Desert Crusts

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Abstract A significant fraction of the world's land surface is covered by arid and semiarid land. Desert crusts, microbial communities formed from cyanobacteria, algae, fungi, and bacteria, are important ecosystems that stabilize and enrich desert soils. Cyanobacteria are key players, often providing physical cohesion, primary production, and life-supporting nitrogen fixation. Here the overall structure of crusts, the important microbial partners, and the microbial diversity that is present are discussed. Some of the special features of these communities and the individual organisms are their tolerances to desiccation and to high levels of UV radiation. Mechanisms to survive long periods of severe dehydration include the synthesis of large amounts of trehalose and the excretion of copious quantities of unique exopolysaccharides. Adaptations that allow survival in spite of high levels of UV radiation include mobility and the synthesis of natural sunscreens, scytonemin, and mycosporines. Much remains to be learned about these ubiquitous microbial consortia, whose functionalities and interrelationships are beginning to be probed at the molecular level. This chapter reviews the general microbial aspects of desert crusts and gives a special emphasis to the involvement of cyanobacteria.

Introduction

Cyanobacteria have had a major influence on the earth for at least the last 2.95 billion years (Planavsky et al. 2014). These organisms are of great ecological importance as they have expanded over time to colonize, in either free-living or symbiotic forms, most of the ecological niches available on the earth (Bolhuis et al. 2014; Makhalanyane et al. 2015a; Moreira et al. 2013; Sukenik et al. 2015). One ecological niche of significant interest is biological soil crusts, in particular desert crusts, found in arid and hyperarid regions. Dry lands make up 41.3 % of the land surface

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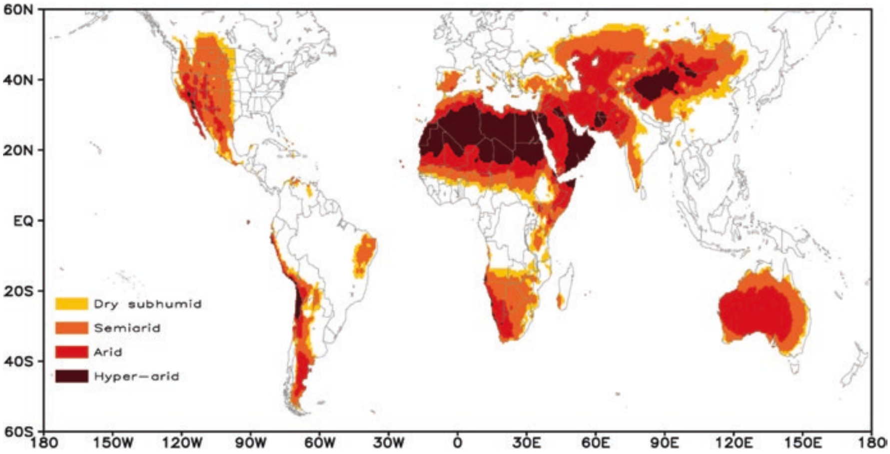

Fig. 1 Global distribution of drylands. Reproduced from Feng and Fu (2013) under the Creative Commons license

with semidesert (arid 10.6 %) and desert (hyperarid 6.6 %) being a significant fraction of that (Fig. 1). Arid and semiarid regions are expanding on an appreciable scale due to land degradation, deterioration in water supplies, and climate changes. Concerns about the lands worldwide that are increasingly threatened with deterioration led the United Nations General Assembly to declare the United Nations Decade for Deserts and the Fight Against Desertification (January 2010 to December 2020) in an effort to promote action to protect the world's dry lands and to prevent further desertification (United Nations 2016).

Biological desert crusts, an assemblage of cyanobacteria, fungi, bacteria, and green algae, cover much of the semiarid and arid regions (Fig. 2). The communities found in these crusts, one type of biological soil crust, are mixtures of algae, cyanobacteria, bacteria, fungi, lichens, and mosses whose exact composition varies with soil type, age, and local environmental factors such as shading, temperatures, rainfall, wind, etc. (Janatkova et al. 2013; Johansen 1993; Li et al. 2013, 2014; Pointing and Belnap 2012; Makhalanyane et al. 2015b). These consortia carry out a variety of ecological functions related to water retention and soil conditioning; fixing nitrogen and carbon dioxide and releasing mineral-bound nutrients such as phosphate, permitting eventually the proliferation of higher life forms (Belnap 2003). Not only is there academic interest in studying desert crust development and the crust-associated communities, but, as the world experiences increased anthropogenic desertification, there is a practical need to understand how to recolonize these lands (Wang et al. 2009; Xu et al. 2013).

The ecological niche where these organisms are found is characterized by high levels of radiation due to incoming solar and reflected light. Soil surface temperatures vary widely, from –20 °C to over 70 °C depending upon time of day and season. Precipitation is sparse and infrequent, and the water content of these crusts can drop to 5 % or less (dry weight basis). Therefore, the key to survival for desert crust

Fig. 2 Mature desert crust from the Colorado Plateau

organisms is their ability to cope with extreme dehydration. Although a great deal is known about desert crusts at the macroscopic level (Wu et al. 2013a; Rosentreter et al. 2007; Makhalanyane et al. 2015b), relatively little information is available at the molecular level. Photoautotrophic organisms are of particular interest and importance in terms of overall desert crust ecology.

While the vast majority of desert crust studies have examined "hot" deserts, as well as what have been called "cold" deserts, such as parts of the Colorado Plateau, very few studies have been done on truly cold deserts, the dry valleys of Antarctica. Initial reports of nearly "sterile" environments were in fact due to the inability to culture any microorganisms from these soils. However, when examined by modern molecular methods, a wide variety of taxonomically unique taxa have been uncovered, suggesting a rich and diverse community despite the inhospitable conditions and extremely oligotrophic soils (Cary et al. 2010). The recent application of GeoChip technology, a technique that would also be extremely useful in the study of more "normal" desert soils, has revealed a diverse functional ecology with genes for various major metabolic pathways, autotrophic and heterotrophic carbon metabolism and diazotrophy (Chan et al. 2012, 2013). Moreover, an examination of the different niche environments available, open soil, hypolithic (growth underneath translucent rocks, i.e., quartz), chasmoendolithic (growth in cracks or fissures), and cryptoendolithic (growth in pores), revealed significant differences in the functional ecologies of the different communities (Chan et al. 2012, 2013). While this review, given the focus of this volume, will highlight the roles played by cyanobacteria, general concepts and advances in knowledge about desert crusts in general and about desiccation resistance will also be covered in order to provide the appropriate context.

