Semi-arid Regions and Deserts

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Summary

Phototrophic microorganisms are mostly endolithic or hypolithic in the more extreme arid environments and are here restricted to situations where sufficient moisture is retained for occasional growth to occur. Slightly less extreme environments frequently have biological soil crusts. In both cases cyanobacteria are the phototrophs most likely to be found and in some cases the only ones. In most cases of crust development *Microcoleus vaginatus* is one of the first cyanobacteria to occur. The crusts play an important role in maintaining soil and sand surfaces in arid regions, so it is important to understand how environmental factors influence communities at a site. In addition to light, water, temperature, salinity, nutrients and carbon dioxide, these include wind action and physical and chemical features of the underlying substratum. Experimental studies have confirmed that some species, such as the semi-desert *Nostoc flagelliforme*, are extremely resistant to damage by high light and UV levels. *N. flagelliforme* and at least some other species require a regular cycle of hydration and dehydration. Cyanobacterial extracellular polysaccharide not only helps cells to withstand desiccation, but aids the development of crust and soil structure. Understanding of crust structure and succession has proved important in planning reclamation programmes in semi-arid regions of China using cyanobacterial inocula. Details of the procedure are described, which sometimes includes techniques to minimize the effects of wind, such as the use a

checker-board arrangement of protective straw to prevent the inocula from being blown away. Reclamation of semi-arid regions in other parts of the world will require similar understanding of the ecology of the cyanobacteria involved.

12.1 Introduction

It has long been known that cyanobacteria can have an important role in environments subject to periods of pronounced water stress, including many desert regions. Much of the earlier literature on deserts dealt with the visually more obvious organisms, such as the mixed colonies of *Calothrix desertica* and *Schizothrix atacamensis* in the Atacama Desert, Chile, described by Schwabe (1960). Early accounts of desert cyanobacteria were mostly taxonomic or floristic, but a study by Friedmann et al. (1967) in another hot desert, the Negev, Israel, helped to raise interest in ecological and physiological problems. Many more accounts of hot desert cyanobacteria followed within a few years. Accounts of cyanobacteria in Antarctic cold deserts also started to be published, but initially these adopted the taxonomic system of Francis Drouet (see Drouet 1981), as did other reports on the Atacama Desert, rendering the data of little value. However, several accounts by E.I. Friedmann on endolithic organisms in rocks of cold as well as hot deserts (Friedmann and Kibler 1980; Friedmann 1982) using mainstream taxonomic conventions stimulated widespread interest in the organisms. Not only did they establish that endolithic cyanobacteria and green algae are widespread in desert rocks, but studies on Antarctic dry deserts raised questions about the environmental limits for life (Friedmann and Ocampo-Friedmann 1984). This in turn led to assessing the possibility for life on Mars, whether organisms with similarities to cyanobacteria might even occur there, and the potential introduction of a cyanobacterium to provide a source of oxygen (Friedmann and Ocampo-Friedmann 1995). In recent years many studies have focussed once more on the Atacama Desert, because of the range of extreme environments there (McCay et al. 2003; Navarro-González et al. 2003) and the fact that it includes the driest non-polar location on Earth, with a mean of only 2.4 mm rainfall a year (Lacap et al. 2011). Wynn-Williams (2000) reviewed the literature up to that date for both hot and cold deserts, although with the emphasis on the latter. This review is 'reprinted' in the online material associated with the present book, so aspects covered by Wynn-Williams are reported only briefly here, while desert epiliths are mentioned in Chap. 10. The present chapter largely deals with biological crusts, considering only briefly those aspects covered in Chaps. 18 and 19. A short account of desert endoliths is given at the end.

Cyanobacteria in the biological crusts are the main primary producers in dry desert or related environments, though other microorganisms are plentiful in later stages of crust develop-ment. The cyanobacteria inhabiting desert crusts usually experience intense environmental stresses, including high daytime temperatures during the summer, low temperatures during the night in the winter, high radiation including visible and UV radiation, and frequent hydration dehydration cycles. Interest in desert microbial communities has increased greatly in recent years, because of concern about the spread of desert and semi-desert regions as a result of how land has been managed in regions with low rainfall and also because of climatic changes. The ways in which algae, and cyanobacteria in particular, can be used to minimize this problem are the particular interest of the authors. Because of the relevance of these studies to improving soil fertility in other regions, the chapter includes a few comments on cyanobacteria in soils.

12.2 Biological Crusts of Arid Regions

12.2.1 Characteristic Species

The relationship between distribution of soil cyanobacteria and environmental parameters has been studied over a long period and much of the earlier literature was summarized by Metting (1981) and the literature to 2000 by Whitton (2000; reprinted in online material). More detailed reviews of biological soil crusts can be found in the volume edited by Belnap and Lange (2001) and the article by Zhao et al. (2009). Based on these and other studies (Roger et al. 1987; Hong et al. 1992; Hu and Liu 2003b; Bhatnagar and Bhatnagar 2005; Chen et al. 2006a; Büdel and Veste 2008); Büdel et al. 2009), it can be concluded that water availability and factors influencing this, such as rainfall frequency of rainfall, and soil moisture content, together with clay and the amount of available phosphate, have the greatest influence on cyanobacterial biomass. However, estimates of diversity based on standard sampling methods still provide inconsistent results. To what extent this reflects weaknesses in sampling procedure and to what extent it reflects real differences in nature is still unclear.

Liu et al. (2001) concluded that higher fertility supports higher diversity, with the maximum number of species occurring in winter after long period of utilization of organic manure. However, a comparison by Zhang et al. (2011) of their results for Gurbantunggut Desert with other those from other deserts indicated that their study region shows the highest diversity of morphotypes, in spite of the fact that the soils are poor in nutrients. The biodiversity of an Antarctic soil decreased with increasing trophic status (Mataloni et al. 2000), while differences in soil chemical composition had no influence on cyanobacterial diversity in the Thar Desert of India (Bhatnagar et al. 2008). The situation will probably only become clear when there are detailed measurements of nutrient concentrations throughout the season for a range of deserts (see Sect. 12.2.3.6). Agricultural ploughing and weeding can

also affect the diversity. For instance, Liu et al. (1999) found fewer species on the surface of soil subsequent to ploughing (Liu et al. 1999). Kirkwood et al. (2008) concluded that a variable environment promoted diversification, and in particular selected for variation in ecotype more than phylotype.

The local distribution of desert algae shows obvious differences between different microhabitats, although the genera *Microcoleus*, *Schizothrix, Scytonema*, *Lyngbya*, *Nostoc* and *Phormidium* have been reported from the soils of many desert environments (Issa et al. 1999; Hu et al. 1999, 2003d, 2004). Among the species recorded as frequent in particular regions are *Microcoleus vaginatus*, *Nostoc punctiforme*, *N. paludosum* and *Tolypothrix distorta* in many deserts of North America (Flechtner 2007), *Microcoleus vaginatus*, *Scytonema javanicum*, *Schizothrix fragile, Phormidium tenue* and *Nostoc* in the hot deserts of North China, and *Microcoleus vaginatus* and *Phormidium murrayi* and closely related taxa in the hot desert of the Colorado Front Range, USA (Belnap and Gardner 1993; Freeman et al. 2009). *Microcoleus vaginatus* is the dominant species in most sandy soils (Belnap 1993; Hu et al. 2003b, d). In the cool part of the Qaidam Basin in China, *Phormidium foveolarum* and *Lyngbya diguetii* are most frequent in the Gobi region, whereas *Microcoleus vaginatus*, *Schizothrix undulata* and *Myxosarcina chroococcooides* occur more often in the eastern part, which is relatively rich in clay (Hong et al. 1992). Whereas filamentous forms are by far the most important among cyanobacteria, the next most important group of algal phototrophs are composed mainly of unicellular coccoid species (Zhao et al. 2009).

Cyanobacteria are sometimes also frequent in dry, but less extreme, regions than the deserts mentioned above. For instance, *Nostoc calcicola*, *Leptolyngbya nostocorum* and *Phormidium autumnale* were very abundant in fallow fields of (the then) Czechoslovakia (Lukešová 1993). In a comparison of four different types of highly cultivated land in N-E. Italy, a cornfield, vineyard, pasture and a field abandoned for 12 years, cyanobacteria were least frequent in the vineyard, being almost absent there (Zancan et al. 2006). In dry farmland of Fenqiu County, Xinxiang, *Dactylococcopsis*, *Fischerella* and *Synechococcus* only occurred in clay, loam and sandy soil, respectively (Liu et al. 2001). However, in the loess area of Lanzhou Wuquanshan and Lanzhou North Hill (Gansu Province) *Phormidium africanum* was the main dominant. In Czech forest soils, *Nostoc calcicola* showed the highest biomass (Lukešová 1993), whereas *Schizothrix telephoroides* dominated in South African savanna soils (Büdel et al. 2009).

12.2.2 Taxonomic Problems in Describing Crust Cyanobacteria

It can still be difficult to name cyanobacteria based on morphological and morphometric data, even if ultrastructure is considered (Vigna et al. 2001; Büdel 2005; Branco et al. 2009) and the problem tends to be especially difficult for dry soils, where the organisms often have fewer obvious features than in some other types of environment. New taxa are still being described (Flechtner et al. 2002). Analyses based only on microscopy generally underestimate the biodiversity of narrow filamentous cyanobacteria, so molecular approaches which may require isolation and culture are required (Schlesinger et al. 2003; Berard et al. 2005). Even molecular analyses can still under-represent signals for conspicuous heterocystous taxa with thick sheaths in biological soil crusts (Garcia-Pichel et al. 2001). However, an improved methodology involving both terminal restriction fragment length polymorphism (TRF or T-RFLP) analysis and 16S rDNA sequence analysis can provide accurate information about the composition and relative abundance of cyanobacterial types (Redfield et al. 2002). A combination of microscopy, DNA sequencing and amplified fragment length polymorphism (AFLP) proved useful in differentiating variation within *Nostoc commune* during extensive sampling across environmental gradients (Novis and Smissen 2006). Automated rRNA intergenic spacer analysis (ARISA) and 16S rRNA gene clone libraries were effective for the investigation of cyanobacterial diversity in a range of soil environments (Wood et al. 2008). Use of STRR1A (primer oligonucleotide 5′-CCARTCCCCARTCCCC-3′) was the most informative and highly effective in diversity analyses of *Anabaena* (Nayak et al. 2009). So, although species composition and frequency failed to show variation at the level of traditional methods due to the low resolution (Mataloni et al. 2000), there were conspicuous differences using two complementary molecular biological approaches (Mataloni and Tell 2002).

