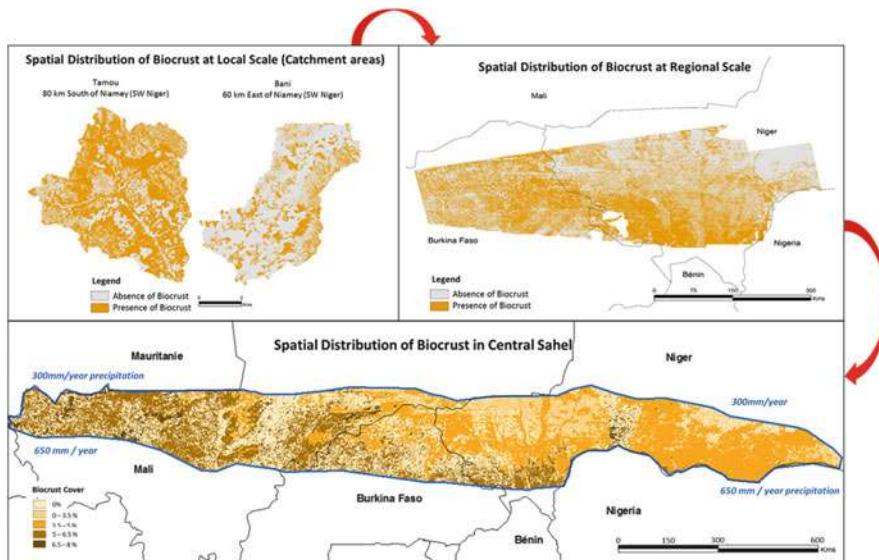


Fig. 10.4 Upscaling of biocrust spatial distribution maps from local scale to ecoregional (central Sahel) based on satellite-derived variables, the ESA GlobCover dataset, and a logistic regression predictive model

precipitation was <350 mm (Malam Issa et al. 2010). A geomorphological gradient was also quite important because it dictated both human use and edaphic properties. Soil cover of biocrusts was observed in the two main representative geomorphological units: ferricrete-capped (erosion-resistant sediment layer cemented by iron oxides) plateau soils with tiger bush vegetation and vegetated sand dune deposits that have lain fallow for up to 10 years.

More extensive data from western Niger and Burkina Faso were used to produce a map of the spatial extent and distribution of biocrusts over the central portion of the Sahel region, based on a logistic regression model that combined annual average rainfall, land use, vegetation cover, and soil types with field data on biocrust fractional soil cover and satellite imagery (Beaugendre et al. 2012; Fig. 10.4). The model was later upscaled for the entire central Sahel (Bontemps et al. 2013). As the region is characterized by two main types of geomorphic surface, a large proportion of the variability in the region is explained by a simple total precipitation gradient.

10.3.2 Case Study: Ecoregional Patterns on the Colorado Plateau (USA)

In contrast to the Sahel, other ecoregions are made up of widely different parent materials and can be expected to exhibit very heterogeneous mosaics of higher and lower quality biocrust habitat. The Colorado Plateau ecoregion is one such area. It is typified by many young soil types and much exposed parent material that ranges from marine limestones and shales to eolian sandstones. A recent ecoregional-scale modeling effort produced a map and statistical model of potential biocrust distribution of the Colorado Plateau (Bryce et al. 2012). The model was based upon an integrated dataset of 593 samples from around the Colorado Plateau and its Northern, Southern, and Eastern ecotones assembled from several sources (summarized in Bryce et al. 2012). All sites were in low-disturbance condition at the time of sampling, and biocrust cover was assumed to be at or near its potential. The models used 16 predictors aimed at capturing key climatic (based on longer-term 1971–2000 averages), edaphic, and topographic influences.

At the ecoregional scale, out of all 16 predictors, the proportional summer precipitation was the single most informative predictor (Fig. 10.5). A threshold was identified, whereby if greater than ~one third of rainfall was received in summer, late successional biocrust cover was only about 2 %, whereas sites receiving a lower proportion of precipitation in summer had anywhere from 6 to 44 % cover, depending on other predictors. The low cover of late successional elements is believed to result from the inability of lichens and mosses to withstand the frequent short wetting events associated with summer precipitation (see discussion above in Sect. 10.2.3; Reed et al. 2012). This result indicates that the seasonality of precipitation can be as influential, or more so, than total precipitation where

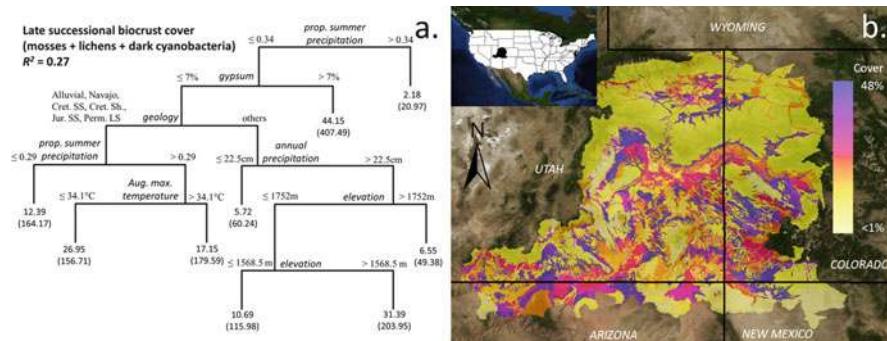


Fig. 10.5 Potential biocrust distribution in the Colorado Plateau ecoregion. **(a)** A regression tree model indicates that the most informative predictor of late successional biocrust cover is proportional summer precipitation. **(b)** A map of potential late successional biocrust abundance based on an ensemble of regression tree models. The palest yellow shades particularly common in the southeastern part of the extent receive mostly summer precipitation and thus have low biocrust potential.

these gradients exist. The next two most informative predictors, percent gypsum and parent material, indicate the tremendous influence that different soil types can have on biocrusts. As the distribution of parent materials on the Colorado Plateau is highly heterogeneous, the map of biocrust abundance and development is a patchwork of biocrust types, with abrupt transitions from very high to very low cover. These characteristics contrast strongly with the more gradual transitions within the Sahel.

10.3.3 Case Study: Ecoregional Patterns in the Mojave Desert (USA)

The Mojave Desert displays typical intermontane basin geomorphology based on a long history of alluvial processes (Peterson 1981). Episodes of erosion, sediment movement, and deposition alternated with periods of stability throughout the Holocene (up to 11,700 years old) and Pleistocene (11,700–2,500,000 years old) eras, creating a mosaic of differently aged soil surfaces that we see today (Miller et al. 2009). It is a more complex geomorphological system than the Sahel, has a greater mixing of soil parent materials than the Colorado Plateau, and is a system where age of surfaces is expected to dictate soil properties and habitat quality.

These geomorphic surfaces are associated with suites of unique environmental factors important to biocrust establishment and propagation, such as surface stability, topography, rock cover, soil texture, and hydrological dynamics. Biocrust cover is greatest on moderately young to intermediate aged (20–7000 years old) surfaces, whereas coverage is negligible on very young (<20 year; e.g., active washes, recent sediment deposits) and very old surfaces covered with well-developed desert pavements (i.e., surfaces of interlocking rock fragments that are at least thousands of years old; Pietrasik et al. 2014; Williams et al. 2013; Belnap et al. 2014).

Moreover, diversity and dominance of biocrust community types varies with geomorphology. Cyanobacterial crusts are most abundant on moderately active sand sheets of Holocene age, suggesting that motile filamentous cyanobacteria can withstand some sand deposition and burial (Williams et al. 2013; Fig. 10.6). In contrast, moss and lichen biocrusts are more prevalent on stable surfaces and are associated with fine-grained substrates that occur between embedded surface rocks (Pietrasik et al. 2014; Williams et al. 2013; Belnap et al. 2014; Fig. 10.5). These conditions are commonly met in soils of early to late Holocene age, with the highest diversity of biocrust types found on moderately young (0.5–1 kyr) surfaces (Pietrasik et al. 2014). Though perhaps less influential than surface age, parent material also influences biocrust type in the Mojave. Soils derived from grussy granites and those containing mixed rock and fine sand show the highest biocrust cover, with cover then decreasing from igneous to limestone to metamorphic-derived soils (Pietrasik et al. 2011a; Belnap et al. 2014; Williams et al. 2013).

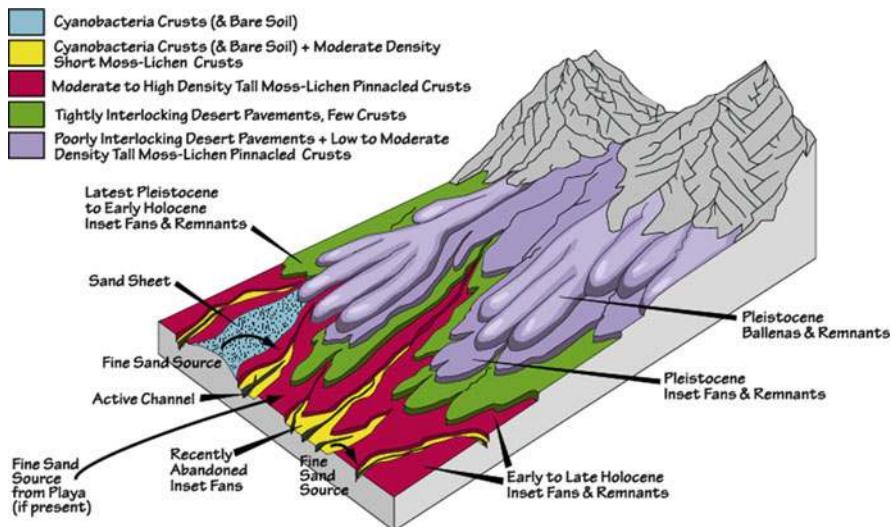


Fig. 10.6 Geomorphic surface type and age predicts interspace cover by biocrusts and desert pavements; reproduced with permission from Williams et al. (2013), courtesy of Elsevier. Fine sand sources include sand sheets, active channels, and alluvial flats or playas (not shown)

10.4 Conclusions: Gaps in Our Knowledge and the Way Forward

Although knowledge has accumulated significantly in the past decade on the distribution patterns of biocrusts and factors controlling the distribution of specific taxa, the state of our collective knowledge is heterogeneous at best. Our missing knowledge can be categorized as geographic gaps and taxonomic gaps.

Most studies on biocrusts have occurred in Australia, China, Europe, Israel, and North America. It has only been in the last few years that surveys have included major portions of Africa and the Indian subcontinent (Büdel et al. 2009; Rosentreter et al. 2014). There remain significant geographic gaps, where few, if any, surveys have been conducted. The biggest gaps currently include central Asia, South America, and the Middle East/Arabian Peninsula (excluding Israel). Data on species composition of biocrusts in South America are especially rare and would benefit from a major research effort in the future. Even within relatively well-studied land masses, there are areas that have received little attention. This is likely a result of uneven distribution of research funding, infrastructure, and the availability of researchers.

Taxonomic gaps arise primarily because few researchers are simultaneously competent in the taxonomy, identification, or molecular characterization of all of the diverse groups of biota encompassing biocrusts and thus do not report on all of them in detail sufficient to build an understanding of their distribution patterns. We

may, for example, have a detailed understanding of lichen distribution, but know little about cyanobacterial distribution, within a given region. A related problem is taxonomic inconsistency, which restrains our ability to compare results from one place to another. In addition, molecular tools are not available to all researchers, making identification of the microbial components of the biocrusts difficult to impossible.

How can we move beyond some of these gaps? The most effective way to fill our information gaps is with more scientific effort. As most of the taxonomists that work on biocrusts are reaching retirement age, this will require training of young scientists in the taxonomy of the different biocrust organisms. To accomplish this, we urge universities to maintain strong programs in taxonomy of these organisms. Also, we should continue to make easily used identification resources such as field guides available to and targeted to the public (rather than taxonomic specialists; e.g., Rosentreter et al. 2007) and transition into web-based resources and smartphone apps.

With additional survey efforts, we can begin filling our data gaps. This information would then allow for intra- and intercontinental comparisons, giving us the ability for truly global-scale studies. The effort required for a global study is clearly too great for any single research group. A promising development has been networked studies, which are becoming increasingly common in a variety of fields. Within the biocrust research community, one such network completed a variety of similarly designed research in multiple arid regions of Africa (Büdel et al. 2009), and another network (Soil Crust InterNational) is currently maintaining a linked set of sites in Europe (Büdel et al. 2014). We envision a multidisciplinary network of international researchers simultaneously sampling biocrusts along key environmental gradients in multiple deserts of the world. The important gradients will differ among ecoregions, but a set of common sampling methods, pooled taxonomic expertise, and pooled analytical capabilities (e.g., soil measurements, GIS, and statistical analysis) will facilitate comparisons among regions.

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Chapter 11

Hypolithic Communities

Stephen B. Pointing

11.1 Introduction

Hypolithic microbial communities develop on the belowground surfaces of translucent stones. These stones are embedded in dryland soils with their dorsal surface exposed, and this allows sufficient light transmission for development of photoautotrophs that dominate these communities. They may be considered as isolated “islands” of biological soil crusts (biocrusts). The major substrates are quartz and marble, and these are ubiquitous in drylands worldwide. They are particularly abundant in desert pavement landscapes that are typical of the most extreme arid drylands, and therefore hypoliths assume a major ecological role under extreme aridity. This chapter describes the hypolithic habitat and how communities assemble at different spatial and temporal scales. Recent advances in understanding the ecological role of hypoliths are discussed, and the potential application of hypolithic systems in applied research is identified.

11.2 The Hypolithic Habitat

Hypolith (derived from the Greek *hypo-* meaning under and *lithikos* meaning stone) is the term used to describe a community largely comprised of microorganisms that develop on the belowground surface of translucent and opaque stones but most typically on quartz (Chan et al. 2012). They are differentiated from other lithic colonizers, such as cryptoendoliths that develop in pore spaces of weathered rocks

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and chasmoendoliths that develop in cracks and fissures of rocks (Pointing and Belnap 2012; Weber and Büdel 2011). They may occur in any environment where substrate exists, although, because this requires an exposed soil surface, it is generally in dryland (herein also referred to as desert) habitats where plant cover is scarce or absent due to aridity. The level of aridity in drylands is defined in terms of moisture deficit within the system by the precipitation: potential evapotranspiration ratio (P:PET), such that dry subhumid regions P:PET <0.65, semiarid regions P:PET <0.5, arid regions P:PET <0.2, and hyperarid regions P:PET <0.05 (UNEP 1992). Many drylands are typified by desert pavement (Fig. 11.1a), a geologically ancient and persistent terrain where quartz and other stones are embedded in the surface soil (Fig. 11.1b; Laity 2008). These extreme arid soils do not generally support a well-developed biocrust, and so a clear ecotone exists between hypoliths and open soil. Hypoliths have also been observed in exposed soils on tropical hillsides and submerged in streams (SB pointing pers. obs.). It is therefore substrate availability, rather than macroclimate per se, that determines the occurrence of hypoliths. Drylands are the largest terrestrial biome and as it is

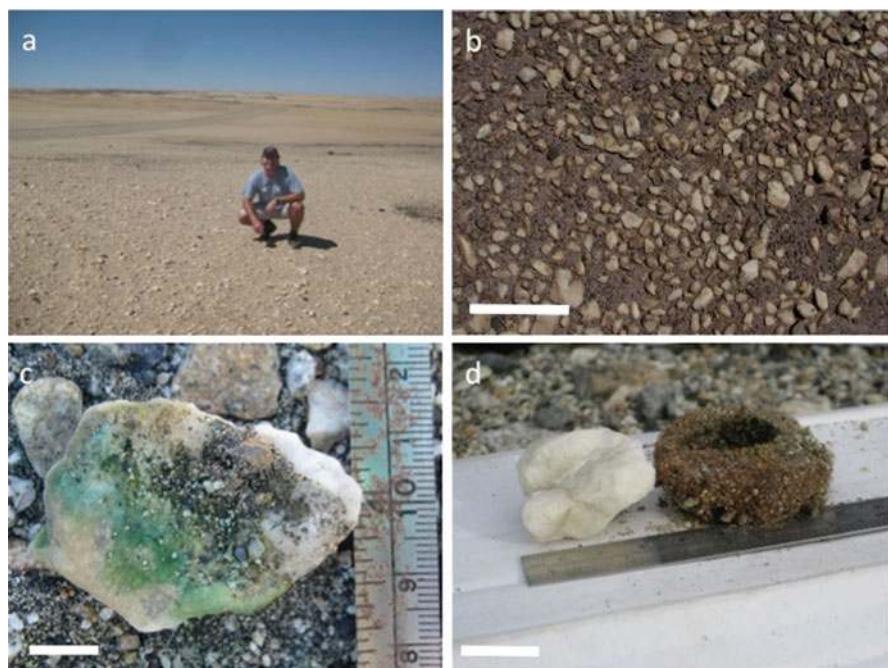


Fig. 11.1 The hypolithic habitat. Desert pavements are extensive in drylands worldwide (a). They comprise quartz and other translucent stones embedded in the soil surface, scale bar 5 cm (b). Hypolithic communities develop on belowground ventral and lateral surfaces, scale bar 1 cm (c). Hypoliths may act as nucleation points for moss development, and this may extend into surrounding soil; here the quartz rock has been removed to show the network of phylloids that develop around the stone, scale bar 2 cm (d)

estimated that up to 50 % of drylands are covered by desert pavement (Laity 2008), dryland hypoliths are therefore of great importance on a global scale.

The dryland hypolithic habitat is characterized by a very specific microclimate that facilitates a level of biocomplexity not possible in surrounding soils. A major factor is the physical size and orientation of the substrate with regard to the soil. Surveys in the Knersvlakte (South Africa), Taklimakan Desert (China), and Tibetan highlands revealed quartz stones were more likely to be colonized if they were physically embedded in the soil (Warren-Rhodes et al. 2007; Weber et al. 2013; Wong et al. 2010). Large stones and boulders may support colonization on below-surface lateral edges, while smaller stones that comprise the majority of hypolithic habitat support hypolithic colonization on ventral surfaces (Chan et al. 2012). The major driver for this is transmittance of photosynthetically active radiation (PAR) and protection from incident UV radiation (Warren-Rhodes et al. 2006, 2013; Wong et al. 2010). The light regime of the hypolithic niche is greatly reduced compared to surrounding exposed substrates, due to the filtering effect of the quartz substrate. This “microbial cabana” effect is a well-documented phenomenon for lithic niches in extreme environments (Pointing and Belnap 2012). Measurements of quartz have shown that near-full exclusion of UV-A and UV-B is achieved under all colonized stones (Cowan et al. 2010; Wong et al. 2010). Levels of PAR reaching the hypolithic niche are typically 50–99 % less than ambient levels (Cowan et al. 2010; Schlesinger et al. 2003; Tracy et al. 2010; Weber et al. 2013; Wong et al. 2010). Quartz of up to 80 mm thickness may be colonized (Tracy et al. 2010), although larger quartz stones are rare since most deposits arise from fragmentation of exposed quartz veins. Hypoliths may also develop on substrates other than quartz, and this includes other translucent rocks such as marble (Cowan et al. 2010), agate, crystals and prehnite (Tracy et al. 2010), and opaque limestone where lateral surfaces receive sufficient PAR to support hypolithic colonization (Cockell and Stokes 2004). Very small stones are less likely to be embedded securely in the substrate and thus do not provide a stable substrate for colonization.

In drylands where moisture input is limiting to biological productivity, the hypolithic substrate provides enhanced moisture availability over surrounding soils. This extends the growing season for hypolithic communities beyond that which macroclimate variables might suggest. The ventral surface of colonized stones has been shown to support higher relative humidity than surrounding open soil surfaces in both hot (Warren-Rhodes et al. 2006; Weber et al. 2013) and polar (Pointing et al. 2009) deserts. Precipitation and fog events may even result in water-saturated soils immediately beneath hypoliths (Warren-Rhodes et al. 2006). Fog has been demonstrated as an important source of moisture to hypoliths in coastal deserts (Azúa-Bustos et al. 2011; Warren-Rhodes et al. 2006, 2013). In polar deserts, the exposed stones may facilitate moisture concentration by trapping wind-blown ice crystals and snow (S.B. pointing pers. obs.). Nonetheless, dryland hypolithic communities face extremely short growing seasons. For example, in the hyperarid core of the Atacama Desert, it has been estimated the growing season for hypoliths is 75 h/year (Warren-Rhodes et al. 2006). Estimates extend to 200–922 h/year in

arid hot and cold deserts of Western China (Warren-Rhodes et al. 2007) and 942 h/year in semiarid Australian desert (Tracy et al. 2010).

The hypolithic niche may also provide a small degree of thermal buffering from extremes of ambient temperature, with less variation on a diurnal basis in hypolithic niches compared to ambient surroundings (Weber et al. 2013). During daylight hours, hypolithic substrates display elevated temperatures relative to surrounding soils and exposed rock surfaces. In the Mojave Desert, hypolithic niche temperatures were 1.1–7.7 °C higher than soils (Schlesinger et al. 2003). In polar hypoliths, this may be a particular advantage where ambient temperatures are very low (Stomeo et al. 2012). Temperature alone is seldom limiting for hypolithic communities in nonpolar deserts (Tracy et al. 2010), although it directly affects moisture availability via freeze thaw and evaporation and influences persistence of moisture.

The combined advantages of stability, radiation, and thermal protection may vary with macroclimate, and this can affect the size of available substrate. For example, a comprehensive field survey of over 13,000 quartz stones in the Atacama Desert (Chile) revealed that the average mean diameter for colonized quartz was 40 mm in semiarid areas, rising to 100 mm in arid and hyperarid areas (Warren-Rhodes et al. 2006).

Hypolithic substrates such as quartz are relatively chemically inert and so have no nutrient value to the community. The underlying soil in drylands is usually extremely oligotrophic, with carbon and nitrogen levels an order of magnitude lower than non-dryland soils (Fierer et al. 2012; Makhalaanyane et al. 2015). The hypolithic substrate can therefore be regarded as an extremely low-nutrient habitat. The more favorable moisture regime in the hypolithic niche beneath quartz has been postulated to lead to increased nutrient levels over time in a small-scale version of the “islands of fertility” that develop in dryland landscapes (Schlesinger et al. 1990; Warren-Rhodes et al. 2007).

11.3 Biodiversity and Biogeography

Hypolithic communities are readily visible to the naked eye as a green biofilm attached to the ventral surface of translucent stones (Fig. 11.1c). Since the hypolithic habitat is characterized by periods of moisture deficit and other environmental stressors, colonists are poikilohydric (desiccation tolerant; Pointing and Belnap 2012) and display adaptations to other stressors in the dryland environment (Chan et al. 2013; Wei et al. 2015a). The protection provided by the stone means that, unlike biocrusts and cryptoendoliths in drylands, hypoliths are not typified by an upper layer of biomass rich in photoprotective compounds (Pointing and Belnap 2012). Instead, they develop as biofilms attached to the stone substrate (Chan et al. 2012). Since the first recorded observations of hypolithic microbial colonization in desert pavements during the 1950s–1970s (Vogel 1955; Cameron and Blank 1965; Friedmann and Galun 1974), a wealth of research has revealed much about their biodiversity and biogeography. Global surveys have revealed the

cyanobacteria are ubiquitous (Bahl et al. 2011; Caruso et al. 2011) and dominant in hypolithic communities worldwide, comprising 47–96 % of recoverable phylotypes (Caruso et al. 2011). Cyanobacteria-dominated hypoliths have been recorded from the Atacama Desert (Chile; Azúa-Bustos et al. 2011; Warren-Rhodes et al. 2006), Australia's northern territory (Tracy et al. 2010), Knersvlakte (South Africa; Weber et al. 2013), Mojave Desert (USA; Schlesinger et al. 2003), Namib Desert (Namibia; Büdel and Wessels 1991; Stomeo et al. 2013; Warren-Rhodes et al. 2013), Negev Desert (Israel; Berner and Evenari 1978), and Taklimakan Desert (China; Warren-Rhodes et al. 2007). Cyanobacteria also dominate hypolithic communities in tundra and polar regions, including Arctic tundra (Cockell and Stokes 2004, 2006), Tibetan tundra (Wong et al. 2010), maritime Antarctic (Cockell and Stokes 2004), and Antarctica's McMurdo Dry Valleys and other ice-free inland areas (Broady 1981, 2005; Cowan et al. 2010; Pointing et al. 2009; Smith et al. 2000; Wood et al. 2008).

The cyanobacterial genus *Chroococcidiopsis* (species names have yet to be agreed for many taxa within this genus) is ubiquitous to hypoliths worldwide and occurs as distinct hot and cold desert variants (Bahl et al. 2011). Hypoliths in less arid locations also support biocrust cyanobacteria such as *Microcoleus vaginatus* and other oscillatorian cyanobacteria (Pointing et al. 2007). An intriguing dichotomy arises between hypolithic cyanobacteria from hot and cold/polar drylands. Hypoliths from warmer nonpolar deserts appear to support mainly the coccoid *Chroococcidiopsis* (Bahl et al. 2011; Friedmann and Galun 1974; Warren-Rhodes et al. 2006, 2007), while those from extreme cold and polar deserts typically have greater abundance of filamentous oscillatorian cyanobacteria (Broady 2005; Cockell and Stokes 2006; Pointing et al. 2007, 2009; Smith et al. 2000; Wong et al. 2010). Comparative deep sequencing of hypoliths from hot and cold drylands supports this delineation (Bahl et al. 2011). The reasons for this are as yet unclear, although one contributing factor may be that *Chroococcidiopsis* is characteristic of a k-selected organism (Pianka 1970). In such organisms, adaptation to the environment is optimized: in this case, the secretion of a copious hygroscopic extracellular polymeric substance (EPS) that may be an adaptive advantage to colonization of hot deserts with prolonged moisture deficit (Chan et al. 2012; Warren-Rhodes et al. 2007; Wong et al. 2010). Conversely, the filamentous Oscillatoriales display relatively rapid growth during favorable conditions of moisture sufficiency that occur briefly during the polar summer and so may be regarded more as r-selected organisms (Pianka 1970). An exception to the cyanobacteria-dominated communities is the unusual red-pigmented hypoliths encountered infrequently in the Atacama Desert, where the dominant taxa are photoheterotrophic Chloroflexi (Lacap et al. 2011). Chlorophyte algae have also been encountered as minor components of some hypoliths (Broady 2005; Cockell and Stokes 2006; Pointing et al. 2009; Smith et al. 2000; Weber et al. 2013). In polar deserts, hypoliths can act as nuclei for localized moss development in the soil adjacent to the quartz stone (B. Weber pers. obs., Chan et al. 2012) (Fig. 11.1d). It has been proposed that the presence of a hypolithic community is a necessary successional stage toward supporting moss development (Makhalanyane et al. 2013; Wong et al. 2010), and this may result in dense networks of phylloids in surrounding soils.

Hypoliths always support a heterotrophic component, and while some phyla are ubiquitous, the heterotrophic component assembles deterministically, according to macroclimate and environmental variables (Caruso et al. 2011). Ubiquitous phyla include the Actinobacteria, Alphaproteobacteria, and Gammaproteobacteria (Makhalaanyane et al. 2012; Pointing et al. 2007, 2009; Valverde et al. 2015; Wong et al. 2010). These may be critical to hypolithic community assembly, whereas others appear to be specific to either polar or nonpolar deserts. For example, the Deinococci appear relatively abundant in warmer deserts (Pointing et al. 2007, 2009; Warren-Rhodes et al. 2006) but are not commonly encountered in polar hypoliths. This may relate to their major adaptation as desiccation-tolerant taxa (Daly 2009). The archaea are absent or a minor component of hypoliths (Pointing et al. 2009; Wong et al. 2010). Fungal phylotypes have been encountered in few studies of hypoliths (Cowan et al. 2012; Pointing et al. 2009; Schlesinger et al. 2003; Wong et al. 2010). Fewer studies have demonstrated lichens growing as true hypoliths, for example, in central Asia (Schubert 1982), the Nama Karoo (Namibia) (Büdel and Schultz 2003), and Tibetan highlands (Wong et al. 2010). Only two studies have attempted to estimate the relative abundance of bacteria, archaea, and eukarya in hypolithic communities, and these suggest that archaea and eukarya comprise <5 % of the overall community in terms of recoverable phylotypes (Pointing et al. 2009; Wong et al. 2010). Higher trophic levels are dominated by nematodes (Smith et al. 2012), although mites, rotifers, springtails, and tardigrades are also encountered patchily and with lower abundance (Courtright et al. 2001; Stevens and Hogg 2002). An as yet unrealized dimension to hypolith biodiversity is that of phages. Studies in other extreme microbial communities indicate phage diversity may be appreciable (Le Romancer et al. 2007), and some exploratory studies on hypoliths suggest they, too, may support diverse phage populations in both hot (Adriaenssens et al. 2014) and polar (Wei et al. 2015b) deserts.

11.4 Patterns of Hypolith Cover

Patterns in hypolithic distribution among colonizable substrate are evident at multiple spatial scales. At a local scale (1–10 km²), evidence of self-organized patchiness has been demonstrated during surveys of arid and hyperarid locations in hot and cold deserts of Western China (Warren-Rhodes et al. 2007). Colonization was characterized by clusters of stones with hypoliths occurring in a spatially predictable manner independent of the underlying pattern of substrate distribution and abiotic variables. Typically, the presence of a colonized stone was a strong indicator that other nearby stones would also be colonized. This was proposed to be driven, at least in part, by biological feedbacks of the hypolith to the local ecohydrological regime and local dispersal dynamics (Warren-Rhodes et al. 2007) in a manner similar to the trigger-transfer-reserve-pulse process observed for vascular plants in drylands (Rietkerk et al. 2004). The proposed mechanism driving this local-scale variability in hypolith cover is shown in Fig. 11.2. Moisture input acts as the *trigger* that results in runoff *transfer* between

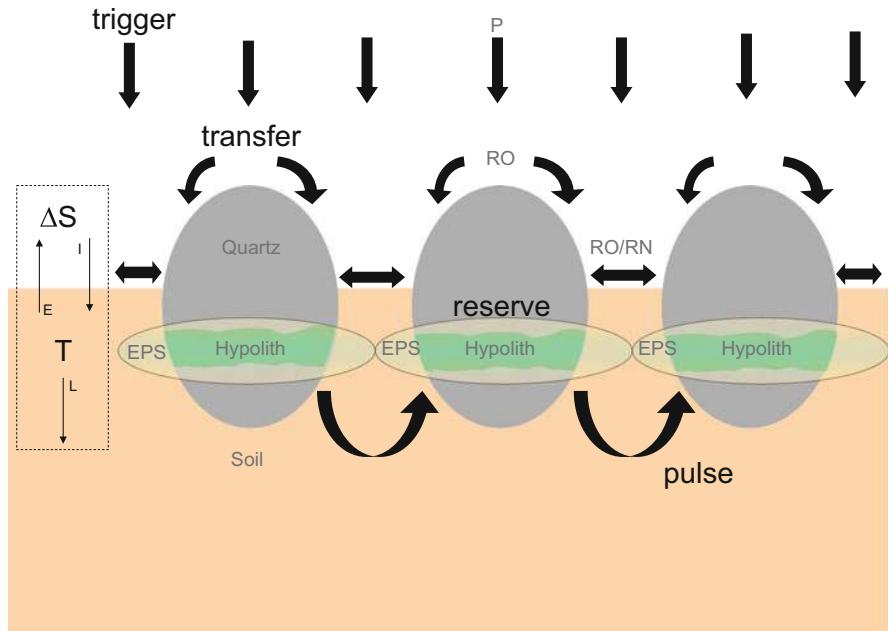


Fig. 11.2 Ecohydrological feedbacks in the hypolithic habitat. Moisture input (trigger) results in runoff (RO, transfer) from the inter-patch, which may be captured as run-on (RN, transfer) by hypolithic patches (reserves). Spatial redistribution of water, soil, and biota may follow trigger events, and large events may move these resources overland to connect patches. Water is stored in soil (ΔS) and hypolithic EPS at rates dependent on EPS properties, soil infiltration (I), and rock/soil properties, such as soil texture (T). Soil water is lost by evaporation (E) or leaching (L). Transfers may result in pulses of hypolithic activity (C, N) and possibly hypolithic colonization of new substrate. Adapted from Warren-Rhodes et al. (2007)

patches of hypolithic colonization. Moisture is then stored within the hypolith EPS as a *reserve* until a *pulse* of favorable conditions allows new hypolithic activity and possible colonization of new substrate.

At landscape scales of tens to hundreds of km², several surveys have reported percentage colonization of available substrate, although others have not factored in total available substrate and so are not true estimates of cover. The largest survey to date was conducted in the Atacama Desert along an aridity gradient from semiarid to hyperarid (Warren-Rhodes et al. 2006). This revealed a gradual decline in colonization of available substrate that occurred from 27.6 % in semiarid landscapes to almost zero at the most hyperarid location. This decrease in cover was also accompanied by a decrease in species richness in the hypolithic communities and shifts in cyanobacterial assemblages toward *Chroococcidiopsis* phylotypes and reduced richness of *Nostocales* phylotypes (Warren-Rhodes et al. 2006). A similar pattern was observed in another large-scale study in the Taklimakan desert and Turpan Depression in China (Warren-Rhodes et al. 2007), where colonization of available substrates declined from 12.6 % to almost zero along an aridity gradient to hyperaridity.

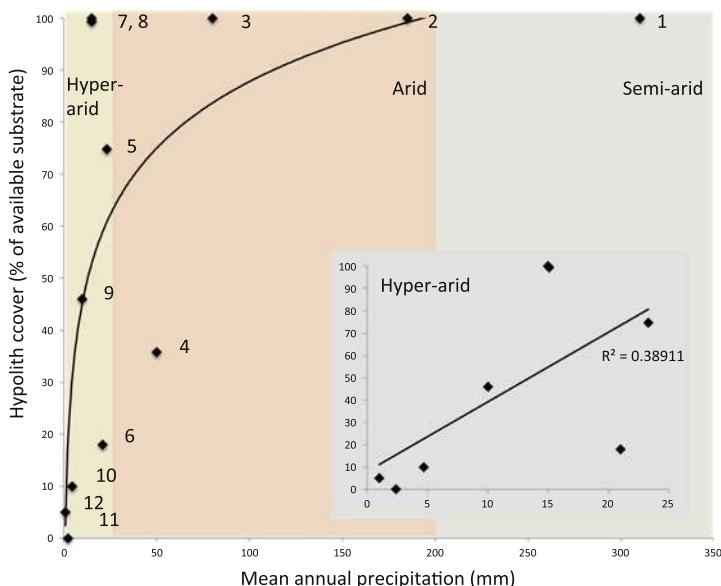


Fig. 11.3 Global scale patterns in hypolith cover. Main graph shows all drylands from semiarid to hyperarid; inset graph shows hyperarid regions only. Numeric labels indicate location: (1) Mojave Desert, USA (Schlesinger et al. 2003); (2) Devon Island, Canadian Arctic (Cockell and Stokes 2006); (3) Namib Desert, Namibia (Stomoeo et al. 2013); (4) Central Tibet, China (Wong et al. 2010); (5) Ruoqiang, Taklimakan Desert, China (Warren-Rhodes et al. 2007); (6) Copiapó, Atacama Desert, Chile (Warren-Rhodes et al. 2006); (7) Sorkuli, Taklimakan Desert, China (Warren-Rhodes et al. 2007); (8) Miers Valley, McMurdo Dry Valleys, Antarctica (Cowan et al. 2010); (9) Turpan Depression, China (Warren-Rhodes et al. 2007); (10) Aguas Calientes, Atacama Desert, Chile (Warren-Rhodes et al. 2006); (11) Yungay, Atacama Desert, Chile (Warren-Rhodes et al. 2006); (12) McKelvey Valley, McMurdo Dry Valleys, Antarctica (Pointing et al. 2009). Values reported are colonized stones as percentage of total available colonizable stones, or inferred from descriptions in the primary literature

An interesting observation was that cold deserts displayed lower cover of available substrate compared to hot deserts, and this was proposed to reflect greater combined thermal and moisture environmental stress (Warren-Rhodes et al. 2007). Clear shifts in hypolithic community structure and a decline in species richness with increasing aridity were also demonstrated for these locations (Pointing et al. 2007). A survey of hypolithic colonization in the polar desert of the McMurdo Dry Valleys in East Antarctica revealed 4.9 % of available substrate was colonized (Pointing et al. 2009). A meta-analysis of hypolith cover from studies of 12 drylands in Africa, Antarctica, China, North America, and South America showed a strong correlation between mean annual precipitation (as a measure of aridity) and hypolith cover globally, regardless of whether the locations are hot, cold, or polar deserts (Chan et al. 2012). Interestingly, within the range for hyperaridity, this relationship displayed a linear correlation, and so predicting cover based on macroclimate may be possible (Chan et al. 2012; Fig. 11.3). A recent study suggests that the magnitude of moisture events may also be important. In the Namib Desert,

the magnitude, rather than the frequency, of precipitation events over time was identified as the greatest predictor of species richness (Frossard et al. 2015). This may, in part, relate to the ability of hypolithic communities to store moisture in EPS (Warren-Rhodes et al. 2007; Wong et al. 2010).

On a temporal scale, hypoliths are assumed to colonize relatively slowly, although evidence is scarce. One study of Atacama Desert hypoliths, using estimates of steady-state residence times of organic carbon, indicated that in semiarid regions, colonization was likely annual, but communities in more arid locations were much older and possibly up to 3200 years old in the most hyperarid location (Warren-Rhodes et al. 2006). It is presently unclear whether hypolithic biofilms have a developmental life cycle and an eventual senescence/dispersal phase (McDougald et al. 2012). The “age” estimates for hypoliths were strongly correlated with estimates of the number of hours per year when hypolithic growth was possible. It may therefore be more appropriate to view the suite of abiotic variables that affect the cyanobacteria-dominated hypolith cover as a collective driver of colonization. In this regard, the botanical concept of the growing season may be applied, where the number of hours in a year when environmental conditions are favorable for photosynthesis to occur will likely prove a strong predictor of cover.

11.5 Biotic Interactions

Biofilms are typically characterized by a level of spatial organization that reflects microbial interactions (Hall-Stoodley et al. 2004). Hypolithic biofilms have been assumed by many researchers to have a relatively amorphous structure, but focused research in this area will likely provide greater insight. It is unlikely that they develop without some level of microscale structure and the interactions that are characteristic of other biofilms (Hall-Stoodley et al. 2004). Current understanding of hypolithic biofilm organization is limited to microscopy studies that have revealed cyanobacteria and other cells embedded in an EPS (de los Rios et al. 2014; Pointing et al. 2007; Warren-Rhodes et al. 2007; Wong et al. 2010).

An understanding of the biotic interactions in hypolithic communities is therefore limited to inference from molecular genetic data. Hypolithic colonists are recruited from low-abundance reservoirs in surrounding soils in less arid deserts (Makhalaanyane et al. 2012), although under extreme aridity locations such as the hyperarid core of the Atacama Desert (Navarro-Gonzalez et al. 2003; Warren-Rhodes et al. 2006) and inland high-elevation parts of the McMurdo Dry Valleys in Antarctica (Pointing et al. 2009), potentially hypolithic cyanobacteria in soils may be undetectable. Antarctic studies have indicated other potential reservoirs for hypolithic colonists in microbial mats from lake margins (Pointing et al. 2009; Wood et al. 2008) and cryptoendolithic communities (Hopkins et al. 2009).

The cyanobacterial component has been identified as a major biotic driver of food web structure in Namib Desert hypoliths (Valverde et al. 2015). Given the ultra-oligotrophic nature of the hypolithic habitat, this may, in part, reflect a role for

photosynthetic exudates and cyanobacterial diazotrophy as nutrient sources for heterotrophic bacteria (Elbert et al. 2012). Another major factor may be the cyanobacterial EPS that serves as a cement for the biofilm likely has an additional role in moisture storage that benefits the community as a whole (Chan et al. 2012). Using ecological network analysis (Valverde et al. 2015), most other co-occurrences of hypolithic taxa have been shown to be positive, suggesting synergistic interactions within the community.

In the absence of significant grazing pressure, it has been suggested that interspecific competition and phage lysis may be important factors controlling community turnover in hypoliths (Wei et al. 2015b). Recent studies lend indirect support to this. Surprisingly high phage diversity has been recorded for hypoliths of hot (Adriaenssens et al. 2014) and polar (Wei et al. 2015b) deserts, and molecular data indicates widespread antibiotic resistance among hypolithic bacteria, which suggests a level of interspecific competition (Wei et al. 2015b).

11.6 Biogeochemical Transformations

Cyanobacteria are photoautotrophs, and thus carbon fixation is a major process in hypolithic communities. Despite this, measurements of photosynthetic activity and carbon fixation in situ are limited to a few exploratory studies (Cockell and Stokes 2004; Schlesinger et al. 2003; Tracy et al. 2010). Estimates of productivity are therefore lacking, but in extreme arid locations where hypoliths are the dominant biomass, they may be the most important source of carbon fixation. Interrogation of Antarctic hypoliths using the GeoChip functional microarray has revealed a diversity of genes for autotrophic carbon fixation among several phyla (Chan et al. 2013). The microarray approach also identified a vast number of carbon catabolism pathways for carbohydrates, proteins, and lipids. A relatively large number of genes for transformation of aromatic compounds were also revealed, suggesting that recalcitrant substrates, including anthropogenic pollutants, could be utilized by hypoliths (Chan et al. 2013).

Nitrogen can be a limiting nutrient in drylands, and so it is not surprising that microarray studies have shown a capacity for nitrogen fixation and full nitrogen cycling in hypoliths (Chan et al. 2013). Potential routes for nitrogen loss from the system (e.g., anammox) have also been demonstrated (Chan et al. 2013). Nitrogen fixation activity has been demonstrated in situ for Antarctic hypolith communities (Cowan et al. 2011) and likely also occurs in nonpolar hypoliths. Several studies have revealed phylotypes of the known nitrogen-fixing genus *Nostoc* in hypoliths from hot, cold, and polar deserts (Cowan et al. 2011; Pointing et al. 2007; Warren-Rhodes et al. 2006, 2007; Wong et al. 2010). It is also likely that the cosmopolitan *Chroococcidiopsis* may be capable of diazotrophy, as acetylene reduction by cryptoendolithic strains has been demonstrated (Boison et al. 2004). An alternate but significant source of diazotrophy in polar deserts may be non-cyanobacterial and derive from Alphaproteobacteria (Chan et al. 2013; Pointing et al. 2009). A

major contribution to dryland biogeochemical transformations may also arise from the physical development of hypoliths. Moisture retention due to EPS secretion and the physical nature of the microenvironment may lead to increased soil fertility over time (Schlesinger et al. 1990), and this may be important for the development of mosses that, in turn, provide soil cohesion and increased nutrient input to soils (Chan et al. 2012). A greater understanding of the functional role for hypoliths in dryland systems should be a priority for future research, particularly since crypto-gamtic covers have been estimated to play a major role in global carbon and nitrogen cycling (Elbert et al. 2012).

11.7 Concluding Remarks

Hypoliths can be viewed as the extreme end of the continuum of colonization for dryland soils. As aridity increases, extensive biocrust cover gives way to a more patchy hypolithic cover, with hypoliths then representing the “last stand” of photoautotroph-dominated biomass in extreme arid drylands. They exhibit distinct biocomplexity, and the keystone cyanobacterial taxa of hypoliths are not those common to biocrusts. In the absence of other significant biota, their contribution to ecosystem processes likely becomes significant, although this is an area that is currently poorly understood.

The ease with which hypoliths can be identified in the field highlights how field ecological research and monitoring can be performed by nonexperts and with minimal reliance on technology, and so it is particularly suitable for study of drylands in developing nations. As a result, greater levels of “citizen science” participation in hypolith surveys are encouraged. The linear relationship between colonization and mean annual precipitation means that measures of hypolith cover may have value in predicting the potential for catastrophic ecosystem shift associated with hyperaridity (Rietkerk et al. 2004). Desert pavements are also under increasing pressure from human disturbance and encroachment (Pointing and Belnap 2014). It may therefore be timely to investigate whether hypoliths can be used in an eco-engineering context (Chan et al. 2012), perhaps to promote colonization of degraded soils by “seeding” them with stone substrate and/or inoculating hypolithic taxa.

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Chapter 12

Remote Sensing of Biological Soil Crusts at Different Scales

Bettina Weber and Joachim Hill

12.1 Introduction

Dryland ecosystems constitute some of the largest terrestrial biomes, collectively covering 41 % of Earth's land surface and supporting over 38 % of the global human population (Maestre et al. 2012). Biological soil crusts (biocrusts) often grow in patches, covering vast regions, making it impossible to accurately assess their spatial distribution patterns based on ground-based mapping techniques. Thus, remote sensing methods are invaluable to classify and characterize biocrusts and to analyze their alteration over time by means of remote sensing change detection analyses.

Remote sensing mapping techniques are based on the spectral characteristics of the studied features, in our case the biocrusts. Prior to developing a classification technique, the spectral patterns, which allow to distinguish between the biocrusts on the one and the underlying and adjoining substrates as well as the surrounding vegetation, on the other hand, need to be studied. Thus, this chapter is divided into two major parts: in the first part, the spectral reflectance properties of biological soil crusts are described and the effects of wetting and disturbance as well as the potential to deviate physiological characteristics from these spectral characteristics are discussed. In the second part, existing methodologies for biocrust classification are presented, their functionality is investigated, and finally their universal applicability and promising new methods for the future are discussed.

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12.2 Reflectance Spectroscopy of Biocrusts

12.2.1 Spectral Reflectance Characteristics of Biocrusts

The method of reflectance spectroscopy is based on electromagnetic radiation, which, according to the “wave” and the “particle model” can be described as an electromagnetic wave or as a particular kind of matter (Jensen 2007). According to the particle model, impacting energy causes the electrons of atoms to jump to a higher energy level (they are excited). After 10^{-8} s, the electrons fall back to the atoms’ lowest empty energy level, giving off radiation, which is a function of the energy that had been absorbed before. According to the quantum theory, this energy is released in discrete packets called quanta or photons. The energy of a quantum is inversely proportional to its wavelength, which is then measured by means of spectroscopy. Thus, the different colors of substances are caused by their differences in energy levels and the selection rules (Jensen 2007). Electron orbital changes are known to produce the shortest-wavelength radiation, near- and/or middle-infrared energy is caused by molecule vibrational motion, whereas long-wavelength infrared or microwave radiation is caused by rotational motion change (Jensen 2007). These spectral characteristics are measured as reflectance spectra displaying the amount of light reflected by a surface along different wavelengths.

As biocrusts comprise photosynthetically active organisms with chlorophyll, i.e., cyanobacteria, green algae, lichens, and mosses, one would expect to find the absorption maxima of chlorophyll within these spectra. In addition to that, the organisms may contain starch, cellulose, and additional pigments, which might be identified in the spectral response.

A general effect of lichen crusts on the variation of reflectance values of bare soils was already observed by Graetz and Gentle (1982), who worked on the reflectance characteristics of Australian semiarid rangelands. They, however, saw biocrusts more as a disturbing issue than as a noteworthy feature on their own.

12.2.1.1 Different Types of Biocrusts

The general spectral characteristics of biocrusts have been investigated in a number of studies, and in all of them, a chlorophyll absorption feature at a wavelength around 667–682 nm has been observed (Table 12.1). At 1450 and 1920 nm, a universal absorption caused by water or OH bonds was observed (Karniel et al. 1999; Ustin et al. 2009). In the medium infrared region at ~ 2300 nm, Escrivano et al. (2010) identified an additional adsorption feature in all biocrusts, which was assigned to the presence of lignin or cellulose.

In most studies, reflectance spectra of different biocrust types have been studied separately. Several studies revealed the overall reflectance values of cyanobacteria-dominated crusts to be lower throughout the spectrum (covering 400–2500 nm: O’Neill 1994; 400–900 nm: Weber et al. 2008; 350–1150 nm: Pinker and Karniel 1995) as compared to bare soil. In contrast to that, other studies report lower

Table 12.1 Spectral characteristics of biocrusts as described in scientific publications

Crust type	Wavelength (nm)	Absorption feature	References	Opposing references
Cyanobacteria-dominated crust	~430	Increased reflectance due to phycobilins	Karnieli and Sarafis (1996)	Not observed by anybody else
Cyanobacterial strains of <i>Coleofasciculus chthonoplastes</i> and <i>Nostoc</i> sp.	~440	Absorption by chlorophyll <i>a</i> or β-carotene	Weber et al. (2008)	
Cyanobacterial strain of <i>Coleofasciculus chthonoplastes</i>	~489	Absorption by carotenoid or phycoerythrin	Weber et al. (2008)	
Cyanobacteria-dominated crusts	~504	Absorption by carotenoids	Chamizo et al. (2012), Rodríguez-Caballero et al. (2014)	
Cyanobacterial strain of <i>Coleofasciculus chthonoplastes</i>	~544	Absorption by phycocyanin or phycoerythrin	Weber et al. (2008)	Ustin et al. (2009)—no absorption in crusts
Cyanobacteria-dominated crust	<550	Higher reflectance than underlying soil	Tsoar and Karnieli (1996), Karnieli (1997)	Pinker and Karnieli (1995), O'Neill (1994), Weber et al. (2008), Chen et al. (2005)
Cyanobacteria-dominated crust	>550	Lower reflectance than underlying soil	Tsoar and Karnieli (1996), Karnieli (1997)	Pinker and Karnieli (1995), O'Neill (1994), Weber et al. (2008), Chen et al. (2005)
Cyanobacterial strain of <i>Coleofasciculus chthonoplastes</i>	~613	Absorption by phycocyanin	Weber et al. (2008)	Ustin et al. (2009)—no absorption in crusts
Cyanobacterial filaments of <i>Microcoleus</i> sp.	~627	Phycocyanin absorption	Karnieli et al. (2003)	
Cyanobacterial strains of <i>Coleofasciculus chthonoplastes</i> and <i>Phormidium</i> sp.	~630	Phycocyanin absorption	Weber et al. (2008)	

(continued)

Table 12.1 (continued)

Crust type	Wavelength (nm)	Absorption feature	References	Opposing references
Cyanobacteria-dominated crust; biocrusts in general	~680	Chlorophyll <i>a</i> absorption	O'Neill (1994), Pinker and Karnieli (1995), Karnieli and Tsoar (1995), Karnieli et al. (1996), Karnieli et al. (2002), Karnieli et al. (2003), Chen et al. (2005), Weber et al. (2008), Ustin et al. (2009), Escribano et al. (2010), Chamizo et al. (2012), Rodríguez-Caballero et al. (2014)	
All crust types	~1450	Water	Karnieli et al. (1999), Chamizo et al. (2012)	
Moss-dominated crust	~1720	Cellulose/lignin/starch/pectin	Karnieli et al. (1999)	
Moss- and lichen-dominated crusts	~1720	Cellulose and lignin	Ustin et al. (2009)	
Biocrust (not specified)	~1920	Water or –OH bonds	Karnieli et al. (1999), Ustin et al. (2009)	
Biocrust (not specified)	~2080	Cellulose, lignin, or other organic components (Escribano et al. 2010) or starch (O'Neill 1994)	O'Neill (1994), Ustin et al. (2009), Escribano et al. (2010)	Absorbing material doubted by Ustin et al. (2009)
Lichen-dominated crust	~2100	Starch and cellulose	O'Neill (1994)	
Moss-dominated crust	~2180	Starch/lignin/wax/tannin	Karnieli et al. (1999)	
Biocrust (not specified)	~2300	Lignin and cellulose	Escribano et al. (2010)	

(continued)

Table 12.1 (continued)

Crust type	Wavelength (nm)	Absorption feature	References	Opposing references
Moss-dominated crust	~2309	Humic acid/wax/starch	Karnieli et al. (1999)	Ustin et al. (2009)—absorption due to carbonate; observed in biocrusts and in soil

reflectance values at wavelengths between 550 and 1100 nm, whereas at shorter wavelengths (400–550 nm), higher reflectance values were measured on cyanobacteria-dominated crusts as compared to bare soil (Karnieli and Tsoar 1995; Tsoar and Karnieli 1996). Karnieli and Sarafis (1996) and later Karnieli et al. (1999) investigated the spectra of cyanobacteria-dominated biocrusts in an experimental approach, showing that phycobilins caused an increased reflectance of 1–2 % at about 430 nm. They claimed that this slightly increased reflectance may be used to differentiate between cyanobacteria-dominated crusts and bare soil and to classify cyanobacteria-dominated crusts within Landsat imagery (Karnieli 1997; see Sect. 12.3.2).

Reflectance spectra of isolated cyanobacterial strains revealed some additional absorption features, which could not be identified in complete crust samples (Table 12.1). On *Coleofasciculus chthonoplastes*, absorption maxima at ~440 nm (chlorophyll *a* or *β*-carotene), ~489 nm (carotenoid or phycoerythrin), ~544 nm (phycocyanin or phycoerythrin), ~613 nm (phycocyanin), and ~630 nm (phycocyanin) were determined by Weber et al. (2008). The absorption maximum at ~440 nm was shared by *Nostoc* sp., that at ~630 nm by *Phormidium* sp.. Karnieli et al. (2002) also observed the phycocyanin absorption maximum on *Microcoleus* filaments at ~627 nm.

On lichen-dominated biocrusts, the effect of chlorophyll, causing an absorption maximum between 670 and 680 nm, could be very weak (Chen et al. 2005), whereas in other cases it was clearly visible (Weber et al. 2008; Escribano et al. 2010). Further shallow absorption features at 2080 and 2100 nm were determined by O’Neill (1994), which he supposed to be caused by starch and a combination of starch and cellulose, respectively. The absorption feature at 2080 nm was also determined by Escribano et al. (2010), who ascribed it to the presence of cellulose, lignin, and/or other organic components.

In spectra of moss-dominated crusts, clear chlorophyll-conditioned absorption maxima were observed (Karnieli et al. 1999; Chen et al. 2005). Additional absorption features were identified at 1720 nm (assigned to cellulose, lignin, starch and/or pectin), 2180 nm (assigned to starch, lignin, wax and/or tannins), and at 2309 nm (assigned to humic acid, wax, and/or starch; Karnieli et al. 1999).

Weber et al. (2008) analyzed an additional type of liverwort-dominated biocrusts. Organisms of the dominating liverwort taxon *Riccia* have a dorsal “epithelium” of

achlorophyllous cells (Perold 1999), causing a silvery reflectance. Thus, this crust type revealed overall higher reflectance values with a chlorophyll absorption maximum being strongly masked.

12.2.1.2 Continuum Removal

The spectral characteristics of biocrusts as opposed to those of bare soil are often characterized by only subtle deviations. In order to identify such slight differences, Clark and Roush (1984) developed a method to model the continuum in a reflectance spectrum as a mathematical function, which is then used to isolate particular absorption features for analysis. This method was used by Escribano et al. (2010) to differentiate between crusts growing in different seasons, whereas Rodríguez-Caballero et al. (2014) illustrated an absorption peak at 504 nm caused by carotenoids, which was present in cyanobacteria, but did not occur in lichen-dominated crusts. Weber et al. (2008) applied continuum removal to set up five rules, which allowed to successfully delimitate biocrusts from both bare soil and vascular plant vegetation, which also proved to work reliably on hyperspectral remote sensing data (see Sect. 12.3.2).

In a later study, Chamizo et al. (2012) used this method to also set up rules, which allowed successful distinction between the spectral response of different crust types. This method was applied to spatial remote sensing data in a later approach (Rodríguez-Caballero et al. 2014).

12.2.2 Effects of Watering

Watering has an instantaneous effect on the reflectance spectra of lichen-dominated crusts, as illustrated by O'Neill (1994). Already 10 min after watering, the absorption maximum at ~680 nm had deepened, and also at wavelengths >1200 nm, reflectance values were considerably lower. Studying cyanobacteria-dominated crusts, also Karnieli and Sarafis (1996) observed overall lower reflectance values upon watering of the crust. After 12 h wet the reflectance at ~680 nm and around 1000 nm had decreased, probably caused by the movement of cyanobacteria within the crust (Danin 1991; Garcia-Pichel and Pringault 2001) or by the initiated growth and formation of new chlorophyll *a*. Analyzing cyanobacteria- and one moss-dominated crust in a dry state, 1 day and 7 days after watering and incubation, Karnieli et al. (1999) observed that the reflectance level decreased and a significant dip ~680 nm developed during the incubation process.

The spectral response following different watering regimes was also studied by Rodríguez-Caballero et al. (2015). Immediately after watering, the reflectance of a cyanolichen-dominated crust with non-lichenized cyanobacteria decreased considerably (Fig. 12.1). After 24 h, wet reflectance values within the visible part of the spectrum (400–700 nm) were below 4 % (Fig. 12.1) and the crust surface had turned dark (Fig. 12.2). Upon drying, the reflectance values increased again, reaching

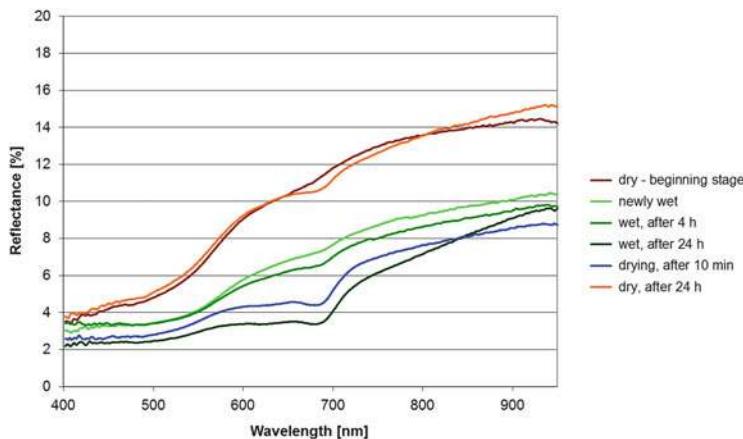


Fig. 12.1 Spectral response of a cyanolichen-dominated biocrust with cyanobacteria in a dry state and at different times during and after a 24-h watering event

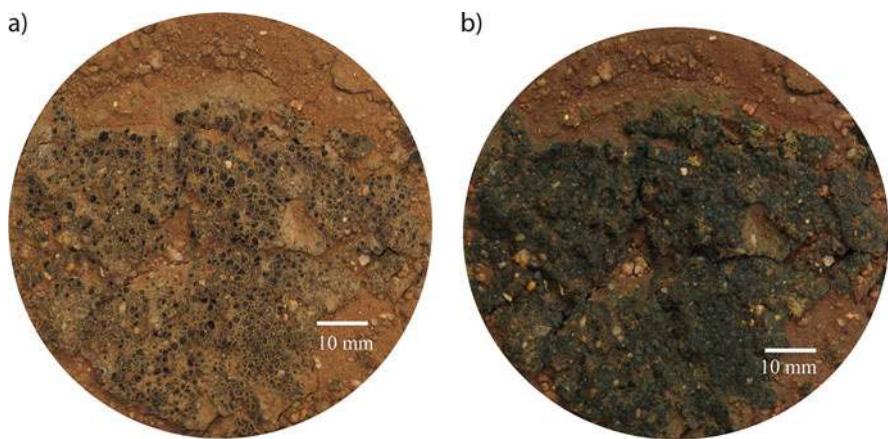


Fig. 12.2 Surface appearance of a cyanolichen-dominated biocrust with cyanobacteria (a) prior to watering, and (b) after 24 h in a wet stage

similar values over a major part of the spectrum, which remained, however, somewhat lower \sim 680 nm (Fig. 12.1), indicating the movement of organisms to the surface or the formation of new chlorophyll.

The spectral and optical response of cyanobacteria-dominated crusts after 10 days wet revealed considerable deviations from the former characteristics (Figs. 12.3 and 12.4b). The crust had turned almost blackish, indicating intense new growth of organisms, and after 1 day of subsequent drying, the overall spectral response was well below the initial spectrum with an intense reflectance minimum \sim 680 nm. During the subsequent 5 weeks of drying, the reflectance values increased gradually and the reflectance minimum \sim 680 nm flattened. Nevertheless,

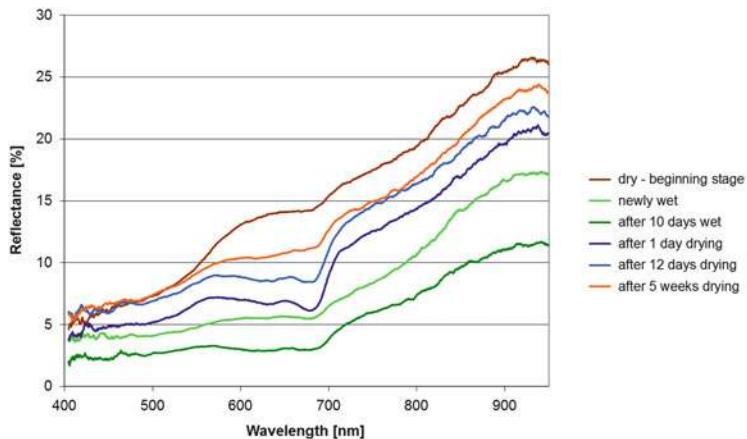


Fig. 12.3 Spectral response of a cyanolichen-dominated biocrust with cyanobacteria in a dry state and at different times during and after a 10-day watering event

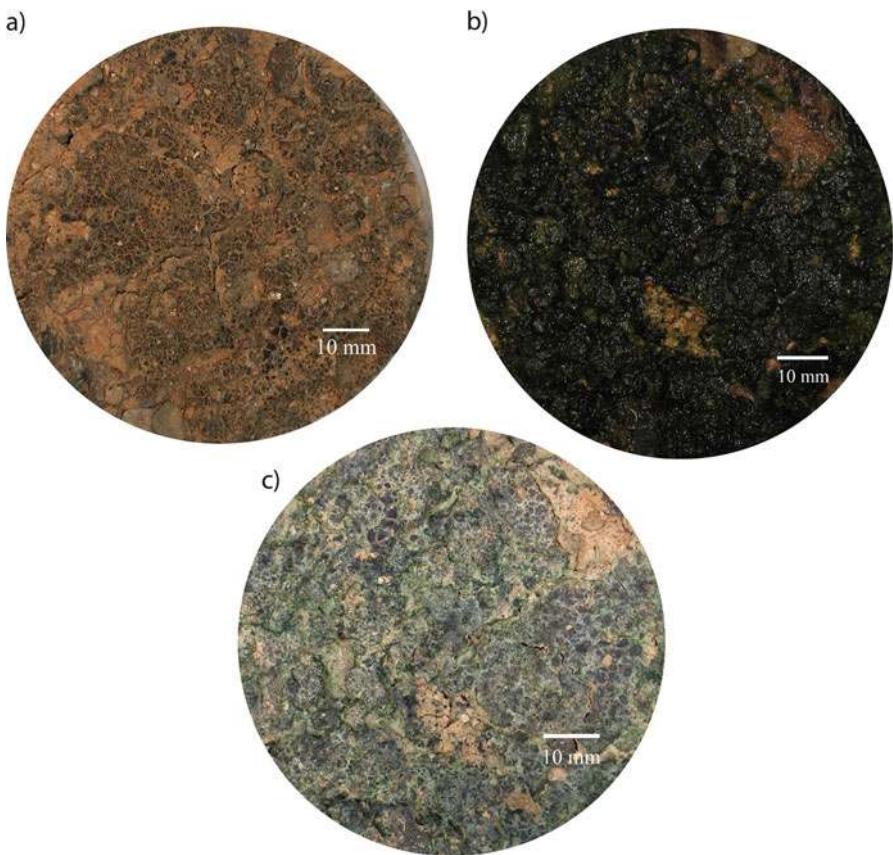


Fig. 12.4 Surface appearance of a cyanolichen-dominated biocrust with cyanobacteria (a) prior to watering, (b) in the end of 10-day watering event, and (c) 5 weeks (in a dry state) after 10-day watering event

reflectance values between 550 and 950 nm remained well below those of the initially measured spectrum and the crust looked still more densely colonized compared to the initial crust habitus (Figs. 12.3 and 12.4a, c). Thus, watering of the crusts over several days seems to have a long-term effect on the spectral characteristics of biocrusts.

Karnieli et al. (2002) studied the spectral reflectance of biocrusts depending on rainy and dry seasons during the year. After 2 weeks of rainfall, they measured well-developed reflectance spectra reminding of vascular plants with a high peak at ~ 550 nm, a distinct absorption maximum at ~ 680 nm, a sharp rise at ~ 700 nm (red edge), and a plateau in the near-infrared (700–1100 nm). During the following dry season the spectrum flattened, the maxima and minima gradually disappeared, and at the end of the dry season the spectra closely resembled those of bare soil (Karnieli et al. 2002). In a different study, biocrusts ($n=5$), which had been collected after the rainy season, were stored for 11 months under dry conditions in the dark. The spectral reflectance of the crusts did not change significantly over the whole time span (Weber unpublished), pointing to the fact that sunlight and/or UV-radiation might be responsible for the spectral alteration of biocrusts during the year.

12.2.3 Effects of Disturbance on the Spectral Characteristics of Biocrusts

Whereas biocrusts generally cause a darkening of the soil surface, their disturbance by both trampling and scraping provokes an increase in albedo (Chamizo et al. 2012). As trampling causes a breakdown of the crust, the lighter-colored soil becomes more dominant in reflectance spectra and after scraping, the spectra closely resemble those of bare soil. Absorption features of pigments ~ 500 and ~ 680 nm and of water ~ 1450 nm were observed to be weaker in trampled and weakest in scraped crusts. A second disturbance effect is the flattening of the surface by both trampling and scraping, also resulting in increased reflectance values (Chamizo et al. 2012).

Mechanical substrate disturbance had similar effects in a study by Ustin et al. (2009), where biocrusts responded with overall higher reflectance values and shallower absorption features at ~ 420 and ~ 500 nm. An absorption feature at ~ 2080 nm, probably caused by organic components, disappeared completely upon disturbance (Ustin et al. 2009).

12.2.4 Spectral Indicators

As previously shown, biocrusts have an absorption feature at ~680 nm in common (Table 12.1), which nicely correlates with the chlorophyll content of dry cyanobacteria-, lichen-, and moss-dominated crusts in a savannah-type ecosystem in Namibia (BIOTA observatories 39, 40; Weber unpublished; Fig. 12.5). This chlorophyll *a* absorption feature is also utilized in vegetation indices, with the most prominent one being the normalized difference vegetation index (NDVI). The NDVI is based on the spectral reflectance of Landsat satellite bands, i.e., the red band (*R*), 600–700 nm, comprising the chlorophyll absorption, and the near-infrared band (NIR), covering 700–1100 nm. It is defined as

$$\text{NDVI} = (\text{NIR} - R) / (\text{NIR} + R)$$

reaching values between –1 and 1.

It was observed that wet cyanobacteria-dominated crusts on sand reached NDVI values up to 0.22 and moss-dominated crusts even gained values of 0.3 (Karnieli et al. 1996, 1999), whereas bare soil had values of 0.08. Thus, they showed that high NDVI values of wet biocrusts may be misinterpreted as vascular plant vegetation dynamics, whereas dry biocrusts only gained negligible NDVI values.

Zaady et al. (2007) used a brightness index (BI) in addition to the NDVI to follow the biocrust succession after a disturbance event. The BI utilizes the reflectance values in the green (*G*: 500–600 nm), red (*R*: 600–700 nm), and near-infrared region (NIR: 700–1100 nm) to calculate the overall brightness of a surface:

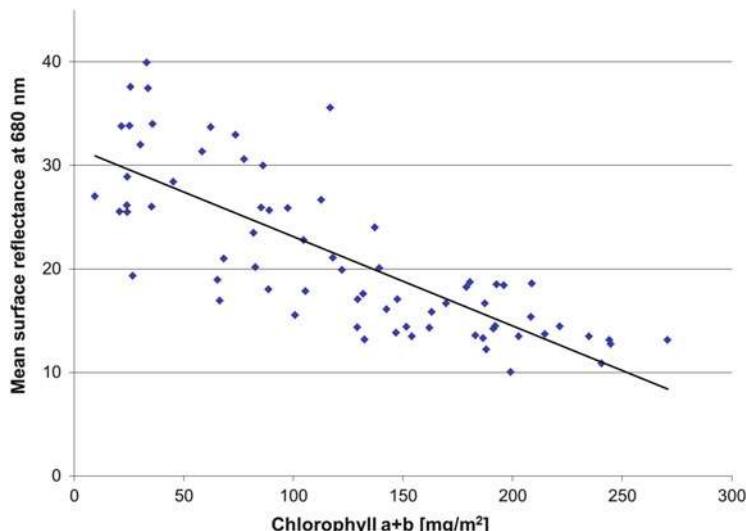


Fig. 12.5 Correlation of mean surface reflectance at 680 nm with chlorophyll *a+b* content of dry cyanobacteria-, lichen-, and moss-dominated crusts sampled in a savannah-type ecosystem in the BIOTA observatories No. 39 and 40 in Namibia. Pearson: $r = -0.78$, $n = 71$

$$BI = \sqrt{G^2 + R^2 + NIR^2}$$

In 6 years after disturbance by scraping, with the crumbled soil being distributed again, the brightness index decreased and the NDVI values increased as expected, but the same development, to a lesser extent, also occurred on non-disturbed control plots. The NDVI values of the controls were significantly higher than those of the treatment plots, but nevertheless, only comparably low NDVI values up to 0.15 were measured on wet crusts.

12.2.5 Spectral Characteristics Related to CO₂ Gas Exchange

As the spectral reflectance at ~680 nm correlates with the chlorophyll content of biocrusts, Burgheimer et al. (2006a, b) investigated the feasibility to derive carbon flux rates from NDVI values of biocrusts. This worked quite well when average data of each 3-day field trip were used. At higher temporal resolution, however, environmental factors like soil water content and light intensity strongly influenced CO₂-gas exchange values, whereas NDVI values remained stable. Thus, only weak correlations were found between both factors measured on biocrusts growing in sandy ($R^2 = 0.44$) and in loess environment ($R^2 = 0.35$; Burgheimer et al. 2006b). Nevertheless, the NDVI was found to be a good tool to represent the biocrusts' seasonal photosynthetic activity. Thus, in a later step, remote sensing methods might be applicable to estimate biocrust assimilation activity (Burgheimer et al. 2006a).

In another approach, chlorophyll fluorescence measurements of cyanobacteria-, lichen-, and moss-dominated crusts were linked to the NDVI and photochemical reflectance index (PRI; Yamano et al. 2006). The PRI is sensitive to changes in carotenoid pigments, which in turn are indicative of photosynthetic light use efficiency. It is calculated as

$$PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$$

with R indicating reflectance and numbers indicating the wavelengths in nanometers. Whereas the NDVI values of wet samples were higher in wet as compared to dry crusts, PRI values of wet crusts had lower values compared to dry ones. Due to inactivity of the crusts, no F_v/F_m was measured on dry crusts. In hydrated moss-dominated crusts, PRI values significantly correlated with F_v/F_m and in wet lichen-dominated crusts F_v/F_m was positively correlated with both the PRI and the NDVI. The authors concluded that the PRI was more effective in estimating the photosynthetic capacity of lichen- and moss-dominated crusts. One, however, has to have in mind that realized CO₂ gas exchange values cannot be directly derived from the fluorescence data measured on the crusts (Raggio et al. 2014).

12.3 Mapping the Spatial Distribution of Biocrusts

Given the significant role of biocrusts in assuring the functioning of desert and steppe ecosystems, there has always been a strong interest in producing spatially explicit distribution maps for improving the estimates of photosynthetic activity and CO₂ exchange retrieved from limited ground measurements (Burgemeier et al. 2006a). The fact that biomass and activity in biological soil crusts are usually concentrated within the uppermost millimeters of the soil surface (see Chap. 13 by Garcia-Pichel et al.) suggests that, in case stable relationships between optically active key variables and crust properties are identified, satellite-based or airborne remote sensing might be employed to assess the presence or absence of biological soils crusts or to differentiate between various crust types (e.g., Karnieli et al. 2003).

While only very limited work has been done on the emissive properties of biocrusts (e.g., Rosenstein and Karnieli 2014), a wealth of studies is available on the use of imaging systems which operate in the reflective optical domain. Already at the time of early Landsat satellites during the 1970s, the nature of the sharp contrast along the Israel–Egypt border has been a matter of scientific interest and debate. Otterman et al. (1974) were the first to explain this by the presence of dark desert plants (either photosynthetically active or senescent) on the Israeli side, while the Egyptian area was almost devoid of vegetation. However, the predominant role of higher plants in producing this spectral contrast was rejected by Karnieli and Tsoar (1995) who claimed that the spectral contrast was not a direct result of vegetation cover but caused by an almost complete presence of biogenic crusts. In his reply Otterman (1996) insisted that even with sparse plant cover (e.g., less than 30 %), the interception of solar irradiance by desert plants, as well as the rays reflected from the soil (i.e., absorption and shadowing), is providing a highly significant contribution to the spectral reflectance.

Besides the fact that the presence of biocrusts in this area is by far more discontinuous and scattered than it was suggested in former studies (Hill et al. 2008), this early scientific debate frames the core problem of mapping biocrusts with multi- or hyperspectral imaging systems: biocrusts are mostly associated with higher plants, and the problem emerging from this fact is that the observed reflectance signal represents a more or less complex mixture of spectral contributions from soil, biocrusts, and vascular plants in varying states and, therefore, partially similar reflectance characteristics. In addition, the contribution biocrusts have on spectral soil surface properties does not depend only on crust composition and state but also on their relative cover (Rodríguez-Caballero et al. 2014). The task is thus to identify different types of biocrusts and to quantify their relative abundance at sub-pixel scale against the background of spectrally similar components.

12.3.1 Image Preprocessing

Monitoring of vegetation and land surface characteristics using passive optical imaging systems largely depends on relationships between biophysical quantities on the ground and their spectral reflectance properties. The different approaches for mapping biological soils crusts discussed in this chapter rely on the availability of calibrated reflectance imagery, i.e., they require that effects of the atmosphere, sun, and sensor positions as well as surface orientation have been properly corrected. The use of atmospheric radiative transfer models to remove atmospheric effects from Landsat imagery has recently been demonstrated in an operational context by a number of authors, such as Richter and Schläpfer (2002), Masek et al. (2006), Vicente-Serrano et al. (2008), and Flood et al. (2013). Since these concepts can be equally applied to a large variety of multispectral imaging systems and are currently included in operational data processing schemes, atmospheric corrections should be considered a necessary prerequisite that can be solved routinely.

12.3.2 Spectral Indices

The work in establishing suitable mapping methods builds on the spectral characteristics of biocrusts which are described in more detail in the first part of this chapter. Accordingly, the prominent chlorophyll absorption feature at ~680 nm, common to cyanobacteria-, lichen-, and moss-dominated crusts, might suggest the use of corresponding ratio indices such as the NDVI. However, since NDVI values in the range of 0.05–0.25 are also typical for a wide range of soil spectra, and because sparse woody vegetation structures as well tend to become spectrally effective from NDVI values around 0.1–0.15 onwards (e.g., Price 1993), this would require that the contribution of such materials to the reflectance signal could be computationally removed.

Karnieli (1997) was one of the first authors to propose a simple spectral index which was based on findings that the presence of cyanobacteria in the biocrusts is the cause for a relatively high reflectance in the blue region. He demonstrated that the spectral index

$$\text{CI} = 1 - \frac{\rho_{\text{red}} - \rho_{\text{blue}}}{\rho_{\text{red}} + \rho_{\text{blue}}}$$

had the ability to differentiate between crusted and uncrusted samples in laboratory experiments. Since the CI can also be derived from any imaging system with spectral bands in the blue and red region of the electromagnetic spectrum (e.g., the Landsat systems, MODIS, or the forthcoming Sentinel-2 and -3 systems), it suggested a wide range of applicability. However, the major problem was that the index enhances the spectral contrast between different geomorphic and lithological

units (e.g., areas with different mineralogies and varying contents of fine-grained material or organic components) in general, but fails to provide a reproducible relationship with increasing biocrust abundance. In addition, the index would by definition be less suitable for biological soil crusts where cyanobacteria are not a dominant constituent (Chen et al. 2005). The obvious conclusion to be drawn is to not only identify spectral ranges which are sensitive to varying abundances of biocrusts but to combine these with bands that are suited to enhance the spectral difference between biological crusts and associated material such as bare soil and photosynthetically active, senescent, or woody plant material.

Based on a study in the cold deserts of N-China, Chen et al. (2005) developed a biological soil crust index (BSCI) which is based on the reflectance in the green, red, and near-infrared range of the electromagnetic spectrum. The proposed index

$$\text{BSCI} = \frac{1 - L \cdot |\rho_{\text{red}} - \rho_{\text{green}}|}{\rho_{\text{AVE}}}$$

uses the average reflectance in the red, green, and near-infrared bands (ρ_{AVE}) to normalize the spectral contrast between the red and green part of the spectrum; L is an adjustment parameter to amplify the absolute difference between these bands. The rationale behind the BSCI is that the red reflectance for biological soil crusts will be much lower than those of bare sand, dry plant material, or photosynthetic vegetation. Chen et al. (2005) demonstrated that the performance of the proposed BSCI is limited to specific bounds, and that these can be substantially extended when atmospherically corrected imagery is used. However, an important limitation of the BSCI is that it must be applied under conditions where higher plants exhibit no photosynthetic activity.

The BSCI had been developed for a specific crust type (with a dominance of lichens) and it was therefore not surprising that transferring the index to a different site in S-Africa was not successful (Weber et al. 2008). However, the availability of hyperspectral imagery (CASI) with a spatial resolution of 1 m allowed the authors to analyze the spectral information content of field-measured biocrust spectra in more detail. Hyperspectral sensors can identify subtle spectral characteristics related to the presence of chlorophyll, carotenoids, and phycobilins in biocrusts (Rodríguez-Caballero et al. 2014). Weber et al. (2008) identified subtle but characteristic differences within the absorption regions around 516 and 675 nm which could be used to define a hyperspectral Continuum Removal Crust Identification Algorithm (CRCIA). When applying this index to hyperspectral CASI data, it was possible to map biological soil crusts as long as those covered more than approximately 30 % per pixel.

The importance of high spectral resolution has been acknowledged in several studies (e.g., Hill et al. 1999; Pinet et al. 2006; Escribano et al. 2010), particularly because additional diagnostic bands in the short-wave infrared region (due to the presence of cellulose, lignin, and other organic components) may support discrimination between biocrusts and soils. Also Ustin et al. (2009) confirmed the important

potential of hyperspectral imagery, since they could identify experimental treatments of biological soil crusts as part of a long-term manipulative experiment. However, it is important to understand that these treatments were applied to homogeneous plots, where the interaction with other materials was largely excluded.

More complicated is the identification when biocrusts are mixed with other soil properties or higher plants. The CRCIA, for example, worked quite reliably also in the presence of plant litter. However, it was observed that spectra of bare soil with minor photosynthetic plant coverage (about 5–10 %) already closely resemble certain types of biocrusts. This implies that biological crusts are almost impossible to map when growing in the proximity of, or even below, photosynthetic shrubs. For this reason an application of the CRCI algorithm on images with coarser spatial resolution was considered critical, owing to increasing spectral mixing effects in the visible and near-infrared (Weber et al. 2008). Similarly, important spectral features of dry and woody plant material (cellulose, starch, etc.) in the 2–2.5 μm wavelength range are also common to certain types of biocrusts. It should therefore not be expected that the availability of hyperspectral data alone can resolve all spectral ambiguities when biocrusts occur spatially mixed with desert plants in photosynthetic or non-photosynthetic states.

12.3.3 Biocrusts as an Element of Complex Spectral Mixtures

In principle the work of Chen et al. (2005) and Weber et al. (2008) already conceptualized the detection of biocrusts as a spectral mixing problem (where biological soil crusts and a background consisting of bare sand, green, or dry plant material and its shadow are main components of the composite reflectance). However, instead of developing optimized spectral indices it might be appropriate to adopt approaches for directly estimating the proportional abundance of materials within an observed surface area. Spectral mixture analysis (SMA) has been advocated as an efficient method to computationally decompose spectra into proportions of pure spectral components (endmembers; e.g., Schowengerdt 1997; Smith et al. 1990). In first approximation, spectral mixing is modeled as a linear combination of pure component (“endmember”) spectra:

$$\rho_i = \sum_{j=1}^n F_j \cdot \rho E_{ij} + \varepsilon_i$$

where ρ_i is the reflectance of the mixed spectrum in band i , ρE_{ij} is the reflectance of the endmember spectrum j in band i , F_j denotes the abundance of endmember j , and ε_i is the residual modeling error in band i .