A variety of cyanobacteria have been identified worldwide in desert crusts, both nitrogen fixing and nonnitrogen fixing. Nitrogen-fixing cyanobacteria are of specific interest for their key role in supplying fixed nitrogen to the desert crust community (Yeager et al. 2007, 2012). Some members have been studied for their ability to carry out hydrotaxis (Pringault and Garcia-Pichel 2004), suggesting that they possess an interesting cellular system for transducing signals related to water availability. Their response to dehydration/rehydration has been studied (Rajeev et al. 2013), and the genome of a ubiquitous member of this family found in desert crusts worldwide has become available (Starkenburg et al. 2011).

General Considerations

Desert crusts, complex microbial communities commonly found in hot and cold desert environments, have long been attributed with a variety of ecological and environmental roles. In particular, a number of early studies credited them with reducing erosion (Johansen 1993). In addition, they undoubtedly act to increase nitrogen inputs, estimated to be of the order of 25 kg N ha^{-1} y^{-1}, through active nitrogen fixation by cyanobacteria as well as heterotrophic bacteria, and act to increase the organic carbon content of the soils they cover, with rates of between 6 and 23 kg C ha^{-1} y^{-1} being estimated for semiarid areas of Southwestern USA. In essence, one function of these communities is to "terraform" and condition the soil for subsequent colonization by other ecosystem communities. Given the large surface areas of the world that are implicated, cryptogamic crusts make a significant overall contribution to global nutrient fluxes, fixing large amounts of atmospheric CO_2 (>2.6 pg C y^{-1}) and N_2 (>49 Tg y^{-1}) (Elbert et al. 2012).

Fixed nitrogen input into the soil through the action of cyanobacteria and heterotrophic bacteria may be of particular importance. Although highly variable on a daily basis, since no fixation apparently occurs in the dry state, or when temperatures are either too high or low, N_2 fixation by cyanobacterial-dominated crusts of the Colorado Plateau, especially those containing the lichen *Collema* (photobiont *Nostoc* sp.), has been estimated to input fixed nitrogen at rates of 9–13 kg ha^{-1} $year^{-1}$ (Belnap 2002). The desert soil crust N cycle appears to lack appreciable anammox or anaerobic denitrification activities, thus suggesting that the major part of the fixed N might find its way into the surrounding environment (Strauss et al. 2012). One study found that mature crusts were much more effective at N_2 fixation (tenfold) than poorly developed crusts and that in all crusts examined *nifH* sequences were mainly (78–100 %) cyanobacterial in origin (Yeager et al. 2004). In fact, rates of both carbon and nitrogen fixation are much higher in late successional crusts than in early ones, strongly suggesting that disturbance of mature crusts, which returns them to early successional stages, has very large impacts (reduction) on primary productivity and nitrogen fixation (Housman et al. 2006).

Cyanobacteria are considered to be the primary producers in most desert crusts, and recent evidence points to the possibility of a significant amount of excretion of fixed carbon compounds with subsequent metabolite "sharing" and cross feeding (Baran et al. 2015). This study used *Microcoleus vaginatus*, a cyanobacterium dominating early crusts (see below), and showed that a broad range of exometabolites were excreted. Additionally, when paired with likely heterotrophic bacterial partners, extensive cross feeding was demonstrated. This suggests that desert crust microbial communities, in addition to being physically associated, may be tied together metabolically. Thus, during early crust formation, when the nonnitrogen fixer *Microcoleus vaginatus* dominates, metabolite excretion may support the heterotrophic bacteria responsible for the fixed nitrogen input into this ecosystem (Pepe-Ranney et al. 2016).

Although not specifically studied, it is very likely that different organisms in these communities solubilize phosphate and trace minerals, thus enriching the soil for growth of the crust and for potential future successional communities. In addition, the filamentous bacteria and fungi that are present undoubtedly contribute to soil stabilization through various mechanisms (Belnap and Gardner 1993; Pointing and Belnap 2012; Ogut et al. 2010; Tao et al. 2008; Pérez et al. 2007; de Oliveira Mendes et al. 2014).

Diversity

General Considerations

As in all of microbial ecology, one debate concerning desert crust diversity has centered around biogeographic issues. Is distribution affected by allopatric speciation or is as suggested by Beijerinck, "everything is everywhere but it is the environment that selects" (O'Malley 2008). Although most past studies have been at the local scale, some recent studies have begun to examine this issue at the continental or even worldwide scale.

As yet, there is no real consensus on this issue. One continental-wide (North America) study of biological soil crusts showed that, at least on the phylum level, no evident biogeographic pattern could be observed (Garcia-Pichel et al. 2013). On the other hand, when a single organism important in desert crust formation, *Microcoleus vaginatus*, was examined on a worldwide scale, appreciable diversity was found and apparent differences in continental distribution was evident (Dvořák et al. 2012). Similarly, another study examined this issue by analyzing the phylogenetics of the ubiquitous desert cyanobacterium *Chroococcidiopsis* using massively parallel pyrosequencing of samples from a variety of desert locations (Bahl et al. 2011). Evidence was presented for divergence in these samples dating to around 2.5 Ga, or at least as far back as the onset of global aridity (~1.8 Ga) at which time two hot desert clades and one cold desert clade were established. The fact that such phylogenies can be established strongly suggests that, in general, there is a lack of dispersal between different habitats, i.e., hot desert into cold, or even within climatically similar deserts. Obviously, these local communities will be structured and shaped by a variety of local variations in factors that are significant in promoting growth; pH, temperature, water activity, fixed nitrogen, minerals, and salinity (Angel et al. 2010; Büdel et al. 2009; Demergasso et al. 2004; Fierer et al. 2012a; Garcia-Pichel et al. 2013; Hagemann et al. 2015; Li et al. 2013, 2014; Schmidt et al. 2012; Stomeo et al. 2012). There is even evidence for local biohistory influencing crust outcome (Lan et al. 2015; Steven et al. 2015).