Molecular studies have been applied to *Microcoleus vaginatus*, which is a very common dominant in biological soil crusts throughout the world, including two of the studies mentioned above. The complete genome of one strain, *M. vaginatus* FGP-2, has been reported (Starkenburg et al. 2011). However, according to the results of 16S rRNA gene and 16S-23S internal transcribed spacer region studies (Boyer et al. 2002), this is not a single species. Combined analysis of sequence and morphological data of 31 strains from desert soils in the USA revealed it to include two species, *M. vaginatus* and *M. steenstrupii*. The latter was suspected of representing several cryptic species, as it showed much greater genetic variability (16S similarities ranging from 91.5% to 99.4%) than the former (97.1–99.9%). The *M. steenstrupii* Boye-Petersen (1923: see Geitler 1932) came from thermal springs, whereas morphologically similar material has been reported not only from the deserts of the Boyer et al. (2002) study, but also hypersaline lakes in Afghanistan and soils in India (Komárek and Anagnostidis 2005). The genus has since been classified into two clades based on 16S rDNA phylogeny, with a new genus *Coleofasciculus* being

proposed (Siegesmund et al. 2008). (For simplicity, the name *Microcoleus* is retained in this chapter).

12.2.3 Environmental Factors

12.2.3.1 Light

The euphotic zones in biological crusts on sand are mostly only 1–2 mm thick due to strong light attenuation by the sand. In a study of cyanobacteria in desert soils in China, 96% could occur within the upper 1.0 mm of crust (Hu and Liu 2003a). Rates of gross photosynthesis and net respiration in the upper 1 to several mm of recently rewetted cyanobacterial crusts in two south.-eastern Utah crusts were sufficiently high to form marked oxygen microenvironments ranging from supersaturation to anoxia; localized pH values sometimes exceeded 10 (Garcia-Pichel and Belnap 1996). The ways in which the cyanobacteria adapt to the light environment include mechanisms for optimizing photosynthesis, protection from damage by visible and UV radiation and sometimes also movement of filaments away from the light. The different layers within soil crusts show differences in how they adapt to light intensity and light quality in the particular layer (Hu et al. 2003c).

Cyanobacteria in the crusts must be equipped with mechanisms to protect themselves against photoinhibition under high light intensities especially during dehydration, since photosystem II (PSII) in most cyanobacteria is highly susceptible, leading to rapid degradation of its core proteins, while subsequent repair requires *de novo* synthesis and reassembly (Niyogi 1999). It is essential for crust species that they can reverse metabolism rapidly and grow in the short periods when water is accessible and then hold back metabolic activity during dehydration. Existing proteins must be stabilized during dehydration to guarantee growth (Potts 2001). In a *Microcoleus* sp. dominated sand crust, over 50% of photosystem II (PSII) activity, assembled phycobilisomes, and photosystem I (PSI) antennae were detected within less than 5 min of rehydration, and energy transfer to PSII and PSI by the respective antennae was fully established within 10–20 min (Harel et al. 2004). Even at exceedingly high light intensities, photoinhibition of PSII occurs only to a limited extent and this is largely balanced by a fast rate of PSII repair. The semi-desert species *Nostoc flagelliforme* tolerates high levels of solar radiation even in the presence of UV (Gao and Ye 2007). In addition soil cyanobacteria can also protect against high light intensity and UV by scavenging reactive oxygen and free radicals (Wang et al. 2007a, 2008).

Other means of minimizing damage by high light intensities include the formation of molecules which dissipate some of the energy at potentially damaging wavelengths before it reaches sensitive regions of the cell. Terrestrial cyanobacteria show marked changes in pigment composition and content in response to visible and UV radiation (Chap. 19), with scytonemins, mycosporine-like amino acids (MAAs) and carotenoids content increasing with solar radiation (Bowker et al. 2002). Sheath-forming filamentous cyanobacteria are the major components in the upper millimetre of blackish-brown crusts, and the dominant species have high contents of carotenoid and MAAa with absorption peaks in the UV or at 507 nm (Tirkey and Adhikary 2005).

Another means of ensuring the population is maintained is for some trichomes to move downwards when light or UV radiation becomes strong. Most soil cyanobacteria can move downwards (Garcia-Pichel and Pringault 2001). Under weak light they can rapidly initiate photosynthesis when light intensity increases, although cyanobacteria deeper in a Baja California mat were shown to recover later than those near the surface (Fleming et al. 2007). There are many records of cyanobacteria at considerable depth in other soil types, such as *Nostoc* and *Leptolyngbya* at 16–18 cm in paddy soils in Osaka, Japan (Fujita and Nakahara (2006), but it is unclear how long such populations can persist in a healthy state.

12.2.3.2 Water

It is not yet possible to generalize on how different water regimes influence the type of crust and its vertical profile, because of the complexity of ways in which the regime can influence both soil formation and crust metabolism at a site. It seems likely that there are considerable differences between sites with rare, but intermittently high, rainfall, versus low rainfall at defined seasons and the almost total dependence on dew of some coastal deserts such as the Namib Desert, Namibia (Lalley and Viles 2005). In the Qubqi Desert of Inner Mongolia (40°21′N, 109°51′E), water vapour from the atmosphere accounted for 25–39% of the total water uptake by man-made crusts with *Microcoleus vaginatus* and *Scytonema javanicum* on a sandy soil (Lan et al. 2010a). This took place mainly by a water vapour adsorption mechanism. However, it did not occur immediately after inoculation of the surface with the cyanobacteria, but there was obvious increase by day 15 and the rate had become markedly enhanced by day 20. It was concluded that growth of cyanobacterial filaments and their associated EPS were the main factors increasing water uptake and content. The inoculated filaments were shown to be in direct contact with the sand and clay particles.

Whatever the particular type of crust, the ability to adapt to desiccation is the top requirement for the cyanobacteria; water content is more important than light, salinity and other factors for their distribution (Tsujimura et al. 1998). Research has shown that terrestrial cyanobacteria have a marked capacity to withstand removal of their cellular water (Potts 1999). The uronic acid of viscous extracellular polysaccharide (EPS) can regulate water retention properties by the transition of gel and sol state (Potts 1994) and is an integral component of cells subject to drying in their natural environment (Helm

et al. 2000; Chap. 18). The presence of a sheath and mucilage can help protect cells against physical desiccation, though not UV shock according to Gupta and Agrawal (2008), unless a UV-absorbing molecule such as scytonemin is immobilized on the EPS. However, Chen et al. (2009a) found that pretreatment of a culture of a desert strain of *Microcoleus vaginatus* with 100 mg L^{-1} EPS effectively eliminated reactive oxygen species and thus provided significant protection from DNA strand breakage and lipid peroxidation. Mager and Thomas (2010) reviewed the overall role of cyanobacterial EPS in soil crusts.

Despite the importance of the water content, a rapid change in it can sometimes be even more crucial for the organisms. The hair-like *Nostoc flagelliforme* can die if it is kept continuously in a very moist environment, because the water loss of physical evaporation is an active process influenced by inhibitors of transcription and translation (Shaw et al. 2003). A regular cycle of dehydration and rehydration is very common in terrestrial cyanobacteria and even indispensable in some cases. The response of *Microcoleus* to a fluctuating water content is especially important in developing the structure of soil biological crusts (Belnap et al. 2001). The bundles of *Microcoleus* trichomes surrounded by their extracellular sheath wind throughout the uppermost soil layers. When sufficiently moist, the trichomes glide out of their sheaths, show positive phototaxis and glide towards the soil surface. Upon drying, the trichomes leave the surface, and the exposed trichomes secrete new sheaths. Frequent changes in moisture content therefore result in copious EPS being dispersed throughout the soil.

Dehydration is, however, a stress process. In studies with desiccation-tolerant *Nostoc commune*, PSI and PSII were both deactivated during dehydration with the loss of photosynthesis; the evidence suggests that dissipation of the light energy absorbed by PSII prevents photoinhibition when subjected to strong light in a dehydrated state (Hirai et al. 2004; Fukuda et al. 2008). Rehydration is an induced process, with over 50% PSII activity and PSI antennae being detected within 5 min of rehydration (Harel et al. 2004). During this period the energy transducing reactions recover first, followed by an increase in ATP pool size (Tiwari and Tripathi 1998); the energy transfer to PSII and PSI can be fully established within 10–20 min of rehydration (Harel et al. 2004). After the recovery of the initial phase, a change in 77 K fluorescence emission spectra began (Qiu et al. 2004a). The recovery can be enhanced by the content of some ions (K, Mg, Ca, PO$_4$), because they enhance the probability of electron transfer beyond Q (A) and the recovery of electron transport flux per PSII reaction centre (Qiu et al. 2004b). From an ecological viewpoint the speed of water uptake depends upon the duration of desiccation (Shaw et al. 2003) and the type of habitat (Tirkey and Adhikary 2005).

Many factors interact in the natural environment and their influence can differ between different desiccation-tolerant

organisms. For instance, Fleming and Castenholz (2007) reported that increased UVA radiation led to a more concentrated scytonemin screen in *Nostoc punctiforme* PCC 73102 and *Chroococcidiopsis* CCMEE 5056, when subjected to periodic desiccation, in comparison with cells maintained fully hydrated. A more concentrated scytonemin screen would reduce the amount of UVR damage accrued when cells are desiccated and metabolically inactive. This might allow the cyanobacteria to allocate more energy during rehydration to systems other than UVR damage repair, which would facilitate recovery. The scytonemin screen is extremely stable, remaining largely intact in the sheaths of desiccated *N. punctiforme* even when continuously exposed to UVA radiation for 2 months. In contrast, scytonemin synthesis in *Chroococcidiopsis* CCMEE 246, a strain producing scytonemin constitutively under low visible light and no UVA was partially inhibited by periodic desiccation.

During the recovery process, extracellular polysaccharides have a very important role in maintaining cell morphology (Chen et al. 2006b). Part of the reason for this is that the extracellular polysaccharide can generate superoxide radicals when rehydration occurs, and the Fe-SOD can counter the effects of oxidative stress (Shirkey et al. 2000). At the same time external carbonic anhydrase can also be activated by rehydration (Ye et al. 2008) and these activations may lead to time-dependent changes in structure and ultrastructure and fluctuations in the composition of the transcriptome. More genes, especially those involved in DNA repair, protein folding, NAD synthesis, nitrogen depletion and CO$_2$ limitation, might be specifically down-regulated or up-regulated (Higo et al. 2007).