Maps of endmember abundances F_j provide the convenience and inter-comparability of standard land cover metrics (e.g., NDVI) while retaining benefits

of physically based estimates, and they can be edited and recombined to produce thematic maps. Hill et al. (2008), for example, could successfully demonstrate that SMA was capable to differentiate between important surface materials (sand, biocrusts, and mineral crusts with different silt/clay contents) on reflectance-calibrated high-spatial-resolution true-color air photos after these had been stratified into areas with and without higher plant coverage. When SMA was applied to hyperspectral imagery, the analysis of mixing residuals (which usually indicate components not represented by the set of endmembers) proved that, in addition to the occurrence of biocrusts, also senescent and woody plants were an essential part of the composite reflectance of the Nizzana dune system in Israel (Hill et al. 1999), thereby confirming the results of Otterman (1996).

Recently, Rodríguez-Caballero et al. (2014) combined a support vector machine classification of hyperspectral CASI data in five ground units (dominated by principal surface components, such as bare soil, green, and dry vegetation, cyanobacteria, and lichen biocrusts) with an analysis of the SMA-derived abundance of different crust types within these units. It was found that all SMA models with a fixed number of spectral endmembers had limited performance (large root-mean-squared modeling errors and/or substantial amounts of abundance estimates smaller than 0 or larger than 100 %), independently of being applied either to the entire image or to more homogeneous ground units. This represents a common problem with linear SMA; it typically occurs when the number of spectral endmembers is greater than the number actually required to unmix an individual pixel in the scene. Material abundances predicted by linear SMA are therefore most accurate when only those endmembers that comprise a given pixel are used. It has therefore been suggested to replace simple SMA by efficient multiple endmember concepts which include the automatic detection of required endmembers (e.g., García-Haro et al. 2005; Rogge et al. 2006). Correspondingly, the application of multiple endmember SMA (MESMA) to pre-stratified ground units in the study of Rodríguez-Caballero et al. (2014) helped to improve results substantially.

12.3.4 Temporal Variability

All methods referred to so far cannot fully resolve the fundamental problem that, depending on the seasonal and short-term variability of phenological conditions, biocrusts may adopt reflectance properties very similar to soils or higher plants of steppe or desert ecosystems. The analysis of an exceptionally long observation record (28 satellite images from two consecutive years) with corresponding field data enabled Burgheimer et al. (2006a) to present a detailed analysis of the spectral reflectance dynamics of cyanobacteria-dominated biocrusts and other ground features in the northern Negev Desert in Israel (Burgheimer et al. 2006a). Although both the photosynthetic activation of biocrusts and the growth of annual plants are triggered by rainfall events during the winter period, it could be demonstrated that

biocrusts and annuals (although spectrally similar) might become separable due to different development rates: biocrusts are responding almost immediately to the availability of water while the emergence of annual plants is slower. Spatial separation of the two will thus depend on the availability of satellite observations during the time span where biocrusts are photosynthetically active but annuals have not yet reached a cover proportion high enough to mask the biocrust reflectance. This period, however, is short (usually not more than 2 weeks) and requires the availability of earth observation systems that combine suitably high spatial resolution with sufficiently high repetition rates. Such systems in principle exist (e.g., the RapidEye, SPOT, and WorldView multi-satellite constellations), but their acquisition management needs to efficiently cope with highly irregular rainfall and diverse temperature regimes common to semiarid and arid ecosystems. The high variability of different biocrust types (i.e., cyanobacteria-, lichen-, or moss-dominated), which frequently will be found associated to or mixed with each other, adds additional complications which render also the exploitation of such multi-temporal observation schemes anything else than trivial.

12.4 Conclusion

Biocrusts are spectrally characterized by a chlorophyll *a* absorption feature at ~680 nm accompanied by spectral features varying between biocrust types, substrates, and studies. Watering causes a rapid intensification of spectral characteristics, whereas disturbance was observed to produce overall higher albedo and flattened absorption features. Few studies showed that spectral indices may also be used to draw conclusions on the photosynthetic potential of biocrusts, but here further studies are needed to evaluate the overall explanatory power of spectral data.

Improving the production of reliable maps of biocrust cover further depends on the availability of imaging systems which provide not only adequate spatial and spectral resolution but are also capable of collecting images sufficiently frequent. Owing to the irregular rainfall regimes in global drylands, short repetition cycles are required to provide observations within the unusually short phenological windows when the spectral contrast between biocrusts and background components is maximized.

This primarily qualifies airborne imaging or, alternatively, space systems which build on multi-satellite constellations for implementing sufficiently dense repetition rates, such as RapidEye (<http://blackbridge.com/rapideye/>), the SPOT-6/7 and WorldView constellations (<http://www.satimagingcorp.com/>), and others. Since 2015 onwards the European Sentinel-2 satellite complements Landsat-8 OLI and forms an additional, powerful EO constellation which covers the visible and near- and short-wave infrared region at intermediate spatial resolution. Hyperspectral information seems able to capture also the more subtle spectral variability of biocrusts and vascular plants during the phenological cycle. Acquiring

hyperspectral images at least twice a year is expected to further improve monitoring capabilities. The German hyperspectral EnMAP mission scheduled for launch in 2018 (<http://www.enmap.org/>) will add important monitoring capacities.

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Part III

Functional Roles of Biological Soil Crusts

Chapter 13

Microstructure and Weathering Processes Within Biological Soil Crusts

Ferran Garcia-Pichel, Vincent John Martin Noah Linus Felde,
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13.1 Introduction

Biological soil crusts (biocrusts) are truly organo-sedimentary systems in which both the organic and the inorganic mineral components play dynamic roles in determining the architecture and evolution of the system, as they interact between themselves and with the physical environment. The relevant organic components include the organismal fraction as well as the extracellular organic substances; the mineral components include the parent soil materials and allochthonous minerals trapped by the crust, and some authigenically precipitated minerals. The underpinning of the interactions between biocrust components occurs at the microscale, but

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results in emergent properties that affect ecosystem-scale phenomena as important as microclimate and hydrological regimes. A basic understanding of the microstructural interactions and dynamics seems thus imperative to attain mechanistic models of biocrust functions and potential responses to a changing environment. Yet, microstructural studies have been few, remain largely descriptive, and have only rarely been integrated with other aspects of biocrust ecology.

Given that the inputs of light energy, most allochthonous minerals, and several nutrients originate from the atmosphere, a strong vertical forcing is imposed upon biocrust architecture. Most generalizations in terms of structure respond to this up/down directionality. While lateral organizational forces do occur, and horizontal variability certainly exists in biocrusts, patterns in this dimension do not lend themselves as easily to generalization and are usually folded into the concept of patchiness. Notably, however, some progress has been attained in describing the structuring influence of aspect exposure in highly three-dimensional, pedicelled crusts.

13.2 Microstructure of Biological Soil Crusts

13.2.1 *Physical Microstructure*

Biocrusts can show a strong vertical layering in their physical microstructure, typically consisting of a physically cohesive upper layer variously called simply crust, topcrust, or bio-rich layer (Fig. 13.1). Topcrust depth is likely determined by the maximal penetration of light into the sedimentary matrix (only a few mm, Garcia-Pichel 1995) that allows for the development of photosynthetic, crust-forming microbial populations. This depth depends on soil texture and the concentrations of microbial pigments. The topcrust layer can often be peeled off and can hold itself together against gravity. The main binding mechanisms may vary. For soils at large [see reviews by Amézketa (1999), and by Bronick and Lal (2005)], abiotic binding mechanisms for soil particles can be the aggregation by carbonates, clay minerals, salts, (hydr)oxides, and phosphates as well as ionic bridging by polyvalent cations. Biotic stabilization can be caused by organic carbon from primary producers as well as the activity of the soil fauna (e.g., earthworms and termites) and microorganisms. The combination and intensity of these mechanisms in biocrusts likely vary, but microbial stabilization is clearly determining in all of them, and abiotic factors have not been examined in much detail. If cyanobacteria are dominant, the stabilization effect can be related to the excreted exo-polysaccharides, often organized as a network of extracellular sheaths (Fig. 13.1). Stabilization by clays in crust roll-ups is demonstrably short-lived compared to stabilization by microbial extracellular polymeric substances (EPS; Beraldí-Campesi and Garcia-Pichel 2010). Cyanobacterial filaments serve as main binding components in cyanobacterial crusts, but fungal hyphae and cyanobacteria

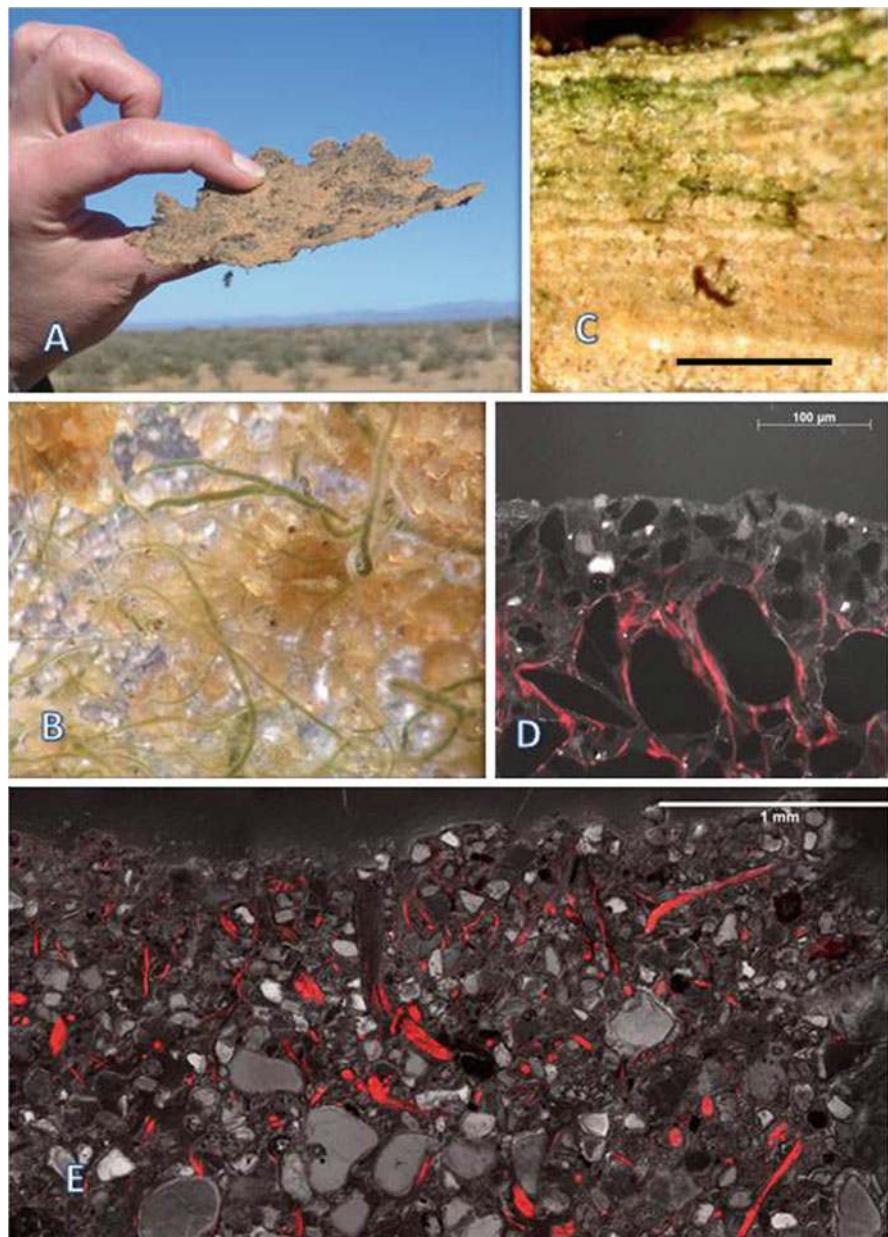


Fig. 13.1 Microstructure of biocrusts: the topcrust. (a) A topcrust from the Jornada del Muerto Valley, New Mexico, Chihuahuan Desert, can hold its own against gravity and can be easily peeled off the soil. (b) Bundle-forming filaments of *Microcoleus vaginatus* weave the organo-sedimentary matrix of a topcrust. (c) Recurrent burial events can result in multilayered crusts, as in this cross-sectioned example from Bardenas Reales in Spain. (d) The topcrust often develops an internal stratification by trapping allochthonous fines from dust, as seen in this example from the Negev Desert, in which a geological thin section is observed with epifluorescence microscopy to highlight red-fluorescent cyanobacterial filaments (Raanan et al. 2016). (e) In a larger view, the

may take on that task in lichen-dominated crusts. In moss-dominated crusts, moss rhizoids and fungi become the relevant binding agents (Lan et al. 2012). Free-living fungi do not seem to play a major role in holding non-lichen crusts together, given their low relative biomass (Bates and Garcia-Pichel 2009; Bates et al. 2010).

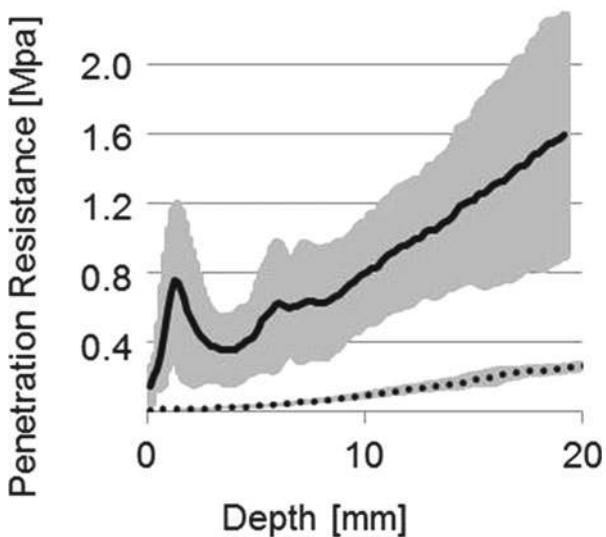
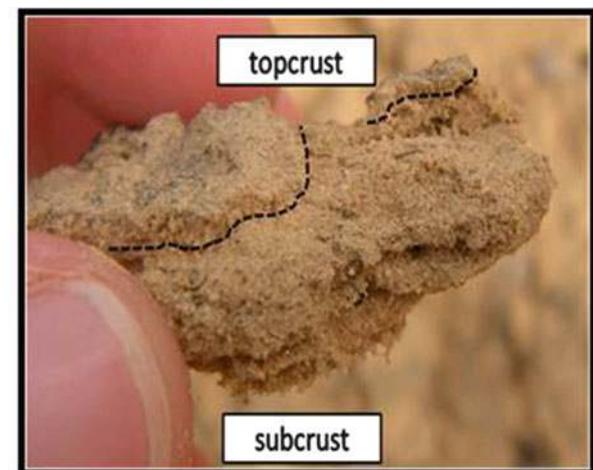
But a biocrust area of influence does often extend deeper than this topcrust, into what has been called a “subcrust” or “undercrust.” For the sake of clarity, we will use the term subcrust throughout this chapter. Several studies describe significant differences between this thin, biologically rich soil surface crust cover, and the underlying soil material (Garcia-Pichel et al. 2003; Malam Issa et al. 2009; Lan et al. 2012; Williams et al. 2012; Drahorad and Felix-Henningsen 2013). Penetration resistance (PR) data of needle-type electronic micro penetrometers are illustrative (Fig. 13.2) because they delimit this small-scale boundary between topcrust and subcrust particularly well (Drahorad and Felix-Henningsen 2013; Drahorad et al. 2013), which is characterized by a reduction in stability at a few mm in soil depth. In this particular case, the subcrust is partly indurated, but this induration does not occur in other crusts. Williams et al. (2012) describe planar voids at this boundary in Mojave Desert crusts. The PR minimum is typical for a breaking point as described by Callebaut et al. (1985) and may indicate a movement of grains into the pore system below or simply a decrease in binding organic substances. PR values among topcrusts vary significantly around the world. Some studies yield values around 49–392 kPa (Guo et al. 2008; Thomas and Dougill 2006, 2007), whereas others report pressures an order of magnitude higher (Maestre et al. 2002). Systematic studies relating PR to biochemical or textural parameters have not been carried out.

There is also evidence that the topcrust itself often contains significant microstructural differences. Early on, it was demonstrated using electron microscopy (Verrecchia et al. 1995) that significant quantities of allochthonous dust fines are trapped in the surface of biocrusts (see Fig. 13.1). In some cases these trapped fines can be transported downwards, even beyond the boundaries of the topcrust. Enrichment in fines has been documented as deep as 5–10 mm, well into the subcrust, in the Negev Desert dunes (Yair 1990), but it is unclear if these are the result of transport or may instead correspond to buried surfaces (see below).

Perhaps not surprisingly, the subcrusts are rarely devoted much attention. Mager (2010) defined a “nonorganic” subcrust in the Kalahari Desert, as did Williams et al. (2012) in the North American Mojave, who defined it as “bio-poor.” However, Garcia-Pichel et al. (2003) showed that zones under the topcrust are still significantly enriched in bacterial populations compared to bulk desert soil (Fig. 13.3). In cryptogam-dominated crusts, rhizines of specific crust organisms can easily reach into the subcrust and influence soil organic matter and stabilization there (Jimenez Aguilar et al. 2009). Beraldí-Campesi et al. (2009) demonstrated that a variety of

Fig. 13.1 (continued) biocrust on sandy soils from the Colorado Plateau is shown in landscape form (courtesy of Estelle Couradeau)

Fig. 13.2 Microstructure of a biocrust: topcrust and subcrust revealed by penetration resistance (PR). Graph shows the PR for a biocrust-covered Arenosol (*solid line, n = 10*) and unconsolidated dune sand (*dashed line, n = 17*). The dotted lines indicate the boundaries of biocrusts between top- and subcrust. From Drahorad and Felix-Henningsen (2013)



subcrusts across different biogeographic provinces in North America differ significantly in geochemical character from the topcrust, the latter being enriched in biogenic elements (C, N, P). Both the topcrusts and the subcrusts are depleted in most other micronutrients and metals compared to neighboring uncrusted soils, speaking for the leaching effect of microbes on micronutrients, and for the necessity and role of allochthonous dust inputs to maintain crust fertility.

When a crust becomes covered by sand, the organisms undergo severe stresses (Rao et al. 2012). Motile organisms can easily move upward to recolonize the new surface (Garcia-Pichel and Pringault 2001), as long as a certain threshold of sand burial depth is not exceeded. In laboratory experiments, Rao et al. (2012) found that

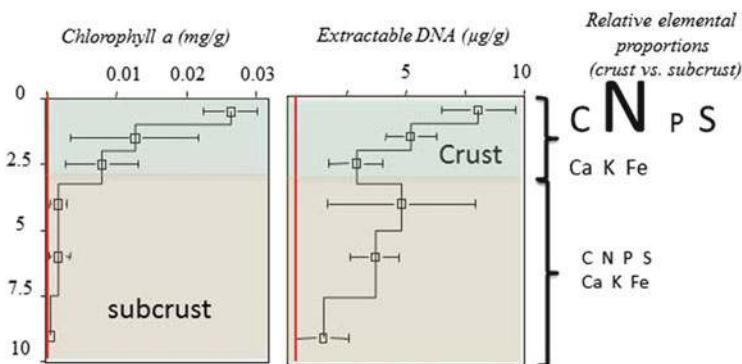
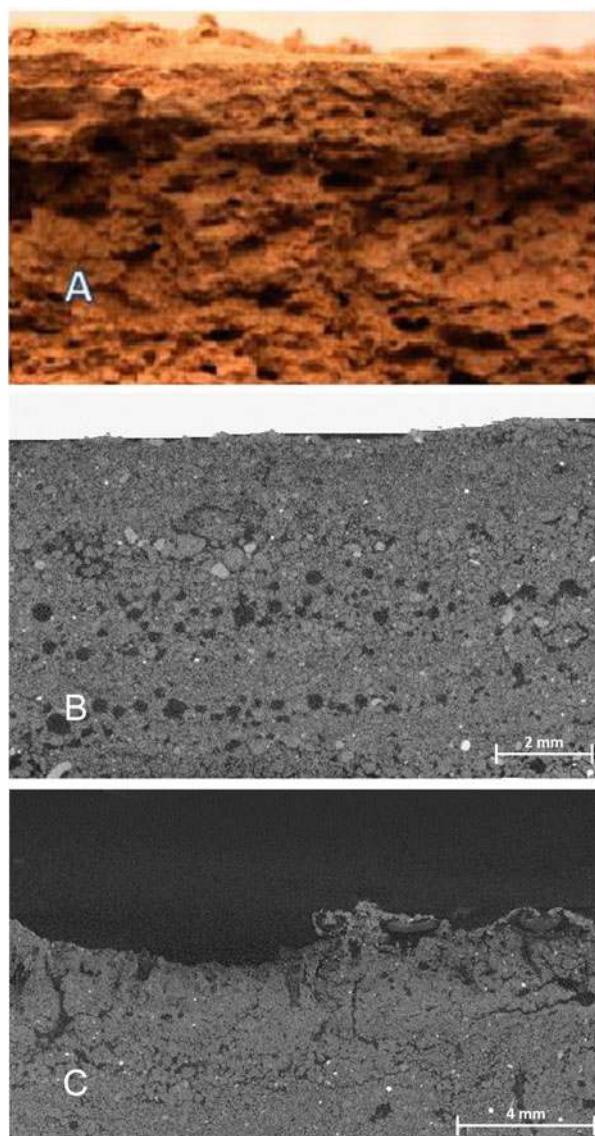


Fig. 13.3 Biogeochemical differentiation in biocrusts as measured in dark cyanobacterial crusts from the Colorado Plateau. The depth (in mm) of the consolidated crust or topcrust is defined by the presence of large phototroph (primary producer) populations, revealed by high concentrations of chlorophyll-a (*left panel*). However, the influence on live microbial biomass (gauged by the concentration of DNA; *middle panel*) extends into, and defines the character of, the undercrust. Red vertical lines reflect the levels of DNA and chlorophyll-a in not crusted, bulk soil from the same area. The differential geochemical character of crust and undercrust is reflected in elemental concentrations (*right panel*), where the relative size of the font for each element denotes relative enrichment or depletion between crust and undercrusts. Data from Garcia-Pichel et al. (2003) and Beraldí-Campesi et al. (2009)

a burial by less than 1 cm of sand has little long-term effect on the crust. Sometimes, in this manner, a new topcrust is created, leading to the buildup of a new subcrust, with perhaps mixed characteristics (Fig. 13.4 and see also Fig. 13.2, where the subcrust shows evidence of an old matrix of cyanobacterial sheaths). Deeper in the soil, ancient buried crusts can sometimes be found (Malam Issa et al. 2009; Drahorad and Felix-Henningsen 2013; Felde et al. 2014), in some cases even recurrently, forming layered sediments (Beraldí-Campesi and Garcia-Pichel 2010). Recently some of these layered fossilized biosurfaces have been recovered from terrestrial sediments as old as 1.2 billion years (Beraldí-Campesi et al. 2014; see Chap. 3 by Beraldí-Campesi and Retallack).

Pore formation seems to be a significant structural trait in many biocrusts. Williams et al. (2012), working in the Mojave Desert, reported that the separation of a crust into two layers coincided with a planar void, likely generated by anastomosis of vesicular pores. These subsurface vesicular pore systems (or vesicular horizons) are common in crusts from various regions (Miralles-Mellado et al. 2011; Badorreck et al. 2013; Beraldí-Campesi et al. 2014; Felde et al. 2014). Unless actively destroyed (e.g., by root growth), they do preserve well in the fossil record and can be used as indicators for paleoenvironmental conditions and “markers” of paleo-crusts (Beraldí-Campesi et al. 2014). Vesicular layers can further decrease infiltration of a crusted soil surface (Hillel et al. 1998). Dietze et al. (2012) conducted comprehensive laboratory experiments that shed light on the genesis of vesicular pores, pointing to a combination of repeatedly descending wetting fronts with a soil surface that is puddled by fines. This sealed surface, due to

Fig. 13.4 Evolution of pores and biopores. (a) Vesicular horizons develop in the subcrust of cyanobacterial biocrusts of the Sonoran Desert (Bernaldi-Campesi et al. 2014). (b) Computer tomography cross section of a cyanobacterial biocrust from the Negev with two vesicular micro-horizons. In addition to the unconnected vesicles that are known to impede water movement, alternating layers of fine and coarse grains cause pore discontinuities, which create a capillary barrier effect that further reduces water infiltration (Feld et al. 2014). (c) Computer tomography cross section of a lichen-dominated crust from the Negev. Increased surface roughness results in a higher dust-trapping efficiency and therefore higher amount of silt and clay. This, combined with the high shrink-swell activity of the lichens, causes expansion-contraction during wetting-drying cycles and ultimately leads to the creation of shrinkage cracks. These cracks can vary in their orientation from horizontally to vertically, which is likely to have different impacts on water and gas fluxes in the crust



the water table on top of the puddled surface, leads to an increased gas pressure and decreased inter-grain connection in the soil, which ultimately results in the formation of spherical, isolated pores. There exists a positive correlation between the size and sphericity of the pores with wetting rates and sand content, but a negative correlation with CaCO_3 content. A necessary biotic influence of microbial metabolic gases can be effectively ruled out because vesicles also formed in sterilized soil (Dietze et al. 2012). For a more detailed description of the connection between

soil crusting and vesicular pore formation, see also Chap. 9 by Colesie et al. and Felde et al. (2014).

Compelling evidence has been presented that EPS play a role in the architecture of biocrusts. Malam Issa et al. (2009) report that EPS can enhance the formation of pores and affect crust geometry. EPS clearly control the formation of microbially induced sedimentary structures (MISS) like roll-ups, folds, desiccation polygons, etc., particularly in non-cohesive substrates like sandy soils (Beraldi-Campesi et al. 2014). Rossi et al. (2012) showed that a simple nondestructive extraction of biocrust extracellular polysaccharides resulted in a much more compacted, “caked up” form that lost significant albedo and the ability to absorb water, all expected outcomes of a collapse of the pore system.

13.2.2 Small-Scale Spatial Structure of Biological Components

Organisms are not spread homogeneously within biocrusts. As was the case with abiotic components, and while lateral patterns (i.e., patchiness) clearly exist, most generalizations can be made regarding the small-scale vertical distribution of organismal biomass and composition.

Examining Colorado Plateau cyanobacterial crusts at millimeter resolution, Garcia-Pichel et al. (2003) found that both bacterial populations and DNA concentrations were tenfold larger in the top centimeter than in deeper, bulk soils. But the maxima in DNA concentration were clearly within the topcrust, either in the surface or the shallow subsurface (1–2 mm), depending on the crust type. Analyses of community structure along the vertical dimension, based on DNA sequencing and microbial community fingerprinting, showed clearly that community composition varied as well, pointing to the presence of differentiated niches within the crust.

Most descriptions of organismal spatial distribution in biocrusts involve the phototrophs, which are visible and largely recognizable by microscopy. Mostly as a consequence of the steep vertical gradients in light and, in arid environments, water availability within the crust, photosynthetic organisms are confined to the topcrust that they help delimit. This is usually only one to a few millimeters deep. Garcia-Pichel et al. (2003) reported that 75 % of all extractable chlorophyll-a can be found in the top 2 mm in Colorado Plateau crusts. But even within this euphotic zone, there is clear evidence of niche partitioning (Elliott et al. 2014). The very surface of the crusts represents a zone of light trapping, where, because of intense light scatter by mineral particles, the irradiance can be significantly higher than that incident down-welling from the outside (Garcia-Pichel 1995). The first colonizers of biocrusts in dryland regions (filamentous cyanobacteria and sometimes green algae) avoid it, and tend to establish subsurface populations below it, a few hundred microns to a few mm deep (Fig. 13.1b, d). Here the light intensities are moderate, there is little chance of abrasion by moving sand, and desiccation happens less

quickly. This gives rise to a subsurface “organic” layer with a largely mineral layer on top. Crusts at this stage are very cryptic and typically referred to as light crusts in the literature. Examples of this are abound in the literature from a variety of locale and climatic regions, for cyanobacteria and eukaryotic populations (Hu et al. 2003; Pringault and Garcia-Pichel 2004; Smith et al. 2004; Zhang 2005; Zhang et al. 2006; Beraldí-Campesi et al. 2009; Chen et al. 2009; Wu et al. 2011; Lan et al. 2012; Rajeev et al. 2013).

Many of these subsurface populations of filamentous cyanobacteria (*Microcoleus vaginatus*, *Microcoleus steenstrupii*, *Trichocoleus* (formerly *Microcoleus sociatus*, *Oscillatoria* spp.) undergo vertical migrations to the surface when the crust gets wet in the dim light of overcast, rainy skies, returning to their subsurface refugium by sensing impending drought, a unique feature among microbes (Garcia-Pichel and Pringault 2001; Pringault and Garcia-Pichel 2004; see videos in Rajeev et al. 2013). Because these cyanobacteria leave a trail of EPS as a mechanism for motility, the movement becomes an efficient form of “weaving” minerals together, and the consolidation encompasses not just their subsurface resting area but the entire topcrust (Fig. 13.1e). Even at this early stage, empty sheaths and EPS left at the surface probably contribute to the dust-trapping ability of early crusts.

The light-trapping surface (0–200 µm deep) is typically only colonized by cyanobacteria that produce large quantities of sunscreens, as in the genera *Scytonema*, *Tolypothrix*, *Nostoc*, *Porphyrosiphon*, etc. (Garcia-Pichel et al. 2001; Hu et al. 2003; Yeager et al. 2007). Most of these cyanobacteria are nonmotile and require the soil to be stabilized before they can thrive, being secondary colonizers after the initial motile filamentous forms (Garcia-Pichel 2002). Their advent during maturation increases a crust’s nitrogen-fixing capacity (Yeager et al. 2007) and lowers significantly soil albedo, due to the high content of scytonemin sunscreens. The top surface can also be colonized by aerophytic cryptogams (lichens and mosses), but these components do not occur everywhere.

Very detailed (submillimeter scale) vertical distributions of cyanobacterial and algal components of crusts from Shapotou (Tengger Desert, China) based on microscopic observations have been presented (Hu et al. 2003; Wu et al. 2011; Lan et al. 2012). These indicate that further vertical organization is possible, depending on the particular locale, but many of the components described in these studies do not seem to be of widespread distribution. Interestingly, they also report a preference of nematodes and protozoa for the topcrusts.

Analogously to cyanobacterial and algal biocrusts, Wu et al. (2011) also observed a layering of the biotic components in lichen-dominated crusts below the lichen thalli, which extend upward from the crust surface (Fig. 13.5). This included a top 1 mm layer with typical phototrophs, underlain by a layer dominated by lichen rhizoids between 1 and 2 mm, and a subcrust below it (subrhizoid layer, down to 6–8 mm). Within moss-dominated crusts, Lan et al. (2012) also distinguished three different layers, i.e., an upper “stem-leaf” layer (~0–2 mm), a rhizoid layer (~2–6 mm), and a subrhizoid layer (~6–15 mm). Pedicellation into mounds in microbiotic crusts appears to produce distinctive microhabitats that result in

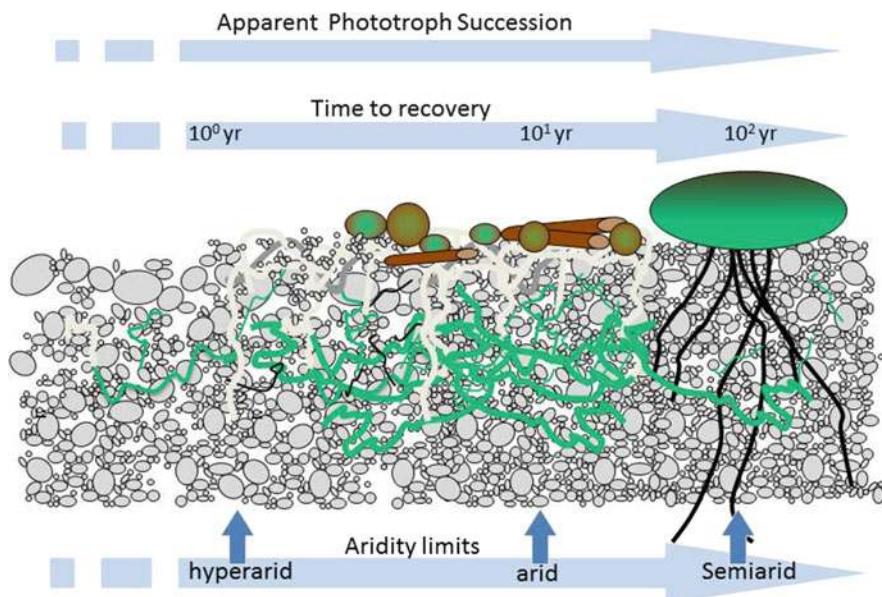


Fig 13.5 Biological succession in biocrusts (depth ~1 cm), conceptualized progressing from left to right, for North America crusts, according to Garcia-Pichel (2002). Early colonization by bundle-forming cyanobacteria (depicted as green filaments, with their sheaths in gray) stabilizes the soil, contributes to the creation of a layer of fines, and enables secondary colonization by heterocystous cyanobacteria (brownish globules and cylinders on soil surface), with eventual colonization by lichens or mosses. Aridity limits the end-point climax of this succession, and the time of recovery to each successive stage increases exponentially

organismal differential distributions and differential organismal cover (George et al. 2000). This is particularly conspicuous for lichens and mosses. Presumably milder micro-aspects (north-north-west, east-north-east, and top) supported greater lichen and moss cover than the warmer, windward, and more xeric micro-aspects (west-south-west and south-south-east (Bowker et al. 2006).

There have been few recent studies on the microbial distributions of non-photosynthetic microorganisms in biocrusts (Steven et al. 2013; Elliott et al. 2014; Maier et al. 2014; see Chap. 5 by Maier et al.). In a first investigation on that topic, Johnson et al. (2005) investigated aerobic chemolithotrophic ammonia-oxidizing bacteria, which build populations covering up to 2.5 mm in the suboxic confines of the active crusts. Here they find optimal “rain down” of ammonium released by cyanobacteria, moderate but sufficient oxygen, and a refuge from intense surface light intensities, to which they are sensitive. Their activity, in turn, contributes to creating a maximum of nitrate concentration at this depth (Johnson et al. 2007). Surprisingly, there are to date no studies on the small-scale distribution of heterotrophic microbes (bacteria, archaea, or fungi) beyond the anecdotal report of Garcia-Pichel et al. (2003), although one could envision a variety of potential niche differences regarding oxygen, pH, light (Garcia-Pichel

and Belnap 1996), nutrients (Johnson et al. 2007; Beraldi-Campesi et al. 2009), and organic carbon (Baran et al. 2015).

13.3 Temporal Dynamics: Biological Succession, Structural Maturation, and Weathering

13.3.1 Biological Succession

Long-term studies on biocrust changes over time are rare. Therefore a “space-for-time” approach has often been applied to infer biocrust temporal dynamics. This “space-for-time” approach includes biocrust types of different perceived developmental stages, in most cases separated into cyanobacteria-dominated crusts (incipient or “light” and more mature or “dark”), lichen crusts, and moss crusts, often assuming that, given sufficient time, crusts will develop in such sequence (see Chaps. 9 and 23 by Colesie et al. and Weber et al., respectively). This is not always the case, given that in many pristine unaltered environments, terminal succession crusts can be lichen, cyanobacteria, or moss dominated (also see Chap. 23 by Weber et al.). Whenever lichen or moss crusts do develop, it is likely that they are preceded by one or more cyanobacterial- or algal-dominated stages. A generalization of the initial stages of biological succession in unconsolidated soils is presented in Fig. 13.5, based largely on results from crusts in Western North America. Loose mineral soil is initially colonized by pioneer cyanobacteria, which are typically motile, filamentous cyanobacteria that form supra-filamentous aggregations into bundles of ropes (Garcia-Pichel and Wojciechowski 2009; Fig. 13.1). They colonize the subsurface, and because of their large size, the rope-shaped organisms stabilize soil particles that come in contact with the extracellular sheaths. Migrations help weave a web of extracellular sheath trails that stabilizes the soil surface. This stage is what is typically referred to as “light crusts” in the literature. Once the surface is stabilized, secondary colonization by other organisms is possible. At depth, we find a variety of other cyanobacteria, which nevertheless remain typically less abundant than the pioneer *Microcoleus* spp. The most significant change occurs close to the surface with the advent of populations of heterocystous, nonmotile cyanobacteria. The three most common clades of such cyanobacteria are *Nostoc* sp., *Tolyphothrix* sp., and *Scytonema* (Yeager et al. 2007). The advent of these heterocystous cyanobacteria brings about significant abiotic changes in albedo and crust surface temperature, that may, in turn, further affect the crust community composition (Couradeau et al. 2016). In a third stage, cryptogamic populations (lichens and/or mosses) may come in. Their presence brings about changes in the original populations as their thalli, external to the soil, can significantly shade the crusts interior, and as their rhizoids and protonemata penetrate and rework the topcrust and subcrust, thereby altering the structure and geometry of the pore system (Felde et al. 2014), which can drastically alter gas and water fluxes in and through the

crust. Similar successions have been described from the Asian deserts (Hu et al. 2003; Zhang et al. 2006). These studies emphasize also the associated changes in visible organization into layers that logically follow the biological succession. Moss thalli constitute, in turn, a habitat for specialized populations of epiphytic cyanobacteria, which are relevant to crust fertility (Veluci et al. 2006).

13.3.2 Structural Development

During ongoing succession of Gurbantunggut Desert crusts, a transition from uncrusted soils to “light crusts” resulted in significant structural maturation, including the formation of a surface layer dominated by aeolian fines, with a dense and tightly packed matrix over an “organismal” layer dominated by cyanobacteria filaments, devoid of fines and developing large voids (Zhang et al. 2006). Studies carried out in the SE Tengger Desert of China showed that not only the vertical stratification was altered with crust successional stage but also that these changes were accompanied by a general increase in thickness and porosity and therefore a decrease in bulk density (Lan et al. 2012). And yet, typically biocrusts of older development stages tend to show increased penetration resistance. Thomas and Dougill (2007) found an almost threefold increase from 55 to 147 kPa with maturation; Guo et al. (2008) report a much more moderate difference: 125 kPa for algal crust vs. 168 kPa for a moss-dominated crust.

In cyanobacterial crusts from the NW Negev Desert of Israel, the porosity of both topcrust and subcrust changes with development. These crusts develop a vesicular micro-horizon and pore discontinuities associated with changes of pore and grain size (Fig. 13.4), which in turn causes a capillary barrier effect that reduces water infiltration. These crusts do show low infiltration compared to the bare soil or more mature crusts (Yair et al. 2011). With ongoing development, lichen crusts establish that develop shrink-swell dynamics caused by wetting cycles of lichen thalli and increased clay contents. This leads to the formation of shrinkage cracks (Fig. 13.4). The number of biopores increases at this stage, due to the growth of annual plants (roots) and lichen rhizoids, leading to increased water infiltration capacity, unless the crust is significantly detached from the soil underneath (Miralles-Mellado et al. 2011). In the successional stages of the Negev crusts, moss crusts show the highest abundance of biologically formed pores. In addition, moss rhizoids and protonemata pierce the complete crust, creating pathways for preferential infiltration and changing the geometry of the pore system from a tortuous to a straight pore network, while increasing pore diameters. The initial layering of coarse and fine grains, which was present in cyanobacterial crusts, disappears from these older crusts, likely as a consequence of active bioturbation. Within this ecosystem, cyanobacterial subcrusts show the highest porosity due to vesicular structures, with the topcrust porosity increasing steadily toward fully formed moss crusts (Feldé et al. 2014).

13.3.3 Weathering and Geochemical Alteration

Investigations of biocrust weathering patterns, mechanisms, and rates are in their infancy. What we can predict to be relevant comes largely from geomicrobial interactions that have been studied in similar environments, i.e., endolithically within rocks, or on temporarily desiccated marine benthic environments. These comparisons have clearly their limits, since the lithic habitat is much more prone to weathering/erosional processes and biocrusts, at the opposing end of the geological spectrum, form on sedimentary settings that are the very results of such processes of weathering and erosion. A crust's main geological role is its stabilizing, erosion-preventing effect on the sedimentary bed it covers. Given the accumulation of relatively large populations of microbes within the confines of a small space, however, biocrusts promote the internal formation of chemical microenvironments that can deviate significantly from the bulk values of the soil (Garcia-Pichel and Belnap 1996). Such microenvironments are thought to be one of the driving forces for increased rates of weathering on the abiotic components of biocrusts, and so the process of weathering cannot be understood but in the light of microstructural considerations. Beraldí-Campesi et al. (2009) surveyed the overall composition of a variety of soil crusts in North America with the specific aim to test the presence of chemical leaching as a process of relevance within biocrusts. The approach they took was to compare the concentrations of a set of 25 elements between crusts and immediately adjacent, uncrusted soils. They also analyzed the concentrations in the crusts and subcrusts. The survey revealed that crusts expectedly enriched the soil with biogenic elements (C, N, P) and generated leaching for many elements, significantly so for several important metals and metalloids (Ca, Cr, Mn, Zn, As, Zr). This leaching effect included the subcrust, indicating that the export of these mineral constituents and important micronutrients extended beyond the reaches of the crust. The authors argued that this leaching effect explains the necessity for allochthonous (dust) inputs to maintain the fertility of biocrusts in the long run.

Some of the physical weathering mechanisms ascribed to cryptogams and microbes in the lithic environment, such as the expansion and contraction of biomass in crevices or pores during wetting and drying (Chen et al. 2000), are clearly less relevant in sedimentary settings, but some of the mechanisms of biochemical weathering can be assumed to potentially work in a similar manner in the clastic milieu of the soil. These include the excretion of oxalic acid, the generation of respiratory CO_2 causing an acidification of the surrounding medium, and the production of biochemical compounds with complexing ability (Chen et al. 2000). In addition, two mechanisms of potential relevance are the alkalization of the substrate caused by CO_2 consumption and the net OH^- increase in the medium (Büdel et al. 2004) and the dissolution of carbonates caused by an active intracellular transport of free Ca^{2+} away from the weathering front and into the medium (Garcia-Pichel 2006).

Generally, silicate substrates are resistant to solubilization by organic acids and acid volatiles like CO_2 . Only some minerals, like the micas, phlogopite, and

muscovite, are prone to acid hydrolysis (Serstevens et al. 1978). Bachmann (1904) described the preferential growth of endolithic lichens between the muscovite mica lamellae of granite. This euendolithic growth was restricted to granites containing mica, whereas in others, organisms were delimited to endolithic growth within fine preexisting cracks or crevices. The exfoliation of micas in granite by growth of chasmoeuendolithic cyanobacteria has been described by de los Rios et al. (2003, 2007). These mechanisms of weathering could potentially impact the mineralogy of soil crusts wherever micas form a substantial mineral component. Beraldí-Campesi and Garcia-Pichel (2010), however, did not find micas to be important silicates in a variety of cyanobacteria soil crust settings, in which silicate clay composition was in fact not altered by the presence/activity of large cyanobacterial populations in those crusts. In young crusts developing in temperate soils impacted by mining, Fischer et al. (2010) found no measurable weathering on silicates after 3 years of development. By contrast, Chen et al. (2009) found a general trend of decrease in primary silicate (K-feldspar) and an opposing increase in secondary hydrous micas along a full-scale space-for-time crust succession, particularly in crusts dominated by lichens and mosses. This is consistent with the well-known role of fungi in driving silicate mineral transformations.

In porous siliceous rocks, organisms form a continuous layer parallel to the rock surface at a few millimeters depth, including lichens (Friedmann et al. 1988; Wessels and Schoeman 1988) and free-living cyanobacteria (Friedmann et al. 1967; Eichler 1981; Friedmann 1982; Bell et al. 1986; Wessels and Büdel 1995; Weber et al. 1996). For the endolithic habitats in South Africa and Antarctica, exfoliative weathering mechanisms along the growth zone of the organisms were observed (Friedmann 1982; Büdel et al. 2004). Büdel et al. (2004) demonstrated that exfoliation results from an alkalization of the substrate by cyanobacteria, which causes both dissolution of silicate in the binding material and mineral grains and precipitation of carbonate crystals. The phenomenon of silicate dissolution by alkali was also predicted to occur in crusts (Garcia-Pichel and Belnap 1996), since photosynthesis-driven alkalization can drive local pH microenvironments above ten, but direct demonstrations are still lacking.

Carbonate rocks and carbonate sediments are colonized and weathered by a variety of microorganisms, such as cyanobacteria, algae, fungi, and lichens. Some grow euendolithically, creating a habitat by the active dissolution of the mineral (e.g., Bachmann 1913; Danin et al. 1983). For heterotrophs, it is thought that the mechanism consists of direct carbonate dissolution by acidification through metabolic CO₂ production (Golubić et al. 1979). Also autotrophic organisms can temporarily show a net release of CO₂ when respiration prevails, which may happen quickly enough to cause dissolution of the substrate (Weber et al. 2011). A new mechanism, by which autotrophs (algae and cyanobacteria) are able to dissolve carbonates, has been proposed by Garcia-Pichel (2006). There is now good evidence that euendolithic cyanobacteria bore by taking up Ca²⁺ ions from the medium selectively at the boring front, thus promoting dissolution of calcium carbonates there, transporting the ions intracellularly and excreting them at the opposing end (Garcia-Pichel et al. 2010; Ramirez-Reinat and Garcia-Pichel 2012). It now

remains to be studied if this mechanism is restricted to cyanobacteria or if it also occurs in eukaryotic phototrophs. Again, in this case there is no evidence that any of these weathering mechanisms are of relevance in soil crusts developing in carbonate-rich soils. A review of molecular tallies of cyanobacteria in a variety of soil crusts, in fact, does not yield any typical euendolithic phylotypes. If any organisms are of importance, it is likely to be lichens, which could contribute to carbonate dissolution through acidification of the medium. Other organisms known to contribute significantly to carbonate dissolution in limestone through the production of nitric acid are the nitrifying microbes. These organisms are widespread and numerous in biocrusts (Marusenko et al. 2013).

13.4 Conclusion

Biological soil crusts (biocrusts) are organo-sedimentary systems in which both the organic and the inorganic mineral components play dynamic roles in determining the architecture and evolution of the system, as they interact between themselves and with the physical environment. We critically reviewed advances in the description of the microstructure of biocrusts with respect to their abiotic and biological components, as well as the interactions between the two in time and space that result in important properties of environmental relevance. We paid special attention to the processes of crust biological and physical succession and to mineral weathering processes.

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Chapter 14

Patterns and Controls on Nitrogen Cycling of Biological Soil Crusts

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14.1 Introduction to Nitrogen Cycling in Biocrusts

Biocrusts play a significant role in the nitrogen (N) cycle within arid and semiarid ecosystems, as they contribute major N inputs via biological fixation and dust capture, harbor intense internal N transformation processes, and direct N losses via dissolved, gaseous, and erosional loss processes (Fig. 14.1). Because soil N availability in arid and semiarid ecosystems is generally low and may limit net primary production (NPP; Hooper and Johnson 1999), especially during periods when adequate water is available, understanding the mechanisms and controls of N input and loss pathways in biocrusts is critically important not only to our broader understanding of N cycling in dryland environments but also of overall dryland fertility. In particular, N cycling by biocrusts likely regulates short-term soil N

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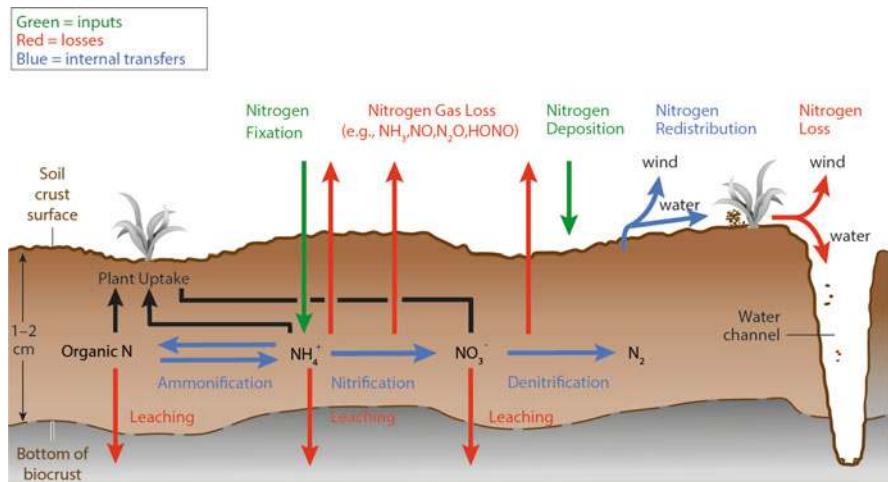


Fig. 14.1 Nitrogen (N) cycling in dryland areas. Nitrogen inputs into biocrusts are by means of N fixation and deposition. Within the biocrusts, N can be internally transferred by wind and water, and it can be metabolically transformed to then be present as ammonium (NH_4^+), nitrate (NO_3^-), organic N, and elemental N_2 . Nitrogen is lost by biocrusts by means of wind and water, leaching into deeper strata, and gaseous losses (e.g., $\text{NH}_3, \text{NO}, \text{N}_2\text{O}, \text{HONO}$)

availability to support vascular plant growth, as well as long-term N accumulation and maintenance of soil fertility.

In this chapter, we review the influence of biocrust nitrogen inputs, internal cycling, and loss pathways across a range of biomes. We examine linkages between N-fixation capabilities of biocrust organisms and spatiotemporal patterns of soil N availability that may influence the longer-term productivity of dryland ecosystems. Lastly, biocrust influence on N loss pathways such as N gas emissions, leakage of N compounds from biocrusts, and transfer in wind and water erosion are important to understand the maintenance of dryland soil fertility over longer time scales. Although great strides have been made in understanding the influence of biocrusts on ecosystem N cycling, there remain important knowledge gaps in our understanding of the influence of biocrusts on ecosystem N cycling that should be the focus of future studies. Because work on the interaction of N cycling and biocrusts up to 2001 was reviewed in Belnap and Lange (2003), this chapter will provide a brief summary of our current knowledge at the beginning of each section and then go on to focus primarily on research findings that have emerged over the last 14 years (2001–2015).

14.2 Biocrust Nitrogen Fixation

Biological fixation of atmospheric N₂ (diazotrophy) is an ubiquitous biogeochemical transformation in biocrusts, and it likely constitutes a dominant source of N in dryland environments (Evans and Ehleringer 1993; Evans and Lange 2003). Multiple studies over years have addressed the environmental controls on N fixation rates and suggest that many factors can be at play [for a summary of the literature up to 2001, see Belnap (2003)]. Studies prior to 2001 showed that the environmental controls on N fixation are generally hierarchical: As biocrust organisms are physiologically active only when wet, moisture is a prerequisite and the first-order control on N fixation. Given sufficient hydration, energy and reduction equivalents are the main metabolic requirements for N fixation. Photochemical processes carried out by nitrogen-fixing cyanobacteria, which are the dominant N fixers in biocrusts, are the ultimate source of this energy required for N fixation. Hence, light intensity can be a prime driver of diazotrophy. Temperature is an important determinant of chemical and biochemical reaction rates, and this applies to N fixation as well. Seasonality, as a compound succession of varying factors such as temperature, light, and moisture, thus drives the major dynamics of N fixation in biocrusts (Bowker et al. 2002; Belnap 2003). Beyond these parameters, antecedent conditions also influence N-fixation rates, as they can determine legacy amounts of reductants, nitrogenase enzyme, and N present in the biocrusts and surrounding soils.

For this chapter, we examined studies post-2001 to explore whether new insights have been gained since the Belnap (2003) review. Because many studies did not report all potentially relevant variables, we restricted our analysis to those studies reporting temperature, season of collection, biome, and biocrust type. In addition, studies using ¹⁵N₂, unless ¹⁵N and acetylene incubations were done simultaneously, are not comparable to those using the acetylene reduction assay (ARA) (see discussion below), and thus we separated our analysis for these two methods. Natural ¹⁵N abundance cannot be used to quantify N inputs in most unmanaged ecosystems but can be used to indicate whether or not N fixation may be occurring and is discussed separately as well.

14.2.1 Studies Measuring Nitrogen Fixation Using the ARA Method

We found 21 publications using ARA under both laboratory and field conditions. Almost all studies in the set used the narrow temperature range of 24–26 °C, so we cannot expect to find useful information on the temperature effects on N fixation. Biocrust type, however, was a significant factor (Fig. 14.2). Light cyanobacterial biocrusts (dominated by low biomass *Microcoleus* spp., which are typically less mature) showed the lowest areal rates (~0.6 nmols C₂H₄ cm⁻² h⁻¹). Recent

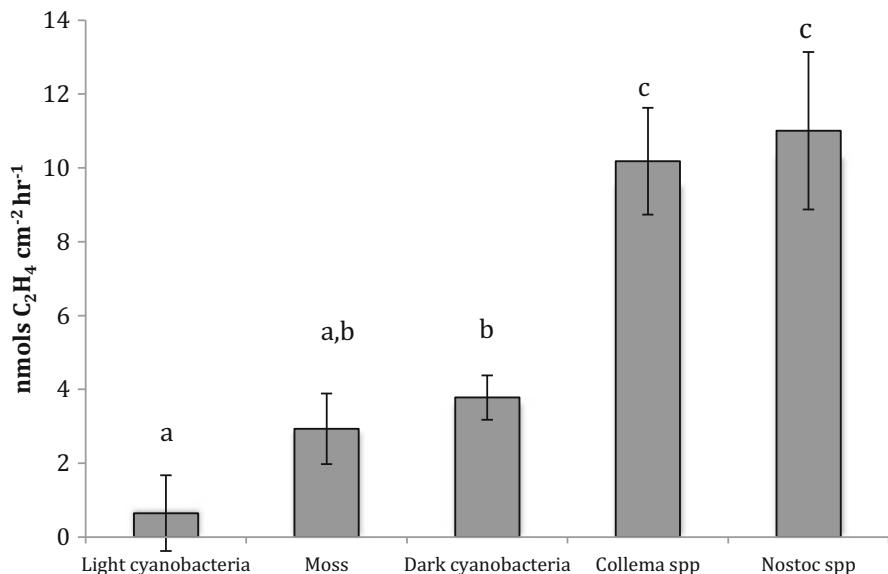


Fig. 14.2 Nitrogen fixation as measured by acetylene reduction assays (ARA) for different biocrust types. Values are means \pm 1 SE. Different lowercase letters above each bar indicate statistical significance at the level of $P < 0.05$. ARA values were obtained from these publications: Aranibar et al. (2003), Barger (2003), Barger et al. (2013), Belnap (2002a, b), Billings et al. (2003), Caputa et al. (2013), Dickson (2000), Housman et al. (2006), Issa et al. (2001), Liu et al. (2009, 2012), Stewart et al. (2011a, b, c, 2012), Strauss et al. (2012), Su et al. (2011 b), Wu et al. (2009), Zhao et al. (2010), and Zielke et al. (2002)

evidence suggests that N fixation in these light cyanobacterial biocrusts is associated with heterotrophic diazotrophic bacteria in the Clostridiaceae and Proteobacteria groups (Pepe-Ranney et al. 2015). Moss biocrusts and dark cyanobacterial biocrusts, dominated by a mix of *Nostoc* spp., *Tolyphothrix* spp., *Scytonema* spp., as well as *Microcoleus* spp., showed an average of ~3–4 times higher rates than light biocrusts, whereas the cyanolichen *Collema* spp. and surface-dwelling sheets of *Nostoc commune* had the highest values of all (Fig. 14.2; \sim 10–11 nmols⁻¹ C₂H₄ cm⁻² h⁻¹, respectively). These patterns are consistent with those reported by Belnap (2003) for studies prior to 2001.

ARA rates across different biomes (i.e., cold, cool, and hot desert) and season of collection (i.e., spring, summer, winter, fall) were highly variable and suggest that seasonality within a biome may have complex and interactive effects on N fixation. For example, Housman et al. (2006) showed that ARA rates peak during cooler, wetter time periods, which varied by biome type (Fig. 14.3). Spring ARA rates were highest in a North American cool desert site, whereas in a North American hot desert site, ARA rates peaked in the fall and winter (Fig. 14.3).

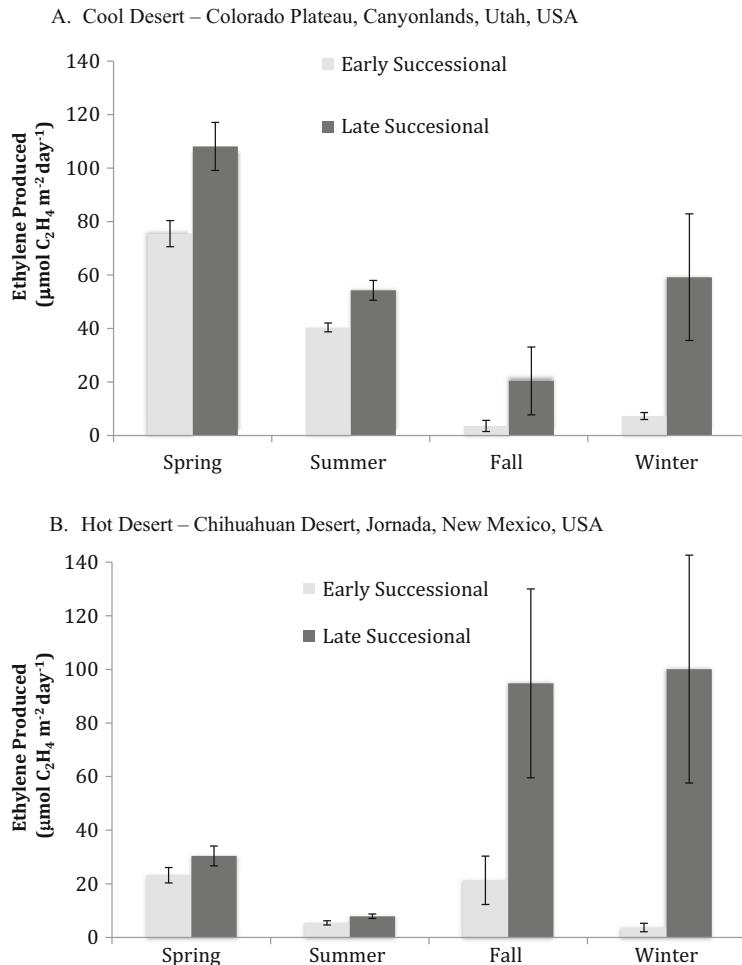


Fig. 14.3 Nitrogen-fixation estimates from acetylene reduction assays in a cool (Colorado Plateau) and hot desert (Chihuahuan Desert) in North America. The figure was modified from Housman et al. (2006)

The high variability in ARA rates reported in the literature may at least partly reflect methodological limitations of the assay. ARA is based on the fact that the enzyme nitrogenase, which is normally responsible for catalyzing the reduction of N₂ to NH₃, can also reduce acetylene to ethylene, the latter reaction being an indirect measure of nitrogenase activity. Optimally, ethylene formation rates are then converted into actual rates of N fixation. The theoretical conversion ratio of ethylene to N₂ fixed is between 3 and 4, depending on whether the H₂ by-product produced during N fixation is driven by a unidirectional (uptake) hydrogenase

[as discussed in Liengen (1999a) and Staal et al. (2001)]. All N-fixing cyanobacteria known contain uptake hydrogenases (Kothari et al. 2012). In a series of early experiments, Hardy et al. (1968) confirmed that this theoretical ratio ranged between 3 and 4 for bacterial cultures and legumes under laboratory and field conditions. Since this time, however, actual results from field and laboratory studies of biocrusts report that conversion ratios can range from 0.022 to 3.49 (Liengen 1999a; Stewart et al. 2011a; Caputa et al. 2013). Deviation (usually downwards) from the 3–4:1 ratio can result from several factors and may include the following: (1) suppressed reduction of H⁺ to H₂ in the presence of acetylene leading to higher conversion ratios of acetylene to N₂ (Jensen and Cox 1983); (2) acetylene is more soluble in water than N₂ thus making acetylene more available to nitrogenase than N₂ (Rice and Paul 1971; Nohrstedt 1983); (3) vanadium-based nitrogenase has lower ratios than molybdenum-based nitrogenase and some organisms can have either (Smith et al. 1987); (4) C₂H₂ can be toxic to microbes (David and Fay 1977); (5) acetylene can be adsorbed onto soil colloids (Rennie et al. 1978); and (6) differential diffusion barriers exist for acetylene. Because N₂ or ¹⁵N₂ only needs to diffuse into the soil, whereas ARA measures require gases to move both in and out of the soil before detection, the effect of these barriers to diffusion is more pronounced with ARA. Therefore, if the intent of a study is to establish absolute rates of fixed N by biocrusts, either ARA determined rates require calibration with ¹⁵N₂ during the ARA measurements or ¹⁵N₂ should be used instead. We note here that any underestimations of rates due to the effect of diffusion limitation will still exist for externally supplied ¹⁵N₂.

¹⁵N₂ Method We could only find three studies since 2001 (Holst et al. 2009; Stewart et al. 2011a; Caputa et al. 2013) and two studies prior to that time (Mayland and McIntosh 1966; Liengen 1999b) that used ¹⁵N₂ to measure N fixation in biocrusts. These studies were not focused on how environmental factors influenced N-fixation rates, as analysis was done under standard temperatures, moisture, and light and with materials collected in the same season. This is unfortunate, as the use of ¹⁵N₂ is required for accurate comparisons among environmental variables and biocrust types. However, these studies do provide data on the appropriate conversion ratio for ARA under those experimental conditions, as all but Mayland and McIntosh (1966) analyzed samples both with ARA and ¹⁵N₂. The most important finding is that ARA can underestimate N-fixation rates in biocrusts, as most studies found conversion ratios to be well below 3–4.

14.2.2 Natural ¹⁵N Abundance

Natural ¹⁵N abundance can be used to determine the overall balance of N inputs and losses or mass balance in those soils, with δ¹⁵N values (i.e., ratio of stable isotopes 15N:14N) close to zero indicating that fixed atmospheric N is likely a dominant source of N available for soils and organisms (Shearer and Kohl 1988). Several

studies have used this method to assess if biocrusts are fixing atmospheric N (Aranibar et al. 2003; Billings et al. 2003; Russow et al. 2005; Marsh et al. 2006; Stewart et al. 2011a). In general, these studies show that soils overlain with biocrusts have lower ^{15}N values than those without biocrusts, consistent with the notion that biocrusts do contribute fixed N to underlying soils and in agreement with global studies prior to 2001 (Evans and Lange 2003). Interestingly, Russow et al. (2005) compared biocrusts dominated by a non-N-fixing lichen to those dominated by *Collema*, showing that *Collema* was responsible for 88 % of the N in biocrusts.

14.2.3 Estimates of Annual Biocrust N Fixation

Similar to the wide range of ARA rates reported above, estimates of annual N inputs from biocrust N fixation are highly variable, ranging from 0.7 to 100 kg N $\text{ha}^{-1} \text{a}^{-1}$ [reviewed by Evans and Lange (2003), Belnap (2002a, b), Russow et al. (2005), Stewart et al. (2011a, b, c), and Caputa et al. (2013)]. Quantification of N fixation by desert biocrusts globally reported an average N-fixation rate of 6 kg N $\text{ha}^{-1} \text{a}^{-1}$ (Elbert et al. 2012).

The potential sources of error in scaling estimates of short-term N-fixation studies to an annual input are (1) inaccurate estimates of the duration of N-fixing activity in biocrusts, either daily or seasonally, (2) the lack of representativeness of the samples analyzed at the landscape level, and (3) the use of inaccurate ARA conversion ratios. As biocrusts are only active when wet, using continuously logged soil moisture data, the potential number of N-fixation activity days may be calculated. Metabolic activity, and thus the ability to fix N, is limited to ~10–12 % of the year in the Namib Desert, Germany temperate steppe, Colorado Plateau Desert, and South African Succulent Karoo (Lange et al. 1991; Lange and Green 2003; Darrouzet-Nardi et al. in press; Weber, unpublished). Thus, constraining the daily periods that biocrusts are physiologically active is critically important to estimating N inputs on an annual time scale. Newly developed biocrust moisture probes, to assess both the activity and the water content of biocrusts, may be a good resource for this (Weber et al. 2015a).

In addition to N fixation, N inputs from the atmosphere through both wet and dry deposition (~2 kg N $\text{ha}^{-1} \text{a}^{-1}$ in relatively pristine air sheds up to 15 kg N $\text{ha}^{-1} \text{a}^{-1}$ in impacted air sheds) may contribute to N inputs and N cycling dynamics within biocrusts. In fact, in air sheds highly impacted by N deposition, this additional source of N may relieve biological N limitation altogether. In a recent study, biocrusts collected from the pristine lower Sonoran desert and then transferred to the high-N atmosphere of the city of Tempe, Arizona, resulted in a complete loss of N-fixation capacity within weeks (Vaugh and Garcia-Pichel, unpublished).

The choice of ARA to N-fixation conversion ratios in estimates of N fixed is also an issue, as this may result in estimates of annual N inputs differing by an order of magnitude (Liengen 1999b; Caputa et al. 2013). Notably, however, upper estimates

of annual N fixation are of similar magnitude as those of annual N fertilization inputs to agricultural systems [reviewed in Evans and Lange (2003) and Caputa et al. 2013]. Clearly then, in the absence of significant N uptake by surrounding vascular plants, there should be evidence of significant system losses in N to offset estimates of high N inputs in order to explain the lack of longer-term soil N accumulation. This is discussed in the following sections.

14.3 Nitrogen Release to the Surrounding Substrate

Extracellular release of nitrogenous compounds, including inorganic forms such as nitrate [NO_3^-] and ammonium [NH_4^+], and small amounts of amide, peptides, and free amino acids, occurs in both cyanobacteria and lichens (Stewart 1970; Millbank 1982). Nitrogen release is especially pronounced in the presence of N-fixing organisms, which can release 5–70 % of N fixed (Magee and Burris 1954; Silvester et al. 1996). Kershaw (1985) reported that 19–28 % of labeled N applied to lichens was later found in surrounding soils. Earlier studies showed more N release when pH, temperature, light, CO_2 , or ionic conditions were suboptimal or during wetting after desiccation (Henriksson 1957; Jones and Stewart 1969a; Millbank 1982; Jeanfils and Rack 1992). Nitrogen release may occur very quickly once biocrust organisms become physiologically active. In *Collema* spp., NO_3^- was released within 30 min of wetting (Garcia-Pichel and Belnap 2003). A recent study showed that a broad range of nitrogen-containing metabolites are continuously released and reabsorbed by biocrust-forming cyanobacteria such as *Microcoleus vaginatus*, a novel process not found across a broad range of other cyanobacteria (Baran et al. 2015). Rainfall patterns seem to affect this release: More NO_3^- was released from dry biocrusts that received a saturating rain event, whereas more NH_4^+ was released from wet biocrusts that received a saturating rain event (Barr 1999). Williams and Eldridge (2011) observed that sand deposition had a strong effect on the release and thus bioavailability of nitrogen (N) after a severe drought. They observed that cyanobacteria-dominated biocrusts covered by sand had up to three times more mineral N (ammonium and nitrate) and twice the mineralizable N than sand-free biocrust samples, likely resulting from autolysis and the subsequent breakdown of cyanobacterial cells rich in N. The compounds released can be readily taken up by surrounding organisms, including reuptake by the organisms or associated vascular plants, fungi, actinomycetes, and/or bacteria (Stewart 1967; Jones and Stewart 1969a, b; Rogers and Burns 1994). This in fact contributes largely to a nice differentiation among allopatric bacteria in biocrust systems (Baran et al. 2015). In the case of NH_4^+ , release from nitrogen-fixing organisms supports very intense rates of nitrification in all biocrusts analyzed (Johnson et al. 2005; Strauss et al. 2012) and significant standing stocks of ammonia-oxidizing archaea and bacteria (Marusenko et al. 2013).

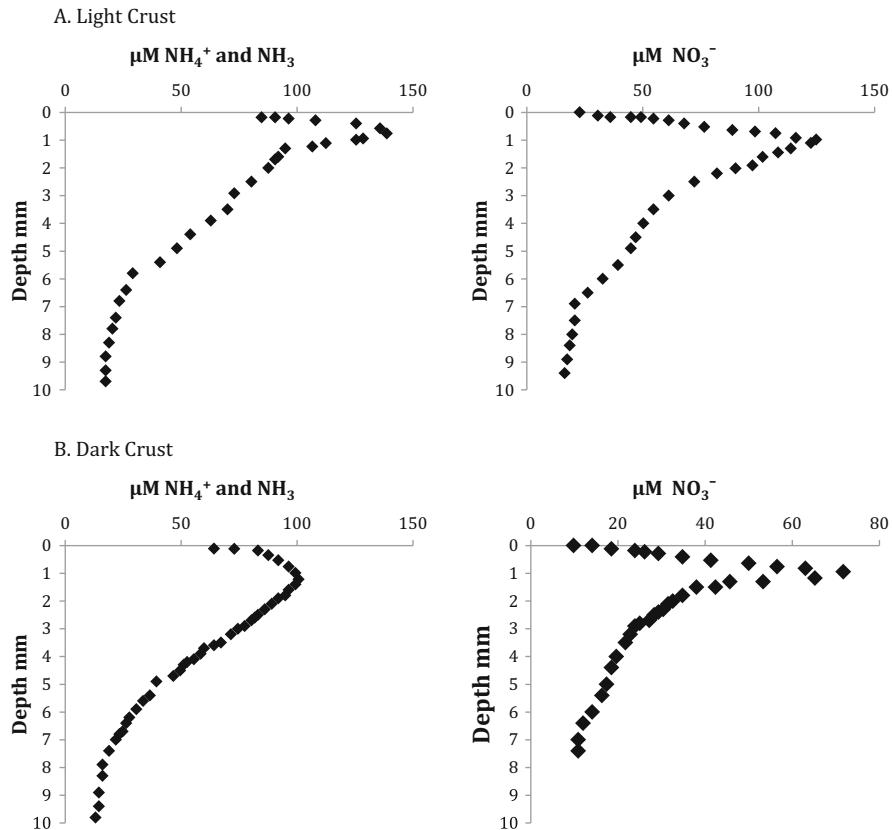


Fig. 14.4 Vertical chemical profiles measured in the soil solution of wetted, active soil crusts using microsensors and obtained 3–6 h after initial wetting. Total ammonium ($\text{NH}_4^+ + \text{NH}_3$) profiles demonstrate accumulation close to the surface. Nitrate profiles also indicate a zone of production 2–3 mm deep, coincident with the maximal activity of ammonia-oxidizing bacteria. Modified from Johnson et al. (2005)

14.4 Biocrust Influence on Soil Inorganic Nitrogen

Nitrogen fixed by diazotrophic organisms not only contributes to the fertility of soils with inherently low nutrient availability but may be an important nutrient source for diverse groups of organisms such as neighboring vascular plants (see Chap. 19 by Zhang et al.), fungi and bacteria (see Chap. 5 by Maier et al.), and mosses (see Chap. 6 by Seppelt et al.). Although N release from biocrust organisms has been well documented across a range of biomes and biocrust types (see Sect. 14.3), results are mixed as to whether this release appreciably enhances inorganic (NO_3^- and NH_4^+) bulk soil N.

The positive influence of biocrusts on inorganic N has been clearly demonstrated within biocrusts at the soil surface (0–2 mm; Fig. 14.4, Johnson et al. 2007). In both light cyanobacterial- and moss-/lichen-dominated biocrusts, inorganic N in pore water was six- to tenfold higher at 1 mm below the soil surface compared to 10-mm depth (Fig. 14.4). The peak inorganic N values were coupled with high O₂ saturation, suggesting that this peak occurred in the zone of high photosynthetic activity. Biocrust N-fixation rates may also influence soil inorganic N levels. Higher amounts of inorganic N were collected on ion exchange resins from biocrust types with higher N-fixation rates (*Collema tenax* vs. *Microcoleus* biocrusts; Belnap, unpublished).

The influence of biocrusts on inorganic N within the bulk soil (>10 mm depth) is mixed with studies showing higher (Guo et al. 2008; Delgado-Baquerizo et al. 2013), lower (Castillo-Monroy et al. 2010), or no difference (Castillo-Monroy et al. 2010) in biocrust inorganic N relative to bare soil. Sampling depth may partially explain these mixed results. The steep gradient in decreasing inorganic N from 0 to 10 mm [as shown in Johnson et al. (2007)] may suggest that the influence of biocrusts on inorganic N may be limited to the top few mm of soil and sampling at deeper soil depths would likely eliminate differences in inorganic N across biocrust types. For example, no differences in inorganic N were reported in the top 5 cm of soil underlying either light or dark cyanobacterial biocrusts on the Colorado Plateau (Barger et al. 2005). However, in a later study of biocrusts from the same sites, NH₄⁺ was 40 % and NO₃[−] was 100 % higher in dark compared to light cyanobacterial biocrusts when sampling the top 2 cm of soil (Barger et al. 2013).

Although few studies have examined the transport of inorganic N from biocrusts at the surface to underlying soils, subsurface inorganic N (5–50 mm depth) was shown to be strongly and positively correlated with biocrust inorganic N at the soil surface (top 5 mm) (Guo et al. 2008). In the few studies on inorganic N transport from surface biocrusts to underlying soils, biocrust type does appear to be an important factor, but not in a predictable manner (Thiet et al. 2005; Veluci et al. 2006; Johnson et al. 2007). In a hot desert environment, no differences were observed in the downward transport of NH₄⁺ in light vs. dark cyanobacterial biocrusts, whereas downward transport of NO₃[−] in light biocrusts was nearly three times higher than in dark biocrusts (Johnson et al. 2007). Veluci et al. (2006) showed the opposite pattern in which NH₄⁺ leaching was higher, and NO₃[−] leaching lower, in lichen-covered as compared to moss-covered or bare soil in a more mesic environment. Although the patterns in inorganic N transport to underlying soil are not consistent and probably also depend on pH and soil characteristics, the magnitude of N transport may be significant. In temperate sand dune soils, inorganic N transport associated with biocrusts ranged from 0.02 to 0.8 g m^{−2} year^{−1}, rates which are similar to N-fixation rates (Thiet et al. 2005).

14.5 Nitrogen Gas Losses from Biocrusts and Biocrusted Soils

Gaseous N loss constitutes a major pathway in which N fixed by biocrusts may subsequently be lost from the ecosystem, either directly from the biocrust itself or from export reservoirs. Thus, the magnitude of gaseous N emissions relative to N inputs via fixation will strongly govern N retained within the ecosystem and longer-term soil fertility. Enhanced NH_4^+ and NO_3^- availability, within biocrusts (as described in Sect. 14.4), may promote N gas emissions through the biotically driven processes of nitrification (oxidation of NH_4^+ to NO_3^-), denitrification (NO_3^- reduction to nitrogen oxides with N_2 as an endpoint), and abiotic losses via ammonia volatilization (NH_4^+ conversion to NH_3 gas) as all of these processes have gaseous end products or intermediaries (Fig. 14.5). Over the past decade, significant advances have been made in measuring N gas emissions from biocrusted soils across a range of biocrust types and biomes (Table 14.1). More recent explorations of anaerobic ammonium oxidation (anammox) rates suggests that while this process does occur, it most likely plays a negligible role in N transformation in biocrusts and is unlikely to contribute significantly to overall N gas emissions (Strauss et al. 2012; Abed et al. 2013). Less explored pathways of N gas loss associated with codenitrification (N gas production during which one N atom of nitrite or nitric oxide combines with one N atom of another N species, as, e.g., amino compound), nitrifier denitrification (NH_3 oxidation to NO_2^- and subsequent reduction of NO_2^- to NO, N_2O , or N_2), and dissimilatory nitrate reduction to ammonium (DNRA) have gained increasing attention in soil ecology and may play a yet unexplored role in biocrust emissions (Wrage et al. 2001; Rütting et al. 2011; Spott and Stange 2011). Although N gas emissions from biocrusts have focused on biogenic processes, abiotic reactive N gas loss, as has been determined to exist in both biocrusted and bulk soils (McCalley and Sparks 2008), may also be a significant loss pathway.

Desert soils provide optimal conditions for ammonia (NH_3) volatilization: Rates are often positively correlated with the generally high soil pH and total salt content found in desert soils, but negatively correlated with the often low organic matter



Fig. 14.5 Pathway of nitrogen fixation, nitrification, and denitrification in biocrusts. During and after N fixation, NH_3 could be released into the atmosphere; during both nitrification and denitrification N_2O , NO , and HONO may theoretically be formed and emitted

Table 14.1 Reactive nitrogen gas flux from biocrust communities across a range of biomes and biocrust types

Measured parameter	References	Soil depth (cm)	Region	Biocrust type	Nitrogen flux ($\mu\text{g N m}^{-2} \text{h}^{-1}$)	Determination method
Potential denitrification rate	Abed et al. (2013)	1–2	Northern Oman	Cyanobacterial Lichen	8181 805	Slurry with acetylene inhibition technique; incubation
Potential denitrification rate	Strauss et al. (2012)	1	Sonoran Mojave Chihuahuan Mojave CO Plateau CO Plateau Sonoran	Dark cyan Dark cyan Dark cyan Light cyan Dark cyan Light cyan Light cyan	16.4 7.4 6.8 4.6 4.2 3.2 2.7	Acetylene inhibition technique; anoxic conditions; incubation
Potential denitrification rate	Johnson et al. (2007)	1	CO Plateau	Dark cyan	0.3	Acetylene inhibition technique; anoxic conditions; incubation
Complete denitrification to N_2	Abed et al. (2013)	1–2	Northern Oman	Cyanobacteria Lichen	0.2 1442 378	$^{15}\text{NO}_3^-$ tracer experiment
Denitrification rate	Barger et al. (2013)	5	CO Plateau	Dark cyan Light cyan	17.4 2.0	Acetylene inhibition technique under varying water conditions; incubation
Denitrification rate	Zaady et al. (2013)	1	Negev	Light cyan Cyano-moss Cyano-moss-lichen	0.10 0.07 0.03	Acetylene inhibition technique; watered to field capacity; incubation

Denitrification rate	Brankatschk et al. (2013)	0.5	Inland dune, Germany	Intense growth of green algae, with cyanobacteria, fungal hyphae, and mosses	23.8	Potential enzyme activity assays
Pot. N ₂ O gas emission	Abed et al. (2013)		Northern Oman	Cyanobacteria and green algae	6.0	
Nitric oxide (NO) emission	Barger et al. (2005)	5	CO Plateau	Initial crust with filamentous cyanobacteria and green algae	2.7	
Nitric oxide (NO) emission	McCalley and Sparks (2008)	15	Mojave	Cyanobacteria	5418	Slurry; microsensors
Nitric oxide (NO) emission	McCalley and Sparks (2009)	8	Mojave	Lichen	434	
Nitric oxide (NO) emission	Weber et al. (2015b)	2.6	Southern Africa	Dark cyano	14.8	Flux measurement with chemiluminescent analyzer
Ammonia (NH ₃) emission	Evans and Johansen (1999)	NR	CO Plateau	Light cyano	9.5	Thermal and chemical decomposition converters
Ammonia (NH ₃) emission	Barger (2003)	5	CO Plateau	Dark cyano	13.3	Passive acid trap (H ₂ SO ₄) trap
					7.6	

(continued)

Table 14.1 (continued)

Measured parameter	References	Soil depth (cm)	Region	Biocrust type	Nitrogen flux ($\mu\text{g N m}^{-2} \text{h}^{-1}$)	Determination method
Ammonia (NH_3) emission	McCalley and Sparks (2008)	15	Mojave	“Crusted” soil with presence of mosses and/or lichens, covering ~20 % of surface	DS: 7.1–21.6 WS: 14.4–336	Thermal and chemical decomposition converters
Ammonia (NH_3) emission	McCalley and Sparks (2009)	8	Mojave	“Interspaces covered in biological soil crust”	DS: 1.5 WS: 45.9	Thermal and chemical decomposition converters
NO_y emission	McCalley and Sparks (2009)	8	Mojave	“Interspaces covered in biological soil crust”	DS: 1.4 WS: 18–88.2	Thermal and chemical decomposition converters
Nitrous acid (HONO) emission	Weber et al. (2015b)	2.6	Southern Africa	Light cyan-o-dominated Dark cyan-o-dominated Chlorolichen-dominated Moss-dominated	333 622 85 127	Continuous flux chambers; mean maximum value during wetting and drying cycle

NR not reported, *DS* dry soil, *WS* wet soil, *CO* Colorado

content, cation exchange capacity (CEC), and clay content (Duan and Hongland 2000). Recent studies suggest that NH_3 volatilization may be a major loss pathway for N relative to other reactive N gases in bulk desert soils (McCalley and Sparks 2008). Reported rates of NH_3 volatilization from biocrusts vary widely, ranging from 1.4 to 336 $\mu\text{g N m}^{-2} \text{ h}^{-1}$ (Table 14.1). In Mojave Desert soils, biocrusts had no influence on NH_3 emissions (McCalley and Sparks 2008). In contrast, in a laboratory incubation of sandy soil from the Colorado Plateau, NH_3 emissions were threefold higher on biocrusted soils compared to soils where biocrusts were removed (Evans and Johansen 1999). Although data on NH_3 emissions by biocrust type are limited, laboratory incubations of Colorado Plateau light and dark biocrusts emission rates were similar (Barger 2003). Similar to NO gas loss, NH_3 loss was consistently observed in dry biocrust soils (McCalley and Sparks 2008, 2009). Estimates of annual NH_3 from biocrusts in Mojave Desert soils were 1.4 $\text{kg N ha}^{-1} \text{ a}^{-1}$ (McCalley and Sparks 2008).