Green Algae

Unicellular green algae have also been found to be components of desert crusts from different parts of the world. Since they are relatively indistinguishable morphologically, the true diversity of this class of organisms to be found in desert crusts was not appreciated until molecular techniques were used. However, more recent studies have shown that at least five different green algal classes are implicated in different desert crust communities which have also been shown to contain many previously undescribed taxa (Lewis and Flechtner 2002; Cardon et al. 2008). Thus, adaptation to this environment appears to have caused a large radiation in diversity, not only genetic but also in terms of physiological adaptation, for example, different photophysiologies and variations in desiccation tolerance. This translates into very significant DNA sequence variations, especially in comparison with the database sequences derived from green algae isolated from aquatic environments (Lewis and Lewis 2005).

Thus, phylogenetic studies demonstrate that desert lineages are distinct from aquatic ones and give evidence for at least 14 separate transitions from aquatic to terrestrial life. Survival under these conditions requires adaptations not normally seen in the aquatic green algae. For example, *Chlorella ohadii*, newly isolated from desert sand crusts, shows remarkable insensitivity to high light intensities, with photosynthetic oxygen evolution unaffected by exposure to 3500 μmol photons m^{-2} s^{-1}

(Treves et al. 2013). On the other hand, at the same time, there was a significant drop (90 %) in variable fluorescence (F_v), strongly suggesting the intervention of a mechanism to dissipate excess light energy. Similar observations have been made with the cyanobacterium *Microcoleus* (see below) (Ohad et al. 2010).

Bacteria

The bacterial population of cryptogamic crusts of the Colorado Plateau (Southwestern USA) have been reported to be dominated by *Actinobacteria* (Garcia-Pichel et al. 2003), whereas this phylum appears to be less abundant in at least some other hot deserts (Abed et al. 2010). A metagenomic analysis has shown that in general both hot and cold desert microbiomes have a significantly different phylogenetic composition than microbiomes from other soil types. Some of this of course might be due to differences in soil pH, previously shown to be a very important factor controlling microbial soil diversity (Fierer and Jackson 2006).

On the other hand, in specific cases, other factors as well might control species composition as seen by an examination of gypsum-containing soils which were shown to have higher amounts of *Actinobacteria* and *Proteobacteria* when compared with shale and sandstone soils, which, on the other hand, had greater amounts of *Cyanobacteria* (Steven et al. 2013). Another study carrying out a PCR-based survey of environmental 16S rRNA genes of the Sonoran Desert found, in order of their importance, members of the *Cyanobacteria*, *Proteobacteria*, *Actinobacteria*, and *Acidobacteria*, with minor amounts of *Bacteroidetes*, *Chloroflexi*, and *Gemmatimonadetes* (Nagy et al. 2005). A very similar distribution was found for desert crusts of the Colorado Plateau where *Microcoleus vaginatus* and *M. steenstrupi* were dominant among the phototrophs, and *Actinobacteria* accounted for 12 %, β-*Proteobacteria* and *Bacteroidetes* each accounted for 10 % of the 16S rRNA recovered (Gundlapally and Garcia-Pichel 2006). Although little studied, it is not surprising that bacterial populations have been found to be stratified over millimeter scales in these desert crusts (Garcia-Pichel et al. 2003).

A recent study using a combination of different pretreatments and isolation strategies showed that it was possible to recover a large number of bacterial isolates from early successional stage desert crust, 105 phylotypes, a significant fraction of the diversity detected by metagenomics (da Rocha et al. 2015). In fact, the distribution of isolates, *Actinomycetes* > *Proteobacteria* > *Firmicutes* > *Bacteroidetes*, roughly mirrors what has been previously found using culture-independent methods. This work sets the stage for detailed physiological analysis of these isolates, important in the desert crust community structure and relatively distant from known and well-studied bacteria.

Nevertheless, a variety of studies have shown that the desert microbiomes have relatively sparse phylogenetic and functional diversity as compared to microbiomes from other environments and, compared to them, are enriched in genes coding for dormancy and osmoregulation while having genes associated with nutrient cycling and catabolism of complex carbon compounds at lower relative abundance (Fierer et al. 2012b). The same study noted that desert soils are also much less rich in genes for antibiotic biosynthesis, suggesting that competitive interactions are of less importance in this environment. Nevertheless, a variety of studies have shown that desert soils typically can be found to contain several different genera, *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria*, with many of the isolates often being novel species (Makhalanyane et al. 2015b).

Fungi

Fungi in desert crusts have been relatively little studied and mostly through cultivation studies, which nevertheless have shown an appreciable degree of diversity. Of course a large number of fungi, principally *Ascomycetes* and, less frequently, *Basidiomycetes*, are found as the mycobiont partners in desert crust lichens. Aside from these, many of the free-living fungi appear to belong to a group of highly pigmented "black," or dematiaceous fungi, with rigid walls and high contents of melanin, carotenoids, and mycosporines, making them highly resistant to environmental stresses (Sterflinger et al. 2012). Among these are often found fungi like *Cladosporium*, *Stachybotrys*, and *Pleospora* and sometimes *Aspergillus* and *Eurotium.* As might be imagined, thermophilic and thermotolerant types can be readily isolated from hot desert crust samples. Fungi are thought to be ecologically important in the desert crust ecosystems potentially contributing to UV resistance, soil stabilization, and solubilization of phosphorous and minerals (Makhalanyane et al. 2015). In this regard, the role and importance of the fungal mycobiont partner in lichens is evident, but the nature and significance of the contribution of free-living microcolonial "black" fungi remains to be determined (Sterflinger et al. 2012). A recent molecular study using rRNA gene fingerprinting demonstrated that desert crusts of the Southwestern USA contain a considerable amount of diversity with the majority of the fungi belonging to either *Ascomycota* or *Pleosporales* (Bates et al. 2012). In addition, evidence was obtained for geographic specificity of assemblages.