The gene *sigJ* is now considered as a fundamental and conducive gene for desiccation tolerance in cyanobacteria, as it up-regulates a large number of genes relating to polysaccharide biosynthesis (Yoshimura et al. 2007). Although *Nostoc commune* can survive several decades of desiccation (probably many more), genomic DNA is still covalently modified during this period, which leads to the loss of supercoiling aggregation, transformation and transfection efficiency. Thus, this response is different from that of *Deinococcus radiodurans* to ionizing radiation (Shirkey et al. 2003). Scondly, acidic WspA may be an important protein in desiccation adaptation, playing a role by modulating the structure and function of the three-dimensional extracellular matrix, or by influencing the distribution and transportation of mycosporine and scytonemin (Wright et al. 2005), as indicated by the influence of drought on scytonemin production in at least some cases (Fleming and Castenholz 2007). Finally, the gene cluster including *treZ*, *treY* and *treH* is very important. This cluster can increase the rate of trehalose production under water-stress conditions (Yoshida and Sakamoto 2009), while trehalose can stabilize membranes (Potts 1994), so the accumulation of trehalose minimize damage to DNA during drought periods (Shirkey

et al. 2003). Trehalose was also one of the substances formed as part of the adaptation by cyanobacteria in the Antarctic fellfields to low temperatures (Arnold et al. 2003).

12.2.3.3 Temperature

Although extreme temperatures may be expected to be detrimental to phototrophs, cyanobacteria still dominate sandy surfaces at 40–52°C and −9°C (Arnold et al. 2003). The soil surface temperature where *Nostoc flagelliforme* grows can exceed 65°C. In the study by Chen et al. (2011) on crust development by this species (Sect. 12.5.2), the authors compared the effects of drying material for 2 h at 60°C with a control on photosynthesis and respiration rates in liquid culture. There was a slight reduction in both activities for the material which had been heated, but nevertheless the rates were still high.

In comparison with most aquatic algae, soil cyanobacteria are much more tolerant to temperature changes and to interactions between temperature and humidity; it is important to consider the response of natural populations to temperature stress together with their response to water stress. Moist cyanobacteria may differ in their sensitivity to heat (Gupta and Agrawal 2006), while the same strain can show obvious differences between different growth stages (Agrawal and Singh 2000). Akinetes usually have a higher tolerance than other stages. Although many akinetes in the study by Agrawal and Singh germinated at 35°C, their formation was markedly suppressed at this temperature, and at no temperature did heat shock promote akinete formation or germination. It was concluded that both wet and dried akinetes tolerated dryness, but not frost. However, such studies must be considered in relation to the particular environment from where the organisms had been sampled.

Most soil cyanobacteria survive equally well or slightly better when exposed to the air on a moist soil surface than when suspended in liquid medium. Desiccation-sensitive algae survive high atmospheric humidity better than desiccation-resistant algae, indicating the importance of atmospheric temperature and relative humidity for a particular species (Gupta and Agrawal 2008). Agrawal and Pal (2003) compared the effects of water stress using agar medium or exposure to NaCl solution on five cyanobacteria and two green algae for various lengths of time. Somewhat surprisingly, two of the three most sensitive organisms were dried mucilaginous small-celled cyanobacteria. Nevertheless the authors concluded that the tolerance of micro-algal forms to water, heat or UV stress depended primarily upon cell-wall characteristics or cellular osmotic properties rather than the original habitat, morphology or whether prokaryotic or eukaryotic.

As part of a programme on the possible effects of climate change, a detailed study was made on the influence of environmental factors on carbon fixation by *Nostoc commune* in Victoria Land, continental Antarctica, where the organism is a very conspicuous terrestrial primary producer (Novis et al.

2007). The study, which involved field and laboratory measurements, together with results from previous years, led to a model describing the process over 1 year. Desiccated *N. commune* mats with a water content ≤30% saturation, showed such a variable rate of net C fixation between replicates that the data could not be modelled. However, for colonies at >30% saturation, the rates of net C fixation and dark respiration depended strongly on irradiance and temperature. Annual net C fixation was 14.5–21.0 g C fixed m^{-2} *Nostoc* mat, depending on the year. Estimates for different seasons correlated with thermal time (accumulated hours above 0°C during the year) rather than irradiance, in contrast to phototroph communities in local (Antarctic) lacustrine environments, where irradiance is the main driver of primary productivity. The relationship between thermal time and net annual C fixation by *N. commune* was strongly linear. *N. commune* appears to compromise between an ability to capitalize on short periods of higher temperature and efficient utilization of lower irradiance at low temperature.

12.2.3.4 Salinity

Although *Dunaliella* spp. are the most abundant phototrophs at the most consistently hypersaline sites in the Salt Plains area of Oklahoma, USA, cyanobacteria have the highest biomass at sites which experience greater fluctuations of salinity (Kirkwood and Henley 2006). They show high diversity in such environments, this diversity spanning a number of cyanobacterial lineages (Kirkwood et al. 2008). Salt stress is accompanied by water stress and can inhibit growth, decrease the Fv/Fm ratio, photosynthetic yield of a mat, slow down photosynthetic recovery, and lead to oxidative damage and lipid peroxidation (Chen et al. 2003b; Fleming et al. 2007; Tang et al. 2007a). Other responses include increases in trehalose and sucrose phosphorylase activation (Page-Sharp et al. 1999) and increases in exopolysaccharides and intracellular sucrose to maintain the cellular osmotic equilibrium between the intra- and extracellular environment (Chen et al. 2003a, b, 2006c). Production of antioxidative enzymes (SOD and CAT) helps counteract oxidative damage (Tang et al. 2007a). Cell morphology may also have an influence, as *Nostoc* with spherical cells showed a higher tolerance to water stress and salinity than *Nostoc* with cells of other shape; the former was able to rectify problematic soil better than the latter (Obana et al. 2007).

As colonizers of desert soil, cyanobacteria often encounter both drought and salinity. Growth and photosynthetic activity of a *Microcoleus vaginatus* crust was significantly inhibited by the double stress; the inhibitory effect increased with increasing intensity of stress and treatment time (Lan et al. 2010b). In contrast to salt stress, drought completely stopped crust metabolic activity, so the crust biomass was conserved at a higher level, which meant that drought alone can provide the crust some protection.

12.2.3.5 Carbon Dioxide

Terrestrial cyanobacteria can directly use CO_2 and HCO_3^{-1} (when hydrated) and an increased CO_2 concentration can enhance diurnal photosynthesis and raise the daily photosynthetic production. However, air-grown mats of *Nostoc flagelliforme* showed higher photosynthetic affinity for CO_2 than high-CO_2-grown ones (Qiu and Gao 2002). Soil CO_2 flux and the influence of soil phototrophs, including cyanobacteria, was studied in some detail at three sites above 3,600 m in the Colorado Front Range, USA (Freeman et al. 2009). The authors grouped such high-elevation areas with other soil-dominated ecosystems – deserts, polar regions and zones of glacial retreat, all of which have often been described as 'barren', despite their potential to host photoautotrophic microbial communities. A combination of soil CO_2 flux measurements and molecular techniques was used to characterize the types of soil phototroph and measure rates of CO_2 uptake. Soil CO_2 flux data from two different years indicated that light-driven CO_2 uptake occurred on most dates. A diverse community of cyanobacteria, "chloroflexi" and eukaryotic algae was present in the top 2 cm, whereas they were nearly absent in deeper (2–4 cm) soils. The cyanobacterial communities were composed of lineages most closely related to *Microcoleus vaginatus* and *Phormidium murrayi*. During the light hours of the 2007 snow-free measurement period, CO_2 uptake was estimated to be 23.7 g C m^{-2} season^{-1}. The authors concluded that photoautotrophic microbial communities play an important role in the biogeochemical cycling of subnival zone soil. (No studies were included to assess the possible contribution of photoheterotrophy.)

Several methods have been used for measuring CO_2 uptake by terrestrial cyanobacteria, but studies by one of the authors (KG) has found that use of an assimilation chamber to hold the sample and measurements of CO_2 concentrations in the inlet and outlet flows with an infrared gas analysis is the most straightforward. Practical details include replacing the cover of the assimilation chamber with a quartz cover and the need to maintain a constant CO_2 concentration in the inlet air flow. This can be achieved with an air bag, which also permits rapid increases in the CO_2 concentration by injecting pure CO_2 into the bag. Reduction of the CO_2 concentration can be achieved by pumping the ambient air though a soda lime column. If required, the open system can be converted to a closed one by circulating the gas.

12.2.3.6 Nutrients

In the Shapotou area of the south-east part of the Tengger Desert, the maximum biovolume of algae (ca. 95% biomass from cyanobacteria) was exhibited in August with the highest precipitation; the minimum value in February with the lowest air temperature (Hu and Liu 2003c). Six microclimate factors (wind speed, air and surface temperature, evaporation, precipitation, humidity) and 27 soil microenvironment parameters (total N, P, K, rapidly available N,P, K, C/N, organic matter, moisture, pH, electric conductivity, Ca^{2+}, Mg^{2+}, SO_4^{2+}, Cl^-, Mn, V, Zn, Cu, Fe, Co, coarse sand grains, fine sand grains, coarse silt, fine silt and coarse clay particles) associated with biovolume were considered. Stepwise multiple regression indicated that biovolume was positively correlated with the amount of local precipitation, total K_2O, soil hydrolyzable N, Fe^{3+} and coarse silt, while negatively correlated with pH, organic matter, Cu and Zn. It was also affected by the trace element Co.

There have been only a few reports on the role of nutrients in determining species composition or succession in crusts, but, judging by the frequency of heterocystous cyanobacteria, nitrogen fixation is an important N source. It therefore seems probable that P and perhaps Fe are the elements whose availability are the most likely to influence cyanobacterial growth. Total P and available P were reported to be the main chemical factors influencing the diversity of cyanobacterial and eukaryotic algal morphotypes soil samples from sand dunes in the Gurbantunggut Desert (Zhang et al. 2011). Mg content was also a factor influencing microalgal biomass and the authors suggested that the contents of P and Mg, soil texture and soil moisture were the main factors influencing distribution in this region. However, in experiments on rewetting dried *Nostoc flagelliforme* collected from Siziwangqi, Inner Mongolia, addition of K^+ had the greatest effect on recovery of photosynthetic activity, whereas Fe^{3+}, Mg, Na, NO_3, PO_4-P and Cl showed little effect (Qiu and Gao 1999). In the case of the cyanobacteria used for inoculation of semi-arid soils, such as the studies by the Liu and Hu group, the P-rich medium BG11 was used to prepare the material. The organisms are therefore probably in a P-rich state when reaching the soil and the cells can be expected to divide several times before becoming entirely dependent on ambient phosphate in the soil. No studies have been reported on the ability to use organic phosphates, but most of the cyanobacterial genera are ones which typically show high surface phosphatase activity in other environments (Whitton et al. 2005). The hypothesis is suggested that surface phosphatase activity per unit biomass is likely to increase during successional stages of crust formation.