A suite of nitrogen oxides are produced biogenically as by-products of nitrification and denitrification processes (Fig. 14.4) and abiotically through chemical formation driven by high temperatures (McCalley and Sparks 2009). Nitric oxide (NO) and nitrous oxide (N_2O) are the dominant by-products in nitrification and denitrification processes with soil water content as a primary control on emissions. Under low soil water conditions, intensive rates of nitrification favor production of NO (Weber et al. 2015b). In contrast, saturated soils and subsequent low O_2 conditions favor denitrification processes and high N_2O emissions (Firestone and Davidson 1989; Hartley and Schlesinger 2000; Pilegaard 2013).

Until recently, denitrification had been a relatively unexplored N loss pathway from biocrusted soils because conditions conducive to the process (e.g., anoxic soils and high levels of soil organic carbon (SOC) and soil NO_3^-) were thought to be limited in dryland environments (Tucker and Westerman 1989). Denitrification is primarily a biological process, whereby denitrifiers (primarily heterotrophic bacteria) use NO_3^- for respiration of organics in the absence of O_2 resulting in the production of NO, N_2O , and N_2 (Fig. 14.4). The high rates of soil respiration prevalent immediately following a precipitation event, however, do deplete biocrust O_2 concentrations, providing the anaerobic conditions required for denitrification. Thus, conditions conducive to denitrification do occur inside of biocrusts at the microscale, with anoxia brought about by respiration, NO_3^- supplied locally by nitrification, and organic carbon in the pore water supplied by export from primary producers (see Johnson et al. 2007). Yet, denitrification rates are typically much lower than those of nitrification or N fixation for any given site and condition or assay (Johnson et al. 2007; Strauss et al. 2012).

Denitrification rates in biocrusts and underlying soils are temporally and spatially variable with estimates varying by five orders of magnitude (Table 14.1, 0.03–8181 $\mu\text{g N m}^{-2} \text{ h}^{-1}$). One must note, however, that much of this variability in Table 14.1 is driven by exceedingly high rates obtained from a single study conducted with a different technique (Abed et al. 2013). Although soil denitrification rates are consistently shown to be highly variable across a broad range of biomes and soil types, the wide range of analytical methods, environmental

conditions in which soils were incubated, and differences in soil sampling depths across the studies may partially contribute to the variability in reported rates (Table 14.1).

Soil organic carbon (SOC) formed by biocrusts may increase denitrification rates (Barger et al. 2013; Brankatschk et al. 2013). In one study on a Central European duneland, denitrification on uncrusted sand was undetectable, whereas rates from three biocrust types ranged from 5 to 48 $\mu\text{g N m}^{-2} \text{ h}^{-1}$ (Brankatschk et al. 2013). An increase in SOC with biocrust development was hypothesized to be driving the higher rates. Additional studies have shown that biocrust development leads to higher denitrification rates (Strauss et al. 2012; Barger et al. 2013; Brankatschk et al. 2013), while other studies have shown the opposite (Abed et al. 2013; Zaady et al. 2013) or no effect (Johnson et al. 2007; Strauss et al. 2012; Zaady et al. 2013), perhaps not an unexpected result given the multiplicity of factors that can influence denitrification.

Simultaneous measurements of denitrification and N fixation reveal that biocrust N fixation generally exceeds denitrification. In both hot and cold desert biocrusts, denitrification rates ranged from 0.1 to 25 % of the N-fixation rates (Johnson et al. 2005; Strauss et al. 2012; Barger et al. 2013; Zaady et al. 2013). The exception to this pattern was a study conducted on an inland dune in Germany, whereby denitrification rates from biocrusts were five- to tenfold higher than N-fixation rates (Brankatschk et al. 2013). Biocrusts from this study experienced historically high levels of N deposition ($12\text{--}15 \text{ kg ha}^{-1} \text{ a}^{-1}$), which may have contributed to the high denitrification rates (Brankatschk et al. 2013). In addition, N-fixation rates in all of these studies were likely underestimated due to the use of high ARA to N-fixed conversion ratios.

Few studies have attempted to estimate annual denitrification rates, but recent estimates from the Negev desert suggest that denitrification from biocrusted soils ranged from 7.2 to $10.8 \text{ kg ha}^{-1} \text{ a}^{-1}$. Biocrust N fixation at these same sites was estimated at $43.2 \text{ kg ha}^{-1} \text{ a}^{-1}$, which suggests that a quarter of the N fixed each year may be lost in denitrification (Zaady et al. 2013). It is important to note that many denitrification estimates are potential rates based on optimal conditions, where conditions of organic carbon supply, anoxia, and long incubation times are all experimentally imposed in the assays relative to the field environment. Thus, potential denitrification rates are likely overestimates and may represent an upper end to N loss.

Nitric oxide (NO) may be produced biogenically both during nitrification and denitrification processes and abiotically through chemical formation driven by solar radiation and moisture (McCalley and Sparks 2009). NO production occurs in both nitrification and denitrification processes with emission rates from 1.1 to $751 \mu\text{g m}^{-2} \text{ h}^{-1}$ from biocrusts and biocrusted soils (Table 14.1). NO loss in dryland soils is positively correlated to nitrification rates (Hartley and Schlesinger 2000; Martin et al. 2003), suggesting that NO is primarily produced during nitrification. Similar to N fixation, soil moisture is a first-order control on NO emissions (Barger et al. 2005; McCalley and Sparks 2008, 2009). In contrast to previous reports of non-detectable levels of NO loss in dry biocrust soils (Barger et al. 2005), results

from McCalley and Sparks (2008, 2009) revealed that low NO emissions occur in dry biocrusts. Biocrust NO emissions also increase with increasing temperature (Barger et al. 2005; McCalley and Sparks 2008, 2009). NO emissions from biocrusts in SE Utah were nearly fivefold higher in the hot summer months relative to the cooler spring and fall time periods (Barger et al. 2005). In summer months, when soil temperatures exceed 50 °C, higher NO fluxes may also be driven by abiotic processes (McCalley and Sparks 2009). Similar to what was the case with denitrification rates, the influence of biocrust type had mixed effects on NO emissions. In SE Utah, NO fluxes from dark cyanobacterial biocrusts were nearly double those of light cyanobacterial crusts, but only during the warmer summer months. In the Mojave Desert, NO fluxes were similar in light cyanobacterial biocrusted and uncrusted soils (McCalley and Sparks 2008). Emissions of biocrusts in the Succulent Karoo showed large variation depending on the type of biocrust with dark cyanobacteria-dominated biocrusts reaching mean maximum emission values of $751 \mu\text{g m}^{-2} \text{ h}^{-1}$ of NO-N, whereas bare soil emitted a mean value of $33 \mu\text{g m}^{-2} \text{ h}^{-1}$ ($n = 4$; Table 14.1; Weber et al. 2015b). Emission values obtained by biocrusts of typical composition during one wetting and drying cycle ($0.74 \pm 0.08 \mu\text{g m}^{-2} \text{ h}^{-1}$ of NO-N) were combined with climate and biocrust composition data to obtain an annual global estimate of 1.1 Tg a^{-1} of NO-N emissions. Former estimates of annual NO gas loss from biocrusts were by far lower ranging from 0.10 to $0.16 \text{ kg N ha}^{-1} \text{ a}^{-1}$ (Barger et al. 2005; McCalley and Sparks 2008).

During both nitrification and denitrification nitrite (NO_2^-) are formed, which, under suitable conditions, can be released to the atmosphere as HONO (nitrous acid). Only recently HONO emissions have been reported from bulk soil (Su et al. 2011a) and soil bacteria (Oswald et al. 2013) and by biocrusts (Weber et al. 2015b). The presence of biocrusts results in higher HONO emissions, whereby all biocrust types released significant amounts of HONO in contrast to the very low emissions reported for bare uncrusted desert soils. As observed for NO, HONO emissions were strongly related to the soil water content. Based on long-term climate and biocrust composition data, global release of HONO-N was estimated at 0.6 Tg a^{-1} . Summarizing the analyzed NO and HONO emissions, 1.7 Tg a^{-1} of reactive nitrogen were found to be emitted, corresponding to ~20 % of the global nitrogen oxide emissions of soils under natural vegetation (Ciais et al. 2013).

14.6 Regulation of Biocrust Nitrogen Transfer in Wind and Water

In dryland ecosystems, water runoff and wind- and waterborne sediment export from plant interspaces are long recognized pathways of N transfer (Ludwig et al. 1997; Ravi et al. 2011). Several studies show that biocrusts influence water and associated nutrient transfers from biocrusted interspace soils to downslope

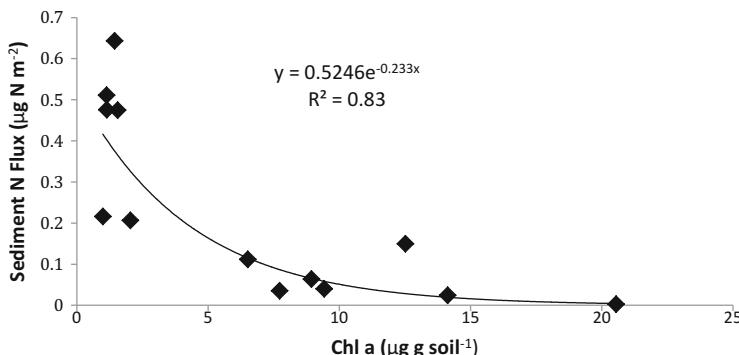


Fig. 14.6 Sediment N flux as a function of soil chlorophyll *a* content in the top 0–2 cm of the soil surface. Modified from Barger et al. (2006) and Barger (2003)

plants (Eldridge et al. 2000, 2002; Maestre et al. 2002). Whereas many studies have found elevated areal N under shrubs relative to interspace soils (e.g., Thompson et al. 2006), many others show no such differences where well-developed biocrusts cover interspace soils (e.g., Allington and Valone 2014). In none of these studies, however, was the role of biocrusts explicitly tested, and inferring transfer rates from standing stocks alone does not adequately describe the specific N transfer mechanisms.

Biocrust type can affect N transfer in overland flow. In a series of 30-min rainfall simulation experiments on sandy soils in SE Utah, sediment N loss was an order of magnitude higher in light cyanobacterial biocrusts (0.6 g m^{-2}) than in the more stable, dark cyanobacterial biocrusts (0.06 g m^{-2}), with over 98 % of the N flux coming from the sediment (Barger et al. 2006). Sediment and thus N loss was a negative function of biocrust biomass, as indicated by chlorophyll *a* content ($R^2 = 0.82$) (Fig. 14.6). In this one high-intensity rainfall simulation event, nearly 3 % of the estimated surface organic N was removed from light biocrusted soils compared to <1 % in dark cyanobacterial crusts. In a similar study on sandy soils in the Tengger Desert, total N flux in runoff and sediment transport from dark cyanobacteria-lichen-moss biocrusts was 0.42 g N m^{-2} (Li et al. 2008), similar to those reported above. Most of the N flux was transported from biocrust patches downslope, and 74 % of the sediment N and 45–73 % of the dissolved N were subsequently trapped by down-slope vegetation (Li et al. 2008). Using silt fences to capture sediment released in natural runoff events from 40 m^2 watersheds over a 4-month period, sites on sandy soils produced an average of 0.05 g N m^{-2} from dark cyanobacterial biocrusted soils, compared to an average of 56 g N m^{-2} from adjacent, recently disturbed uncrusted soils (J. Belnap, unpublished). On clay soils, the dark cyanobacterial biocrusted soils produced an average of 0.05 g N m^{-2} and the disturbed uncrusted soils an average of 0.66 g N m^{-2} over the same 4-month time period. In contrast to these patterns, higher runoff from biocrusted soils relative to bare soils in some settings can result in loss of water and nutrients at the watershed level (Yair et al. 2011).

Wind redistributes sediments in drylands, at the local (e.g., to nearby shrubs; Ravi et al. 2010) to regional (e.g., to nearby mountains; Neff et al. 2008) scale, and often moves more sediment than water does (Field et al. 2011). Biocrusts reduce sediment loss via wind erosion by up to 66 times compared to uncrusted surfaces (see Chap. 16 by Belnap and Büdel; Field et al. 2011). Because sediments contain N, biocrusts will therefore reduce N transfer by wind. However, we could find only one study quantifying this process (J. Belnap, unpublished). In SE Utah, sediment was collected by dust samplers (units expressed as the collection area of the sampler) from perennial and annual grasslands with varying crust types. Nitrogen lost from the grassland dominated by perennial native plants and dark cyanobacterial biocrusts was very low in all years ($\sim 0.1 \text{ mg N cm}^{-2} \text{ a}^{-1}$ to $\sim 2 \text{ mg N cm}^{-2} \text{ a}^{-1}$ in a wet and dry year, respectively). In contrast, a nearby area on the same soil type but dominated by annual plants and light cyanobacterial biocrusts lost a similar amount of N in wet years ($0.2\text{--}0.4 \text{ mg N cm}^{-2} \text{ a}^{-1}$) but much higher amounts in a drier year ($\sim 70 \text{ mg N cm}^{-2} \text{ a}^{-1}$). Areas with only annual plants and no biocrusts had very high N losses in both wet and dry years, losing up to $10 \text{ mg N cm}^{-2} \text{ a}^{-1}$ and $\sim 160 \text{ mg N cm}^{-2} \text{ a}^{-1}$ in a wet and dry year, respectively. While this difference may not have been entirely due to the difference in biocrusts, as the plant type and/or cover also varied, wind erosion models show that dark cyanobacterial biocrusts completely stabilize soils, even when no plant cover is present (Munson et al. 2011). Wind and water also interact to move N in drylands (Belnap et al. 2011), but unfortunately the role of biocrusts in such coupled transfers of N has not been studied.

Nitrogen has also been reported to be moved from biocrusts to nearby plants, with the proposed agent being biocrust fungi (Green et al. 2008). Three studies showed that labeled N added to interspace biocrusts could be found within hours in plant tissue 1 m away. An expanded discussion on this topic is found in Chap. 19 by Zhang et al.

Nitrogen movement by wind and water erosion may result in both N loss from the system but also N transfer within the system. For example, estimates of N fixation by biological soil crusts on the Colorado Plateau ranged from $1.3 \text{ kg N ha}^{-1} \text{ a}^{-1}$ in light cyanobacterial biocrusts up to $9 \text{ kg N ha}^{-1} \text{ a}^{-1}$ in dark cyanolichen biocrusts (Belnap 2002a, b). In a high-intensity rainfall simulation event, N flux from light cyanobacterial biocrusts was 6.3 kg N ha^{-1} (sixfold higher than annual N inputs) as compared to only 0.6 kg N ha^{-1} lost from dark cyanobacterial biocrusts. Early successional light cyanobacterial biocrusts have low N-fixation potential, and N losses of this magnitude would require a significant number of years for recovery. Thus, a single high-intensity rainfall event may dramatically alter N balance within biocrusts.

14.7 Ecosystem Nitrogen Budgets

The very fact that nitrogen fixation is such a prominent and ubiquitous trait of biocrusts speaks clearly for a permanent state of N limitation and requires that much of the N fixed is exported away from the crust in some form or another. The fate of N fixed by biocrusts and whether this N is retained in the system or lost via the broad range of pathways (described in earlier sections) determines ecosystem N balance over longer time scales. Given that N-fixation estimates may be quite high but soil N accretion rates are generally low (10 % of N fixed, Peterjohn and Schlesinger 1990) suggests that either major errors in estimates or scaling of biocrust N fixation plague our current approaches as described in the previous section or annual N losses are several orders of magnitude higher than what would be anticipated in these relatively low-nutrient environments. Additionally important pools or processes may yet to be adequately considered and measured (e.g., N transfer to plants; see Chap. 19 by Zhang et al.). Although numerous studies of N losses and transfers from biocrusts have contributed to our understanding of the fate of N fixed by biocrusts over the past decade, significant uncertainties related to biocrust N balance still remain. Specifically, the challenges in measuring all pathways of N inputs, losses, and retention simultaneously under environmentally relevant field conditions have limited our ability to “close” the N cycle.

Over longer time scales, the balance between N inputs and losses is reflected in accumulation of soil organic N. A recent survey in North America showed that biocrusts accumulate very significant levels of total N (severalfold) above the

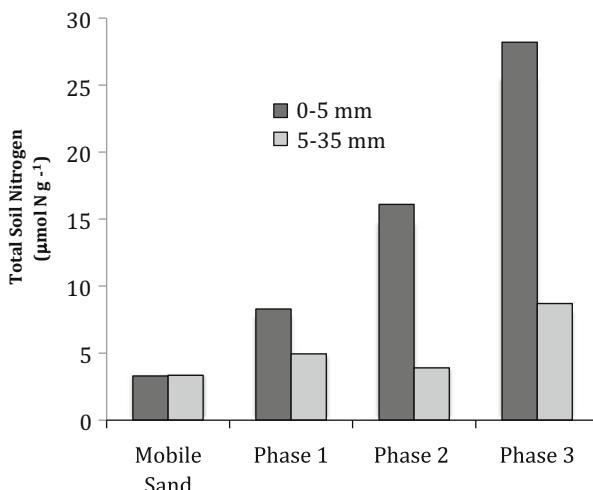


Fig. 14.7 Soil organic N accretion with biocrust development on a Central European inland dune. Mobile sand = bare substrate with no biocrust development; Phase 1 = sand grains that are stabilized at their contact zones by filamentous cyanobacteria and green algae; Phase 2 = cyanobacteria and green algae; Phase 3 = filamentous and coccoid green algae, some cyanobacteria, fungal hyphae, and mosses. Modified from Brankatschk et al. (2013)

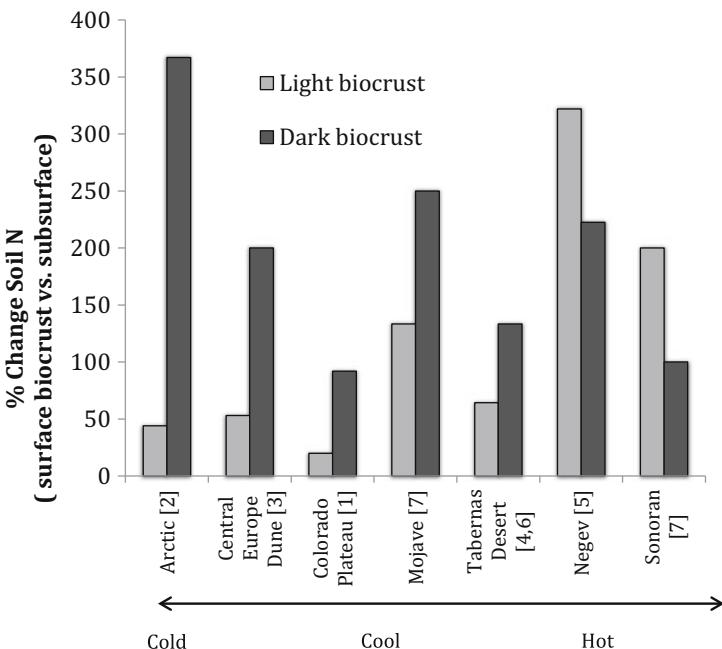


Fig. 14.8 The influence of biocrust type on soil surface enrichment of soil organic N across biomes. “Dark” biocrusts included both dark cyanobacterial biocrusts and dark cyanolichen biocrusts. Numbers next to each site name on the x-axis denote the publication in this order: [1] (Barger 2003; Barger et al. 2013); [2] (Breen and Lévesque 2008); [3] (Brankatschk et al. 2013); [4] (Chamizo et al. 2012); [5] (Drahorad et al. 2013); [6] (Miralles et al. 2012); [7] (Strauss et al. 2012)

background levels found in uncrusted, neighboring soils (Beraldi-Campesi et al. 2009). An example taken from a Central European duneland shows that soil organic N was similar across the top 35 mm of the soil surface in undeveloped, mobile sands (Fig. 14.7, Brankatschk et al. 2013). As cyanobacteria colonized soil surfaces, organic N increased in the zone of biocrust activity (0–5 mm). In later successional stages (algal-cyanobacteria-moss biocrust), soil organic N in these duneland ecosystems was more than ninefold higher than that of the mobile sands (Fig. 14.7). Soil N in subsurface soils was similar across all development stages and suggests that any N transfer from surface soils does not result in significant N accretion in subsurface soils.

A similar pattern of soil organic N accumulation in surface soils was observed across a range of biomes. In a review of seven studies, the presence of biocrusts consistently increased soil surface N relative to subsurface soils (Fig. 14.8). In cold and cool desert environments, the pattern of higher N in surface soils was much greater in dark biocrusts (cyanobacterial and cyanolichen) relative to light cyanobacterial biocrusts. Interestingly, this pattern was not consistent in hot desert environments. Soil N accretion in surface soils in a study in the Negev and the

Sonoran Desert studies was lower in dark biocrusts relative to light biocrusts relative to subsurface soils (Fig. 14.8).

14.8 Summary of Biocrust N Cycling

In low-nutrient environments with few vascular plant symbiotic N fixers, biocrusts play an important role in ecosystem N cycling. A large number of studies across a wide range of biomes clearly confirm that not only the presence of biocrusts but biocrust community composition strongly influences N-fixation activity, with N fixation increasing with level of development (cyanobacterial-lichen biocrusts > dark cyanobacterial biocrust (e.g., *Nostoc* spp. and *Collema* spp.) > light *Microcoleus*-dominated biocrust). Nitrogen fixation by biocrusts results in N release to the soil in a variety of N forms (inorganic and organic N), thus elevating soil inorganic N pools in the top few millimeters of soil. The influence of N release on the bulk soil at greater soil depths is less clear, with biocrusts either elevating or having no influence on bulk soil inorganic N pools. The fate of N fixed and released by biocrusts, and whether this N is retained in the ecosystem in either soils or plants, determines ecosystem N balance over longer time scales, and results on the influence of biocrusts are mixed. Whereas we have multiple studies that examine a single compartment of N budgets, we lack studies that simultaneously address N inputs, losses, and soil and plant pools, thus precluding the construction of definitive N balances. One of the most consistent impact biocrusts have on ecosystem N is reducing N loss via wind and water erosion, with such losses consistently decreasing with increasing biocrust development.

14.9 Research Challenges

1. *Biocrust N fixation*—On a global scale, N fixation by biocrusts was estimated to account for $\sim 26 \text{ Tg a}^{-1}$ or half of the global N fixation as estimated in the latest IPCC report (Elbert et al. 2012; Ciais et al. 2013). Thus, well-constrained estimates of biocrust N fixation at larger spatial scales are important for our broader understanding of global N cycles. To better estimate biocrust N fixation across biocrust types and biomes, future biocrust N-fixation studies should (1) report antecedent conditions such as the amount of time biocrusts were metabolically active before measurements, (2) measure temperature within the biocrust rather than air, (3) use $^{15}\text{N}_2$ or calibrate ARA with $^{15}\text{N}_2$, and (4) increase incubation times to avoid diffusion limitation (Johnson et al. 2005).
2. *Spatiotemporal scaling of biocrust N cycling*—Many of the studies described in this chapter examine biocrust N input and loss pathways on short time scales (i.e., minutes, hours) and small spatial scales (i.e., centimeters to meters). Although these detailed studies of biocrust N cycling have been critical to

increasing our understanding of the important environmental controls on N transformations in biocrusts, temporally scaling short-term N loss rates to annual losses still remains a challenge due to the high spatial and temporal variability in rates.

3. *Soil moisture and temperature monitoring*—Since biocrust organisms are physiologically active only when adequate water is available, continuous monitoring of moisture in soil lichens, mosses, and surface soils (0–0.5 cm or less) is important for constraining N budgets.
4. *Use of common methodologies and units*—Future studies are encouraged to use common methodologies and units during reporting in order to compare across all aspects of biocrust N cycling, especially for N fixation. To facilitate future meta-analyses and reviews, N cycling rates should be reported on both a mass and area basis in the supplementary material for comparison across studies. Ancillary soil data such as soil texture, moisture, temperature, SOM, total N, and inorganic N pools are the most important measures for biocrust N cycling studies in addition to adequately characterizing the biocrust community with measures of chlorophyll *a* and biocrust species composition.
5. *Biocrust N release and uptake*—Understand the environmental conditions that result in N release and subsequent uptake by soil microorganisms and surrounding plant communities and how these dynamics may change with anthropogenic atmospheric N deposition.
6. *Simultaneous measures of N inputs, losses, and all pools (soil and plant)*—Examine covariation of integrated cycling (many processes) with fundamental environmental drivers (i.e., temperature, moisture). Studies focused solely on one type of transformation are by now of very limited value, in view of the large variability of each process in space and time.
7. *Understand the limits of denitrification in biocrusts*—As reported in previous sections, conditions within active biocrusts are prime for denitrification (i.e., anoxic conditions, organic matter supplied by photosynthetic release, and nitrate supplied by strong nitrification), and yet rates are generally low (in many but not all studies) compared to the potentials.

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Chapter 15

Carbon Budgets of Biological Soil Crusts at Micro-, Meso-, and Global Scales

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15.1 Introduction

Biological soil crusts (biocrusts) inhabit extensive parts of different terrestrial ecosystems and are especially abundant under conditions where vascular plants encounter natural limits of growth (Belnap and Lange 2003). Due to their poikilohydric character, biocrusts show resilience under extreme conditions, as well as a remarkable adaptation to the various combinations of different climatic factors found throughout all latitudes from the tropics to the poles (Grote et al. 2010; Colesie et al. 2014). Because biocrusts can fix carbon (C) through photosynthetic activity, they are important in local scale C cycles. In addition, due to their broad distribution, they can also be relevant on ecosystem and global scales (Elbert et al. 2012; Porada et al. 2013, 2014).

In this chapter, several different terms are used when considering CO₂ balance. Net photosynthesis (NP) and dark respiration (DR), respectively, refer to the uptake and release of CO₂ measured with CO₂ gas exchange systems. CO₂ gas exchange

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measurements under controlled conditions allow the identification of cardinal points for photosynthesis (e.g., temperature optimum, light saturation, optimum water content). In long-term observations, an important value is the net primary production (NPP), which is the difference between the gross primary production (GPP) and the autotrophic respiration (AR; Chapin et al. 2006). A further highly relevant variable is net ecosystem production (NEP), which is the difference between gross primary production (GPP) and ecosystem respiration (ER; Randerson et al. 2002). Similar values, net ecosystem carbon balance (NECB) and net ecosystem exchange (NEE), are the net rate of carbon accumulation in (or loss from) ecosystems. NECB can be determined by measuring changes in carbon stocks in vegetation and soil. NECB and NEE differ from NEP if inorganic carbon enters or leaves the system in dissolved form or if fluxes other than C fixation and respiration occur. In addition, we use the term net soil exchange (NSE) for chambers that include only bare or biocrusted soil surfaces and exclude vascular plants.

It must also be remembered that in arid soils, biological activity is not the only driver of CO₂ exchange. It has been recently reported that inorganic CO₂ fluxes in alkaline and saline substrates can exceed those caused by organic activity (Xie et al 2009; Shanhun et al. 2012; Ma et al. 2013). Before producing an accurate approach to the CO₂ balance in arid lands, it is therefore necessary to determine whether inorganic activity in calcareous soils needs to be considered as a sink or a source of carbon, and the abiotic conditions need to be specified. On the other hand, in the most extreme habitats, photosynthetic activity in the soil is mainly restricted to the especially protected microhabitat that occurs under semitransparent pebbles, the so-called hypolithic communities, which are extensively considered in Chap. 11 by Pointing.

In the following sections, we use a multiscale approach to discuss the usefulness of available measuring techniques and methods calculating the CO₂ balance of biocrust communities. In the first section, we focus on the microscale, that is, the individual organism such as a single lichen or bryophyte thallus or a well-defined cyanobacteria colony. We then address CO₂ exchange of a complete ecosystem or at the community level (mesoscale). Finally, we will look at recent approaches to assess the contribution of biocrusts on a global scale.

15.2 The Microscale: Individual Organism Performance

15.2.1 *Proposed Methodologies on the Microscale*

Direct Measurement of CO₂ Exchange Quantitative measurements of CO₂ fluxes in biocrust organisms are feasible using CO₂ gas exchange systems. The major advantage of CO₂ exchange measurements is that they can provide both accurate response curves of NP to environmental factors, as well as actual exchange rates in the field under quasi-natural conditions. On the other hand, a major disadvantage is

that data are not provided for CO₂ uptake nor do they discriminate between abiotic and biotic CO₂ production.

Lange et al. (1997a) developed an automatically operating cuvette with which they measured quantitative CO₂ exchange in lichens. A major limitation to the use of these systems is that they are expensive, only quasi-automatic (i.e., they need regular, often daily checking), and usually only a small number of samples (often only one) can be measured. Many other studies on quantitative CO₂ exchange measurements are available, but mainly cover only short time periods. Nevertheless, these are often used for calculations and modeling of biocrust C cycling. Lange (2003a) intensively discusses the differences between different extrapolation methods and also the difficulties in upscaling fixation rates to yearly averages. Bader et al. (2010) use the same dataset to show that lower sampling frequencies both within the day and on less than 365 days of the year cause deviations in modeling results and propose supporting extrapolation approaches.

Indirect Measurements Based on Activity Detection Fluorometers, which detect fluorescence of chlorophyll *a*, provide a method to record the activity time of poikilohydric photosynthetic organisms (Schroeter et al. 1992; Schlenzog and Schroeter 2001). Recent innovations allow the establishment of long-term chlorophyll fluorescence monitoring systems, which are online and report via telephone or satellites (Büdel et al. 2014; Raggio et al. 2014). The systems not only provide an excellent background on activity periods of the organisms *in situ* but often also allow determination of the mode of activation (humid air, dew, or rain) to be identified. Such data are necessary for any calculations of productivity over time (Fig. 15.1). Recently, a biocrust wetness sensor was developed, which allows determination of the activity status and water content of biocrusts by means of electrical conductivity measurements (Weber et al. 2016). As these sensors are inexpensive, robust, and easy to use, they can be employed for long-term measurements. Installation of multiple sensors in the field allows assessment of spatio-temporal variability in biocrust C exchange under field conditions. However, these methods do not provide quantitative data on CO₂ uptake or loss. Therefore, in order to obtain measures such as NPP, these methods must be combined with CO₂ gas exchange measurements under varying environmental conditions that can account for the relationship between chlorophyll fluorescence or water content and CO₂ exchange in lichens, algae, and bryophytes. Nevertheless, both techniques have an unquestionable advantage of allowing for unattended long-term noninvasive monitoring of metabolic activity.

Direct Measurement of Mass Gain A relatively easy way to relate microscale CO₂ measurements to the productivity of lichen- or moss-dominated systems (i.e., the NECB) is to use lichenometric data as a baseline to calculate mass gain over a selected time interval. Lichenometry has been widely used to date surfaces, mainly in studies on glacier retreat in both hemispheres (Innes 1988; Winchester and Harrison 2000; Roberts et al. 2010), or to calculate the growth rate of a thallus by direct measurements at time intervals (Armstrong and Bradwell 2010; Sancho and Pintado 2004; Sancho et al. 2011). Annual thallus enlargement measured in

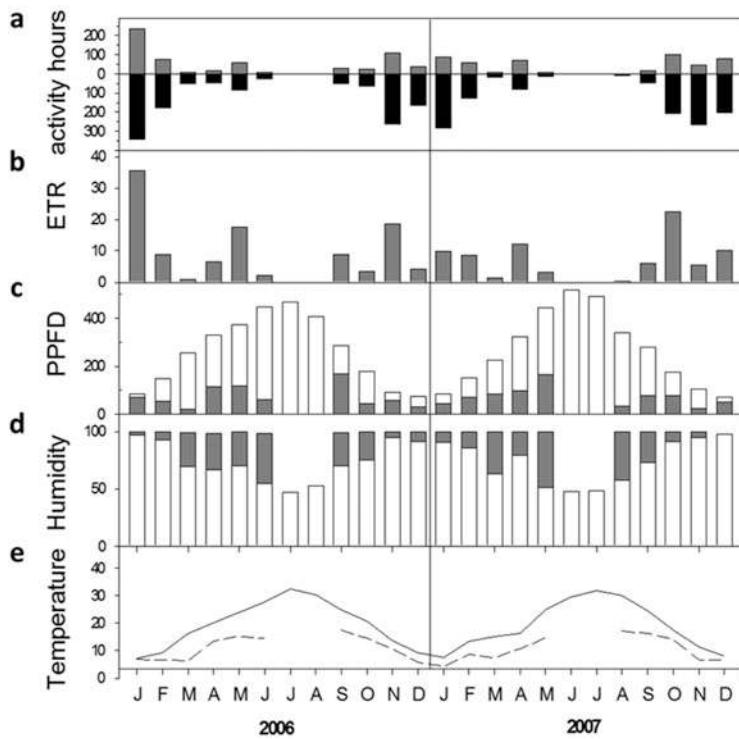


Fig. 15.1 Summary of the activity detected as fluorescence of chlorophyll a and microclimate measured for *Diploschistes diacapsis* assessed in continuous measurements over a period of 2 years, 2006 and 2007, in Almería (Spain). (a) Lichen activity in number of hours active per month: gray upper part of bar indicates fluorescence activity under photosynthetic active radiation and black lower part indicates fluorescence activity in the dark. (b) Sum of electrons transported per month ($\text{mol electrons } m^{-2} \text{ month}^{-1}$). (c) Mean PPFD ($\mu\text{mol photons } m^{-2} s^{-1}$) for each month: white bars indicate mean value of the complete month and gray bars indicate the mean value for times when the lichen was active. (d) Mean relative humidity next to the lichen at the soil surface in each month (%): white bars indicate the mean RH for the entire month; the total bar is the mean value of times when the lichen was active. (e) Mean lichen temperature of all measurements in each month (solid line) and for the periods when the lichens were active (dashed line, missing data indicates no activity in those months)

lichenometric studies can be transformed to thallus weight gain after determining the thallus weight per unit area (Raggio et al. 2012). The obtained annual C gains are fully comparable across different ecosystems in the world and improve our understanding of the contribution by lichens, especially epilithic communities, to the global C balance (Table 15.1). Theoretically, a combination of high quality digital photographs, appropriate image analysis programs, and an accurate determination of thallus weight on a surface basis could allow long-term productivity monitoring of crustose lichens without using any expensive and complicated systems.

Table 15.1 Net carbon uptake of different lichen species calculated as (a) dry weight accumulation (g m^{-2}) and (b) carbon assimilation (g m^{-2}). The carbon content in lichens typically ranges between 30 and 40 %, thus values in (b) need to be multiplied by values between 2.5 and 3.3 in order to estimate dry weight accumulation

Lichen species	Growth form	Habitat	Annual growth	References
<i>Buellia frigida</i>	Crustose	Continental Antarctica	0.1 g m^{-2} (a)	Sancho, unpublished
<i>Rhizocarpon geographicum</i>	Crustose	Bipolar	2–5 g m^{-2} (a)	Sancho, unpublished
<i>Buellia latemarginata</i>	Crustose	Maritime Antarctica	7–10 g m^{-2} (a)	Sancho, unpublished
<i>Caloplaca sublobulata</i>	Crustose	Maritime Antarctica	8–11 g m^{-2} (a)	Sancho, unpublished
<i>Placopsis perrugosa</i>	Crustose	Tierra del Fuego, Chile	50–80 g m^{-2} (a)	Sancho, unpublished
Lichen tundra	Mainly fruticose	Boreal Woodland, Canada	100 g m^{-2} (b)	Coxson and Marsh (2001)
<i>Lecanora muralis</i>	Crustose	Temperate Region, Germany	65.0 g m^{-2} (a)	Lange (2003a, b)
<i>Cetrariella delisei</i>	Fruticose	High Arctic	5.1 g m^{-2} (b)	Uchida et al. (2006)
Biocrust	Mainly crustose	Mojave Desert, USA	11.7 g m^{-2} (b)	Brostoff et al. (2005)
Biocrust	Mainly crustose	Chinese Desert	3.46–6.05 g m^{-2} (b)	Feng et al. (2014)

Modeling Methods Modeling is used to estimate annual C budgets. Continuous cuvette measurements, providing data over more than a year, as conducted by Lange (2000, 2003a, b), are an exception. Most commonly, a series of field measurements of CO_2 gas exchange is connected with the concurrent environmental factors. Different types of algorithms or models are then used to link field and laboratory measurements with long-term records of those same environmental factors. The methodological approach is to combine CO_2 gas exchange rates assessed during typical activity days (see Lange and Green 2004) with records of long-term chlorophyll *a* fluorescence and microclimate data (at least one continuous year). These measurements are conducted for the most abundant biocrust types of each area. This approach minimizes theoretical assumptions and extrapolations in the modeling. Several important ecophysiological phenomena in biocrusts have been shown to influence these modeled estimates of CO_2 gas exchange, including depression of photosynthesis at high water contents (Lange et al. 1995; Fig. 15.2) and more frequent than expected biocrust activity at suboptimal light and temperature conditions in the field (Lange and Green 2004). As these phenomena are relevant for productivity calculations, they also need to be analyzed in detail by means of constructing gas exchange estimates at different light and water values in the laboratory. Other factors that have to be taken into account during modeling are

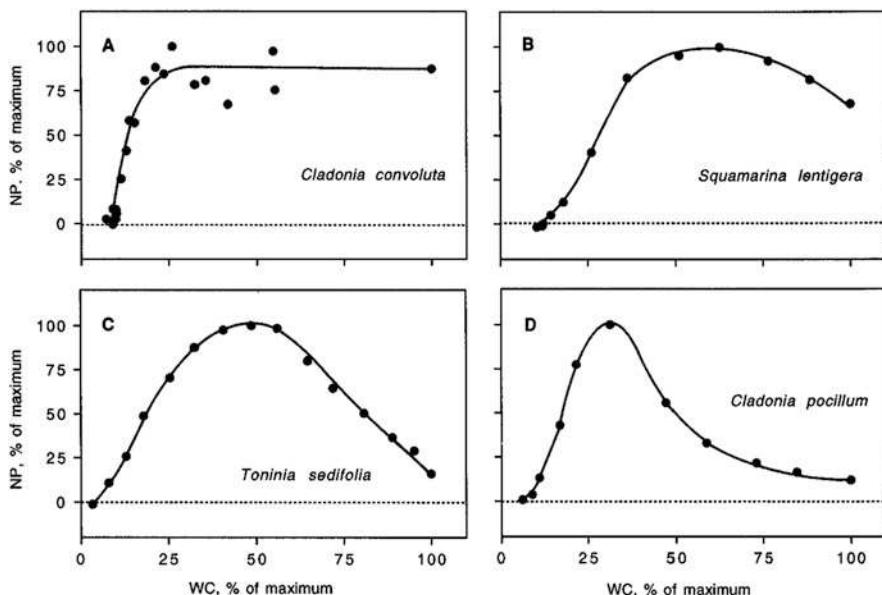


Fig. 15.2 Dependence of net photosynthesis (NP, % of maximum) and thallus water content (WC, % of maximum) in different soil crust lichen species collected in the same locality. Different responses of NP are observed at maximum WC (100 %), from high depression of NP at high WC (c, d) to low (b) or nonexisting depression (a). Modified from Lange et al. (1995)

the biotic and abiotic CO₂ fluxes from the soil (Ma et al. 2013; Rey et al. 2014; Weber et al. 2012). These are potentially a major problem in modeling biocrust-derived C fluxes. The large differences between modeled respiration (see Castillo-Monroy et al. 2011) and NPP for desert biocrusts shows that the calculated NPP will be very sensitive to non-biocrust-derived C. However, the literature indicates that abiotic fluxes from soil carbonates, the obvious potential source of C flux from soils, can be very low (Serna-Perez et al. 2006; although see Rey 2015). A combination of the datasets accumulated in the SCIN project (Büdel et al. 2014) with the current knowledge regarding CO₂ fluxes in biocrusts from arid and semiarid environments will allow modeling the behavior of these communities in a global change scenario (Fig. 15.3).

Some other approaches do not produce models for final C balance, but provide useful datasets for future modeling because they contain empirical measurements of gas exchange at the microscale (field and/or laboratory datasets). Lange (2003a) showed that the annual C balance of the lichen approximates its annual increase in biomass, stating that the potential annual primary production of lichen-dominated systems reaches around 8 % of the global mean for terrestrial productivity. Weber et al. (2012) published relevant CO₂ fluxes in mosses from a semidesert in South Africa, underlining in their results the physiological importance of measuring complete biocrusts against measuring isolated components of them (see also Sommerkorn et al. 1999). Finally, some works link CO₂ fluxes at the biocrust

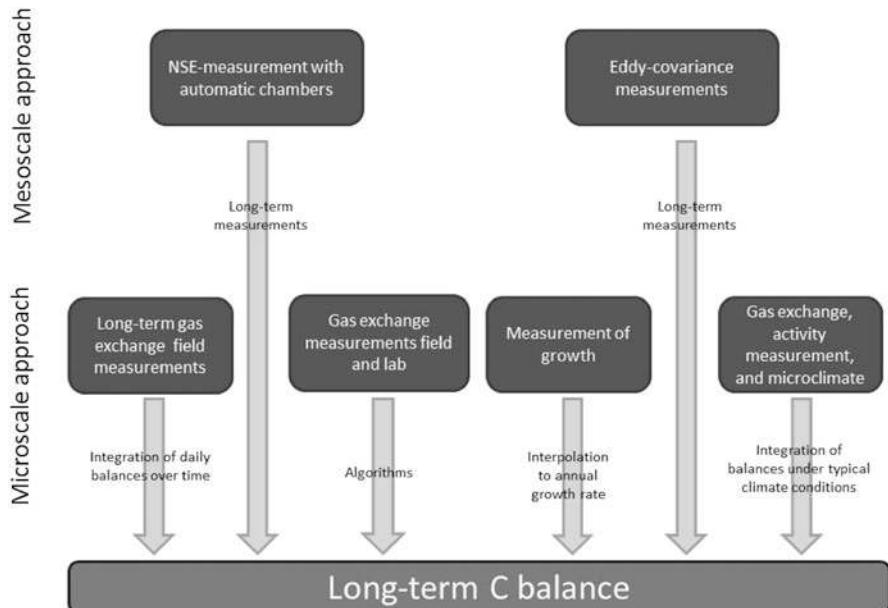


Fig. 15.3 Conceptual model showing how to integrate measuring methods at meso- and micro-scale to calculate long-term C balance in biocrust systems

microscale level with future climate change scenarios (Grote et al. 2010; Maestre et al. 2010, 2013). These works provide large datasets that will help to understand possible consequences of environmental change for C balances in arid or semiarid environments where biocrusts are abundant.

15.2.2 Available Datasets on the Microscale

Tundra In tundra habitats, poikilohydric organisms form a major part of the overall vegetation. Here, annual C budgets have been estimated. Maximum photosynthesis rates for lichen species in tundra vegetation range from $0.8 \text{ nmol g}^{-1} \text{ s}^{-1}$ for *Sphaerophorus globosus* to $8.0 \text{ nmol g}^{-1} \text{ s}^{-1}$ for *Dactylina arctica* (Tenhunen et al. 1992; Table 15.2). Lichens dominate biocrust communities in well-drained evergreen shrub vegetation as well as in rocky fell-fields and contribute up to 400 g of photosynthetically active biomass m^{-2} (Tenhunen et al. 1992). Along a gradient of increasing water availability, there is a transition from lichen-dominated biocrusts to those dominated by mosses. The NP rates of typical tundra mosses are about three times higher than those of lichens [e.g., maximum NP for *Polygonatum alpinum* is $27.8 \text{ nmol g}^{-1} \text{ s}^{-1}$ (Oechel and Collins 1976) and *Sphagnum squarrosum* is $18.9 \text{ nmol g}^{-1} \text{ s}^{-1}$ (Murray et al. 1989)]. The relatively high NP rates and the generally moist conditions lead to substantial estimates for annual C fixation rates

Table 15.2 Net carbon uptake ($\text{g C m}^{-2} \text{ year}^{-1}$) of different crust types from the tundra and desert biome

Net carbon uptake ($\text{g/m}^{-2} \text{ year}^{-1}$)	Biome	Organism	References
38.5–171	Tundra	Moss	Oechel and Collins (1976)
10	Tundra	Moss	Billings (1987)
2–68	Tundra	Lichens and mosses	Shaver and Chapin (1991)
4.7–20.4	Tundra	Lichens	Lange et al. (1998)
24.80	Tundra	Moss	Bisbee et al. (2001)
6.5	Tundra	Moss	Uchida et al. (2002)
12–60	Tundra	Moss	Schuur et al. (2007)
5.3–29	Desert	Lichen	Klopatek (1992)
4–11.3	Desert	Lichen	Lange et al. (1992)
0.07–1.5	Desert	Cyanobacteria	Jeffries et al (1993)
16	Desert	Lichen	Lange et al. (1994)
0.54	Desert	Cyanobacteria	García-Pichel and Belnap (1996)
25.8	Steppe	Lichen	Evans and Lange (2003)
11.7	Desert	Cyanobacteria	Brostoff et al. (2005)

in tundra areas, where particularly bryophytes are important in C and N cycling (Turetsky 2003). For example, estimated NPP of feather mosses in the boreal forests reach about $24.80 \text{ g C m}^{-2} \text{ year}^{-1}$ (Bisbee et al. 2001), and in wet areas *Sphagnum* species are also very productive with up to $19 \text{ g biomass m}^{-2} \text{ year}^{-1}$. Fenton (1980) estimated that mean productivity of Antarctic *Polytrichum alpestre* ranges from 213 to $350 \text{ g m}^{-2} \text{ year}^{-1}$, while productivity of *Chorisodontium aciphyllum* averages $162 \text{ g m}^{-2} \text{ year}^{-1}$.

Temperate Habitats In temperate regions, there has only been one study addressing annual C budgets for individual biocrust lichens. Lange (2002, 2003a) measured *Lecanora muralis* using the Klapp cuvette for 15 months and determined its annual C fixation rate to be $21.494 \text{ g C m}^{-2} \text{ year}^{-1}$ (Lange 2002, 2003a). Lange (2000) also used this system on the gelatinous lichen *Collema cristatum* to show very good agreement between NP responses measured in the laboratory and field.

Deserts In deserts, due to restricted water availability, organisms are only sporadically active (Lange et al. 2006; Sponseller 2007; Pintado et al. 2010), causing NPP to be generally much lower than in temperate or polar regions, but as higher plants are sparse, biocrust cover can be very high and thus still play an important role in overall C cycles. However, as biocrust organisms are only metabolically active when wet and precipitation in deserts is highly variable, estimates for NPP of biocrust components are highly variable as well, ranging between 0 and $29 \text{ g m}^{-2} \text{ year}^{-1}$ (Table 15.2). In general, biocrusts in temperate deserts are more easily damaged, and their carbon fixation reduced, by compressional disturbances than those in tundra habitats. In addition, as temperatures are higher in deserts, moisture evaporates more quickly than in tundra, and thus their overall photosynthetic gain is less. However, biocrusts

can access a range of water sources, many of them not being available to higher plants. Some desert lichens (e.g., *Acarospora cf. schleicheri*, *Caloplaca volkii*, and *Lecidella crystallina*) can mainly use fog to reactivate their photosynthesis (Lange et al. 1994) and reach an estimated photosynthetic carbon gain of $16 \text{ g C m}^{-2} \text{ year}^{-1}$. Not only scarcity of water affects C cycles in biocrusts but also surplus water with contents above 60 % generally results in a decline in GP in many biocrust species, probably caused by water-filled pores restricting gas diffusion (Grote et al. 2010; Lange et al. 1997b; Green et al. 1994).

The type of biocrust organism also plays an important role in C fixation at a site. On the Colorado Plateau and in the Chihuahuan Desert, Housman et al. (2006) showed that later successional biocrusts dominated by the cyanobacteria *Nostoc* and *Scytonema* and the lichens *Placidium* and *Collema* typically had a 1.2–1.3-fold higher daily C fixation than early cyanobacterial crusts dominated by the cyanobacterial genus *Microcoleus*. Biocrusts dominated by *Microcoleus vaginatus* growing on dunes are estimated to fix $11.7 \text{ g C m}^{-2} \text{ year}^{-1}$ (Brostoff et al. 2005). Early successional biocrusts from highly disturbed areas, dominated by algae or cyanobacteria, show lower carbon fixation values than those from undisturbed sites where lichens and mosses occur (Table 15.2; Zaady et al. 2000), being in agreement with the photosynthetic capacities found for the individual biocrust components.

15.2.3 Modeling on the Microscale

Castillo-Monroy et al. (2011) proposed that biocrusts in a semiarid ecosystem in Spain were responsible for the greatest proportion of the total soil respiration. Their model was based on the assumption that 85 % of soil respiration could be explained by soil temperature and moisture and predicted a C release between 240.4 and $322.6 \text{ g C m}^{-2} \text{ year}^{-1}$. Wilske et al. (2009) used a model based on vascular plant studies but adapted that to work only when there is water available in the ecosystem. The model is sustained by (a) the link between biocrust CO₂ fluxes and an indicator of annual metabolic activity and (b) a more simplistic precipitation-driven alternative. The final results showed a large interannual variation in C uptake for biocrust NEE ranging between 0.7 and $5.1 \text{ g m}^{-2} \text{ year}^{-1}$. An alternative approach is the algorithm proposed by Brostoff et al. (2005), where the NPP is calculated as the difference between maximum NP and maximum DR measured in the field multiplied by the percentage of cover and meteorological indicators of possible biocrust metabolic activity. Using this method, the NPP of biocrusts in the Mojave Desert was $11.7 \text{ g C m}^{-2} \text{ year}^{-1}$ and between 3.46 and $6.05 \text{ g C m}^{-2} \text{ year}^{-1}$ for different biocrust types in a Chinese Desert (Feng et al. 2014). Finally, Uchida et al. (2006) developed a model for the dominant terricolous lichen *Cetrariella delisei* in deglaciated areas of the high Arctic. In their productivity model, they obtained a mean NPP value of $5.1 \text{ g dw m}^{-2} \text{ year}^{-1}$ (about 2295 mg C m^{-2}) per snow free season (Table 15.1). They based their model on the interaction between abiotic factors and CO₂ exchange, always assuming in their algorithms that NP and DR are firstly dependent on water availability and secondly on temperature and radiation.

Water is often available under a suboptimal combination of environmental factors, typically low radiation and low temperature, which usually limits biocrust NP in the field (Lange and Green 2004; Raggio et al. 2014). This is considered to be a reliable approach to model NPP of cryptogams (Lange 2003a, b).

15.3 The Mesoscale: Net Ecosystem Exchange in Biocrusted Soils

15.3.1 Available Datasets on the Mesoscale

Continuous long-term measurements of net ecosystem C exchange (NEE) in biocrust-dominated soils are only available for two desert regions.

Colorado Plateau, USA The first study region is the Colorado Plateau Desert, USA, where there have been three studies on two different soil types. These studies, despite using different measurement techniques and on different soils, obtained very similar results. The first study used large auto-chambers with an internal diameter of 0.36 m² and contain dark, late-successional biocrusts consisting of ~10 % moss (mostly *Syntrichia caninervis*), ~5 % lichen (*Collema tenax* and *Collema coccophorum*), and 85 % cyanobacteria (dominated by *Microcoleus vaginatus*) (Darrouzet-Nardi et al. 2015). Measurements were made hourly for 21 months (from winter 2006 through summer 2007). Except following large rain events (ideal conditions for photosynthesis), the soil surface acted as a small C source to the atmosphere. The highest C losses were observed in spring (327 mg C m⁻² day⁻¹) and the lowest in winter (65 mg C m⁻² day⁻¹). Of the 627 measurement days, only 6.4 % showed a positive NSE. These data indicated that only larger or extended events kept soils wet long enough for the biocrust activity to result in uptake outweighing losses, whereas smaller events resulted in net C loss.

The second study on the Colorado Plateau occurred on fine sandy loam soils at a site 120 km from the first site, using the same auto-chamber design as above (Fig. 15.4; Bowling et al. 2011). Measurements were done over the course of 300 days (Julian 0–299), although gaps occurred during that time due to equipment malfunction. Soils were covered with a biocrust dominated by the cyanobacterium *Microcoleus vaginatus* with some *Bryum argenteum* moss present as well. Results were very similar to the first study. During the measurement time, only large or almost contiguous smaller rain events resulted in small C uptake (414.7 mg C m⁻² day⁻¹) by the biocrusted soils (Fig 15.4). As these events were rare, the soil surfaces were mostly a small C source (up to 985.0 mg C m⁻² day⁻¹) over the course of the experiment.

The third study was at the same site as the second study, but measurements were done using eddy covariance (Bowling et al. 2010). This study further corroborated the results obtained in the first two studies: Biocrust soil surfaces at these sites were

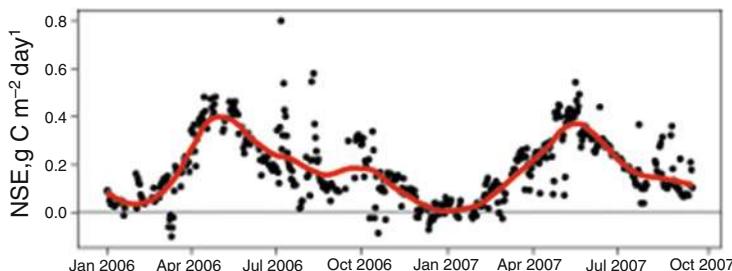


Fig. 15.4 Daily average net soil exchange (NSE) of $\text{CO}_2\text{-C}$ in control plots from the daily sums dataset over the 21-month measurement period of the study. Positive values indicate net loss of C from soils. Red curve is a local regression (loss) with span = 0.2

mostly small sources of C (up to $518 \text{ mg C m}^{-2} \text{ day}^{-1}$), with large rain events resulting in small C uptake (up to $933 \text{ mg C m}^{-2} \text{ day}^{-1}$). However, there was a sparse cover of vascular plants at this site, and thus these measurements also reflect their influence on C fluxes.

Gurbantunggut Desert The third desert is the Gurbantunggut Desert in northwest China. Su et al. (2012, 2013) measured C fluxes of different soils dominated by various types of biocrusts (moss, lichen, and cyanobacteria). As in the Colorado Plateau studies, the results show small C losses from the soil during most of the time, with only short intervals of small C uptake. The similarity in magnitude of the losses and uptake compared to the Colorado Plateau data is striking [−2281 to $1244 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the Gurbantunggut Desert (all biocrust and soil types) and −623 to $1660 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the Colorado Plateau Desert].

It is unfortunate that we have so few continuous measurements of NEE for biocrusts, as these few studies strongly suggest that spot measures, whether in the laboratory or field, are not sufficient when trying to understand the role of biocrusts in ecosystem C dynamics. Interpretation of the data from any of these studies is complicated by the fact that it is currently not feasible to separate out the role of biocrusts from that of underlying soil factors, such as respiration from roots, deeper biota, and abiotic losses, as well as effects from the somewhat artificial environment created by our measurement techniques. Despite this complication, the similarity of the values obtained from the two studies at geographically distinct sites indicates that the overall photosynthetic contribution of biocrusts in temperate deserts can mostly offset soil abiotic and biotic losses.

15.4 The Macroscale: Global Carbon Budgets

Two different studies have investigated the contributions of cryptogams to carbon budgets on a global scale (Elbert et al. 2012; Porada et al. 2013). In the first study, Elbert et al. (2012) compiled the available data from more than 200 studies on the

carbon fixation rates of cryptogamic organisms occurring on soil, rocks, and leaves of plants. In most cases, short-time measurements with net photosynthesis rates under optimum conditions had been conducted. These values were scaled to annual NPP rates and assigned to major ecosystems (desert, extratropical forest, steppe, tropical forest, and tundra) to obtain mean NPP values, which were then extrapolated to a global scale. Considering only biocrusts occurring under more arid conditions, comparably high flux rates were obtained for steppe ecosystems ($16.0 \text{ g C m}^{-2} \text{ year}^{-1}$) compared to deserts ($5.2 \text{ g C m}^{-2} \text{ year}^{-1}$).

Based on their calculations, Elbert et al. (2012) estimated C uptake in these cryptogamic covers to be $\sim 3.9 \text{ Pg C year}^{-1}$, corresponding to $\sim 7\%$ of the net primary production of terrestrial vegetation. When only cryptogamic ground covers are considered, annual C uptake was estimated at $\sim 2.4 \text{ Pg C year}^{-1}$ (Fig. 15.5). When restricted to biocrusts, uptake values of $\sim 0.6 \text{ Pg C year}^{-1}$ were obtained. This value is $\sim 1\%$ of the NPP of terrestrial vegetation ($\sim 56 \text{ Pg year}^{-1}$, Zhao et al. 2005), but in the desert ecosystem, biocrusts account for about 9 % of the total NPP ($\sim 0.07 \text{ Pg year}^{-1}$ compared to a total NPP of $\sim 0.8 \text{ Pg year}^{-1}$; Zhao et al. 2005; Elbert et al. 2012). As mostly measurements of single cryptogamic organisms were used for these calculations with only few data available on complete communities (e.g., biocrusts), these results may be higher than balances of complete biocrusts with fungi, bacteria, and archaea involved.

In this first upscaling approach, several assumptions were made to facilitate an upscaling from short-term measurements to a long-term global scale. In order to come up with long-term data of higher accuracy, the natural cycles of hydration and dehydration and the resulting productivity have to be followed ideally over several years. This knowledge can greatly improve the understanding of seasonal and interannual variability of CO₂ fluxes and allow the development of strong predictive models to assess the behavior of biocrusts in a global change scenario.

In a second approach, Porada et al. (2013) used a process-based model to estimate the global C uptake by lichens and bryophytes across all habitats. In this “Lichen and Bryophyte Simulator,” the organisms are described by a reservoir approach that consists of pools of biomass, sugar reserves, water, and internal CO₂ concentration. These pools are changed by input and output flows of C and/or water that are driven by climatic factors and the biotic environment (e.g., location relative to the surrounding vegetation). Utilizing this model, the authors predict a global terrestrial NPP ranging between 0.34 (average method) and 3.3 Gt C year⁻¹ (maximum weighing method) by lichens and bryophytes. This is the first approach analyzing the NPP of cryptogams based on a photosynthesis model. Thus, it still contains uncertainties, as for some physiological parameters, little data are available for lichens and mosses. Also, C losses have not been considered and thus NEE/NSE may be very small.

The global patterns of the ground-based NPP rates calculated by Porada et al. (2013) generally agree with those of Elbert et al. (2012), with the highest NPP values in both studies being reached in extratropical forests and the lowest (zero) in the Sahara Desert, due to the lack of water (Fig. 15.5). The overall values, however, are smaller in the study of Porada et al. (2013) compared to Elbert et al. (2012). This is

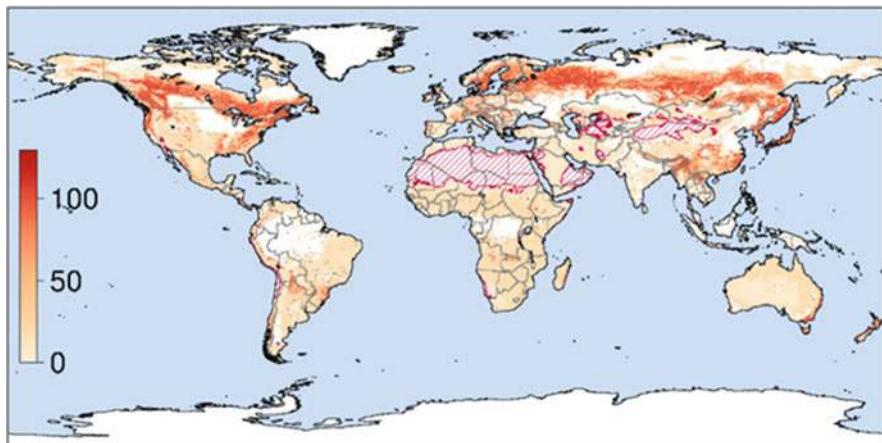


Fig. 15.5 Geographic distribution of atmospheric carbon dioxide fixation by cryptogamic ground covers. The *color coding* indicates the flux intensity in $\text{g m}^{-2} \text{ year}^{-1}$. *White areas* indicate ecosystems for which no data are available; *hatched areas* were excluded from global budget calculations (annual mean precipitation $< 75 \text{ mm year}^{-1}$, and desert areas designated as dune sand/shifting sands and rock outcrops)

possibly, in part, because cyanobacteria and algae were not taken into account in the study, despite their extensive global cover. Nevertheless, this approach allows completely new insights into the global relevance of cryptogamic organisms in C cycles. In addition, Porada et al. (2014) also used this model to calculate the potential N fixation, phosphorus uptake, and chemical weathering by lichens and bryophytes. Investigating global estimates, one has to keep in mind that biocrusts may also indirectly enhance CO₂ uptake by plants through cyanobacterial nitrogen enrichment of the soil (Belnap 2002; Elbert et al. 2012).

15.5 General Future Research Needs and Directions

Despite the potential importance of biocrusts in C cycles at all scales, we have little quantitative data by which to understand their role. Using common protocols, we need to better document how biological (e.g., species composition, organism condition) and physical factors (e.g., activity rates and times as determined by climatic factors, soils) influence C fixation and loss. Across all scales, we need to better understand observed NPP/NSE rates: that is, what portion of the measured NSE is due to biocrust photosynthesis and respiration, and what portion of C losses is due to other sources, such as bacteria, fungi, and soil carbonates? At the microscale, we need more studies on how biological and environmental factors interact to determine photosynthesis and respiration. At the mesoscale level, only eddy covariance and flux towers provide real estimation of CO₂ fluxes of whole

ecosystems. However, these studies are still very rare in biocrust communities, thus seriously limiting our understanding of the role of biocrusts in landscape or larger-scale CO₂ balances and budgets. For this reason, we suggest more such installations, with care paid to standardize protocols and measurements. In addition, because eddy covariance offers direct measurements of C fluxes, these studies could be linked to the modeled outputs at the microscale, giving an opportunity for cross-validation. A validated model could allow predicting the influence of environmental change on C cycling across all scales.

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Chapter 16

Biological Soil Crusts as Soil Stabilizers

Jayne Belnap and Burkhard Büdel

16.1 Introduction

Soil movement via aeolian and fluvial processes provides important local, regional, and global biogeochemical linkages between the atmosphere, hydrosphere, biosphere, and pedosphere (Schlesinger et al. 1990; Syvitski 2003). However, this soil redistribution has had detrimental and often irreversible consequences in the past that are likely to continue into the future (Bridges and Oldeman 1999; Lal 2001; Valentin et al. 2005). Dryland regions are particularly vulnerable to soil erosion because of the low levels of vascular vegetation, soil moisture, and soil organic matter. In addition, many soils are a mix of sand and fine particles that are especially prone to wind erosion. As a result, erosion resistance depends mostly on the presence of physical or biological soil crusts to stabilize the large exposed interspaces between plants (Sivakumar 2007; Belnap 2003). Because drylands are inhabited by one-third of the world's population, human-related disturbances often disrupt biocrusts (UNDP/UNSO 1997; Eldridge and Belnap 2003), with the result that ~ 24 million km^{-2} , or approximately 17.5 % of the global land area, is being degraded by wind and water erosion (Williams and Balling 1996; Bullard and McTainsh 2003).

In dryland regions, soil loss can greatly exceed formation rates, as it can take thousands of years to form a few centimeters of soil (Pillans 1997; Cuff and Goudie 2009). Eroded soils are less fertile, as wind and water can winnow out the fine clay

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particles to which nutrients are adsorbed, leaving behind coarser soils with fewer nutrients (Neff et al. 2005). Soils are often very shallow in desert areas and can be completely stripped away when soil protection is lost (Jayne Belnap, personal observation). Eroded soils are often deposited in streams by either wind or water, negatively impacting water quality. In addition, dust deposited on nearby mountains increases the melt rate of the snowpack, decreasing both late season water and the total amount of water entering streams (Painter et al. 2010). Dust can also place human health at risk (e.g., respiratory disease, highway fatalities).

In this chapter, we will explore the role that biocrusts play in preventing wind and water erosion in dryland regions. We will emphasize studies that have occurred since 2000, as studies prior to that time were reviewed in Belnap (2003), Warren (2003a, b), and Belnap and Lange (2003). As almost all studies have found that biocrusts stabilize soils from both types of erosive forces, we will be focusing on the factors that influence the degree to which biocrusts confer resistance.

16.2 Biocrust Characteristics that Confer Resistance and Resilience to Soil Erosion

The major biocrust characteristics that influence soil protection from wind and water erosion include the morphology of individual species, as well as the developmental stage and biomass of the biocrust community as a whole. The extent, intensity, and time since disturbance are also important, but these factors are reflected in the species composition and biomass of the biocrust community. Because these characteristics vary with climate, soils, and other factors, erosion resistance and resilience can vary within short distances.

16.2.1 Species and Biocrust Developmental Stages Affect Resistance to Wind and Water Erosion

There have been a substantial number of studies examining the effect of biocrusts on wind and water erosion. In almost all cases, biocrusts increase the resistance of soils to erosion. However, very few studies have addressed how individual species influence soil loss, and most have been wind tunnel studies. Fortunately, we have many more studies that have compared the differential protection offered by various levels of biocrust community development from both wind and water.

16.2.2 Individual Species Affect Resistance to Soil Loss

Biocrust development begins with the colonization of cyanobacteria and fungi. Hu et al. (2002) examined the stabilization capability of four filamentous cyanobacteria (*Microcoleus vaginatus*, *Phormidium tenue*, *Scytonema javanicum*, and *Nostoc* sp.) and one green alga (*Desmococcus olivaceus*), all species commonly found in early successional biocrusts. Using a wind tunnel run at 6 m s^{-1} , they showed that *Microcoleus vaginatus* and *Phormidium tenue* needed the least biomass (0.6–1.3 and 1.4–2.3 mg chl a g^{-1} dry soil, respectively) of all tested species to withstand this wind speed. The remaining species required substantially more biomass, with *Scytonema javanicum* needing 6.3–13.0 and *Nostoc* sp. 34.7–55.6, mg chl a g^{-1} dry soil. *Desmococcus olivaceus* was unable to stabilize soils at any application rate. A blend of 80 % *Microcoleus vaginatus* and 5 % each of the other four species required less biomass to stabilize soils than an equal mix of the five species, again indicating the superiority of *Microcoleus vaginatus* in stabilizing soils.

Measuring threshold friction velocities (TFV, the wind speed at which soil particles are moved), this same study (Hu et al. 2002) showed that *Microcoleus vaginatus*, *Phormidium tenue*, and the *Microcoleus vaginatus*-dominated mix had higher TFVs than *Nostoc* sp., *Desmococcus olivaceus*, or the mix with equal proportions of the species. Similarly, McKenna-Neuman et al. (1996) found the cyanobacterium *Nostoc commune* or a mixture of the cyanobacteria *Nostoc commune* and a *Lyngbya* species was superior to the green alga *Chlamydomonas acidophila* in stabilizing soil surfaces. However, in contrast to this general pattern of cyanobacteria being better at stabilization of soils than green algae, the filamentous cyanobacterium *Lyngbya* sp. was the least resistant of the three species they tested (and, coincidentally, has a firm, narrow sheath that is not sticky; Burkhard Büdel, personal observation). Interestingly, Hu et al. (2002) found that small amounts of dust, when incorporated slowly into a *Microcoleus* biocrust, increased biocrust cohesion and thus resistance to wind erosion.

In another study, McKenna-Neuman and Maxwell (1999) examined the resistance of three monospecific fungal biocrusts (*Aureobasidium pullulans*, *Trichoderma harzianum*, and *Absidia corymbifera*), a cyanobacterial biocrust (*Nostoc commune*), and a green algal biocrust (*Chlamydomonas acidophila*). All three artificial fungal biocrusts were thicker and more resistant to wind erosion than the photoautotrophic biocrusts. The order of resistance was *Trichoderma harzianum* > *Absidia corymbifera* > *Aureobasidium pullulans* > *Nostoc commune* > *Chlamydomonas acidophila*. They also showed that the breakdown of biocrusts can occur either during a high-energy wind event or, surprisingly, by slow abrasion during chronic low-energy wind events (McKenna-Neuman et al. 1996; McKenna-Neuman and Maxwell 1999, 2002). Thus, biocrust integrity depends on growth rates in excess of the chronic loss as well as loss imposed by high-energy velocity wind events. The only study we could find on how individual microbial species influenced water erosion was Kidron

et al. (1999). Similar to the findings on wind erosion, they found *Scytonema* sp. to be more effective at stabilizing surfaces than *Nostoc commune*.

As mosses and lichens colonize biocrusts, wind resistance continues to increase. A wind tunnel study showed that biocrusts dominated by either the moss *Tortula ruralis* or *Pohlia nutans* were equally protective of the soil surface when exposed to sand-containing winds at 6 or 7.5 m s⁻¹ (McKenna-Neuman and Maxwell 2002). An additional and interesting finding of this study was that the breakdown of biocrusts, regardless of whether cyanobacterial or moss-dominated biocrusts, can result from a slow, constant abrasion of the biota as well as from acute wind events. Unfortunately, this was the only study that could be found looking at the resistance of individual moss or lichen species.

There are many ways in which species can vary in their ability to stabilize soils. For microbes, these include (1) size and strength of individual cells to enable resistance to abrasion and breakage; (2) ability to form filaments, giving the organism the ability to wrap around soil particles as well as connect them together into soil aggregates (Belnap and Gardner 1993); (3) amount of exo-polysaccharides secreted, as these provide the “glue” that enables the filaments to adhere to the soil particles and other organisms; (4) length of filaments, enabling them to cover more soil particles; (5) strength of cell linkages along the filament so the filaments do not break with stress; and (6) mobility in the soil, enabling the organism to both cover more soil particles with EPS and cells/filaments, as well as incorporate newly deposited material, thus avoiding death by burial and increasing the strength of the biocrust. In leaving their old sheath envelope behind when moving into the new soil layer, the microbial sheaths continue to stabilize the older soil layers. This leads to a characteristic soil layering that can be easily observed in soil cross-fractures or even in the fossil record (see Fig. 9.2h). For example, the internal and external morphology of the microbial species tested in McKenna-Neuman et al. (1996) and McKenna-Neuman and Maxwell (1999, 2002) may explain the observed order of resistance. *Trichoderma harzianum* has a robust external structure and internal septa to reinforce the cells. *Absidia corymbifera* has an exterior similar to *Trichoderma harzianum* but lacks the internal septa. *Aureobasidium pullulans*, in contrast, consists of a chain of weakly linked cells. All three fungal biocrusts were thicker than the photoautotrophic biocrusts, all of which had lower resistance to wind erosion.

For lichens and mosses, important factors conferring stability are (1) size of continuous thallus on the surface that prevents wind from touching the soil, (2) ability to withstand abrasion from both chronic and acute events, and (3) depth and extent of anchoring structures, which prevents the organisms from being uprooted. As can be seen, there is a large amount of variation in the factors listed above. However, we do not know the relative importance of these factors. Because many efforts are currently focused on using biocrusts for soil stabilization, further research on which traits are the most important for stabilization is a critical research need.

Figures 16.1a–h and 16.2a–e show photographs of the different dominant phototrophic species important in stabilizing soils. Unicellular green algae

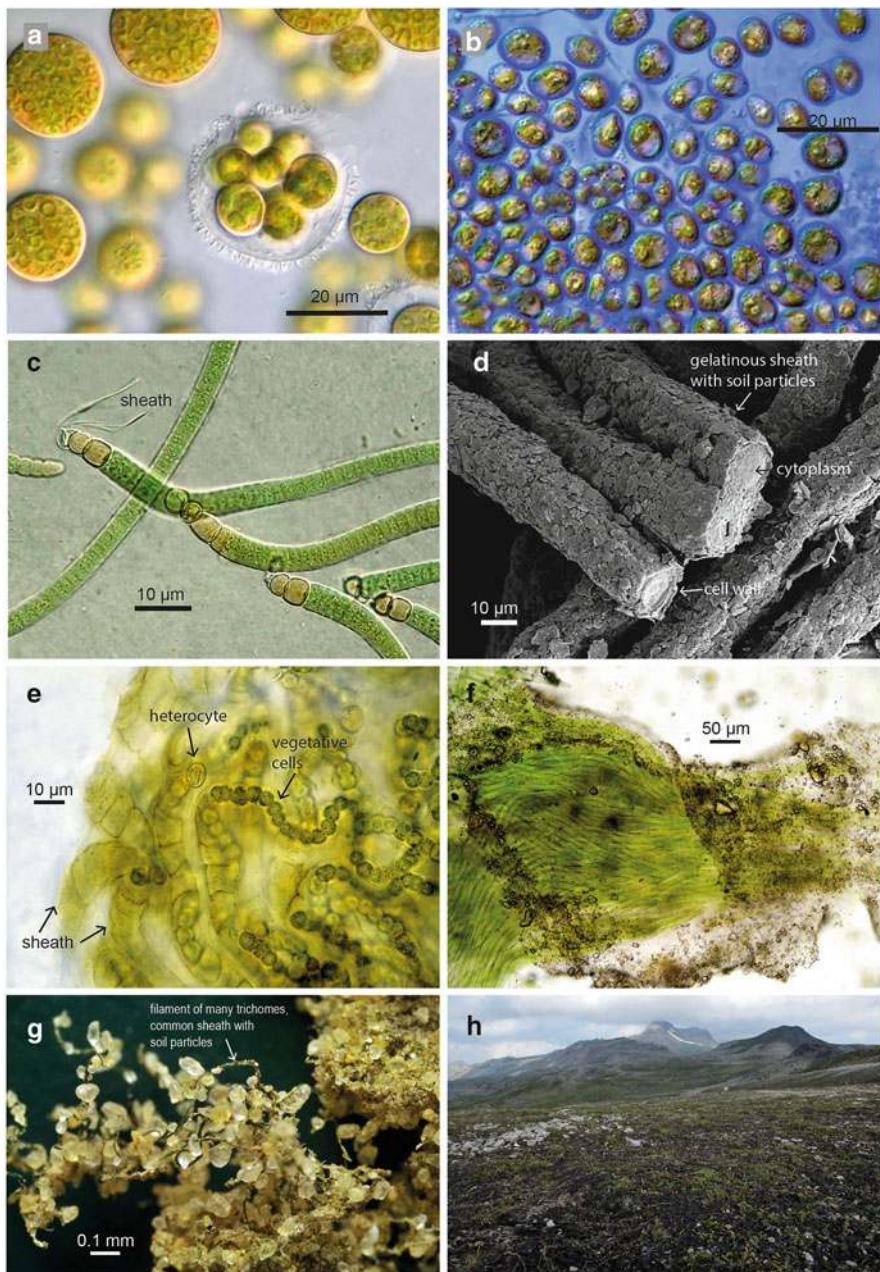


Fig. 16.1 (a) The unicellular green alga *Bracteacoccus giganteus* is common in biocrusts but produces only a limited amount of slimy sheath material (micrograph courtesy of Darienko and Friedl). (b) Unicellular green biocrust alga *Neochlorosarcina negevensis*, gelatinous sheath stained blue with 0.1% methyl blue (micrograph courtesy of Darienko and Friedl). (c) The filamentous cyanobacterium *Calothrix* sp. occurs in low densities and produces only thin

(Fig. 16.1a, b) and filamentous green algae and cyanobacteria (Fig. 16.1c–f) glue soil particles together (Fig. 16.1g) and can form an almost continuous cover in many ecosystems (Fig. 16.1h). The internal structure of the stabilizing layer can consist of both living and abandoned sheath layers (Fig. 16.2a). Liverworts (Fig. 16.2b), moss (Fig. 16.2c), and lichens (Fig. 16.2d, e) are also important stabilizers, and in fact, as they occur above the actual soil surface, they often offer better protection than cyanobacteria or green algae. Fungi are also critical in stabilizing soils and act similarly to the filamentous cyanobacteria.

16.2.3 Developmental Stage Affects Resistance to Soil Loss

At very low biomass levels, cyanobacterial biocrusts do not confer resistance to wind erosion. In the Mojave Desert of southern CA, USA, a minimum of $0.01 \text{ mg chl } a \text{ g}^{-1}$ soil was needed to stabilize soils (Belnap et al. 2007). Hu et al. (2002) reported this threshold to be higher at $0.6 \text{ mg chl } a \text{ g}^{-1}$ soil. Belnap et al. (2014) used regression tree analyses and found that the most important factor predicting TFV was cyanobacterial chlorophyll *a*, with soils containing $>0.014 \text{ mg g}^{-1}$ soil having twice the stability of those below that value. Belnap et al. (2008) also found a strong relationship between cyanobacterial chlorophyll *a* and soil stability ($R^2 = 0.77$). Unfortunately, we do not have data on the lowest threshold for resistance to water erosion.

Among young biocrusts, there is an exception to the pattern of increasing resistance to erosion with increasing biomass. At a certain point in development when biomass is low, the biocrust organisms have created enough cohesion to hold the soil surface particles together but are insufficiently anchored to the soil to withstand acute stress created by high winds or water. Under these conditions, large cyanobacterial/fungal-bound soil flakes can be seen detaching from the soil surface and blowing or washing away (McKenna-Neuman et al. 1996; McKenna-Neuman and Maxwell 1999, Belnap pers. obs.).