Archaea

Relatively little is known about archaeal populations of desert crusts. At least one metagenomics survey has suggested that they are present as a relatively minor fraction, ~6 %, in hot deserts, which nevertheless represents a greater abundance than found in other soil types examined (Fierer and Jackson 2006). The principle group detected belonged within the relatively recently described *Thaumarchaeota*, well known for their involvement in the nitrogen cycle in many habitats.

Cyanobacteria

General Distribution of Cyanobacteria in Desert Crusts

Cyanobacteria have long been recognized as essential components of desert crusts, and early studies demonstrated that these crusts were dominated by filamentous cyanobacteria, with *Microcoleus*, *Phormidium*, *Plectonema*, *Schizothrix*, *Nostoc*, *Tolypothrix*, and *Scytonema* being described as common genera found worldwide in hot and cold deserts (Johansen 1993). As noted above for bacteria and in common with many other biofilms, cyanobacteria have been found to be stratified with desert crusts, with maximal photosynthetic activity being observed one millimeter below the surface (Raanan et al. 2016a). The dominance of cyanobacteria in this environment implies that they play the role of keystone species, probably through their abilities to appropriately modify the physical matrix, to provide fixed carbon as primary producers and, in most cases, to provide fixed nitrogen.

Although it has been long supposed that one of the significant roles played by cyanobacteria was to establish and maintain crust integrity, in realty there has been little direct proof for this hypothesis. One relatively recent study has now shown this to be the case by testing the ability of four different filamentous cyanobacteria, previous isolated from desert crusts, *Microcoleus vaginatus*, *Phormidium tenue*, *Scytonema javanicum*, and *Nostoc* sp., to consolidate sand (Hu et al. 2002). Erosion was then studied using a wind tunnel, permitting the researchers to test the effects of a number of variables.

One study, by combining phylogenetic and morphological analysis, was able to define six distinct clusters of cyanobacteria observed in four biological crust types from the Colorado Plateau (Garcia-Pichel et al. 2001). One of these did not appear to have a cultivated representative strain with which to compare, and another, although "*Phormidium*-like," contained only sequences from desert crust cyanobacteria and was quite distant from *Phormidium* species. A new name, *Xeronema*, was proposed for this cluster. However, this seems like a poor choice since it is already the name of a genus of flowering plants. Nonetheless, DGGE analysis suggests that members of this group are ubiquitous and therefore certainly deserving of further study.

Arid grasslands in some areas of the Southwestern USA have been shown to contain three types of crust even though they are growing on the same red sandstone soil substratum: cyanobacterial crust, lichen-dominated crust, and moss-dominated crust (Redfield et al. 2002). The cyanobacterial diversity in the three types of crusts was analyzed using terminal restriction fragment length polymorphism (TRF or T-RFLP) and 16S rDNA sequence analysis. The results showed that the cyanobacterial crust, while containing other genera, was dominated by strains of *Microcoleus vaginatus*, which also the most abundant cyanobacterial species in the moss crust. On the other hand, this organism was only a minor component of lichen-based crusts where strains related to *Chroococcidiopsis* and *Oscillatoria* were in the majority.

Similarly, a study of biological soil crusts in the Gurbantunggut Desert, China, showed that diverse morphotypes and phylotypes can exist in the same desert depending upon local conditions: position on a sand dune, type of soil texture, and available phosphate (Zhang et al. 2011). In most cases, filamentous cyanobacteria predominated in this study. It was study found that the upper layers of the crusts were dominated by *Microcoleus vaginatus*, with appreciable amounts of *Oscillatoria aeruginosa*, *Synechococcus parvus*, *Oscillatoria tenuis*, *Chlorococcum humicola*, *Navicula* sp., and *Hantzschia amphioxys*. At least in these samples, morphotype diversity was largely influenced by phosphate concentrations.

Hypolithic and Endolithic Cyanobacteria

Cyanobacteria are in the majority in hypolithic communities observed worldwide, representing 47–96 % of the bacterial phylotypes recovered (Caruso et al. 2011). Rocks supporting hypolithic growth include quartz, prehnite, and agate. There is some evidence that hypoliths from warm deserts are mainly coccoid *Pleurocapsales* of the genus *Chroococcidiopsis*, whereas the hypoliths from extreme cold and polar deserts are more likely to be filamentous oscillatorian morphotypes (Chan et al. 2012). The contribution of cyanobacteria to the overall ecology of hypolithic communities is probably key due to their autotrophic carbon fixation. In many hyperarid desert hypolithic communities, cyanobacteria may well be the only primary producers.

A study of hypoliths found in deserts of Northern Australia found that up to one-third of the OTUs recovered grouped within *Chroococcidiopsis* and that photosynthetic activity required a minimum soil moisture content of 15 % (Tracy et al. 2010). As well, the most common cyanobacterial 16S rRNA sequences recovered from hypoliths from the hyperarid Atacama Desert were related to *Chroococcidiopsis* (Warren-Rhodes et al. 2006). Not surprisingly, this study found that abundance, diversity, and the residence time of organic carbon decreased significantly with decreasing annual rainfall. However, even under extremely low rainfall conditions (<1 mm/year), hypolithic communities can be found if local conditions, such as fog along the coast, permit (Azúa-Bustos et al. 2011). Even under these conditions, DNA analysis showed that strains related to *Chroococcidiopsis* appeared to be in the majority with some strains related to other well-known desert inhabitants, *Microcoleus*, *Nostoc*, and *Scytonema*, also being recovered.

A more recent, more complete study of organisms of this hyperarid region, part of a continuing effort where more than 480 cyanobacterial cultures have been isolated, found a variety of species richness and distribution patterns depending upon sampling site, with it being impossible to culture any cyanobacteria form the majority of the sites (88) examined (Patzelt et al. 2014). Nevertheless, molecular analysis demonstrated a surprising diversity with a variety of filamentous forms belonging to Nostocophycideae, Synechococcophycideae, and Oscillatoriophycideae, along with the coccoid *Chroococcidiopsis.*

Endolithic environments, where microorganisms can grow inside translucent rocks, such as halites, gypsum, and carbonates, are very related microhabitats. These minerals might help trap some moisture as well as provide some light at short distances (~mm) beneath the surface while at the same time largely blocking UV radiation and greatly attenuating the intense solar visible light. A variety of bacteria and a unique cyanobacterium, related to *Halothece*, have been recovered from halite samples (Robinson et al. 2015). Cyanobacteria associated with both halites and gypsum have been reported to make large quantities of carotenoids and scytonemin, a UV-protectant compound (see below). The known hypolith, *Chroococcidiopsis*, has been found to be an active colonizer of gypsum (Wierzchos et al. 2015).