12.2.3.7 Wind and Burial by Sand

Many desert regions are subject to strong wind action and hence cyanobacterial species and strains may be expected to dispersed widely and hence organisms best suited for growth at any particular site are likely to arrive quite often. The use of artificial inoculation (Sect. 12.4.1) in semi-arid regions merely shifts the ratio of cells to soil. The possibility that such organisms in desert dust in southern Iraq might have been sufficiently dense to act as a factor causing ALS (amylotrophic lateral sclerosis) disease in troops involved in the 1990–1991 Gulf War was raised by Cox et al. (2009).

The role of biological crusts in stabilizing soil against wind action was first described by Booth (1941) and subsequently there have been many comments on the importance of the filamentous microorganisms in the crusts (e.g. Issa et al. 1999; Tirkey and Adhikary 2005). This is especially important in sandy soils, because of their lower resistance to wind erosion than other types of soil (Zhang et al. 2006). These authors showed that the extent of erosion of biological soil crusts in the Gurbantunggut Desert, northern Xinjiang, Northwestern China, paralleled the extent of which the crusts had been disturbed. Wind tunnel comparisons showed that the maximum velocity tested, 25 m s^{-1}, caused no erosion of the surface of a crust with 100% cover, while the highest disturbance occurred without crusts. The wind erosion rate of sandy soil with 0% crust cover was 46, 21 and 17 times that of soil with 90% crust cover at wind velocities of 18, 22 and 25 m s^{-1}, respectively. The authors emphasized the importance of minimizing crust disturbance in desert regions. In addition to reducing trampling, strategies should be developed to manage livestock and oil exploration in order to avoid concentrated zones of impact. In a less extreme semi-arid region of southern Australia, biological soil crusts were shown to recover quite rapidly after livestock had been removed (Read et al. 2011). The authors compared their estimate of 20 years for recovery with the results of three other studies on recovery from livestock damage in desert regions of other parts of the world. The recovery rates were surprizingly similar, in spite of wide differences in annual rainfall (390 mm in Australia and 95–230 mm for the others). Read et al. concluded that mosses were the dominants colonizers in their region, but no studies were included on possible changes in cyanobacterial populations immediately after the livestock had been removed. However, it seems clear that recovery from livestock damage is quite different from colonization of a bare surface.

As cyanobacteria are usually the main component of the crusts, their ability to withstand wind force is important. Wind force is a stress factor and can decrease PSII activity and electron transport rate. In the case of *M. vaginatus* increases were recorded in proline, total soluble sugar, reducing sugar, extracellular sugar and protein contents (Xu et al. 2010). However, the fact that natural crusts are a mixture of several species makes it difficult to quantify the contribution by individual species, especially to cohesion. Several authors have proposed methods to deal with the problem (Liu et al. 1994; McKenna-Neuman et al. 1996). Hu et al. (2002a) isolated the dominants (*Microcoleus vaginatus*, *Phormidium tenue*, *Scytonema javanicum* and *Nostoc* sp.) from crusts in the Tengger Desert (37°32′N, 105°02′E), NingXia Autonomous Region, and measured their cohesion in stabilizing shifting sand. Biomass, species, community composition, niche within the crust, crust thickness, growth phase, soil moisture and dust accretion could all could increase the strength of cohe-

sion. The threshold friction velocity (TFV) was increased significantly by all the species tested, but the increase was much greater with filamentous species. Among the four species *Microcoleus vaginatus* was the strongest, though *Phormidium tenue* was also strong indoors, but not outdoors. Thick crusts were less easily eroded than thin crusts, but biomass was more effective than thickness.

Cyanobacterial crusts throughout the world often encounter burial by sand during the course of their development at lower sites. In a greenhouse experiment Wang et al. (2007b) found that EPS content and *Fv/Fm* decreased correspondingly with the increase in the burial time and burial depth; however, the degradation of chlorophyll *a* commenced only at 20 or 30 burial days. This suggests that burial by sand is not an important stress, because, although cyanobacterial crusts may often be covered by sand, but they are seldom buried for long periods in naturally windy environments. Growth and/or motility give the organisms some ability to move upwards and this is probably an important part of the process of crust formation in such environments.

12.3 Development and Succession of Biological Soil Crusts

12.3.1 Crust Structure

The fact that the blackish-brown colour of many biological soil crusts is due to filamentous sheath-forming cyanobacteria has been shown by many authors (e.g. Tirkey and Adhikary 2005). The results indicate that microbiotic cover is an important determinant of sand fixation in the Gurbantunggut Desert, northern part of Xinjiang, Northwestern China. The crusts consist of an intricate network of filamentous cyanobacteria and EPS, which in sandy regions binds and entraps the sand grains, and conglutinates fine particles (Zhang et al. 2006). The crusts resemble other microbial mats and stromatolites in that there is a vertical stratification of different functional groups of microorganisms (Davey and Clarke 1992; Garcia-Pichel and Belnap 1996; Stal 2000; Hu et al. 2003c). The crusts are often distinctly laminated into an uppermost, partially inorganic, layer (*ca* 0.0–0.02 mm), a middle phototroph-dense layer (*ca* 0.02–1.0 mm) and the lower phototroph-sparse layer (below ca 1.0 mm) (Davey and Clarke 1992; Hu et al. 2003c). Cyanobacteria are distributed throughout the whole crust profile, and trichomes can move in response to light and water, as described for *Microcoleus* in Sect. 12.2.3.2 (see also Garcia-Pichel and Pringault 2001; Pringault and Garcia-Pichel 2004). Nevertheless, *Scytonema*, *Nostoc* and *Calothrix* are typically organisms of the uppermost layer (Hu et al. 2003c; Rosentreter and Belnap 2003), *Microcoleus vaginatus* of the middle layer, and *Phormidium* and *Lyngbya* of the deep layer (Hu

et al. 2003c). An experimental study (Wu et al. 2011) on crusts from a non-irrigated area of the Tengger Desert showed that 60% of the total algal biomass (presumably mostly cyanobacteria) occurred in the top 1 mm of the soil profile in algal soil crusts, but 80% in lichen soil crusts. The authors suggested that most of the algae in the latter were symbiotic.

A study of the micromorphology of the crusts under plane polarized light found no soil aggregates, apart from some micro-aggregates (Hu et al. 2003c). However, some inter-locked micro-beddings exist in the profiles of older crusts, which are composed of fine clay particles formed by the deposition of fine silt; the shapes of these micro-beddings were thought to be related to the direction of water move-ment on the soil surface, and were the main factor reducing infiltration of the soil (Hu et al. 2004).

12.3.2 Crust Development

Once biological crusts start to develop, the sand surface becomes stabilized and the uppermost several millimetres of topsoil undergoes various changes. *Nostoc*, *Scytonema, Calothrix*, *Microcoleus* and hyphae within the soil profile were found to be nearer to the surface in older crust (Hu et al. 2003c; Rosentreter and Belnap 2003). It was suggested this aided the transformation from algal crusts to the lichen crusts of later stages (Hu et al. 2003c). There are also differences in the relative proportions of biomass. When lichens and mosses accounted for less than 41.5% of the crust surface, algal biovolume became higher in the older crusts, but the opposite applied when they covered more than 70% of it (Hu and Liu 2003a).

During development of the crusts there are many changes in physical and chemical properties. The amount of dew for-mation increases with the development level of the microbiotic crusts (Liu et al. 2006; Rao et al. 2009a), as do the concentra-tions of organic matter and nutrients, conductivity, porosity, silt, clay, secondary minerals, the bulk density and the num-ber of microlayers of the crusts (Hu and Liu 2003c; Guo et al. 2008). CO_2 exchange rates have also been used as an indica-tor of the state of the development level (Zaady et al. 2000). In a study by Yan-Gui et al. (2011), the net photosynthetic rate was significantly higher at 51-year old restoration site in the Tengger Desert than a 15-year old site (1.57 versus 0.92 μmol m^{-2} s^{-1}). Accumulated carbon fixation also increased with restoration time, but with a slower phase ini-tially and then higher one after 43–51 years of restoration. The accumulated carbon fixation was correlated with soil organic carbon content. Later successional crusts have been shown to have not only greater photosynthetic activity, but also greater nitrogenase activity and N_2 fixation, and daily Fv/Fm (Housman et al. 2006; Rao et al. 2009b).

Other biological phenomena have been reported with the progress of the successional stages. Desert protozoa were shown to be adapted to a specific temperature and precipi-tation regime during crust development (Darby et al. 2006), their numbers increasing during succession from *Microcoleus* to lichen to bryophyte crusts (Bamforth 2008). The mecha-nism of this aboveground – belowground link is probably due to the increase in food, habitat, nutrient inputs, moisture retention and environmental stability provided by the bio-logical soil crusts. Isopods have an important role in nutri-ent cycling (Shachak et al. 1976). Nematode status has been used as a biological indicator of soil condition, with succes-sionally more mature communities (abundance, richness and diversity) beneath well-developed, late-stage crusts than beneath immature, early-stage crusts (Darby et al. 2007). The desert snail *Sphincterochila zonata* was on a loess plain in the Negev Desert an important role in grazing the surface algal community, in spite of the fact that it was only active on 8–27 winter days annually (Shachak and Steinberger 1980). Other reports concern organisms higher in the food web, such as the distribution of lizards (Zaady and Bouskila 2002). CO_2 exchange rates have also been used as an indicator of the state of the development level (Zaady et al. 2000). Later successional crusts had greater photosynthesis, nitrogenase activity, higher daily C and N fixation, and daily Fv/Fm (Housman et al. 2006; Rao et al. 2009b). It is clear that the formation of biological soil crusts can speed up development of the soil ecosystem (Chen et al. 2002).