With time, cyanobacterial biomass increases past the stage of the flaking issue and later-successional mosses and lichens colonize, conferring increased resistance to soil erosion as cover and biomass increase [reviewed in Belnap (2003) and Warren (2003a, b)]. Because lichens and mosses actually protrude above and cap

Fig 16.1 (continued) gelatinous sheaths. Photo by B. Büdel. (d) Filaments of the green alga *Klebsormidium* sp. inside biocrusts with soil particles attached to the sheath. Photo by B. Büdel. (e) The filamentous cyanobacterium *Nostoc* cf. *microscopicum* occurs in medium density but produces thick sheaths. Photo by B. Büdel. (f) The filamentous cyanobacterium *Microcoleus vaginatus* occurs in large amounts in biocrusts and produces a huge amount of sheath that remain in the substratum even after the trichome left; attached soil particles mark the extent of the sheath. Photo by B. Büdel. (g) *Microcoleus vaginatus* filaments with up to $100 \mu\text{m}$ large soil particles attached to its thick, sticky sheath. Photo by B. Büdel. (h) Well-developed cyanobacterial biocrust forming a dense cover in the high European Alps, 2600 m a.s.l. Photo by B. Büdel

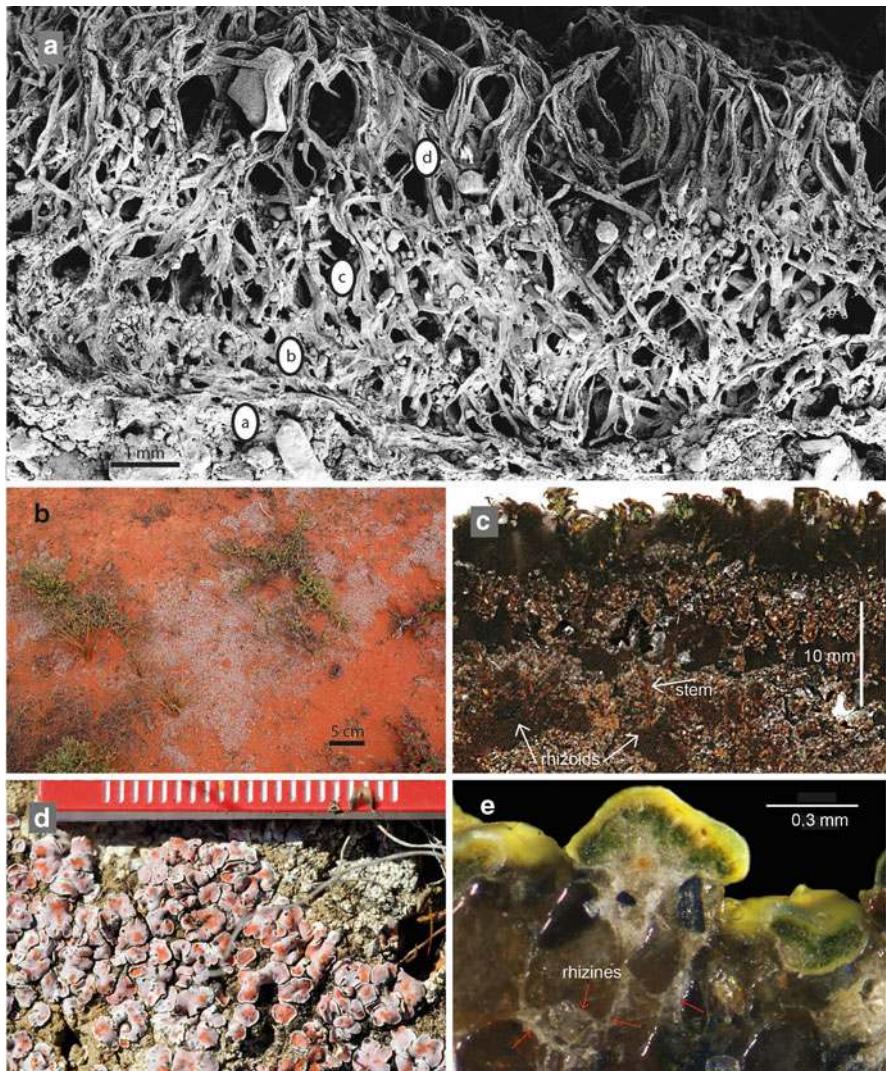


Fig. 16.2 (a) Crust structure of a *Symplocastrum* cf. *purpurascens*-dominated biocrust. a = basal layer with compressed empty sheaths; b = 2 seasons old layer with empty sheaths; c = new layer with trichomes inside the sheaths. Photo by B. Büdel. (b) Liverwort (*Riccia* sp.)-dominated biocrusts covering large parts of the soil, Western Cape region, South Africa. Photo by B. Büdel. (c) Cross section of a moss-dominated biocrust. The moss covers the soil surface almost completely, with rhizoids (reddish filaments) penetrating several millimeters into the soil. Photo by B. Büdel. (d) Dense biocrust dominated by the green algal lichen *Psora decipiens*, covering the soil surface more or less completely. Photo by B. Büdel. (e) Cross-fracture of a lichen-dominated (*Acarospora gwynnii*) biocrust, with rhizines penetrating the soil surface up to 1 mm. Photo by B. Büdel

the soil surface and add relatively deep (up to 5 cm) anchoring structures, later-successional biocrusts are better able to withstand both the abrasion of soil particles driven by wind and raindrop erosion associated with water erosion than cyanobacterial crusts, regardless of the cyanobacterial biomass (Qin and Zhao 2011; Zhao et al. 2014). In addition, water velocity can be a major factor in determining sediment production in some settings, as slower water carries less sediment and has lower erosive power. The external morphology of biocrusts has a large effect on velocity. In hot deserts and some temperate regions, cyanobacteria smooth and flatten the soil surface, increasing water velocity (Belnap 2006). In contrast, many of the biocrusts found in cool and cold deserts have an extremely roughened soil surface created by freezing, pushing the soils upward and rain differentially eroding downward and this roughened surface greatly slows water velocity. However, the specific interaction of water velocity and biocrust roughness has not been quantified in enough studies to understand its importance. In addition, better developed biocrusts contribute significant amounts of organic carbon to soils via carbon fixation (Lange 2003) and decaying organic matter (Danin and Ganor 1991), both of which contribute to aggregate formation and thus soil stability.

Studies since 2000 have uniformly verified the relationship between the developmental stage of biocrusts and resistance to erosion. Belnap et al. (2009) showed that under natural field conditions in average rainfall years, a site covered with thin cyanobacterial biocrust and annual plants (due to grazing impacts) under average rainfall conditions produced 2.8 times the sediment of a site covered with lichen-moss biocrust and a sparse but perennial grass cover (Fig. 16.3). In drought years, this difference became 5600-fold between the sites. Regression analysis showed that biocrust cover was the most important predictor of site stability (Belnap et al. 2009). Using a wind tunnel in the field, Goossens (2004) reported that well-developed biocrusts better stabilized soils from wind erosion than cyanobacterial biocrusts. Again with a wind tunnel in the field, Belnap et al. (2014) found that the most stable biocrusts were those with lichens and mosses when compared with cyanobacterial biocrusts. Reynolds et al. (2001) showed that moss-lichen biocrusts collect and retain dust for multiple decades. Using a wind erosion model, Munson et al. (2011a, b) showed that well-developed moss-lichen biocrusts could prevent any soil loss from wind erosion even in the absence of all vascular plants.

Well-developed biocrusts similarly decrease or prevent water erosion. Using a rain simulator, Eldridge and Leys (2003) found soil erosion decreased by almost two orders of magnitude as biocrust cover increased from 0 to 100 % and Bowker et al. (2008) found that cyanobacterial biomass was a moderate to excellent predictor of soil stability ($R^2 = 0.21–0.75$), depending on soil type. Barger et al. (2006), using rainfall simulation, found that erosion was five times higher from soils covered by low-biomass (light) crusts than from soils covered by better developed (dark) biocrusts. At the small watershed scale (~1 ha), silt fences were used to collect natural sediment off the adjacent biocrusted and uncrusted surfaces (Jayne Belnap, unpublished). On clay and sandy soils, two and five times as much sediment, respectively, was collected from the uncrusted compared to biocrusted soils. Some work in temperate regions has been done as well. Knapen et al. (2007)

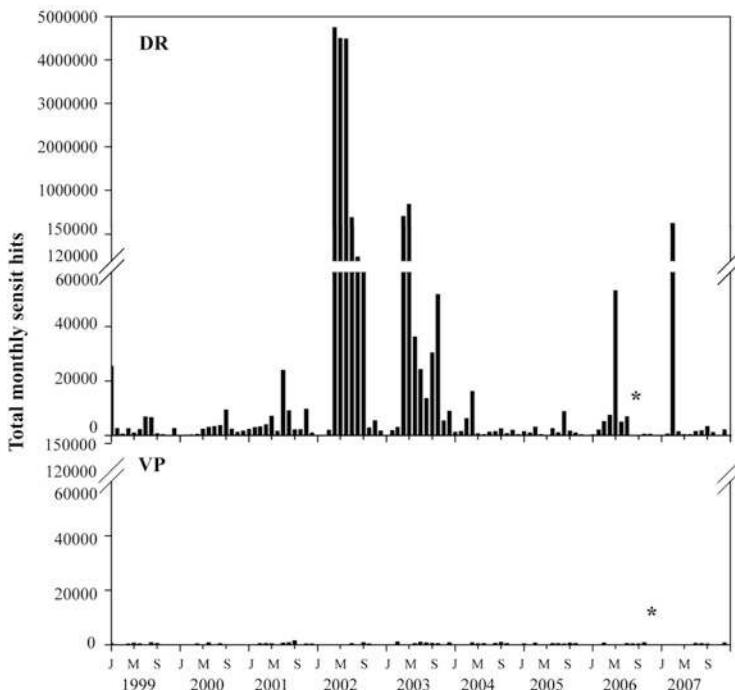


Fig. 16.3 Movement of soil particles detected by SENSITs (SENSIT probes protrude above the soil surface ~15 cm, counting the number of saltating particles upon impact, thus estimating the amount of sediment movement) in an area (DR) dominated by cyanobacterial biocrusts and a nearby one (VP) dominated by moss-lichen biocrusts. Sediment movement was always greater at the DR site compared to VP. However, this difference was greatly exacerbated during the exceptionally dry months of May–Sept 2002 and 2003. During this time, sediment movement was greatly increased at the DR site, whereas little change was noted where moss-lichen biocrusts covered the soils [Adapted from Belnap et al. (2009)]

investigated the effect of biocrusts on croplands in central Belgium and found that they decreased soil erosion. At the large watershed scale, Cantón et al. (2011) found that bare soil or physical crusts produce up to 20× more sediment as biocrusted soils on marl, mica schist, and limestone-derived soils. Gaskin and Gardner (2001) found that biocrusts reduced soil losses by up to 50 % compared with a maize crop devoid of groundcover.

Belnap et al. (2008) developed a level of development (LOD) that visually divided biocrusts into six classes of development, with 0 being bare soil and 6 being a well-developed lichen-moss biocrust. Using a rain simulator on biocrusts present in plant-free interspaces between *Coleogyne ramosissima* shrubs and storm sizes equivalent to >500 year events, mean sediment loss from early cyanobacterial crusts (LOD 1) was ~300 g m⁻², whereas there was almost no sediment produced from LOD 6 biocrusts (Fig. 16.4, upper panel; Belnap et al. 2012). Data from this study were used to parameterize the Rangeland Hydrology and Erosion Model

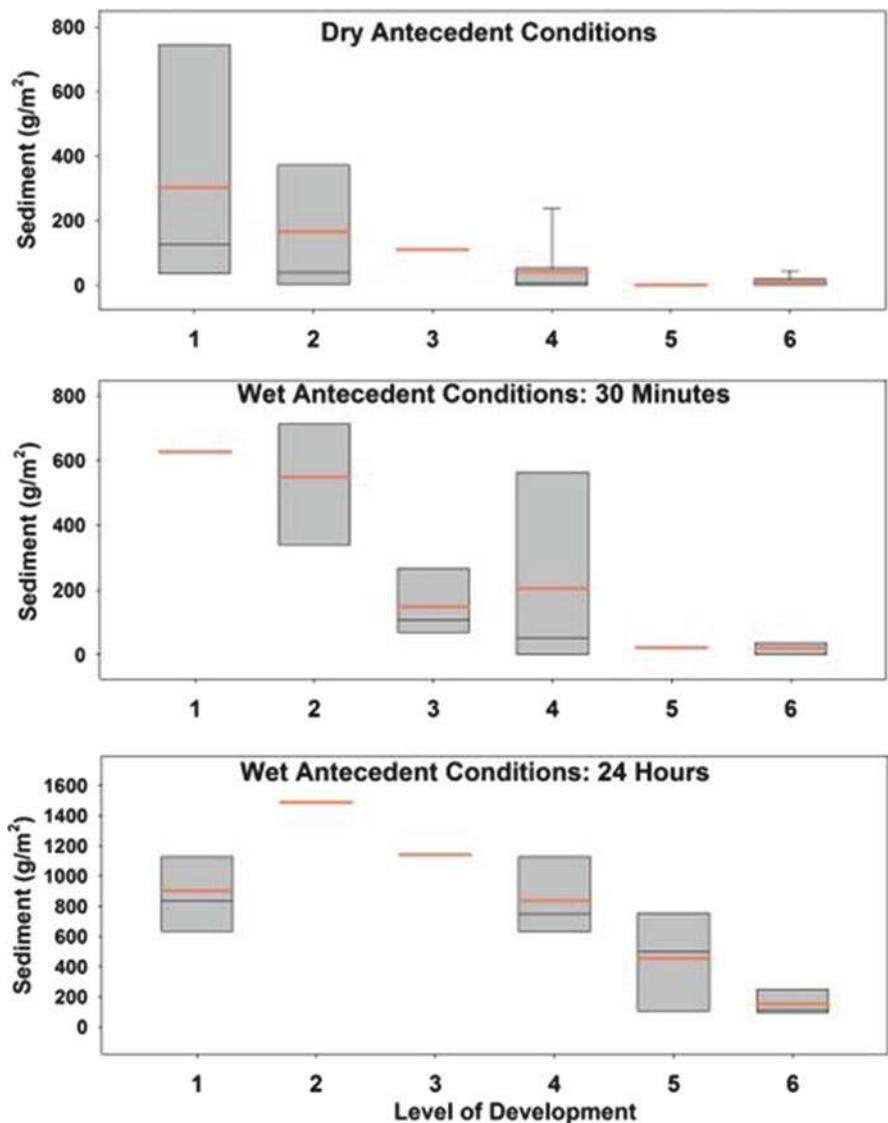


Fig. 16.4 Box plots of sediment production for each biocrust LOD class, with 0 being bare soil and 6 being a well-developed lichen-moss biocrust. The ends of the boxes define the 25th and 75th percentile, the error bars define the 10th and 90th percentiles, the black line is the median, and the orange line is the mean. Where error bars or boxes are lacking, there were only 2–3 replicates. Experimental plots were located in plant-free interspaces between *Coleogyne ramosissima* shrubs [Adapted from Belnap et al. (2012)]

(RHEM), and model runs showed that sediment production was much more sensitive to changes in slope length and gradient when biocrusts were in their least developed condition (LOD 1 and 2). Thresholds of slope length (10 m) and gradient (10 %) were observed, beyond which erosion increased sharply. With more

developed biocrusts (LOD 4–6), sediment production was relatively insensitive to changes in either slope length or gradient. In addition, model runs showed runoff, and thus sediment production, occurred with only 10 mm of rain in LOD 1 biocrusts under dry conditions, whereas events of ~40 mm were required for runoff and sediment production in LOD 2–6 biocrusts. As storms of this size are extremely rare in most deserts, these better developed biocrusts offer almost complete erosion resistance. Chaudhary et al. (2009) demonstrated that biocrust cover had over three times the explanatory power of any other variable measured ($r^2 = 0.60$).

16.2.4 Antecedent Moisture Affects Resistance to Soil Loss

Antecedent moisture also plays a substantial role in determining how much eroded sediment a given rain event will produce (Fig. 16.4, middle and lower panels; Belnap et al. 2012). When a rainfall simulator was used to apply events to dry soils, LOD 1–2 biocrusts produced some sediment, whereas LOD 4–6 biocrusts were stable. However, when soils were pre-wetted for 30 min, the mean sediment produced by LOD 1–4 biocrusts was up to twice that when the rain event was applied to dry soil. Biocrusts with LOD 5 and 6 remained stable. When rain events were applied to biocrusts that had been pre-wetted for 24 h, the increase in sediment production was dramatic: for biocrusts with LOD 1–5, sediment production increased by up to 11-fold, with biocrusts of LOD 6 remaining stable. Thus antecedent moisture not only resulted in more sediment being produced, but the longer the soils were moist, the more likely better developed biocrusts were to produce substantial amounts of sediment.

16.3 Disturbance to Biocrusts Reduces Resistance to Soil Loss

All studies show an increase in both wind and water erosion when biocrusts are disturbed, as disturbance essentially reduces biomass and developmental stage of the biocrusts. Early studies with wind tunnels showed a four- to fivefold increase in sediment production when a biocrusted surface is disturbed [reviewed in Belnap (2003)]. These findings have been corroborated with later studies. Eldridge and Leys (2003), using a wind tunnel, determined that at least 20 % cover is required to keep sediment transport below an erosion control target of $5 \text{ g}^{-1} \text{ s}^{-1}$ for a 65 km h^{-1} wind at 10 m height. Neff et al. (2008) showed that dust input to high-elevation lakes has increased 5–8 times during the period when large-scale agriculture, including livestock, appeared in the Western USA. Although we cannot know the degree to which biocrust disruption contributed to this spike in dust production, it is likely significant, as most undisturbed soils in this region are covered and stabilized by biocrusts. Wind

tunnel work by Belnap (in Field et al. 2010) shows that across a wide range of soil textures, disturbed biocrusts produce up to $400\times$ the sediment of undisturbed biocrusts. In China, no sediment was produced from sandy biocrusted soils at a wind velocity of 25 m s^{-1} (Zhang et al. 2008). However, sediment production rates were 46, 21, and 17 times higher on bare soils than biocrusted soils at wind speeds of 18, 22, and 25 m s^{-1} , respectively. In addition, TFV for an undisturbed surface was 19 m s^{-1} higher than a disturbed biocrust.

16.4 Nutrient Loss with Erosion

Nutrients are also lost with sediment movement. In southern New Mexico, USA, wind erosion after disturbance of the soil surface removed up to 25 % of total organic carbon and nitrogen from the top 5 cm of soil in four windy seasons (Li et al. 2007). Because carbon and nitrogen are the first to mobilize and other cations (e.g., potassium, sodium) are less likely to move, the spatial heterogeneity of nutrients is altered, which can then affect plants and biogeochemical cycling in the soil (Li et al. 2008). Another study in southern Utah, USA, showed that wind erosion had depleted silt by 38–43 %, soil carbon and nitrogen by 60–70 %, and other essential nutrients (magnesium, sodium, phosphorus) by 14–51 % (Neff et al. 2005).

Using a rain simulator, Barger et al. (2006) showed that there was up to a fivefold higher loss of sediment-bound carbon and nitrogen (N) from plots covered by low-biomass biocrusts compared to plots covered by high-biomass biocrusts. Total N loss from dark crusts (dissolved plus sediment-bound) was an order of magnitude lower than light crusts (dark = 0.06 g N m^{-2} , light = 0.63 g m^{-2}). Jayne Belnap (unpublished) found that soils collected by silt fences from uncrusted sandy sites contained more phosphorus (11 vs. 4 ppm), potassium (K; 79 vs. 48 ppm), N (344 vs. 104), and silt (19 vs. 9 %) compared to the biocrusted soils. At the clay sites, uncrusted soils lost significantly more K (286 vs. 163 ppm) and silt (33 vs. 21 %) than the biocrusted sites. Kidron (2001) showed that eroded soils may be enriched in organic matter as well, with 0.3–0.4 % being measured in collected sediment versus $\leq 0.1\%$ found at the source.

16.5 Soil Movement at the Local to Global Scale

Soil movement has implications for nutrient and water cycles at the local, regional, and global scales. Where biocrusts are disturbed, or in regions where hot, dry conditions keep them at a low developmental stage (e.g., hyperarid deserts); they offer little protection from soil erosion. At the local scale, this has several implications. First, far-traveled fine dust falls more or less equally across the landscape. If biocrusts are lacking, this dust is redistributed by water downslope or by wind to

nearby obstructions, resulting in a heterogeneous distribution of nutrients and soil particle sizes (Shachak and Lovett 1998; Reynolds et al. 2001). In addition, movement by wind and water can also deposit the soil in nearby stream channels, where stream waters export the sediment from the system (Belnap et al. 2011). Particles suspended by the wind can also be exported from the system. This results in soil fertility being reduced locally, as discussed in Sect. 16.4, and sediment entering the water reduces its quality locally and regionally. Dust particles are deposited on the snowpack of nearby mountains, decreasing albedo and hastening snow melt. This exposes soils and allows plants to germinate earlier in the spring, increasing both evaporative and transpiration losses to the atmosphere. This can result in substantially less overall water entering small to large rivers and aquifers and thus lowering water quality as well (Painter et al. 2010).

16.6 Future Research

Despite the uniformity in studies finding that biocrusts reduce soil movement by wind or water, we still have limited understanding in the specifics of how biocrusts stabilize soils. Only a handful of studies have evaluated the relative ability of individual species and many others remain to be evaluated. We also need to test suites of species. Once this is done, we need a better understanding of why some individual or combinations of species are better than others. For example, we assume that the amount of exo-polysaccharides a species exudes is important, but we have little information on the circumstances under which this is true, how much is enough, or under what circumstances exo-polysaccharides are produced. This understanding will become increasingly important as biocrust inoculants are increasingly used to stabilize disturbed lands and the composition of the inoculant needs to be decided. This information could also inform whether artificial products (e.g., polyacrylamide gels to substitute for exo-polysaccharides) might augment stabilization efforts.

As later stages of biocrust development better stabilize soils than earlier stages, we also need a better understanding of growth rates for different biocrust species, both under current and future climate conditions. These are only a few examples of further studies that can help elucidate how biocrusts stabilize soils.

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Chapter 17

The Role of Biocrusts in Arid Land Hydrology

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and Oumarou Malam Issa

17.1 Introduction

The role of biocrusts in many key dryland processes has been well recognized in a number of studies. Their influence on hydrological processes has been one of the most widely studied, but also the most controversial aspects, with findings varying markedly among different regions. Studies in the early 1990s focused mainly on the deserts of North America, Australia, and Israel. Over the past decade, however, a considerable number of studies have emanated from Europe, Africa, and, particularly, China.

We used published and unpublished data to develop a conceptual model of how biocrusts affect hydrologic processes across different scales (Fig. 17.1). Our model indicates that different climatic regimes at regional to global scales create a wide range of biocrust types of different morphology, biomass, and species composition, all of which influence hydrological cycles. Across a gradient from hyperarid to temperate cool and to high-altitude/high-latitude cold climates, which also corresponds to a gradient from low to high rainfall and high to low potential

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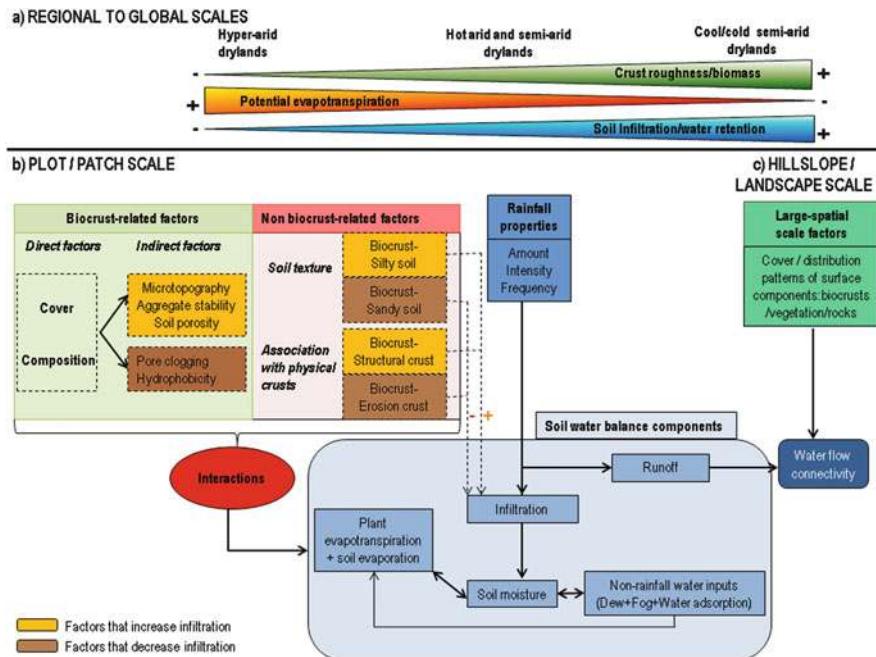


Fig. 17.1 Conceptual model illustrating the factors, which regulate biocrust influence on hydrological processes across scales. At a regional to global scale, biocrust biomass increases and morphology changes from smooth, rugose, and pinnacled to rolling and from hyperarid to temperate cool and to high-altitude/high-latitude cold climates (and thus from low to high rainfall and high to low potential evapotranspiration). The increase in soil surface roughness and biocrust biomass across this gradient increases water infiltration and retention (a). At a given site, direct biocrust factors such as cover and composition, and indirect factors related to the modification of soil properties by biocrusts, such as roughness, porosity, aggregate stability, and hydrophobicity, influence soil water retention at the plot/patch scale (b). Non-biocrust factors such as soil texture and association with physical crusts and other factors as the type of rainfall and antecedent soil moisture can modify the influence of biocrusts on hydrological processes (b). At larger hillslope and catchment/landscape scales, land use, cover, and spatial distribution of surface components (biocrusts, plants, rocks) control runoff generation and water flow connectivity (c)

evapotranspiration, crust biomass increases and biocrust morphology changes from smooth via rugose and pinnacled to rolling (Belnap 2006, see Chap. 9 by Colesie et al.). As a general trend, this increase in soil surface roughness and biocrust biomass causes an increase in water infiltration and retention (Fig. 17.1a, Belnap 2006).

Our model illustrates how biocrust properties, soil type and cover, and distribution patterns of biocrusts and vegetation, as well as land use and climate (temperature and precipitation), interact to influence the effects of biocrusts on soil hydrological cycles at both the plot/patch and hillslope/landscape scale (Fig. 17.1b, c). These different scales are interconnected through multiple feedback

loops. Consequently, biocrusts have a profound influence on hydrology and therefore ecosystem structure and functions.

Despite the recent advances in our understanding of how biocrusts influence hydrological processes, we are yet to develop definitive predictions of how climate, soil type, disturbance, scale, type of measurement, and biocrust characteristics interact to influence these processes. In this chapter, we explore how these factors are involved in assessing the role of biocrusts in soil hydrological processes. We focus here on studies published after 2003. Earlier reviews can be found in Eldridge (2003), Warren (2003a, b), and Yair (2003).

17.2 Infiltration and Runoff

17.2.1 *Biocrust-Related Factors Influencing Infiltration and Runoff*

Biocrusts can affect infiltration directly by their cover and composition and indirectly through modification of soil properties that affect infiltration (Fig. 17.1a, b), including (i) roughening of the surface, increasing water retention time, and slowing down water velocity (Rodríguez-Caballero et al. 2012); (ii) exopolysaccharide (EPS) production, as EPS absorbs large amounts of water (Chamizo et al. 2012a) and increase hydraulic conductivity (Rossi et al. 2012), and their swelling upon wetting modifies microtopography, increasing surface roughness (Rodríguez-Caballero et al. 2015); (iii) increasing soil aggregation, creating macro-pores that enhance infiltration (Feldé et al. 2014; Malam Issa et al. 2009; Miralles-Mellado et al. 2011); and (iv) absorptivity of biocrust organisms (Mazor et al. 1996). On the other hand, biocrusts can decrease infiltration by (i) trapping fine particles that clog soil pores (Verrecchia et al. 1995), (ii) swelling and clogging pores when produced EPS absorbs water (Colica et al. 2014; Fischer et al. 2010), and (iii) hydrophobicity of some biocrust species (Souza-Egipsy et al. 2002; Tighe et al. 2012).

17.2.1.1 **Biocrust Roughness Effects on Infiltration and Runoff**

Infiltration and runoff are heavily influenced by soil surface roughness (Fig. 17.1a, b). In hot hyperarid and arid deserts, most biocrusts are cyanobacteria dominated. As there is no frost heaving causing a roughening of the surface, the presence of only cyanobacteria smoothes the surface. Some studies, mostly in Israel, have shown that landscapes dominated by these smooth biocrusts are characterized by low infiltration and high runoff (Yair 2003). However, even a millimeter-scale increase in microtopography in these biocrusts or an increase in the moss/lichen component can increase surface permeability and reduce runoff in these regions

(Kidron 2007). For example, in sand dunes of the Negev Desert, Israel, thin, smooth cyanobacterial biocrusts found in the more arid southern sites (90 mm average annual rainfall) absorbed very little rain, thus generating extensive runoff, whereas slightly rougher and more absorptive moss-dominated biocrusts at the wetter northern sites (165 mm annual rainfall) decreased runoff (Almog and Yair 2007; Yair et al. 2011).

In hot semiarid regions, undisturbed biocrusts are generally rugose, being roughened by the presence of scattered lichens and mosses (e.g., southern Arizona and California, USA), or are rolling when the moss and lichen cover is high (e.g., southern Spain). During low-intensity rainfall, surface micro-depressions of biocrusts temporarily pool water and slow overland flow, thus increasing infiltration and reducing runoff flow connectivity compared to bare soils (Chamizo et al. 2012b; Rodríguez-Caballero et al. 2012, 2013). However, under intense or large rain events, these micro-depressions fill quickly and runoff generation is similar in both biocrusts and bare soils.

In cool semiarid regions, undisturbed biocrusts are pinnacled (e.g., Gurbantunggut Desert, China; Colorado Plateau, USA) or rolling (e.g., southern Idaho, USA; Belnap et al. 2003). Both biocrust types increase the roughness and absorptivity of the soil surface and have high biocrust biomass (Belnap 2006). All experiments with these biocrust types show they reduce runoff (Belnap 2006; Belnap et al. 2013).

17.2.1.2 Biocrust Successional Stage and Species Composition Effects on Infiltration and Runoff

In both cool and hot semiarid regions, multiple rainfall simulation experiments show infiltration generally increased with greater biocrust development, which is accompanied by increased biomass (Barger et al. 2006; Belnap et al. 2013; Chamizo et al. 2012c; Li et al. 2002; Xiao et al. 2011). As shown in Fig. 17.2, infiltration and runoff differences between a biocrust of a low and high development level can be dramatic (Belnap et al. 2013). However, some studies have shown the opposite: infiltration decreased with greater biocrust cover and biomass (Li et al. 2010; Wu et al. 2012; Zhao and Xu 2013), attributed to finer soil texture and greater water holding capacity and pore clogging in the well-developed biocrusts.

Studies addressing the effects of biocrusts on infiltration and runoff in temperate environments are scarce, probably because the high coverage of vascular plants exerts a strong control on soil hydrology and the relative cover of biocrusts is low. Nevertheless, several authors have found that biocrusts have considerable influence on local hydrology. Drahorad et al. (2013), Fischer et al. (2012a, 2013), and Lichner et al. (2010, 2012) all showed that water repellency increased and sorptivity and conductivity decreased with biocrust development.

The species composition of biocrusts can also influence infiltration (Fig. 17.1b). The sheaths surrounding cyanobacteria and the gelatinous fungal material

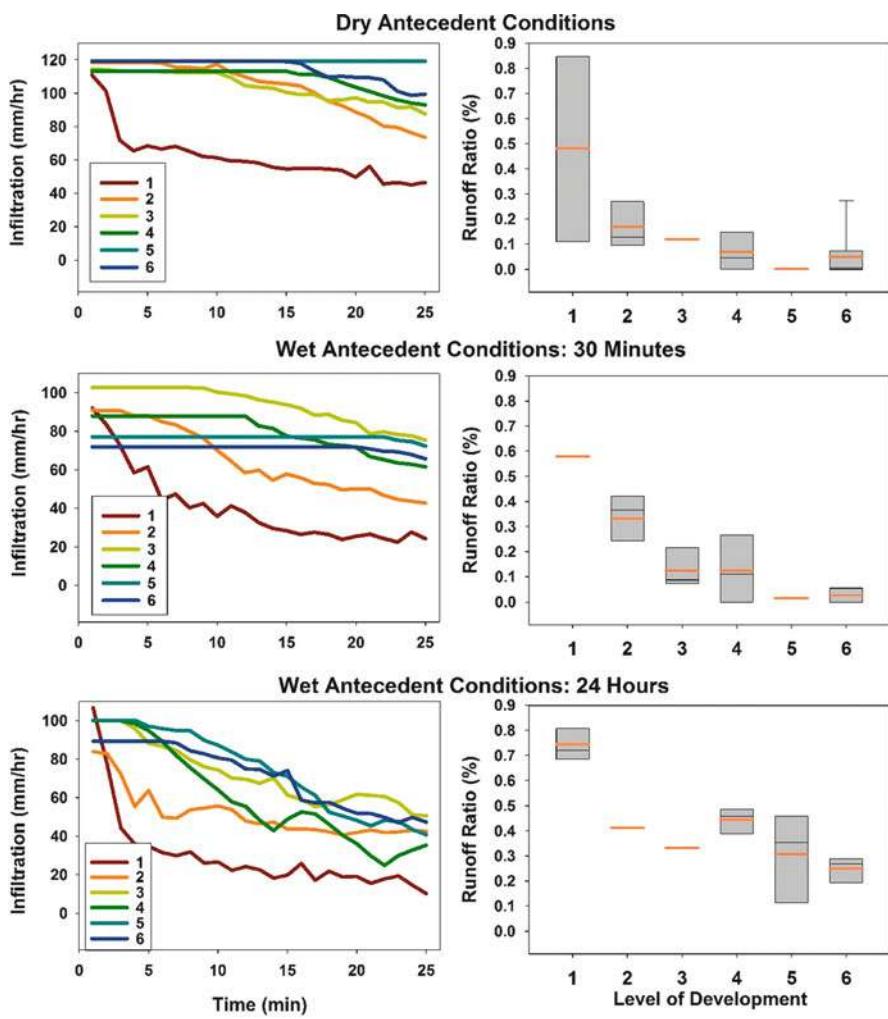


Fig. 17.2 Infiltration rate and runoff ratio of biocrusts depending on crust developmental stage and antecedent soil moisture, under a rainfall simulation experiment (rain intensity between 110 and 125 mm h⁻¹) conducted on the Colorado Plateau (SE Utah, USA). Level of development (LOD) was determined according to the crust parameters' color (light to dark), presence of mosses/lichens, and roughness. The ends of the box plots represent the 25th and 75th percentiles, the black line is the median, error bars define the 10th and 90th percentiles, and the orange line is the mean [For more information, see Belnap et al. (2013)]

surrounding cyanolichens such as *Collema* and *Endocarpon* spp. can absorb considerable quantities of water; however, once saturated, they shed water. A study of man-made algal biocrusts showed that compared to bare sand, *Klebsormidium subtile* biocrusts decreased hydraulic conductivity, whereas *Choriciystis minor* and *Tribonema minus* had no effect, suggesting that *Klebsormidium subtile* more

effectively clogs soil pores, likely reducing infiltration (Lichner et al. 2013). Mosses can absorb large amounts of water, as well as hold water between their leaves (Chamizo et al. 2012c; Eldridge et al. 2010; Xiao et al. 2011). In contrast, many crustose, foliose, and squamulose lichens (e.g., *Psora* spp., *Diploschistes* spp., *Squamaria* spp.) have hydrophobic surfaces (Souza-Egipsy et al. 2002; Tighe et al. 2012) and thus can decrease infiltration where their cover is substantial (Chamizo et al. 2012c; Eldridge et al. 2010). These species cap the soil surface, and as they often form large contiguous patches, their presence increases runoff over small to medium spatial scales. In the semiarid woodlands in eastern Australia, many inter-canopy patches are dominated by such species, making them zones where infiltration is low and runoff is generated. In the Tabernas Desert, SE Spain, crustose and squamulose lichen-dominated biocrusts cover large areas of the landscape. Under intense rainfall events, these biocrusts show runoff similar to physical crusts (Chamizo et al. 2012c).

17.2.1.3 Effects of Exopolysaccharides on Infiltration and Runoff

EPS compounds may represent up to 75 % of the carbohydrates synthesized by cyanobacteria-dominated biocrusts (Mager 2010). Several laboratory studies have analyzed the influence of EPS on soil hydraulic conductivity and have generally found that EPS decrease hydraulic conductivity by creating hydrophobic soil layers (Lichner et al. 2013) and blocking soil pores when wet, especially in well-developed biocrusts on sandy soils (Colica et al. 2014; Fischer et al. 2010, 2013; Mager and Thomas 2011; Malam Issa et al. 2009). These compounds also facilitate dust entrapment, which can also decrease soil porosity (Belnap 2006). Consequently, higher EPS contents are sometimes correlated with increased runoff. In contrast, Rossi et al. (2012) suggested that EPS could enhance hydraulic conductivity as they created pores in the soil, increasing the pathways for infiltration. Unfortunately, only a few field tests on how EPS affect runoff have been done. Kidron and Büdel (2014) compared runoff from two sand dunes, one covered by cyanobacterial biocrusts and one by green algal biocrusts. Cyanobacteria produced higher levels of EPS than green algae, and accordingly, the cyanobacterially covered dune produced most runoff. However, in the northern Chihuahuan Desert, New Mexico, the relationship between runoff and EPS content analyzed on silty alluvial deposits, gypsum sand, and quartz sands was very low ($R^2 = 0.03–0.05$). In the sandy soils, biomass (as indicated by chlorophyll *a*) was the most important factor, although the R^2 was still low (0.18–0.29, $p = 0.02$; Kidron et al. 2012).

17.2.2 Other Biocrust-Mediated Soil Factor Effects on Infiltration and Runoff

Soil properties such as soil texture and physical crusts strongly affect the permeability of the surface and can be affected by the presence of biocrusts (Fig. 17.1b, Warren 2003a). On fine-textured soils, biocrusts are thought to increase infiltration by maintaining the integrity of surface bio-pores and contributing to the structural stability of near-surface layers by maintaining macroaggregate structure (Bowker et al. 2011). A likely exception to this is soils containing high amounts of shrink-swell clays, as these soil particles swell and restrict infiltration despite a biocrust cover. Very sandy soils are generally characterized by rapid infiltration, but pore clogging by biocrusts is thought to increase runoff unless the soil surface is sufficiently roughened to prevent runoff (see Sect. 17.2.1.1).

Biocrust development atop physically crusted soils is a common feature in many arid and semiarid environments (Eldridge et al. 2000; Eldridge and Greene 1994; Greene et al. 1998; Malam Issa et al. 1999, 2011), which can modify the role of biocrusts in infiltration. Runoff coefficients, where biocrusts have developed on erosion crusts covered with fine particles, are higher than those obtained for biocrusts on structural crusts covered with coarse sand grains, suggesting that the pore-clogging effect by biocrusts is higher on the finer soil materials (Fig. 17.1b, Malam Issa et al. 2011).

17.2.3 Antecedent Soil Moisture and Precipitation Characteristics Affecting Infiltration and Runoff

The temporal variability of hydrological processes related to antecedent soil moisture and rainfall characteristics (timing, intensity, amount) strongly affects the role of biocrusts in infiltration and runoff (Fig. 17.1b). Antecedent moisture is critical in determining the effect of biocrusts on these processes, especially if soils have been wet for an extended period of time. On dry clay soils, the presence of numerous cracks can increase water infiltration. However, when wetted, these cracks seal and, together with EPS swelling, result in increased runoff (Verrecchia et al. 1995). A study on sandy soils showed that runoff more than doubled on soils wetted 24 h prior to water application compared to water applied to dry soils (Fig. 17.2, Belnap et al. 2013). This response was especially pronounced in the well-developed biocrusts. Similarly, in a rainfall simulation experiment in the Tabernas Desert, SE Spain, runoff from a biocrusted soil under wet antecedent soil moisture was also double that of dry biocrusts (Chamizo et al. 2012c). As it is typical for deserts that multiple rain events occur within a short time period, it is critical to include antecedent soil moisture in runoff models.

The interaction of biocrusts and rainfall characteristics (e.g., intensity, event size) also affects infiltration. During low-intensity rainfall events, well-developed

biocrusts decreased runoff compared to bare soils (Chamizo et al. 2012b; Rodríguez-Caballero et al. 2013). However, under high-intensity and prolonged rainfall, which saturated soils and biocrusts, well-developed biocrusts showed the same or higher runoff than bare soils (Chamizo et al. 2012b, c). Yu et al. (2010) modeled the influence of biocrusts on water flow in two revegetated sites in the Tengger Desert. They found that no runoff was generated when rainfall intensity was low, but during higher-intensity events, the lower hydraulic conductivity in biocrusted soils compared to bare soils resulted in greater runoff. In semiarid regions with highly pinnacled biocrusts, runoff is generally nonexistent under natural conditions except during extreme events (Belnap et al. 2013).

Event size can influence the relationship between biocrusts and infiltration. Runoff was reduced or nonexistent with small rain events that failed to saturate the biocrusts in the Negev (Kidron and Yair 1997). In the Tengger Desert, small events (~10 mm) infiltrated further into bare soils than biocrusted soils, whereas the opposite occurred with larger events (~60 mm) (Wang et al. 2007). Similarly, Li et al. (2010) reported that infiltration depth decreased with biocrust development (from algae to lichen to moss biocrusts) with low rainfall amounts (<20 mm), but there was no difference among them with higher rainfall amounts (>20 mm). Wu et al. (2012) found that light algae, dark algae, and moss biocrusts generated similar runoff when rainfall amount was low (12 mm), but with higher rainfall (22 mm), runoff was greater in the more developed biocrusts (dark algae and moss). One explanation of these patterns is that biocrusts are able to absorb small rainfall events, thus decreasing runoff, but at the same time holding the water at the surface and limiting water infiltration depth. Under high rainfall amounts, the absorptivity of the biocrusts is overcome, thus runoff is not affected or increased.

17.2.4 Influence of Biocrust Disturbance on Infiltration and Runoff

The degree of disturbance or time since disturbance affects how biocrusts influence hydrological processes, and this will vary with biocrust and disturbance type. For example, in the Negev Desert, mowing by cutting and spreading vegetation and vehicle tracks increased hydraulic conductivity and reduced runoff, whereas biocrust removal and killing with an herbicide led to reduced hydraulic conductivity and increased runoff (Zaady et al. 2013). In some soils, removal of the biocrust can initially increase infiltration (Eldridge et al. 2000), but the later development of a physical soil crust by exposure to raindrop impact can result in higher runoff compared to biocrusted soils (Chamizo et al. 2012c). Human and animal trampling also affects infiltration. In semiarid regions with pinnacled and rolling biocrusts, trampling can reduce infiltration by reducing the biocrust biomass, converting lichen-moss biocrusts into ones dominated by cyanobacteria and compacting the soil, thus facilitating the development of physical soil crusts (Belnap and Eldridge

2003; Herrick et al. 2010; Chamizo et al. 2012c). In contrast, at sites covered with heavy physical crusting, smooth cyanobacterial crusts, or hydrophobic lichens, disturbance such as grazing can increase infiltration by breaking up these hydrophobic surfaces (Belnap and Eldridge 2003; Bowker et al. 2011; Chamizo et al. 2012c; Bowker et al. 2013). In desert settings with a high cover of biocrusts that promote high connectivity of runoff-generating areas, surface disturbance by soil-foraging animals results in small infiltration zones (Eldridge et al. 2011). In Australian rugose biocrusts, increased grazing on clay loam soils resulted in reduced biocrust cover, increasing infiltration (Eldridge unpublished data). However, in a second study on fine-textured soils with a relatively long history of moderate grazing, biocrusts had no significant effect on infiltration. On coarse-textured soils subjected to grazing during the past 30 years, increasing biocrust cover was associated with substantial increases in infiltration. A likely explanation for the grazing effect at sites dominated by sandy soils is that grazing induces successional shifts in biocrust communities (Bowker et al. 2011), reducing the size of hydrophobic patches of lichen biocrusts (Bowker et al. 2013) and increasing the alternation of sparse and discontinuous patches of cyanobacteria and cyanolichens. A paired watershed-scale (four pairs ranging from 6 to 51 ha) study that ran for 20 years in the semiarid lands of western Colorado, USA, showed that grazing reduced biocrust cover, soil surface roughness, and soil stability. Accordingly, runoff from the ungrazed watersheds was 30 % less than from the grazed watersheds during the 13 years after the treatments began, and during the next 6 years, runoff from grazed watersheds was 40–45 % higher (Lusby 1970). This study is still ongoing and increased runoff from the grazed areas continues to be observed (Duniway and Belnap unpublished data).

In hyperarid and arid environments, smooth to slightly rugose biocrusts can create highly conductive zones that facilitate runoff to downslope heterogeneously distributed and retentive plant patches (Ludwig et al. 2005; Cantón et al. 2011). Increased infiltration following biocrust disturbance reduces water harvesting to downslope shrub patches, leading to a loss of ecosystem function and a decrease in plant productivity (Eldridge et al. 2000, 2002; Li et al. 2008). In contrast, in regions with pinnacled and rolling biocrusts, both vegetation and biocrust patches retain resources, including water, and only extreme rainfall events produce runoff from either patch type. In these landscapes, most landscape components and functions are homogenously distributed, including infiltration, vegetation, and biocrust patches.

17.2.5 The Critical Importance of Scale in Infiltration/Runoff Studies

Landscape functions, including hydrological processes, are strongly controlled by the type, size, and distribution pattern of surface components of different sizes (e.g.,

plants, rocks, biocrusts; Fig. 17.1c; Arnau-Rosalén et al. 2008; Cantón et al. 2011). Plants generally create retentive patches that capture water and other resources such as sediment and organic matter (Wilcox et al. 2003; Ludwig et al. 2005). Biocrusts, depending on landscape position, biocrust type, and scale, can create highly retentive to conductive patches. Scale dependency is determined by the degree of connectivity among patch types (in this case, mostly plants and biocrusts), the nature of the biocrust patch (here, retentive to conductive), and the number and size of roughness elements introduced as plot size increases (e.g., large rocks, plants, washes; Belnap et al. 2005; Ludwig et al. 2005). In general, infiltration increases with spatial scale, as more surface roughness elements are included (Wilcox et al. 2003). Only during large or high-intensity rainfall events is the infiltration capacity of the vegetation exceeded and water lost from the system. In the Tabernas Desert, measurements from a 1.8 ha microcatchment over 20 years showed that runoff from biocrust patches during smaller rain events (<20 mm) was captured by downslope vegetation, whereas during events >20 mm, runoff coming from biocrust patches surpassed vegetation capacity and reached the catchment outlet (Rodríguez-Caballero et al. 2014a).

To examine the effects of scale (understood as an increase in plot size), we compiled results from 48 cases reported in 27 studies that measured biocrust runoff or runoff indicators (e.g., hydraulic conductivity, sorptivity). These studies were done with various plot sizes, ranging from point measurements at the cm scale (e.g., tension infiltrometers, infiltration depth, raindrop tests) to plots of varying sizes ($<2\text{ m}^2$, $>2\text{ m}^2$) and to the catchment scale. In these studies also varying biocrust types (smooth, rugose, rolling, and pinnacled) with different species dominance (cyanobacteria, lichen, and moss) were investigated (Table 17.1). The 14 cases (from nine studies) conducted at the point scale showed that biocrusts increased runoff indicators in 53 % of the cases, whereas these were decreased or not affected in 33 % and 13 % of the cases, respectively (Fig. 17.3). At this scale, smooth and rolling biocrusts most often increased runoff indicators (60 % and 67 %, respectively), whereas rugose and pinnacled biocrusts most often decreased it (67 % and 100 %, respectively). Biocrusts on sandy soils increased runoff more often than not (70 %), whereas the opposite was true for silt and gypsum soils. At the $<2\text{ m}^2$ plot size, results were similar to the point scale when all 17 cases (from ten studies) were combined: 50 % showed biocrusts increased runoff, whereas in 50 % they either did not affect or decreased it. The few studies on rugose and pinnacled biocrusts showed mostly decreased runoff. Half of the studies on sandy soils showed that biocrusts increased runoff. Moss and rolling biocrusts still mostly increased runoff. However, unlike the point scale, most lichen and cyanobacteria biocrusts reduced runoff (Fig. 17.3) and smooth biocrusts equally increased or decreased runoff.

Interestingly, when experiments were done at larger plot sizes ($>2\text{ m}^2$) and at catchment scales, results were quite different (Fig. 17.3). Runoff was more often reduced than not when all 17 cases (from nine studies) were combined (71 %) and when categories were created based on biocrust developmental stage (runoff reduction: 50–100 %), morphological types (50–100 %), or soil type (64–100 %). Thus, at the larger scale all categories showed that biocrusts decreased runoff more

Table 17.1 Effect of biocrusts on infiltration and runoff according to different studies

Site	Ground cover/ biocrust type	Biocrust morphology	Soil texture	Method	Effect on runoff/ runoff indicators	References
Shapotou, Tengger Desert, China	Shrub-lichen, shrub-no biocrust, bare soil	Ro	Sandy	Infiltration depth (field)	– (rain ~10 mm) + (rain ~60 mm)	Wang et al. (2007)
Aranjuez, Spain	Lichen, moss	Ru	Gypsum	Infiltrometer (field)	– (moss) + (lichen)	Eldridge et al. (2010)
Shapotou, Tengger Desert, China	Algae, lichen, moss	Ro	Sandy	Infiltration depth (field)	+ (rains < 20 mm) no effect (rains > 20 mm)	Li et al. (2010)
Negev Desert, Israel, Lieberose, Germany	Algae, moss	Sm	Sandy loam Sandy	Infiltrometer (lab)	+	Fischer et al. (2012a, 2013)
Mojave, Colorado Plateau, Sonoran Desert and Chihuahuan Desert, USA	Cyanobacteria	Sm	Varying soil texture	Infiltrometer (lab)	± (influence of soil texture)	Rossi et al. (2012)
Southwest Slovakia	Cyanobacteria, lichen-moss	Ro	Sandy	Infiltrometer (field)	–	Drahorad et al. (2013)
Southwest Slovakia	Algae, bare sand	Sm	Sandy	Infiltrometer (field)	+	Lichner et al. (2013)
Hobq Desert, Inner Mongolia, China	Inoculated cyanobacteria	Sm	Sandy	Infiltrometer (lab)	+	Colica et al. (2014)
Shapotou, Tengger Desert, China	Algae, moss	Ro/Ru		Rainfall simulation (field plots 1 m ²)	+	Li et al. (2008)
S Sahel, Niger	Cyanobacteria	Sm/Ru	Sandy	Rainfall simulation (field plots 1 m ²)	–(biocrust-struc- tural crust) +(biocrust- erosion crusts)	Malam Issa et al. (2011)

(continued)

Table 17.1 (continued)

Site	Ground cover/ biocrust type	Biocrust morphology	Soil texture	Method	Effect on runoff/ runoff indicators	References
Loess Plateau, China	Inoculated moss	Ro/Ru	Loess soil (39 % sand, 29 % silt, 32 % clay)	Rainfall simulation (field plots 0.4 m ²)	—	Xiao et al. (2011)
Colorado Plateau, SE Utah, USA	Dark cyanobacteria, lichen	Pi	Sandy loam	Rainfall simulation (field plots 0.5 m ²)	— (> biocrust development)	Belnap et al. (2013)
Tabernas Desert, SE Spain	Physical crust, cyanobacteria, lichen, moss	Ru/Ro	Silty loam Sandy loam	Rainfall simulation (field plots 0.25 m ²)	— (cyanobacteria, moss) + (lichens)	Chamizo et al. (2012c)
Hilly Loess Plateau, N Shaanxi, China	Low to high development	Ru/Ro	Silty	Scouring experiments (field plots 0.4 m ²)	+	Zhao and Xu (2013)
Negev Desert, Israel	Algae, cyanobacteria	Sm	Sandy	Rainfall simulation (field plots 2.8–4.1 m ²)	— (algae) + (cyanobacteria)	Kidron and Bridel (2014)
Israeli–Egyptian border, Israel	Cyanobacteria, moss	Sm/Ru	Sandy loam Sandy	Field runoff plots (8 m ²)	— (moss) + (cyanobacteria)	Almog and Yair (2007) and Yair et al. (2011)
Negev Desert, Israel	Cyanobacteria, moss, scalped soil	Sm	Sandy	Field runoff plots (3.6–6.3 m ²)	—	Kidron (2007)
S Sahel, Niger	Cyanobacteria	Sm	Sandy	Field runoff plots (9 m ²)	+	Malam Issa et al. (2009)
Tabernas Desert, SE Spain	Cyanobacteria, lichen	Ru/Ro	Silty loam	Field runoff plots (1–10 m ²)	— (low-intensity rain) + (high-intensity rain)	Chamizo et al. (2012b)

Chihuahuan Desert, New Mexico, USA	Algae, cyanobacteria, lichen	Ru	Gypsum sands Sandy Silty alluvial deposits	Field runoff plots (1.9–6.4 m ²) + (sandy) – (silty)	No runoff (gypsum sands) + (sandy) – (silty)	Kidron et al. (2012)
Tabernas Desert, SE Spain	Cyanobacteria, lichen	Ru/Ro	Silty loam	Field runoff plots (1–10 m ²)	– (low-intensity rain) + (high-intensity rain)	Rodríguez-Caballero et al. (2012, 2013)
Jingbian Desert, Shaanxi, China	Light algae, dark algae, moss	Ro	Sandy	Field runoff plots (0.13 m ²) 12 mm + (rain ~22 mm)	no difference (rain 12 mm) + (rain ~22 mm)	Wu et al. (2012)
Tabernas Desert, SE Spain	Lichen	Ro	Silty loam	H-type flumes (microcatchment 1.8 ha)	– (rain < 20 mm) + (rain > 20 mm)	Rodríguez-Caballero et al. (2014a, b)
SE Utah, USA	Moss	Pi	Sandy	H-type flumes (two pairs of 20 ha catchments: grazed/ ungrazed)	– (ungrazed)	Lusby (1970) and Dunaway and Belnap (unpublished data)

Biocrust morphology: Sm smooth, Ru rugose, Ro rolling, Pi pinnacled. Runoff indicators refer to hydrological variables that do not imply a direct measurement of runoff yield but provide information of the effect on runoff, e.g., hydraulic conductivity, infiltration depth, infiltration rate, etc. The symbol + indicates a positive effect of biocrusts on runoff, while the symbol – indicates a negative effect

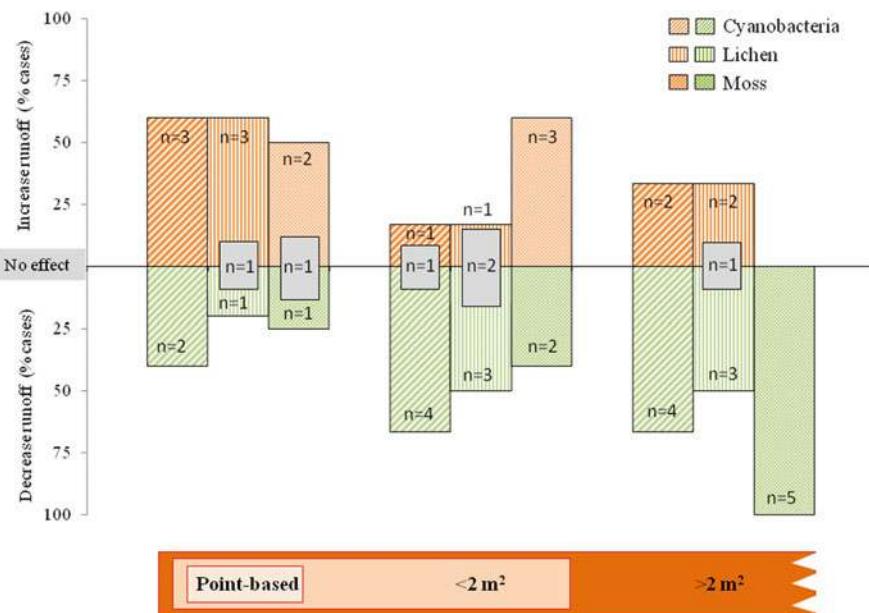


Fig. 17.3 Percentage of cases compiled from 27 reported studies showing positive (orange-colored bars), negative (green-colored bars), or no effect (gray-colored bars) of different dominant biocrust types on runoff at different plot sizes (point based, $<2 \text{ m}^2$ and $>2 \text{ m}^2$). The N-value indicates the number of cases of each crust type that increases, decreases, or has no effect on runoff at each plot size. For the “no effect” cases, the percentage is obtained as the sum of the values of the gray bars above and below the X-axis

often than increasing it, regardless of developmental stage, morphological type, or soil.

Sixteen cases examined runoff or indicators of runoff using small ($<20 \text{ mm}$) and larger ($>20 \text{ mm}$) wetting events at the three scales (point, $<2 \text{ m}^2$ and $>2 \text{ m}^2$). At the point scale, runoff indicators increased with small events and were not affected by larger events. At both of the two larger scales, events $<20 \text{ mm}$ showed that biocrusts decreased runoff regardless of biocrust developmental stage. For events $>20 \text{ mm}$, runoff was either increased or not affected.

Comparison among these studies illustrates the critical aspect of considering scale when assessing how biocrusts influence infiltration-runoff. As has been pointed out, the hydrological response at hillslope and catchment scales will depend on the spatial distribution of biocrust and vegetation patches as well as interactions among these patches. Accurate information of the spatial distribution of these surface components is needed to reliably understand the role of biocrusts in runoff processes at larger scales. Recent methodologies to map biocrusts based on remote sensing data (Weber et al. 2008; Rodríguez-Caballero et al. 2014b; Rozenstein and Karnieli 2014; see Chap. 12 by Weber and Hill) are presented as promising tools to advance to this goal. Thus, reliable cartography of biocrust and vegetation

Table 17.2 Effect of biocrusts on soil moisture and evaporation according to different studies

Site	Ground cover/biocrust type	Biocrust morphology	Soil texture	Method	In situ/ex situ	Depth (cm)	Soil moisture	Evaporation	References
S Utah, USA	Cyanobacteria, lichen, bare soil	Pi	Sandy loam	Probes	Ex situ (field)	1–3, 4–6, 7–9	+	–	George et al. (2003)
Cape Cod National Seashore, Massachusetts, USA	Algae		Sandy	Micro-lysimeter	Ex situ (indoors)	0–20	+	–	Smith et al. (2004)
Tabernas Desert, SE Spain	Lichen, physical crust	Ru	Silty loam	Probes	In situ	3	+		Cantón et al. (2004)
Israeli–Egyptian border, Israel	Cyanobacteria, mosses	Sm/Ru	Sandy	Oven-drying method	Ex situ (indoors)	0–80	+ (surface) –(deep)		Almog and Yair (2007)
Shapotou, Tengger Desert, China	Well-developed crust, bare soil	Ro	Sandy	Micro-lysimeter	Ex situ (field)			–(low rain) + (high rain)	Liu et al. (2007)
Shapotou, Tengger Desert, China	Shrub with biocrust, shrub without biocrusts, and bare soil	Ro	Sandy	Probes	In situ	5, 10, 15, 20, 30, 40	–(low rainfall ~10 mm) + (high rainfall ~60 mm)		Wang et al. (2007)
Shapotou, Tengger Desert, China	Algae, moss, bare soil	Ro	Sandy	Ex situ			+ (early stage) –(late stage)	Zhang et al. (2007)	
Shapotou, Tengger Desert, China	Lichen, moss, bare soil	Ro	Sandy				+ (early stage) –(late stage)	Li et al. (2009) (review)	

(continued)

Table 17.2 (continued)

Site	Ground cover/biocrust type	Biocrust morphology	Soil texture	Method	In situ/ex situ	Depth (cm)	Soil moisture	Evaporation	References
Shapotou, Tengger Desert, China	Algae, lichen, mosses, bare	Ro	Sandy	Micro-lysimeter	Ex situ (field)	0–30		–(rain < 10 mm) + (rain > 10 mm)	Li et al. (2010)
Inner Mongolia, N China	Moss	Ru	Sandy	Oven-drying method	Ex situ (indoors)	Every 5 cm to a depth of 60 cm	+ (high soil water content) –(low soil water content)		Gao et al. (2010)
Loess Plateau, China	Moss	Ro	Sandy Sandy loam	Micro-lysimeter	Ex situ (field)	0–15	1°: Moss > bare 2°: Moss < bare	Sandy: – –(early stage) + (late stage) Sandy loam: –	Xiao et al. (2010)
Shapotou, Tengger Desert, China	Biocrust, bare soil	Ro	Sandy	Neutron probes	In situ	0–30, 30–60, 60–90, 90–120, 120–150, 150–200, 200–250, 250–300	+ (0–5 cm) – (5–120 cm)	+ (early stage) –(late stage)	Yu et al. (2010)
Loess Plateau, Shanxi, China	Algae, bare soil	Ro/Ru		Micro-lysimeter	Ex situ (field)			+ (early stage) –(late stage)	Wang et al. (2011)
Negev Desert, Israel	Cyanobacteria, moss	Sm/Ru	Sandy	Petri dishes Core sampling	Ex situ (indoors outdoors)	Petri dishes: 1 cm	+ (1 cm) –(0–10 cm)		Kidron and Tal (2012)
Tabernas Desert, SE Spain	Cyanobacteria, lichen, bare soil	Ru/Ro	Silty loam	Micro-lysimeter	Ex situ (field)	0–5		bio crust ~ bare	Chamizo et al. (2013a)

Tabernas and Cabo de Gata-Níjar, SE Spain	Cyanobacteria, lichen, moss, bare soil	Sm/Ru/Ro	Silty loam Sandy loam	Probes	In situ	3, 10	+ (high water content) no effect (low water content)	– (high water content) no effect (low water content)	Chamizo et al. (2013b)
Inner Mongolia, China	Inoculated cyanobacteria, bare soil	Ru	Sandy	Oven-drying	Ex situ (indoors)	0–1	+	–	Colica et al. (2014)
Aranjuez, Spain	Lichen, mosses	Ru	Gypsum	Probes	In situ	0–5	+	+ (>75 % cover)	Berdugo et al. (2014)

Biocrust morphology: Sm smooth, Ru rugose, Ro rolling, Pi pinnacled

distribution will allow incorporating their effects at coarser spatial scales and have more accurate information on hydrological dynamics in arid and semiarid regions.

17.3 Soil Moisture Evaporation

Our review of the literature showed congruence among the studies examined, as a majority of cases (15/23; 65 %) showed that biocrusts reduced evaporation compared to bare soils (Table 17.2), whereas only two studies showed no significant difference.

The influence of biocrusts on soil evaporation may depend on the stage of the evaporation process. Four studies on coarse dune sand (Zhang et al. 2007; Li et al. 2009; Yu et al. 2010; Wang et al. 2011) found that evaporation rates were faster in biocrusts compared with bare soil during the early stages of evaporation, but slower during the later stages of evaporation as the soil dried out, due to the higher water retention capacity of biocrusts. In contrast, one study showed the opposite, with biocrusts increasing evaporation at the end of the evaporation process by prolonging the time water was kept at the surface, especially on sandy soils (Xiao et al. 2010). On coarser dune sand, Liu et al. (2007) and Li et al. (2010) found no difference in evaporation between biocrusts and bare soil during small rain events (2, 5 and 10 mm), but larger rainfall events (20 mm) resulted in higher evaporation rates in biocrusts compared to bare soil.

Some studies have shown that biocrust cover of <60 % or between 25 and 75 % decreased evaporation relative to bare soil, whereas when cover was >75 %, evaporation was greater (Harper and Marble 1988; Berdugo et al. 2014), likely due to soil surface temperatures increasing with cover (Harper and Marble 1988; Kidron and Tal 2012). However, some studies showed no impact of biocrust temperature on evaporation rates (Xiao et al. 2010) or, although they may have increased soil temperatures, they reduced evaporation rates by increasing water retention capacity (George et al. 2003). Ambient temperature can also be a factor. Under warm ambient temperatures (~30°), both biocrusts and bare soils lost water very quickly and no significant differences were found in their evaporation rates (Chamizo et al. 2013a). Under mild ambient temperatures, however, biocrusts reduced evaporation and increased soil moisture compared to soils without biocrusts (Chamizo et al. 2013b).

Surface soil water content can also affect the influence of biocrusts. When soil water content is high, evaporation is reduced and soil moisture is retained longer in biocrusts due to their effect on pore clogging, especially in well-developed lichen-moss biocrusts. In contrast, when soil water content is low, unblocking of soil pores in biocrusts causes soil moisture to be similar in both biocrusts and bare soils (Chamizo et al. 2013b).

Given that most biocrust organisms absorb water to some degree, most studies reported that biocrusts increase moisture in the first few centimeters of the soil (~5 cm) (Cantón et al. 2004; Chamizo et al. 2013a, b; Colica et al. 2014;

Gao et al. 2010; Yu et al. 2010), and a positive correlation has been found between chlorophyll *a* content of the crust and daylight surface wetness duration (Kidron and Benenson 2014). On the contrary, some studies have shown that moisture is lower in deeper soil strata below biocrusts than under bare soils (Gao et al. 2010; Yu et al. 2010). However, these studies were conducted at soil depths expected to be well past any influence that biocrusts may have on evaporation. As the composition of biocrusts can influence the composition of the vascular plant community (see Chap. 19 by Zhang et al.), and different plants have different rooting patterns, the effect of biocrusts on soil moisture at depth may be mediated through the vascular plant community.

17.4 Dew, Vapor, and Fog Inputs

Biocrusts can also increase non-rainfall water inputs such as dew, vapor, and fog into the soil. In many deserts, particularly more arid deserts, these are essential additional water sources for biocrusts and soil biota. For example, atmospheric water vapor has been described as the greatest source of moisture intercepted by lichens in coastal deserts (Maphangwa et al. 2012). The harvesting of non-rainfall water inputs has the potential to create a positive feedback loop wherein harvested water stimulates biocrust activity, including photosynthesis and growth, enabling biocrusts to harvest more non-rainfall water inputs.

Most studies of non-rainfall water inputs have been reported from Asian deserts, including the Gurbantunggut Desert (Chen 2012; Tao and Zhang 2012a, b; Zhang et al. 2009a, b), the Hopq (Kubuqi) Desert (Lan et al. 2010; Rao et al. 2009, 2011), the Tengger Desert (Liu et al. 2006; Pan et al. 2010) and the Mu Us Sandy Land (Sun et al. 2008; Zhang et al. 2008). These studies have shown that the amount of dew harvested varies widely among biocrust and desert types, with the greatest average amount being around 0.5 mm day^{-1} (precipitation equivalent) in the Tengger Desert (Liu et al. 2006).

Biocrust type likely affects dew harvesting because the efficiency of harvesting dew varies with the roughness, surface area, and capacity of crusts to absorb moisture. Several authors have reported an increase in dewfall deposition with increasing biocrust development. Liu et al. (2006) found that the amount of dew increased from physical crusts to algae and moss crusts. Similarly, Zhang et al. (2009a) reported that dew deposition increased from bare sand to cyanobacterial, lichen, and moss biocrusts. However, they found that the moss biocrusts were wet for a shorter time compared to bare sand. This was explained because mosses were cooler at night, enhancing dew formation, but warmed faster during the day, resulting in greater evaporation rates. Wang et al. (2014) also reported that moss-dominated biocrusts harvested significantly more dew and water vapor than bare sand in the Tengger Desert, China. A study on sand dunes in northeastern Germany reported higher dew formation with increasing biocrust development (from low to high algal cover and to high algal cover with few mosses)

with the greatest amount of dew being 0.2 mm day^{-1} . The most important factors contributing to dew formation were found to be organic matter content (EPS amount), crust thickness, and coverage (Fischer et al. 2012b).

Interestingly, the type of moss can also affect dew deposition rates. Tao and Zhang (2012a) compared the water content, evaporation ratio, and dew deposition in mosses with and without hair points on their leaves. Mosses with hair points increased water content by 25 % compared to those without. Hair points also retarded evaporation rates and increased the total and daily amounts of dew.

17.5 Exploration of Contradictory Results

Although this literature review has identified many similarities among studies of biocrust effects on hydrologic processes, they also indicate a number of conflicting results. While some are caused by variability in soils and biocrusts within a site, there may also be other factors:

First, comparisons are usually made between undisturbed crusted soils and disturbed soils by scalping or trampling or between undisturbed crusts with varying cover and composition, so any observed differences at a site may be due to alteration of soil structure by disturbance or to different inherent characteristics under biocrust types (Eldridge 2003). Moreover, what is often identified as bare soil is often colonized by cyanobacteria and other microscopic organisms.

Second, even when similar biocrust types are compared among studies, different results may be due to differences in underlying soil properties such as soil texture, soil structure, parent material, soil organic matter content, aggregate stability, porosity, or association with physical crusts (reviewed in Belnap 2006).

Third, studies have used a variety of techniques or measured different variables, making it difficult to compare results across studies or different scales, or to scale up from the plot to the landscape scale (Belnap 2006). Scaling is probably the most critical issue. Most studies that address infiltration of biocrusts use tension infiltrometers, water drop repellency tests, or rainfall simulations at small spatial scales. However, these laboratory or plot-level studies are limited because they are unable to account for differences in temporal (variability in rainfall intensity and size, distribution and kinetic energy of drops) and spatial (responses at hillslopes or across landscapes) scales, where plant cover, soil surface roughness, and other variables alter the way that biocrusts influence hydrology (Chamizo et al. 2012b; Rodríguez-Caballero et al. 2014a). The results of small-scale tests, therefore, can be highly misleading and give an inaccurate account of how biocrusts affect water cycles at the landscape scale.

Finally, studies of soil moisture and evaporation have used techniques and equipment such as microlysimeters, moisture probes, and oven-dried samples that vary in accuracy. Most studies have been conducted *ex situ* (taking the crust out of its natural environment) under field or laboratory settings, which may alter many soil, water, and environmental variables that influence the results. Studies may also

show different results depending on the soil depth at which measurements are made.

17.6 General Conclusions

A number of general conclusions can be drawn from our review on the role of biocrusts in soil hydrological processes. First, when runoff is measured at a larger scale ($>2 \text{ m}^2$), most studies have shown that biocrusts reduce runoff, irrespective of biocrust species composition or external morphology, rainfall type, or soil type. Runoff is always reduced under three situations: lichen-dominated biocrusts, pinnacled biocrusts, and small rainfall events ($<20 \text{ mm}$). Biocrusts have been found to reduce evaporation and increase soil moisture content of the upper soil layer in most cases. Dew, vapor, and fog inputs can also influence the water budget of biocrusts.

The balance between direct and indirect factors, and their interaction with soil physical properties, rainfall characteristics, and spatial scale, will ultimately govern how biocrusts influence hydrological processes at a given site. We maintain that the important issue is not to try to determine whether biocrusts increase or decrease infiltration, runoff or evaporation per se, but to understand more about how different variables moderate the response of biocrusts at different scales (*sensu* Bowker et al. 2013). At very small (microplot or plot) scales (up to about 1 m^2), the effect of microtopography on infiltration is underestimated, making other factors such as biocrust hydrophobicity or pore clogging more important than any influence of soil roughness. As spatial scales increase, surface roughness created by both biocrusts and vascular plants become more important, as does the connectivity among different patch types. Rainfall characteristics can have a major effect on how biocrusts influence infiltration and runoff processes. During low-intensity rainfall events, biocrusts often reduce runoff by creating greater roughness and water absorption capacity. However, during large and intense rainfalls that saturate the crust, the roughness effect may be overridden, and biocrusts increase runoff compared to bare soils.

To date, most research on the influence of biocrusts on hydrological processes has been based on studies conducted at very small spatial scales ($<1 \text{ m}^2$) that do not account for the high variability in space and time that characterize hydrological processes. This spatial and temporal variation has important implications for the upscaling of biocrust hydrological effects and for infiltration-runoff modeling in arid and semiarid areas, where biocrusts are a significant component of the soil surface. Studies at larger spatial scales (hillslope, landscape, catchment) incorporating temporal variability are an essential component of future biocrust research. The adoption of standardized methodologies would help in assessing the role of biocrusts in dryland hydrological cycles.

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Chapter 18

Physiology of Photosynthetic Organisms Within Biological Soil Crusts: Their Adaptation, Flexibility, and Plasticity

T.G. Allan Green and Michael C.F. Proctor

18.1 Introduction

All photoautotrophic organisms (called “plants” for the purpose of this chapter) in biological soil crusts (abbreviated to biocrusts for this chapter) are small and *poikilohydric* in that their hydration status tends to equilibrate with the water status of their environment. Unlike vascular plants, they lack adaptations to maintain a quasi-constant internal water content by regulating water loss, coupled with water uptake from the soil. However, that does not mean that the water content of *their cells* fluctuates continuously with the changing availability of water in the atmosphere, which is for most of the time far below the range of water potentials at which metabolism is possible. The photosynthetic cells in biocrusts are generally intimately associated with greater or lesser amounts of external capillary water at near-zero water potential, so if liquid water is present at all in their surroundings, they are at full turgor (when wall pressure is numerically equal to osmotic potential) and to some extent buffered against immediate changes in environmental water status. There is a complex interaction between photosynthesis and water storage, and many features of shoot and leaf architecture in bryophytes, and thallus form in lichens, act through surface tension to store and to regulate the distribution and movement of this extracellular water, maintaining cell turgor while minimizing interference with gas exchange (Buch 1945, 1947; Dilks and Proctor 1979; Green

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et al. 1985; Proctor 1979a, 2000a, 2009). The extracellular gelatinous material secreted by many cyanobacteria and algae probably performs a similar function. As long as any extracellular liquid water remains in contact with them, the photosynthetic cells remain fully turgid. When evaporation exhausts the extracellular water, the cells themselves quickly dry out and cease metabolism (Proctor 2002). Most terrestrial biocrust organisms are desiccation tolerant (DT)—able to lose the greater part of the cell water (down to 5–10 % RWC)—suspend metabolism when dry, and recover within an hour or two upon rewetting (Proctor and Tuba 2002). When dry, they often need and are able to withstand high temperatures and intense photosynthetically active radiation (PAR) and UVB. Despite their apparent simplicity, there is growing evidence of physiological agility with acclimation to environmental factors such as light, UV, and temperature being reported.

In this chapter we look at the response of biocrust photosynthetic organisms to the main factors of light, temperature, CO₂, and thallus water content, but we emphasize the special features of the poikilohydric lifestyle and the biocrust environment; that means that these organisms cannot be treated as small higher plants but show important differences in their physiology and ecology.

18.2 The Importance of Scale

Scale is of paramount importance. Area is proportional to the square and volume to the cube of linear dimension. Surface tension acts on *linear* interfaces. Gas exchange and interception of radiation are proportional to *area*, mass, and with it metabolic capacity (and demand) and weight are proportional to *volume*. The consequence is that gravity, a limiting factor for mammals or trees, is trivial at a scale of millimeters, while surface tension, which is a trivial force for us, is among the most powerful forces to which a small organism is exposed. A consequence of scale relationships is that most plants larger than about 10 cm are vascular plants and most smaller than about 1 cm are a varied collection of “lower plants” including cyanobacteria, various “algae,” mosses, liverworts, and lichens. There is a “window” between about 1 cm and 10 cm in which both strategies are viable and coexist. All plant organs (and organelles) have a minimum size, and there would simply not be the space to pack the necessary complexity of a vascular plant in a plant body less than about 1 cm (all gardeners know the vulnerability of small seedlings). Conversely, the poikilohydric plant is limited beyond ~10 cm by water supply and support.

18.3 Climate and Microclimate

18.3.1 Boundary Layers

Scale enters also into relations with the atmospheric environment. The ground or any other solid object in contact with the atmosphere influences the airflow around it. Trees, buildings, crops, and shelter belts all have their effect (intended or otherwise) on airflow. This region of interaction between air and ground is the *boundary layer*. Close to the ground (or any object), the streamlines are parallel with the surface—the airflow is *laminar*. Farther from the surface, the airflow breaks up into eddies—the airflow becomes *turbulent*. The importance of this is that, within the laminar boundary layer, diffusion of heat, water vapor, CO₂, etc. takes place by the slow process of molecular diffusion, whereas away from the laminar boundary layer, turbulent mixing becomes dominant, which may be orders of magnitude faster. The laminar boundary layer has no sharp upper limit, but gradually gives way to the turbulence of the surrounding air. Roughly, the laminar boundary layer at the scale of a biocrust, at a wind speed of 1 m s⁻¹, is around 1–2 mm. At 0.1 m s⁻¹ (conventionally taken as “still air”), the thickness of the laminar boundary layer will be ~3–6 mm. Even if conditions are such, that turbulence is being generated, there will always be a laminar sub-layer close to the surface (Monteith and Unsworth 1990). The figures imply that biocrust organisms exist largely within the laminar boundary layer in all but windy weather. In vascular plants, the stomata mark the transition between the predominantly turbulent air outside the leaf and the predominant molecular diffusion in the mesophyll; the diffusion path in the mesophyll is typically around 0.5 mm.

18.3.2 Microclimate

“Climate” is in the perception, and on the scale, of the organism that experiences it. Many climatic and environmental variables, such as temperature, humidity, CO₂ concentration, and wind speed, show more or less steep gradients near the ground. Standard meteorological air temperature and humidity measurements are taken about 1.5 m above the ground, with the instruments freely exposed to the air but shaded from direct sun, as in a louvered Stevenson screen. That gives air (“shade”) temperatures appropriate to our own scale or to the scale of our farm livestock and tall crops or trees. We measure “grass minimum” temperature because many crops (and grasslands) are low growing, and “ground frosts” can occur, while the air temperature is still several degrees above freezing. Were we to measure our climate parameters on the scale of biocrust organisms, we should get an entirely different picture; the average might be almost the same but the extremes would be very different. This is reflected by the much wider latitudinal distributions of mosses and lichens, which can productively use the temperature maxima near the ground,

compared with forest trees, which are constrained by air temperature. For example, the moss *Bryum argenteum* (a common constituent of biocrusts) occurs from the Arctic to the Antarctic and at all latitudes in between. For more on climate and microclimate, and plant responses thereto, see Geiger (1950, a classic, still worth consulting), Gates (1980), Campbell (1977), Monteith and Unsworth (1990), Jones (1992), and Barry and Chorley (2003). An outline on bryophytes is given by Proctor (2011).

18.4 Water Relations of Poikilohydric Plants

The water relations of poikilohydric plants are basically the same as those of vascular plants, but with two crucial differences. In the Höfler diagram of Fig. 18.1, the cells of homoiohydric vascular plants function between *full turgor* (100 % RWC and 30 % RWC) (0 to -5 MPa). If the cell water content drops below

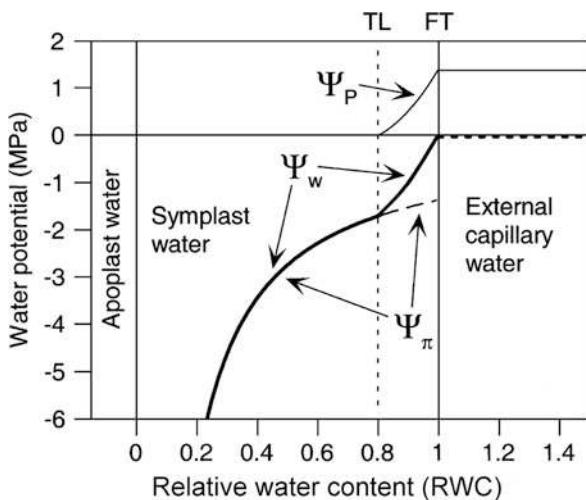


Fig. 18.1 Höfler diagram for a typical bryophyte, based on thermocouple psychrometer measurements on the leafy liverwort *Porella platyphylla* (Proctor 1999). The body of the diagram shows the relation of *relative water content* to water potential (Ψ) and its components: Ψ_w = water potential of the cell, Ψ_π = osmotic potential of the cell sap, and Ψ_P = turgor pressure. The water potential of the cell (Ψ_w) is zero at full turgor (FT); the cell is in equilibrium with liquid water in its environment. As the cell loses water, turgor pressure (Ψ_P) falls and becomes zero at the point of turgor loss (TL). The tissue then becomes flaccid, and Ψ_w becomes equal to Ψ_π . Bryophytes share this much of the diagram with vascular plants. But in addition to water inside the cell, turgid metabolically active bryophytes (or lichens) have *external capillary water* held in spaces at near-zero water potential outside the cells, and this water is physiologically important, too. The external capillary water is physically continuous with the *apoplast water* in the cell walls (which needs a diagram to itself), spanning a range of water potentials from zero to negative values far outside the limits of metabolism

about 30 % RWC, the cell dies. The regions of interest in cells of poikilohydric plants extend far beyond these limits. Vascular plants are basically *endohydric*; all the physiologically important water is inside the plant. Poikilohydric plants are *ectohydric*; much of the water associated with plant is held in capillary spaces outside the plant, and this water too is physiologically important to the functioning of the plant. This externally held water can vary widely in quantity, but while it is present, the photosynthetic cells remain fully turgid. Whereas the full-turgor water content of a vascular plant is easily established by weighing a fully turgid leaf, and weighing the same leaf after oven drying, it is not so easy to obtain for poikilohydric plants because of the external capillary water. Full-turgor water content of a poikilohydric plant is difficult to measure without recourse to thermocouple psychrometry, but acceptable approximations can often be obtained (at least for bryophytes and lichens) by careful blotting with soft absorbent paper (Beckett 1995, 1996, 1997; Green et al. 1985; Proctor et al. 1998; Proctor 1999; Nardini et al. 2013; Merinero et al. 2014). Saturation (maximal) water content is an entirely different thing from full-turgor water content, with the latter being *essential* for physiological work. “Relative water contents” based on “saturated” water content are meaningless. The only easily reproducible datum is oven-dry weight.