Desiccation Tolerance

Obviously an important attribute of many desert crust microorganisms is the ability to survive extended periods of desiccation. Desiccation tolerance, also referred to as anhydrobiosis, is as yet poorly understood (Potts 2001). It is likely that a number of different strategies and mechanisms are involved, from means for maintaining protein stability in the absence of structurally important water of hydration, to repair processes involved in responses to UV damage and reactive oxygen species (ROS) (Billi and Potts 2000, 2002).

For a thorough discussion of the relevant biophysical properties of water and the biological structural and functional considerations related to the consequences of its loss or reduction through various drying processes, see the discussion by Potts (1994). Different cellular components and structures are either directly or indirectly sensitive to dehydration. For one thing, membrane integrity and fluidity are affected since membranes are held together by the surface tension of water and drying can affect the membrane transition temperature (T_m) with potentially disastrous and lethal effects on permeability. How desiccation-tolerant microbes escape this fate is not known, perhaps they have a different polar/nonpolar nature of their membranes. Likewise, proteins depend upon bound water to maintain their three-dimensional structure, and removal of intracellular water below the levels required to maintain a surface layer covering cellular proteins can cause irreversible denaturation of key proteins. On the other hand, cellular DNA is probably indirectly affected with the impossibility of carrying out repair during the desiccated dormant state.

The water content of a "normal" microbial cell is around 70 %, whereas desiccated cells can reach 3–10 % by weight (Potts 1994). Coping with such a loss of water and surviving intact pose special problems. For example, the driest state, 3 %, is well below the amount of water required to fully cloak cellular proteins in a monolayer of water, 30–40 %. It seems that one mechanism of surmounting this problem is the synthesis of large amounts of sucrose or trehalose, and some desert crust organisms can accumulate large amounts of these compounds, up to 20 % by weight. However, it would seem that, although these same compounds are used by some organisms when challenged osmotically, through what is called "preferential exclusion," a different mechanism applies when these compounds are made as protectants against desiccation.

In fact, a wide variety of compatible solutes are made by a range of microbes, and these compounds have been suggested to serve a variety of purposes, from desiccation tolerance and osmoregulation to reserves of carbon, nitrogen, and energy (Welsh 2000). "Preferential exclusion" by so-called compatible solutes, sugars, amino acids, polyols, etc., act to stabilize proteins by forcing the remaining water to form shells around the proteins, hydrating them. However, this cannot be the mechanism of action of sucrose or trehalose in anhydrobiosis since, as noted above, desiccated cells do not even contain enough water to fully hydrate their complement of proteins. Instead, these polyhydroxy compounds are thought to act through a replacement mechanisms, serving to "hydrate" cellular proteins through the formation of the requisite hydrogen bonds. In fact, by the same mechanism, trehalose could stabilize the cellular membrane if it was present on both sides. Finally, these compounds could act in another manner, through the formation of aqueous glasses, a property of some solutes at low enough water activity or low enough temperature, thus avoiding the complete dehydration of the microbial cell at temperatures below the "glass" melting point, 90 °C for trehalose/water (Potts 1994, 2001).

Similarly, some desiccation-resistant cyanobacteria produce large amounts of extracellular polysaccharide which presumably offers resistance. For example, up to 60 % of the dry weight of a colony of *Nostoc commune* can be formed of the glycan matrix, a novel polysaccharide composed of a 1-4-linked xylogalactoglucan backbone decorated with D-ribofuranose and 3-*O*-[(*R*)-1-carboxyethyl]-D-glucuronic acid (nosturonic acid) groups (Helm et al. 2000). The unusual properties of this compound and its abundance may be put to use, either through the formation of a biological glass, or, otherwise, to protect the cells from desiccation.

Relatively little is known about how the special challenges faced by photosynthetic organisms are met. One of the challenges for photosynthetic microorganisms like cyanobacteria is how to survive in a desiccated state where metabolism is necessarily dormant, but the photosynthetic pigments, chlorophyll, and phycobiliproteins are still potentially capable of absorbing photons and generating high-energy states whose dissipation can be quite deleterious. One response is to synthesize chromophores which can safely absorb potentially damaging light (see below). However, some organisms, like *Leptolyngbya*, lack this capacity and hence must rely on another strategy for survival.

One study has suggested that this organism is spared from excessive photochemical reactions in the dry state by small changes in the thylakoid membranes which appear sufficient to totally quench the absorbed light energy (Bar-Eyal et al. 2015). Another study showed that over 50 % of photosystem II (PSII) activity could be recovered within 5 min of rehydration of a desert crust sample that had been kept in the dry state for over 1 month (Harel et al. 2004). As well, this study suggested that one survival mechanism of the cyanobacteria within the crust is the unusual ability to increase the rate of PSII repair with light intensity and time of exposure, resulting in only very low levels of photoinhibition under high light intensity.

A study of the tolerance of desert green algae to desiccation examined the recovery of the quantum yield of photosynthesis (F_v/F_m) upon rehydration and found that desert algae showed remarkably different recovery abilities than their aquatic relatives. Cells incubated over extended periods of time in darkness after desiccation were more likely to recover than cells which had been illuminated during this time period (Gray et al. 2007). As with the isolated green algae, reactivation of photosystem II in lichen soil crusts exposed to repeated dehydration/rehydration cycles occurs over a remarkably short time period, several hours (Wu et al. 2013b). An early study examined the responses of several different *Nostoc*, *N. flagelliforme*, *N. commune*, and *Nostoc* sp., rewetting after 2 years of dryness (Scherer et al. 1984). Rapid rewetting was noted with respiration recovering the fastest (30 min), followed by photosynthesis (~7 h), and, much later (~140 h), nitrogen fixation.