By comparison with the methods of mineralogy and agrology, biomethods (such as algal distribution and biovol-ume) are more precise in judging algal crust development because the changes in minerals and soil are very slow (Hu et al. 2003c). The results of molecular fingerprinting (Garcia-Pichel et al. 2001; Redfield et al. 2002) also indicate that a particular microbial community corresponds to the degree of crust successional maturity (Gundlapally and Garcia-Pichel 2006). With respect to diazotrophs, the abun-dance of *nifH* sequences and nitrogenase activity were both higher in mature crusts than in poorly developed ones (Omoregie et al. 2004). Yeager et al. (2004) also demonstrated a transition from a poorly developed crust to mature crusts harboring a greater percentage of *Nostoc* and *Scytonema* spp.

With respect to the developmental stage, Li et al. (2002) divided crust development into the three stages, a non-biologi-cal crust, crusts enriched with mosses, and crusts dominated by abundant algae, mosses and liverworts. However, this classification merely reflected the distribution pattern in a natural environment rather than the biological development process. Development has usually been considered in three stages, cyanobacteria-dominated, lichen-dominated and moss-dominated ones (Rivera-Aguilar et al. 2006). This classification fits neatly with the evolutionary position of the

three types of dominant and is consistent with the typical process of biological development. However, it can be difficult to differentiate crusts at the middle and late stages, because they are often a mixture. In studies by researchers at Wuhan records are based on the dominant coverage and crusts with similar cover of one of the dominants are treated as the same transition stage (Lan et al. 2011b).

Particular interest has been given to the development of, and crust formation by, *Nostoc flagelliforme* because of its economic value (Sect. 12.3.3 and Chap. 26). Growth has been studied on filter paper, various soil types (Hu et al. 1987), transparent plastic sheets (Gao and Yu 2000) and sand (Chen et al. 2009b, 2011); apart from the plastic, all the tests were conducted in petri dishes. Comparison of coarse (between 5 and 14 Tyler mesh) and fine sand (<32 Tyler mesh) showed that growth was faster with the fine sand. Electron microscopy showed that cells of the filaments adhered closely to the sand surface. The biological crust was a multilayer network formed by EPS mingled with filaments intertwined around each other.

12.3.3 Succession

Studies of succession on newly exposed surfaces where conditions are unfavourable for rapid invasion by rooted plants have provided many examples where cyanobacteria have an important role during the early stages. In the case of gypsum rocks in S-E. Spain succession started with domination by cyanobacteria, which was then followed by green algae (Dana and Mota 2006). In the Tengger Desert succession fell into three stages, with *Microcoleus vaginatus*, *Scytonema javanicum* and *Microcoleus vaginatus* dominating, respectively, at the three different stages (Hu et al. 2003d). *M. vaginatus* was the first colonizer on all microenvironments and had a marked success over other algae. The process was affected by water content, nutrient concentrations and extent of shading, with shortage of water being the most important Under irrigation conditions and where the slope was less than 45°, a succession of dominants could occur within the first 1–2 months, by which time nutrient levels were low and *S. javanicum* took over. Unconsolidated sand on a sandhill in the Laarder Wasmeer, an inland dune area in The Netherlands, was colonized initially by *Oscillatoria* spp., this being followed in turn by *Klebsormidium*, *Synechococcus* and *Zygogonium* (Pluis 1994). The algal crust seldom reached maturity on the dunes due to wind action, but the crust was more stable on flat areas. However, when the green alga *Zygogonium* did form a pronounced cover on slopes, the crust became water-repellent when dry, leading to higher surface run-off during rainfall. This region merits further study, because the importance of unsheathed cyanobacteria at the first stage of succession contrasts with reports from most other areas.

The usar soils (alfisol, solonetz, alkaline) of India have been the subject of many studies on colonization following the pioneer research of R.N. Singh (1950) and his students. In a study by Pandey et al. (2005), the obvious growths of cyanobacteria after the first monsoon rainfall appeared in the order: *Microcoleus* sp., *Calothrix brevissima*, *Scytonema* sp., *Cylindrospermum licheniforme*, *C. fertilissima*, *Nostoc calcicola*, *Nostoc punctiforme*, *Aphanothece parietina*, *Nostoc commune*, *Aulosira fertilissima*, *Phormidium* and *Oscillatoria*. Among these, *Nostoc calcicola* was the dominant. It was suggested that differences in colonization were related to local climate, the importance of air-borne inocula and other factors concerning soil and biology.

The next stage in succession typically leads from the algal crusts to crusts dominated by lichens and/or mosses. Hu and Liu (2003b, c) found that the abundance of cyanobacteria decreased gradually during succession, especially that of *Scytonema javanicum*, whereas biodiversity increased gradually. Biomass increased at an early stage, but then decreased again. Studies on crusts in South Africa showed that crust thickness and chlorophyll content increased significantly as the early successional types progressed to late successional types (Büdel et al. 2009). However, the speed of natural succession was so slow that the community-building species were still the first dominant species after 42 years, although the degrees of dominance had decreased slightly. Hu and Liu (2003a) found that the speed of succession and trends at sites in the Tengger Desert were affected by water, vegetation coverage, terrain, time and soil physical and chemical properties, especially the Mn content in the soil, which appeared to have a threshold effect.

In a study (Büdel et al. 2009) of drylands in South Africa, the main factors influencing diversity and distribution patterns of biological soil crusts were rain frequency and the duration of dry periods rather than total precipitation. Silt and clay had a significant positive correlation with the number of crust types, and cyanobacterial diversity was significantly higher in the winter rain zone than the summer rain zone. This led the authors to suggest that fine grain-size could promote crust succession and their biomass content. However, Li et al. (2002) thought the most significant driving factor in the development of microbiotic crusts in the Tengger Desert was the spatial variability of rainfall infiltration depth (Li et al. 2002). Some insight as to how such variability can occur was provided by Gao et al. (2010) in a study on Mu Us Sandland soils. Under high water conditions, soil water in the surface soil layer (0–10 cm) was higher in soils with biological surface crusts than those without them, while the opposite was true in the deep soil layer (30–55 cm). However, under low water conditions, surface water was lower in the presence of crusts than in their absence.

Many studies have been reported on the influence of soil crusts on the next stage in succession, the colonization and

subsequent growth of vascular plants. However, it is still often unclear what cyanobacteria contribute at this stage (Büdel 2005). The importance of nitrogen fixation in soil crusts is often stressed and much of this is likely to be contributed by cyanobacteria, whether free-living or a lichen symbiont. In a study (Lesica and Shelly 1992) of the effect of biological crusts on growth of the rare endemic *Arabis fecunda* in S-W. Montana, USA, the crusts were the pinnacle type, which has a highly dissected surface. At least three of the four phototrophs listed (*Microcoleus vaginatus*, *Nostoc commune*, *N. muscorum*, *N. punctiforme*) and several of the lichens are N$_2$-fixers. The presence of a crust favoured survival of older plants of *Arabis*, but not its recruitment.

12.4 Applications

12.4.1 Desert Reclamation

Cyanobacteria as the pioneers of biological soil crust formation can have a range of effects. These are ability to stabilize the topsoil (Hu et al. 2004), increase and maintain soil fertility (Tirkey and Adhikary 2005; Yan-Gie et al. 2011), adsorb and capture dust (Hu et al. 2002b), enhance topsoil moisture (Garcia-Pichel and Pringault 2001; George et al. 2003) and facilitate soil reclamation (Liu et al. 2001; Pankratova 2006; Obana et al. 2007). This all supports the suggestion that inoculation of cyanobacteria is a suitable biotechnological approach for reclaiming desert soils (Acea et al. 2003). However, until recently only natural soil crusts, discrete fragments and a slurry of mixed cyanobacteria and lichen have been tried in an experimental scale (Belnap 1993; Hu et al. 2002b) and on a degraded soil (Maestre et al. 2006). Several authors therefore concluded that this was underexploited opportunity for restoring soil ecosystems (Liu et al. 2001; Bowker 2007).

The practical application of cyanobacterial inoculation on the shifting sand dunes of the Qubqi (Hobq) Desert of Inner Mongolia (Fig. 12.1) commenced in 2001 (Chen et al. 2006a; Tang et al. 2007b; Xie et al. 2007). By 2005, at the end of this particular programme, the inoculated area had reached ca. 0.033 km^2 and the coverage of biological crusts was over 70%. During this period spraying of the inoculum was carried out by workers.

Since 2007 more than 4,880 m^2 race-ponds for algal culture have been built and about 25 km^2 sand dunes had been inoculated (up to 2010) in the Qubqi, Ulan Buh and Mu Us Deserts. By October 2010 another 15 km^2 had been inoculated in the Horqin (Keerqin) Sand Land and the Hulun Buir Sand Land. The results so far indicate that the crustal cover can reach 40–50% in the first year, 60–70% in the second year and more than 70% by the third year, except for sites subject to strong winds. Inoculation is accomplished using a truck (tanker)

Fig. 12.1 The flat, shifting sand region of the Qubqi Desert, Dalateqi, Inner Mongolia, with sparse short shrubs (*Parthenocissus tricuspidata*) and the grass *Elymus dahuricus* in August 2007. The area will be sprayed with a suspension of 50% *Microcoleus vaginatus*, 20% *Scytonema javanicum* and 30% *Phormidium tenue*

(Fig. 12.2) modified to provide the spray (Figs. 12.3 and 12.4). The technology combines cyanobacterial inoculation with planting shrubs (Fig. 12.5), branches or straw, the latter two being arranged in a checker-board pattern (Figs. 12.6 and 12.7). This procedure has been applied mainly to the sides of railways and highways passing through arid land and to the margins of oases and farming-pastoral zones in north China. The principle of the technology is to inoculate different cyanobacterial communities onto an unstable sandy surface taking into account the local climate, soil texture, vegetation cover and characteristics of the terrain. In lower land among sand dunes and flat patches inoculation by cyanobacteria alone has usually proved sufficient, but on steep slopes (Fig. 12.8) this needs to be combined with the branch (or straw) checker-board technique, or shrubs planted to reduce the slope before inoculation.

The short-term aim is to speed up the formation of biological soil crusts to stabilize the shifting sand surface; while the long-term or final objective is to facilitate the restoration of the soil ecosystem as a whole, including the establishment of other cryptogamic plants (eukaryotic algae, fungi, lichens, mosses), vascular plants (grass and shrub) and heterotrophs (protozoa etc.), and the enhancement of soil fertility and the reclamation of soil structure.