Because of their impermeable cuticularized epidermis, vascular plants operate between full turgor and ~30 % RWC; if the soil is dry or saline, the plant is water stressed. For a poikilohydric plant, all habitats are mesic when the cells are fully turgid, and all habitats are arid when the cells are desiccated. Water stress is confined to (relatively brief) intervals between the two states, and the difference between mesic and xeric habitats is a matter of the time spent in the two states (Proctor 2000b).

18.5 Desiccation Tolerance (DT)

Desiccation tolerance in bryophytes and lichens has been defined as the ability to equilibrate its internal water potential with that of moderately dry air and then resume normal function when rehydrated (Alpert 2000). This means equilibration with 50 % relative humidity at 20 °C, which leads to a thallus water content (WC) around 10 % and a water potential of –100 MPa. This threshold of 10 % WC seems to have physiological meaning and to correspond to the point at which there is no longer enough water to form a monolayer around macromolecules thus stopping enzymatic reactions and metabolism (Billi and Potts 2002). In the laboratory, much lower hydrations, less than 1 %, can be achieved by drying over P_2O_5 , and levels almost as low, around 2 %, can occur in the field when dry lichens are heated by the sun to temperatures that can reach 70 °C. Desiccation tolerance is shown by bacteria (including Cyanobacteria), many “algae,” mosses, liverworts, and lichens and among animals by many “infusoria,” rotifers, nematodes, tardigrades, etc. What is it that enables them to do this? Several mechanisms seem to be required to achieve DT. There is evidence of the importance of vitrification (glass

formation) of the cell contents to DT (Crowe et al. 1992, 1998; Buitink et al. 2002). Solutes, such as sucrose, oligosaccharides, fructans, polyols, and trehalose; protective proteins, LEA (late embryogenesis abundant) proteins and HSPs (heat-shock proteins); and amphiphilic metabolites, are important in membrane stabilization; antioxidants are important against accumulation of reactive oxygen species (ROS) that can occur during dehydration and rehydration (Smirnoff 1993; Asada 2006; Green et al. 2011a; Proctor and Smirnoff 2011).

Some bryophytes of frequently desiccated habitats (and lichens in general) are constitutively DT (CDT). *Syntrichia ruralis* (formerly *Tortula ruralis*), *Grimmia pulvinata*, and *Schistidium apocarpum* (s.l.) can withstand drying from full turgor to a water content of 5%–10% of their dry mass in half an hour or less, and on remoistening after a few hours or days of desiccation, recover positive net assimilation within a few minutes, and return to a positive net carbon balance within an hour or less. Most molecular work has been done on *Syntrichia ruralis*, which does not need a transcriptional activation of a distinct set of “tolerance genes,” but rather relies heavily on the more rapid response afforded by translational controls (Oliver and Bewley 1997; Oliver 2009). The response is certainly not as rapid in all bryophytes. Abel (1956) screened detached leaves of 66 mosses and found that they formed a nearly perfect continuum from *Schistostega pennata*, *Sphagnum* sp., and *Bryum schleicheri*, killed by 24 h exposure to 96 % RH, to *Syntrichia ruralis* and *Grimmia* sp., whose leaf cells would still plasmolyze even after 24 h over concentrated sulfuric acid. Over half the species tested showed a dramatic increase in tolerance following pre-desiccation at 96 % RH, a phenomenon also demonstrated for biocrust mosses in the Mojave Desert (Stark et al. 2005, 2011, 2012). Stark and Brinda (2015) emphasize the continuum that exists between CDT plants and plants in which desiccation tolerance is induced by slow drying (induced drought tolerant: IDT). Many small mosses important in biocrusts in seasonal climates are IDT. The relationship between the normal habitat conditions of a bryophyte or lichen and degree of survival following drying and desiccation is important and should be taken into account at all times. The CDT mosses and lichens represent one extreme in desiccation tolerance, while, at the other extreme, there are examples of species that have almost zero tolerance of dehydration, let alone desiccation. For lichens, *Pseudocyphellaria dissimilis* cannot survive even 20 h equilibration at 12 % relative humidity (Green et al. 1991), while species of the moss order Hookeriales and many (not all) thalloid liverworts are also desiccation intolerant (Proctor and Pence 2002). It is important to remember that most bryophytes and lichens fall between these extremes of desiccation tolerance, but, because of the open environments of most biocrusts and the wide range of climatic (and often seasonal) conditions to which they are exposed, their component species span a wide range of the DT spectrum. Both CDT and IDT species occur in the Mojave Desert (and in the UK). Smaller seasonal gregarious species seem to be predominantly IDT, but larger perennial mosses of dry places are CDT.

18.5.1 Recovery from Desiccation

The general pattern of recovery from desiccation after rewetting is similar in both lichens and bryophytes although generally more rapid (and less studied) in lichens (Ried 1960; Hinshiri and Proctor 1971; Farrar 1976a, b; Farrar and Smith 1976; Bewley 1979; Bewley and Krochko 1982; Oliver 1991; Oliver and Bewley 1997; Tuba et al. 1996; Proctor et al. 2007a, b; Proctor 2009, 2010). Respiration, protein synthesis, and the activity of the photosystems begin immediately on rewetting. The enzymes of the “dark reactions” of photosynthesis take a few minutes to be fully functional. Gas exchange measurements immediately on rewetting show enhanced respiration. This “resaturation respiration” is different from basal respiration; it is cyanide sensitive in the lichen *Hypogymnia physodes* (and perhaps generally), which basal (dark) respiration is not, and decays in a comparable time that it takes for the fine structural changes to be completed (Farrar and Smith 1976; Proctor et al. 2007a). Recovery from desiccation takes place regardless of the presence of protein synthesis inhibitors (Proctor and Smirnoff 2000; Proctor et al. 2007a, b; Pressel et al. 2009). The pattern of protein synthesis alters dramatically in the first hours following rewetting, and the sequence of events during recovery is complex (Oliver 2009). Morphological change at the subcellular level is most active in the first few hours of rehydration, but full return of organelles to their pre-desiccation form and disposition, and reassembly of the cytoskeleton may take 24–48 h (Pressel et al. 2006, 2009). This is essential for active translocation (Ligrone and Duckett 1994; Pressel et al. 2006) and for the cell cycle, cell division, and cell growth (Mansour and Hallet 1981), but apparently not for photosynthesis or carbon fixation (Pressel et al. 2009).

Recovery follows much the same course for liverworts, although data are available for only a few species. The “oil bodies” of liverworts appear to play a crucial role in recovery of *Southbya nigrella* and probably other species (Pressel et al. 2009; Proctor 2010). Some species of liverworts, particularly small Marchantiiales (*Corsinia*, *Exormotheca*, *Mannia*, *Oxymitra*, *Plagiochasma*, and *Riccia* spp.), are DT and are prominent in biocrusts in the Mediterranean region with cool wet winters and summer drought and in comparable climates elsewhere.

In general there is a positive and not unexpected link between time to achieve recovery and length of time active once rehydrated. Lichens recover rapidly but then remain active only briefly, while, at the other extreme, many mosses recover slowly but then remain active longer (Green et al. 2011a; Kappen and Valladares 2007; Proctor 2004; Zotz et al. 2000; Zotz and Rottenberger 2001). The greater time and thallus water content required by mosses to recover full activity, plus the enhanced respiratory activity after rehydration (Dilks and Proctor 1976; Farrar and Smith 1976; Schlenzog et al. 2004) means that partial hydration followed by rapid drying, as found in hot desert environments, can lead to damage and death (Coe et al. 2012, 2014; Barker et al. 2005; Stark et al. 2011). In view of the longer recovery times and ability to utilize heavier rainfall events, it is also not unexpected

that bryophyte biomass in biocrusts will be positively linked to overall precipitation and they show a greater representation in wetter habitats (Wu et al. 2015).

18.6 Sources of Water to Biocrust Plants

Poikilohydric organisms such as lichens and mosses can become hydrated from rain, humid air, dew, and fog, with only the first being usually available to homoiohydric plants. The rate and extent of hydration differs between the different sources, and the actual effectiveness depends on the individual organisms.

18.6.1 Rainfall

Rain is the most obvious and the easiest to deal with; rainfall records are among the most widely available of meteorological data. At the Tabernas Desert, Almeria, rainfall greater than 0.1 mm fell on 23 occasions in 2013, and all events would have hydrated the lichens enough for activity to start and all but two to reach the WC optimal for photosynthesis (WC_{opt} ; see Table 18.1). Sixteen of the events would have fully saturated the lichens and mosses. Biocrust organisms can remain active for long periods after hydration by rain, but the actual carbon gain depends on the photosynthetic response at high WC (see Sect. 18.8.1).

18.6.2 Humid Air

Laboratory studies (e.g., Bertsch 1966; Lange et al. 1988) have often shown that lichens with green algal photobionts can become active from humid air alone and that lichens with cyanobacterial primary photobionts do not. As hydration by humid air is not a rapid process, at 97 % relative humidity the majority of green algal lichens need 6 h or longer to reach 60 % WC, it seems improbable that moistening by humid air alone can be significant in practice for most biocrusts and almost certainly not for those with cyanobacteria. A small number of examples are known where positive net photosynthesis occurs by late afternoon high humidity although the ecological significance is questionable (Lange et al. 2008). There could, however, be an important indirect effect through the water content gain from humidity lowering the amount of water required for full activity from other sources such as dew or impaction of water droplets from mist. This could be important for both lichens and bryophytes. There are also a few examples where some green algal lichens in arid areas do not show activation by high humidity (Del-Prado and Sancho 2000; Colesie et al. 2014a; Hovenden and Seppelt 1995).

Table 18.1 LMA (mass per unit area), thallus water contents in % dry weight, and mm rain equivalent

Species	Thallus water content						Depression	Dew fall required	Maximal net photosynthetic rate	Dark respiration	Chlorophyll mg m ⁻²
	LMA g m ⁻²	% dry weight	mm	MCP Opt	Max %	MCP Opt					
<i>Collema cristatum</i> ¹	310	42	500	1700	0.16	1.52	5.2	80	10	95	2.8
<i>Fulgensia fulgens</i> ²	440	11	56	270	0.05	0.25	1.2	100	3.1	15.6	5.2
<i>Lecanora muralis</i> ³	510	29	106	310	0.15	0.55	1.6	100	9.4	34.4	6.5
<i>Cladonia convoluta</i> ⁴	630	38	150	500	0.24	0.95	3.2	0	15	59.4	5.4
<i>Squamaria lenigera</i> ⁵	684	10	53	120	0.08	0.4	0.9	30	5	25	4
<i>Collema tenax</i> ⁶	1190	18	84	210	0.22	1	2.5	85	13.8	62.5	3.9
<i>Diploschistes diacapsis</i> ⁷	2000	3	25	60	0.06	0.5	1.2	60	3.8	31.3	5

Source of data: ¹Lange (2000), ²Lange et al. (1995), ³Lange (2002), ⁴Lange and Green (2003), ⁵Lange and Green (2004), ⁶Lange et al. (1998), ⁷Pintado et al. (2005)

MCP moisture compensation point for NP; Opt water content at maximal NP; Max maximal measured water content; depression—NP at maximal water content as % maximal NP; dewfall required in mm to achieve MCP and Opt; maximal net photosynthetic rates on area (μmol m⁻² s⁻¹) and dry weight (nmol g⁻¹ s⁻¹) basis; dark respiration on area basis (μmol m⁻² s⁻¹); QE quantum efficiency (initial slope of NP response to PPFD); and chlorophyll content (mg m⁻²) for seven BSC lichen species

18.6.3 Dew

Hydration by dew is well known for lichens and less so for mosses (Lange 1969, 2001; Csintalan et al. 2000) and produces the so-called “gulp” effect in which the organism activates during clear radiation nights, giving a brief period of positive net photosynthesis when the sun rises, before the temperature increases and the lichen or moss dries rapidly and photosynthesis ceases. The length of the active period and the total carbon gain will depend on two main factors, the amount of dew fall that has occurred during the night and the degree of hydration required by the individual species to achieve positive net photosynthesis (NP). Dew fall occurs commonly in desert areas because of the clear skies and the consequent radiative cooling of the soil surface. The number of nights with dew fall can be very large, for instance, 78 % of nights in a coastal arid zone near Almeria, Spain (Uclés et al. 2014; Fig. 18.2). Quantity of dew fall is normally not high, and a summary by Uclés et al. (2014) suggests that amounts up to 0.17 mm (precipitation equivalent) are normal, while occasional falls up to 0.3 mm can occur. The amount of dew fall appears to be strongly linked to the length of time that the surface is below the dew point. A rate of 0.014 mm h^{-1} was demonstrated by direct measurement for El Cautivo, Tabernas Desert, Spain, by Uclés et al. (2015), with dew fall lasting for up to 15 h in winter. Dew fall appears to be slower at most other sites (Zhang et al. 2014). Lichens are best studied, and species differ considerably in the amount of dew fall needed to become active. The moisture compensation point (MCP) is reached at 0.05 mm (about $3\frac{1}{2}$ h dew fall) by *Fulglesia fulgens* (Table 18.1), while 0.24 mm (17 h dew fall) are needed by *Cladonia convoluta*; so this species does not benefit from dew.

18.6.4 Interception of Fog and Cloud Water Droplets

Higher hydration levels can be achieved by interception and capture of droplets of water from fog or clouds. This is a dynamic process, which depends on the mass of the water droplets and the diameter of the target; it is most effective with a heavy mist and target of negligible diameter, as spiders’ webs are on misty autumn mornings (Monteith and Unsworth 1990). *Teloschistes capensis* in the Namibian coastal lichen fields reaches optimal levels of hydration from fog, which can occur on more than 250 days a year (Lange et al. 2006). Rundel (1978) gives details of lichen communities that are supported by fog. Although there are few studies, fog or clouds are also important for alpine biocrusts both for rehydration and extending activity in the light (Reiter et al. 2008). Growth forms in biocrusts, such as those of *Racomitrium* and *Teloschistes*, appear well adapted to the interception of droplets of water from mist or clouds.

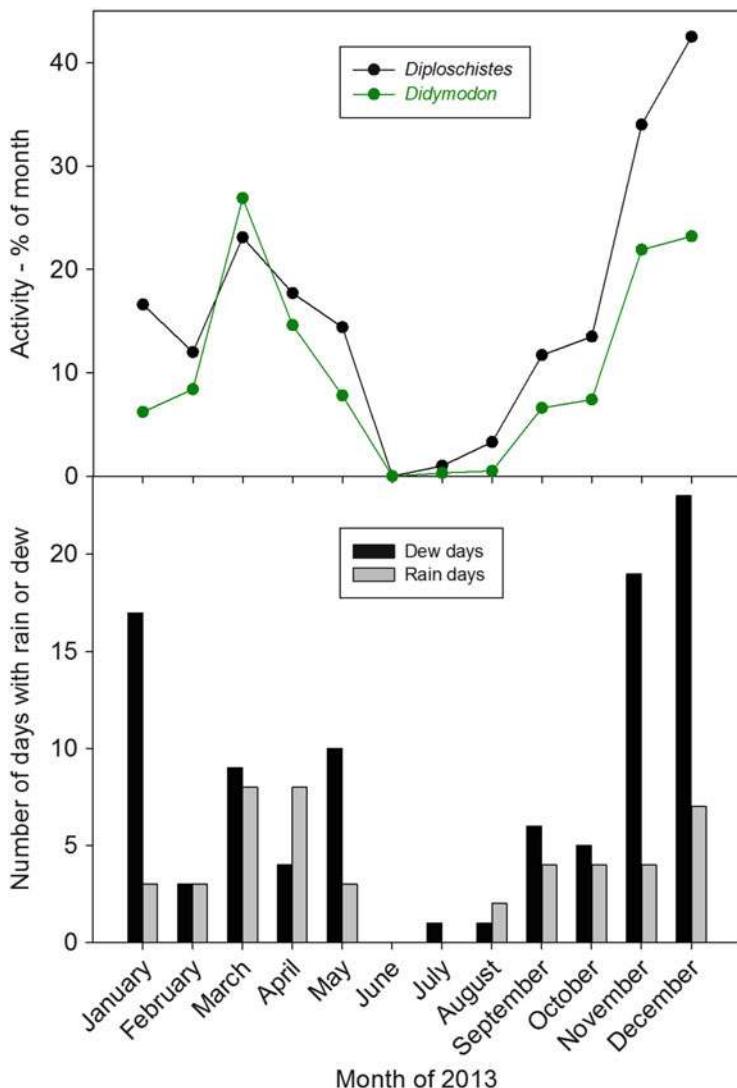


Fig. 18.2 Activity (% of each month) for the lichen *Diploschistes diacapsis* and the moss *Didymodon rigidulus* in the Tabernas Desert in 2013. The number of days in each month when there was dew or rain is shown in the lower part of the figure. The lichen shows higher activity especially in the three winter months (November to January) when dew occurrence is particularly common

18.7 Mass per Unit Area and Thallus Water Content

In almost all studies of lichens and mosses, plant water content is expressed as percentage of dry weight ($\% \text{ dw} = [\text{wet weight} - \text{dry weight}] * 100 / \text{dry weight}$). For biocrusts it is more common to use millimeter precipitation equivalent, because this

is not only how the inputs, rain or dew, are measured, but also there is often great difficulty to separate individual organisms from the crust.

There is a wide range in leaf mass of biocrust lichens per square meter (mass per area: LMA) from 310 g for *Collema cristatum* to 2000 g for *Diploschistes diacapsis* (Table 18.1). Biocrust lichens are heavy in comparison to foliose lichens from forests. Merinero et al. (2014) report that *Lobaria scrobiculata* and *Lobaria pulmonaria* range from 50 to 200 g m⁻² (mean 86 and 97 g m⁻², respectively), while *Pseudocyphellaria crocata* ranges from 40 to 100 g m⁻² (mean 73 g m⁻²); Snelgar and Green (1981) give *Pseudocyphellaria dissimilis* from inside a New Zealand rain forest as 59 to 91 g m⁻². Similar LMA is shown by a wide range of lichens summarized in Green and Lange (1994). Merinero et al. (2014) link the changes in dry mass per unit area with habitat; the wetter the habitat, the lower is the lichen mass per unit area. Lichens in biocrusts fit with this suggestion as they grow in extremely dry habitats and have the highest LMA. In comparison, normal C3 leaves average about 110 g m⁻² (Vile et al. 2005), but the leaf area index is commonly around 5.

For lichens and bryophytes, LMA provides the link between water inputs in millimeters and thallus water content in % dry weight. A precipitation equivalent of 0.1 mm corresponds to 100 g m⁻², so a lichen or bryophyte with 100 g m⁻² would be hydrated to a water content of 100 % dw (assuming all incoming water is taken up by the organisms). It might be expected that the lower the LMA then the less water (in mm) would be needed to achieve a WC high enough to activate the lichens. However, this depends on the species. In Table 18.1, *Collema cristatum* has the lowest mass per square meter but the highest MCP and WC_{opt}. In contrast *Diploschistes diacapsis* has the highest LMA and lowest MCP and WC_{opt}. Although the input rate of water is not under the control of biocrusts, it appears that the response to the input is determined by the species.

Net photosynthesis increases with relative water content (full turgor = 1.0) and maximal rates are not reached until full turgor (Proctor 2009). The water content needed to reach maximal net photosynthesis also depends, therefore, on the cell structure and interactions with water location. An unusual form is the gelatinous homoiomerous lichens such as *Collema* and *Leptogium* species. Here, a very small mass of (high molecular weight) gelling agent is used to capture a large amount of “internal” water that actually lies outside the outer cell membrane. However, again, optimum net photosynthesis will not be reached until full turgor (near-zero water potential) is reached for the whole system.

Maximum net photosynthesis (NP_{max}) on an area basis is independent of LMA which, as a consequence, means that biocrusts with low LMA will have higher NP_{max} on a dw basis (Fig. 18.3, $P = 0.0004$, $R^2 = 0.92$). There is a similar situation for dark respiration (DR), which also shows no significant changes on an area basis, but which shows a linear decline with increasing LMA on a dw basis ($P = 0.016$, $R^2 = 0.66$). These relationships suggest that there is an increase in metabolically inactive mass at higher LMA. The manipulation of water-holding capacity by differential mass allocation appears to offer a method for lichens and mosses to adapt their water relations to the local environment.

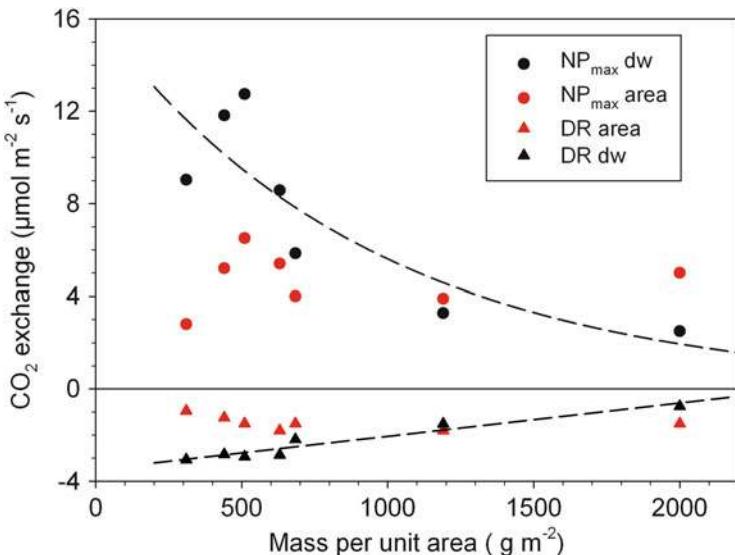


Fig. 18.3 Relationship between maximal net photosynthesis (NP_{max} , circles) and dark respiration (DR, triangles) on an area basis (red symbols, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and dry weight basis (black symbols, $\text{nmol g}^{-1} \text{s}^{-1}$) for the seven biocrust lichens in Table 18.1. The fitted curves for the dry weight basis data are significant, $P = 0.0004$, $R^2 = 0.92$, for DR, and $P = 0.016$, $R^2 = 0.66$ for NP_{max}

18.7.1 Chlorophyll Content and Photosynthetic Rates

Lange (2001) gives a summary of the then available maximal net photosynthetic rates under optimal conditions (NP_{max}) for a wide variety of soil crusts, and these span over two orders of magnitude between around 0.1 and $11.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, the latter being for a green algal lichen-dominated biocrust in Germany. NP_{max} is mainly between 2 and $5 \mu\text{mol m}^{-2} \text{s}^{-1}$, which are high rates compared to the more typical 1 – $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ for rain forest lichens (Lange et al. 1993). The rates are comparable to the leaves of phanerogamic vegetation at the biocrust sites (Lange 2001); however, the annual carbon uptake per surface area will certainly be much lower, because the poikilohydric nature of biocrusts means that they are often dry and they are often active under nonoptimal conditions (see later Sect. 18.9.1) and also because phanerogamic plants can build canopies, i.e., have a higher leaf area index.

Chlorophyll contents of biocrust lichens span a wide range from a low 42.7 mg m^{-2} for *Collema cristatum* to an exceptional 1350 mg m^{-2} for *Diploschistes diacapsis* (Table 18.1; Lange 2001). Other soil crusts can have even lower contents, such as 20.7 , 29.0 , and 38.1 mg m^{-2} for algal, mixed, and moss-dominated biocrusts from Tengger Desert in China (Zhao et al. 2014), and 16.7 to 43.4 mg m^{-2} for cyanobacterial biocrusts, and 53.2 mg m^{-2} for moss-dominated biocrusts in the Negev Desert (Kidron et al. 2012). Lan et al. (2012), for

the Qubqi Desert, Mongolia, found a large increase in chlorophyll content with biocrust development from 30 mg m^{-2} in cyanobacteria-dominated early crusts to 210 mg m^{-2} for fully developed moss-dominated crusts. The chlorophyll contents for lichen-dominated biocrusts can, therefore, be comparable with those of average C3 leaves, which require $500\text{--}700 \text{ mg chl m}^{-2}$ to achieve maximal quantum yield of CO_2 uptake (Lange 2001). Utilizing the data from Table 18.1 and from Lange et al. (1997), there appears to be no significant link between biocrust chlorophyll content (mg m^{-2}) and maximal NP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). The two cyanobacterial *Collema* species (Table 18.1) have the lowest chlorophyll contents and NP_{\max} , which is a little unexpected as cyanobacterial lichens often have high NP (Lange 2001) and also higher nitrogen availability through their nitrogen fixation. *Diploschistes diacapsis* presents an interesting situation, as the same NP_{\max} is supported by $210 \text{ mg Chl m}^{-2}$ in Utah but requires $1350 \text{ mg Chl m}^{-2}$ in Almeria (Pintado et al. 2005). This suggests that two different strategies are in use by the same species.

Overall, the higher LMA and NP_{\max} in comparison with other lichens conform with trends in other plants that are adapted to high light conditions.

18.8 Responses of Biocrust Plants When Active

18.8.1 Responses to Hydration

Fundamentally, poikilohydric plants have similar responses to vascular plants in their cell water relations below full turgor. What makes the difference is the external capillary water. Consequently, poikilohydric plants that are fully turgid in the field carry variable amounts of this external water. On an RWC scale, setting full turgor as 100 %, poikilohydric plants can be carrying water equivalent to 200–300 % RWC (or more). The presence of this external water can have a large effect on the photosynthetic rate. The diffusion coefficient of CO_2 in water is about 10,000 times less than in air, so superincumbent water increases resistance to CO_2 uptake at higher (total) water contents. Depressed NP at higher WC has been commonly found for lichens (e.g., Kershaw 1972; Lange et al. 1994) but it is equally true for bryophytes (Stålfelt 1938; Dilks and Proctor 1979; Alpert and Oechel 1987), except that bryophytes commonly have adaptations which minimize the conflict between water storage and gas exchange (Proctor 1979a, 2002, 2009; Fig. 18.4). Cowan et al. (1992) working on *Ramalina maciformis* confirm the greatly increased diffusion resistances at high WC. There is little change in the respiration rate with WC beyond full turgor.

Despite the overall similarity in the response of both NP and DR to WC (below full turgor) for bryophytes and lichens, there is a high level of variability in detailed response and absolute values (Fig. 4 in Lange 2001; Table 18.1). Many green algal lichens have a maximal NP first at about 100 % WC with maximal WC below

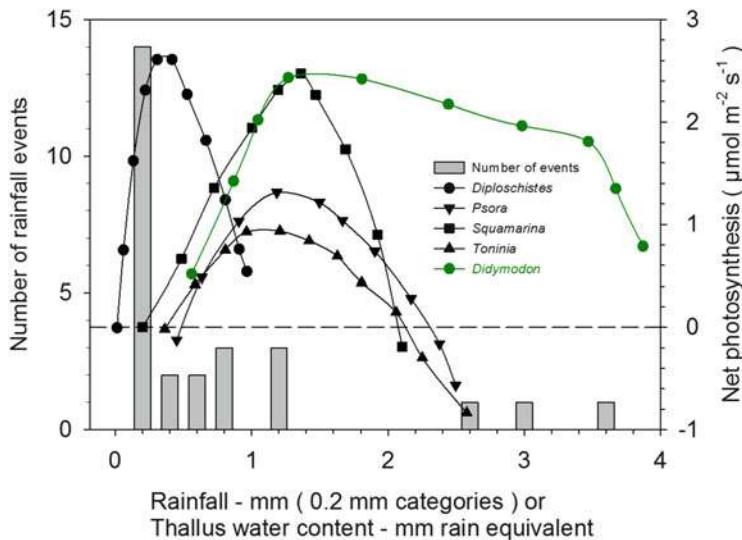


Fig. 18.4 Line graph: response of net photosynthetic rate (right hand axis, $\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at saturating PFD and 15 °C to thallus water content (mm precipitation equivalent) for four lichens and one moss from Tabernas Desert, Almeria, Spain. Bar graph: distribution of rainfall occurrence with each bar representing the number of occurrences of a rainfall event of a particular size; X axis is rainfall event size in 0.2 mm categories. Note the “plateau” of the moss (green points)

200 % and various levels of depression in NP at high WC. In contrast, many cyanobacterial lichens have both high WC for optimal NP (around 300 %) and a very high maximal WC, reaching 1200 %. Mosses often reach maximal NP at WC around 100 %, but thalloid liverworts (and some mosses, e.g., Hookeriaceae, Sphagnaceae) can have very high maximal WC, reaching 2000 %, with a less pronounced depression in NP. In general, there is a positive linkage between a high WC for maximal NP and maximal WC.

The difference between mosses and lichens is usually explained as resulting from the greater ability of mosses to separate stored extracellular water from photosynthetic exchange surfaces (Green and Lange 1994). How the external water is controlled in bryophytes is well understood (Buch 1945, 1947; Dilks and Proctor 1979; Proctor 1979a; Proctor and Tuba 2002). A lot of the detailed architecture of bryophyte shoots and ornamentation of their surfaces reflects adaptations to provide capillary spaces for water storage while at the same time leaving surface clear for gas exchange (Buch 1945, 1947; Dilks and Proctor 1979; Proctor 1979a, b, 2009). For lichens, some of the same principles apply. The medulla has wide airspaces, to which the algal cells in the gonidial layer have free access—an efficient “pseudo-mesophyll.” The interior of the thallus is water repellent and protected against waterlogging (like the mesophyll of higher plants); connection to the atmosphere at large probably varies with the species between upper and lower cortex. Storage of water is probably partly internal, and partly in the immediate

environment, depending on species and habitat. At present, there are few morphological explanations for the differences between lichens in the level of depression of NP at high WC, although such changes in structures will be difficult to discover as even a fully active lichen at optimal WC for NP needs a very small proportion of its surface to be air-filled pores for CO₂ exchange. The most robust estimate is 0.2 % for *Ramalina maciformis* (Cowan et al. 1992).

An important result of the depressed NP at high WC is that heavy rain may not lead to increased carbon gain and this effect is clearly shown by *Lecanora muralis* (Lange 2003). When this lichen was thoroughly wetted by heavy rain for 74 days of its active time, the heavily depressed NP and unaffected respiration meant that these days contributed only 4.2 % of its net annual carbon gain compared to the 40.0 % contributed by the 105 days with dew. This contrasts with *Cladonia convoluta* (= *foliacea*), which has no depression at high WC and makes most of its carbon gain following wetting by heavy rain (Lange and Green 2003). Most bryophytes would be expected to behave like *Cladonia convoluta*, as they usually show efficient adaptations, tending to keep surfaces free of water for gas exchange, and only small depressions (up to ~50 %) in NP at high WC (Dilks and Proctor 1979; Alpert and Oechel 1987). Bryophytes are more prominent in wetter and shadier habitats and in more oceanic areas, and lichens are more prominent in drier and more brightly lit places and in continental regions, but there is a great deal of overlap between the two groups.

Bryophytes are suggested to be particularly vulnerable to the effects of partial hydration, probably because they need longer to reactivate photosynthesis than lichens. Stark (2005) found that to fully hydrate patches of dry *Crossidium crassinerve* in the Mojave Desert, a rain event of at least 2 mm was required, and that lesser amounts, together with the rapid drying after rain, can contribute to substantial carbon losses and death (Barker et al. 2005). It is often noticeable that dry bryophytes are water repellent when first wetted; this could be interpreted as insuring that recovery is not started by trivial amounts of rain. The influence of rain on biocrust productivity depends, therefore, not only on the amount of rain but also on the rate of recovery and the quantity of water needed to achieve saturation.

In terms of contribution to overall productivity, the minimum water potential, at which photosynthesis is detectable, is only of academic interest. Respiration is rather different. Even a modest level of carbon loss over weeks could negate a brief period of carbon gain. This is one reason why, once a poikilohydric plant is dry, it needs to be dry enough to stop metabolism altogether. Dryness also prevents fungal attack.

18.8.2 CO₂ Concentration

Biocrusts show the typical and expected saturation curve relationship between NP and CO₂ concentration, but Glime (2007) points out that there is a major difference between lichens and bryophytes for the CO₂ concentration required to saturate

NP. Many lichens studied have their NP at optimal water content saturated with CO₂ at close to present ambient levels (400 ppm; Green and Snelgar 1981), whereas NP of bryophytes is typically not saturated at 1000 ppm CO₂ (Pannewitz et al. 2005; Glime 2007). The compensating CO₂ concentration (the value when NP matches respiratory loss) is around 100 ppm for most bryophytes as might be expected for typical C3 plants. Hornworts (*Anthocerotae*) have a CCM (see below). Lichens show more variability, and all cyanobacterial species and many green algal species possess CO₂ pumps (CCM; Raven et al. 2008) and can have CO₂ compensation points close to zero ppm (Badger et al. 1993; Palmqvist 2000).

The higher CO₂ requirement by bryophytes appears to be related to the absence of a CO₂ pump and to the liquid-phase diffusion resistance between the wet cell wall and chloroplasts of the leaf cells. This liquid-phase diffusion resistance affects lichens as well, but its effect is moderated by the higher effective “ A_{mes}/A ” (area of mesophyll to surface area of leaf) of the gonidial layer. This is in addition (and quite unrelated) to the superincumbent water, which is usually given as the cause of the strong depression of NP in lichens.

Most bryophytes have unistratose leaves; calculation suggests that at current ambient CO₂ concentrations, and assuming a reasonable value for the liquid-phase diffusion resistance between the moist leaf surface and the chloroplasts, the maximum rate at which CO₂ can diffuse into a single surface could be matched by the energy available from a photon irradiance of $\sim 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ —around 14 % of full sunlight (Proctor 2005). A unistratose leaf has two surfaces, and leaves generally overlap on bryophyte shoots. However, not all of that area is available for gas exchange, and in practice photosynthesis is saturated below $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in most mosses (Marschall and Proctor 2004). Many estimates of saturation irradiances are higher, but the actual quantity of light reaching the active centers will also be lowered by filters and refractive surfaces. If CO₂ diffusion limits photosynthesis at high irradiance in many bryophytes, their CO₂ uptake would be expected to respond positively to enhanced CO₂ concentration. The data of Silvola (1985) for mire and forest bryophytes in Finland and Pannewitz et al. (2005) for three Antarctic mosses show that this is indeed so. As Fig. 18.5 shows, temperature and CO₂ concentration interact in their effect on net CO₂ uptake.

Biocrusts are close to the ground by definition, so they exist within the steep gradients of microclimatic factors near the surface. There is some evidence that elevated ambient CO₂ levels can occur in biocrusts, with the highest values observed on moss carpets in the Antarctic, where up to ten times normal ambient CO₂ has been measured (Tarnawski et al. 1992; Green et al. 2000a). Higher levels, 60 % higher than normal ambient concentrations, have also been reported from forest floor moss communities (Tarnawski et al. 1994) meaning that the CO₂ flux is always from the soil to the atmosphere and there is no net CO₂ uptake from the atmosphere by the bryophytes. CO₂ efflux is also reported from biocrust communities and this may be abiotic as it occurs when the surfaces are dry (Rey 2014).

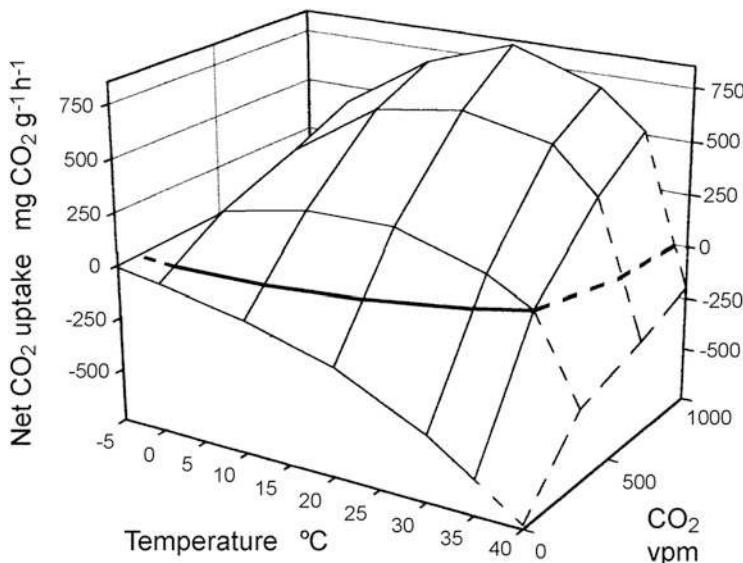


Fig. 18.5 Diagrammatic response of net CO₂ uptake to temperature and CO₂ concentration, at an irradiance (photon flux) of 500 μmol m⁻² s⁻¹, in a boreal forest moss, based on the data of Silvola (1985) for *Dicranum majus*. Broken lines are extrapolated beyond the range of the measurements. The **bold line** shows the compensation point. Note that the temperature optimum for net CO₂ fixation tends to increase with rising ambient CO₂

18.8.3 Light

The response of net photosynthesis to photosynthetically active photon flux density (PFD) for biocrusts is the typical saturation curve (Lange 2001). The light level required to saturate NP (PFD_{sat}) of biocrusts is almost always at, or above, about 700 μmol photons m⁻² s⁻¹ and, because of this, biocrusts have often been referred to as being similar to sun plants (Lange 2001), but they do not reach the NP_{max} associated with such plants although they certainly have higher NP_{max} than species from shadier habitats (Proctor 2014; Robinson and Waterman 2014). It is probable that the high PFD_{sat} (and NPQ) provides protection against occasional high incident PFD. The latter is the situation for lichens in shady rain forests (Green et al. 1997) and is probably also the case for biocrusts (see Sect. 18.9 on activity). PFD_{sat} is dependent on thallus water content, being lower at WC below WC_{opt}, and remains constant or occasionally lower at higher WC (Lange 2001). The light compensation point (PFD_c) is correlated with high PFD_{sat}, and, therefore, biocrusts have relatively high values, often 60 to 100 μmol photons m⁻² s⁻¹, which are also influenced by temperature, being lower at low temperatures.

The maximal apparent quantum efficiency for CO₂ fixation (Φ) is relatively constant at WC greater than WC_{opt} and declines rapidly at lower WC (Proctor et al. 2007a). It also declines with temperature, indicating a negative effect on

photosynthetic fixation pathways (Lange 2001). In general, Φ for biocrusts is around 0.011–0.016 (Table 18.1), which is low compared to higher values for shade lichens (around 0.05) and higher plants, which are around 0.06 and higher.

Overall, the high PFD_{sat} enforces higher compensation points of NP and lower Φ , which make biocrusts less efficient at low light. To some extent this is moderated by lower temperatures.

18.8.4 Responses to Excess Light

Bryophytes and lichens show excellent protection against possible damage by high UVB and PAR (Büdel et al. 1997; Robinson and Waterman 2014). This protection seems to be constitutive, and when the plants are dry and inactive, chlorophyll fluorescence is near zero. Heber et al. (2006a, 2007) conclude that the incoming solar energy is dissipated harmlessly as heat in the reaction centers and antenna of photosystem II (PSII). Where high light prevails, when the organisms are active, different mechanisms operate (Heber et al. 2006b; Kranner et al. 2002, 2008). The Antarctic lichen *Umbilicaria aprina* showed no negative effects after exposure to full sunlight immediately following the first rehydration after a winter buried under snow (Kappen et al. 1998). The Antarctic moss *Bryum argenteum* showed no effects of full sunlight, whether a shade or sun form, and always maintained a high level of xanthophyll cycle constituents (Schroeter et al. 2012). Different mechanisms are used by *Bryum argenteum* to protect against UV radiation and high PFD. Samples with low UV protection replaced the protection within days after renewed exposure to UV, and their NP was not negatively impacted during this time (Green et al. 2000b).

Desiccation-tolerant bryophytes and lichens in sun-exposed situations must be exposed while turgid and metabolically active to light greatly in excess of that needed for carbon fixation, at least for short intervals (Heber et al. 2006b; Demmig-Adams and Adams 2006). In many (perhaps all) of these species, photosynthetic electron flow inferred from chlorophyll fluorescence does not saturate, but continues to rise (often near linearly) at high irradiance (Marschall and Proctor 2004; Proctor and Smirnoff 2011). Similar non-saturating electron flow has been reported by Pannewitz et al. (2003) for *Hennediella heimii* in the Antarctic. In the species that have been investigated (*Schistidium apocarpum* (s.l.), *Syntrichia ruralis*, *Racomitrium lanuginosum*), CO₂, and O₂ act as interchangeable electron sinks, and the non-saturating component of electron flow is to photoreduction of oxygen. It is always associated with high levels of non-photochemical quenching (Proctor and Smirnoff 2011, 2015). Vascular plants and algae prevent reactive oxygen species (ROS) formation by activation of non-photochemical quenching (NPQ), which dissipates excess excitation energy by zeaxanthin-mediated photoprotection harmlessly as heat (Asada 1999, 2006; Niyogi et al. 2005). Although NPQ is found in both algae and plants, these organisms rely on two different proteins for its activation, light-harvesting complex stress-related (LHCSR) protein and

photosystem II subunit S (PsbS). In the moss *Physcomitrella patens*, both proteins are present and active (Gerotto et al. 2012). The algal protein has yet to be demonstrated in other mosses, but the presumption is that it will occur. The presence of alternative quenching systems is also present in lichens, as shown by the constant yield at all incident PFD for many Antarctic lichens (Schlensog and Schroeter 2000). One result of the presence of an alternative electron sink is that electron transport rate (ETR) calculated in fluorescence measurements is a poor indicator of CO₂ fixation, although useful in other ways for interpreting performance.

18.8.5 Temperature

Many mosses and lichens maintain modest (sometimes substantial) net CO₂ uptake at or even a few degrees below 0 °C. Limitation of photosynthesis and respiration probably arises mainly from water loss, as ice forms outside the cells. As temperature increases, net CO₂ uptake rises to a maximum at the optimal temperature, before declining again at higher temperatures, ultimately reaching a point where photosynthesis fails to balance respiration, and net CO₂ exchange again becomes negative. Thus, there is an upper temperature compensation point, which sets a limit to the highest temperature at which the bryophyte can grow. As Fig. 18.6 shows, the

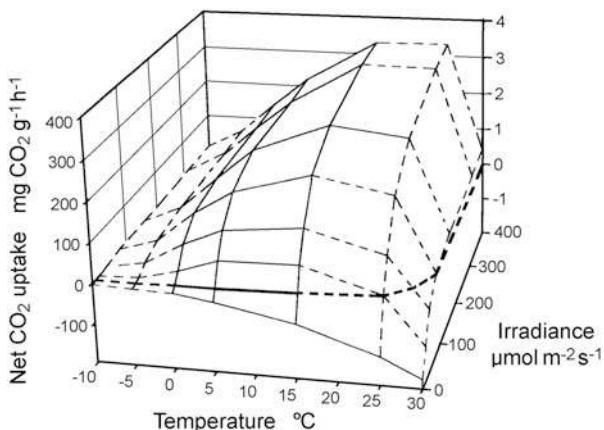


Fig. 18.6 Diagrammatic response of net CO₂ uptake to irradiance and temperature at ambient CO₂ concentration in a common temperate moss, based on the data of Stålfelt (1938) for *Hylocomium splendens*. Irradiances in the original measurements were expressed in kilolux and have been roughly converted to equivalent quantum flux units. Broken lines are extrapolated beyond the range of the measurements. The *bold line* shows the compensation point, the line of zero net CO₂ exchange. Note that the temperature optimum for net CO₂ fixation tends to increase with irradiance, and the light saturation level rises with increasing temperature (modified from Proctor 2011)

compensation point is in fact one line varying with irradiance and temperature. Cyanobacterial lichens provide an interesting exception by being unable to carry out positive NP below freezing point (Lange 1965). As a result, they are excluded from the main continent of Antarctica (Green et al. 2011b) and also from high-elevation habitats.

Biocrusts show a wide range of optimal temperatures for net photosynthesis (T_{opt}) that show a strong link to the temperatures of their habitats. Optimal temperatures in polar regions are low. Mosses from the Ross Sea region had optima of 6.8 °C for *Ceratodon purpureus*, 9.1 to 15.9 °C for *Bryum argenteum*, and 12.0 °C for *Bryum pseudotriquetrum* (Pannewitz et al. 2003), while green algal lichen biocrusts ranged from 5 °C at Darwin area (80°S latitude) to 17 °C at Homburg (Germany, 50°N; Colesie et al. 2014b). Biocrusts in arid areas range from 21 °C (*Fulgensia fulgens*, *Diploschistes diacapsis*) to 29 to 32 °C, *Collema tenax*, *Cladonia convoluta*, *Squamaria lentigera*, and *Collema cristatum* (Table 18.1). This wide range for temperature optima contrasts with the limited range in PFD required to saturate photosynthesis.

It is known that some soil crust lichens can almost fully acclimate their respiration rates, so that there is no change in DR at mean habitat temperatures (Lange and Green 2005). This ensures that respiration rates do not increase at warmer times of the year, but it also means, because gross photosynthesis will be increasing with temperature, while DR remains relatively constant, that optimal temperatures for NP will also rise (Sun and Friedmann 2005). The means by which the acclimation in respiration occurs is not known, but it also offers a mechanism to adjust the optimal temperature for NP.

18.9 Reality: The Duration of Active and Inactive Periods

18.9.1 Background

Biocrusts are all poikilohydric and being terrestrial will almost certainly be desiccated on many occasions and for various lengths of time. When desiccated, the biocrusts are dormant and can withstand extremes in temperature (cold and hot) and light. Tolerance to these extremes is adaptive and does not occur in poikilohydric organisms that do not meet these environmental stresses (e.g., Green et al. 1997, 2011a). They represent a different set of adaptations to those utilized when the biocrusts are active when they are under much more moderate conditions (Green et al. 2007). In order to interpret the response of CO₂ exchange of biocrusts to environmental factors, it is necessary to know when biocrusts are active and under what conditions. Knowledge about the times when biocrusts are active can also inform the choice of conditions in laboratory-based investigations and assist interpretations of field manipulations. If the object is simply to record inactive and active periods, electrical resistance with a suitable data logger is an obvious choice

(Proctor 2004); it can be employed at various levels of sophistication (Weber et al. 2016). Some bryophytes look strikingly different wet and dry (e.g., *Syntrichia ruralis* and related species); for these a visual system can be used, based on a web camera (Graham et al. 2006). Hamerlynck et al. (2000) used changes in albedo to follow the hydration state of *Syntrichia ruralis*. Monitoring of environmental conditions such as air temperature, thallus temperature, incident PFD, wet/dry, and relative humidity is now a routine matter with data loggers coupled with sensors with response times that match environmental changes.

Two main forms of monitoring have been used to track photosynthetic activity, CO₂ exchange and chlorophyll fluorescence. Gas exchange is the gold standard to monitor biocrusts. The significant advantage is that, because actual CO₂ exchange is measured, it is possible to calculate carbon budgets with accuracy only limited by the capabilities (and errors!) of the system. Modern portable CO₂ infrared gas analyzer (IRGA) systems require only minutes to make measurements on samples, and, provided such measurements are made at suitable time intervals, then information about diurnal or daily activity patterns can be obtained (e.g., Lange et al. 1990, 1994). Automatic systems have been produced, with which measurements for periods up to 16 months have been made, and allow calculation of annual carbon budgets for biocrust plants. The major limitation with gas exchange-based systems is that only one sample can be measured, and, as with the manual systems, the sample has to be enclosed to make the measurement, leading to uncertainties about whether microclimate is representative.

The major advantage of chlorophyll fluorescence (Maxwell and Johnson 2000; Baker 2008) is that it is noncontact and noninvasive, so that samples can be measured *in situ* without disturbance or harm, and is also quick and easy. Of the commonly calculated parameters, F_v/F_m , which measures the maximum quantum yield, is often used in vascular plant physiology as a measure of “stress” and recovery. Effective quantum yield (Φ_{PSII}) is the fraction of excitation energy flowing through photosystem II, and with some crop plants, it is a reasonable (and much more easily measured) surrogate for photosynthesis. Non-photochemical quenching (NPQ) is largely a measure of the harmless dissipation of excitation energy as heat. These three measures are dimensionless ratios and are not influenced by, for instance, distance of measuring probe from the sample. Automatic systems have been developed, which allow measurements at suitable intervals for long periods, sometimes years (Pintado et al. 2010; Raggio et al. 2014; Barták and Váczí 2014).

Measurements of chlorophyll fluorescence in vascular plants are an unreliable guide to its use to best effect with poikilohydric plants. The use of maximal quantum efficiency, F_v/F_m , as a stress-and-recovery measure presupposes that F_m remains constant. A higher plant leaf is a population of cells, all of the same age, functioning as an integrated whole; a moss shoot is a population of cells of different ages. It is reasonable to expect the cells of the leaf to behave in more or less the same way. In the moss shoot, the older cells may die and the younger recover; it only takes a small proportion of tissue to survive to create a wholly misleading impression of the response of the tissue as whole. That makes changes in F_m

important, too. Similarly, ETR (relative electron transport rate) is not a good indicator of net photosynthesis for biocrust photosynthetic organisms because some of the electron flow (sometimes the majority at high irradiance) through PSII is related to photoprotection rather than to carbon fixation (Green et al. 1997; Proctor and Smirnoff 2011). However, the presence of a chlorophyll fluorescence signal for Φ_{PSII} is an excellent indicator that the studied photosynthetic organism is hydrated and has active photosystems, and from this, the active time and relationships between activity and concurrent environmental conditions can be determined.

Considerable confusion exists because some authors specifically report chlorophyll fluorescence studies as photosynthesis (Hui et al. 2014 among others) or have incorrectly utilized Φ_{PSII} as an indicator of photosynthetic capacity (e.g., Wertia et al. 2012). Chlorophyll fluorescence is at its most powerful when used in conjunction with gas exchange.

18.9.2 Dry (Inactive) Periods

Long periods of continuous dryness are surprisingly rare. The longest “rainless” (<0.2 mm of rain) period recorded in the British Isles in the twentieth century was 59 days, from August to October 1959; there were five other “rainless” periods of 45 days or more, all between April and October, and all in the second half of the century (Dukes and Eden 1997). In two years’ recording of *Grimmia pulvinata* cushions on a wall top in Devon, UK (Proctor 2004), the longest dry periods recorded were 367 h (15.3 days) in April–June 1989 and 268 h (11.2 days) in October–December the same year (Table 18.2).

Table 18.2 *Grimmia pulvinata*

Time interval	Quartile 1	Median	Quartile 3	Maximum	Midpoint of logistic fit
Dry					
Jan–Mar 1989	1.8	5.5	12.0	123.5	4.76
Apr–June 1989	2.3	5.5	29.1	367.0	7.30
Jul–Sep 1989	6.5	25	104.5	255.0	52.94
Oct–Dec 1989	2.8	9.8	27.1	267.5	9.48
Wet					
Jan–Mar 1989	2.1	14.5	37.3	161	26.59
Apr–June 1989	1.5	6.5	17.0	72.0	13.83
Jul–Sep 1989	1.5	10.0	17.5	152.5	10.91
Oct–Dec 1989	0.9	11.0	103.8	669.0	17.66

Length of moss-wet and moss-dry intervals recorded at Murchard Bishop, Devon, UK, during 1989: descriptive parameters (hours). The logistic fit tends to be truncated at its upper end for wet periods in winter and for dry periods in summer; its midpoint (representing the steepest point on the fitted curve and the mode of the fitted distribution) is then substantially greater than the (nonparametric) median value of the raw data

Rainless periods in more arid climates can be much longer, but may be punctuated by summer thunderstorms and by nighttime dew deposition. Stark (2005) monitoring the moss species *Crossidium crassinerve* in the Mojave Desert reported dry periods generally being <25 days, but with one or two periods from 26 to 150 days and one exceptional period of 191 days in 2002. In Tabernas Desert the longest period without activity was 48 days but dry periods longer than 16 days occurred only twice in the year.

Survival for very long periods of desiccation (tens of years) have been reported (Bristol 1916; Malta 1921; Maheu 1922; Keever 1957; Breuil-Sée 1993), but are probably of little ecological relevance. That is subject to the qualification that biocrust organisms pass a substantial fraction of the time at temperatures up to 60 °C; Hearnshaw and Proctor (1982) found that survival time of dry bryophytes declined steeply with temperature, while Lange (1955) showed that dry mosses showed an annual cycle in the lethal temperature (30 min treatment) being around 15 °C higher in summer at around 93 to 105 °C. Surprisingly, lichens seem to show a lower ability to tolerate long periods of desiccation than bryophytes and even DT vascular plants (Green et al. 2011a).

18.9.3 Wet (Active) Periods

On a wall top in Devon (UK), the longest “moss-wet” period in 1989 was 669 h (27.9 days, Table 18.2). This accords well with expectation and with autumn as the season when mosses grow the most. But the medians of the data and the estimates derived from the logistic fits tell a different story, which is, there is surprisingly little difference between the length of the moss-wet periods between the summer and winter seasons of the year. Stark (2005) found in the Mojave Desert that longest continuous hydration was 17 and 14 days and that most of wet periods were 4 days or shorter. In Tabernas Desert the longest period in which activity occurred during each day (i.e., could be a dew event) was 33 days. However, for biocrusts at more temperate sites, active periods in winter can last several months, up to around 140 days. At alpine sites, the active period could be most of the year depending on snow coverage and also on the activity state of biocrusts under snow.

Desiccation-tolerant bryophytes (and lichens) are preeminently organisms adapted to frequent, and often short, dry–wet cycles, but it is also clear that in wetter, temperate, or alpine sites, the wet periods are definitely not short.

Considering data obtained from monitoring periods of around 1 year or longer, annual activity varies over a large range from 4.6 % for the lichen *Umbilicaria aprina* at Botany Bay, 77°S; in Antarctica through 46 to 55 % for *Usnea aurantiaco-atra* at Livingston Island, 62°S; and to 65.6 % for *Cladonia convoluta* in Germany, 52°S (Schroeter et al. 2000, 2010; Lange and Green 2003). In the Tabernas Desert, the driest area of Europe, *Diploschistes diacapsis* was active for only 20 % of the year (Pintado et al. 2010). The differences in the length of the active periods in these examples certainly reflect the different severity of the

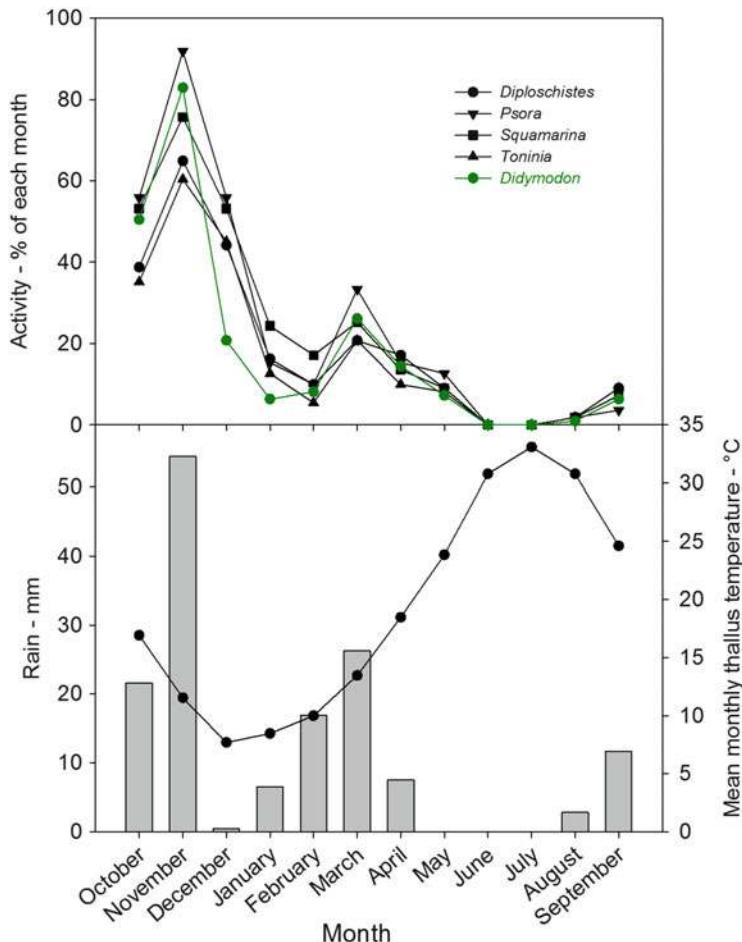


Fig. 18.7 Upper panel: monthly activity (% of month) for four lichens and one moss at Tabernas Desert, Almeria, Spain, from October 2012 to September 2013 (modified from Raggio et al. 2014). Lower panel: monthly rainfall (mm) and mean thallus temperature ($^{\circ}\text{C}$, mean of all species) for the same period

habitats, particularly in terms of available water for hydration. Belnap and Lange (2005) give the activity periods for six lichens, which were all monitored at the same location. Annual activity varies from 34.4 % for *Fulgensia fulgens* to 65.6 % for *Cladonia convoluta* and this must reflect different hydration strategies by the species.

Activity also varies through the year, as can be clearly seen in the data for four lichens and a moss in the Tabernas Desert, Almeria, southern Spain (Fig. 18.7, modified from Raggio et al. 2014). Monthly activity is zero for the two dry months June and July, but reaches around 80 % in November. The activities of the lichens

and moss all follow a similar general pattern, tracking rain and dew events, suggesting that activation by humid air, only reported for lichens, is not significant.

18.9.4 Activity, Light, and Temperature

Because biocrusts will desiccate and become dormant especially under high incident radiation, conditions when they are active may diverge from the overall distribution of an environmental factor. An example is given in Fig. 18.8 for thallus temperature of *Diploschistes diacapsis* in Tabernas Desert. Very high temperatures can occur in summer months, reaching over 50 °C, but the lichen is inactive at these times. Most activity occurs between 10 and 15 °C and only rarely above 20 °C. *Psora decipiens*, also in the Tabernas Desert, also shows this divergence for both thallus temperatures and incident PFD (Fig. 18.9). This deviation has been reported for many species from diverse ecosystems such as temperate steppe vegetation (Lange 2003), Tabernas Desert (Pintado et al. 2010; Raggio et al. 2014), and Antarctica (Schlensog et al. 2013; Green et al. 2007). An impressive example is that of *Umbilicaria aprina*, which had almost identical temperature when active in continental (77°S) and maritime (62°S) Antarctica, despite a difference of around 10 °C in annual mean temperature (Green et al. 2011b). Schlensog et al. (2013) compared the summer activity of lichens and bryophytes at a single site on Leonie Island, Antarctic Peninsula, and showed that the bryophytes in the wetter flush area were much more active than the lichens, which dried regularly, and that species with high activity were more strongly coupled to the general environment than those with low activity. This can be seen in Fig. 18.9, where active and overall conditions of PFD and temperature converge in the winter, the period of higher activity, and most strongly diverge in the autumn and spring.

Fig. 18.8 Distribution of thallus temperatures of *Diploschistes diacapsis* for the year 2013. The x-axis is thallus temperature in 5 °C categories; and the y-axis is the number of data points (reading taken every 30 min) with these temperatures. The height of the bar is the total number of times that temperatures in a particular band occurred and each bar is divided into the active (dark portion) and inactive (gray portion) periods

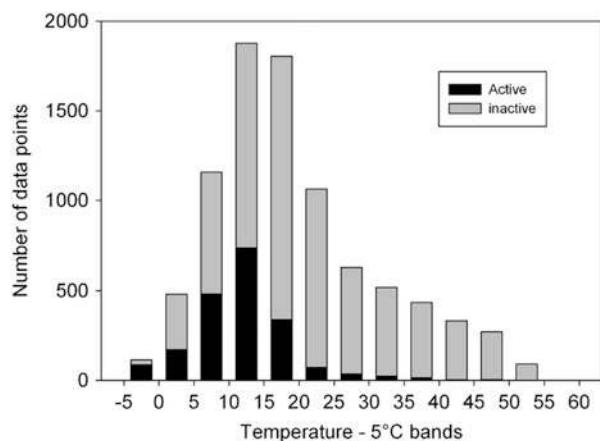
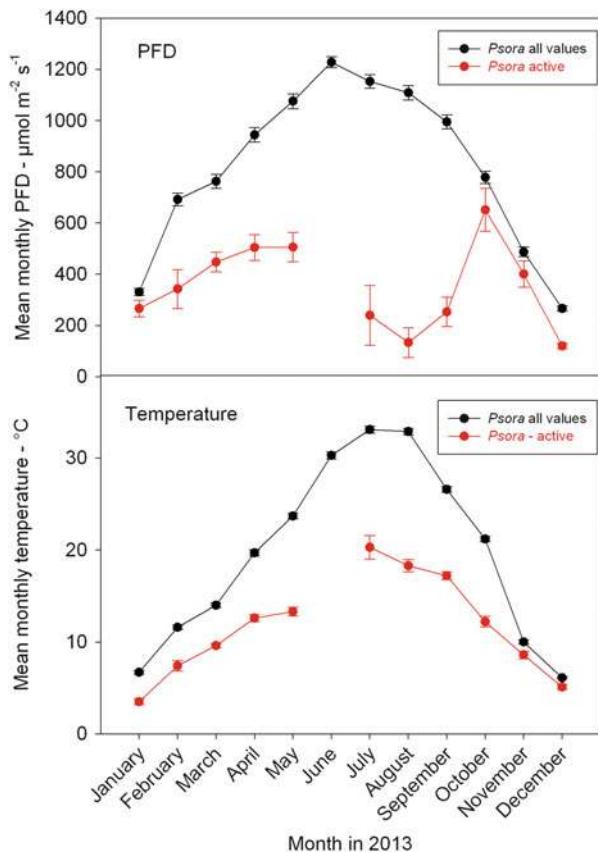


Fig. 18.9 Mean monthly values for incident photon flux density (PFD, upper panel) and thallus temperature (lower panel) for the lichen *Psora decipiens* for the year 2013 at Tabernas Desert, Almeria, Spain. In each panel, the black symbols represent the mean of all values (in the case of PFD, zero values are excluded) and the red symbols are when the lichen is active. The lichen was not active in June



18.10 Conclusion: Adaptation, Flexibility, and Plasticity

By necessity of their lifestyle, all biocrust organisms are small, and, because of this, the organisms making up biocrusts are often regarded as being “simple” in contrast to vascular plants. Ever since their origin in the Paleozoic, cells of vascular plants have been subject to entirely different selection pressures from those of poikilohydric plants. Vascular plant cells have a (quasi)-constant water supply, and water potential is constrained within narrow limits, thanks to a combination of roots, a conducting system, an impermeable cuticle, and stomata. Poikilohydric plant cells have, by contrast, to live with whatever diverse conditions their environments throw at them. This arises partly as a result of the difference in scale and partly from the difference in life strategy (Proctor and Tuba 2002; Proctor 2014). Neither does small size mean simple metabolic ability, there is growing evidence that lichens and mosses, in particular, are metabolically versatile and show a large

range of acclimation to environmental factors. We should not, therefore, be surprised when we find evidence for such adaptive changes or acclimation. The scale of the changes and ability to adapt or acclimate will, of course, be species dependent and can be expected to vary between organisms, even within a single habitat. It follows that while some species can span many environments, with the moss *Bryum argenteum* being one of the better examples (Longton 1981), in most cases a change in environment will bring about a change in species. For example, strong relationship between water regime and lichen, moss and hepatic diversity is present across the latitudinal gradient of Antarctica (Green et al. 2011b). Major changes with climate will result in alterations in biodiversity due to the arrival of better-adapted species and the inability of existing species to sufficiently adapt and remain competitive.

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Part IV

**Interactions Between Biological Soil Crusts
and Vascular Plants**

Chapter 19

Interactions of Biological Soil Crusts with Vascular Plants

Yuanming Zhang, Asa L. Aradottir, Marcelo Serpe, and Bertrand Boeken

19.1 Introduction

In most dryland ecosystems, biological soil crusts (biocrusts) coexist alongside herbaceous and woody vegetation, creating landscape mosaics of densely vegetated and biocrust-covered patches (Boeken and Shachak 1994; Belnap 2003; Cortina et al. 2010; Maestre et al. 2010). The patterns and dynamics of these patches are affected by multiple direct and indirect interactions between vascular plants and biocrusts and include negative and positive effects (Fig. 19.1).

In general, the influence of biocrusts on vascular vegetation is the result of interactions among biocrust type, vascular plant characteristics, and local climatic, environmental, and edaphic conditions. Differences in biocrust composition and substrate result in diverse morphological, physical, and chemical features that create unique microenvironments of temperature, nutrient and water availability, and trapping of organic matter and seeds. The manner in which biocrusts affect the capture and retention of plant seeds, the availability of water and nutrients, and the

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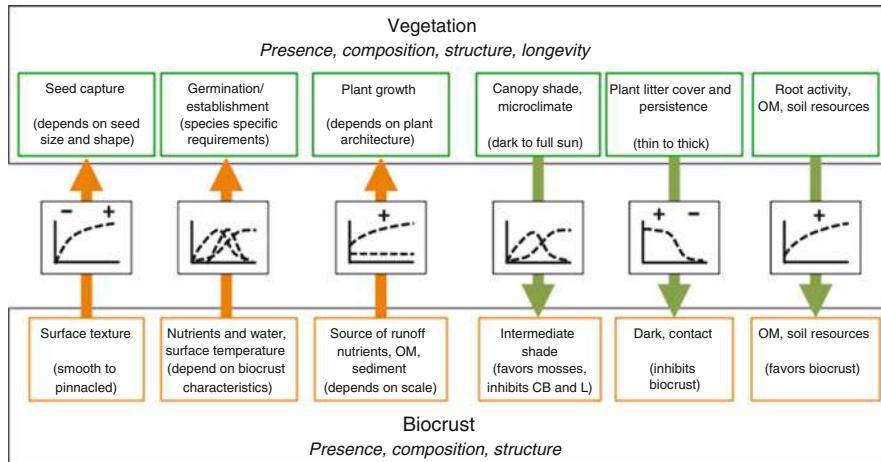


Fig. 19.1 Schematic diagram of the positive and negative mutual interactions between biocrust and vegetation and their dependence on various functions and properties of both (CB cyanobacteria, OM organic matter, M mosses, L lichens, Sp species)

temperature of the soil surface will ultimately determine whether crusts promote, inhibit, or have negligible effects on vascular plant communities. Furthermore, the effects of biocrusts on plants are not restricted to the crust-covered patches themselves, as they alter local hydrology (see Chap. 17 by Chamizo et al.) and nutrient cycles (see Chaps. 14 and 15 by Barger et al. and Sancho et al., respectively), thus influencing the availability of water and nutrients reaching nearby plants (Boeken and Orenstein 2001). The vascular plant communities, in turn, can affect biocrust presence, development, and composition through canopy shade, water relations, litterfall, and root activity, all of which vary depending on plant density, composition, and phenology.

19.2 Influences of Biocrusts on Colonization and Seedling Emergence of Vascular Plants

19.2.1 Seed Arrival, Retention, and Accumulation

Widespread seed dispersal is common in open habitats, where wind and water move seeds across the soil surface until they are trapped by depressions or barriers (Boeken and Shachak 1994; Jumpponen et al. 1999; Marteinsdottir et al. 2010). Biocrusts have diverse microtopographies (George et al. 2000; Davidson et al. 2002; Bowker et al. 2006; Langhans et al. 2009) that affect their ability to trap seeds, mainly depending on surface roughness in relation to secondary seed dispersal. In addition, external seed morphology, such as seed appendages, is

believed to influence germination via effects on water absorption (Harper 1977; Fenner and Thompson 2005; Baskin and Baskin 1998) and to affect dispersal through either enhancing seed movement (e.g., to escape competition or predation) or inhibiting it (e.g., retention in a favorable environment) (Harper 1977; Fenner and Thompson 2005; Gros et al. 2006; Boeken and Shachak 1994). The appendages may also reduce the ability of seeds to fall through cracks in the biocrust. This may explain observations in the Gurbantunggut Desert (NW China), where seeds with appendages were virtually absent in the soil beneath moss and lichen biocrusts. Furthermore, plants having seeds with appendages were rarely found in these biocrusts. In contrast, plants having seeds with appendages were present in bare soil following biocrust disturbance or in cyanobacterial crusts (Zhang unpublished data).

The effects of biocrusts on seed retention and the soil seed banks are highly species specific and range from positive (Bliss and Gold 1999; Boudell et al. 2002) to minimal (Boeken et al. 2004; Megill et al. 2011) to negative (Boeken and Shachak 1994; Li et al. 2005; Clements et al. 2007). This variability is primarily related to the type of biocrust, as pinnacled and rolling crusts found in cool and cold deserts are able to trap seeds more effectively than smooth crusts common in hot deserts (Belnap 2003). For instance, two biocrusts with high surface roughness due to the presence of foliose lichens or mosses promoted both seed entrapment and seed bank accumulation in arid lands of Patagonia (Bertiller and Ares 2011) and Northern China (Su et al. 2007), respectively. However, increases in roughness due to biocrusts do not enhance seed entrapment in all cases (Olano et al. 2005; Clements et al. 2007). For example, Li et al. (2005) found that a moss biocrust decreased seed entrapment and seed density in the soil seed bank despite the added roughness.

On undisturbed surfaces of smooth cyanobacterial crusts typical for hyperarid deserts, seeds are exposed to removal by wind, surface water runoff, and granivory (Boeken and Shachak 1994). Therefore, soils under this type of crust often have limited seed banks (Prasse and Bornkamm 2000; Boeken et al. 2004; Li et al. 2005). Some species overcome the physical barrier formed by flat, dense cyanobacterial crusts (and generally underlying physical crusts) by specific adaptations. For instance, the annual grass *Stipa capensis*, which dominates the smooth and dense cyanobacterial crusts in semiarid zones of North Africa and the Middle East, has specialized soil positioning and penetration mechanisms mediated by hygrocastic awn movement (Boeken and Shachak 1994, 2006). Seeds of the annual forb *Plantago coronopus*, which are dispersed from the dead parent plant during rainfall, adhere to cyanobacterial crusts by means of a mucilaginous seed coat and are thus relatively well protected against removal by water and granivores (Gutterman and Shem-Tov 1997).

19.2.2 Seed Germination and Seedling Emergence

Seed germination requires water imbibition under adequate temperature, which is followed by an increase in seed metabolic activity and subsequent radicle growth and emergence (Fenner and Thompson 2005; Finch-Savage and Leubner-Metzger 2006). Most studies on the effect of biocrusts on germination are not limited to the events leading to radicle emergence, but also include subsequent seedling growth and early survival. These stages are collectively the most precarious in the life cycle of most vascular plants, and the environmental conditions required for germination and establishment may determine the niche of many plant species (Grubb 1977).

According to Belnap et al. (2003), biocrusts generally enhance germination and emergence in cool deserts, but the response is more ambivalent in hot deserts. Recent studies summarized below support this analysis and furthermore demonstrate that the effect of biocrusts is both species specific and dependent on the biocrust type. Species-specific effects were, for example, reported by Godinez-Alvarez et al. (2012), who found positive effects of both a cyanobacterial biocrust and a mixed moss–cyanobacterial biocrust from a tropical desert in Mexico on the germination of *Agave marmorata*, but no effects on either *Prosopis laevigata* or *Neobuxbaumia tetetzo*. Similarly, positive but species-specific effects of biocrusts on seedling emergence were reported for herb species in a xeric Florida shrubland (Hawkes 2004) and for germination of arctic species in moss-covered patches as compared to bare gravel moraines in Svalbard (Muller et al. 2011). The subshrub *Atractylis serratuloides* (Asteraceae), also common to shrub- and grasslands in the same region, germinates well on cyanobacterial biocrusts (Elbaz 2012). This is partly because single seeds germinate within the intact *capitulum* after being stuck near small exposed rock fragments (Elbaz 2012). Most other annual and perennial dryland plants of North Africa and the Middle East lack mechanisms enabling germination on undisturbed biocrusts (Boeken and Shachak 1994; Boeken 2008). Unlike *Stipa capensis*, native grass species of the region, like *Bromus*, *Avena*, and *Schismus*, are therefore found more in disturbed, fragmented biocrust areas (Boeken and Shachak 1994; Boeken and Orenstein 2001; Zaady et al. 2003; Boeken 2008). In these grasses, seeds are dispersed within complete spikelets, ensuring efficient movement by wind across intact biocrusts and increased seed trapping in places with biocrust disturbance (Boeken and Shachak 1994). These mechanisms may play an important role in the invasiveness of Mediterranean annual *Bromus* and *Schismus* species (especially *Bromus tectorum*) in areas with extended biocrust disturbance in the western USA, South Africa, and Australia (Hernandez and Sandquist 2011; Peterson 2013; Belnap and Weber 2013; Milton 2004). Biocrust restoration may reduce these invasive species, but may enhance biocrust specialists such as *Stipa capensis*.

The inhibitory effects of biocrusts can be species specific, as reported by Zhang et al. (2010), who found not only dissimilar effects of biocrusts on the germination of desert species on semifixed sand dunes in China, but that the effect on different species varied depending on environmental conditions (dry or wet soil).

Germination experiments with three annual species on intact, crushed, or autoclaved cyanobacterial biocrust from a semiarid Negev shrubland (Zaady et al. 1997) also showed species-specific inhibition that was mechanical, related to the presence of cyanobacteria, or a combination of both. Seed size seems to be an important factor determining whether biocrusts inhibit germination. Briggs and Morgan (2011) found reduced germination of the large-seeded subshrub *Maireana excavata* in southeastern Australia on intact moss biocrusts, while three other species with smaller seeds had similar final germination success on intact and disturbed biocrusts. A number of other studies have demonstrated effects of biocrust type on germination and emergence of vascular plants. Higher seedling emergence has been reported in biocrusts dominated by mosses than algae (Su et al. 2007) or lichens (Deines et al. 2007; Serpe et al. 2006) and higher germination in a mixed biocrust with lichens and mosses than in a biocrust dominated by crustose lichens (Serpe et al. 2008). Greater seedling emergence was found after sowing on the foliose lichen *Squamaria cartilaginea* than on the crustose lichen *Diploschistes diacapsis* (Escudero et al. 2007). Furthermore, as biocrust characteristics may change with time, their effect on germination may vary with biocrust age as showed by Langhans et al. (2009), who found higher seedling emergence on older, stable biocrusts than on early successional biocrusts. On the other hand, Su et al. (2007) found no clear trend in germination with biocrust age.

19.3 Influence of Biocrusts on Seedling Establishment

19.3.1 Survival and Growth of Seedlings

Once vascular plant seedlings have emerged, biocrusts may provide favorable conditions for their survival and growth (Belnap et al. 2003; Boeken 2008). Such positive effects have been observed under greenhouse and field conditions (Danin and Nukrian 1991; Elmarsdottir et al. 2003; Godinez-Alvarez et al. 2012; Lesica and Shelly 1992; Seghieri et al. 1997; Zhang and Nie 2011). In a controlled environment, St. Clair et al. (1984) observed that the establishment of three grass species was higher in an undisturbed mixed biocrust than in a trampled one. On eroded areas in Iceland, higher seedling densities and reduced seedling mortality of several species were observed in microsites with biocrusts compared to sparsely biocrusted ones; these effects have been attributed to less soil erosion and frost heaving in the more biocrusted microsites (Aradottir and Arnalds 2001; Karlsdottir and Aradottir 2006). Biocrust effects on seedling survival and growth can also vary according to both biocrust type and plant species. In an algal-dominated biocrust from a temperate region (Cape Cod, USA), seedling survival of two plants, *Deschampsia flexuosa* and *Morella pensylvanica*, was higher than in a lichen–moss biocrust (Thiet et al. 2014). However, a moss-dominated biocrust increased

the survival of *Morella pensylvanica* as compared to the bare soil control, but did not influence *Deschampsia flexuosa* (Thiet et al. 2014).

In contrast to the above results, various studies have shown that disturbance or removal of biocrusts can cause an increase in survival and growth of seedlings (Beyschlag et al. 2008; Hernandez and Sandquist 2011; Langhans et al. 2010; Li et al. 2006). These studies included cyanobacterial, mixed, smooth, and rugose biocrusts. In some cases, the specific biocrust characteristics that were responsible for reduced establishment are unclear. Nevertheless, the results suggest that physical, chemical, and biological conditions created by intact biocrusts limit seedling establishment in many plant species. Disturbance can temporarily increase nutrient release from biocrust organisms, which may be particularly beneficial for seedling establishment in nutrient-poor soils (Beyschlag et al. 2008). In semiarid Negev ecosystems, seedling establishment in annuals benefits from biocrust disturbance and removal, perhaps because these events can increase water infiltration rate and reduce runoff (Eldridge et al. 2000, also see Chap. 17 by Chamizo et al.).

Most biocrusts are not considered a barrier to root penetration or root growth (Belnap and Gardner 1993). However, biocrust organisms may slow down these processes, extending the period when the seedlings are more vulnerable to environmental stresses (Escudero et al. 2007; Zamfir 2000). Even when seeds germinated, the establishment of two grasses on the crustose lichen *Diploschistes muscorum* was negligible because the roots were not able to penetrate the lichen thallus and many root tips became necrotic (Serpé et al. 2008).

Apart from a mechanical effect, the extracellular components of crust organisms may affect root elongation by other mechanisms. Lichens in particular are known to produce compounds that affect the soil pH or have allelopathic properties (Concostrina-Zubiri et al. 2013; Frahm et al. 2000; Molnar and Farkas 2010). Some of these compounds have been shown to reduce seedling growth under laboratory conditions (Favero-Longo and Piervittori 2010; Tigre et al. 2012) although field tests of allelopathy are lacking. Moreover, biocrust types vary in their hydrophobicity (Drahorad et al. 2013; Kidron and Büdel 2014). A more hydrophobic environment will tend to be less favorable for water uptake by emerging roots (Blackwell 2000), thus reducing root growth and potentially decreasing survival. Presently, however, little is known about the significance of crust hydrophobicity on early seedling growth under field conditions.

It is worth noticing that negative effects of biocrusts on seedling establishment may be important for the functioning of arid and semiarid ecosystems as a whole. The inhibitory effect of biocrusts on vascular plant establishment appears to be more common for large-seeded weedy and exotic species than for native plants, which may increase habitat resistance to exotic plant invasions (Hernandez and Sandquist 2011; Li et al. 2006; Morgan 2006). Moreover and independent of species-specific effects, the decrease in seedling establishment can reduce biocrust fragmentation over the landscape, contributing to a patchy vegetation distribution. In arid environments, such mosaics can increase biodiversity, reduce fuel loads, and result in a better utilization of limited resources such as water and nutrients (Shachak et al. 1998; Boeken and Orenstein 2001; Eldridge et al. 2002; Peters

et al. 2006). For example, in arid regions, runoff of water and nutrients from biocrusted areas may be required to support downslope vegetation patches, whereas if biocrusts are broken, the resulting highly localized infiltration prevents sufficient water and nutrients from reaching downslope vegetation (Eldridge et al. 1999). This runoff also creates “islands of fertility” (Shachak et al. 1998; Boeken and Orenstein 2001) or bands of vegetation, which can be critical for plant survival and growth (Belnap 2006; Rodriguez-Caballero et al. 2013). Thus, limitations of vascular plant establishment on the biocrust *per se* may benefit plant growth at larger spatial scales (Bowker et al. 2010; Eldridge et al. 2002).

19.3.2 Biomass Accumulation and Allocation

Many studies have reported a positive effect of biocrusts on biomass and productivity of vascular plants (DeFalco et al. 2001; Pendleton et al. 2003; Langhans et al. 2009), although species-specific (Lan et al. 2014) or negative (Boeken and Shachak 1994; Thiet et al. 2014) effects have also been observed. The positive effects of biocrusts on biomass production are ascribed to enhanced soil conditions under biocrusts compared to bare soil, including greater content of soil organic matter and inorganic nitrogen (N; DeFalco et al. 2001; Pendleton et al. 2003).

Under natural conditions, the presence of biocrusts has been correlated with increases in plant biomass in different habitats (Langhans et al. 2009; Liu et al. 2013; Zhang and Nie 2011). In cold deserts of western North America, biomass of native plants was higher in biocrust-covered soils than adjacent bare areas (Belnap and Harper 1995; Brotherson and Rushforth 1983). Similarly, in the sandy Gurbantunggut Desert of northwestern China (Zhang and Nie 2011), the presence of biocrusts was associated with higher biomass of vascular plants, but only of herbaceous species. However, another study from the same area indicates that biocrusts can increase biomass accumulation of woody species as well. Liu et al. (2013) compared the growth of a clonal shrub, *Eremosparton songoricum*, on two microsites, one with naturally moving sand and one where the sand had been fixed by the straw checkerboard method. Sand fixation by well-developed biocrusts was correlated with higher plant biomass per unit area than in non-fixed sand. Similar observations of higher herbaceous and woody plant cover and biomass on biocrust-stabilized dunes were made in the sandy deserts of the Negev (Tsoar 2005), where biocrusts prevent plant burial and denudation and reduce deep infiltration (Kidron and Yair 1997). In contrast to sandy soil, absence or removal of biocrusts on heavier, loessial, or loamy soils increases plant biomass (Boeken and Shachak 1994; Eldridge et al. 2000). This may be partly due to higher water and seed capture.