Dynamics of Resuscitation

Of course, there is a great deal of interest in understanding how the individual organisms and entire community structure responds to cycles of desiccation and rehydration. Nevertheless, this is a difficult study to make in any great detail and was not really amenable to examination until the advent of modern molecular tools. One recent study followed the dynamic changes in microbial community structure following rewetting by analyzing rRNA using a stable isotope approach and H_2O^{18} (Angel and Conrad 2013). Cyanobacteria were found to be the dominant group two weeks after rehydration and incubation in the light.

In order to attempt to mimic natural cycles, but under controlled conditions, another study employed a chamber which allowed desiccation to take place at controllable rates (Raanan et al. 2016b). A strain of *Leptolyngbya ohadii* isolated from the desert crust obtained from the Negev desert was used and examined under conditions, light cycle and drying rate, that corresponded to local meteorological data. Just as observed with the whole crust, recovery was strongly dependent upon the previous rate of dehydration, with slower rates favoring recovery (Raanan et al. 2016b). Insight into the molecular programming leading to responses to desiccation and rehydration by *Microcoleus vaginatus* were gained by carrying out an in situ whole-genome transcriptional time course (Rajeev et al. 2013). This analysis shows that the onset of desiccation triggers the induction of genes for C and N storage and response to osmotic, oxidative, and photooxidative stresses. Hydration led to the immediate induction of genes for DNA repair and regulatory processes, with photosynthesis being reestablished within one hour of wetting.

Production of Exopolysaccharides

In general, cyanobacteria as a group have the capacity to synthesize and excrete a wide variety of extracellular polysaccharides (De Philippis and Vincenzini 1998; Pereira et al. 2009; Rossi and De Philippis 2015). Most polysaccharides synthesized (80 %) contain six to ten different monosaccharides, about 90 % have one or more uronic acids, and as well most contain noncarbohydrate groups such as sulfate, peptides, acetyl, or pyruvoyl groups (De Philippis et al. 2001). Although this has been little exploited, many have interesting properties that suggest biotechnological uses as emulsifying or thickening agents, for cation absorption, etc.

For terrestrial cyanobacteria, some of which are found in desert crusts, exopolysaccharides have been proposed to serve a variety of functions: the stabilization of the physical matrix upon which they are growing, the sequestration of metal cations, as a matrix to absorb excreted UV-protectant compounds, protection against desiccation, and, perhaps, the basis for gliding motility. In fact, the rapid rehydration of *Nostoc* colonies upon rewetting to give macroscopic gelatinous masses leads to the naming of this genus in the Middle Ages, before the invention of the microscope (Potts 1997)!

Besides stabilizing the physical structure of the growth matrix and providing a store of fixed carbon to support growth of heterotrophs (Mager and Thomas 2011), cyanobacterial exopolysaccharides improve its hydraulic conductivity (Rossi et al. 2012). The cohesive ability necessary for stabilization of fine sand particles seems to be a function of the specific composition of the polysaccharide (Hu et al. 2003). Simple amendment of desert soil with cyanobacterial polysaccharide appears to enhance shrub growth (Xu et al. 2013). Interestingly, given the rampant desertification that is underway in many parts of the world, cyanobacteria and their excreted polysaccharides may play an important role in restoration efforts through the use of induced biological crusts. Recent research indicates that these cyanobacterial compounds impart many beneficial properties in terms of stabilization and improved hydrological behavior (Chen et al. 2014; Colica et al. 2014, 2015).

Protection Against High Levels of UV Radiation

Desert crust cyanobacteria might be thought to have high levels of resistance to radiation. Even the aquatic *Anabaena* sp. PCC7120 has been found to be relatively resistant to gamma radiation, with 50 % survival at a dose of 5.4 kGy (Singh et al. 2013). The same study also found that this strain showed desiccation tolerance with 50 % survival after 6 days. Another more pertinent study has shown that cyanobacteria of relevance to desert crusts, *Microcoleus vaginatus*, *Nostoc* sp., and *Scytonema javanicum*, are relatively resistant to UV-B radiation (Chen et al. 2013).

Of course, desert crust microorganisms are by nature exposed to relatively high levels of UV radiation, and cyanobacteria from this environment have been shown to have a number of mechanisms for evading or combating UV exposure: avoidance, defense, and repair (Ehling-Schulz and Scherer 1999). Most filamentous cyanobacteria possess gliding motility and therefore in principle can escape too high light intensities through downward migration. In this regard, it is interesting to note that UV-B has been shown to induce migration of the marine cyanobacterium *Microcoleus chthonoplastes* in a microbial mat, implying that it contains an as yet to be described sensor capable of perceiving light of these wavelengths (Bebout and Garcia-Pichel 1995). In addition, UV damage is avoided in at least one cyanobacterium through the replacement of the normal D1 protein, integral part of the PSII reaction center, with a UV-B inducible isozyme (Campbell et al. 1998). Additionally, changes in PSII may enable some desert crust cyanobacteria to survive high light intensities in general (Ohad et al. 2010).

Many desert crust cyanobacteria have been shown to produce UV-absorbing compounds, natural "sunscreens," as protection against UV-induced photodamage.

The classic example is scytonemin, a unique UV-A absorbing pigment, which has a dimeric indole-phenolic structure and is produced only by terrestrial cyanobacteria (Garcia-Pichel and Castenholz 1991; Gao and Garcia-Pichel 2011; Proteau et al. 1993). This specialized pigment is made by a unique, specialized biosynthetic pathway, one known to be possessed by a number of cyanobacteria (Sorrels et al. 2009).

In addition to scytonemin, many cyanobacteria, as well as other lower organisms, are capable of synthesizing water-soluble mycosporine amino acids (MAAs), amino acids, and amino alcohols linked to a cyclohexanone chromophore, which absorbs between 310 and 360 nm. Indeed, studies have shown that MAAs protect cyanobacteria against harmful UV radiation (Ehling-Schulz et al. 1997). One study, using *Nostoc commune* isolated from desert crust, showed that exposure to UV-A and UV-B increased the synthesis of scytonemin and a UV-absorbing mycosporine along with extracellular polysaccharide (Ehling-Schulz et al. 1997). There were differences in induction patterns depending upon whether UV-B or UV-A was supplied, suggesting that synthesis is regulated by different UV photoreceptors.