What have proved to be the ideal inocula for these Chinese semi-desert regions are approximately 60% *Microcoleus vaginatus*, 20% *Scytonema javanicum* and 20% *Phormidium tenue* (*Leptolyngbya tenuis*). The principle in selecting materials has been to use inocula simulating nature. It is useful to consider the roles of these three species. In more than 90% natural crusts, *Microcoleus vaginatus* contributes the most cohesion in stabilizing a sandy surface; it is the first dominant

Fig. 12.2 The vehicle carrying water for sites adjacent to the road in the eastern part of the Qubqi Desert, Jianchai, Inner Mongolia

Fig. 12.4 Spraying water up to c 100 m distance onto an area already inoculated with algal suspension. Qubqi Desert, Jianchai, Inner Mongolia

Fig. 12.3 Truck equipped with an improved sprinkler head spraying an algal suspension up to a distance of 50 m. Qubqi (Hobq) Desert, Dalateqi, Inner Mongolia, in August 2007

Fig. 12.5 The space between two rows of *Salix psammophila* planted in an area of shifting sand to be sprayed with algal suspension. Qubqi (Hobq) Desert, Dalateqi, Inner Mongolia, in August 2008

and often forms the middle layer of an algal crust. *Phormidium tenue* often forms the deep layer within the crust; although it is able to stabilize the sand surface quickly because it provides the strongest cohesion; however, it is unable to survive on most surfaces due to its weak tolerance of radiation. In the case of *Scytonema javanicum,* its ability to provide cohesion in stabilizing the sand surface is not so strong as the other two species, it is the strongest against radiation damage (both high light and UV). If often occurs in the most uppermost layer, thus protecting the species below. The combination of the three provides strong resistance to damage by wind and radiation. As all the strains were taken from local natural crusts, nothing has been done that might influence the genetic composition of natural communities.

The group involved with the project at Wuhan considered that this approach was indispensable and should be at the forefront of research in areas prone to desertification. Before this the most promising biological technique to control desertification had been limited to the planting of vascular plants in fields (Kang 1999). The trees needed several years to grow and, even if they had survived and grown, the sandy surface remained unstable due to the shrub or tree cover being less than 30%. The inoculation technology solves this problem and suits the ecological characteristics of the drought region and represents the direction in which desertification control should be achieved (Yang et al. 2001). The main difficulty is the high cost, because the mass culture of cyanobacteria is expensive and long distance trans-

Fig. 12.6 Because of the strong winds in the region, a checker-board pattern of areas is marked out with small branches before the surface is inoculated with algae. Qubqi Desert, Dengkou, Inner Mongolia, in August 2008

Fig. 12.8 The process of placing the straw checker-board on slopes before inoculation. Qubqi Desert, Dalateqi, Inner Mongolia, August 2008

Fig. 12.7 The high dunes of the Ulan Buh Desert are covered with a checker-board of branches before the surface is inoculated to reduce the effect of strong winds. Dengkou, Innner Mongolia, in March 2007

port of fresh material is not easy; unfortunately, the activity of dry powder is always much lower than that of liquid inoculum. Up to now the project has used liquid material which is harvested once the algal density has reached the required density. Culture is not synchronized, so every 1 or 2 days there is a pond ready for material to be collected, transported and inoculated.

From 2011 onwards, a Chinese private enterprise company will support the Wuhan team to extend this technique to another 133 km² in the next 5 years. The cost has to be reduced much more, as the present cost is ca. 0.15¥ per m², without taking into consideration the building expenses for the culture

ponds. The costs include the salary of occasional workers, electricity, water and transport up to a distance of 300 km.

In spite of the concern about cost, the technique has many advantages, with the formation of a biological soil crust being speeded up markedly following inoculation. Changes measured by Wang et al. (2009) were increases in soil organic carbon, total N; total salt, calcium carbonate, conductivity, crustal thickness, cohesion and chlorophyll a content. Other reported changes include increases in soil enzyme activities with inoculation time (Tang et al. 2007b), an enhanced net CO_2 exchange rate (Maestre et al. 2006), appearance of a few moss species in the second year (Wang et al. 2009) and establishment of grasses and shrubs (Wang et al. 2009). All this has convinced researchers that the technology is effective in the recovery of biological soil crusts and the restoration of soil ecosystems (Maestre et al. 2006; Wang et al. 2009). Liu et al. (2008) have even suggested that the use of inocula could be tried in controlling dust on the moon and Mars and this idea was considered in more detail by Cockell (2010). Belnap (2003) speculated on the importance of cyanobacterial crusts in the development of soils in the early history of the earth, while Beraldi and Farmer (2010) provided evidence which seems to support this. Biogenic features of the Dripping Stone Quatrzite, a siliciclastic formation in Arizona compared closely to modern biological soil crusts.

12.4.2 Soil Fertilization

Because cyanobacteria have an important role in many soil ecosystems, it is also possible to improve soil characteristics by modifying cyanobacterial populations in less extreme

situations than the deserts discussed above. Many of the ways in which cyanobacteria can influence soil were considered by Whitton (2000), but increasingly the information about these processes at particular sites is becoming more quantitative. Among more recent studies are ones on increases in available combined N resulting from cyanobacterial nitrogenase (Aranibar et al. 2003; Tirkey and Adhikary 2005), increases in available P, K, Mg, Ca, Mn and Zn (Pardo et al. 2009), total organic carbon, soil organic carbon, cation-exchange capacity, water infiltration (Warren 2001), water-holding capacity, hydraulic conductivity, mean weight diameter (Nisha et al. 2007; Obana et al. 2007), porosity (Issa et al. 1999), improved soil aggregation and seedling emergence (Rogers and Burns 1994). All of these have the potential for helping to reclaim degraded soil ecosystems (Obana et al. 2007). More specifically, cyanobacterial activity can cause agglomeration of soil particles and improve the tilth, while their application as biofertilizer and soil conditioner can reduce the use of chemical fertilizers for sustainable agriculture (Malliga and Subramanian 2002; Ibraheem 2007).

Caution must be used in trying to extrapolate results from one region to another, but the detailed information in some accounts can provide much of interest for projects elsewhere. Issa et al. (2007) reported a laboratory study on the effect of a *Nostoc* inoculum on a 1-cm layer of poorly aggregated soil from the Eastern Cape, South Africa. The *Nostoc*, which was grown from a strain isolated in Tanzania producing a large amount of EPS, was sprayed on the surface of one set of samples at an inoculum density of $3\,g\,L^{-1}$, leading to a dense superficial network of *Nostoc* and its EPS after 4–6 weeks. There was a rapid improvement in aggregate stability and this increased gradually with time and cyanobacterial growth. While it is clear that the cyanobacterium was responsible for the increased aggregation, no experiments were included to see if an equivalent addition of nutrients would have eventually stimulated growth of local strains of N_2-fixing cyanobacteria. Acea et al. (2003) tested the effect of cyanobacterial inocula on heated soil samples from N-W. Spain, which represented a sort of temporary desert that might occur after a fire. Four strains were used (*Oscillatoria*, *Nostoc*, *Scytonema* or a mixture). Inoculation induced great microbial proliferation near the surface of the heated soils, together with high increases in organic matter and nutrients. In general, cellulolytics were increased by four logarithmic units, amylolytics and ammonifiers by three logarithmic units and nitrifiers by more than two logarithmic units. No explanation was suggested for the marked increase in cellulolytics, when the cyanobacteria themselves would not have formed cellulose. Among the available nutrients the highest increase was for Ca, followed, respectively, by Mg, K, Na and P.

The authors concluded that inoculation of burned soils with N_2-fixing cyanobacteria was a very useful biotechnological approach to promoting microbiotic crust formation, enhancing C and N cycling microorganisms and increasing organic matter and nutrient contents in soils damaged by heating. It is unclear whether the most suitable strains were selected for the soils in this study, so there is considerable potential for developing the method in regions prone to fire risk. It should be easy to store suitable inocula on a sufficiently large scale to deal with problems when they occur.

The microbial cover can transform the region from an accumulation zone of water to a source zone with consequences on regional fertility transfer (Valentin et al. 2004). Reclamation is not just an accumulation process, because excess ammonium and nitrate can be leached away (Veluci et al. 2006). Addition of other material can sometimes speed the rate of development of the cyanobacterial community, such as the incorporation of pyrite, as tested by Pandey et al. (2005).

Although the extensive literature on the use of cyanobacteria and *Azolla* in rice-fields to enhance nitrogen fixation and reduce or even avoid the need for nitrogen fertilizer lies outside the scope of this chapter, it does suggest guidelines for research on the use of inocula in the development of biological crusts in arid regions. Some, though not all, the earlier research on biofertilizer in rice-fields was rather uncritical and sometimes led to conflicting results (Whitton 2000). While studies at some sites showed that soil inoculation had no effect on rice yield (e.g. Reddy et al. 1986), others did seem to provide convincing evidence of positive effects of adding cyanobacteria on the growth, yield and mineral composition of rice plants (Dhar et al. 2007; Tripathi et al. 2008). Soil inoculation also reduced the absorption by rice of Cd, Ni and As (Tripathi et al. 2008). One of the most important findings is convincing evidence for the need to use local cyanobacterial strains (Nisha et al. 2007; Swarnalakshmi et al. 2007), something that was all too often ignored in early studies on rice fields.

In arid and semiarid areas the uptake of water from the atmosphere serves as an important water source for biological soil crusts, and also vascular plants, insects and small animals. For instance, in the Qubqi Desert water uptake from the atmosphere accounted for 25.0–39.8% of total water uptake was obtained by a water vapour adsorption mechanism, the remainder being from the soil (Lan et al. 2010a). The formation of crusts promoted water uptake, but the increased uptake did not occur immediately after inoculation or crust formation. The water taken from the atmosphere increased significantly from day 15 after inoculation and the soil water content was markedly enhanced from day 20. The authors concluded that the growth of algal filaments and their secretions were the main factors increasing the rate of water uptake by the crusts and the resulting higher water content.