Allocation of biomass to roots is expected to decrease with increased soil fertility (Van Wijk 2011). Consequently, root-shoot ratios of plants growing on biocrusts may be lower than those of plants growing in uncrusted soils. In agreement with this hypothesis, Bliss and Gold (1999) and Pendleton et al. (2003)

reported lower root–shoot ratios of plants associated with biocrusts than those growing without crusts. Langhans et al. (2009) found that root–shoot ratios decreased with biocrust age, indicating less allocation to roots with improved fertility. Furthermore, Thiet et al. (2014) showed that seedlings in biocrusts had shorter roots than bare ground controls. However, the presence of biocrusts is not always related to a decrease in the root–shoot ratio. For example, Liu et al. (2013) found higher root–shoot ratios on fixed than non-fixed sand, even though the fixed sand had a higher content of organic matter and N than the non-fixed one. Perhaps, under the dry conditions of desert sand with high infiltration rates, the low water status of the plants was a more important factor in determining the root–shoot ratio than soil fertility.

Overall, our literature review indicates that biocrusts tend to increase biomass of vascular plants. In addition, disturbance of biocrusts caused by trampling can transiently enhance biomass accumulation. At a small scale, these disturbances may be important for plant establishment in certain environments (Beyschlag et al. 2008; Zhang unpublished data). However, large-scale or frequent disturbance of biocrusts most likely reduces biomass accumulation by altering patterns of water infiltration and runoff and by preventing the buildup of organic matter and nutrients associated with the crust presence (Belnap 2006; Eldridge et al. 2002).

19.3.3 Phenology and Sexual Reproduction

Very little is known about the influence of biocrusts on the phenology of vascular plants. Nevertheless, some results suggest that biocrusts may promote early flowering and greater production of reproductive structures. In a study by Pendleton et al. (2003), an annual forb, a perennial grass, and a perennial forb flowered earlier and/or produced more reproductive biomass on crushed than intact biocrusts or sand. An effect of biocrusts on flowering time was also observed by Zhang and Nie (2011) in the field, where flowering and fruiting of annual forbs and grasses occurred sooner in biocrusted than uncrusted areas. Other studies have shown variable effects of biocrusts on flowering, fruiting, and/or seed production. For *Arabis fecunda* (Lesica and Shelly 1992), the number of inflorescences and fruits per plant was similar in biocrusted and uncrusted areas, while Bliss and Gold (1999) reported species-specific effects of biocrusts on the number of seeds per fruit and weight per seed.

19.4 Influences of Vascular Plants on Biocrusts

19.4.1 Canopy Shade

Although biocrust organisms are adapted to high light intensities (Harel et al. 2004), they often benefit from some shading by vegetation (Belnap 2003; Cortina et al. 2010; Singh et al. 2012), as the shade reduces light damage and desiccation. Some studies indicate that enhanced UVB radiation intensity causes significant reduction in photosynthetic function, destruction of chloroplast ultrastructure, and disordering of antioxidant enzyme systems in the moss *Bryum argenteum* (Hui et al. 2013), the lichen *Umbilicaria aprina* (Niemi et al. 2002), and the cyanobacterium *Microcoleus vaginatus* (Xie et al. 2009). On the other hand, complete canopy shade could also cause severe damage by light deprivation, but its occurrence is rare in dryland ecosystems due to the scattered distribution, open canopies, and low stature of the shrubs and trees and the short life span of the annuals.

In many dryland ecosystems, a woody plant canopy creates a gradient from deep shade near the stem to maximal irradiance outside the canopy, reflected in an uneven thickness of biocrusts and a radial distribution (zonation) of some biocrust organisms, particularly mosses (Eldridge et al. 2000; Martinez et al. 2006; Cole et al. 2010). Eldridge et al. (2000), for instance, found preference for shrub canopy shade in a number of moss species (*Aloina bifrons*, *Crossidium* sp., *Bryum* sp., and *Pterygoneurum subsessile*), particularly at sites with a northerly aspect. Cole et al. (2010) demonstrated that the Mojave Desert moss *Syntrichia caninervis* transplanted into exposed sites lost significantly more cover than those moved into shaded sites.

Shrub canopy shade also affected reproductive behavior in biocrust mosses, as it increased the density of sexual organs in male *Bryum dunense* in sandy deserts of the Negev (Herrnstadt and Kidron 2005), possibly caused in part by differential desiccation tolerance between the sexes (Benassi et al. 2011). In another study of two pleurocarpous mosses (*Rhytidadelphus squarrosus* and *Calliergonella cuspidata*), lower irradiance beneath the shrub canopy decreased evaporation rates (Van der Hoeven et al. 1998). This prolonged photosynthesis compensated for the lower photosynthetic rates found under the shrub canopy. In addition, at low irradiance, the morphology of shoots of *Rhytidadelphus squarrosus* changed, as the main axis lengthened and the branches shortened. In contrast, higher solar insolation in interspace habitats induced rapid drying and prolonged drought periods, limiting the metabolic activity of biocrusts (Hamerlynck et al. 2002). The combined stress of drying and heat-accelerated water loss in the biocrust moss *Syntrichia caninervis* was followed by a decrease of photosynthetic activity (Xu et al. 2009). In contrast to mosses, lichens were often promoted by higher light intensities (i.e., less shade) (Sedia and Ehrenfeld 2003).

In many cases, variation in biocrust thickness, cover, and composition under woody plant canopies is correlated to other factors besides shade. For instance, Martinez et al. (2006) showed that the abundance of moss and lichen biocrusts

under canopies in Spain was also related to cover of litter, soil respiration, potassium content, and aggregate stability. Under the canopy of patch-forming dryland shrubs and in the exposed intershrub space, surface texture, surface cover, and soil properties tend to vary along with shade (Boeken and Orenstein 2001; Golodets and Boeken 2006).

19.4.2 Plant Litterfall

Litter deposition is probably the most important mechanism of biocrust disturbance by vegetation (Boeken and Orenstein 2001). Litter cover may affect the microenvironment of biocrusts in many ways: physical contact, soil properties, soil nutrient status, microbial composition and structure, and particularly light, temperature, and moisture (Belnap 2003; Jensen and Gutekunst 2003; Xiong and Nilsson 1999; Facelli and Pickett 1991). Biocrust burial by plant litter accumulated under woody plants can restrict its development under canopies (Boeken and Orenstein 2001; Berkeley et al. 2005) due to light reduction. In Negev shrublands, heavy and persistent litter cover kills the biocrust organisms (mainly the cyanobacterium *Microcoleus vaginatus*) and in many cases allows termites to remove the remaining physical crust structure (Boeken and Orenstein 2001).

Temporary or light litter cover can protect the biocrusts from photodamage (Serpe et al. 2013), reduce heat stress, and maintain suitable surface temperatures for photosynthesis (Lange 2003). Shade of moderate litter cover also creates favorable temperature and humidity conditions for increased microbial activity and litter decomposition, increasing soil organic matter and soil fertility (Zaady et al. 1997; Li et al. 2007). The changes in the microenvironment can ultimately lead to changes in the photosynthetic capacity of biocrusts (Serpe et al. 2013). Biocrust organisms are unequally affected by litter cover, due to the differences in metabolic requirements and the ability of mosses, and some lichens, to grow up through the litter (Lange 2003; Marschall and Proctor 2004). Briggs and Morgan (2008) found some moss species were competitively superior to lichens where litter cover was moderate.

Litter accumulation from invasive species may impede the recovery of biocrusts after fire (Hilty et al. 2004). Areas previously invaded showed reduced moss crust and lichen cover (Belnap et al. 2006). Some studies have shown that invasive species can hinder biocrust recovery in early successional stages, while mature biocrusts resist invasion (Dettweiler-Robinson et al. 2013). A rather dense litter cover (23.5 mg cm^{-2} of biocrust) of the exotic annual grass *Bromus tectorum* reduced the chlorophyll content and the rate of gross photosynthesis and dark respiration of biocrusts dominated by either the moss *Bryum argenteum* or the lichen *Diploschistes muscorum* (Serpe et al. 2013).

19.4.3 *Soil Properties*

In addition to litter production affecting biocrusts and underlying soils, vegetation also alters subsurface soils by increasing soil organic matter, water holding capacity, and soil nutrient content (Maestre et al. 2010). However, little is known about the effects of vegetation-induced changes in the soil on biocrusts. Furthermore, in some instances, changes in soil conditions beneath vascular plants do not parallel those beneath biocrusts. For example in the northern Negev, the 0–20 cm soil under vegetation had higher moisture in the rainy than in the dry season, while soil covered by a cyanobacterial crust appeared unaffected (Golodets and Boeken 2006).

19.5 Nutrient Uptake by Vascular Plants as Influenced by Biocrusts

19.5.1 *Availability and Uptake of Mineral Nutrients*

In arid and semiarid environments, biocrusts can be the main source of available N (Evans and Belnap 1999; Elbert et al. 2012). The contribution of biocrusts to N availability tends to be higher for upper soil layers (Breen and Levesque 2008; Zhao et al. 2014). Gao et al. (2010) compared the organic content and total N in fixed and moving sand dunes. The biocrusts on fixed sand increased the organic matter and total N content of the soil, but only in the upper 5 cm. This unequal effect of biocrusts on N content may lead to differences in N uptake among plant species. Plants with shallow roots usually benefit more from the biocrust presence than deeper rooted plants (DeFalco et al. 2001; Yan 2009; Zhang and Nie 2011).

Biocrusts secrete phosphatase, and higher phosphorus (P) availability beneath biocrusts is associated with higher concentrations of P in plant tissue. For example, in southeastern Utah foliar levels of P in *Festuca octoflora* were 78 % higher in plants growing in biocrust covered as compared to uncrusted soil (Belnap 2011). Positive effects of biocrusts on plant P uptake were also observed in the Kubuqi and Gurbantunggut deserts, although the extent of this effect varied among plant species. Overall, the enhancement of P uptake was greater for herbaceous than shrub species (Yan 2009; Zhang and Nie 2011).

Cyanobacterial biocrusts can synthesize anionic polysaccharides that bind cations (Reddy et al. 1996; Chen et al. 2003; Parker et al. 1996). Moreover, the increase in organic content of the soil caused by the biocrust presence increases the cation exchange capacity of the soil (Breen and Levesque 2008; Guo et al. 2008; Zhao et al. 2014). Notwithstanding this increase in cation retention, the effects of biocrusts on plant uptake of cations have ranged from negative to positive (Harper and Belnap 2001; Pendleton et al. 2003). This range of responses may be attributed to other effects of biocrusts on the soil such as moisture or pH, which influence the

availability of cations and other nutrients (Concostrina-Zubiri et al. 2013; Wu et al. 2013; Zhao et al. 2014). In addition, competition for nutrients with microbes in biocrusts might cause lower concentrations of available cations in the soil and thus in plant tissue. Although conflicting results are found in the literature, the uptake of some cations, including Cu, K, Mg, and Zn, tends to increase in the presence of biocrusts (Harper and Belnap 2001; Pendleton et al. 2003; Zhang and Nie 2011). In contrast, plant Fe uptake appears to be lower in soil covered with biocrusts. For other cations, such as Ca, Mn, and Na, positive, minimal, and negative effects of biocrusts on plant uptake have been reported (Harper and Belnap 2001; Pendleton et al. 2003). Similar to P and N, differences in cation uptake among plant species reflect, in part, differences in root architecture. The increase in soil cations caused by the biocrust is mainly limited to the upper soil layers. Consequently, ephemerals rooted primarily within the surface soil benefited more from the biocrust presence than more deeply rooted shrubs (Harper and Belnap 2001; Yan 2009; Zhang and Nie 2011).

19.5.2 Fungal Linkages Between Biocrusts and Vascular Plants

The nutrients released from biocrusts to the soil and those that become available following mineralization are generally thought to enter plants via direct absorption by the roots or through arbuscular mycorrhizae (AM) that form symbiotic associations with the roots. In dryland ecosystems, fungi rather than bacteria likely dominate the nutrient cycles, given their ability to function at much lower soil water potentials (Allen 2007; Porras-Alfaro et al. 2011). Biocrusts are heavily dominated by dark septate endophytes (DSE), although they also contain AM (Allen 2007; Bates et al. 2012; Porras-Alfaro et al. 2011). Except for liverworts, AM are not known to form associations with organisms present in biocrusts, and AM lack any significant saprophytic capability (Hodge 2014; Ligrone et al. 2007). Nevertheless, the higher levels of organic matter and nutrients beneath biocrusts relative to bare soil may promote hyphal proliferation and growth, increasing the potential for transferring nutrients to plants (Gryndler et al. 2005; Joner and Jakobsen 1995). The role of AM on enhancing P uptake from deeper soils is well established (Smith et al. 2011), but P transfer mechanisms from biocrusts to plants are not known. Several lines of evidence indicate that AM may contribute to N transfer (Tu et al. 2006). Pioneer work by Hawkes (2003) showed that the $\delta^{15}\text{N}$ values of a cyanobacterial–algal crust were similar to those of mycorrhiza-associated plants and lower than the $\delta^{15}\text{N}$ values of non-mycorrhizal plants. Further work is needed to determine the forms of N transferred from biocrusts to plants via AM since these fungi can transfer NO_3^- , NH_4^+ , as well as several amino acids to roots (Jin et al. 2005; Ngwene et al. 2013; Whiteside et al. 2012). Similarly, it would

be valuable to determine the carbon cost to the plant associated with N transport since both symbionts have large demands for N (Johnson 2010).

A recent intriguing hypothesis is that a fungal bridge may largely control nutrient transformation and translocation between biocrusts and vascular plants (Green et al. 2008; He and Xu 2009; Zhuang et al. 2014). As DSE dominate the biocrusts, it is believed they play an important role in this nutrient transformation and transport. Dark septate fungi can increase the pool of nutrients available to plants through solubilization of P complexes and mineralization of proteins, peptides, and amino acids (Barrow and Osuna 2002; Newsham 2011). The DSE may stimulate mineralization by facilitating breakdown of organic matter derived from biocrusts. They may also contribute to exchange of nutrients between biocrusts and plants. Spot application of ^{15}N -NO₃ and $^{13}\text{C}_5$, ^{15}N -glutamic acid to biocrusts demonstrated that ^{15}N compounds can be transferred to plants 1 m away in 24 h through root-free soils, presumably via DSE, which were the dominant fungi in the soil and on the roots (Green et al. 2008; Zhuang et al. 2014). Because DSE can enter plants through plant tissue (Barrow and Osuna 2002), it is possible this translocation is bypassing roots. In addition, spot application of ^{13}C from $^{13}\text{C}_5$, ^{15}N -glutamic acid to plant leaves showed a transfer of C to biocrusts, again through root-free soils, which suggests that plants may provide metabolic support to biocrusts during active periods (Green et al. 2008).

Combined, these studies indicate that exchange of nutrients between biocrusts and vascular plants can occur through different pathways. Knowledge in this area is still very limited. Mesocosm studies are needed to determine the specific organisms that mediate nutrient transfer between biocrusts and plants and to quantify how important fungal transfers are to plant nutrition.

19.6 Conclusions

Biocrusts can have positive and negative effects on vascular plants, depending on species, development, and life cycle stage. During seed dispersal, biocrusts with high surface roughness tend to increase seed entrapment, while entrapment is low in biocrusts with smooth surfaces. Following entrapment, the proportion of seeds reaching microsites favorable for water imbibition and germination varies with biocrust microtopography and seed morphology. Similarly, root growth during seedling establishment may be affected by biocrust characteristics such as pH and hydrophobicity, as well as biocrust effects on nutrients and water. Given these various factors and differential responses of seedlings to a particular environment, generalizations about the effect of biocrusts on seed germination and seedling establishment are presently difficult to make. Modeling approaches that evaluate the contribution of different factors and interactions may help to identify those that are particularly important. In addition, further work is needed to determine whether certain biocrust types are overall more conducive to seed germination or seedling establishment than others. A meta-analysis of the meanwhile rather numerous

studies on biocrust effects on seeds and seedlings may reveal general trends that are not obvious from the various and often contrasting results found in the literature.

Following establishment, the effects of biocrusts on plant growth are for the most part positive. It is also likely that biocrusts increase plant reproductive output; however, more studies will help to verify this. Promotion of plant growth by biocrusts has been attributed to changes in the distribution of water and in the levels of organic matter and nutrients. Effects on plant growth may also reflect biocrust-induced changes in the soil biota. Such changes have been studied in relation to nutrient mineralization and, to a lesser extent, nutrient acquisition. It is plausible that biocrusts mediate other changes such as the abundance of microorganisms, which promote growth via alterations in plant hormone concentrations or decreases in pathogens (Wardle et al. 2004). Studies on this topic and on the specific and overall responses of plant communities to biocrusts are needed, as overall responses are often unknown or unreported (Boeken and Shachak 1994; Boeken and Orenstein 2001).

Canopy shade tends to benefit biocrust development, and effects of litter on biocrusts can range from positive to negative depending on litter thickness and persistence. The cover provided by canopy and light litter alters the duration of hydrated periods and the rates of photosynthesis, changing the biocrust carbon balance and ultimately influencing its taxonomic composition and functioning. Invariably, a thick, persistent litter layer seems to inhibit or eliminate biocrusts, likely as a combination of a negative carbon balance in the dark and physical contact. The precise litter levels that begin to cause damage to biocrusts are unknown, warranting further analysis.

The positive and negative interactions between biocrusts and vascular plants play a role in determining their coexistence. An interesting hypothesis claims that the types of interactions that promote coexistence vary with the degree of aridity. Under high aridity, plant growth is predominantly restricted by lack of water, and negative effects of biocrust on establishment and growth of vascular plants are minimal. Under this scenario, biocrust effects would be predominately beneficial, resulting from reduced soil erosion and increased availability of nutrients and water. Similar conditions occur in dry arctic environments, where frost and erosion severely limit plant growth. This hypothesis, that evolution has led to biocrusts with distinct effects on vascular plants based on differences in aridity or prolonged frost, requires further investigation. It would be worthwhile to test this notion in a global study on the spatial interactions between biocrusts and vegetation in relation to aridity and other environmental stressors. Within this framework, detailed positive and negative biocrust–vegetation interactions, including those on entire communities, can be compared and modeled. Of particular interest would be to identify patch-forming ecosystem engineer species and distinguish between transient and more persistent interactions between plants and biocrusts and between the scales at which they operate.

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Chapter 20

Biological Soil Crusts as a Model System in Ecology

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20.1 Introduction

The interest of the scientific community in biocrusts, and the amount of information on the specific properties of these communities currently available, has fostered their use to test ecological theories, particularly at community and ecosystem levels. Some examples include the relationship between biodiversity and ecosystem functioning (Maestre et al. 2005, 2012), the ecological consequences of climate change on organisms (Escolar et al. 2012; Maestre et al. 2015) and ecosystem processes (Maestre et al. 2013; Reed et al. 2012), the interplay between abiotic stress and the outcome of biotic interactions (Bowker et al. 2010a) or the functional

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role of spatial patterns (Maestre et al. 2012), to name a few. These studies have provided novel insights into the topic being studied and the refinement of existing theory (e.g., Bowker et al. 2010a), highlighting the potential of biocrusts to act as a model system to advance ecological theory.

When a model is being studied, the researcher's interest lies in the ecological process or property rather than the system itself, and the system becomes a tool for learning about the process or property (Vitousek 2002). Can biocrusts be a good model system in ecology? To answer this question, we must define first what we understand as a model system. It can be defined as "a gene, a species, a community, or an ecosystem displaying a general process or property in an understandable way" (Vitousek 2002). Useful model systems may or should (1) be simpler than alternative systems, such that the property or process of interest is not confounded by other properties or processes, (2) display the processes being studied faster than other genes/organisms/communities/ecosystems, (3) be smaller than alternative systems, (4) be idiosyncratic or distinctive in a useful way that makes them instructive, and (5) be both generalizable and amenable to experimentation (Bowker et al. 2014; Vitousek 2002). In certain contexts, biocrusts exhibit all of these model system characteristics. Biocrusts exemplify favorable combinations of small size, useful idiosyncrasy, and manipulability in experiments (Table 20.1), which make them a suitable and very useful model system for ecologists (Bowker et al. 2014). Throughout this chapter, we emphasize the main biocrust features that make them special and well suited to advance our understanding of important questions in community and ecosystem ecology. Because of space limitations, this chapter does not discuss in detail all the relevant literature and questions that can be explored using biocrusts. Rather, we aim to provide readers with arguments about why biocrusts are an excellent model system in community and ecosystem ecology and to foster their use in novel ways by ecologists.

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Table 20.1 Desirable attributes of a model system, with an explanation of how biocrusts fit them

Attributes	Description
Simple	<ul style="list-style-type: none"> • Biocrust diversity levels are tractable • Visible biocrust components can be easily identified at the functional group or species level
Fast	<ul style="list-style-type: none"> • Biocrusts may change their abundance within the year (Belnap et al. 2006) and can recover from disturbances in just some years (Lázaro et al. 2008) • Some biocrust species can be cultivated and grow quickly under controlled conditions (Xu et al. 2008)
Small	<ul style="list-style-type: none"> • Natural variation in biocrust communities can be found in the field within a square meter • The size of biocrust constituents facilitates their use in community and ecosystem ecology studies
Idiosyncratic or distinctive	<ul style="list-style-type: none"> • The distinctive features in the biology of biocrust constituents makes them particularly interesting model systems to study issues such as how intransitive interactions (Ulrich et al. 2014) and parasitism (Hawksworth 1982) determine overall species diversity
Amenable to experimentation	<ul style="list-style-type: none"> • Biocrust taxa can be readily cultured or easily transported, allowing researchers to construct custom communities in small-sized experimental units • Features of biocrusts make them highly suitable for conducting manipulative experiments in a cost-effective manner

Adapted from Bowker et al. (2014)

20.2 Exploring the Biodiversity–Ecosystem Functioning Relationship with Biocrusts

The value of biodiversity for ecosystem functioning has been both a long running theme in the ecological sciences and a powerful argument to justify the conservation of natural areas (Cardinale et al. 2012). Many studies conducted in the last decades have demonstrated a positive monotonic relationship between biodiversity and a variety of ecosystem processes, establishing a useful generalization bridging community and ecosystem ecology (Cardinale et al. 2011). Biocrusts may play a useful role as a model system in refining biodiversity–ecosystem functioning theory. Two properties in particular lend them to this task: (1) biocrust diversity can be manipulated and (2) the small size of biocrust organisms decreases the economic costs of experimentation. Biocrust-forming lichens can be transplanted relatively easily (Maestre et al. 2012; Castillo-Monroy et al. 2015), and bryophytes can be transplanted or cultured (Xu et al. 2008; see Chap. 24 by Zhao et al.). Thus, it is possible to assemble customized biocrusts of varying levels of lichen and moss diversity, manipulating species richness, evenness, and β -diversity simultaneously (Maestre et al. 2012, Fig. 20.1). Cyanobacteria and algae can also be cultured using liquid culture (Wang et al. 2008), thus their richness can also be manipulated, but this control does not extend to most other bacteria, archaea, and fungi which cannot be cultured. The small size of biocrust organisms allows meaningful variation in



Fig. 20.1 Examples of the use of biocrusts in a biodiversity–ecosystem functioning experiment (Maestre et al. 2012). (a) Intact lichen pieces collected from the field, cut into homogeneous 0.5 cm side square fragments, (b) fragments of lichens added to the surface to achieve a 60 % coverage of each microcosm unit, (c) examples of microcosms after the set up, and (d) small spatial footprint of two multifactor replicated experiments. Reprinted from Bowker et al. (2014), with permission from Springer

diversity levels at small scales (Bowker et al. 2013a) and reduces the space needed to assemble experimental communities. Therefore, complex experiments can be conducted in a few square meters, drastically lowering costs when comparing with experiments conducted with vascular plants (e.g., the Jena, Cedar Creek or Sabah experiments, Hector et al. 2011; Pasari et al. 2013; Roscher et al. 2004).

Although biodiversity is a complex concept, the large majority of research thus far has focused on species richness as the focal metric of biodiversity (Cardinale et al. 2011). Biocrusts have proven no exception to the general principle of positive richness–function relationships; these communities commonly exhibit approximately linear relationships between the number of macroscopic species (bryophytes and lichens) and various indicators of nutrient cycling, hydrological, and soil development and retention functions (Bowker et al. 2010b). Positive richness–function relationships are supported in multiple observational field studies (Bowker et al. 2010b, 2013b). An experiment conducted using constructed biocrusts of varying richness found that many additional functional indicators were influenced, both positively and negatively, by richness (Maestre et al. 2012). Together, these studies show that most functional indicators are correlated, either negatively or positively, with species richness. Increasingly, ecologists are moving beyond the

consideration of single ecosystem functions, such as productivity, to multifunctionality: the simultaneous performance of multiple ecosystem functions (Pasari et al. 2013). To date, two studies have suggested that a greater number of biocrust species promote greater multifunctionality and that a greater number of species are required to sustain multiple functions than a single function (Maestre et al. 2012; Bowker et al. 2013b). Other studies are also using biocrusts to study changes in multifunctionality along environmental gradients (Delgado-Baquerizo et al. 2016).

Components of biodiversity other than species-level taxonomic richness have the potential to influence ecosystem functions or multifunctionality (Pasari et al. 2013; Tilman et al. 2014). These include taxonomic diversity at other levels (familial, generic), species evenness, β -diversity (species turnover), trait diversity, functional group diversity, phylogenetic diversity, and within-species genetic diversity. Only some of these elements of biodiversity have been investigated using biocrusts. In general, biocrust evenness is not commonly related to ecosystem functioning, except in interaction with other biocrust properties such as spatial patterning (Bowker et al. 2010b; Maestre et al. 2012). Species richness was found to be a better indicator of function than the richness of *a priori* functional groups, perhaps because our knowledge of functional traits does not properly group species according to their impacts on ecosystem functioning (Bowker et al. 2010b). Alternatively, it may mean that biocrust moss and lichen species tend to have unique suites of functional traits (Bowker et al. 2011; Concostrina-Zubiri et al. 2014), and perhaps a trait diversity index would prove even more informative than species richness. In contrast to the weak effects of evenness and functional group richness on ecosystem functioning, β -diversity, measured as differences in community structure among samples, has been shown to strongly determine infiltration (Eldridge et al. 2010; Bowker et al. 2013a) and nutrient cycling (Bowker et al. 2011; Maestre et al. 2012). Much remains to be learned about the relative influence of these different components of biodiversity, but based on currently available information, species richness and β -diversity are among the most influential biocrust properties regarding ecosystem functioning. These biodiversity effects are as strong or stronger than those of other community properties such as total cover or spatial patterning (Maestre et al. 2005, 2012).

To date, very little information is available on biocrust microbial biodiversity effects on function. Castillo-Monroy et al. (2011) found that lichen richness, rather than bacterial richness, appeared to drive multiple ecosystem functions related to nutrient cycling. Hu et al. (2002) found that artificial biocrusts composed of multiple cyanobacterial species aggregated soil more strongly than single species cultures. Next-generation molecular techniques now provide greater capacity to measure microbial biodiversity and functional traits, and the generalization of their use will allow us to test biodiversity–function hypotheses more fully in the near future.

20.3 Biocrusts as a Model System to Study Nitrogen Cycling

The convenience of biocrusts as a model system is magnified when they are targeted to study nutrient cycling processes. First, simplicity becomes crucial to evaluate inputs and outputs of nutrients from and to the atmosphere. In this regard, both atmospheric nitrogen (N) fixation, nitrification, and denitrification can occur in a more local and coupled manner in biocrusts than in plant-centered systems, in part, because of the lack of a complex root system in biocrusts. For example, processes such as N fixation and denitrification occur simultaneously in direct contact with biocrust-forming lichens and mosses (Belnap 2002; Barger et al. 2005). However, in plants these processes can be spatially disconnected; while N fixation usually occurs in highly specialized root structures (e.g., root nodules), processes such as denitrification can be highly influenced by plant rhizosphere exudates (Baggs and Philippot 2011). Thus, biocrusts can provide a simpler model to achieve a better understanding of N cycling in terrestrial ecosystems. Second, studying the internal cycling of nutrients within the biocrust area of influence also benefits from simplicity. For example, in ecosystems dominated by vascular plants, the rhizosphere and the bulk soil represent two different C sources in terms of C quality, but also in terms of their temporal and spatial availability for microorganisms; this adds a level of complexity that is absent in biocrust-dominated ecosystems. On the contrary, the local effects of biocrusts on soils, as well as the intimate contact between their surfaces, can provide unique opportunities to improve our knowledge on important processes such as nutrient mineralization, organic acid exudations (e.g., oxalic acid), and N uptake (Whitton et al. 2005; Delgado-Baquerizo et al. 2013a, b). Finally, the soil under the influence of biocrusts is restricted to a few centimeters beneath them (Pointing and Belnap 2012), avoiding the complexity of integrating different soil horizons with different (and sometimes antagonist) physical and chemical properties.

Given the rapid response of biocrusts to disturbance (see Chap. 21 by Zaady et al.), these organisms may provide a good model system to study the effect of global environmental change on the soil N cycle. For example, the cover of biocrust-forming lichens and mosses can decrease by 40 % or more in a few years as a response to simulated climate change (Maestre et al. 2013; Reed et al. 2012). Such changes would take much longer for dominant vascular plants, particularly those located in areas such as drylands. Biomass turnover rates are also faster in biocrust-dominated systems than in vascular plant-dominated systems and are also highly variable (e.g., Belnap et al. 2006). Parallelisms could be found between lichens and mosses as equivalents to the woody component of terrestrial plant systems and algae and cyanobacteria as equivalents to its herbaceous component (Bowker et al. 2014). The smaller dimension of biocrust systems has also been proven to be advantageous for studying nutrient cycling, allowing the detailed description of the spatial pattern and scale of nutrients under biocrusts (Delgado-Baquerizo et al. 2013a) or the response of the N cycle to dew events or nutrient

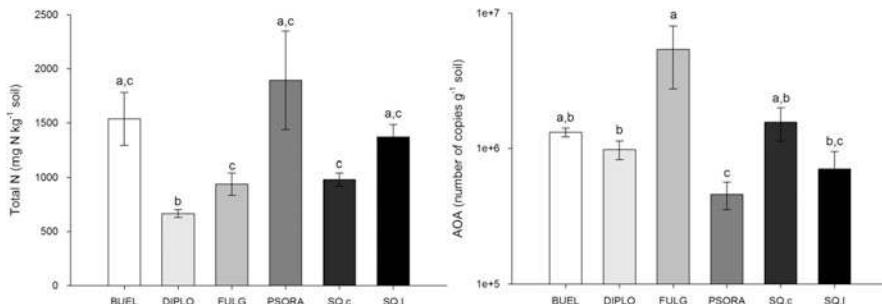


Fig. 20.2 Values of total N and ammonia-oxidizing archaea (AOA) in the upper soil (0–1 cm depth) under different biocrust-forming lichens. Species abbreviations as follows: *Buellia epipodium* (BUEL), *Diploschistes diacapsis* (DIPLO), *Fulgensia subbracteata* (FULG), *Psora decipiens* (PSORA), *Squamaria cartilaginea* (SQ.c), and *Squamaria lentigera* (SQ.I). Different letters indicate significant differences among the lichen species studied for total N and ammonia-oxidizing archaea (AOA; $P < 0.05$, post hoc test after semi-parametric PERMANOVA analyses). Values represent means \pm SE ($n = 5$). Source: Delgado-Baquerizo et al. (2015)

additions (Delgado-Baquerizo et al. 2013b, c) at a significantly lower cost than in ecosystems dominated by vascular plants.

Biocrusts have another distinctive property difficult to find in a single plant community: the possibility to find a wide spectrum in litter quality (Palmquist et al. 2002). In biocrusts, such a range goes from highly labile cyanobacteria to the recalcitrant lichen tissues, with significant impacts to nutrient cycling. For instance, Miralles et al. (2012a) showed that soils under late-successional lichen species such as *Diploschistes diacapsis* and *Lepraria crassissima* have higher respiration rates, organic C content, and inorganic N concentrations than those located under cyanobacteria. Results from a biocrust community in central Spain showed that biocrust-forming lichens had species-specific effects on the availability of N and their related microbial communities and that these effects were related to the nutrient content of lichen tissues (Delgado-Baquerizo et al. 2015; Fig. 20.2). For example, species such as *Psora decipiens* where more strongly correlated with the concentration of total N in soil than others such as *Diploschistes diacapsis*. Similarly, *Fulgensia subbracteata* showed a stronger correlation with the abundance of ammonia-oxidizing archaea than species such as *Psora decipiens*. These micro-organisms carry out the first step of nitrification, and there is evidence that they can dominate over other nitrifiers such as ammonia-oxidizing bacteria in drylands (Delgado-Baquerizo et al. 2013b).

The proven ability of biocrusts to influence the different processes and microbial communities driving the N cycle, together with their small size and manageability and the versatility shown by different co-occurring biocrust types (e.g., mosses, lichens, and cyanobacteria) and species (e.g., *Psora decipiens* and *Diploschistes diacapsis*), indicates that biocrusts can be considered a useful and suitable model to check for multiple hypotheses regarding N cycling to achieve a more integrated understanding on how N cycling works in terrestrial ecosystems.

20.4 Using Biocrusts to Study Biotic Controls on Ecosystem Functioning: The Hydrology of Drylands as an Example

Hydrological processes, and therefore water availability, in drylands are largely controlled by the activity of organisms such as plants (Whitford 2002). The study of biotic controls on ecosystems is a topic of major concern among ecologists, but current approaches have tended to focus on vascular plants (Aguiar and Sala 1999; Cortina and Maestre 2005). Biocrusts are also relevant for understanding processes that control water availability, as well as source–sink and infiltration–desiccation dynamics in drylands (Belnap 2006; see Chap. 17 by Chamizo et al.).

Source–sink relationships and the movement and fate of water in drylands operate at a number of spatial scales. At landscape (ecosystem) scales, water usage and movement are controlled by geomorphology and slope processes (Puigdefábregas et al. 1999; Rodríguez-Caballero et al. 2014). At smaller spatial scales, water movement is controlled by patterns of vegetation, with greater infiltration and soil moisture and lower rates of runoff and evaporation beneath plants than in their interspaces (Bhark and Small 2003). Frequently overlooked in the literature are smaller-scale effects (10^{-1} to 10^{-3} m) that are driven largely by biocrusts (Belnap 2006). Here, we present three propositions, based on work from Australia and Spain, which illustrate how we can use biocrusts as model systems to improve our understanding of source–sink dynamics in drylands.

- (1) **The crust morphology–function proposition:** *Source–sink relationships are highly dependent upon the particular functional group to which the biocrust-resident taxa belong. Specifically, in sink areas, biocrust organisms will tend toward taxa and morphologies that increase infiltration and capture resources, while in source areas, biocrusts will evolve toward types that reduce infiltration (increase runoff) and shed resources.* Given the strong relationship between biocrust form and function (e.g., Eldridge and Rosentreter 1999), we would expect source areas to be dominated by gelatinous, crustose, and squamulose lichens and sparse, small mosses. This is because they are very short in stature and therefore less likely to trap runoff water. Conversely, dense, clump-forming mosses, fruticose lichens, and thallose liverworts, which are associated with resource capture, would be expected to dominate the sinks. Support for this proposition comes from studies of dryland systems with low slopes (<3 %) in Spain and Australia where crustose and squamulose lichens are typically found in source areas while others (typically mosses) are most abundant in sink regions (Eldridge 1999; Maestre et al. 2002; Rodríguez-Caballero et al. 2013).
- (2) **The autogenic engineering proposition:** *Organisms forming biocrusts actively engineer their environment to maximize the amount of moisture they receive while minimizing moisture shed to vascular plants, with which they compete directly for space and resources.* Biocrusts growing in plant inter-spaces can engineer an environment that gives them an advantage over vascular

plants. For example, the accumulation of cyanobacterial filaments dominated by polysaccharides often reduces infiltration by binding together surface sand particles (Mager and Thomas 2011). Water is thus directed away from vascular plants, giving cyanobacteria, which tolerate low moisture, a competitive advantage over vascular plants. On the Colorado Plateau, micro-pinnacled surfaces dominated by cyanobacteria create a distinct microclimate, due to differences in slope and aspect (Bowker et al. 2002). These roughened surfaces retard runoff, trap more seeds, and allow more water to soak into the soil. For other crust types, however, smoother surfaces commonly behave in the opposite fashion. Biocrusts resemble diminutive landscapes where source–sink processes operate in miniature. Thus, they can be useful models to test whether source–sink dynamics in whole ecosystems can be downscaled to these microsystems. For example, within a small area of less than 1 m², patches of biocrusts dominated by mosses might act as sinks, analogous to dense woodland or forest ecosystems, while patches of lichens, particularly those comprising dense squamules, will act as sources.

- (3) **The rainfall–crust morphology proposition:** *The degree of morphological complexity of biocrust taxa is likely greater in areas of higher rainfall or in areas with greater soil moisture.* Consistent with landscape theory, we would expect source–sink ratios to decline with increasing rainfall, and, in areas with smaller sources, a dominance of water-shedding/resource-releasing crust forms. In higher rainfall areas, biocrust taxa would be relatively small, due to competition (e.g., overtopping) from vascular plants. Biocrust taxa in the zone where source areas meet the sinks have been shown to be dominated by bryophytes rather than lichens and cyanobacteria because these areas receive the most runoff (Eldridge 1999).

Biocrusts can also improve our understanding of desiccation processes in drylands. Preliminary results from the analysis of a long-term (6.5 years) dataset on surface soil moisture indicate that biocrust-forming lichens both increase the amount of rainfall reaching the soil during rain events and accelerate the loss of water during desiccation (Berdugo et al. 2014). In this study, species such as *Diploschistes diacapsis* favored the channeling of water into the soil, hence increasing infiltration rates. At the same time, this species enhanced the soil desiccation rate after rainfall events; this effect was likely due to the increase in surface soil temperature promoted by *Diploschistes diacapsis*. The hydrophobic exudates that these lichens secrete at small spatial scales when wet (Contreras et al. 2008) also reduced the permeability of the soil once moisture reached a threshold, for both desiccation and wetting processes. These results exemplify the utility of biocrusts as a model system to study how organisms modulate water dynamics in drylands.

20.5 Studying Biotic Interactions Using Biocrusts

The study of facilitative and competitive interactions in drylands has been a major research topic in community ecology over the last two decades (see Brooker et al. 2008 and Soliveres et al. 2015 for reviews). While studies on biotic interactions between saxicolous and epiphytic lichens have been carried out since the early 1980s (see Armstrong and Welch 2007 for a review), analogous studies using biocrusts were not initiated until 20 years later. Maestre (2003a, b) and Maestre and Cortina (2002) used spatial pattern analyses to study the covariation between biocrust-forming mosses and lichens and to explore the effects of vascular vegetation on the patterns of co-occurrence between these biocrust constituents. This work has been expanded to study biotic interactions between biocrust-forming lichens and mosses at the community level. For example, research carried out in central Spain has shown that competition is more intense than facilitation in biocrust communities dominated by lichens (Maestre et al. 2008) and that the intensity of competition varies with the availability of water and nutrients (Maestre et al. 2009). Bowker et al. (2010a) examined the intensity of biotic interactions in the field at the community level along a regional abiotic stress gradient (driven primarily by temperature and aridity) in Spain. Based on the spatial aggregation or segregation patterns of all the species in the community, these authors inferred that negative species interactions were prevalent in the biocrust communities studied and that competition intensity increased with abiotic stress (Fig. 20.3). This response is just the opposite of what has been predicted for vascular plants (Brooker et al. 2008, but see Soliveres et al. 2015). Spitale (2009) investigated how the growth of the moss *Warnstorffia exannulata* was influenced by the presence or absence of two adjacent species, *Sphagnum warnstorffii* and *Scapania undulata*. He found that natural climatic fluctuations, by affecting the length of the water gradient, changed the competitive hierarchies of the species on a seasonal scale but did not result in a switch from competition to facilitation under more stressful conditions along a water stress gradient. Other studies have evaluated how interactions among microorganisms changed along a stress gradient determined by biocrust development in China (Li et al. 2013). These authors found that interactions within the soil phototroph community shifted from facilitation to competition with microhabitat improvement (from algal-dominated to a moss-dominated biocrust community). Mosses have also been found to facilitate the lichen *Peltigera rufescens* by enhancing its photosynthetic activity and growth in Germany (Colesie et al. 2012).

We strongly believe that the insights gained by this research, and the commonalities and differences found among biocrusts and other organisms, can largely advance research in biotic interactions. For example, a high species specificity in the outcome of these interactions, regardless of the prevailing environment, has been observed in both vascular plants (Soliveres et al. 2011) and biocrusts (Bowker et al. 2010a) despite that their interactions are determined by strikingly different mechanisms. Lichens and bryophytes exhibit a remarkable array of secondary

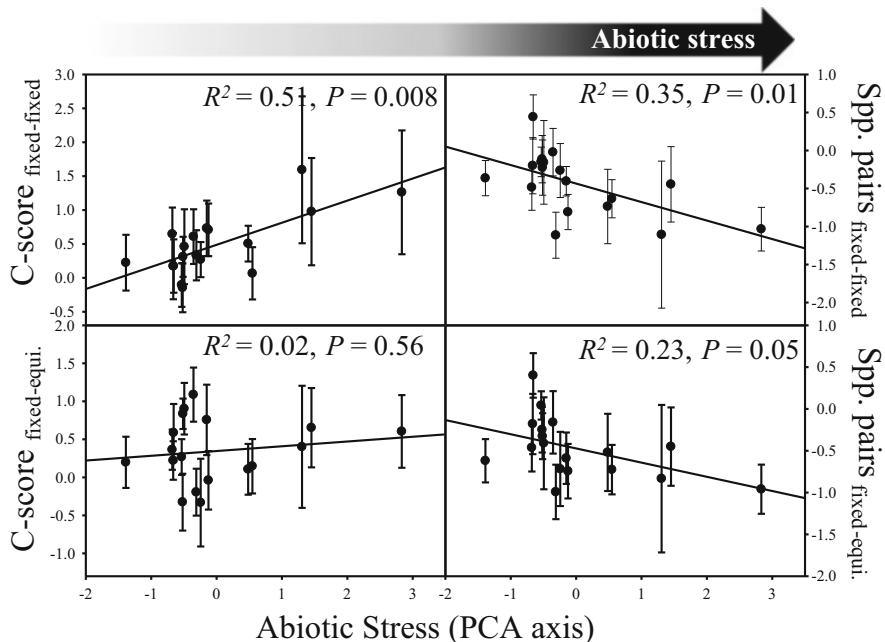


Fig. 20.3 Outcome of biotic interactions among biocrust-forming lichens and mosses in the field, as measured with standardized effect sizes of mean co-occurrence statistics (C-score and species pairs), along a natural gradient of abiotic stress (the first component—axis—of a principal component analysis (PCA) conducted with climatic variables) in Spain. Each point represents one site, and each error bar reflects the standard deviation among replicated transects (usually ten) measured within sites. High values of the C-score indicate that different species tend to segregate from one another in space, whereas high values of the number of species pairs indicate that different species tend to aggregate together in space. Results from two null models (fixed-fixed and fixed-equitable) are shown. Reprinted from Bowker et al. (2010a), with permission from the British Ecological Society and Wiley

chemicals, some of which can promote the uptake of essential micronutrients, reduce the intracellular concentration of toxic compounds, and lessen the growth of pathogenic bacteria and fungi (e.g., Lawrey 1986; Hauck 2008; Hauck et al. 2009; Kowalski et al. 2011); thus, species with complementary chemical arsenals (e.g., those facilitating nutrient uptake and promoting defense against pathogens) may be mutually benefitted by association. Mosses can reduce the desiccation of adjacent lichens (Colesie et al. 2012), a mechanism that could lead to facilitative species combinations (Spitale 2009), despite the predominant competition for space found in biocrust communities (Maestre et al. 2008). Thus, the study of facilitative and competitive interactions among biocrust constituents, and the explicit consideration of the mechanisms underlying them, may lead to conceptual advances that will help to move this field forward (see Bowker et al. 2010a for an example).

20.6 Aboveground–Belowground Interactions in Biocrust-Dominated Ecosystems

Because they are a complex of photoautotrophs and heterotrophs, biocrusts may function as a microcosm of the plant–soil or aboveground–belowground interaction. Biocrust-forming photoautotrophic lichens behave similarly to a miniature vascular plant, and associated bacteria are not unlike rhizosphere bacteria (Bowker et al. 2010a). For example, different biocrust species secrete significant amounts of substances such as glycolate, vitamins, and auxin, which promote plant growth (Fogg 1966); chelators, which keep nutrients available to plants (Lange 1974); and exopolymers, which enhance microbial activity (Mager and Thomas 2011). This, together with the fact that biocrusts play key roles in an unusually wide array of ecosystem functions (Belnap 2006; Bowker et al. 2011; Maestre et al. 2011), makes them a suitable model system to study aboveground–belowground interactions.

Properties of the autotrophic community members can often be linked to the heterotrophic community. García-Palacios et al. (2011) found that biocrust cover is associated with high soil stability and high soil microbial functional diversity in late-successional roadside grasslands. In a microcosm experiment where the biodiversity and spatial pattern of biocrusts were manipulated, soil microorganisms were strongly influenced by biocrust attributes (Castillo-Monroy et al. 2015). These authors found that microbial functional diversity was maximized in those microcosms with a random pattern, high species richness, and maximum evenness level. In the same experiment, changes in different community attributes of biocrust autotrophs had a diverse array of impacts on ecosystem functions (e.g., some enzymatic activities related to nutrient cycling; Maestre et al. 2012), suggesting that they could be mediated by the modifications in soil microbial communities induced by biocrust autotrophs. Delgado-Baquerizo et al. (2013c) found that biocrusts control changes in the microbial functional diversity of nutrient-amended semiarid soils. They found that diversity was higher under biocrusts than in bare ground when carbon and phosphorus were added. Castillo-Monroy et al. (2011) evaluated the influence of biocrusts on associated microbial communities; while biocrust abundance and richness did not affect bacterial richness/abundance, some bacterial species were sensitive to the abundance of particular biocrust-forming lichens. Wedin et al. (2015) assessed how the infection of *Cladonia symphycarpa* by the parasitic lichen *Diploschistes muscorum* affects associated microbiomes and photobionts. These authors found a gradual microbiome shift during this process, including a notable decrease in relative abundance of Alphaproteobacteria and a concomitant increase in Betaproteobacteria. In a climate change experiment conducted in a semiarid *Pinus halepensis* plantation, Maestre et al. (2015) found that warming increased the physiological stress of the Gram-negative bacterial community, as indicated by the ratio between the phospholipid fatty acids cy17:0 and 16:1ω7. This response was, however, modulated by lichen-dominated biocrusts, as the increase in this ratio with warming was higher in areas with a low biocrust cover. Microbes are not the only organisms that can be affected by

aboveground biocrust constituents, but also soil microfauna such as nematodes, springtails, and mites (see Chap. 8 by Darby and Neher).

20.7 Biocrusts as a Model System to Study Resistance and Resilience

The properties of biocrusts (Table 20.1) make them ideal model systems to study resistance and resilience (i.e., the ability of a given variable to endure disturbances without experiencing substantial changes and its capacity to recover afterwards, respectively, Seybold et al. 1999). Biocrust constituents are poikilohydric (i.e., they can withstand desiccation to very low levels of dehydration of cells or tissues without damage and recover when water returns to be available; Green et al. 2011) and thus are strongly resilient to aridity. For example, Rajeev et al. (2013) showed how water availability quickly triggers metabolic changes in dormant cyanobacteria that allow them to recover their photosynthetic activity in less than one hour. Orlando et al. (2010) reported a biodiversity explosion of cyanobacteria as a consequence of a “desert bloom” event in the Atacama Desert. Well-developed biocrusts almost always resist the force of rainfall drops (splash erosion, Lázaro et al. 2008), and their constituents can resist wide ranges of temperatures, humidity, or radiation. For example, the biocrust-forming lichen *Psora decipiens* is a common species in environments as distinct as drylands from Almería (SE Spain) and pavements in Sweden (Büdel et al. 2014). While biocrusts dominated by lichens are often highly sensitive to disturbances such as trampling, those dominated by cyanobacteria can be quite resistant to mechanical disturbance (see Chap. 21 by Zaady et al.) and also resilient: after 10 years of foot trampling, cyanobacteria-dominated biocrusts lost approximately one half of their extractable DNA (Kuske et al. 2012), but kept the key cyanobacterial species *Microcoleus vaginatus*.

In fact, biocrusts have already provided insights on ecosystem resistance and resilience. Miller et al. (2011) showed that the loss of biocrusts can seriously affect ecosystem resilience in drylands. Miralles et al. (2012b) found that indicators of soil organic matter quality provided valuable information about ecosystem resilience and degradation in biocrust-dominated areas. Besides, the limits of resistance and resilience are marked by thresholds, and thresholds in key ecosystem processes have been found by studying biocrusts. For example, Rodríguez-Caballero et al. (2013) found that below a rainfall intensity threshold (average I_5 max 20–25 mm/h), runoff is mainly driven by rainfall volume; beyond this threshold, runoff is controlled by both rainfall intensity and biocrusts, which exert strong direct and indirect effects on infiltration. Well-developed biocrusts have also been found to promote stabilizing ecohydrological feedbacks in drylands (Turnbull et al. 2012).

20.8 Biocrusts as a Model System to Study Ecosystem Restoration

The use of biocrusts in ecological restoration represents an opportunity to reach the desired targets (Bowker 2007, see also Chap. 24 by Zhao et al.). Current knowledge on the ecological role of biocrusts, the availability of production and application protocols, and the existence of commercial products provide unique conditions to test the principles of restoration ecology. Biocrusts may be used to explore emerging concepts in ecological restoration, such as restorability (i.e., the inverse of the effort needed to restore a degraded area), restoration efficiency (Cortina et al. 2006), and novel ecosystems (Hobbs et al. 2009). They may also contribute to the ongoing discussion on the use of alien species and genotypes in ecological restoration (McKay et al. 2005), particularly as commercial inoculum is being transferred across the globe. Unfortunately, only little information on these topics is currently available.

20.9 Concluding Remarks and Future Directions

In the preceding sections, we have highlighted the virtues of biocrusts as a model system to investigate a wide variety of timely and relevant ecological questions. As such, they have a tremendous potential to contribute to the future development of many important ecological areas. For example, biocrusts can provide important insights into how biodiversity at multiple levels (taxonomic, functional, and phylogenetic) affects multifunctionality, a current priority topic for biodiversity–ecosystem functioning research (Naeem et al. 2012). There is also a growing recognition that these coordinated experimental networks are needed to understand complex processes such as ecosystem responses to climate change and to improve our ability to forecast future ecosystem states (Fraser et al. 2013). Biocrusts are ideal to conduct multisite, multi-community, coordinated global experiments aiming to elucidate a range of topics, varying from the recovery of ecosystem structure and functioning after disturbances to the effects of climate change on biotic attributes (e.g., cover, richness, spatial pattern) and associated ecosystem processes. Future investigations should take advantage of the opportunities offered by biocrusts when studying how the interplay between above- and belowground communities shape the structure and functioning of terrestrial ecosystems. Of particular interest are studies focusing on the role of particular species and functional traits in the availability of N and the abundance of microbial communities involved in C and N cycling. Similarly, studies which address the direct impacts of global change on biocrust composition and abundance, which are important drivers of nutrient cycling and availability, will be necessary to advance our understanding of the modulatory effects of biocrusts in nutrient cycling in a future world. Evaluation of the impact of restoration practices and artificial biocrust establishment on

community dynamics and ecosystem function provide ample opportunities to combine advances in ecological theory with improvements in environmental management.

Many challenges remain ahead, however, before biocrusts can be considered as a fundamental part of the ecologists' toolbox of organisms for developing/testing new methods and theories. Perhaps the main challenge is to convince fellow scientists that these organisms have advantages over other model systems and that they play multiple and important ecosystem roles in a wide array of terrestrial ecosystems. If we realize the potential of biocrusts for advancing our understanding of the natural world and start using them as described throughout this chapter, we will both advance ecology and increase the awareness of the ecological importance of these communities.

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Part V

Threats to Biological Soil Crusts

Chapter 21

Effects of Local-Scale Disturbance on Biocrusts

Eli Zaady, David J. Eldridge, and Matthew A. Bowker

21.1 Introduction

Disturbance is a primary cause of spatial heterogeneity in ecosystems, as it affects composition and structure of ecosystems and influences competition, environment, substrate, and resource availability (Eichberg et al. 2007; White and Pickett 1985). As such, disturbance has a wide variety of both positive and negative impacts on ecosystems. The ecological success or failure of a wide range of species is closely tied to local natural disturbance events such as wildfires, droughts, floods, and windstorms. For example, some disturbances can be valuable and help maintain ecosystem diversity by creating areas at different stages of recovery, where organisms that may have otherwise been eliminated can survive. Nevertheless, high-intensity disturbances can alter species composition and decrease diversity. Conversely, some species cannot tolerate much disturbance and become extinct if their ecosystem is highly disturbed, potentially lowering the diversity of the ecosystem (Landres et al. 1999; Pickett et al. 1989). Anthropogenic disturbances may be extreme in nature and outside of the evolutionary environment of an ecosystem.

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Disturbances, such as removal of topsoil by heavy equipment or excessive grazing beyond the carrying capacity of the ecosystem, almost invariably have negative consequences for ecosystem structure and function.

It is well known that dryland biocrusts are very vulnerable to anthropogenic and natural disturbances and remain, for many years following disturbance, in a degraded state in many areas worldwide, leading to soil surface degradation (Belnap and Eldridge 2001). Minimizing or preventing disturbance of biocrusts, or mitigating the disturbance through rehabilitation, may preserve and improve the functional recovery of degraded dryland ecosystems due to the varied functions that biocrusts provide (Belnap 2003a, b). These functions include provisioning of soil surface stability and resistance to wind and runoff erosion (Chaudhary et al. 2009), improving soil nitrogen (Barger et al. 2006), and nontrivial contributions to primary production (Jasoni et al. 2005). The influence of the disturbance on the biocrust depends on the nature of the disturbance (type, severity, frequency) and other factors such as soil type (texture, structure, and bulk density), site characteristics (climate, i.e., radiation, temperature, and rainfall regime), geomorphology (aspect, plateau), and timing (Belnap and Eldridge 2001).

There are some examples where limited disturbance (small scale, low intensity) of biocrusts leads to positive ecosystem outcomes. Occurrence of small-scale local disturbance events of moderate intensity and intermediate frequency, such as typical natural disturbances caused by native grazers, burrowing animals, or natural wildfires, in some natural biocrust habitats, seems to promote the successful coexistence of biocrust organisms and higher plants in some nutrient-poor environments (Beyschlag et al. 2008; Boeken et al. 2004; Jeschke and Kiehl 2008; Li et al. 2005).

In mesic systems, which would otherwise be highly vegetated, disturbances may actually favor biocrust development by opening the vegetation canopy and allowing sunlight to reach the soil surface. One example is inland dunes of Germany that were previously used as military training areas (Düming et al. 2014; Jentsch and Beyschlag 2003). Biocrusts of mesic systems tend to be early successional series which diminish in importance as vascular vegetation recovers to a closed canopy (Bowker 2007).

The disturbances we discuss in this chapter include (1) direct human activities such as livestock grazing and other agricultural practices, military training activities, human recreation disturbances, and mining and (2) natural disturbances, which may be augmented or altered by humans such as fire, sand deposition, and drought. In this chapter, we focus on research findings mainly from the last decade, as the previous literature was covered in Belnap and Eldridge (2001).

21.2 Direct Anthropogenic Activities

21.2.1 Agricultural Activities

Transforming natural semiarid areas to agricultural land for crop production will invariably reduce and may even locally eliminate biocrust components. Other types of agricultural activities have variable impacts on biocrusts, ranging from neutral to highly negative.

21.2.1.1 Tillage and Mechanical Clearing

The degree of soil disturbance associated with tillage and mechanical clearing is known to have long-lasting effects on biocrusts. In a study in a mesic grassland in Australia, Briggs and Morgan (2012) assessed the recovery of biocrust richness and cover at sites ranging from recently to never cultivated lands. Recently cultivated sites generally had significantly lower total cover of biocrusts and morphological type diversity than sites with a recovery time of 60 years since disturbance. Plowing for woody plant control has also been shown to reduce the cover and spatial arrangement of biocrusts (Daryanto et al. 2013). Zaady et al. (2013) experimentally simulated common agricultural disturbance scenarios occurring in Israel: (1) scalping (removal of the top 2 cm of topsoil), simulating light harvesting and minimum tillage practices, and (2) mowing and spreading of perennial vegetation simulating covering of the soil surface with plant debris. Sixteen years after treatment, both scalping and mowing were found to have long-term effects on the biocrusted soil surface and its related properties. Mowing and, to a lesser degree, scalping reduced runoff production and increased hydraulic conductivity. Infiltration rates were $7.6 \pm 1.7 \text{ ml min}^{-1}$ in the mowed plots and $4.8 \pm 1.1 \text{ ml min}^{-1}$ in scalped plots, compared to only $0.2 \pm 0.1 \text{ ml min}^{-1}$ in control-biocrust plots. The role of complete biocrust removal by scalping on infiltration processes was also examined in three contrasting environments (a loess-covered hillslope, a sandy dune, and a loess floodplain) at three sites in the Negev Desert, Israel. At the sandy dune and loess-covered hillslope sites, both sorptivity (e.g., capacity of the medium to absorb or desorb water by capillarity) and steady-state infiltration were enhanced by three- to fivefold where the biocrust was removed, and also at the loess floodplain site sorptivity was increased (Eldridge et al. 2000b). The removal of the biocrusts in these three very distinct landscapes influenced resource flows, particularly the interception and redistribution of runoff water to more productive patches, which are essential for ecosystem productivity in patterned landscapes.

The impact of tillage and clearing of biocrusts may also negatively impact agricultural systems which mimic the natural function of patterned landscapes. Man-made contour dikes are a central component of water harvesting systems for tree planting, herbaceous biomass production, and soil conservation in dry areas such as the Middle East (e.g., Egypt, Israel, and Jordan), Africa (e.g., Burkina

Faso), and South America (e.g., Chile). Efficient water capture depends on the presence of a stable biocrust upslope that directs surface runoff into the dikes where it is stored (Zaady et al. 2001). Complete destruction of the shrubs and biocrusts by cultivation reduced the runoff production available for the water harvesting systems to 6 % of the rainfall, in comparison to up to 32 % when the shrub hummock and biocrusts were left undisturbed (Eldridge et al. 2002). These results reinforce the view that biocrusts are critical for the efficient operation of water harvesting systems (Eldridge et al. 2002; see Chap. 17 by Chamizo et al.).

Afforestation is another land use which involves substantial disturbance or removal of the soil surface layers, so that the effects on biocrusts are likely to mirror those of agricultural practices such as tillage. These activities invert and mix soil horizons, bringing deeper material to the surface and dramatically altering soil surface characteristics (see also Chap. 9 by Colesie et al.).

21.2.1.2 Herbicides

Herbicides are commonly used as a weed control method in cropping ecosystems or in rangelands to produce desired changes in vegetation. For example, their use is expanding in the North American West as a tool to combat exotic plant invasions, but despite the wide usage, published data displaying the effects on biocrusts are scarce. Herbicide impacts strongly depend on the specific herbicide being applied, the composition of biocrusts, and the timing of application. In drylands, two studies have shown that glyphosate herbicides (e.g., Roundup, Accord), which function as broad-spectrum post-germination herbicides, do not negatively impact biocrusts. In the first study by Youtie et al. (1999), direct application of Roundup (N-(phosphonomethyl)glycine) and Accord (glyphosate dimethylamine) on moss-dominated biocrusts had no short-term negative impact on bryophyte cover. In fact, bryophyte cover decreased significantly in control plots due to the buildup of litter from exotic annual grasses that had invaded the site, while in the treated plots, the cover remained stable or increased slightly. A second study in an afforested area of Park Shaked, a long-term ecological research site in the northern Negev Desert, Israel, confirmed that spraying of Roundup had no effect on the biocrust components and did not alter the amount of runoff. The experiment in Park Shaked also quantified the effects of the herbicide simazine (2-chloro-4,6-bis(ethylamino)-s-triazine) on biocrust components and on the patchy structure of the landscape (Zaady et al. 2004). Simazine, a photosynthesis inhibitor, is a pre-germination herbicide (WSSA 1989; Kodama et al. 2001). Application of simazine affected biocrusts by decreasing chlorophyll levels and moss density dramatically, practically eliminating the photoautotrophic organisms (Fig. 21.1), whereas their organic and inorganic structures remained in place and continued to behave similarly to living biocrusts with regard to hydrology (Fig. 21.2).

When the experimental plots were reinvestigated 16 years after treatment, it was found that spraying of simazine decreased the biocrust cover by 23 % and perennial plants by 13 %, while promoting the annuals, whose coverage had risen by 64 %

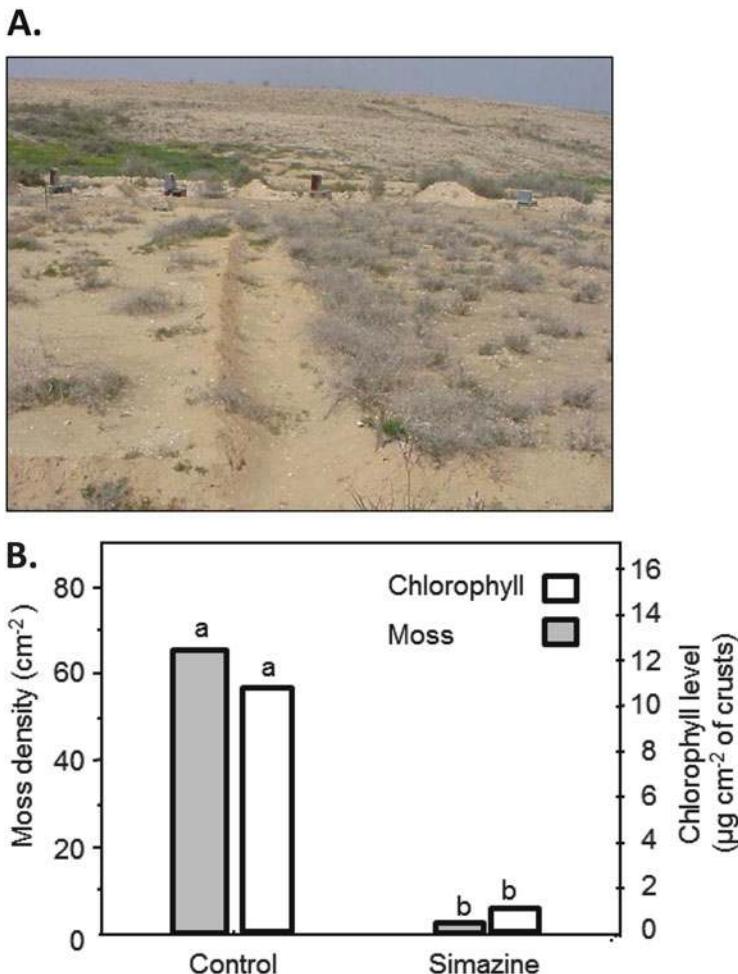


Fig. 21.1 (a) Plot with simazine, 3 years after application showing its *bright color* (left) compared to the *dark color* of the control biocrusts (right). (b) Simazine application reduces moss density and chlorophyll levels of biocrusts

(Zaady et al. 2013). Residual herbicides remain active within the soil for a long period of time and prevent germination of seeds, growth of roots, and regrowth of biocrusts. Thus, the biocrust disintegrated along with entrained sediment and organic material. This combination of impacts on biocrusts and vascular plants caused an increase in sediment yield in runoff water (Zaady et al. 2004, 2013).

In another experiment conducted in the Negev Desert highlands, simazine was sprayed onto freshly autoclaved biocrust samples to prevent recolonization. The samples were placed in trays in the field, and after 42 months, the role of biocrusts in the accumulation of atmospheric particles was examined. Once a month, the trays were weighed to quantify the accumulation of atmospheric particles on each.

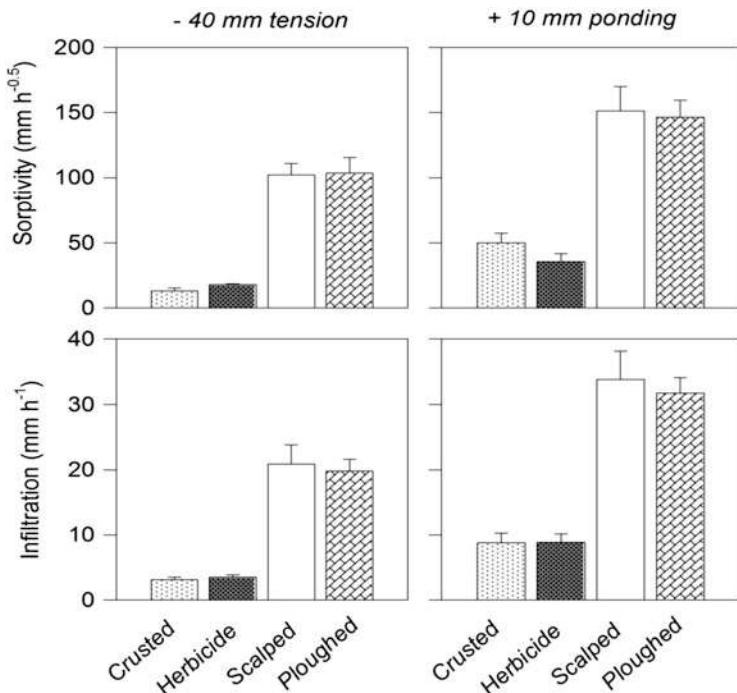


Fig. 21.2 Effects of herbicide application, scalping (physical removal of the biocrusts), and plowing (complete removal of the crust and disturbance of soil) on sorptivity and steady-state infiltration under -40 mm of tension and ponded ($+10 \text{ mm}$) conditions

Atmospheric particles were found to accumulate on sprayed biocrusts at a significantly lesser rate (228 g m^{-2} per annum) than on live, intact biocrusts (277 g m^{-2} per annum). This result shows the drastic long-term effect that simazine may have on soil depth accretion rate (Zaady and Offer 2010).

In conclusion, from the herbicides examined, simazine, but not glyphosate, was found to have a long-term effect on the biocrusted soil surface and its properties. Spraying treatments led to increased runoff production and decreased hydraulic conductivity. These practices had a long-term residual impact on biocrust succession and on related soil surface properties, which affected the hydrological processes and system functioning (Zaady et al. 2013).

21.2.1.3 Grazing of Livestock

The effects of grazing-induced disturbance on biocrust cover, composition, and function are manifold and variable and have been the subject of several reviews during the past two decades (e.g., Belnap 2003a, b; Eldridge and Greene 1994; Harper and Marble 1988; Warren and Eldridge 2001; West 1990). A critical review

of recent literature suggests a number of overarching propositions on the response of biocrusts to grazing.

Negative and Unequivocal Effects of Grazing

Perhaps the most clearly defined effect of grazing is the general observation that grazing almost always results in simplification of biocrust community structure and reduction of biocrust function. These disturbances are caused by surface trampling by the livestock hooves. Grazing reduces the total biocrust cover (Beymer and Klopatek 1992; Daryanto and Eldridge 2010; Golodets and Boeken 2006; Hodgins and Rogers 1997; Ponzetti and McCune 2001; Thomas 2012) and biomass (Beymer and Klopatek 1992) while increasing the biocrust cover spatial variability (Gomez et al. 2012; Pietrasik et al. 2011). Grazing reduces biocrust richness (Ponzetti and McCune 2001; Root and McCune 2012) and alters biocrust composition, e.g., by increasing cyanobacterial cover at the expense of lichens (Eldridge et al. 2000a). Grazing results in reduced C and N fixation (Aranibar et al. 2008) and C sequestration (Thomas 2012) and greater levels of sediment production (Belnap et al. 2009), but can reduce levels of runoff (Eldridge et al. 2000a, b; Pueyo et al. 2013; see also Chap. 17 by Chamizo et al.). Grazing-induced effects on biocrusts can indirectly influence a number of key ecosystem processes such as infiltration (Eldridge et al. 2010) or the invasibility of exotic plants (Reisner et al. 2013). Grazing may also influence the species-specific effects on ecosystems, for example, by reducing the effects of the lichen *Diploschistes diacapsis* on soil pH, K, Na, Ca, and Zn concentrations (Concostrina-Zubiri et al. 2013, 2014).

Legacy of Grazing Effects

Past levels of grazing are thought to have a large influence on the speed with which biocrusts can recover from disturbance (Beymer and Klopatek 1992). Shrublands in the Western USA that had an extensive biocrust cover and have never been grazed are thought to be largely resistant to invasion by the Eurasian grass *Bromus tectorum*, although substantial changes in biocrust richness were found in plots with even intermittent grazing (Belnap et al. 2006). Historic grazing may sometimes be more influential than contemporary grazing because many of these surfaces have already lost much of their upper soil layers, and subsurface horizons may better resist grazing-induced trampling (Eldridge and Greene 1994).

Taxon-Dependent Grazing Effects

The effects of grazing on biocrust taxa are likely to be species, morphological group, or functional group dependent. Concostrina-Zubiri et al. (2013) found that soil heterogeneity, caused mainly by the different physicochemical properties

exerted by the different biocrust taxa, decreased sharply with increasing grazing intensity and frequency. Lichens with continuous thalli have been shown to be more vulnerable to grazing than those with semicontinuous thalli (Scutari et al. 2004; Jimenez Aguilar et al. 2009) and foliose lichens more susceptible than squamulose lichens (Rogers and Lange 1971). Mosses have also been shown to be more susceptible than fruticose lichens (Muscha and Hild 2006). Some individual species or taxonomic groups may be advantaged by low levels of grazing, for example, those that rely on fragmentation for dispersal (Eldridge and Leys 1999; St. Clair et al. 2007).

Landscape- and Season-Dependent Effects of Grazing

Sensitivity of biocrusts to disturbance varies according to landscape properties and setting. Read et al. (2008) found that biocrusts were more strongly impacted by grazing animals in small patches such as livestock shelters in woodlands, but as the size of the patch increases, the impact is more dispersed. Heterogeneous landscapes of partially fixed dunes also influence the effects of disturbance on biocrusts. Proximity to mobile portions of dunes can lead to chronic deposition of sand which can in turn interact with other forms of disturbance (Zhang et al. 2013). There are also seasonal effects of grazing on attributes such as biocrust abundance (Holst et al. 2009). While grazing in the cooler, wet season, when the biocrust becomes soft and hoofprints are clearly visible (Fig. 21.3), often has a lesser effect on biocrust cover and individual taxa (e.g., moss), summer grazing can have marked negative effects (Memmott et al. 1998; Wang et al. 2009). This generalization may only hold in deserts which receive cool season precipitation.

Effects of Grazing Intensity

Effects of grazing depend on relative grazing intensity (e.g., Concostrina-Zubiri et al. 2013, 2014). Even limited grazing can cause significant shifts in vegetation and damage to soil biocrusts (Lovich and Bainbridge 1999). Generally, higher levels of grazing lead to more substantial effects on biocrust taxa and therefore on functions such as N input and soil stabilization (Liu et al. 2009). Biocrust cover and richness likely decline with increased grazing intensity, as evidenced by multiple studies (Graetz and Ludwig 1978; Williams et al. 2008). Examination of grazing effects on biocrust richness, cover, and abundance from 44 studies in Australia (Eldridge, unpublished data) indicates the generally negative effect of any level of grazing, even a change from ungrazed to lightly grazed, on biocrust cover, richness, and abundance. The large variability among attributes would be expected across any continent and could be accounted for by differences in the complement of grazing animals, landforms, and soil types. Despite all the studies conducted so far, there is still little information on how biocrusts respond to different rotational strategies or stocking levels.

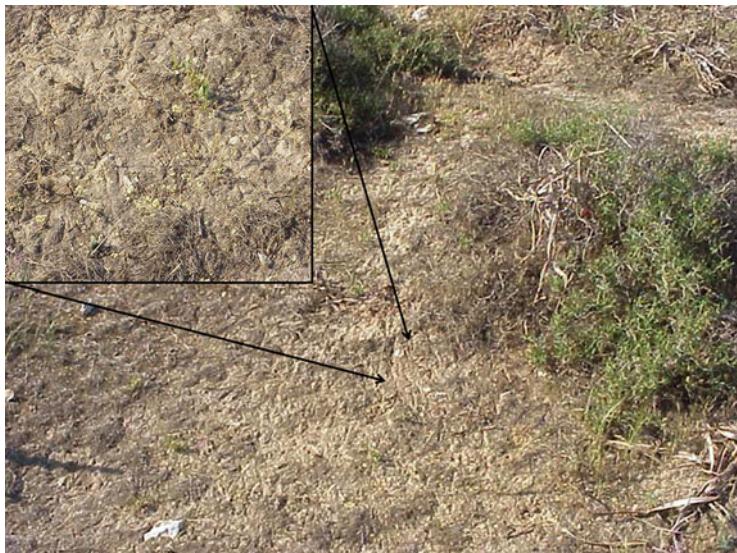


Fig. 21.3 Hoofprints of sheep on wet biocrusts after herd crossing. The biocrust is still seen in a good condition, although the microtopography is not flattened as undisturbed one. It is not becoming crumbled and loose as in the case of dry crust (E. Zaady)

21.2.2 Nonagricultural Direct Human Disturbances

There are several types of disturbance impacting biocrusts that are not linked to crop or livestock production. Drylands tend to be more sparsely populated and in some nations have been used for military training activity. With an increasing global population, more urbanization of drylands is occurring, bringing with it new housing development and road construction. Linked to this urban expansion, more natural drylands are being used for recreation. Recreational disturbances to biocrusts are caused by human foot traffic, mountain bikes, and four-wheel drive vehicles. Other disturbances are caused by new housing development and road construction.

21.2.2.1 Military Activity

Another disturbance, which occurs over large scales in less populated areas of deserts worldwide, is military training. Military training results in loss and degradation of soil surface habitat due to varying site-specific combinations of foot traffic, camping activities, vehicle traffic ranging from jeeps to tanks, and artillery practice. Prosser et al. (2000) reported that two years of moderate to heavy tracked

vehicle training increased the percentage of bare soil by 17 % on a military reservation in North Dakota.

Large areas of the California desert, which covered more than 46,800 km², were impacted by military training during World War II between 1942 and 1944 and exemplify the many impacts of military training including tent sites, roads, and tank tracks (Lovich and Bainbridge 1999). Belnap and Warren (2002) studied the recovery of soil properties in this area approximately 55 years after disturbance. They reported that tracks from military vehicles were still visible, particularly in areas of desert pavement. Based on biomass estimates, the cyanobacterial component of biocrusts had recovered 46–65 % of their biomass in tracks compared to outside the tracks. Overall recovery of lichen cover has been much slower. Under plant canopies, coverage of *Collema tenax* was not significantly different between areas inside and outside the tracks; however, recovery of *Catapyrenium squamulosum* was only 36 % of its biomass. In plant interspaces with less favorable moisture and temperature conditions, *Collema tenax* showed a 6 % recovery and *Catapyrenium squamulosum* a 3 % recovery of their biomass. Assuming that the recovery of biocrusts is linear, it may require almost two millennia for full recovery of these areas.

In mesic, central European sandy areas, past military disturbance is thought of as a force which maintains biodiversity and provides opportunities for biocrusts to grow (Jentsch and Beyschlag 2003; Fischer et al. 2010; Düming et al. 2014). Since many of these areas have ceased to be used for military training, some have proposed simulating military disturbances for promotion of early successional vegetation, inclusive of biocrusts (Jentsch et al. 2009).

21.2.2.2 Human Foot and Vehicular Traffic

While most compressional disturbances (such as from vehicles and trampling by people or animals) result in similar types of impacts, severity can vary widely depending on disturbance source, intensity, timing, frequency, duration, and extent. In Grand Canyon National Park, only 15 passes of hikers wearing lug-soled boots were required to destroy biocrusts (Cole 1990). Visual evidence of biotic components was reduced to nearly zero after 50 passes. The results of Cole's experiment clearly illustrate the vulnerability of biocrusts by trampling. Zaady et al. examined the effects of mountain bicycles on cyanobacterial crusts on loess soils in the Zin Valley, Negev Desert highlands (E. Zaady, unpublished). The results suggested that, although it took up to 3 years for biocrusts to recover, the major damage was to the organisms that rely on the cyanobacterial crusts (Shachak and Steinberger 1980; Shachak et al. 1976). The cyanobacterial crusts comprise the basis for the ecological system in the Negev Desert. Species density of organisms such as isopods (*Hemilepistus reaumuri*) and snails (*Sphincterochila zonata*) that feed on the cyanobacterial crusts decreased markedly, and these declines were followed by a

decrease in the burrow density of the large-clawed scorpion (*Scorpio maurus palmatus*), their main predator (E. Zaady, unpublished). Belnap and Eldridge (2001) suggested that motor vehicles exert compressional and shear force and may often crush, crumble, or bury biocrust organisms. The long-term effects of car tires on biocrusts and their influence on the hydrological aspects of a semiarid ecosystem were simulated using a heavy roller (Zaady et al. 2013). Even 16 years after treatment, reduction of biocrusts and their runoff-generation functions was apparent.

21.2.2.3 Mining

Mining in general involves removal of the topsoil layers. Deep soil layers are exposed and the soil surface characters change dramatically. Mining influences particle size distribution and porosity of the substrate, particularly those with a relatively high content of silt and clay (Spröte et al. 2010). There are no published studies on the effects that mines have on biocrust communities, but we can expect them to be similar to other activities which completely destroy existing biocrusts and strongly alter soil surface physical and chemical properties such as deep tillage and earthworks associated with urbanization. Some researchers have suggested or attempted initiating mining rehabilitation with cyanobacterial crusts (Doudle and Williams 2010; Zaady et al. unpublished). Assisted recovery of biocrust is discussed more fully in Chap. 24 by Zhao et al.

21.3 Indirect Anthropogenic Activities

Local pollution such as elevated tropospheric ozone concentration, heavy metal pollution, and oil spills also pose a threat to biocrust communities in arid lands worldwide (Fig. 21.4), particularly those in the vicinity of urban and/or industrial areas (Maestre et al. 2012). The potential effects of these pollutants can be related to direct physiological stress and are probably followed by significant community alterations (Belnap and Eldridge 2001), which may give them a competitive advantage over other biocrust components, changing the community composition. For example, Cuny et al. (2004) found that the lichen *Diploschistes muscorum* was able to limit the damage caused by heavy metal (Cd, Pb, and Zn) pollution to a certain extent by antioxidant mechanisms. However, to the best of our knowledge, no data are currently available on how these pollutants may affect biocrust communities as a whole, making any conclusion on these topics rather speculative.



Fig. 21.4 Crude oil pipeline leakage covering the cyanobacterial biocrusts in the Negev Desert Arava valley (E. Zaady)

21.4 Natural Disturbances

21.4.1 Fire

Johansen (2001) described the effects of fire on biocrusts and post-fire recovery. Burning has been shown to have dramatic and often varied effects on biocrusts. Biocrusts could be directly burned or killed by heat from the fire or indirectly impacted by vegetation removal or ash deposition. The mechanism by which fire impacts biocrusts depends on fire frequency, intensity, and patchiness, which in turn is impacted by fuel loads (Johansen 2001). Fires are typically patchy because of sparse and irregular distribution of available fuels.

High-intensity fire may directly decrease biomass or cover of biocrusts, alter community composition, or alter functional properties of biocrusts. Fire typically resets the biocrust successional process, reducing late successional species or all species and sometimes favoring early successional species. Hawkes and Flechtner (2002) found that species composition generally did not change after fire in Florida, but the abundance of organisms was significantly reduced. Similar patterns have been observed by other investigators. However, others found a decline in species richness as well as in cover, often associated with altered community composition

(Schulten 1985; Hilty et al. 2004; Dettweiler-Robinson et al. 2013), sometimes with a greater cover of short mosses, but a reduced cover of lichens and tall mosses. Fire impacts on biocrusts also extend to their functions. Fire reduces surface stability compared with unburned sites, possibly by reducing the extent of cyanobacterial filaments in the soil (Bowker et al. 2004). Burning, even during seasons when biocrust taxa are dormant, can still lead to reduced nitrogen fixation and chlorophyll *a* content (Ford and Johnson 2006).

