

# Microbial diversity in desert ecosystems

Ashish Bhatnagar\* and Monica Bhatnagar

Department of Microbiology, Maharshi Dayanand Saraswati University, Ajmer 305 009, India

**Deserts are apparently lifeless. Yet there appear a number of microhabitats that are inhabited by microorganisms. Since stress allows only the tolerant forms to grow, the microorganisms not only dominate such habitat but also grow sufficiently to impart special visible features to the habitat. We discuss here diversity and microbiology of specialized habitats of deserts, viz. patina (desert varnish), cryptobiotic crusts, saline playas and rhizosheath.**

THE Earth Summit of 1992 in Rio de Janeiro brought into focus the danger of desertification that affects some 40% of global lands and nearly one billion people. It is caused primarily by human activities that increase it at an alarming rate of some half million hectares annually.

Deserts are characterized by lack of moisture (annual rain  $\leq 254$  mm) as a result of which biological activities are regulated by ephemeral water availability. However, total water availability is defined by the interaction of precipitation, temperature, evaporation and evapotranspiration. Based on the vegetative cover and total precipitation, arid ecosystems are called desert, semidesert, steppe, subdesert, semiarid or arid grasslands. These are often located in regions along both, the Tropic of Cancer and the Tropic of Capricorn. Deserts are composed of sand that is larger and rounder than the sea beach sand. There are 22 deserts in the world. Meigs<sup>1</sup> estimated that 19% ( $27.6 \times 10^6$  km<sup>2</sup>) of the global land is arid deserts and 14.6% ( $21.2 \times 10^6$  km<sup>2</sup>) covers area defined as semi-arid deserts excluding Antarctica. Due to extreme variations in geoclimatic patterns, the global arid biome consists of highly diversified and heterogeneous ecosystems.

The dry climates of the continents occur in five great provinces separated from one another by oceans or by wet equatorial zones. Of these five provinces, North African-Eurasia is larger than rest of the four combined. The world's largest desert Sahara and a series of other hot deserts and semi-arid areas continue eastward through the Arabian peninsula along the Persian Gulf of Pakistan, and India fall in this province<sup>2</sup>. It also includes cold deserts from states of the former Soviet Union through China to Iran. The tropical desert of Asia extends to India through Rajasthan and Gujarat where it is called the Thar. The Thar lies west of Aravalli Range in Rajasthan and covers an area of about 196,150 km<sup>2</sup>. It is subjected to intense

winds and wide variations in temperature ranging from a minimum of 5°C to a maximum of 45°C. It is dotted with numerous water reservoirs including four major inland saline playas.

## Soil microorganisms

Microbial activity in desert soils is highly dependent on characteristics such as temperature, moisture and the availability of organic carbon<sup>3-5</sup>. Of these, moisture availability is the major constraint affecting microbial diversity, community structure and activity. Populations of aerobic bacteria in deserts across the world are reported to vary from  $< 10$  in Atacama desert to  $1.6 \times 10^7$  g<sup>-1</sup> in soils of Nevada<sup>6</sup>. Sand dunes from Thar are reported to have relatively smaller population ( $1.5 \times 10^2 - 5 \times 10^4$  g<sup>-1</sup> soil)<sup>7,8</sup>. Gram-positive spore formers are dominant and the populations do not decline significantly even during summers<sup>9</sup>. Actinomycetes may constitute ~50% of the total microbial bacterial population in desert soils. However, Hethener<sup>10</sup> reported only 1–2% representation of actinomycetes in the sandy soils of Tassili N' Ajjer. Dominant microflora of desert soils is made up of coryneforms, i.e. *Archangium*, *Cystobacter*, *Myxococcus*, *Polyangium*, *Sorangium* and *Stigmatella*; sub-dominant forms comprise *Acinetobacter*, *Bacillus*, *Micrococcus*, *Proteus* and *Pseudomonas*. Cyanobacteria also contribute significantly ( $0.02$  to  $2.63 \times 10^4$  g<sup>-1</sup> soil) to the biota of hot arid regions in terms of primary productivity and nitrogen fixation<sup>11</sup>. The dominant cyanobacterial forms of Thar desert are *Chroococcus minutus*, *Oscillatoria pseudogeminata* and *Phormidium tenue*; *Nostoc* sp. dominates amongst heterocystous forms. Fungal populations as viable propagules range from nil to  $6.3 \times 10^3$  in Uzboi desert Takyr<sup>12,13</sup>. The dominant genera include *Aspergillus*, *Curvularia*, *Fusarium*, *Mucor*, *Paecilomyces*, *Penicillium*, *Phoma* and *Stemphylium*. Xeric mushrooms such as *Coprinus*, *Fomes*, *Terfezia* and *Termania* have also been reported from deserts<sup>14</sup>.

## Rhizosphere

Rhizosphere is an important site of microbial activity in desert soils, since it provides ample carbon substrate in an otherwise organic matter poor arid soil. The rhizosphere effect is therefore more pronounced in deserts both, qualitatively and quantitatively than in other soils<sup>3,15</sup>. Despite this, rhizosphere and rhizosheaths in desert plants have been studied only scantily.