12.4.3 Food Exploitation

Although "Spirulina" (*Arthrospira*) is the cyanobacterium which has acquired the widest acceptance as a high nutrient food (Chaps. 25 and 26), three species of *Nostoc, N. flagelliforme*, *N. commune* and *N. sphaeroides*, have long been considered another good food; these have been a traditional delicacy in China and other parts of east and south-east Asia for many centuries. *N. flagelliforme* is the one most closely associated with semi-desert regions and its biology and practical use were reviewed by Gao (1998). The method of harvesting material with rakes was causing such environmental damage in Inner Mongolia and adjacent provinces of China, that harvesting was banned, with marked sociological effects (Roney et al. 2009). This in turn stimulated research on its possible commercial large-scale culture. Its developmental stages in indoors have been described in some detail (Gao and Ye 2003; Liu and Chen 2003; Su et al. 2007), but so far no breakthrough has been achieved in culture techniques permitting large-scale culture. Further research is needed to establish how to get rapid growth while providing what may prove to be an obligate requirement, the alternating wet and dry conditions mentioned earlier. It may also be possible eventually to combine methods for the development of biological soil crusts with ones that permit growth of *N. flagelliforme* without harvesting leading to the crusts being damaged.

The macroscopic colonies of *Nostoc commune* are found world-wide, although the name is known to include genetically diverse organism (Potts 2000). It is easy to collect large amounts from many sites world-wide, where it is subject to alternate wetting and drying, though typically a greater proportion of the time in the wet state than *N. flagelliforme*, which suggests that it should be easier to develop large-scale culture methods for *N. commune* if it proved economically worthwhile to do so. Nevertheless Chen et al. (2011) established laboratory conditions where showed a 250% increase in *N. flagelliforme* in 25 days under laboratory conditions with much lower temperatures and light flux than likely to occur in natural populations in summer, so it may prove economically possible to grow this species as well. *N. sphaericum* is the species most associated with wet environments and its life cycle was described by Becerra-Absalon and Tavera (2009).

Mass culture of the near-spherical colonies has been achieved at the Institute of Hydrobiology, Wuhan, and the product is being widely sold in markets in China, with a good profit. Nevertheless, it is important to remember the possibility of toxic strains when developing methods for large-scale culture of *Nostoc*. All 21 *N. commu*ne samples bought at markets in Peru showed the presence of β-N-methylamino-L-alanine (BMAA), a neurotoxic amino-acid (Johnson et al. 2008) The diversity of forms, especially those named *N. commune*, means that every species or strain grown for food should be tested rigorously before it is marketed. *Nostoc* culture is considered further in Chap. 26.

12.4.4 Utilization of Exopolysaccharides

The importance of cyanobacterial EPS in biological crust formation and improving soil structure has already been mentioned several times and the biological roles for the organisms are discussed in Chap. 18. Pereira et al. (2009) reviewed its composition, function and factors affecting synthesis and an investigation of the factors important in its formation by *Microcoleus vaginatus* was reported by Xie et al. (2008). Many studies have reported on how the various properties could be put to practical use. There is information about protection from desiccation, tolerance to salt and alkali, antibiotics, ultraviolet radiation (Mazor et al. 1996; Stal 2000; Chen et al. 2002, 2003a, b; Tang et al. 2007a), increase in crust cohension (Hu et al. 2002b), the formation of soil aggregates, utilization of phosphorus and release of trace elements, and removal of heavy metals (De Philippis et al. 2001, 2003, 2007; Micheletti et al. 2008) and immobilization of enzymes, especially phosphomonoesterase (Whitton et al. 2005). These indicate the possible uses of EPS in amelioration of desert soil (Painter 1993) and removal of heavy metals from polluted water (De Philippis et al. 2003, 2007; Micheletti et al. 2008), whether as isolated EPS or by growth of organisms with a high EPS content.

The most important feature of EPS is its high and varied bioactivity (Garbacki et al. 2000). In order to understand and perhaps exploit the EPS of edible *Nostoc* their chemical properties have been analyzed in some detail (Huang et al. 1998; Helm et al. 2000). Several desert strains have been used for the analysis of monosaccharide linkages, chemical structure and physical properties (Hu et al. 2003a; Hokputsa et al. 2003). Other studies include ones on anti-tumour and anti-inflammatory activities (Garbacki et al. 2000; Zhang et al. 2008) and the positive nematicidal potential of culture filtrates of *Microcoleus vaginatus* (Khan et al. 2005).

12.4.5 Other Substances of Potential Use

Because cyanobacteria in arid environments are under stress, it seems likely that these will prove an important source of molecules with potentially useful properties. Among the many studies investigating the effects of cyanobacterial extracellular materials on other organisms, soil isolates were tested by Safonova and Reisser (2005) and terrestrial ones by Svircev et al. (2008). A number of researchers have shown an interest in possible uses for the photoprotectants, scytonemin and the mycosporine-like amino acids (e.g. Kulik 1995; Rastogi and Sinha 2009). Scytonemin production

increases in cyanobacteria which can form the molecule (Harel et al. 2004; Fleming and Castenholz 2008; Pattanaik et al. 2002: see Chap. 19). Genomic and gene analysis of scytonemin biosynthesis in *N. punctiforme* has been carried out (Soule et al. 2007, 2009) and the initial biosynthetic steps established (Balskus and Walsh 2008).

12.5 Practical Methods

12.5.1 Stabilization of Topsoil

12.5.1.1 Wind-Tunnel Testing

The effects of wind speed have been tested on both individual colonies and soil crusts. A wind of 2.0 m s^{-1} led to the mass of *Nostoc flagelliforme* colonies decreasing to 50% 2.8 times faster than in still air, while a further rise to 3.4 m s^{-1} led to it being 4.9 times faster; this was the stage at which photosynthetic efficiency started to be affected (Gao et al. 1998). Proper wind tunnels are needed for tests on the stability of soils against wind erosion and experiments have been conducted on both biological and physical crusts (Liu et al. 1994; McKenna-Neuman et al. 1996; Hu et al. 2002a). Earlier studies (Liu et al. 1994; McKenna-Neuman et al. 1996) expressed results as the change in mass of an eroded soil, so the data failed to reflect actual cohesion of the topsoil. The method has now been modified to express the results on an areal basal – the portion of erosion area affected (Hu et al. 2002a). Another problem is that natural crusts are often a mixture of cyanobacteria, eukaryotic algae, fungi, lichens and mosses in varying proportions, so it is necessary to make a cyanobacterial crust in order to measure cyanobacterial cohesion. Test are carried out in a straight-line suction wind tunnel, which provides laminar air flow at a slow velocity.

The practical methods are as follows.

Preparation of artificial algal crust

1. Fill flat rectangular containers (e.g. 30×40×2.8 cm trays with small holes at the bottom for drainage) with unconsolidated local sand to a depth *ca*. 5 mm below the height of containers. The surface of the sand is levelled by drawing a straight bar along the edges of the top of the tray from end to end, then soaked with water, but without any water accumulating on the surface.
2. Inoculation. A slurry of ground and homogenized cyanobacterial material is sprayed onto the sand surface for a fixed time using a water jug with spray nozzle. Four replicates are used for each treatment in every experiment. The containers are then moved outdoors or to a greenhouse for at least a week in order to be 'trained' – an essential step. If a greenhouse is used, it should have natural light conditions (canopy of transparent plastic sleeting). The final water content and cyanobacterial biomass of air-dried sands are determined before the wind tunnel experiments by subsampling the plots outside the test area (Hu et al.

2002a). The control surfaces are not inoculated, but are treated similarly with water or BG11 medium.

Wind-tunnel test

1. Sufficient local unconsolidated sand is delivered into the air stream at the entrance of the tunnel working section, upstream of the crust surface.
2. The floors of the working section of the tunnel is covered with a thin wood sheet and the containers are placed in the tunnels with their long dimensions parallel to the tunnel. The cyanobacterial crusts are level with the tunnel ground to maintain laminar, non-turbulent flow.
3. The degree of wind erosion is expressed as % of a 30×30 cm square showing damage to the crust. Wind speed is measured with a pitot tube, with different speeds tested during the course of the studies. Prior to testing the crusts, the effects of very low moisture on threshold friction velocity are tested, so that the effect of moisture can be separated from the effect of cyanobacterial growth.

Field data can be used to indicate the wind velocity required for the initiation of saltation, the threshold friction velocity (TFV), the aerodynamic roughness length and the wind profile above sand surfaces covered by biological crusts. The drawback of this laboratory tunnel is that it cannot be moved easily. Basis on a similar principle, a portable wind tunnel was invented, which has been used by Belnap and Gillette (1998) and Eldridge and Leys (2003) for many studies. They found TFVs of undisturbed crusts well above the wind forces experienced at the sites and the cover of biological crusts was significantly positively correlated with dry aggregation levels greater than 0.85 mm.

12.5.1.2 Press-Resistance Testing

As well-developed natural crusts can withstand more than a 25 m s^{-1} sand-holding wind, the method of sand wind tunnel is unable to reflect differences in their strength (Hu et al. 2002a), so testing the press-tolerance strength is very important. The press-resistance cohesion can measure by using a penetrometer (A-0152), which has been used in a number of studies (Hu et al. 2002a). The calculated formula is

$$\rho = 100X / 0.7952 (40 - X)^2$$

where ρ is press-resistance cohesion (g cm^{-2}), X is recoiled length (mm).

Concerning this instrument, an important question is the angle of penetration.

12.5.1.3 Flexure Testing

The flexure test was invented and used by McKenna-Neuman et al. (1996), the principle of apparatus being to test the blending moment resisted by interial stresses set up in the crust. The modulus of elasticity for a load is determined from

$$E = Wl^3/48I(\Delta y)$$

where W is load at the elastic limit, *l* is length of the crust, *I* is the moment of intertia, Δy is the deflection of the crust in the direction of the applied force.

As samples need to be collected and separated from the soil below when measured, the results of such flexure tests may not always be suitable for assessing cohesion *in situ*. Although direct comparisons have not yet been made, we suggest that flexure testing provides more realistic information for biological soil crusts, while the penetrometer is more useful for physical crusts. Langston and Neuman (2005) found that strong salt crusts tested with a penetrometer were easier to break down and erode than relatively weak biotic crusts. This may be the reason why the relationship between algal biomass and press-cohesion is not as tight as that of the cohesion against wind erosion (McKenna-Neuman et al. 1996; Belnap et al. 2007; Xie et al. 2007). Inorganic minerals and soil texture are mainly affected by press cohesion, organic matter and biological components by flexure cohesion, whereas the data from wind tunnel studies reflect an integrated cohesion (Hu et al. 2002b).

12.5.1.4 Visual Technique

In order to assess conveniently the stability of cyanobacterial dominated crusts, Belnap et al. (2008) put forward a visual technique based on soil surface darkness. The research team at Wuhan also had realized this phenomenon and used the principle when collecting samples (Hu et al. 2003c), and found there was high repetition in the results. Two problems remain to be solved. (1) The effect of soil texture and light regime on darkness of the crust needs to be validated further. (2) How the index categories can be applied under different climatic still needs to be investigated.