While high-intensity fires may have large direct effects on biocrusts (Greene et al. 1990), low-intensity fires may have few effects (Warren and St. Clair 2009). Low-intensity fires in the Palouse Prairie in the Western USA, for example, resulted in few differences in lichen and moss composition compared with unburned sites (Bowker et al. 2004). In some productive ecosystems, the greatest indirect effect of fire on biocrusts may be to reduce competition from vascular vegetation. For example, relatively frequent fires (every 2 years) in grasslands in eastern Australia have been shown to lead to increased abundance and diversity of biocrust taxa by reducing vascular plant biomass and cover and providing niches for biocrust establishment (O'Bryan et al. 2009). Frequent fires prevent the recovery of lichens and mosses, leaving only a few species of cyanobacteria. The cover of cyanobacteria can increase a few months after fire in response to the removal of competing vascular vegetation and dense litter (Eldridge and Bradstock 1994).

21.4.2 Sand Deposition

Very thin layers of wind- or waterborne sediments can cover photosynthetic organisms and dramatically reduce site fertility (Belnap and Gillette 1997; Berkeley et al. 2005). Deposition of sediment may favor those groups that have a greater tolerance to burial, such as bundled filamentous cyanobacteria (Hu et al. 2003; Rao et al. 2012; Thomas and Dougill 2007) or certain species of mosses (Jia et al. 2008). Few moss species can overcome sand burial and their survival depends on the depth of the sand cover layer (Martínez and Maun 1999).

Rao et al. (2012) conducted field-based studies to evaluate the effects of sand burial (depths of 0, 0.5, 1, 3, and 5 cm) on biocrusts in the Hopq Desert, China. Their study demonstrated that sand burial imposed severe stresses on the cyanobacterial crusts, such as a reduction in chlorophyll *a* content, restriction of scytonemin synthesis, damage of PSII activity, as well as reductions in total carbohydrate reserves. These observations are similar to those of Wang et al. (2007), who examined the effects of sand burial on biomass, chlorophyll fluorescence, and extracellular polysaccharides on human-made cyanobacterial crusts. Their results indicated that extracellular polysaccharide content decreased with increases in burial time and depth. Chlorophyll *a* content did not degrade until 30 days of burial. Declines in the content of extracellular polysaccharides were also observed in the cyanobacterium *Microcoleus vaginatus* (Wang et al. 2007).

Williams and Eldridge (2011) studied the effects of sand deposition on the bioavailability of N in cyanobacteria-dominated soil biocrusts during and after a severe drought. They found that sand-covered biocrusts had up to three times more mineral N (NH_4^+ and NO_3^-) and twice the mineralizable N than sand-free samples. They suggested that increased N bioavailability probably results from autolysis and a subsequent breakdown of N-enriched cyanobacterial cell material, mediated by changes in the soil surface microenvironment. Their findings suggest that landscape-level processes of sand deposition have a marked effect on soil nutrient pools by enhancing the accumulation of plant-available N on cyanobacterial crusted surfaces. Inappropriate land management or the loss of cyanobacterial soil crusts during drought would compromise the long-term bioavailability of soil N.

21.4.3 Drought

Biocrusts can rapidly decrease in abundance when conditions are poor (Belnap et al. 2006; Bowker et al. 2008; Williams et al. 2008). Because hydration time is among the most important determinants of biocrust growth rate, biocrusts can be negatively impacted by drought despite their desiccation tolerance (Williams et al. 2008; Barker et al. 2005). The effects of normal desiccation events on desiccation-tolerant organisms are well reviewed elsewhere (Kranner et al. 2008; Oliver et al. 2005). In contrast, a drought is a distinct complex of stressors composed of longer than normal desiccation events, punctuated by fewer and shorter hydration events. During an extended drought, biocrust organisms are subject to photooxidative degradation of their pigments, nucleic acids, and proteins and physical degradation of their tissues. They are deprived of activity and, therefore, of opportunities to repair damage. Thus, the length of a desiccation period has been shown to exert a negative influence on biocrust organisms (Coe et al. 2012; Gray et al. 2007).

Altered precipitation patterns, including amount, seasonality, and frequency of precipitation, have been projected as major climate change factors in the coming decades (Christensen et al. 2007). For this reason, several studies have applied experimental alterations of precipitation to biocrusts in an effort to simulate climate change (Coe et al. 2012; Reed et al. 2012; Escolar et al. 2012). These climate change experiments are the subject of Chap. 22 by Reed et al. Here, we focus on the response of biocrusts to nonexperimental drought in the field.

21.4.3.1 Drought Effects on Biomass and Cover

In general, drought conditions in the field cause a decrease of biocrust biomass and pigment concentrations. Biocrust cover (differentiated into moss, lichen, and dark cyanobacteria) and chlorophyll *a* content were measured at 109 relatively undisturbed ~2 ha sites in Grand Staircase-Escalante National Monument, USA

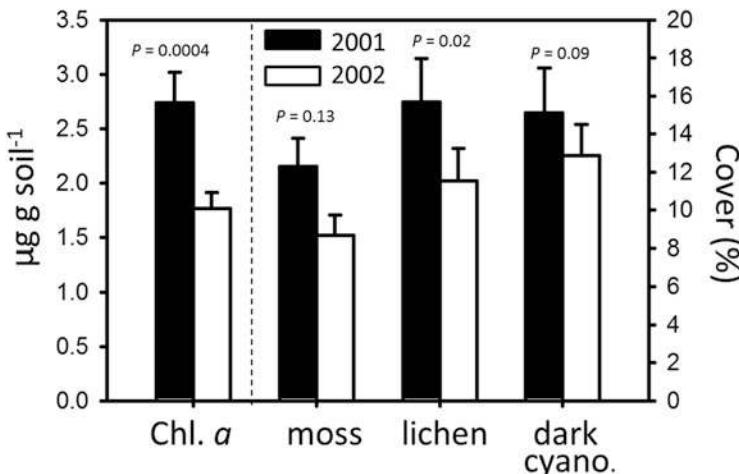


Fig. 21.5 Chlorophyll concentrations and cover of various biocrust types sampled before the drought and during a severe drought (2002) in Grand Staircase-Escalante National Monument. Statistical tests account for both soil type and long-term precipitation averages as covariates

(Fig. 21.5) (Bowker et al. 2006). Samples were taken from various soil types across 0.8 million hectares. Sampling was conducted in late spring–early summer of 2001, a moderately dry year, and in the extreme drought year of 2002. The cover of all biocrust components was somewhat lower in 2002, especially the lichen cover, which decreased by nearly one-third ($p = 0.02$). Chlorophyll *a* declined most clearly by over one-third ($p = 0.0004$), indicating either less cyanobacterial biomass in soils or a lower pigment concentration within cyanobacteria.

Similar results were observed in semiarid Queensland, Australia, where cyanobacterial crust cover was suppressed by more than 50 % during and following a major drought event (Williams et al. 2008). Belnap et al. (2006) documented a decrease of similar magnitude in cover of biocrust mosses and lichens from 1967 to 2003, with an extreme drought year in 2003 on the Colorado Plateau, USA.

An alternating series of droughts spanning 19 years (1992–2009) brought about a decline in annual average precipitation from more than 200 mm to 150 mm, and two years with less than 100 mm, in the northern Negev Desert. The drought period triggered a change of the landscape from one dominated by shrubs to one dominated by biocrusts. Most of the *Noaea mucronata* (Chenopodiaceae) and *Atractylis serratuloides* (Asteraceae) shrubs died and were not replaced by new recruitment. This caused biocrust components to take over with the moss *Aloina bifrons* (Pottiaceae) dominating south-facing and *Crossidium crassinerve* var. *laevipilum* (Pottiaceae) dominating north-facing slopes. The cyanobacteria are dominated by *Microcoleus vaginatus* (Chroococcales), which grows 0–2 mm below the soil surface, and *Nostoc punctiforme* and *Scytonema* spp. (Nostocales), which grow on the soil surface. Other species present in small numbers are *Chroococcus turgidus* (Chroococcales), *Calothrix* sp. (Oscillatoriales), and the green alga

Palmella sp. (Tetrasporales). The soil cover of biocrust increased from 30 to 70 % (Zaady et al. 2004, 2013, unpublished data).

21.4.3.2 Drought Effects on Species Composition and Diversity

In some cases, organisms are universally negatively impacted by drought, but in other cases, some species seem to be more susceptible than others, possibly paving the way for community shifts (Mueller et al. 2005; Verwijmeren et al. 2014). In a drought following an exceptionally wet period in the Mojave Desert, Belnap et al. (2007) found a universal decline of biocrust organisms rather than a shift in composition. A similar study on the wetter and cooler Colorado Plateau found that chlorolichens and mosses were most clearly negatively impacted by drought, whereas lichens of the genus *Collema* were more strongly influenced by other climatic factors. Barker et al. (2005) confirmed moss susceptibility to drought in the form of widespread bleaching of moss tissues in response to drought. Furthermore, drought may indirectly favor those groups that better tolerate burial, such as bundled filamentous cyanobacteria (Rao et al. 2012; Thomas and Dougill 2007) or mosses (Jia et al. 2008).

21.4.4 Conclusion

Disturbances can have direct and indirect effects on several aspects of the structure and function of biocrust communities. Human activities (i.e., mechanical agricultural practices, herbicides, livestock grazing, military activities, hiking, off-road vehicles, mining, and air pollution) and natural factors (i.e., fires, sand deposition, and drought) cause disturbances resulting in crushing, crumbling, or burial of biocrust organisms or degradation of their tissues or physiology, leading to reductions and changes in biocrust community structure, biomass, and function. The severity of local disturbances depends on the spatial extent, frequency, timing, disturbance source, relative intensity, and duration.

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Chapter 22

Biocrusts in the Context of Global Change

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22.1 Introduction

A variety of global environmental changes—including increased temperature, altered precipitation regimes, increased nutrient deposition, and elevated atmospheric CO₂ concentrations—are affecting ecosystems worldwide, and drylands are no exception. Multiple lines of evidence suggest that arid and semiarid ecosystems may experience particularly large changes in climate (IPCC 2013; Garfin et al. 2014) and that interactions among global change factors (e.g., elevated CO₂ × warming) could have strong synergistic effects in these ecosystems (Shaw

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et al. 2002; Shen et al. 2009; Morgan et al. 2011). Drylands are characterized by extremes in temperature and aridity, as well as by relatively low soil fertility (Hooper and Johnson 1999; Li et al. 2009). Thus, predictions for a warmer, drier climate and increased nutrient deposition pose important questions about dryland resilience in the face of environmental change. For example, increased temperature may reduce the photosynthetic rate of dryland vascular plants, both by exceeding photosynthetic temperature optima and through reduced soil water availability (Wertin et al. 2015). Over longer timescales, climatic changes and physiological effects may result in significant modifications to dryland vascular plant community composition, productivity, and phenology (Miranda et al. 2009; Munson et al. 2011).

Alongside vascular plants, it is equally important to consider how biocrusts will respond to environmental change, because much of the arid land surface is covered by biocrusts and because of their global role in ecosystem function (Pointing and Belnap 2012; Büdel et al. 2009; Elbert et al. 2012; Porada et al. 2013, 2014; Lenhart et al. 2015). A growing body of evidence suggests that global changes have the potential to dramatically affect biocrust communities and the range of ecosystem services they provide. In this chapter, we examine data exploring the effects of environmental change on biocrust structure and function, as well as the potential for changes to biocrusts to create feedbacks to global change. We focus on biocrust responses to elevated atmospheric CO₂ concentrations, climate change (warming and changes in precipitation patterns), and nitrogen (N) deposition and consider both the observed responses and the mechanisms behind the effects.

22.2 Elevated Atmospheric CO₂ Concentrations

Atmospheric CO₂ concentrations have increased faster than most “worst case” model predictions, and concentrations continue to rise (IPCC 2013). Numerous studies have assessed the effects of elevated CO₂ on vascular plants (for reviews see Poorter 1993; Wand et al. 1999; Poorter and Navas 2003), but little is known about how biocrusts will respond to increasing atmospheric CO₂ concentrations. There are several mechanisms by which elevated CO₂ could affect biocrusts, including

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direct effects on photosynthesis and indirect effects via changes to vascular plant and/or biocrust community composition, soil moisture, carbon (C) allocation, and alteration to soil nutrient availability. Available data regarding biocrust responses to increased atmospheric CO₂ come mostly from laboratory studies, growth chamber experiments (e.g., Lane et al. 2013), and results from the Free Air CO₂ Enrichment (FACE) elevated CO₂ experiment conducted in the Mojave Desert, USA, which ran from 1997 to 2007 (the Desert FACE experiment; http://web.unlv.edu/Climate_Change_Research/NDFF/NDFF_index.html).

Under controlled laboratory conditions (optimal light, moisture, and temperature), biocrust organism photosynthesis is often limited by CO₂ availability (Tuba et al. 1998; Jauhiainen and Silvola 1999; Lange 2002; Botting and Fredeen 2006; Toet et al. 2006), and gas exchange studies consistently show that biocrust photosynthetic rates increase proportionally with the partial pressure of external CO₂ before saturation is reached (e.g., Fig. 22.1a; Lange 2002). For example, net photosynthesis rates at 350 ppm CO₂ for the biocrust lichens *Fulgensia fulgens*, *Diploschistes muscorum*, and *Diploschistes scruposus* were only 70–80 % of their photosynthetic rates at 480 ppm CO₂ (Lange et al. 1999), suggesting strong positive responses of each lichen to increased CO₂. For biocrust mosses, exposure to elevated CO₂ has been shown to enhance photosynthetic rates (Tuba et al. 1998). These results, together with an overall increase in soil water availability resulting

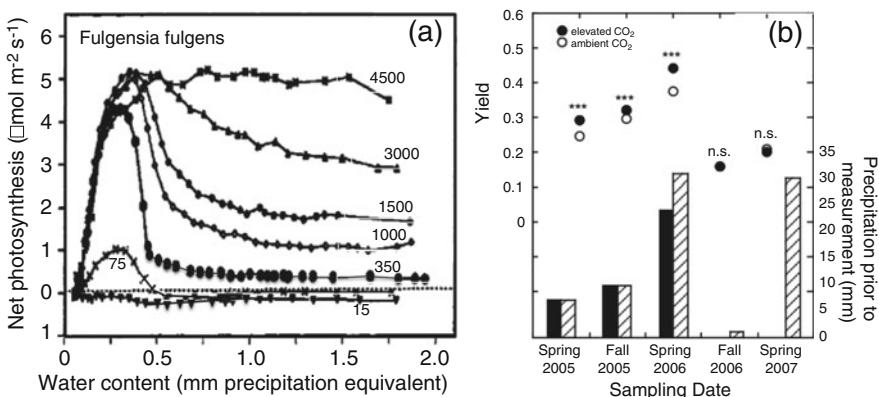


Fig. 22.1 (a) Response of net photosynthesis (at saturating photosynthetic photon flux density) of the lichen *Fulgensia fulgens* to thallus water content at different external CO₂ concentrations. External CO₂ concentrations ranged from 15 to 4500 ppm (as indicated on each curve), and incubations occurred at 17 °C. Data are reprinted from Lange et al. (1999) with permission from Elsevier. (b) Field data showing the effects of elevated CO₂ on lichen effective quantum yield in relation to different amounts of precipitation. Bars show precipitation totals for 7 days (black bars) and 14 days (dashed bars) prior to each effective quantum yield measurement. Symbols represent means of *Collema coccophorum* effective quantum yield ($n = 60$ per value) for the ambient (open circles) and elevated CO₂ (filled circles) treatments of the Nevada Desert Free-Air Carbon Dioxide Enrichment (Desert FACE) experiment. Elevated CO₂ treatment effects on effective quantum yield values are shown as *** $P < 0.001$ or not significant (n.s.). Figure modified from Wertia et al. (2012)

from reductions in vascular plant transpiration under elevated CO₂ [(Morgan et al. 2011), but see (Nowak et al. 2004)], suggest that elevated CO₂ could increase net photosynthesis of bryophyte and chlorolichen biocrust communities. Increased photosynthesis may allow for greater production of biomass, secondary osmoprotectants, and pigments (e.g., melanin, mycosporines) that could enhance stress tolerance relative to biocrusts under current ambient conditions.

The effects of altered CO₂ concentrations would be strongly dependent upon biocrust moisture content and its effect on the diffusion of CO₂ (e.g., Lange 2002; Lange and Green 2008), and net photosynthesis responses observed under laboratory conditions may not translate into an observable effect on biocrust function or structure in the field. In addition, biocrust autotrophs may not consistently experience an increase in CO₂ when atmospheric CO₂ concentrations increase, as soil surface and soil atmosphere CO₂ concentrations can be much greater than that of the atmosphere (e.g., Pumpanen et al. 2003). Wertin et al. (2012) used the Desert FACE experiment to investigate how elevated CO₂ affected the abundance, community composition, effective quantum yield (a proxy for photosynthetic capacity), and pigment concentrations of Mojave Desert biocrust mosses and lichens. They found that, during a drought, elevated CO₂ (550 ppm, compared with a ~370 ppm control) did not alleviate water stress or increase photosynthetic capacity enough to mitigate a dramatic, drought-induced reduction in moss and lichen cover. Lichen-effective quantum yield and biocrust pigment concentrations were more strongly dependent upon recent precipitation than the CO₂ treatment although, when hydrated, elevated CO₂ did increase lichen photosynthetic potential (Fig. 22.1b; Wertin et al. 2012).

These data make sense in the context of increased CO₂ availability resulting in increased photosynthesis at times of optimum saturation (e.g., Lange 2002) and are well aligned with a vascular plant study at the same Desert FACE site. Photosynthesis and new shoot production of a dominant shrub was markedly increased by the elevated CO₂ treatment in a high rainfall year; however, elevated CO₂ did not have effects in a drought year (Huxman et al. 1998; Hamerlynck et al. 2000; Smith et al. 2000). Elevated CO₂ also resulted in increased C content per unit mass in shoots of the moss *Syntrichia caninervis* (Brinda et al. 2011; Coe et al. 2012a), although this did not consistently translate into increased shoot growth (Brinda et al. 2011). Taken together, these results suggest that increases in atmospheric CO₂ may benefit biocrust lichens and mosses but only when precipitation is sufficient and depending upon allocation. Thus, the results support the idea that, in arid ecosystems, there would be a minimum threshold of precipitation necessary for elevated CO₂ to have a positive effect on the photosynthetic activity of biocrust components.

In addition to lichens and mosses, cyanobacteria in biocrusts contribute significantly to surface soil biomass and to net photosynthesis (e.g., Johnson et al. 2012). At the same Desert FACE site, molecular and metagenomic analyses of the biocrust bacterial community showed that cyanobacteria exhibited reduced total biomass and constituted a lower proportion of the biocrust bacterial community after 10 years of elevated CO₂ relative to the ambient CO₂ controls

(Haimovich-Dayan et al. 2011; Steven et al. 2012). Functional analyses of biocrust metagenomes showed that cyanobacterial genes related to oxidative stress responses were higher in biocrusts exposed to elevated CO₂ conditions compared to ambient conditions, suggesting that increased oxidative stress may play a role in the cyanobacterial response (Steven et al. 2012). Thus, the photosynthetic cyanobacteria in biocrusts responded negatively to long-term elevated CO₂ conditions in the field, highlighting the complexity of biocrust community responses to changing CO₂ concentrations.

It is interesting to consider the potential variation in the mechanisms behind vascular plant versus biocrust responses to increased CO₂. For vascular plants, a higher concentration of CO₂ could increase the amount of C fixed per unit water transpired (i.e., a higher water use efficiency). However, biocrusts lack stomata and thus are not transpiring H₂O, and the water content of biocrusts is a strong regulator of C fixation via its effect on CO₂ diffusion rates. In effect, in some organisms and at some moisture levels (e.g., Lange 2002), a higher CO₂ would increase the amount of C fixed by biocrusts per unit time of activity, which is more accurately described by the integrated water-driven C budget [IWCB, which assesses the amount of C fixed for a given amount of water during one wetting and drying cycle within the lifetime of a plant or biocrust (Mishler and Oliver 2009)]. Biocrusts are active only when wet, and reductions in their moisture occur via evaporation and the leaching of water to deeper soil layers. Thus, altered CO₂ concentrations could affect C fixation directly for some biocrust organisms via changes to fixation rates but not indirectly via an ability to stay wet longer. In contrast, vascular plants can increase the length of time they can access soil water with elevated CO₂-induced reductions to transpiration loss (Morgan et al. 2011). In areas with enough vascular plant cover, if increased CO₂ does result in greater soil moisture via reduced vascular plant transpiration (*sensu* Dermody et al. 2007; Morgan et al. 2011, but see Nowak et al. 2004), then increased CO₂ concentrations could indeed increase the length of the biocrust photosynthetic period based on vascular plant-driven increases in soil moisture. However, it is important to note that many crust organisms have reduced photosynthesis in wet conditions, showing a unimodal relationship between moisture content and photosynthetic rate regardless of atmospheric CO₂ concentration (e.g., Lange 2002). Another potential interaction is CO₂-induced increase in the cover of vascular plants, including exotic annual grasses (Smith et al. 2000). If elevated CO₂ enhances vascular plant net primary productivity (e.g., Smith et al. 2000; Housman et al. 2006; Morgan et al. 2011), biocrusts may experience reduced light availability and increased fire susceptibility, which could affect biocrust photosynthesis, performance, and composition.

Multiple lines of evidence suggest that biocrust N₂ fixation represents a vital and potentially dominant source of N to many drylands (Belnap 2002; Reed et al. 2011; Elbert et al. 2012; Yeager et al. 2012), and CO₂-induced changes in biocrust composition and/or C cycling could indirectly affect soil fertility via effects on processes such as N₂ fixation (Norby and Sigal 1989). Nevertheless, the one dryland field study of which we are aware that manipulated CO₂ and assessed N₂ fixation (Desert FACE) found no significant effect on the process (Billings et al. 2002).

However, biocrust soil N mineralization rates did decline by 35 % under elevated CO₂ at the site.

Less is known about the effects of elevated CO₂ on the microfaunal consumers that inhabit biocrusts. In a temperate forest system, Neher et al. (2004) found that elevated CO₂ decreased the total abundance of nematodes. However, neither Ayres et al. (2008) nor Blankinship et al. (2011) found a consistent, significant effect of elevated CO₂ on soil fauna in a variety of temperate field experiments, and questions of how changes in atmospheric CO₂ concentration translate into soil surface and within-soil CO₂ concentrations remain (Pumpenan et al. 2003). After eight years of the Nevada FACE experiment, Darby et al. (in preparation) found that elevated CO₂ did not have a significant effect on biocrust soil microfauna, although some taxonomic groups were significantly affected by an interaction of CO₂ with other environmental variables, such as soil depth or proximity to vascular plants. For example, elevated CO₂ increased the abundance of fungivorous nematodes beneath grass cover but not beneath shrub cover or plant interspaces. Additionally, multivariate analysis showed that a number of desiccation-intolerant nematode species were more abundant under ambient CO₂, while several desiccation-tolerant species were more abundant under elevated CO₂. Collectively, these results suggest that the effect of elevated CO₂ on biocrust microfauna will not be simple, but instead a complex interaction with plant exudates and soil hydrology.

22.3 Climate Change

The biophysical characteristics of drylands make them highly vulnerable to climate change (Sala et al. 2000; Reynolds et al. 2007; Maestre et al. 2012; IPCC 2013). While it is sometimes suggested that biocrusts are so well adapted to aridity that they could maintain resilience in even the hottest and driest of climates, a number of studies suggest that, in fact, biocrusts may respond dramatically to even seemingly subtle climatic changes.

22.3.1 Temperature

Important changes in the phenology, distribution, and functioning of biota are linked with the effects of warming (e.g., Gonzalez-Megias and Menendez 2012; Visser and Both 2005), and questions of temperature thresholds and tipping points are increasingly recognized as critical aspects of climate modeling (e.g., Livina et al. 2011). Models forecast notably warmer temperatures for the already warm desert biome, as well as increases in the frequency of extremely warm years by the late twenty-first century (IPCC 2013; Garfin et al. 2014). Without increases in precipitation, this would increase the aridity of drylands and may expand the dryland area worldwide 10 % by the end of this century (Feng and Fu 2013). A

growing body of work suggests the potential for warming to markedly affect biocrust community composition and function. Continental-scale compositional surveys of biocrust cyanobacterial communities across arid and semiarid North America showed a latitudinal switch in the dominance of two key biocrust cyanobacteria (Garcia-Pichel et al. 2013). Laboratory incubation data confirmed that this latitudinal sorting was driven largely by cyanobacterial preferences for temperature: *Microcoleus vaginatus* was less thermotolerant than *Microcoleus steenstrupii* (Garcia-Pichel et al. 2013). In view of predictions for much warmer temperatures in the southwestern USA (Garfin et al. 2014), *Microcoleus steenstrupii* may replace *Microcoleus vaginatus* in much of the studied area within the next few decades, with unknown ecological consequences for soil community composition, fertility, and stability.

A study on the Colorado Plateau, USA, compared the response of biocrust communities to 10 years of altered precipitation and experimental warming (using infrared warming lamps, which warmed soils 2–4 °C above ambient) with 15 years of physical disturbance from repeated human trampling (Ferrenberg et al. 2015). Although biocrust responses to warming took >5 years to manifest, warming considerably reduced moss and lichen cover relative to control plots, and the cover of lightly pigmented cyanobacterial biocrust significantly increased. Importantly, the extent of visible biocrust community change in the climate manipulation plots was the same as that observed with physical disturbance, suggesting the potential for biocrusts to respond dramatically to warming: climate treatments and physical disturbance led to a similar early successional community state (Ferrenberg et al. 2015). Genetic techniques were used to assess biocrust cyanobacteria and soil microbial communities from the same climate and physical disturbance experiments, and, in contrast to the visual assessments of biocrust community, microbial data suggested that the climate and physical treatments differentially impacted the resident soil bacterial communities and the community functional profile (Steven et al. 2015). Taken with the cover data (Ferrenberg et al. 2015), these genetic results highlight how different components of biocrust communities (i.e., visible crusts vs. microbial communities) can respond differently to the same perturbation and show that different methods of assessment (i.e., cover vs. abundance) provide distinct insights (Steven et al. 2015).

Escolar et al. (2012) used open-top chamber warming to show that an average 2.4 °C increase in soil temperature brought about a significant decrease in the diversity of a well-developed biocrust community (Fig. 22.1a). This was driven by a 40–70 % decline in the cover of lichens (such as *Diploschistes diacapsis*, *Squamaria lentigera*, and *Fulglesia subbracteata*); however, warming slightly increased moss abundance. A warming experiment in the Arctic also showed negative effects on peatland lichen diversity and mixed effects on peatland moss diversity (Lang et al. 2012). While peatland organisms are distinct from dryland biocrusts, the data have implications, not only for the health of biocrusts in a warming world but also for the C cycling processes they control. Taken together, these field manipulation studies provide important insight in the potential of

biocrust organisms to respond significantly to climate warming, with important implications for ecosystem function.

In an experiment conducted at two sites in Spain, Maestre et al. (2013) used open-top chambers to show that passive warming (1.5–2.7 °C) significantly increased midday soil CO₂ efflux to the atmosphere from biocrust soils dominated by mosses and lichens, an effect that was not observed when biocrusts were absent (Fig. 22.2b). Similarly, results from infrared heating experiments conducted on the Colorado Plateau support the idea that warming increases the likelihood of net CO₂ loss from biocrusts (Darrouzet-Nardi et al. 2015). Net soil CO₂ exchange with the atmosphere represents the sum of many biotic and abiotic gross fluxes, including root respiration, heterotrophic respiration, photochemical CO₂ production, and thermal expansion of soil pore space (Rey 2015; Darrouzet-Nardi et al. 2015). Traditional assessments of net flux cannot partition CO₂ into component gross fluxes, and more work partitioning flux is a high research priority (Rey 2015), but evaluation of net flux patterns does lend insight into how warming affects the net exchange of CO₂ between soils and the atmosphere. In the Colorado Plateau experiment, plots from control and warmed plots (2 °C above ambient) were assessed for soil net ecosystem exchange every hour for 21 months. The results showed strong relationships between CO₂ flux and soil temperature, moisture, and light, with warming resulting in significant increases in net soil CO₂ loss during fall and winter. In fact, taking into account these three physical factors (temperature, moisture, and light) explained ~80 % of the natural variability observed over the course of the measurement period (Darrouzet-Nardi et al. 2015). Further, the experiment in Spain showed warming reduced C fixation in biocrust-dominated microsites, suggesting that higher temperatures may result in a reduced capacity for biocrusts to act as a C sink (Ladron de Guevara et al. 2014). Another experiment in an arid ecosystem in South Africa that experimentally increased temperatures (2.1–3.8 °C above ambient using passive chambers) found that populations of four lichen species showed dramatic declines in photosynthetic effective quantum yields over the course of a year (Maphangwa et al. 2012). Reductions in effective quantum yield do not directly translate into reductions in CO₂ uptake, and short-term results may significantly diverge from patterns seen in the long-term. Nevertheless, taken together, these studies suggest the possibility for increased temperatures to affect the net balance of CO₂ exchange between biocrusts and the atmosphere by affecting photosynthesis, respiration, or both (Mishler and Oliver 2009).

Physiological information from laboratory incubations supports the idea that the differential responses of photosynthesis and respiration may help explain increased C loss with warming (Lange and Green 2005; Grote et al. 2010). Gross photosynthesis and respiration both increased with warming, but the relative increase in respiration rate was much larger than that of photosynthesis (Fig. 22.2c; Grote et al. 2010). Thus, even though both gross fluxes are stimulated by higher temperatures (measurements went up to 35 °C), the magnitude and rate of change differed, which resulted in more CO₂ moving from biocrusts into the atmosphere. In the Grote et al. (2010) study, biocrust photosynthesis also showed a decline with

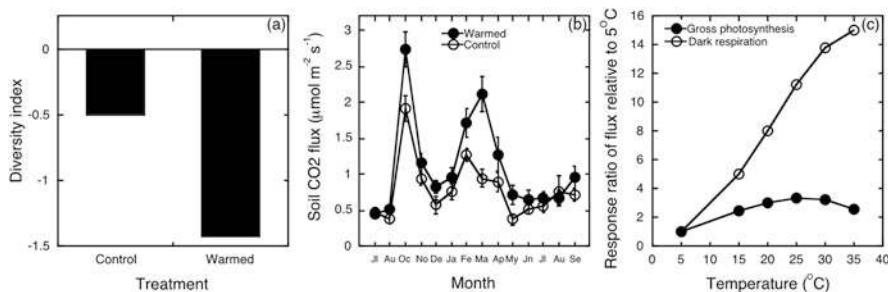


Fig. 22.2 (a) Changes in biocrust diversity between June 2008–May 2011 for control and warmed plots of a semiarid site in Spain. Warming treatments were performed using open-top chambers and warmed plots maintained soil temperatures on average 2.7 °C warmer than control plots. Biodiversity, as assessed using the exponential Shannon diversity index, significantly declined over the measurement period in warmed plots ($P < 0.05$), but not in control plots. Data are from Escolar et al. (2012). (b) From the same climate manipulation plots as described in (a), data showed warming treatment-induced increases in biocrust soil CO₂ efflux to the atmosphere. Values are means ($n = 10$) for daytime measurements made monthly from July 2008 through September 2009 and two letter codes for month are presented on the x-axis. Standard errors are shown. Data are from Maestre et al. (2010). (c) Laboratory gas exchange data showing the response of late successional biocrusts from the Colorado Plateau, USA, gross photosynthesis (filled circles) and dark respiration (empty circles) to increasing temperature. Values are response ratios of each flux relative to the flux at 5 °C and are from samples that were at 40 % relative water content. Data are from Grote et al. (2010)

temperatures above ~25 °C, while dark respiration consistently increased with temperature and showed no decline (Fig. 22.2c). These laboratory experiments demonstrate mechanistically how higher temperatures can negatively impact biocrusts by causing less favorable C balances for biocrust organisms.

Warming also has the potential to affect soil nutrient cycling under biocrusts, both directly via effects on crust and non-crust processes (e.g., soil mineralization enzyme activity, N₂ fixation rates; Sardans et al. 2006; Su et al. 2011) and indirectly via changes to the community composition (Fig. 22.2a). Drylands are strongly constrained by nutrient availability, and biocrusts are known to significantly affect nutrient inputs and cycling (e.g., Belnap 2002; Reed et al. 2012; Delgado-Baquerizo et al. 2013b). Recent research indicates that the effects of biocrusts on nutrient pools and cycles are species specific (Bowker et al. 2011; Miralles et al. 2012, 2013; Delgado-Baquerizo et al. 2015), as typically found with vascular plants (e.g., Bardgett et al. 1999). Thus, the effects of warming could significantly alter nutrient cycling and availability via changes to biocrust community composition and activity (Hu et al. 2014). For instance, Delgado-Baquerizo et al. (2014) found that the dynamics of N availability diverged progressively from original conditions with 46 months of 2.7 °C experimental warming for biocrust and bare soil areas. Warming increased N availability, promoted the dominance of inorganic over organic N, and increased the fungal/bacterial ratios. While biocrusts did play an important role in slowing the soil N cycle responses to climate treatments, taken together, the results suggested that warming had a negative indirect effect on the resistance of the site's N cycle to change via alteration to its community structure.

Finally, it is important to note that all experimental warming treatments have caveats and that considerations of warming methodology are critical for interpreting results (e.g., Aronson and McNulty 2009). As the data discussed in this section show, the use of sustained heating methods is needed to predict and respond to coming changes on both large and small spatial scales. To this end, field warming studies provide important insight. Warming methods, either “active” and “passive,” have different advantages and disadvantages. For example, active infrared warming more directly warms surfaces (such as plants and biocrusts) without the significant concomitant increases in air warming expected with global warming, and active warming is notably expensive and cannot be performed at remote sites without a power source. In turn, passive warming can result in altered moisture and light environments that complicate treatments and can cause strong diurnal variability in warming with daytime warming potentially reaching problematic levels. Collectively, the scientific community will continue to need a mix of warming techniques (Aronson and McNulty 2009; Amthor et al. 2010; and Kimball 2011).

22.3.2 *Precipitation*

Dryland structure and function are largely driven by precipitation (Noy-Meir 1973), and thus changes to the timing, frequency, and amount of precipitation are expected to result in significant transformations to dryland biota. Indeed, the importance of moisture in moderating or exacerbating the impacts of elevated CO₂, warming temperatures, and changes in nutrient availability on biocrusts has been noted in previous sections. Studies of vascular plants suggest that altered timing and size of individual precipitation events may be as or more important for dryland ecosystem function than changes to the total amount of annual rainfall (Sala and Lauenroth 1982; Ojima et al. 1993; Weltzin et al. 2003; Cable and Huxman 2004; Schwinnning et al. 2004; Potts et al. 2006). This makes understanding biocrust responses to altered precipitation even more complex, as multiple aspects of precipitation change—even those that do not greatly alter annual inputs—have the potential to strongly affect biocrust communities, either alone or in combination with other environmental factors. For example, a rainfall manipulation experiment on the Colorado Plateau showed that increasing the frequency of small summer monsoonal rainfall events led to the pronounced mortality of the dominant moss *Syntrichia caninervis* (reducing this moss’s biocrust cover from >25 % to ~0 %; Fig. 22.3a; Reed et al. 2012; Zelikova et al. 2012). The experiment quadrupled the long-term average frequency of 1.2 mm summer rainfall events and had the potential to stress biocrusts in multiple ways, including heat and light stress. Notably, this die-off event was not only sizeable; it was rapid: mortality was observed after a single season of treatment, and the moss did not recover with normal fall-spring rainfalls (Fig. 22.3a). An exploration of the physiological mechanisms driving the mortality revealed that smaller rainfall events resulted in a

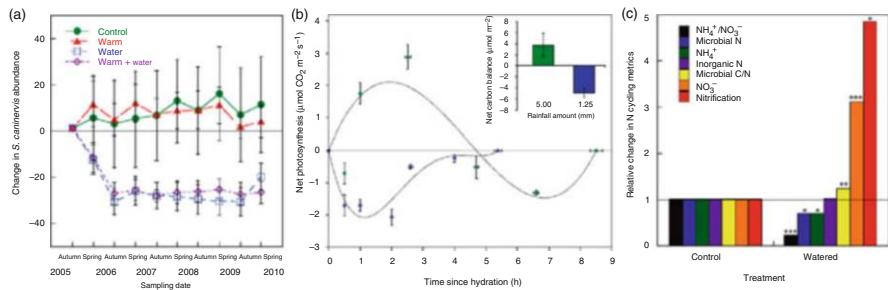


Fig. 22.3 (a) Moss abundance relative to the first measures of the climate manipulation experiment for each treatment. Values were calculated by subtracting the moss abundance data from each subsequent date's data. Repeated measures analyses showed significant interactions between time and moss cover ($P < 0.001$) such that cover in the control and warmed (2–4 °C above ambient) plots increased over time. In contrast, cover in plots receiving increased frequency of small precipitation events declined significantly by autumn 2006 and remained low (averaging <1 % of total crust cover in spring 2010). Values are means ± 1 S.E. (b) Net CO_2 exchange of *Syntrichia caninervis* over the course of the wet–dry cycle following a simulated 1.25 mm rainfall event (blue symbols; $n = 11$) and a 5 mm rainfall event (green symbols; $n = 13$). The inset shows the resulting mean C balance (± 1 S.E.) following exposure to a 5 mm (green bar) or 1.25 mm (blue bar) magnitude event. The green and blue circles show average CO_2 exchange values within 1 h time intervals (1/2 h intervals between 0 and 1 h following hydration) for the moss wet with 5 mm and 1.25 mm events, respectively. The x-axis error bars represent 1 S.E. of the time since hydration within intervals and the y-axis error bars represent 1 S.E. of the CO_2 exchange rates. Best-fit polynomial curves depict trends in net CO_2 exchange and were used to calculate integrated C balance following simulated rainfall events. (c) Nitrogen pools and fluxes in watered plots relative to control plots: watered plots maintained lower NH_4^+ concentrations, $\text{NH}_4^+/\text{NO}_3^-$ ratios and microbial biomass N concentrations, and higher microbial biomass C/N ratios, soil NO_3^- concentrations, and potential nitrification rates. Values are means, and asterisks depict significant differences among samples taken from the control plots and those taken from watered plots: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All figure panels are reproduced from Reed et al. (2012)

negative moss C balance, such that the low-volume rainfall did not allow the moss to stay wet long enough to receive a net C benefit from photosynthetic activity (Fig. 22.3b; Reed et al. 2012). Indeed, for *Syntrichia caninervis* on the Colorado Plateau, rainfall event size may be the strongest predictor of C balance based on its effect on how long crusts remain wet, with the largest C gains associated with the largest precipitation events, and with small precipitation events resulting in C deficits (Coe et al. 2012b; Reed et al. 2012; Darrouzet-Nardi et al. 2015). In the same climate experiment, cyanobacteria, including both N_2 -fixing and non-fixing species, decreased significantly after two summers of altered precipitation (Yeager et al. 2004; Johnson et al. 2012).

Miranda et al. (2009) used a greenhouse experiment to show how a 3-month delay in the onset of autumn rainfalls (i.e., an increased summer drought) could reduce the cover of mosses from 44 % (no delay) to 0 %. These moss responses also underscore the fact that dryland responses to precipitation change can be rapid and substantial, and a seemingly subtle climatic change can induce effects similar to or larger than those from physical disturbance (e.g., grazing, off-road vehicle use;

Ferrenberg et al. 2015). Furthermore, the observed mortality in the Colorado Plateau experiment was the result of the *addition* of water but applied in smaller, more frequent events, highlighting the complexity in relationships among climate, organisms, and biogeochemical cycles in dryland ecosystems.

Field experiments conducted in Spain did not find negative effects of a ~30 % rainfall reduction on the cover and physiological performance of biocrusts dominated by mosses and lichens (Escolar et al. 2012; Ladron de Guevara et al. 2014). Indeed, such a reduction had a positive effect on the growth of dominant biocrust components in this area, such as *Diploschistes diacapsis* and *Squamaria lentigera*, and on the net photosynthesis of the whole biocrust community in times with abundant rainfall. Detailed analyses of the physiological data obtained from the experiments suggest that this lack of response to rainfall reduction is likely due to the importance of non-rainfall water inputs—such as dew, fog, and water vapor adsorption—in the performance of biocrusts (Ladron de Guevara et al. 2014; McHugh et al. 2015). The apparent lack of sensitivity to the overall reduction in rainfall also points to the importance of biocrust-specific responses to changes in the size, duration, and timing of rainfall events, as discussed above. Moreover, these data highlight the importance of considering how experimental treatments (e.g., warming infrastructure) could inadvertently affect experimental results via unintended effects on the inputs of dew and water vapor adsorption.

Dryland climates select for desiccation tolerance in vascular plants and biocrusts (Oliver et al. 2000, 2005; Proctor et al. 2007). In the context of climate change, the issue is not only how biocrusts prepare themselves for desiccation (Buitink et al. 2002; Marschall and Proctor 2004; Oliver et al. 2005) or how they handle rewetting (Proctor and Smirnoff 2000), but also how activity may either be a benefit or a disadvantage to biocrust health. In a large part, this may depend on the amount of time the precipitation can keep them wet (i.e., IWCB; Mishler and Oliver 2009). Thus, beyond the size of the precipitation event, environmental factors that affect soil moisture, such as temperature and soil texture, can play an important role in mitigating the effects of altered precipitation (Cable et al. 2008). Assessments of the relationship between natural rainfall patterns and biocrust health are in line with results suggesting detrimental effects from precipitation changes that result in less water or an increase in the frequency of small rainfall events (Coe et al. 2012b; Reed et al. 2012). For example, Barker et al. (2005) showed that rainfall events of <3.5 mm occurring during warmer months resulted in biocrust physiological stress, due to partial hydration/rapid dehydration cycling and by inference, in negative IWCBs (Mishler and Oliver 2009). Data from another manipulation experiment on the Colorado Plateau supported the idea that responses in photosynthesis can create feedbacks to biocrust health via alterations to the amount of C available for the production of protective pigments (Belnap et al. 2004). These data also showed that different biocrust species can respond in markedly different ways to altered precipitation (Belnap et al. 2004).

Field data from the Mojave Desert suggest that in addition to precipitation effects on biocrust health via effects on C cycling (Fig. 22.3b; Belnap et al. 2004; Reed et al. 2012), these effects could represent a feedback to climatic change. For

example, a rainfall manipulation experiment in the Sonoran Desert, USA, showed that, following small precipitation pulse sizes, biocrusts contributed 80 % of the soil CO₂ flux to the atmosphere (Cable and Huxman 2004). In contrast, larger precipitation events resulted in CO₂ efflux that was dominated by root and soil heterotrophic sources. A 3.5-year field experiment in Spain evaluated the spatiotemporal heterogeneity of soil respiration and estimated that biocrusts accounted for 42 % of C released by soil respiration (Castillo-Monroy and Maestre 2011). Taken together, these results show how climate change effects on biocrust communities can markedly alter the exchange of CO₂ between dryland soils and the atmosphere, representing a potentially large feedback to climate change.

As with temperature, changes in precipitation have the potential to affect dryland structure and function through alterations to nutrient cycling. For example, the large mortality of *Syntrichia caninervis* in response to the increased frequency of small monsoonal rainfall events had significant effects on N cycling. The soil in plots with moss mortality had significantly altered N pools and fluxes (Fig. 22.3c), and plots with moss mortality had higher nitrate (NO₃⁻) and lower ammonium (NH₄⁺) concentrations, thus lower NH₄⁺/NO₃⁻ ratios than plots with living moss. Increased nitrification rates could explain the higher NO₃⁻ and lower NH₄⁺ concentrations, as elevated nitrification may be rapidly converting NH₄⁺ to NO₃⁻ (Fig. 22.3c). The switch to NO₃⁻ dominance has important implications for soil fertility, as well as for the trajectory of biocrust recovery after the loss of a dominant community member. For example, in these systems NO₃⁻ is more likely to be lost through leaching and gaseous N loss pathways (Weier et al. 1993; McCalley and Sparks 2009), and over longer timescales this could result in lowered total soil N abundance and availability. In addition, results from another dryland ecosystem suggest that the identity of soil N species (e.g., NH₄⁺ vs. NO₃⁻) may be a more important regulator of ecosystem function than the absolute quantity of available N (Austin et al. 2006).

Changes in biocrust community composition also have the potential to affect the energy balance of dryland ecosystems; for example, the dramatic mortality of crust in the small-volume precipitation plots on the Colorado Plateau (Reed et al. 2012; Ferrenberg et al. 2015) resulted in a 33 % increase in soil albedo (Rutherford et al. In Review). Because drylands make up such a large proportion of the Earth's terrestrial surface and receive solar irradiance at near potential, these changes to albedo could have important consequences to future climate at the global-scale. Questions of soil stability and dust production are receiving increasing attention, often in the context of how physical disturbance greatly reduces the strong capacity biocrusts maintain for reducing wind and water erosion (Belnap et al. 2014). Biocrusts in later-successional states (i.e., moss- and lichen-dominated) are more effective at stabilizing soils (e.g., Belnap and Gillette 1998); thus, if climate change or physical disturbance cause biocrust communities to revert to earlier-successional states (e.g., Ferrenberg et al. 2015), we can expect to see significant feedbacks to future climate and other issues of societal concern, such as dust production.

Finally, biological soil crusts themselves affect hydrological cycling. A nearly seven-year study of a semiarid grassland in central Spain showed that well-developed biocrusts dominated by lichens (75 % cover) gained more water from rainfall events relative to bare ground, but they also lost the water more quickly (Berdugo et al. 2014). Many other studies have shown that biocrusts can reduce evaporation and either decrease or increase water infiltration, depending on the biocrust type and scale being measured (see Chap. 17 by Chamizo et al.). In the northwest Negev Desert, Felde et al. (2014) showed that biocrust developmental stage greatly affected the soil pore system and influenced water redistribution. In the context of climate change, these patterns show biocrust composition and cover could play a critical role in affecting soil moisture and mitigating (or exacerbating) dryland soil moisture responses to climate change.

22.3.3 Climate Interactions and Extremes

Because multiple environmental changes occur simultaneously across a heterogeneous landscape, teasing apart individual and interactive effects of climate change is a significant research challenge. Full-factorial climate manipulations and modeling studies do suggest strong interactions among climate change factors that would have been difficult to determine by studying a single factor in isolation (e.g., Shen et al. 2009). Indeed, central challenges to the creation of a general framework with which to consider and predict biocrust responses to climate change include (1) the mosaic composition of widely spaced plants and inter-plant biocrusts, (2) the pulsed nature of dryland moisture availability and consequent activity, (3) the potential for biocrusts to respond dramatically and nonlinearly to environmental changes (e.g., Figs. 22.1, 22.2 and 22.3), (4) the fact that different biocrust organisms are likely to respond differently (Belnap et al. 2004) and vary in adaptation/acclimation strategies, and (5) our incomplete knowledge of how biocrust communities interact with changing climate to regulate ecosystem function and future change (e.g., Delgado-Baquerizo et al. 2013a), including changing patterns in vascular plants. Since 1950, historical observations of precipitation and drought indices have shown increased aridity levels in terrestrial ecosystems worldwide, including many drylands (Dai 2011a, b). Some modeling results indicate that the frequency and intensity of droughts will be increased in drylands across the globe with climate change (Dai 2013), as will the risk of lengthy drought periods or “megadroughts” (Ault et al. 2014). Such extreme climate events will further reform our understanding of biocrust relationships with climate and will help elucidate the mechanisms through which these organisms cope with stress. In particular, dramatic changes to climate have the potential to push the boundaries of biocrust physiology and to offer unique opportunities to assess the relationships between the severity of stress and the nature of biotic interactions among biocrust populations (e.g., competition vs. facilitation among different species of lichens, mosses, bacteria, etc.; Chap. 5; Maestre et al. 2008, 2009, 2010; Bowker et al. 2010).

In addition to relationships among biocrust species, climatic changes are likely to affect multiple classes of organisms concurrently; for example, the relationships between biocrusts and microfauna suggest important but rarely studied interactions (Neher et al. 2009; Darby et al. 2010). Nematodes, tardigrades, and rotifers survive extreme temperature by entering a dormant state called anhydrobiosis, while protozoa survive extreme temperatures as cysts (see Chap. 8 by Darby and Neher). Entering and exiting these dormant states is metabolically costly for the individual, and some species do not tolerate frequent wetting by precipitation or rehydration during high temperatures. Thus, the combination of frequent wetting cycles in the presence of elevated temperatures is expected to cause more mortality of microfauna than either frequent wetting in mild temperatures or extreme temperatures while anhydrobiotic alone (Darby et al. 2006, 2011). Changes in drought will also likely affect biocrust-plant interactions (see Chap. 19 by Zhang et al.). For example, it has been found that moss-dominated biocrusts lengthened the emergence time of the grass *Poa ligularis* under drought conditions, a response that was not observed when water availability did not limit seed germination (Funk et al. 2014). Predicted changes to aridity (Feng and Fu 2013) could also significantly affect coupled C and nutrient cycling in drylands. Delgado-Baquerizo et al. (2013a) showed that predicted increases in aridity with climate change could reduce the concentrations of soil C and N in global drylands but increase soil phosphorous (P) concentrations. Such changes could effectively uncouple dryland C, N, and P cycles, which could have large consequences for the provision of key services provided by these ecosystems.

It is important to note that, despite the importance of biocrusts in global biogeochemical cycles (Elbert et al. 2012; Porada et al. 2014; Weber et al. 2015) and their potential for rapid change (e.g., Escobar et al. 2012; Ferrenberg et al. 2015; Lenhart et al. 2015; Reed et al. 2012), biocrust biota and their functioning are absent from most Earth System Modeling (ESM) efforts. Thus, the prevalence and significance of biocrusts in drylands, as well as their responsiveness to climate change, calls into question the accuracy of global models that do not include them. Due to the nature of biocrust responses and to some important similarities between vascular plants and biocrusts, incorporating biocrust responses to climate change may be relatively straightforward (e.g., Darrouzet-Nardi et al. 2015) and could result in substantial effects on ESM results and implications.

22.4 Nitrogen Deposition

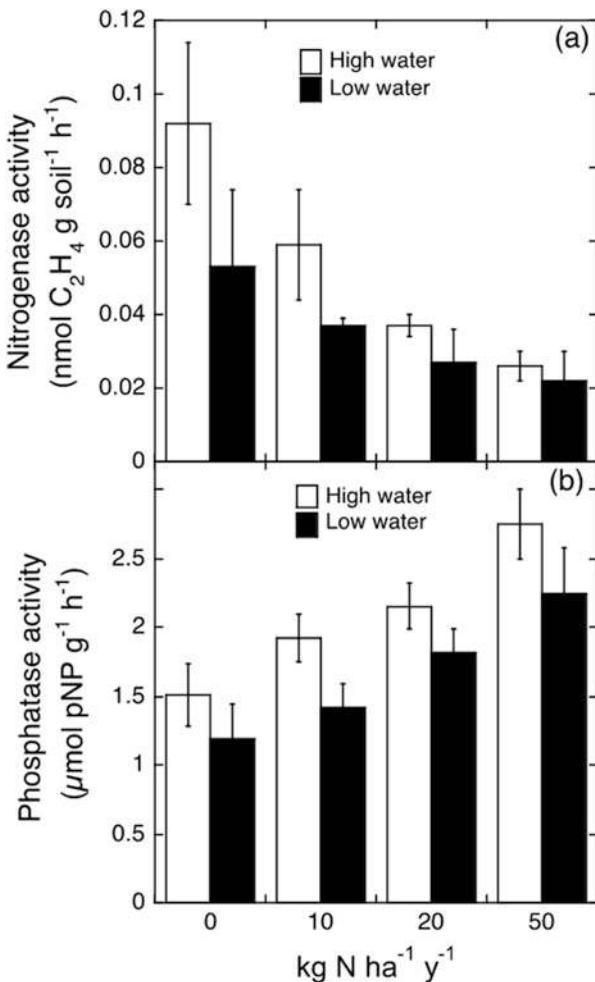
Anthropogenic activities are causing dramatic changes to the global N cycle (Blett et al. 2014; Galloway et al. 2008; Pardo et al. 2011; Vitousek et al. 2013), and increased N deposition—stemming from human activities such as fertilizer use and fossil fuel combustion—is having significant effects on terrestrial ecosystems worldwide (Gruber and Galloway 2008). Nitrogen deposition is on the rise in many drylands, and these systems typically maintain relatively low N stocks.

Accordingly, N deposition may be expected to have significant effects on the structure and function of biocrust communities. Biocrust responses to increased N deposition include reductions in photosynthesis and N₂ fixation rates (Sheridan 1979), changes in concentrations of photosynthetic and ultraviolet (UV)-protective pigments such as scytonemin, increases in electrolyte leakage, increases in denitrification rates, and shifts in lichen community composition (Ochoa-Hueso et al. 2013a). Nitrogen deposition also commonly results in a lower soil pH and loss of base cations (Horswill et al. 2008), and this too can affect the composition and function of biocrust communities (Ochoa-Hueso et al. 2011b). Further, continued increases in atmospheric N deposition are predicted (Phoenix et al. 2006; Galloway et al. 2008), and thus the effects of N deposition on biocrusts are likely to intensify.

Another central way in which N deposition can affect biocrusts is through effects on vascular plants (Ochoa-Hueso and Manrique 2013). Nitrogen deposition commonly increases soil N availability (e.g., Ochoa-Hueso et al. 2014) and thus can stimulate plant growth, at least to a certain extent (Ochoa-Hueso and Manrique 2010). For example, N deposition could result in an increase in the cover of exotic plants, particularly grasses, which can alter the recurrence frequency of wildfires by providing large amounts of highly flammable fuel (Rao et al. 2010; Ochoa-Hueso and Manrique 2014). Increases in plant productivity and altered fire frequencies could negatively affect biocrust communities, and could set a trajectory of ecosystem change (Bowker et al. 2004; Ochoa-Hueso et al. 2011a). That being said, some biocrust communities may have more positive interactions with fire (e.g., if trees that were previously shading soils are burned), and further work exploring biocrusts in the context of fire is warranted.

It has been suggested that increased N deposition could have a lessened effect on ecosystems if N₂-fixing organisms responded to anthropogenic N inputs by lowering N₂ fixation rates. Because most N₂-fixing organisms can downregulate fixation rates when N is available in the environment, rates are likely to decline with increased N inputs. Although the form of N (e.g., NO₃⁻ vs. NH₄⁺) could still be greatly affected by deposition, a reduction in N₂ fixation would decrease overall inputs of “new” N to the ecosystem. A multifactorial N and P greenhouse fertilization study of *Collema tenax* collected on the Colorado Plateau, USA, did show large reductions in the lichen’s N₂ fixation with increasing concentrations of N inputs. As commonly observed for many systems, P additions stimulated N₂ fixation rates (Reed et al. 2007, 2011) and, interestingly, showed strong interactions with N inputs to determine overall rates of lichen fixation (Roybal and Reed In Review). More generally, there are many ways in which N deposition may significantly affect ecosystems via coupled interactions with other biogeochemical cycles, such as C and P cycles. For example, Ochoa-Hueso et al. (2014) found that increasing N inputs decreased N₂ fixation rates, as well as stimulated the activity of the phosphatase enzyme (Fig. 22.4). These same increases in phosphatase were observed with *Pleurochaete squarrosa* (Ochoa-Hueso and Manrique 2013) and *Cladonia foliacea* (Ochoa-Hueso et al. 2013b). While N is known to have significant effects on ecosystem structure and function (Vitousek and Howarth

Fig. 22.4 (a) Nitrogenase and (b) phosphatase enzyme activity as affected by N addition and watering treatments. Nitrogen treatments (NH_4NO_3) were designed to simulate N deposition rates of 0, 10, 20, and $50 \text{ kg N ha}^{-1} \text{ per year}$ and increasing N inputs resulted in significant declines in nitrogenase activity ($P = 0.01$) and significant increases in phosphatase activity ($P = 0.02$). Samples received higher and lower watering treatment to mimic altered moisture availability and these treatments are shown with white and black bars, respectively. Values are means with standard error shown ($n = 4$, except for the $0 \text{ kg N ha}^{-1} \text{ per year}$ low water treatment, where $n = 2$). Data are from Ochoa-Hueso et al. (2014) and are shown here with permission from Elsevier



1991), P availability also exerts important control over terrestrial vascular plant communities (LeJeune and Seastedt 2001; Phoenix et al. 2004; Suding et al. 2004; Gross et al. 2005; Van den Berg et al. 2005). If elevated N inputs result in increases in P mineralization rates and P availability, this could represent a significant indirect effect of N deposition.

Finally, an interesting linkage between biological soil crusts and N deposition is the use of lichens and mosses as bioindicators to evaluate the impacts of chronic N inputs. Lichens and mosses are considered highly sensitive to N deposition, and it has been shown that they can respond rapidly to changes in atmospheric chemistry (Pinho et al. 2008, 2009; Bobbink et al. 2010; Branquinho et al. 2010; Ochoa-Hueso et al. 2014).

22.5 Conclusions

Biocrusts are crucial components of many drylands, as they interact with vascular plants and soil fauna, and play fundamental roles in maintaining soil stability, biogeochemical cycling, and water balance. As with the loss of any keystone functional group (Chapin et al. 1997), shifts in biocrust communities have the potential to result in sizeable and enduring changes to ecosystem structure and function. Here we show that biocrusts respond to a wide variety of environmental changes, including rising CO₂ concentrations, altered climate, and increasing N deposition. Biocrust responses to climate change appear to be particularly strong and, while different biocrust organisms will respond differently to changing climatic conditions, the data suggest that increasing temperatures and altered precipitation patterns, as well as strong interactions between the two, are greatly modifying the structure, function, and resilience of biocrust communities. Future research can help to elucidate the generality of crust responses to the suite of global changes with which they are faced, as well as increase our understanding of the mechanisms that drive this change. In addition, information about how biocrusts will respond to global change could inform restoration research and planning efforts (e.g., Chap. 24 by Zhao et al.), such that considerations of future environmental conditions could help predict the biocrust communities most likely to succeed.

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Part VI

**Natural and Enhanced Recovery and
Management**

Chapter 23

Natural Recovery of Biological Soil Crusts After Disturbance

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23.1 Introduction

When a habitat is newly formed under natural conditions (e.g., after the retreat of a glacier) or after disturbance (e.g., fire, trampling and grazing, mining, off-road vehicles), natural succession follows general patterns which have already been described in the first Ecological Studies Volume on biological soil crusts (biocrusts, Belnap and Lange 2003). The authors describe natural succession as generally starting out with large filamentous cyanobacteria that stabilize the soil, followed by smaller cyanobacteria, green algae, lichens, and bryophytes (Belnap and Eldridge 2003). Succession patterns and recovery rates vary, depending on a variety of factors including the type of disturbance, soil type, conditions of adjoining substrates, types of vascular plant vegetation, climatic conditions, and availability of inoculation material. This impedes the comparison of results obtained in

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different studies. Overall, the 2003 review concluded that natural recovery rates were slow under most conditions.

In the present chapter, we do not describe these results again, but concentrate on studies done since 2000 and how they have altered our understanding of biocrust succession and recovery rates. We focus on natural processes occurring after either natural or man-made disturbance without any human assistance (i.e., rehabilitation or restoration measures). The latter, named as enhanced recovery of biocrusts after disturbance, is treated in a separate chapter (see Chap. 24 by Zhao et al.).

23.2 Stages and Timing of Recovery

One of the most widely known properties of biocrusts is that in many environments, natural recovery from disturbance tends to be slow (Belnap and Eldridge 2003). Sites with greater effective precipitation, natural site stability (afforded by finer soil texture, embedded rock, shallower depth, and denser plant spacing), and low disturbance frequency or intensity are likely to recover more quickly than when the opposite conditions occur (Belnap and Eldridge 2003). We believe this heuristic model still largely holds, and more recent estimates of recovery time appear to be largely consistent with it (Table 23.1). However, recent studies show a wide variability in recovery rates among different localities, with recovery ranging from only a few years (Dojani et al. 2011) to millennia under hyperarid conditions (estimated, Belnap and Warren 1998).

Variability and dependency on multiple factors remains the overarching generalization that can be made about recovery times. Some studies also estimated different recovery times for different biocrust properties. Kidron et al. (2008) show full recovery of chlorophyll *a* and protein takes 6–8 years, whereas carbohydrate recovery is accomplished within 8–9 years in cyanobacteria-dominated biocrusts. Also, we note that a large number of studies are based on only one or a few observations in time, which generally only provides an upper or lower bound, rather than an estimate, of recovery time. Studies which use linear extrapolations have a strong tendency to generate very long recovery times; however, this method should only be applied where recovery times are likely to be longer than can reasonably be monitored. Initial colonization of many biocrust components is likely a rate-limiting step in recovery; thus, linear extrapolations are likely to be overestimated (Belnap and Warren 1998).

Table 23.1 Estimated recovery times of biocrusts

Location	Climate regime	Precipitation timing	Soil texture	Method	Disturbance	Estimated years to recovery			Citations
						Cyanobacteria algae	Bryophytes	Lichens	
Namib Desert, Namibia	Hyperarid, hot	W (fog)	Various	a	Construction or high vehicle traffic			99–527	1
Namib Desert, Namibia	Hyperarid, hot	W (fog)	Various	a	Vehicle traffic—multiple passes		12–28	12–28	1
Namib Desert, Namibia	Hyperarid, hot	W (fog)	Various	a	Vehicle traffic—single pass		5–7	5–7	1
Negev Desert, Israel	Arid, hot	W	Sandy	b	Scalping ($\geq 1 \text{ m}^2$)	8–9	17–22	17–22	2
Mojave and Sonoran Deserts, USA	Arid, hot	W or S and W	Sandy	a	Vehicle tracks	3	10–90	10–90	3
Sonoran Desert, USA	Arid, hot	S and W	Sandy	b	Military encampment (prior clearing)	>56	>56	>56	4
Sonoran Desert, USA	Arid, hot	S and W	Sandy	b	Vehicle and other surface disturbance	≤ 56		≤ 56	4
Negev Desert, Israel	Arid, hot	W	Sandy loess	b	Scalping ($< 1 \text{ m}^2$)			>5	5
Maralinga, Australia	Arid, hot	W	Calcrete	c	Vehicle and other surface disturbance			>40	>40
Maralinga, Australia	Arid, hot	W	Calcrete	c	Vehicle and other surface disturbance			>60	6
Mojave Desert, USA	Arid, hot	W	Desert pavement	a	Tank tracks	85–120	100 to almost 2000	100 to almost 2000	7,8
Mojave and Sonoran Deserts, USA	Arid, hot	W or S and W	Fine	a	Vehicle tracks	2–3	4–15	4–15	3

(continued)

Table 23.1 (continued)

Location	Climate regime	Precipitation timing	Soil texture	Method	Disturbance ($<1\text{ m}^2$)	Estimated years to recovery			Citations
						Cyanobacteria algae	Bryophytes	Lichens	
Succulent Karoo, South Africa	Semiarid, hot	W and A	No data	b	Scalping ($<1\text{ m}^2$)	≤ 2.7	variable	>2.7	9
Victoria, Australia	Semiarid, hot	W	Fine	c	Cropping	<15	15–60	15–60	10
Mojave—Great Basin ecotone, USA	Semiarid, cool	W	No data	c	Burning	>19	>19	>19	11
Great Basin, USA	Semiarid, cool	W	No data	b	Chemically killed	<1		<1	12
Great Basin and Colorado Plateau, USA	Semiarid, cool	S and W or W	Various	c	Grazing	≤ 18	≤ 18	≤ 18	13
Colorado Plateau, USA	Semiarid, cool	S and W	Sandy	a	Vehicle tracks	7–4	26–39	10–71	3
Colorado Plateau, USA	Semiarid, cool	S and W	Sandy	b	Human foot traffic—varying intensity	3–5		>10	15
Colorado Plateau, USA	Semiarid, cool	S and W	Sandy	b	Grazing	>10		>10	15
Colorado Plateau, USA	Semiarid, cool	S and W	Fine	a	Vehicle tracks	2–3		4–15	3
Tengger Desert, China	Semiarid, cool	S	Sandy	c	Dune mobility	>55		>55	16
Tengger Desert, China	Semiarid, cool	S	Sandy	b	Scalping ($<1\text{ m}^2$)	3–4		3–4	17

Loess Plateau, China	Semiarid, cool	S	Sandy loess	b	Scalping ($\geq 1 \text{ m}^2$)	3		3	18
Colorado Plateau, USA	Semiarid, cool	S and W	Sandy or gypsiferous	a	Scalping ($< 1 \text{ m}^2$)	35–65	250	45–85	250
Colorado Plateau, USA	Semiarid, cool	S and W	Sandy or gypsiferous	a	Scalping ($< 1 \text{ m}^2$)	14–34	42	40–766	40–766
Columbia Basin, USA	Semiarid, cool	W	Fine	b	Burning	>11	>11	>11	21
Columbia Basin, USA	Semiarid, cool	W	Fine	b	Burning (followed by seeding)	>11	>11	>11	21
Columbia Basin, USA	Semiarid, cool	W	Fine	b	Burning	>11	>11	>3	22
Victoria, Australia	Semiarid, cool	W	Fine	c	Grazing			20	23
Great Basin, USA	Semiarid, cool	W	Fine	b	Fire	≤ 5		≤ 5	24
Great Basin, USA	Semiarid, cool	W	Fine	b	Grazing	≤ 7		>7	25
Inland Dunes, Germany	Mesic, cool	YR	Sandy	b	Scalping or raking ($< 1 \text{ m}^2$)	>5	>5	>5	26
Florida Rosemary scrub, USA	Mesic, hot	S	Sandy	c	Fire	10–15		10–15	27

All included studies compared some form of disturbed area to a control. Linear extrapolations beyond the data are included only if the original authors used this methodology. Precipitation timing: W = winter, S = summer, A = autumn, YR = year round. Method: a = control impact and linear extrapolation, b = control impact, c = space for time (multisite, varying disturbance age). Citations: 1. Lalley and Viles (2008), 2. Kidron et al. (2008), 3. Belnap unpublished, 4. Kade and Warren (2002), 5. Zaady et al. (2007), 6. Eldridge and Ferris (1999), 7. Belnap and Warren (1998), 8. Belnap and Warren (2002), 9. Dojani et al. (2011), 10. Briggs and Morgan (2012), 11. Callison et al. (1985), 12. Lynn and Cameron (1973), 13. Anderson et al. (1982), 14. Cole (1990), 15. Jeffries and Klopatek (1987), 16. Li et al. (2004), 17. Tian et al. (2014), 19. Belnap (1993), 20. Belnap and Eldridge (2003), 21. Hiltz et al. (2004), 22. Rychert (2002), 23. Read et al. (2011), 24. Johansen et al. (1984), 25. Johansen and St. Clair (1986), 26. Langhans et al. (2010), 27. Hawkes and Flechtner (2002)

23.3 Factors Affecting Stages and Timing of Natural Recovery

23.3.1 Climate

Precipitation is a central determinant of natural recovery rates, as already outlined in the first Ecological Studies Volume on biocrusts (Belnap and Lange 2003). This has been corroborated by more recent studies. Drier climates (e.g., Lalley and Viles 2008; Kade and Warren 2002) appear more likely to have multidecadal or even multi-century recovery times than wetter climates (e.g., Hawkes and Flechtner 2002; Belnap and Warren 2002). Higher precipitation was observed to be positively correlated with the growth of green algae and mosses during succession of biocrusts in the Tengger Desert, China. Hu and Liu (2003) and also Zhang et al. (2007) observed an increase in biocrust cover along a precipitation gradient in the Gurbantunggut Desert, China.

23.3.2 Soil

Succession of biocrust organisms is well known to be faster on fine-textured soils, which form stable physical crusts more readily than coarse-textured soils (Belnap and Eldridge 2003). Information on additional soil properties influencing succession are rare, as most studies investigate the soil properties of already developed crusts, whereas only few analyze the impact of soil properties on biocrust development.

Recent examples of slow (multidecadal) biocrust recovery are observed when soils are inherently unstable, such as previously mobile dunes (Li et al. 2004), compared to more stable soils (Xiao et al. 2014). In some cases, long-term disturbance seems to have altered soil conditions to the point that a return to the original state may take a very long time or will even never occur (Belnap and Warren 1998). Investigating the microbial community assemblages during succession after glacial retreat in the High Arctic, Kaštovská et al. (2005) observed that cryoconite sediments being created when windblown material melts into ice surfaces are more suitable for the development of microbial assemblages than barren, vegetated, and subglacial soils. The high abundance of auto- and heterotrophs was also here positively influenced by the high proportion of fine sediment fractions, whereas nutrient levels were low and often below detection limits.

A fertilization experiment in recently deglaciated unvegetated soils in South-eastern Peru revealed that a single treatment with +NP fertilizer caused the soil bacterial community structure of 3-year-old soil to most closely resemble 85-year-old soil only one year after treatment (Knelman et al. 2014). Soil edaphic properties of treatment differed widely from late-successional plots (i.e., pH, soil moisture, carbon content), suggesting that nutrients alone, independent of other edaphic

factors that change with succession, may control soil microbial development. This observation on microbial communities in recently deglaciated soils needs to be evaluated for biocrusts in other climatic regions.

23.3.3 *Severity of Disturbance*

Some studies show that duration of recovery is also influenced by the severity of disturbance. High-intensity disturbances, for example, tank traffic (Belnap and Warren 1998) or long-term tillage (Briggs and Morgan 2012), tend to have longer recovery times than small-scale or low-intensity disturbances (Tian et al. 2006; Lalley and Viles 2008).

In a xeric rosemary shrubland in Florida, Hawkes and Flechtner (2002) applied disturbance of two severity grades to biocrusts. In one set of plots, biocrusts were crushed and raked until no aggregates remained, whereas in the second set of plots, biocrusts were removed to a depth of ~4 cm. After 6 months, chlorophyll *a* in the plots with removed biocrusts was lower than that in crushed or control plots, which did not differ from each other. Also in other studies, complete removal of crusts had more severe effects than crushing without removal. Langhans et al. (2010) measured higher ruderalization indices (the ratio of ruderal species cover to overall vegetation) on strongly disturbed plots compared to weakly disturbed and control plots 2 years after disturbance, due to typical species decreasing after the severe disturbance. A study in the hyperarid Namib Desert estimated recovery time of removed biocrusts to be many times longer than recovery of moderate impacts created by tire tracks (345–527 years versus 12–28 years, respectively; Lalley and Viles 2008). Thus, complete removal of biocrusts generally had more severe effects on recovery rates compared to disturbance where biocrusts material remained in place.

Fire generally is reported as a severe disturbance having major effects on biocrust abundance, but often not obviously affecting the subsequent successional sequence. Hawkes and Flechtner (2002) describe that the abundance of cyanobacteria and algae declined dramatically immediately after fire, peaking again 10–15 years after fire, with no major taxonomic changes between pre- and post-fire communities. Also Johansen et al. (1993) observed no major changes in species composition after fire in a semiarid sagebrush desert of the Lower Columbia Basin, USA. Here, immediately after the fire, the morphological structural aspects of the crust were still very much intact, although the organisms were dead, and algal recovery was already observed during the second winter after disturbance. Also Hilty et al. (2004) observed a significant decline in biocrust cover and diversity after a wildfire in a sagebrush shrub-steppe in Idaho, USA. Here, fire did affect species composition, with an increase in short mosses and a decreased coverage of lichens and tall mosses.

Low-intensity fires, which are a natural feature in the Palouse prairies of the Northwestern USA, were observed to have much less drastic effects on biocrusts

than in other systems (Bowker et al. 2004). Whereas 1 year after the fire soil stability and microbe pigmentation were still significantly lower on burnt compared to control plots, there was no difference in lichen and moss species composition, and also nutrients and surface rugosity did not differ between treatments. The high resistance of biocrusts in this habitat to wildfire was assumed to be favored by low-intensity fires and growth of biocrusts in spaces away from vascular plant fuel load.

Thus, the disturbance intensity of fire seems to be variable and may be influenced by fire intensity and adaptation of the biocrust community to wildfires.

23.3.4 Timing of Disturbance as Influenced by Climatic Conditions

In addition to severity, the timing of disturbance can play a role in natural recovery rates, as recovery rates depend on climate, and climate conditions can vary depending on when the disturbance occurs. For example, Dojani et al. (2011) removed biocrusts on 25 plots at the end of the dry season in the Succulent Karoo, South Africa. Six months later, at the end of the rainy season, initial cyanobacteria-dominated biocrusts had already established, covering the same surface area as crusts on undisturbed control plots. The authors suggest that timing of the disturbance before a wet season was instrumental in rapid recovery, as the loose soil was not blown away during the dry season, but soon fixed by rain and reestablishing cyanobacteria. The relevance of favorable climatic conditions after disturbance has also been pointed out by Hawkes and Flechtner (2002). They removed the biocrusts to 4 cm depth in $100 \times 1 \text{ m}^2$ plots and observed a quick recovery of biomass (measured as chlorophyll *a* contents), probably being favored by the unusually high winter rainfalls after disturbance. Johansen et al. (1993) observed a sudden and quick algal and cyanobacterial recovery in the second winter after a fire in the sagebrush desert of the Lower Columbia Basin. Also in this case, the quick recovery of biocrusts may have been promoted by a particularly wet winter, as speculated by the authors. Consequently, timing of disturbance with regard to climatic conditions and especially precipitation events appear to influence the initial stages of succession, whereas they probably do not influence later successional stages.

23.4 Hidden Dynamics

Most estimates of biocrust recovery are based on only a few observation points, for example, estimating biocrust abundance in a habitat after a known period of time has passed since the last disturbance. Underlying the apparent slow growth rates is a

surprising level of temporal dynamics. Increasingly, biocrusts are being viewed as dynamic, rather than slowly changing and static communities (Belnap et al. 2006, 2007; Dojani et al. 2011).

Biocrust recovery rates are not linear through time and may vary from year to year or even seasonally (Belnap et al. 2006; Lázaro et al. 2008). Periods of very fast growth may occur during wet seasons or especially wet years (Dojani et al. 2011; Belnap et al. 2007). In contrast, cover or biomass may decline substantially during drought or other stressful conditions, as also observed in the spectral response of biocrusts (see Chap. 12 by Weber and Hill and Chap. 21 by Zaady et al.; Bowker et al. 2008; Karnieli et al. 2002). These findings suggest we should adjust our view of biocrust recovery from a slow and steady process to a view of pulses of rapid growth punctuated by either static growth or regression of cover or biomass. In addition, estimates of recovery times can vary widely, depending on conditions preceding sampling (Belnap et al. 2006, 2007).

23.5 Successional Trajectories

Like most ecosystems, biocrust recovery from disturbance has characteristic successional dynamics. Belnap and Eldridge (2003) proposed a successional sequence for arid and semiarid regions throughout the world, where large filamentous and mobile cyanobacteria (e.g., *Microcoleus* spp.) are the initial colonizers, followed by smaller surface-bound cyanobacteria (e.g., *Nostoc* and *Scytonema*) and algae, followed by very early-successional lichens such as nitrogen-fixing *Collema* spp. A series of early- to late-successional bryophytes and lichens join the community later at various times. The successional sequence may terminate earlier in regions with less effective precipitation and be richer in later successional moss and lichen species in wetter regions. For the most part, this succession does not constitute complete replacement of one successional type by another, but rather is an addition of species and shifts in relative species abundance over time.

This successional sequence, or minor variations of it, might be thought of as the “general sequence”, because it is commonly reported in a variety of regions (Dojani et al. 2011; Büdel et al. 2009; Hu and Liu 2003; Kidron et al. 2008; Belnap et al. 2008; Yeager et al. 2004). In sandy deserts of China and Israel, researchers have further illuminated the initial colonization stages, in which a weak physical crust may be formed by eolian dust deposition (Yair and Verrecchia 2002; Zhang 2005), although this initial physical crust is not always observed (Kidron et al. 2008). The newly created surface may be colonized by heterotrophic bacteria prior to the arrival of the large, filamentous cyanobacteria (Zhang 2005). It is not currently known how universal this heterotrophic successional stage is. Large, bundled, and mobile filamentous cyanobacteria (generally *Microcoleus* spp.) engineer an increasingly stable biocrust up to 1 cm thick. Later, surface-bound cyanobacterial colonizers are favored by the stable surface created by the

filamentous cyanobacteria. These taxa are rich in sunscreen pigments and, combined with an increase in biomass, give biocrusts their common dark color, as well as the often-cited gradient from light to dark biocrusts, which indicates succession (Belnap et al. 2008; Darby et al. 2007; Dojani et al. 2011; Yeager et al. 2004). As biocrusts darken and host more species, the ecological maturity of the microfauna also increases (Darby et al. 2007). In regions where succession proceeds beyond “dark” cyanobacterial crusts, typically mosses and/or lichens are reported as becoming more abundant or even dominant (Belnap et al. 2008; Kidron et al. 2008; Jia et al. 2008; Lan et al. 2012; Lázaro et al. 2008; Büdel et al. 2009).

After establishment of dark cyanobacterial biocrusts, other successional pathways are also possible. In the Kalahari Desert, burial by sand is a constant force pushing succession back toward lighter crust stages, while slightly higher microtopographic features may advance to darker later successional phases (Thomas and Dougill 2006). Later successional dynamics may be linked to chronic burial in sandy regions. For example, Jia et al. (2008) note a successional sequence in the Tengger Desert, involving moss colonization prior to gelatinous lichen colonization in a sequence corresponding to burial tolerance (*Bryum argenteum*, *Didymodon vinealis*, *Syntrichia caninervis*, *Collema tenax*). On the Colorado Plateau, fragments of normally late-successional moss species may be deposited with sand in the low-lying areas of pinnacled crusts. This may lead to spatial heterogeneity in biocrusts, whereby pinnacles which are tall enough to avoid burial may advance successional from light to dark cyanobacterial crusts. In contrast, lower microsites may either regress in succession to lighter cyanobacterial crusts or follow an alternative trajectory toward moss (*Syntrichia caninervis*) dominance (Bowker unpublished data). Thus, chronic deposition of sand may represent one mechanism by which mosses may be earlier colonizers than lichens. In a study conducted in semiarid woodlands in South West Queensland, Australia, Williams and Eldridge (2011) investigated the effects of sand deposition on the bioavailability of nitrogen (N) after a severe drought. They observed that cyanobacteria-dominated biocrusts covered by sand had up to 3 times more mineral N (ammonium and nitrate) and twice the mineralizable N than sand-free biocrust samples. They concluded that the increased N availability likely resulted from autolysis and the subsequent breakdown of cyanobacterial cells rich in N.

Lan et al. (2012) also note two divergent successional trajectories, one roughly following the Belnap and Eldridge (2003) model (cyanobacteria, gelatinous lichens, mosses), whereas the other trajectory may skip lichen dominance, transitioning directly from cyanobacterial crusts to moss crusts. Areas with finer soils, such as gypsiferous marls in the Tabernas Badlands of Southern Spain, do not have a major moss component. Rather, dark cyanobacterial crusts develop quickly and are replaced by lichens. Early-successional lichens include *Placynthium nigrum* and *Squamaria lentigera*, but there are multiple end points of succession based on microclimate (Lázaro et al. 2008). These multiple pathways of succession, such as toward moss or lichen dominance, are depicted in a state-and-transition model in Fig. 23.1.