Recently, microarrays were used to examine the global expression response of *Nostoc punctiforme* to UV-A exposure (Soule et al. 2013). Roughly 10 % of the genes (573/6903) were affected, with upregulation of 473 and downregulation of 100. Notably the downregulated genes included those for photosynthetic pigment biosynthesis, while the upregulated genes included genes encoding scytonemin biosynthesis as well as antioxidant enzymes (catalase, superoxide dismutase, etc.). Strikingly, almost half the upregulated genes could not be assigned to functional categories, demonstrating that much remains to be learned about this response. The extremely desiccation- and radiation-resistant *Chroococcidiopsis* can even survive the intense UV radiation of outer space for more than 1 year (Cockell et al. 2011).

Nitrogen Fixation

One study carried out on desert crusts of the Colorado Plateau combined a *nifH* (encodes Fe-protein of nitrogenase) environmental survey with the isolation of representative nitrogen-fixing cyanobacteria and concluded that 89 % of the recovered *nifH* sequences were from cyanobacteria of the *Nostocales* order (Yeager et al. 2007). This suggests that the majority of nitrogen fixation maybe carried out by cyanobacteria with only a minor role for heterotrophic nitrogen fixation, in contrast to some earlier proposals (Billings et al. 2003; Johnson et al. 2005). The isolated strains were morphologically identified as *Nostoc commune* and *Scytonema hyalinum* and strains belonging to *Tolypothrix* and *Spirirestis*, but as noted elsewhere here final taxonomic designation should rely on more detailed molecular analysis.

Specific Desert Crust Cyanobacteria

Much remains to be discovered in terms of specific taxa of cyanobacteria associated with desert crusts, and it is relatively easy to isolate new species and even new genera (Řeháková et al. 2007). Nevertheless, years of standard microbiological

Table 1 Cyanobacterial morphotypes found in desert crusts of the Colorado Plateau[a]

Morphotype	Type	Relative abundance			
		Sandy soil	Shale	Gypsum	Silt
Ensheathed filaments	*M. vaginatus*	++++	++	n.d.	++++
Ensheathed filaments	*Schizothrix* sp.	++	++	+	++
Single filaments	*Phormidium* sp.	+	n.d.	++	+
Heterocystous filamentous	*Scytonema* sp.	+	++	++	++
Heterocystous filamentous	*Nostoc* sp.	n.d.	n.d.	+++	+++
Heterocystous filamentous	*Chlorogloeopsis* sp.	n.d.	n.d.	n.d.	+

[a] Adapted from Garcia-Pichel et al. (2001)

work has enabled the isolation and characterization of some of the major cyanobacterial players in desert crust communities. Some of the relevant details are given briefly in what follows. Typical morphotypes of cyanobacteria found in the desert of the Colorado Plateau are given in Table 1.

Nostocales

A variety of organisms falling in this order can often be isolated from desert crusts, in particular mature ones. In one study, two new *Nostoc* species, *N. indistinguendum* sp. nov. and *N. desertorum*, sp. nov. as well as a new genus and species within this order, *Mojavia pulchra*, were identified (Řeháková et al. 2007). A great deal of evidence, particularly on the molecular level, supports these assignments and also suggests that various isolates previously identified as known terrestrial species isolated from humid soils based on morphological considerations have been misidentified. Strains often identified, based on old morphological criteria, as *Scytonema*, are commonly observed in and isolated from desert crusts (Fig. 3a). There is some

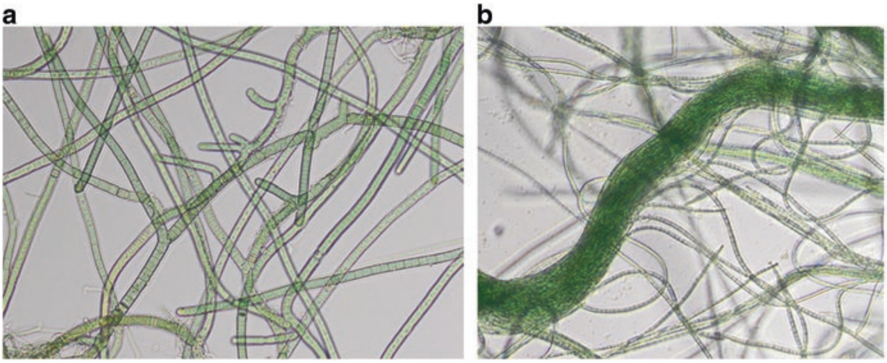

Fig. 3 Desert crust cyanobacteria. Typical isolates from Colorado Plateau desert crusts are shown. (**a**) *Scytonema* sp. (**b**) Ensheathed trichomes of *Microcoleus vaginatus*

suggestion that this genus is in fact polyphyletic, and a new taxonomy for these strains will probably emerge in the near future with the application of molecular approaches. Already a number of draft genome sequences of strains isolated from diverse habitats have recently become available.

Microcoleus

It has long been assumed that cyanobacteria have, as with other free-living microorganisms, a ubiquitous occurrence. This has certainly been true for *Microcoleus*, a genus within the *Oscillatoriales* order with reports of the isolation of *M. vaginatus* from sites spread around the globe. One classical distinguishing morphological feature is that the filaments are often found as ensheathed bundles of trichomes (Fig. 3b). An early application of molecular analysis of 16S rRNA and 16S rRNA–18S rRNA internal transcribed spacer (ITS) sequences showed that many strains of *M. vaginatus* isolated from desert soils in the Southwestern USA were in fact *M. steenstrupii* and that there was enough divergence within these to suggest that this group contains several cryptic species (Boyer et al. 2002). Some variation even within the much more closely related “true” *M. vaginatus* strains was also noted.