12.5.2 Assessment of Biomass

Selecting the best ways to measure biomass has been a persistent and complex problem throughout the study of terrestrial algae. Some of the earlier problems and successes were included in the review by Whitton (2000). Hu and Liu (2003b), who attempted to compare direct counts, dilution plate techniques and measurements of biovolume and chlorophyll a, then put forward a relatively exact method to quantify algal biomass to the species level. This was a version of the biovolume technique, but it is time-consuming and rather inconvenient. When studying saline land in Japan, Tsujimura et al. (2000) concluded that culture dilution was suitable for spatial, but not seasonal studies. Prasanna et al. (2006) developed the most probable number method to isolate and count cyanobacteria simultaneously. This was a more elaborate approach to a procedure which has sometimes been used in rice-field studies. It involved the use of 96-well plates holding 0.3 mL per well. The technique could also be used for isolating cyanobacteria by isolating colonies in the gel matrix; sampled

could be stored at room temperature without loss of viability for 5–6 weeks. This technique was suitable for large sample sizes. Nevertheless the Wuhan team prefers direct observation or a combination of direct counting and molecular analysis; enrichment culture is used just for identification.

Chlorophyll a content is commonly used as an indicator of cyanobacterial biomass (Bowker et al. 2002), while the presence of chlorophyll b in addition can provide an estimate of crust recovery, with an increasing ratio between the two indicating an increasing contribution by green algae and mosses (Rychert 2002). Pigment extraction is a particular problem with crusts, because of the range of other pigments that may be present, especially those associated with lichens, becomes an increasing problem as crusts develop. Lan et al. (2011a) reported significant differences in the efficiency of various organic solvent. Dimethyl sulphoxide (DMSO) provided the highest extraction efficiencies, but was unsuitable for crusts containing a substantial proportion of other pigments. N,N-dimethyl-formamide not only showed low extraction efficiencies, but also the efficiency was easily affected by interfering pigments in well-developed crusts. In general, ethanol was more effective than acetone and also provided more stability and greater safety. Methanol has been used in many previous studies on chlorophyll extraction of dried cyanobacterial samples, usually following the procedures of Marker et al. (1980) and Marker (1995). However, its use for the projects at Wuhan and elsewhere in China has largely ceased because of its greater toxicity than ethanol.

12.6 Desert Endoliths

When conditions become too severe for cyanobacteria to grow in soils, they are restricted to chasmolithic, endolithic or hypolithic growths (see Chap. 10) associated with rocks. In extreme cases, such as in Beacon Valley in the McMurdo Dry Valleys, Antarctica, studied by Pointing et al. (2007, 2009; Sect. 14.2.1), rocks provide isolated "islands" of colonization, as soils in the more extreme environments appear to be free of phototrophs. Deserts with translucent rocks almost always have endolithic or hypolithic cyanobacterial growths, though the colonization frequency in the most arid regions may be very low (see below). In the case of deserts where quartz forms a pavement, the cyanobacterial layer occurs under the pavement i.e. truly hypolithic. Such communities have been described from the Mojave Desert (Schlesinger et al. 2003) and the deserts in China studied by Warren-Rhodes et al. (2007a, b) and also several regions in Antarctica (Broady 2005; Wood et al. 2008). The growths are usually dominated by the form-genus *Chroococcidiopsis*, which is extremely resistant to ionizing radiation and desiccation (Billi et al. 2000; Cockell et al. 2005). Desert sandstones, which typically have chasmoliths as well as endoliths, usually also have *Chroococcidiopsis* morphotyes. Phylogenetic

analyses of *Chroococcidiopsis* populations from deserts in 18 different regions of the world showed no evidence of recent inter-regional gene flow, indicating that populations have not shared common ancestry since before the formation of modern continents (Bahl et al. 2011). The authors concluded that the global distribution of desert cyanobacteria has not resulted from widespread contemporary dispersal, but is an ancient evolutionary legacy. However, their study dealt only with Chroococcidiopsis, perhaps the organism most closely adapted to the desert environment, so caution should be used in generalizing to other genera until phylogenetic studies have been done on them.

In contrast to most studies of desert quartz, Pointing et al. (2007) found that quartz in the McMurdo Dry Valleys of the Antarctic is dominated by Oscillatoriales; in this case the range of cyanobacterial genera increased as conditions become slightly more favourable. The communities are usually visible as green layers or clumps, but Lacap et al. (2011) reported that some hypolithic communities in the Atacama Desert are red due to dominance by diverse chloroflexi, which they suggested might occur under more nutrient-rich conditions.

The extent to which individual translucent rocks have cyanobacterial communities differs markedly between sites. Near-100% colonization was reported for the warm Mojave Desert (Schlesinger et al. 2003). A small-scale ecological survey in the central southern region of the Tibet Autonomous Region in China (29°07′ N, 85°05′E, alt. 4,638 m) found that 36% of quartz rocks were colonized. Lower values occur in the Taklimakan and Qaidam Basin deserts of western China, where colonization of the available habitat ranged from 0.37% to 12.6%, with the lowest values at cold dry desert sites (Warren-Rhodes et al. 2007b). In the last study differences between sites were most strongly correlated with moisture-related variables, but patchiness within sites was correlated with local geology, there being more frequent colonization on large rocks; dispersal during rainfall was also an important factor. In the study of the hyper-arid core of the Atacama Desert by Schlesinger et al. (2003), the frequency of colonization was very low – only 3 out of 3,723 stones in an area >2,000 m^2. Further studies on the limits for cyanobacterial growth in the Atacama Desert have been reported by Warren-Rhodes et al. (2006) and Wierzchos et al. (2006). *Chroococcidiopsis* morphotypes were absent at the most extreme arid sites, but one was recorded in halite evaporite rocks in the driest part of the desert, where not even quartz rocks were colonized (Wierzchos et al. 2006). Warren-Rhodes et al. (2006) concluded that hypoliths in the Atacama are very long-lived, possibly persisting for thousands of years. However, disturbed hypoliths seldom survive, indicating the importance of the substrate being stable (Lacap et al. 2011).

Several studies have provided detailed accounts of diversity at particular sites using molecular techniques. In the case of the quartz pavement in central Tibet, where a cold desert tundra environment has persisted over a geological timescale, profiling using terminal restriction fragment length polymorphism revealed no significant difference in community structure between rocks (Wong et al. 2010). The hypolithon was dominated by cyanobacterial phylotypes, with relatively low frequencies of other bacterial phylotypes. In addition to four *Chroococcidiopsis* clones, the cyanobacteria included many filamentous ones (*Nostoc*, *Leptolyngbya*, *Phormidium*, *Pseudanabaena*, *Oscillatoria*, *Microcoleus*, *Plectonema*).

Among the many questions still requiring clear-cut answers is the extent to which maintenance of populations in endolithic communities depends on long-lived cells repairing stress damage or whether there is a turn-over of cells, with those dying being replaced by new cell growth. This was investigated by Billi (2009) for a laboratory strain of *Chroococcidiopsis* (CCMEE 029), which had been stored in a desiccated state for 4 years. Live and dead cells were found in dried cell aggregates and the author suggested that subtle modifications to the cell environment are required to dry without dying. The cells avoiding or reducing subcellular damage showed a variety of responses, including avoiding or limiting genome fragmentation and genome covalent modifications, and preserving intact cell surface membranes and phycobiliprotein autofluorescence.

The importance of nutrient cycling within the sandstones of the Beacon Valley was made clear by Banerjee et al. (2000b), who compared phosphomonoesterase and phosphodiesterase activities of the endolithic communities from three different types of rock, which had three different dominants: *Chroococcidiopsis*, mixed *Gloeocapsa* and the green alga *Trebouxia*. Although some dead cells were observed (B.A.W., unpublished), no attempt was made to compare the ratio of live to dead for the three genera. The optimum pH values for phosphomonoesterase activity were 9.5, 5.5 and 8.0, respectively, all of which corresponded quite closely to the pH values of the three aqueous rock extracts. The communities showed significantly higher phosphomonoesterase activity at 5°C than 1°C, and two of them showed much higher activity at 5°C than 10°C. All three had slightly lower activity in the light (8 µmol photon m^{-2} s^{-1}) than the dark and prior exposure to light also led to lower subsequent activity in the dark. However, an axenic isolate of *Chroococcidiopsis* showed various physiological differences from that of the same organism in crushed rock fragments, especially a much higher temperature optimum (Banerjee et al. 2000a); this suggests that the physiology of the organized is influenced by being immobilized within the rock. As P is scarce in the Beacon Sandstone and more likely to be a limiting element for growth than C or N, its cycling within a particular rock type is probably a key factor influencing metabolic activity of the community.

Another unanswered question is the extent to which *Chroococcidiopsis* fixes nitrogen in these environments.

Friedmann and Kibler ([1980]) concluded that polar and other endolithic cyanobacteria largely used abiotic nitrogen sources, but N$_2$ fixation was reported in *Chroococcidiopsis*-dominated communities endolithic in gypsum in an alpine environment (Boison et al. [2004]) and all eight strains of *Chroococcidiopsis* mentioned by Rippka et al. ([2001]) synthesized nitrogenase under anoxic conditions. In view of the phylogenetic diversity of the form-genus *Chroococcidiopsis* (Billi et al. [2010]; Bahl et al. [2011]), it will require studies on a wide range of communities before the situation is clear.

12.7 Conclusions

There is now a great deal of information about cyanobacteria and other microalgae in desert and semi-desert regions, especially in areas where at least part of the surface is covered in biological soil crusts. The role of these crusts in stabilizing soils, reducing desertification and in some cases helping to reverse it, is well established. Examples of reclamation are increasing, especially in China, and the review makes clear the importance of research on the biology of the crusts and the practical methods for encouraging their development, including inoculation and minimizing damage by trampling and livestock. Most accounts mention the importance of cyanobacteria, especially during the early stages. However, it is still difficult to generalize on the organisms and processes leading to biological soil formation under different types of desert environment – for instance those dependent on rare rainfall events versus those dependent on dew formation, or the effects of different light regimes. It is essential to be able to do this, if the research and practical experience gained in countries such as China are to be applied to parts of the world like East Africa, where steps to reduce desertification are urgently needed, yet there is little local scientific knowledge or skill to put them into practice. Greater standardization of sampling and analytical methods, together with a more critical statistical evaluation of the data would make it easier to generalize between studies.

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