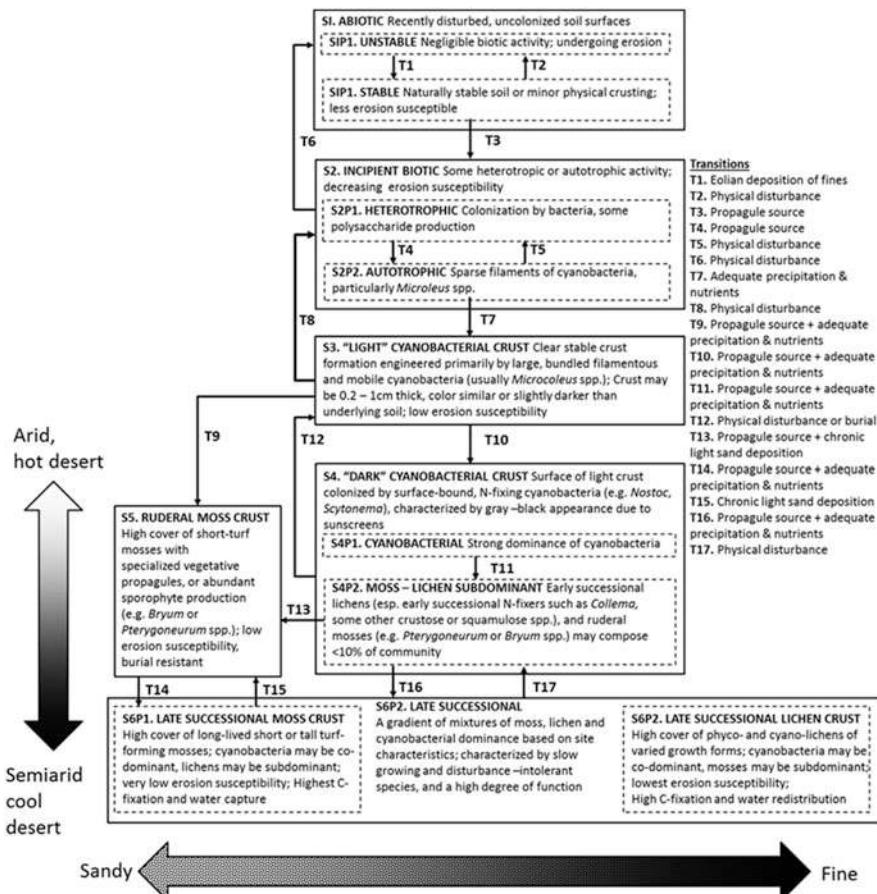


Fig. 23.1 The general biocrust succession sequence expressed as a state-and-transition model. Solid boxes represent ecosystem states, drawn here to emphasize successional series. States have unique functional and structural properties and are stable unless a transition occurs. Dashed boxes represent phases (e.g., S1P1, state 1 phase 1), variants within a state that often shift back and forth. Arrows represent transitions, each associated with a trigger (listed to R). Aridity axis (left side) indicates that succession in arid, hot deserts may terminate in dark cyanobacterially dominated states, while later successional moss- or lichen-dominated states are possible in semiarid, cool deserts. Soil texture axis (bottom) indicates that sandy textures favor moss-dominated late-successional communities, and fine textures favor lichen dominance

This general successional sequence is by no means the only successional sequence that has been reported. The following are alternative successional sequences that have been observed in other specific situations such as post-fire recovery, fog deserts, mesic dunes, and favorable environments.

23.5.1 Successional Pathways After Fire

Disturbance due to fire may lead to distinct successional pathways as compared to mechanical disturbances (compression, trampling, removal, and burial); this has been most frequently documented in cooler semiarid steppes. The distinctiveness of post-fire disturbance trajectories may be due to unique effects of heat addition or to ash influx. There is some evidence that colonization by heterotrophs, particularly Firmicutes and Actinobacteria, may occur prior to colonization by photoautotrophs (Aanderud and Blair 2013). Green coccoid algae and diatoms may be earlier photoautotrophic colonizers post-fire than cyanobacteria (reviewed by Johansen 2003). Bowker et al. (2004) also found that one year after a low-intensity fire in a cool semiarid grassland, diatoms were more abundant and filamentous cyanobacteria were less abundant than in unburned sites. Johansen (2003) generalizes that ruderal mosses and heterocytic cyanobacteria are the next suite of colonizers. This observation is supported by Hilty et al. (2004), who found that short turf-forming ruderal mosses (e.g., *Ceratodon purpureus*, *Funaria hygrometrica*, *Bryum argenteum*) were actually more abundant in burned plots than unburned controls after 10 years, suggesting a relatively early-successional role. Similar flushes of mosses early in succession have been observed after fire in former shrublands in the Northern Colorado Plateau (Bowker personal observation) and burnt forest stands (Hardman and McCune 2010). Also in temperate European habitats, the moss *Funaria hygrometrica* has been observed to be one of the first colonizers after fire (Castoldi et al. 2013). Lichens of all growth forms tend to be much less abundant in burned plots, suggesting a later successional role (Hilty et al. 2004; Johansen 2003).

23.5.2 Fog and Dew Desert Successional Pathways

Arid and hyperarid deserts receiving a substantial proportion of precipitation in the form of fog and dew support unique species assemblages dominated by fruticose and foliose lichens. The hypolithic environment is mainly made up by cyanobacteria with few green algae in-between (see Chap. 11 by Pointing; Büdel et al. 2009). Almost nothing is known about the recovery of disturbed hypoliths. For aboveground components, disturbed surfaces in the Namib Desert were observed to support lichen communities distinct from adjacent undisturbed ones (Lalley and Viles 2008). Disturbed areas always had fewer species, although in many cases, they had the same dominant species as the undisturbed controls. There was little convergence on a particular early-successional community at the various sites, but some species such as *Xanthoparmelia walteri*, *Lecidella crystallina*, and *Caloplaca eudoxa* were sometimes more abundant in disturbed areas compared to adjacent controls.

23.5.3 Inland, Mesic Sandy Habitat Successional Pathways

Locally xeric- or desert-like conditions can be found in inland dunes or other sand deposits in mesic regions. This property makes them more stressful than might be expected based on rainfall totals, and due to relatively low vascular plant cover, these areas may be biocrust habitat. Reported successional dynamics differ considerably on a case-by-case basis. The pH of the sandy environment may be a major determinant of succession. Green algae tend to achieve similar or greater abundance than cyanobacteria in acidic soil; thus, we can hypothesize that acidic soils will have distinct successional trajectories from the general sequence. On inland acidic dunes in Germany, Fischer et al. (2010) identify a high abundance of green algae and cyanobacteria as early successional and coccoid green algae and bryophytes as indicative of later successional crusts. Also studying a former military area in northwestern Germany, Paus (1997) observed that succession either started out with green algae (*Zygogonium* sp.) or mosses and lichens occurred as first colonizers. Similarly, on acidic sandy soils of former military areas in southwestern Germany, cyanobacteria are rare, and filamentous green algae (*Klebsormidium* sp.) stabilize unconsolidated soils (Weber and Büdel unpublished data).

On inland calcareous and alkaline dunes in a mesic climate in Germany, Langhans et al. (2009) suggest that initial crusts are composed of filamentous cyanobacteria (*Oscillatoria* sp., *Microcoleus vaginatus*) and algae (*Zygogonium ericetorum*, *Klebsormidium*). More established “stable” crusts support a greater abundance of mosses (e.g., *Syntrichia ruraliformis*, *Tortella inclinata*). In a locally xeric sand barren in Ohio, USA, Veluci et al. (2006) describe a fairly typical progression of algae and cyanobacteria to dominance by roughly similar proportions of mosses (unidentified) and lichens (mostly *Cladina* and *Cladonia*). The relative abundance of algae to cyanobacteria was not measured, but the presence of cyanobacteria was inferred due to measured N fixation (Veluci et al. 2006). Hawkes and Flechtner (2002), working in Florida rosemary scrub habitats, report a similar mixture of green algae and cyanobacteria early in succession and a greater abundance of *Cladina* and *Cladonia* later.

There are important differences between mesic inland sandy systems and other biocrust successional pathways. Under mesic conditions, where biocrusts develop upon disturbance or removal of vascular plant vegetation, biocrust communities are not the endpoint of succession but are eventually replaced by vascular plant vegetation if no further disturbances occur (Büdel et al. 2014).

23.5.4 Succession in Favorable Environments

The combination of relatively mesic conditions and stable, water-retaining fine soils might be considered a “favorable environment” for biocrusts (Read et al. 2011). In habitats like these, deviations from the general successional

sequence have been observed. In Australia, Read et al. (2011) observed mosses, and not cyanobacteria, to be the first colonizers in their study region in Northwest Victoria, which receives about 370–410 mm rainfall per year and has stable clay-rich soil. Dark cyanobacterial crusts became more prominent through time, and lichens were the slowest organisms to colonize (Read et al. 2011). They hypothesize, that the stable, fine-textured soils create favorable conditions for the primary colonization by moss.

In regions with dry climate or unstable soils, the ability of filamentous cyanobacteria is essential to engineer stability so that other taxonomic groups which require stable substrates may colonize. Thus, the general successional sequence is characterized by early facilitation of later successional taxa by the filamentous cyanobacteria. In more stable habitats (e.g., clay soils or higher vegetation cover), biocrusts do not necessarily need a consolidation stage with cyanobacteria fixing and dominating the biocrust. This response has also been observed in mesic portions of Germany after removal of biocrusts on calcareous soils rich in silt and clay (Paus 1997; Weber et al. unpublished).

In the Australian case, the sequence of species arrival in favorable environments is hypothesized by Read et al. (2011) to be related to traits of the colonizing species and competition rather than facilitation among species. They argue that in favorable environments, species with high “structural density” (shorter-statured species that are more tightly adherent to the soil surface, inclusive of dark cyanobacteria, and many lichens) tend to be late successional, possibly because these traits lead to a slow relative growth rate and stronger competitive ability, whereas species with a lower structural density (e.g., loose cushion tall mosses and fruticose lichens) tend to be capable of faster growth and earlier colonization. Read et al. (2016) also acknowledge the existence of ruderal species that specialize in rapid colonization from vegetative propagules. This hypothetical alternative successional model, and proposed novel mechanisms, should be further tested in other environments.

23.5.5 *Multiple Successional Pathways*

The large majority of biocrust succession studies treats recovery from disturbance as a deterministic process culminating in a single predictable stable state. As expressed in Fig. 23.1, this is likely an oversimplification even of the general sequence. A recent study conducted in the Chihuahuan Desert of Mexico provides additional evidence of multiple successional trajectories (Concostrina-Zubiri et al. 2014). The authors compared biocrusts of rangelands in exclosures released for 11 and 27 years from continuous high-intensity grazing and released for 6 years from seasonal high-intensity grazing. Their results suggest different successional pathways depending on whether biocrusts are recovering from continuous or seasonal high-intensity grazing.

Like Read et al. (2016), the authors explain successional dynamics based upon traits of species but emphasize resistance and resilience to disturbance rather than

structural density and advance four groups of species: high resistance and high resilience (e.g., cyanobacteria), high resistance and low resilience (e.g., semicontinuous squamulose lichens), low resistance and high resilience (e.g., ruderal mosses), and low resistance and low resilience (e.g., other lichens). These traits would determine not only what happens after disturbance ceases but also the starting community structure.

23.6 The Changes of Soil Properties During or After Recovery of Biocrusts

The formation and development of biocrusts can profoundly alter a wide array of ecological functions (Castillo-Monroy and Maestre 2011; Williams et al. 2012; Pietrasik et al. 2013), including the improvement of soil properties (Kidron et al. 2010; Drahorad et al. 2013; Miralles et al. 2013). Soil physicochemical properties are one of the key indicators for the assessment of recovery direction and process of some ecosystems. Natural recovery of biocrusts usually adds silt and clays to soils (e.g., Yair and Verrecchia 2002) and improves soil organic matter and soil nutrients (Guo et al. 2008; Gomez et al. 2012). The recovery rate of these properties is related to biocrust type (dominated by cyanobacteria, lichens, or mosses) and the climate conditions (e.g., precipitation and temperature; Langhans et al. 2010; Tian et al. 2005; Xiao et al. 2014).

Soil particle size, organic matter, and nutrient contents show similar patterns during natural recovery of biocrusts. In most studies, silt and clay contents consistently increase after cessation of disturbance and the beginning of biocrust recovery (e.g., grazing; Chen et al. 2009; Zhao et al. 2010, 2011). For instance, silt and clay contents accounted for 2 % in mobile sand dunes and 33 % in the uppermost 2.5 cm of moss-crusted soil after ~30 years of natural recovery (Zhao et al. 2010). The increased ratio of silt and clay is caused by well-described dust trapping of the biocrust (Williams et al. 2012) and the production of secondary minerals by biocrust weathering, primarily of quartz and feldspars (Wang et al. 2007; Chen et al. 2009; Gomez et al. 2012).

Many studies show that soil nutrient contents increase with biocrust recovery (e.g., Jia et al. 2003; Li et al. 2007; Zhao et al. 2010). Analyzing four successional biocrust types and uncrusted shifting sand, Hu and Liu (2003) found higher Mn contents were associated with well-developed as compared to less-developed biocrusts. Guo et al. (2008) found increased organic matter, total N, available N, available phosphorus (P), and calcium carbonate in biocrusted compared to uncrusted soils in the Horqin Sand Land, Inner Mongolia, China. Li et al. (2007) showed an increase in fine particles, total N, P, K, and organic matter in biocrusted compared to unconsolidated soils in the Tengger Desert, China. Investigating biocrust recovery across 21 sites, where grazing had ceased between 1 and >50 years ago, Read et al. (2011) showed that the soil available P and K, total N, nitrate,

and organic carbon increased during biocrust recovery in a dryland agricultural region of Northwest Victoria, Australia.

Soil C:N ratio is an important index for element cycling rates. Reviewing the literature, we observed that during biocrust recovery, the C:N ratio often decreases significantly within the biocrust, likely due to N inputs by the biocrusts (e.g., Li et al. 2007; Zhao et al. 2011). In one study, soil C:N ratio at 0–3 cm depth dropped from 27.7 to 6.6 within 9 years of biocrust restoration (Li et al. 2008).

Few studies have investigated the role of biocrust development on soil electrical conductivity (EC) and pH. Guo et al. (2008) reported pH values increased from 7.37 to 7.59 with biocrust development after grazing exclusion and to 8.03 after 44 years of recovery (Li et al. 2003). EC increased from $47.3 \mu\text{s cm}^{-1}$ in physically crusted soils to $111.5 \mu\text{s cm}^{-1}$ in moss-crusted soils (Guo et al. 2008).

Many studies show soil hydrology is impacted by biocrust development. In one study, soil surface moisture was up to 8 times higher on a 15-year-old biocrust compared to mobile sand dunes in a sandy land (Zhao et al. 2011). Similarly, soil moisture in the upper 10 cm soil profile was ~2 times higher after 2 years of recovery of a moss crust compared to the control in a semiarid environment in the Loess Plateau region of China (Xiao et al. 2014). The number of days and the amount of dew trapped increased with biocrust development stage (Liu et al. 2006; Pan et al. 2010, 2014; Zhang et al. 2009). There are many studies investigating the effects of biocrusts on local hydrology, being treated extensively in Chap. 17 by Chamizo et al.

23.7 Conclusion

Natural recovery of biocrusts is influenced by various parameters, such as soil conditions, climate, and the severity and timing of disturbance, with the latter again influencing the climatic conditions following disturbance. Recent research has shown that biocrust recovery rates through time are not linear, but may vary widely, depending on nonlinear external parameters, e.g., extraordinary climatic conditions. Natural recovery often follows a general succession pattern, starting out with cyanobacteria and algae, which is then followed by lichens and bryophytes at a later stage. However, this general sequence can be altered by parameters like dust deposition, fire effects, and special climatic conditions as in fog and dew deserts and under mesic climates. Recent studies have proposed that under favorable, stable soil conditions, the initial soil-stabilizing cyanobacteria-dominated succession stages may be omitted and moss-dominated biocrusts can develop in the initial phases of biocrust development. During natural recovery of biocrusts, soil properties change, e.g., soil nutrient and organic matter contents increase. Also, silt and clay contents of encrusted soils increase with biocrust maturity, which may be caused by two mechanisms, i.e., entrapment of fine soil particles by biocrusts and the new formation of smaller particles by weathering of the existing substrate.

Finally, soil hydrology is affected by biocrust development with the soil moisture content of surface soils increasing with biocrust succession.

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Chapter 24

Enhanced Recovery of Biological Soil Crusts After Disturbance

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24.1 Introduction

Biological soil crusts (biocrusts) are very sensitive to anthropogenic and natural disturbance, such as trampling, grazing, and fire and remain in a degraded state in many areas following such disturbances (Belnap and Eldridge 2003; see Chap. 21 by Zaady et al.). Considering their highly relevant ecological functions, like increasing stability of surface soils against wind and water erosion, improving soil fertility, and their considerable primary production in arid and semiarid regions, rehabilitation of biocrusts may improve the functional recovery of degraded ecosystems (Belnap 1993; Bowker et al. 2005; Liu et al. 2013). Often, biocrusts can naturally recover after disturbance when stressors are eliminated owing to the pioneer nature of some component organisms, like many of the cyanobacteria and some mosses (Booth 1941; Belnap et al. 2003; see Chap. 23 by Weber et al.). However, natural recovery rates of biocrusts are often too slow, and,

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consequently, the process takes too long to recover satisfactory ecological functions in many arid and semiarid regions, especially under chronic disturbance regimes. It has been estimated that the natural recovery rates of biocrusts range from a few years to several hundred years or millennia depending on severity, type, season, and duration of disturbance, as well as the soil properties and climate conditions of the region, especially the precipitation amounts and frequencies (see Chap. 23 by Weber et al.). On the other hand, the pioneer nature of some biocrust organisms and exceptional vegetative reproduction capacity of most biocrust organisms create the possibility of speeding up the process of biocrust formation and succession by inoculating the soil surface with fragments of these organisms together with resource supplements such as water and/or fertilizer.

Numerous studies have been conducted related to artificial cultivation of biocrust organisms for rehabilitation purposes in the laboratory and field in the United States, China, Israel, Spain, Africa, and Australia (Belnap 1993; Dodi and Zaady 2006; Maestre et al. 2006; Malam-Issa et al. 2007; Wang et al. 2008; Zheng et al. 2011; Zhang et al. 2013; Liu et al. 2013; David J. Eldridge, unpublished). Also, several studies have evaluated ecological functions of artificially recovered biocrusts (Malam-Issa et al. 2007; Xiao et al. 2008b, 2011; Zheng et al. 2011; Wu et al. 2013). Theoretical foundations, principles, methods of biocrust rehabilitation, and its effect on biocrusts' ecological function are reviewed in this chapter.

24.2 Theoretical Foundation for Rehabilitation of Biocrusts

As detailed in Sect. 24.4, many biocrust organisms can be grown artificially (Chen et al. 2003, 2009; Stark et al. 2004; Bi and Hu 2006; Robin and Rosentreter 2006; Bu et al. 2011; Liu et al. 2013). The reason for that is that many biocrust organisms are successional pioneers having developed various modes of vegetative reproduction (Johri and Srivastava 2001). Subsequently, we will briefly review the traits and reproductive modes of these organisms to understand how they might be grown artificially.

24.2.1 *Cyanobacteria*

Cyanobacteria are prokaryotic, photoautotrophic organisms which occur in nearly all terrestrial environments (Whitton and Potts 2000). They are often the first photosynthetic species to appear on disturbed soils and can survive under extreme environmental conditions, such as high temperature, pH, and salinity, low precipitation, strong irradiation, and desiccation (Booth 1941; Whitton and Potts 2000; see Chap. 4 by Büdel et al.). As prokaryotic organisms, unicellular reproduction

occurs by simple division of the cell. Vegetative propagation of filamentous cyanobacteria often takes place by hormogonia and pseudohormogonia (Krishnamurthy 2001). These biological characteristics and simple vegetative reproductive modes make cyanobacteria highly suitable organisms for biocrust rehabilitation.

24.2.2 *Mosses*

Mosses are generally the most prevalent bryophytes in biocrusts. Two key properties of mosses make them highly relevant to dryland restoration and specifically rehabilitation of biocrusts: (1) They are totipotent, meaning that any vegetative tissue of a plant may serve as a propagule that may grow into new plants (Memon and Lal 1981). (2) Moss propagules can be stored and retain viability for long periods of time under the right conditions (Stark et al. 2004). The spore is the product of sexual reproduction and a means of long-distance dispersal of mosses. However, in dryland environments, vegetative reproduction is much more important, because liquid water is required for a fertilization event and subsequent spore production (Nath and Asthana 2001; Goffinet et al. 2008). Further, many of the most common desert mosses have highly skewed sex ratios and high abortion rates of sporophytes, both reducing the efficacy of sexual reproduction (Stark et al. 2000). Some mosses utilize specialized asexual propagules, like deciduous shoot apices, flagellae, caducous branchlets, bulbils, rhizoidal tubers, endogenous gemmae, and gemmae. However, almost any portion of the gametophyte of a moss, like shoot apices, leaves, stems, and even rhizoids, can potentially act as a propagule, although there are significant differences in reproductive potential among these different types of tissue (Glime 2007; Goffinet et al. 2008).

24.2.3 *Lichens*

Lichen reproduction can involve one or both bionts and can be sexual or asexual (Krishnamurthy and Upreti 2001). Sexual reproduction of lichens involves only the fungal mycobiont which produces a fruiting body that contains and disperses spores. The sexual formation of new lichen thalli by mycobiont spores is extremely difficult because of the challenging relichenization process. It has been reported that the formation of a new lichen thallus from the ascospore-derived mycelia occurs in about one out of several million cases (Honegger 2008). However, several modes of vegetative propagation are well developed in lichens. Fragmentation is the simplest and one of the most common methods of vegetative reproduction, whereas isidia and soredia are specialized vegetative propagules of lichens, containing both the mycobiont and photobiont. Thus, at least in theory, it should be feasible to restore lichen crusts by inoculation.

24.3 Principles Underlying the Practice of Biocrust Rehabilitation

Biocrusts are often crucial structural and functional components of many ecosystems, and biocrust rehabilitation may be an important part of restoration of a degraded ecosystem (Belnap and Eldridge 2003; Bowker 2007). The principles of economics, technical operability, and sustainable development provide guidance for biocrust rehabilitation. Below we outline several principles to guide the setting of goals, selecting species and restoration materials to work with and selecting which sites are most likely to benefit from biocrust rehabilitation, and understand the challenges which constrain success.

24.3.1 Rehabilitation Goals

Setting a practical and suitable goal is the first and most important step for biocrust rehabilitation (Bradshaw 1996; Falk et al. 2006; van Andel and Aronson 2006; Bowker 2007). In a given degraded ecosystem, a suitable target may be based on a desired ecosystem structure (e.g., species composition, biomass, coverage, and/or thickness similar to what existed before degradation, if known) or ecosystem function (soil stabilization, N fixation, etc.) to meet rehabilitation objectives (Aronsen et al. 1993). In addition, the rehabilitated biocrust should be able to sustain or advance succession of the entire ecosystem when rehabilitation measures are terminated.

A suitable rehabilitation goal defines successful rehabilitation (hereafter “target”) and will alert us when we have reached the endpoint. However, development of a functional target is somewhat complex. It should be a trade-off between the practical objectives of rehabilitation (such as to alleviate water or wind erosion, to restore biodiversity or a specific biotic community, to enhance vegetation succession rate, to enhance soil fertility, etc.), local environmental constraints, and the economic costs of the rehabilitation process. For example, many studies have determined the minimum coverage and development of biocrusts to achieve erosion control (Belnap and Gillette 1998; Zhao and Xu 2013). Thus the minimum sufficient amount of biocrust coverage may be used as a functional target if the rehabilitation of biocrusts is intended to combat desertification by alleviating soil erosion.

Predictive models of potential biocrust distribution, abundance, and composition that are based on correlation between biocrust community properties in less disturbed areas and abiotic environmental factors are a useful tool for developing structural targets for biocrust recovery (Bowker et al. 2006a, b). Unfortunately, only a few efforts have been made toward such models, despite that many studies have been conducted on the development and distribution of biocrusts in various arid ecosystems (see Chap. 10 by Bowker et al.). Based on identifying environmental

factors that correlate with biocrust occurrence on different spatial scales, Bowker et al. (2006a, b) developed a spatial model of biocrust “potential” distribution over a landscape. In practice, to be used more widely, this approach requires an understanding of the quantitative relationship between abiotic environmental factors and the structure of biocrusts, and many low-disturbance sites to be used as a structural target, which is challenging in many parts of the world where there is a paucity of such sites. However, an alternative approach is to locate a less degraded site, which is otherwise similar to the area that will be rehabilitated. These relicts of local natural biocrust are useful structural targets for full rehabilitation of an ecosystem, but it is important to note that full recovery may not always be attainable if too many degradation thresholds have been surpassed. Pragmatic rehabilitation efforts may seek to establish a successional trajectory toward the structural target, rather than actually attaining it. Bowker (2007) proposed suggestions on the principles and methods for selection of potential “reference” sites.

So far, few studies have specifically addressed how to determine restoration targets; most studies have focused on how to increase biocrust abundance rather than state a specific endpoint (Maestre et al. 2006; Wang et al. 2008; Xiao et al. 2011; Zhang et al. 2013; Liu et al. 2013). However, although the topic was not specifically addressed, most studies on biocrust cultivation actually followed some of the principles and methods mentioned above in that they used locally sourced organisms in keeping with a site-specific structural target (Belnap 1993; Maestre et al. 2006; Malam-Issa et al. 2007; Xiao et al. 2008a; Chen et al. 2009; Wang et al. 2008; Zheng et al. 2011; Zhang et al. 2013; Liu et al. 2013).

24.3.2 *Choice of Species*

Several principles come into play when selecting species to be used in rehabilitation after disturbance. Often, early colonizers in the successional sequence are chosen (e.g., *Microcoleus* spp.) because their presence may facilitate later colonizers. It is also common practice to choose species or ecotypes adapted to the local climate and soil conditions, both to increase the probability of success and to avoid introducing exotic or invasive species. Species or ecotypes chosen for inoculation may also be those capable of tolerating unfavorable environmental conditions, like high temperature, pH, and salinity, strong irradiation, and frequent desiccation. Additionally, species may be chosen due to diverse reproductive strategies (e.g., mosses and lichens) and/or because they are easy to culture, or because of a particular ecological function to which they contribute. As mentioned in Sect. 24.6, improved knowledge on species’ biology and ecology will definitely benefit the choice of appropriate species to be used in biocrust rehabilitation.

Often, cyanobacteria are the earliest photosynthetic organisms to colonize soil surfaces after disturbance because of their ability to grow fast and resist environmental stress. In other ecosystems, mosses may be early colonizers (Hilty et al. 2004). Thus, cyanobacteria and mosses are most often the preferred cultured

organisms for biocrust rehabilitation. Further, the differences in tolerance of unfavorable environmental conditions and adaptability among species of those groups provide a practical strategy for species selection. As examples, the cyanobacterium *Microcoleus vaginatus*, which is the dominant pioneer organism in many arid and semiarid ecosystems, has been widely investigated in many studies on biocrust rehabilitation (Xie 2006; Xie et al. 2007; Xu and Ning 2010; Xu et al. 2010; Zheng et al. 2011; Zhang et al. 2013; Liu et al. 2013). *Bryum argenteum*, a cosmopolitan moss species and common component in biocrust communities in many dryland ecosystems, showed a much broader ecological niche than *Syntrichia caninervis*, *Didymodon tectorum*, and *Didymodon vinealis*, based on photosynthetic activity (Yunge Zhao and Jayne Belnap, unpublished), and could thus be a better species for cultivation and wide application.

To date, cyanobacterial species that have been most often investigated in biocrust rehabilitation include *Microcoleus vaginatus*, *Scytonema javanicum*, and *Phormidium tenue* (Xu et al. 2010; Zheng et al. 2011; Zhang et al. 2013; Liu et al. 2013). In addition, *Nostoc sp.* was artificially cultivated in a few studies (Bi et al. 2005; Malam-Issa et al. 2007). Moss species that have been experimentally grown include *Aloina bifrons*, *Bryum argenteum*, *Bryum recurvulum*, *Bryum pallescens*, *Barbula unguiculata*, *Ceratodon purpureus*, *Didymodon nigrescens*, *Didymodon constrictus*, *Didymodon rigidulus* var. *ditrichoides*, *Didymodon tectorum*, *Didymodon vinealis*, *Pterygoneurum lamellatum*, *Pterygoneurum ovatum*, *Syntrichia caninervis*, and *Syntrichia ruralis* (Robin and Rosentreter 2006; Xu et al. 2008; Chen et al. 2009; Stark et al. 2004, 2009a, b, 2010; Bu et al. 2011; Stark and Brinda 2013; Antoninka, Doherty and Bowker, unpublished). All of the cyanobacteria and moss species investigated showed potential for artificial cultivation. However, rehabilitation of biocrusts would definitely benefit from the exploitation of more candidate species with broader ecological aptitudes and functions.

24.3.3 Site Selection

Theoretically, biocrusts can be rehabilitated in most terrestrial degraded ecosystems to exploit their role as either pioneers or stress-tolerant communities or both. There are two primary considerations in prioritizing a site for biocrust rehabilitation. First, the site should have greater potential for success of rehabilitated biocrusts than other sites. Second, the site should benefit from the assisted recovery of biocrusts more than alternative sites.

Potential for success is largely constrained by soil properties and climatic conditions. These challenges are important to understand and are dealt with in detail below (Sects. 24.3.4 and 24.3.5). In addition to these overarching challenges, suitability of sites for biocrust rehabilitation differs, because biocrusts are strongly influenced by microenvironmental conditions and disturbance sensitivity. Results of field surveys in many arid and semiarid ecosystems demonstrated that the

greatest microbial biomass and/or coverage were often found on ENE and NNW exposed slopes in the northern hemisphere, in the shade of vascular plants (especially mosses), and at the foot of slopes and sand dunes, where microenvironmental conditions are less extreme than in other habitats (Garcia-Pichel and Belnap 2003; Davidson et al. 2002). Thus, site selection in a given degraded ecosystem must carefully consider physical, biological, and logistical constraints (e.g., transportation conditions and water availability). Pre-existing microenvironmental properties, like the slope aspect, position on slopes, position relative to vascular plants, and even micromorphology, are known to have a critical influence on formation and succession of biocrust communities (Garcia-Pichel and Belnap 2003; Davidson et al. 2002). Thus, sites with facilitative microenvironmental properties for biocrust succession should be preferentially inoculated.

There are several types of priority areas for biocrust rehabilitation, which suffer from unstable soils and would largely gain from the addition of biocrusts. These include abandoned mines, roadsides (where annuals and shrubs will not grow; García-Palacios et al. 2011), mobile dunes (especially when they encroach upon agricultural fields, roads, and populated areas; Wang et al. 2008; Liu et al. 2013), deserted military and contaminated areas, decommissioned large-scale solar power facilities, and roads and drilling pads associated with energy exploration and extraction. For example, abandoned mines and quarries generally must be reclaimed to some degree by law, by recreating the previous topography of the land. This is often insufficient, as during the first rainfall events, considerable soil surface erosion occurs. However, this could be mitigated by the rehabilitation of biocrusts (Fig. 24.1).

24.3.4 Challenges: Soil Conditions

The condition of soils is one major constraint of successful assisted recovery of biocrusts. Soils in degraded ecosystems may have a low water holding capacity, coarse texture and unstable surface (sandy ecosystems), low organic material and nutrient content, high pH and salinity (arid and hyperarid ecosystems), and high bulk density due to compaction (old mines) or may be composed of unweathered parent materials (roadsides). While a large body of literature has addressed the influence of biocrusts on soil properties (Rao and Burns 1990; Chamizo et al. 2012), few researchers have focused on the impact of soil properties on the growth and community succession of biocrusts.

Biocrust organisms often can colonize these challenging sites (Belnap et al. 2003), and soil amelioration may even facilitate their colonization and growth. For instance, Maestre et al. (2006) found that recovery of biocrusts could be enhanced in Mediterranean semiarid areas by addition of organic residues such as composted sewage sludge, which might increase soil fertility and microbial activity. For mobile sandy surfaces, stabilizing measures, like straw checkerboard and/or bush planting, have been efficacious for biocrust rehabilitation in northwestern



Fig. 24.1 A few cases which are priority areas for biocrust rehabilitation from the Negev Desert, Israel; (a) topography reclamation of an old phosphate mine surrounded by naturally occurring dark cyanobacterial crusts; (b) rainfall events producing overland water runoff, creating gullies at the soil surface; and (c) heavy soil surface erosion in reclaimed area



Fig. 24.2 Mobile sand surface stabilized by the checkerboard method, which facilitates development of cyanobacterial biocrusts; conducted in Inner Mongolia, China. Often made of straw, these checkerboards were constructed from twigs of *Salix psammophila*. (a) Newly made checkerboards on mobile sand dunes. (b) Some of the twigs in the checkerboards developed into new *S. psammophila* plants which were beneficial to surface stabilization. Cyanobacterial crusts developed in the open spaces within the checkerboards. (c) Dark cyanobacterial crust developing within the checkerboards (Photo by Dunhai Li)

China (Fig. 24.2; Wang et al. 2008; Wu et al. 2013; Liu et al. 2013). In the Tengger Desert, northwestern China, recovery of biocrusts was enhanced by straw checkerboard combined with shrub planting, which resulted in a sustainably stabilized ecosystem composed of biocrusts and sand-binding vegetation (Li et al. 2010). Polyacrylamide, a chemical sand-fixing agent, can stabilize surfaces and is not harmful to cyanobacterial cells. In addition, its high water holding capacity is beneficial for the inoculated cyanobacterial cell growth in sandy soil (Park et al. 2014). Yunge Zhao (unpublished data) also tested a water-retaining polyacrylamide to stabilize a loess parent material for moss cultivation. However, the results showed a prominent swelling–shrinking of the soil surface caused by drying–wetting cycles of the agent, which made the surface unsuitable for moss fragments to colonize, despite the fact that polyacrylamides may improve cyanobacterial biocrust growth in the lab (Park et al. 2014). Soil-aggregating polyacrylamides have mostly exerted negative effects on the establishment of biocrust organisms under field conditions (Davidson et al. 2002). In the case of fixation of sand dunes by filamentous cyanobacteria, the physical gaps between the large sand particles cause a decreased colonization rate. Here, using 5–10 % silt and clay with the inoculant is recommended to provide some stability and help

Table 24.1 Impact of nutrient addition on moss crust formation in 30 days of cultivation

Nutrient	Optimal concentration (g L^{-1})	Average moss cover (%)	Average moss density (plant cm^{-2})	Average moss height (mm)
Control	–	9.8	8.0	0.8
Glucose	30	18.6	15.1	1.0
Nitrogen (NH_4NO_3)	1.0	18.1	16.3	0.9
Phosphorous (KH_2PO_4)	2.0	14.3	12.5	0.9
Magnesium (MgSO_4)	0.5	16.2	11.0	1.0

Note: Data shown here are the results of a growth chamber culturing experiment of *Didymodon tectorum* (Chen et al. 2011). Five concentration levels were independently tested for each kind of nutrient. The optimal concentrations are listed in the Table. Approximately 1.8 L m^{-2} of each nutrient solution was sprayed on the soil surface prior to inoculation. Nutrient solutions showed significant negative influences on moss crust formation when the concentrations of NH_4NO_3 , KH_2PO_4 and MgSO_4 were over 4.0 g L^{-1} .

cyanobacteria to overcome these gaps (Dodi and Zaady 2006; Zaady, personal communication).

Despite many soil amelioration methods in use for degraded soils, it is mostly problematic to utilize the methods developed to assist vascular plant growth directly for biocrust rehabilitation because of the tremendous differences between vascular plants and biocrust organisms. As an example, Yunge Zhao (unpublished data) has attempted to ameliorate the loess soil by adding organic manure (cow dung), hoping to improve the nutrient content for moss growth. However, large amounts of fungi introduced along with the manure exerted serious negative effects on moss establishment, even with as little as a 5 % addition rate (manure mass/soil mass; Yunge Zhao, unpublished). However, a modicum of glucose and nutrients (nitrogen, magnesium, and phosphorous) showed positive influence on moss crust formation (Table 24.1). Nevertheless, very little research has been done on this topic to date.

24.3.5 Challenges: Climate Regimes

The other major constraint to success of biocrust rehabilitation is climate. Water, in the form of rainfall, dew, fog, and melting snow, is essential for biocrust propagules to grow because biocrust organisms are active only when hydrated (Belnap et al. 2003). Thus, to rehabilitate biocrusts in arid and semiarid regions, one needs to take full advantage of the relatively moist season of the year. Liu et al. (2013) observed a significant increase in biomass of inoculated cyanobacteria after a rainfall. We can still expect better recovery rates of biocrusts that were inoculated just before or during the moist season as compared to the dry season. In

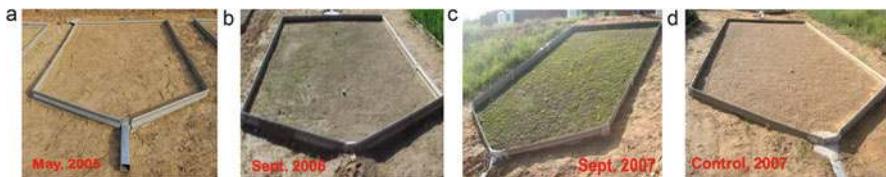


Fig. 24.3 Successional dynamics of artificial moss crusts in the Loess Plateau region. (a) Beds of soil in May 2005. The plots were inoculated with field-collected moss crust material after they were set up. (b) Inoculated plot in September 2006. Moss crust covered 30 % of the plot surface. (c) Inoculated plot in September 2007. Nearly complete coverage of moss crust was attained. (d) Control plot in September 2007. No obvious moss crust had developed

the Loess Plateau region, Xiao et al. (2008a) inoculated moss crusts in the beginning of August 2005 (early monsoon), which resulted in a 30 % moss cover crust after the monsoon (Fig. 24.3).

Another approach for microclimate regulation, in addition to taking full advantage of a naturally moist season, is creating artificial microclimate conditions by planting shrubs or other native vascular plants when inoculating biocrusts, especially when irrigation will be applied at the beginning of rehabilitation (Liu et al. 2013).

24.4 The Practice and Advancement of Biocrust Rehabilitation

From the beginning of this century, many studies related to biocrust rehabilitation have been carried out in arid and semiarid regions because of the increasing attention to soil desertification in such regions around the world. With differing levels of success, cyanobacteria-, moss-, and lichen-dominated biocrusts have been either cultured in laboratory settings or promoted under field conditions. The literature on culture of cyanobacterial crusts in China has been extensive enough that a scientific monograph, *Environmental Biology of Desert Cyanobacteria and Combating Desertification with Biological Soil Crusts*, was published in 2013 (Liu et al. 2013, In Chinese). The book provides a collective review of environmental tolerance of desert cyanobacteria, culture methods and techniques in the laboratory, greenhouse and field conditions, and methodology and technology of cyanobacterial crust rehabilitation in sandy desert ecosystems. These rehabilitation methodologies include isolation and mass cultivation of cyanobacteria and application techniques. The methods have been successfully demonstrated in large-scale experiments in an area of approximately 200 ha in Hopq Desert, Inner Mongolia, China, and are instructive for biocrust rehabilitation in other regions. In this section, the practice of biocrust rehabilitation will be discussed. We will mainly focus on measures and procedures that may allow the successful growth of biocrusts *ex situ*, or encourage their growth in the field.

24.4.1 Artificial Cultivation of Cyanobacterial Biocrusts

Generally, artificial rehabilitation of cyanobacterial biocrusts includes four successive steps, which are (1) isolating propagules from natural biocrusts, (2) mass cultivation of propagules, (3) propagule preparation, and (4) field application and establishment.

- (1) Isolating propagules: Cyanobacteria propagules are mostly isolated from natural biocrusts using a relatively mature, well-established microbial cultivation technology (Yan et al. 2004; Rao et al. 2009; Liu et al. 2013). Field-collected biocrust material is ground and incubated under optimum environmental conditions. Afterwards, the strains are isolated and identified. As an alternative, Dodi and Zaady (2006) proposed an easier method of cyanobacteria propagule collection, which is based on the collection of overland runoff water, generated by natural rain or an artificial rainfall system on a biologically crusted site, thereby obtaining a suspension that contains cyanobacterial propagules. The water with the propagules can be used immediately by spraying on the target areas or after drying at 40 °C to produce a powder of propagules to be used later. Propagules can be obtained by both methods. The isolation approach is optimal when a specific organism is targeted, but has the additional requirement of professional facilities and skills.
- (2) Mass culture of propagules: The isolated cyanobacterial species must be mass cultured to obtain a sufficient quantity for inoculation. A multigrade upscaling procedure was developed for mass cultivation of propagules in China (Liu et al. 2013). First, the isolated target cyanobacteria species (such as *Microcoleus vaginatus*, *Scytonema javanicum*, *Nostoc* sp.) are grown in BG-11 medium without microelements in small closed transparent containers (ranging from 0.5 to 18 L) to achieve more propagules. Then, the cultures are inoculated and cultivated in a series of various size raceway culture ponds until the biomass of cyanobacteria has achieved the desired level (Fig. 24.4). Mixers are necessary to maintain optimal ratios between oxygen and carbon dioxide in the propagule suspension. BG-11 or BG-11₀ (used for nitrogen-fixing species) medium is used for mass culture. Although the optimal photosynthetic temperature of *Microcoleus vaginatus* is around 25 °C, it was reported that they grew well in the culture ponds between 15 and 30 °C (Liu et al. 2013). Using this procedure, it was estimated that 120–180 kg (fresh weight) could be produced in a culture pond with a volume of 48 m³ within 5–10 days (Liu et al. 2013).
- (3) Propagule preparation: Normally, the propagule suspensions can be applied on the target sites after concentration by evaporation or filtration (Wang et al. 2008; Liu et al. 2013). This procedure can also be continued to create a dry powder of propagules (Dodi and Zaady 2006; Liu et al. 2013). Full drying allows long-term storage of propagules in little space (Liu et al. 2013). But before applying dried propagules to the disturbed target area, a 1-day resuspension in water is required. Another possibility is to mix the propagule powder with a polymer, which can create a porous film attached to the soil after



Fig. 24.4 Mass cultivation procedure and equipment used for cyanobacteria (*Microcoleus vaginatus*) culture in Inner Mongolia. (a) The first grade mass culture of isolated cyanobacteria in flasks; (b) Small raceway culture ponds for further mass culture; (c) A large raceway culture pond. (Photo by Weibo Wang)

applying the mixture onto the soil surface (Dodi and Zaady 2006; Liu et al. 2013). Unfortunately, although these alternative preparation strategies exist, there are no studies that we are aware of comparing their relative success rates side by side in the field.

- (4) Application and establishment: Both powders and suspension of cultured cyanobacteria propagules have been experimentally applied for biocrust rehabilitation in the field. Zhang et al. (2013) developed artificial biocrusts in a greenhouse using different inoculum doses of cyanobacteria powder (0.5, 1, 3, and 7 g m^{-2}) and found that the resulting cyanobacterial biomass (in terms of chlorophyll a content) increased with the inoculum dose. They recommended a dose of 7 g m^{-2} for the Gurbantunggut Desert, northwestern China. However, most field inoculation trials have used a liquid suspension of cyanobacterial propagules (Xie 2006; Wang et al. 2008; Zheng et al. 2011). For example, cyanobacterial crusts with a biomass of $3.8 \text{ mg chlorophyll a m}^{-2}$ had formed 27 days after inoculation with mixed cyanobacterial cultures (*Microcoleus vaginatus*, *Scytonema javanicum*, and *Nostoc* sp.) at a ratio of $0.22 \text{ mg chlorophyll a m}^{-2}$ in field plots with the automatic micro-irrigation in Inner Mongolia (Liu et al. 2013). Wu et al. (2013) also reported that a well-developed cyanobacterial crust had formed 7 years after inoculation with the cultured cyanobacterial suspension. However, despite these successful experiences, it still remains uncertain whether liquid-cultured material will generally be able to adapt to harsh field conditions.

With respect to successful establishment of propagules after inoculation, soil moisture management is vital for survival and succession of the inoculated propagules. A significant decrease in biomass of inoculated cyanobacteria was observed by Liu et al. (2013) when no water was supplied after inoculation. So far, although in different amount and frequency, irrigation has always been utilized in experimental and practical biocrust rehabilitation as a necessary measure (Wang et al. 2008; Zhang et al. 2013; Wu et al. 2013). For example, 20 mm per day, irrigated by automatic micro-irrigation sprinkling from 9:00 to 16:30 for 15–18 days, were used by Wang et al. (2008) in Inner Mongolia. Also in Inner Mongolia,

Wu et al. (2013) watered the inoculated cyanobacteria-dominated crusts with 3 L m⁻² every 3 days for a total of 15 days.

Given the successful experiences, amount and frequency of irrigation for biocrust rehabilitation are worthy of further study. The balance between watering time, amount, and frequency exerts a significant influence on the fate of the propagules. However, given the importance of water for the formation and development of artificial biocrusts, only a few studies have been designed to evaluate effectiveness of frequency and amount of watering (Maestre et al. 2006; Zhang et al. 2013). According to the mean annual precipitation in the Gurbantunggut Desert (79.5 mm), five different moisture treatments (no water added, 1, 2, 3, and 4 L m⁻²) were applied during the first 3 weeks by sprinkling evenly at 10:00 a.m. Two to three liters (equivalent to 2–3 mm of rain) per square meter were recommended for artificial biocrust cultivation in the region (Zhang et al. 2013).

In addition to moisture, the BG-11 medium has been used during the establishment period as a nutrient supplement to promote succession of artificial cyanobacterial biocrusts in several studies (Wang et al. 2008; Wu et al. 2013; Liu et al. 2013). Measures that may create more benign microenvironmental conditions, like straw barriers or bush planting, have been used in Inner Mongolia and have been proven as an effective measure for artificial biocrust development (Wang et al. 2008; Liu et al. 2013).

24.4.2 Artificial Cultivation of Moss Crusts

To date, most moss cultivation research is still tentative, investigating culturing methods for different species. Only one study has upscaled artificial culturing of moss crust to field plots (Xiao et al. 2011).

A few studies investigated the propagation potential of different inoculation material, like spores, vegetative fragments, and field-collected moss crusts (Chen et al. 2009). The results showed that the field-collected moss crust was the best performing inoculum, although spores and vegetative fragments also could develop into new moss plants (Chen et al. 2009, 2011). So far, most of the artificial moss crusts have been inoculated with moss material collected directly from field sites, without an intervening mass culture step. This approach is suitable only in certain situations and is unlikely to ever be sustainable at larger scales.

Fortunately, biocrust mosses have proven very amenable to cultivation, for example, in growth chambers, either from spores or from gametophyte fragments. Tissue culture is another useful technique that may provide purified plants through an in vitro model under well-defined environmental conditions within a short period of time (Glime 2007). Studies have been conducted on tissue cultivation of drought-tolerant mosses, and researchers have developed a feasible culture procedure for *Syntrichia caninervis* (Xu et al. 2008). In addition, tissue cultivation is a potential method to solve the problem of providing sufficient material for field inoculation. There are two main forms of reproduction: (1) stems continually branch and



Fig. 24.5 Tissue culture of the desiccation tolerant moss *Syntrichia caninervis*. (a) Tissue culture in Knop's solution. (b) The fragments of *Syntrichia caninervis* could form new moss shoots when cultivated on a surface covered with 2 mm of sand. (c) Stems continually branch and produce young plants. (d) Young plants and the fragments of the stems and leaves repeatedly and extensively produce protonemata

produce young plants (Fig. 24.5c); (2) young plants and the fragments of the stems and leaves repeatedly and extensively produce protonemata which develop into a large number of new plants (Tian et al. 2005, 2006; Nie et al. 2006; Fig. 24.5d).

In general, mosses can be grown on a variety of substrates. Placement of gametophyte fragments onto a bed of soil or artificial substrate (e.g., perlite) with addition of water and nutrient media (e.g., Knop's solution) will result first in protonematal growth and an eventual growth of new shoots (Robin and Rosentreter 2006; Stark et al. 2004; Yunge Zhao, unpublished). Yuanming Zhang et al. (unpublished data) were able to develop a moss-dominated incipient crust population in the lab within 2 months of cultivation. Sterilized Knop's solution has proven to be the best of several media for culturing moss tissue in the lab (Xu et al. 2008). In the Tengger Desert, four moss species, *Bryum argenteum*, *Didymodon nigrescens*, *Didymodon constrictus*, and *Didymodon rigidulus* var. *ditrichoides*, were collected and artificially cultured on a sand surface (instead of Knop's solution) under greenhouse conditions. Except for the species *Bryum argenteum*, no mosses showed any growth on the sand surface. It was observed

that new shoots came out on top of old shoots or fragments of stems and leaves (Bai et al. 2003). Results from the Gurbantunggut Desert also showed that, after 1 month, the fragments of the desert moss *Syntrichia caninervis* could form new moss shoots when they are cultivated both in Knop's solution and on sand (Fig. 24.5a, b; Nie et al. 2006). Regarding the amount of inoculant, Chen et al. (2009) demonstrated 500–750 g m⁻² to be suitable for cultivation of *Didymodon tectorum*-dominated crusts when inoculated with the moss crust (with soil material).

In the Loess Plateau region, Chen et al. (2009) found that soil moisture greater than 60 % field capacity was the most critical factor for both formation and development of moss crusts. Further, 17 °C was the optimal temperature for *Didymodon tectorum*. Also, in the Mu Us Sandy Land (China), Bu et al. (2011) showed that the optimal culture temperature is around 15 °C, which is similar to results with mosses from the Loess Plateau (China) by Chen et al. (2009). Xiao et al. (2011) pioneered an upscaled outdoor moss-culturing technique, dispersing moss fragments onto beds of soil with enhanced nutrient supply, watering, and a glass cover for heat and moisture conservation. This approach yielded 100 % cover in 448 days (Xiao et al. 2011). In addition, Xiao et al. (2011) established moss crusts in field plots by inoculating the soil surface with field-collected moss crust material at the beginning of monsoon, combined with watering and an addition of KH₂PO₄ solution. Within only 2 months, a coverage of 30–60 % was reached, exemplifying the promise of moss crust rehabilitation.

Recently, upscaled culturing techniques have been applied in a greenhouse setting in the United States using a novel automatically irrigated system that relies on capillary action of water upward through beds of sand in plastic containers (Doherty et al. 2015; Fig. 24.6). The advantage of such a system is its uniform watering to field capacity at a frequency chosen by the researchers and the relative lack of surface disturbance associated with other water delivery mechanisms. Initial results have illuminated optimal combinations of hydration period and frequency of fertilizer application, for both *Syntrichia caninervis* and *Syntrichia ruralis* sourced from Northern Utah (Antoninka, Doherty, and Bowker, unpublished; Fig. 24.6). Additional early results suggest that populations of *Syntrichia ruralis* sourced from different climates respond differently to length of hydration period (Doherty 2014).

24.4.3 Artificial Promotion of Lichen Crusts

Although lichens are important components of biocrusts, and there are sound biological foundations for enhancing recovery of lichen crusts by inoculation with the fragments of lichen thalli, there is no literature on the artificial cultivation of dryland lichens for the purpose of rehabilitation of biocrusts. Studies that have used field-collected inocula and reapplied them to the field have met success in enhancing lichen cover or richness (Belnap 1993). Other studies have sought to determine the natural limiting factors of lichen growth in the field hoping that these

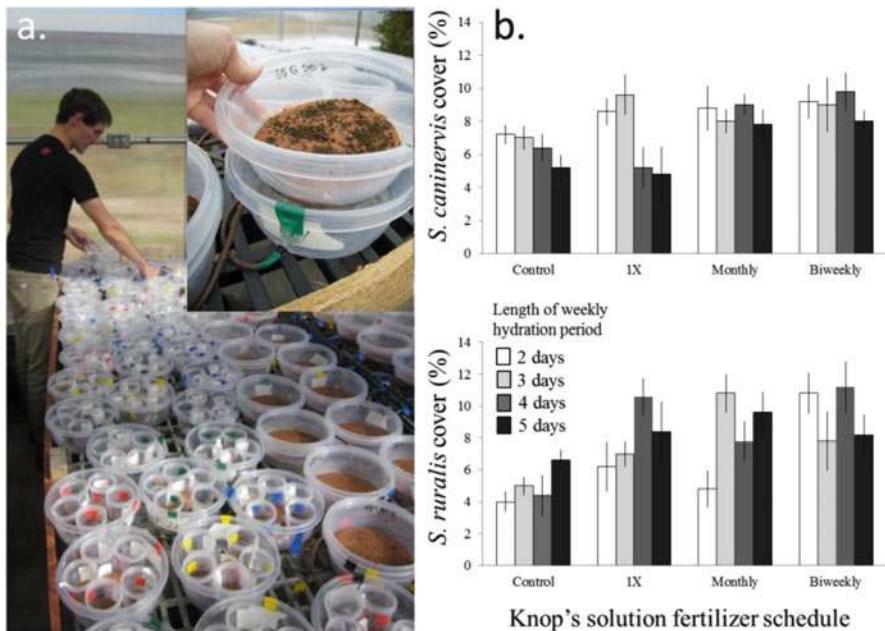


Fig. 24.6 An experimental moss cultivation system. **(a)** Irrigation water is pumped to a lower water basin, which drains slowly. A second container, equipped with holes for wicking in the bottom, is filled with sand and a moss culture. Through capillary action, the water hydrates the surface uniformly and then drains to field capacity. **(b)** Cover percentage of two moss species after 4 months, as a function of different irrigation and fertilizer regimes

factors may be manipulated to promote growth of lichens. One such series of studies on the Colorado Plateau (USA) focused on the lichen genus *Collema* and sought to determine what constrained its natural recovery and which, if any, human interventions might facilitate its growth. Davidson et al. (2002) investigated influences of different restoration treatments such as fertilization, watering, cyanobacterial addition, stabilization with polymers, and micro-aspect on the success of transplanted lichen thalli (*Collema* spp.; ~1 cm diameter). This experiment revealed that the most consistent determinant of successful lichen transplantation was microclimate, suggesting that generation of microtopography might be a measure to promote lichen success. A later experiment confirmed that microclimate was a major filter for establishment of *Collema* isidia or thallus fragments (Bowker et al. 2010). Davidson et al. (2002) also crossed the effects of addition of cultured *Collema* photobionts (*Noctoc* sp.) and the addition of *Collema* spores on initiation of new lichen thalli. New thalli were promoted by spore addition but not by photobiont addition. From a practical standpoint, this result is discouraging because culturing the photobiont is feasible, but there is no practical method to culture large quantities of the lichen mycobiont nor to produce spores. Extensive field surveys repeatedly found correlations between biocrusts, including key lichen species, and

micronutrients such as Mn and Zn, suggesting the hypothesis that biocrusts grow better where these nutrients are more available (Bowker et al. 2005, 2006a). Later experiments showed no clear benefit of growth from the addition of these micronutrients, neither in the lab (Bowker et al. 2008) nor in the field (Matthew A. Bowker, unpublished data). As a major component of biocrust communities and a major contributor to the nitrogen cycle, artificial cultivation of lichens clearly deserves more exploration.

24.4.4 Enhanced Recovery of Biocrusts by Inoculation with Natural Biocrust Material

There are several cases of experimental enhanced recovery of biocrusts by inoculation with fragments of field-collected biocrust material (Belnap 1993; Scarlett 1994; Bowler 1999; Maestre et al. 2006; Xiao et al. 2008a; Chen et al. 2009; Chiquoine 2012). Virtually every study that attempted this approach has succeeded in increased recovery rates of biomass, coverage, and diversity. This practice is limited in its applicability because it requires one collection area to be compromised by biocrust removal, so that another area can be rehabilitated. The only situations in which this may be viable are (1) small-scale applications in which a large amount of inoculum is not needed and (2) situations where biocrusts might be salvaged in advance of a disturbance and stored for later use at small or medium scales. Chiquoine (2012) details the construction of a new routing of a road in the Mojave Desert (USA), in which biocrust materials were stockpiled and used to inoculate the previous road. This method is not sustainable in large-scale applications, and it has long been realized that methods for *ex situ* cultivation of biocrust organisms are needed in order to scale up biocrust rehabilitation.

24.5 Recovery of Ecosystem Functions via Biocrust Rehabilitation

Almost without exception, studies on rehabilitation of biocrusts achieved by inoculation at both laboratory and field scales have demonstrated significant recovery of biocrusts in terms of reducing the time of recovery and enhancing species diversity, biomass, and coverage (Belnap 1993; Maestre et al. 2006; Malam-Issa et al. 2007; Wang et al. 2008; Wu et al. 2013; Liu et al. 2013). Rehabilitation measures had positive effects on recovery of biocrust functions in the greater ecosystem, such as surface stabilization, soil nutrient enrichment, and erosion alleviation.

24.5.1 Impact of Rehabilitated Biocrusts on Physical Properties of Soil Surface

Soil surface properties, like darkness, compressive strength, and stability increased significantly with succession of the rehabilitated biocrusts. Wu et al. (2013) observed a darkening process (fawn-gray-dark gray-black) on the soil surface over the course of 7 years of succession in rehabilitated cyanobacterial crusts, caused by increased pigment contents, mainly chlorophyll *a* and scytonemin. Dark colors would be expected to increase soil temperatures, perhaps increasing production of cyanobacterial biomass in cool seasons. Xie et al. (2007) found that the compressional strength of rehabilitated cyanobacterial crusts was enhanced with increasing cyanobacterial biomass of *Microcoleus vaginatus* in Inner Mongolia, China. The highest compressional strength detected was 0.89 kg cm^{-2} , which was approximately eightfold higher than that of control sites. In addition, the compressional strength of rehabilitated cyanobacterial crusts did not decrease immediately with cyanobacterial biomass decrease. Similar results were obtained by Zheng et al. (2011) in the Xinjiang Province.

Provision of soil stability by rehabilitated biocrusts is a key topic studied by many scientists. Previous research has shown that quantity and stability of microaggregates are significantly improved by the presence of rehabilitated crusts (Xie 2006; Malam-Issa et al. 2007; Zheng et al. 2011; Liu et al. 2013), and, for some cyanobacterial species (*Nostoc* sp.), the effectiveness may be observed only 6 weeks after inoculation (Malam-Issa et al. 2007). With enhanced soil aggregate stability, a reduction of soil erosion can be expected.

24.5.2 Impact of Artificial Biocrusts on Soil Biotic Activity and Fertility

Several studies have indicated that inoculation with artificial cyanobacteria cultures significantly enhances soil fertility (Acea et al. 2003; Xiao et al. 2008b; Zheng et al. 2011; Wu et al. 2013). This effect is due to three mechanisms. First, biocrust rehabilitation may restore microbial populations of the degraded soils, which is critical for soil nutrient cycling. By inoculating heated soil with cyanobacterial strains of the genera *Oscillatoria*, *Nostoc*, or *Scytonema* and a mixture of them, Acea et al. (2001) found counts of cyanobacteria increased by 8 logarithmic units, while heterotrophic bacteria, actinomycetes, algae, and fungal propagules rose by 14 logarithmic units and acidophilic bacteria and *Bacillus* spp. by ~3 logarithmic units, and fungal mycelia showed an 80-fold increase. They also detected a relatively high number of NH_4^+ producers ($7.4 \times 10^9 \text{ g}^{-1}$ crust), starch-mineralizing microbes ($1.7 \times 10^8 \text{ g}^{-1}$ crust), cellulose-mineralizing microbes ($1.4 \times 10^6 \text{ g}^{-1}$ crust), and nitrifiers (NO_2^- and NO_3^- producers; 6.9×10^4 and $7.3 \times 10^3 \text{ g}^{-1}$ crust, respectively) because of the formation of artificial biocrusts (Acea

et al. 2003). Similarly, Tang et al. (2007) indicated that enzymatic activities in desert soil following *Microcoleus vaginatus* and *Phormidium tenue* inoculation were significantly higher than those in a mobile sand dune.

Secondly, C and N contents in soil increased because of increasing biotic activities, especially photosynthesis and nitrogen fixation directly promoted by the inoculated cyanobacteria. Several studies demonstrate increased C and N contents after inoculation with biocrust cyanobacteria (Acea et al. 2003; Nisha et al. 2007; Xiao et al. 2008b). Acea et al. (2003) found increased soil C and N contents in soil at average values of 275 g C kg^{-1} soil and 50 g N kg^{-1} after the artificial biocrusts were cultured for 2 months. Xiao et al. (2008b) reported that the contents of organic material and nitrogen of the top 4 cm soil were increased by 42.9 g m^{-2} and 2.73 g N m^{-2} per year, respectively, in an artificially formed moss crust, and they found a higher nutrient accumulation rate for artificial moss crusts compared to the naturally developed ones. Wu et al. (2013) found a doubling of soil total N and available P and a quadrupling of available N, when comparing 2-year-old to 7-year-old rehabilitated biocrusts. In addition, Maestre et al. (2006) found higher rates of net CO_2 exchange and nitrogen fixation when the crust was inoculated as slurry and under a high watering frequency treatment, compared to dry applications with lower watering frequency. Soil content of inorganic nutrient elements (e.g., Ca, Mg, K, Na, and P) was also higher at sites with biocrust inoculation (Acea et al. 2003; Wu et al. 2013).

Thirdly, soil pH and salinity, which have an indirect influence on availability of soil nutrients, may be reduced by artificial biocrusts. Wu et al. (2013) found an obvious decline ($\sim 0.8\text{--}1.0$ units) in pH in biocrust layers after 7 years of succession. Increases in soil biotic activity and fertility are indicators of recovered ecological function of the artificial biocrusts, which will promote succession of the entire ecosystem.

24.5.3 Impact of Artificial Biocrusts on Soil and Water Loss from Slopes

Although rehabilitation of biocrusts is mostly aimed at combating desertification by alleviation of soil erosion, only a few studies have been conducted on erosion control of rehabilitated biocrusts. Xiao et al. (2008a) found that sediment loss from artificial biocrusts with 30–60 % moss cover was reduced by 26 % on average (artificial biocrust only) and 39 % (with *Caragana korshinskii* Kom. planted) under nine natural rainfall events compared with those plots without inoculation or planting. The results confirmed the effectiveness of biocrust rehabilitation in soil erosion control.

24.6 Questions Worthy of Future Study

Given the many advances of the past 10–15 years, there are questions related to biocrust rehabilitation worthy of further study. First, we need a better theoretical foundation and more empirical data to enable a more successful biocrust rehabilitation practice. In particular, the differences among biocrust organisms in ecological tolerance, adaptability, and reproductive biology deserve further investigations. This autecological foundation would allow the development of new culturing techniques and expand our ability to select the correct species for rehabilitation activities. We also do not have a strong body of published data on the relative influences of abiotic environmental factors like temperature, humidity, and soil conditions, such as texture, moisture, pH, salinity, and nutrients on rehabilitation success. It will be valuable to determine species interactions between biocrust organisms, because positive or negative interactions could impact both inoculum production efficiency and successional trajectories after field application. In addition, the influence of storage length and conditions on the ability of biocrust inocula to grow under field conditions should be explored.

Second, we must effectively develop methods that allow us to operate at larger scales. Appropriate methods and techniques of inoculation are critical for biocrust rehabilitation on multi-hectare or greater scales. To date, only a few studies have applied inoculation methods at these scales (Liu et al. 2013), which may be related to the limitation of theoretical research on biocrust rehabilitation. Liu and his research team used a vehicle that carried large-range sprayers (over 50 m wide) to inoculate biocrusts at the field scale (Liu et al. 2013), but the equipment relies too much on roads to be universally useful. As a potential alternative, an aircraft is proposed in biocrust inoculation (Sears and Prithiviraj 2012), but this approach has not been implemented to date.

In addition, much work is still needed with respect to the post-inoculation management of newly created biocrusts under field conditions. There may be multiple practices which could enhance success rate or growth rate based upon reduction of environmental stress, either actively or passively, by avoiding high-stress seasons. Such strategies like creation of microtopography, provision of shade, and water management have not been thoroughly investigated yet.

24.7 Conclusions

Several studies carried out on various continents have demonstrated the feasibility of biocrust rehabilitation by inoculating the soil surface with biocrust organisms in degraded arid and semiarid ecosystems, and this human intervention may be necessary in some cases to recover ecosystem functions. The recovery of ecological functions of biocrusts may in turn improve rehabilitation of the degraded ecosystem by restoring soil nutrient cycling, fertility, and erosion resistance. To rehabilitate

biocrusts in degraded ecosystems, practitioners should follow the underlying principles of restoration ecology, such as the principle of the limiting factor, eco-structure theory, and ecological suitability principles. Thus far, there have been some highly successful experiences with cyanobacterial crust cultivation. The technique of creating artificial cyanobacterial crusts has been used to combat soil desertification in an area of about 200 ha in Inner Mongolia, China (Liu et al. 2013). Artificial moss crusts have been successfully developed at laboratory scales, but techniques have yet to be scaled up. There are still many questions worthy of future study before we rehabilitate moss crusts in large areas under field conditions, especially regarding the ecological suitability and adaptability of different species. In addition, much attention should be paid to the effectiveness of inocula, especially for moss species. Rehabilitation of lichen crusts is the least successful and also least explored approach at present, but because of the role of cyanobacterial lichens in N fixation, this should be pursued further.

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Part VII

Future Research on Biological Soil Crusts

Chapter 25

Synthesis on Biological Soil Crust Research

Bettina Weber, Jayne Belnap, and Burkhard Büdel

25.1 Introduction

This second Ecological Studies volume on biological soil crusts (biocrusts) covers the research progress made during the last ~1.5 decades, which is the time-span since the release of the first volume of Ecological Studies covering biocrusts (Belnap and Lange 2003). Many topics in the first volume, such as biocrust bacterial composition, their microstructure, and remote sensing, were only presented in a preliminary fashion. Some topics were not covered at all (e.g., biocrusts in the fossil record, history of biocrust research). However, since the publication of this first volume, there has been an exponential increase in biocrust research, recently reaching well over 100 publications per year (Fig. 25.1) and covering a wide variety of topics, ranging from theoretical to experimental, basic to applied, and microscopic to global scales. Thus, biocrust research started to be also recognized by the general scientific community, as is reflected by first publications appearing in transdisciplinary highlight journals. However, despite these efforts, there are many knowledge gaps remaining.

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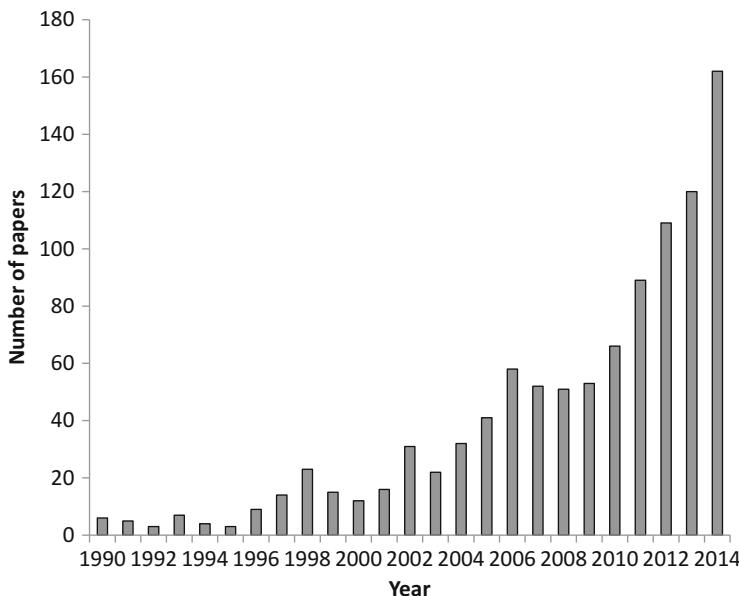


Fig. 25.1 Number of studies on biological soil crusts per year, covering the time-span from 1990 to 2014. Please note the increase in annual publications after publication of the 1st and 2nd edition of the first Ecological Studies volume on biocrusts (Belnap and Lange 2003). Data based on a Scopus search on January 4, 2016, searching for the key words “biological soil crust,” “microphytic crust,” “biocrust,” “cryptogamic crust,” and “microphytic crust” (courtesy: Emilio Rodríguez-Caballero)

25.2 Major Advances in Research

The biocrust research covered within this volume reports on some major recent scientific advances that are propelling the field in new directions. By using different lines of origin, comprising both geological and molecular analytical techniques, an evolutionary cycle for biocrusts could be established (see Chap. 3 by Beraldí-Campesi and Retallack). According to this structure, microbial communities similar to today’s marine microbial mats, with cyanobacteria-like organisms performing non-oxygenic photosynthesis, likely existed up to 3.5 Ga BP (before present) (Fig. 25.2; Noffke et al. 2013). About 2.6 Ga BP, cyanobacteria with oxygenic photosynthesis evolved, starting to make the Earth habitable for oxytrophic organisms. Fossil data suggest that around 2.4 Ga BP, the first biocrusts may have occurred (Beraldí-Campesi 2013). It was much later that eukaryotic algae (~500 Ma BP), lichens (~450 Ma BP), and bryophytes (~410 Ma BP) developed and thus became components of biocrusts (Heckman et al. 2001; Delaux et al. 2015; Leliaert et al. 2012). Adaptations of modern biocrust microorganisms to desiccation and high UV-light radiation most likely developed well before the appearance of macroscopic plants (~300 Ma BP), making the biocrusts particularly suited for colonization of desert environments. Grasslands, which like deserts are regularly

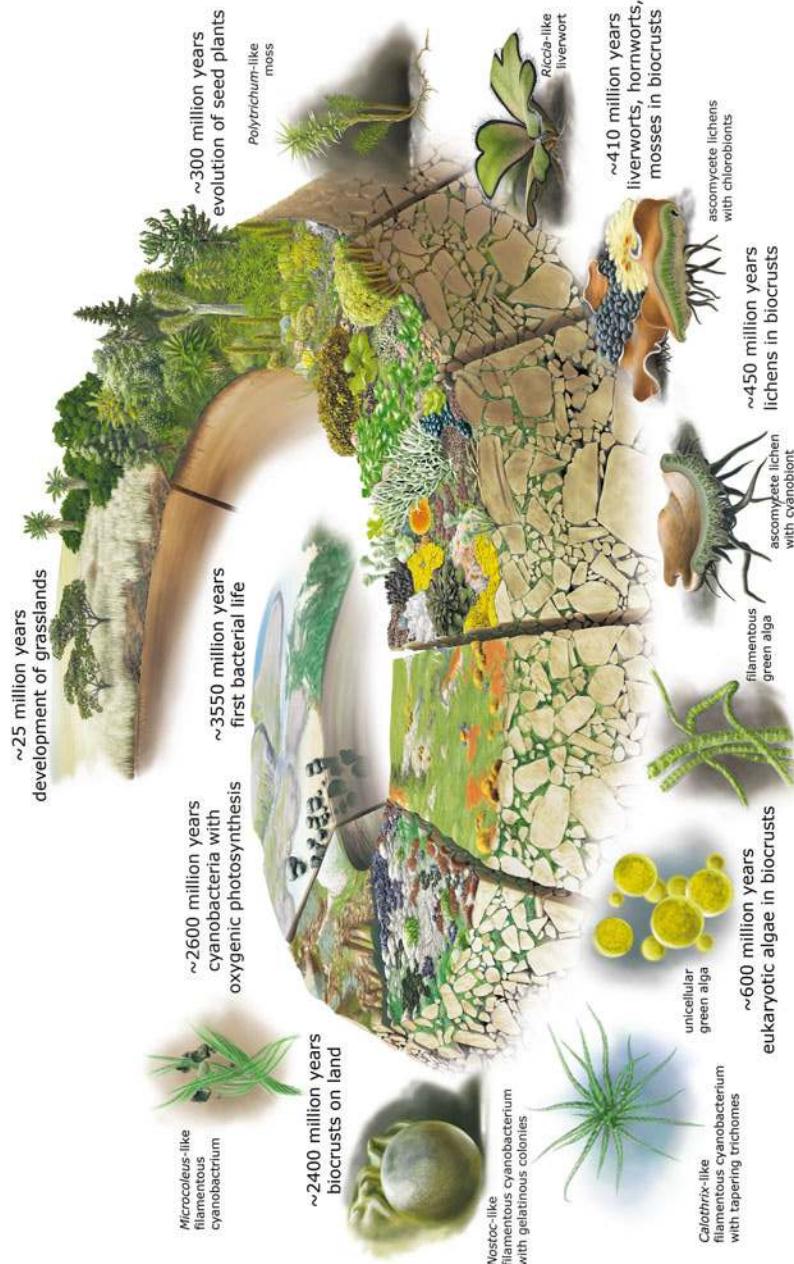


Fig. 25.2 Hypothetical evolution of biocrusts on land. Segments one to seven follow the evolution of cyanobacteria and algae to the seed plants. With the advent of sed plants and their strong competitiveness, biocrusts continued to occur but became restricted to drylands and other extreme habitats (e.g., after major disturbances). Even though occurring in rain forest areas after major disturbances, they only last for short time periods before being replaced by vascular plant vegetation. The last segment was selected as one of several options showing the presence of biocrusts in semiarid lands (savannas), as one representative dryland habitat. Apart from savannas, biocrusts are a regular vegetation component in desert, steppe, and tundra vegetation. Drawing by B. Büdel and F. Spindler

colonized by biocrusts, only developed ~25 million years BP (Smith 2015; Strömberg 2011).

The first studies reporting on biocrust organisms were about 240 years ago, when Peter Simon Pallas described an extensive soil lichen cover in the semiarid steppe of Kazakhstan (Pallas 1776), and bryophytes typical for biocrusts were taxonomically described (Linné 1774; see Chap. 2 by Lange and Belnap). Recognition of soil encrustations with algae, which fulfill ecological tasks, started only in the 1950s, when both Booth (1941) and Fletcher and Martin (1948) investigated their effects on local hydrology. During recent years, studies of biocrust organisms together with their ecological roles showed that biocrusts constitute complete ecosystems, with photoautotrophic cyanobacteria, algae, lichens, and bryophytes acting as producers and heterotrophic bacteria, archaea, and fungi as decomposers. A large array of protozoa, nematodes, tardigrades, rotifers, mites, collembolans, and even larger arthropods and mollusks are important consumers (Darby et al. 2010; see Chap. 8 by Darby and Neher). Thus, biocrusts indeed may be suitable model ecosystems (Bowker et al. 2014; see Chap. 20 by Maestre et al.). On the other hand, we still see some obstacles in using this approach, as there are major knowledge gaps regarding the diversity and response of microbial organisms. For example, despite being miniature ecosystems, the biodiversity contained within is huge, with ~320 species of cyanobacteria, ~350 eukaryotic algae, ~320 species of biocrust bryophytes, and ~550 lichen species currently identified (see Chaps. 4, 6 and 7 by Büdel et al., Seppelt et al., and Rosentreter et al., respectively), together with an uncounted number of bacteria and fungi (see Chap. 5 by Maier et al.). Many of these organisms are extremely difficult to identify and for most of them, their ecological role still needs to be identified.

Recently, biocrusts have also been shown to play a role in global biogeochemical cycling. An upscaling approach based on published literature shows that while they provide only a minor fraction of the biological terrestrial net primary productivity (NPP; ~1 %), they may contribute ~27–53 % of the biological terrestrial nitrogen (N) fixation at the global scale (Elbert et al. 2012), according to the latest Intergovernmental Panel on Climate Change report (Ciais et al. 2013). Nitrogen flux measurements also revealed that biocrusts release reactive N compounds, like nitric oxide (NO) and nitrous acid (HONO) into the atmosphere, which may total up to 1.7 Tg per annum, accounting for ~20 % of the globally emitted reactive N compounds from natural soils per year (Weber et al. 2015; Ciais et al. 2013). These studies indicate that biocrusts may not only play a relevant role at the ecosystem scale, but may also perform important functions in global biogeochemical cycles, which need to be investigated in more detail.

Recent studies have demonstrated that biocrusts are particularly sensitive to global change. Only minor changes in precipitation regime can have detrimental effects on the often-dominant moss *Syntrichia caninervis* (Reed et al. 2012). On the other hand, the species composition of biocrusts may well adapt to climate change patterns. For instance, it has been shown that under warmer climatic conditions, the cyanobacterium *Microcoleus vaginatus* is gradually being replaced in dominance by *Microcoleus steenstrupii*, with the latter being more thermotolerant (Garcia-Pichel et al. 2013; see Chap. 22 by Reed et al.). Also in other studies, e.g., along a latitudinal

gradient of Antarctica, a strong relationship between water regime and lichen and bryophyte diversity was observed (Green et al. 2011), and only some species, as the moss *Bryum argenteum*, can span many environments (Longton 1981; see Chap. 18 by Green and Proctor). Thus, climate change will likely cause a shift of biocrust species during the next decades. Increased land use, which is under way, has been well described to cause major damage in biocrusts, as a reduction in biomass and changes in biocrust community composition (Daryanto et al. 2013; Root and McCune 2012). This may not only affect biocrusts themselves but also vascular plants, as the species composition of biocrusts can affect plant germination and growth (Godinez-Alvarez et al. 2012; Zhang and Nie 2011), as well as nutrient fluxes from biocrusts to vascular plants (Green et al. 2008; Zhuang et al. 2014; see Chap. 19 by Zhang et al.). In addition, increased land use change is also expected to affect global nutrient cycling and dust emissions (Field et al. 2010; see Chap. 16 by Belnap and Büdel). Recent advances in the rehabilitation of biocrusts, utilizing cultivation of biocrust organisms and inoculation of desert soils (Wu et al. 2013; Doherty et al. 2015; see Chap. 24 by Zhao et al.), can help to mitigate the most extreme effects of increased land use and may confine desertification.

25.3 Future Research Challenges

Despite the large increase in biocrust research, there are still major knowledge gaps which need to be tackled in the decades to come. Considering biocrust diversity studies, there are many regions where few, if any, studies have been conducted, such as South America, northern Africa, the Arabian Peninsula, and Central Asian regions, yet large expanses of biocrusts are expected to be found. Here, a global universal mapping methodology, such as using newly established remote sensing technologies, could be extremely helpful to identify particularly promising regions (see Chap. 12 by Weber and Hill). While the general composition, structure, and distribution patterns of biocrusts and also hypolithic crusts has been characterized quite well during the last years in a few deserts (see Chaps. 9, 10, and 11 by Colesie et al., Bowker et al., and Pointing, respectively), we know almost nothing about their effects on weathering and geochemical alteration of the substrate, which up to now has only rarely been studied (see Chap. 13 by Garcia-Pichel et al.). Regarding molecular identification techniques, there is the challenge of linking the characterized genetic entities (operational taxonomic units) with morphologically identified biocrust organisms. This step is essential to identify the effects of environmental factors upon their function and thus to understand the overall ecological roles of biocrusts.

Although there has been a large body of research examining the role of biocrusts in water cycling, nutrient (especially C and N) fixation, and release patterns, scientific knowledge is still far from closing the overall cycles. Whereas it is clear that biocrusts play a major role in dryland hydrology, overall mechanisms functioning across scales have not been identified and described yet (see Chap. 17 by Chamizo et al.). Recent long-term CO₂ gas exchange measurements of biocrusted soils have largely measured small, but overall negative, values (see

Chap. 15 by Sancho et al.). It is not known what specific soil factors are offsetting the photosynthetic gains from biocrusts, or the role of abiotic versus biotic losses. In addition, as an ecosystem cannot maintain a negative balance for very long, yet these exist and organisms are growing, our understanding of the C cycle in these ecosystems is clearly not complete. Studies on N cycling turned out to be particularly complex, as a variety of different compounds are formed and may be released both into the surrounding substrate and into the atmosphere during metabolic processes (see Chap. 14 by Barger et al.). In order to obtain a closed cycle, all the different sources, cycling processes, and sinks need to be assessed by means of suitable methods, some of which will require new analytical methods. The role of phosphorus as a potentially essential element and its cycling within biocrusts remains largely unstudied up to now.

We also need a greater understanding of how to reduce impacts to biocrusts when planning surface-disturbing activities (e.g., grazing, driving vehicles off-road), whether it be by altering their timing, intensity, and/or location or avoiding the disturbance. There has been a great deal of interest in whether biocrusts can be used to increase the fertility of agricultural soils and thus the growth and nutritional content of crops. This is an area that has received almost no attention, but could provide some intriguing results.

In order to fill existing research gaps, also novel scientific approaches are needed. We expect that global scale research networks could be extremely helpful in a range of different applications: They could be used to conduct the same experimental approaches across a range of conditions, so we may better understand the underlying mechanisms. Global networks could also be used for long-term monitoring of biocrust dynamics, for which there is almost no data. Furthermore, such networks may be used to conduct meta-analyses of already existing data.

Finally, the experimental results obtained during multiple local studies need to be integrated and extrapolated to ecosystem and global scales in order to identify the overall role of biocrusts in the Earth system through time.

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