The degree of identity of *M. vaginatus* from various locales and the possible role of geographic barriers, which could lead to some kind of allopatric speciation, were investigated in a relatively recent study using the 16S rRNA and 16S–23S rRNA ITS sequences of *M. vaginatus* isolates from three different continents (Dvořák et al. 2012). Analysis showed that a broad genetic diversity was present and that strains isolated in Europe were a separate lineage from strains isolated in North America and Asia. Thus, geographic isolation, at least on the continental scale, can lead to differential evolution of local strains over the more than 4 million years since the estimated divergence. Thus, seemingly cosmopolitan strains can possess cryptic divergence when examined at the molecular level (Boyer et al. 2002; Dvořák et al. 2012).

A metabolomics study has shown that *Microcoleus vaginatus* PCC 9802 is capable of producing mercaptohistidine betaine (ergothioneine) and, more interestingly, unlike nine other cyanobacteria examined, a series of unusual oligosaccharides, possibly based on seven carbon sugar alcohols (Baran et al. 2013). These compounds may be important in promoting gliding motility in this organism, known to be capable of vertical migration in desert soils (Garcia-Pichel and Pringault 2001; Garcia-Pichel et al. 2001).

These cyanobacteria normally have a very characteristic sheath encasing multiple filaments (Fig. 3b). Microscopic studies have shown that this sheath, by virtue of its polysaccharide content, binds soil particles and, most likely, cationic minerals. In addition, electron micrographs show that filaments are completely encased in sheaths when dry, suggesting that they might also confer desiccation tolerance to this organism (Belnap and Gardner 1993). *Desertifilum tharense*, a novel cyanobacterium related to *Microcoleus*, but with more than 5 % 16S rRNA sequence divergence, has been described from crusts of the Thar Desert in India (Dadheech et al. 2012). On the basis of their 16S rRNA sequence, this is a distinct lineage while sharing some morphological features with *Microcoleus* and *Phormidium*.

Pseudoanabaenales

This is an order that was recently split off from *Oscillatoriales* and contains the polyphyletic *Leptolyngbya*. Within the *Leptolyngbya* lie organisms that have been isolated from desert crusts from a variety of locations and which have been recently recognized as a new genus, *Nodosilinea* (Perkerson et al. 2011). Another group has identified a number of new *Oculatella* species in this order, *O. atacamensis* and *O. mojavensis*, isolated from different desert habitats (Osorio-Santos et al. 2014).

Gloeocapsopsis

Recently a novel *Gloeocapsopsis* (order *Chroococcales*), a hypolith isolated from the Atacama Desert, was described. This cyanobacterium appears to be highly tolerant to desiccation with 69 % survival after 2 years at 0.4 a_w (Azua-Bustos et al. 2014). Upon desiccation, this organism was found to increase the synthesis and its content of sucrose and trehalose, compatible solutes. There is some indication that desiccation tolerance requires the capacity to repair DNA, and thus there is potential overlap with radiation resistance.

Chroococcidiopsis

Indeed, when *Chroococcidiopsis* strains (order *Chroococcidiopsidales*), important members of desert crusts from hyperarid areas and known for their robust desiccation tolerance, were examined for radiation resistance, there was 35–80 % survival of doses of 2.5 kGy (Billi et al. 2000). As noted above, representatives of this genus have been isolated from a large number of hyperarid habitats. They are characterized as being spherical, unicellular cells, commonly found in groups or clumps where they can be covered by a common envelope or sheath.

Responses of Desert Crusts to Climate Change

Although not enough is known presently about the ecophysiology of desert crusts to be able to predict with any certitude how they might respond to the different challenges of a climate-induced change in the desert environments in which they are found, several studies have recently suggested several possible scenarios. Analysis of a large-scale, long-term (10 years) experiment where a desert area as kept under elevated CO_2 shows that, in contrast to expectations, cyanobacterial biomass actually decreased under prolonged exposure to elevated CO_2 and that this decrease was due to a reduction along multiple lineages as there was no apparent reduction in taxonomic richness (Steven et al. 2012a, b). Additionally, total microbial biomass was the same between elevated and ambient CO_2 samples, suggesting that the decline in cyanobacterial biomass was accompanied by an equal increase in other groups. A study of the biogeographic distribution of two *Microcoleus* species, *M. vaginatus* and *M. steenstrupii*, found that *M. vaginatus* was more prevalent at coder sites and *M. steenstrupii* more prevalent at hotter sites, suggesting that *M. vaginatus* will be replaced by *M. steenstrupii* as the earth warms (Garcia-Pichel et al. 2013).

Biotechnological Aspects

Although relatively little exploited until now, the different organisms found in desert crusts can be imagined to have the capacity to make a number of compounds of potential biotechnological interest. At some point therefore, there may be an interest in the cultivation of specific organisms in order to carry out large-scale production of particular compounds. Recently, a specific type of photobioreactor has been proposed for this end (Kuhne et al. 2014). In this case, the cyanobacterium *Trichocoleus sociatus* was grown in an immersed fashion instead of the normal submerged mode, leading to a 35 % increase in growth rate and a sevenfold increased production of product, extracellular polymeric substances (EPS).

Microcoleus vaginatus has been reported to produce an unusual mixture of four normal and a relatively low concentrations, more than 60 alkanes, with the dominant compounds being heptadecane (12 %), 7-methylheptadecane (7.8 %), hexadecanoic acid (6.5 %), (Z)-9-hexadecenoic acid (5.6 %), 4-ethyl-2,2,6,6-tetramethylheptane (2.8 %), (Z)-9-octadecenoic acid (2.8 %), and 4-methyl-5-propylnonane (2.7 %) (Dembitsky et al. 2001).

Conclusion

Desert crusts, with their keystone cyanobacteria, are important ecological communities covering relatively significant areas of land under what can be considered largely inhospitable climatic conditions. They have evolved special adaptations permitting survival and proliferation under adverse conditions. A fair amount is already known about diversity and biogeography of some of the various crust organisms and about some of the desiccation protection and UV protection mechanisms involved. The future should bring much more detailed information about the important physical and metabolic interactions between the key microbial partners and the details of the molecular mechanisms of adaptation to desiccation and rehydration, including the cellular programs involved. Finally, given the cryptic metabolic capacities involved, it is likely that desert crust organisms represent a largely untapped resource of compounds of potential biotechnological interest.

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