\*For correspondence. (e-mail: aridgaba@hotmail.com)

Generally R : S (rhizosphere : soil) ratio is high in arid soils for nearly all metabolic types of bacteria (viz. heterotrophs, diazotrophs, cellulolytes and nitrifiers) and fungi in most plants studied<sup>8,16-18</sup>. Yet the rhizosphere effect on different groups of microorganisms varies from one plant species to other<sup>8</sup>. Of six desert range plant species of Iraq, namely *Acillea* sp., *Aristida plumosa*, *Artemesia herba-alba*, *Haloxylon articulatum* and *Heliotropium ramosissimum*, rhizosphere of *Aristida plumosa* had maximum *Azotobacter* population while *Artemesia* sp. the least<sup>19</sup>. Khathuria<sup>8</sup> observed that *Datura metal* did not have any significant effect on total heterotrophic count, but showed a high R : S ratio for diazotrophs, nitrifiers, actinomycetes and fungi. The high density of microorganisms in a shrub rhizosphere is suggested to have an important effect upon root litter decomposition<sup>20</sup>.

The soil zone penetrated by fine roots and held together by mucilage is called the rhizosheath. Numerous tiny fine roots present on the main root, coat the surrounding soil with mucilage and modify the soil in contact<sup>21</sup>. The largest, most coherent soil rhizosheaths are formed on the roots of grasses in dry soil<sup>22</sup>. Although ascribed to many plant species, it is especially pronounced in various species belonging to the family Poaceae<sup>6</sup>. Dry conditions allow formation of rhizosheaths that are larger, more coherent and more strongly bound to the roots than those formed in wet soils. Drier soil also enhances adhesiveness of rhizosheath mucilage and the formation of root hairs; both effects stabilize the rhizosheath. Young<sup>23</sup> found that rhizosheath soil was significantly wetter than bulk soil and suggested that exudates within the rhizosheath increased the water-holding capacity of the soil. Furthermore, it has been proposed that in dry soil, the source of water to hydrate and expand exudates is the root itself. The exudates released from the roots at night allow the expansion of the roots into the surrounding soil; when transpiration resumes, exudates begin to dry and adhere to the adjacent soil particles<sup>24</sup>.

*Bacillus polymyxa* and the fungus *Olpidium* are found associated with rhizosheaths. *Ancalomicrobium* and *Hypomicrobium*-like organisms are also present<sup>25</sup>. Rhizosheaths are important because of the associated diazotrophs and enhanced water retention and nutrient uptake<sup>22,26,27</sup>.

In the rhizosphere of desert plants mycorrhiza play a very significant role in plant nutrition and stabilization<sup>28</sup>. Well-developed mycorrhizal communities from deserts are often instrumental in determining the community structure of the area. Most species in families of Asteraceae, Fabaceae, Poaceae, Rosaceae and Solanaceae usually form endomycorrhizal associations in arid habitats<sup>6</sup>. Trappe<sup>14</sup> listed 264 plant species from arid and semi-arid environments that had mycorrhizal-based root colonization, and approximately 25% species exhibited specific associations with endomycorrhizal fungi. *Glomus deserticola* is indigenous to many desert soils<sup>14</sup>. Kiran Bala *et al.*<sup>29</sup> reported >50% infection by vesicular-arbuscular

mycorrhizal (VAM) fungi in 17 tree species of the Indian desert, with genera *Glomus* and *Gigaspora* being dominant. *Opuntia* and *Euphorbia* showed considerable root infection. *Gigaspora margarita*, *Glomus fasciculatum*, *G. mossae* and *Scutellospora calospora* have been reported from the rhizosphere of *Prosopis juliflora*<sup>30</sup>. In desert, incidence of arbuscular mycorrhiza (AM) infection varies with the availability of water<sup>31</sup> and with composition of the plant community<sup>32</sup>. Therefore deep-rooted habit along with AM infection of desert vegetation is an important survival mechanism to compete for water and nutrients with the shallow rooted and fast-growing plant species. During the slow succession process, a characteristic of arid habitats, mycorrhizal plant species gradually replace the nonmycorrhizal plants<sup>33</sup> due to the competitive edge that the former possesses. Cul and Nobel<sup>34</sup> reported improved hydraulic activity, increase in CO<sub>2</sub>, water and nutrient uptake in the desert succulents, viz. *Agave deserti*, *Ferocactus acanthodes* and *Opuntia ficus-indica*. Mycorrhizae are also known to restore soil productivity by ameliorating and enriching soil organic carbon, as observed in *Prosopis juliflora* inoculated with *G. caledonium*<sup>30</sup>.

Desert truffles, as they are known, are members of the family Terfeziaceae, order Tuberales that include several genera of hypogeous mushrooms, renowned for their culinary value. Members of *Terfezia* and *Termania* sp. are mycorrhizal on the roots of members of family Cistaceae such as *Helianthemum*<sup>35,36</sup> and are found in arid and semi-arid zones of the Mediterranean basin in Iraq and Kuwait, the Sahara and Saudi Arabia<sup>37</sup>, Hungary<sup>38</sup>, China<sup>39</sup> and in the Kalahari desert<sup>37</sup>. They are also found in South Africa in association with other plants since the family Cistaceae does not occur in this region. Termanias and Terfezias are variable in their mode of mycorrhizal association. While *Terfezia leptodenia* forms special Terfezia type ectomycorrhizal associations, *T. claveryi* forms endomycorrhizal associations<sup>40</sup>.

Mycorrhiza also help in desert reclamation and soil stabilization. They link soil particles to each other and to the roots in part by producing glomalin, an important glue that holds aggregates together. Panwar and Vyas<sup>41</sup> reported beneficial effects of *Acaulospora mellea*, *Gigaspora margarita*, *G. gigantea*, *Glomus deserticola*, *G. fasciculatum*, *Sclerocystis rubiformis*, *Scutellospora calospora* and *S. nigra* on *Moringa concanensis* and proposed use of such AM fungi in conservation of this endangered multipurpose tree species in the Indian desert.

## Surface features of the soils

A considerable portion of global desert is covered by hardened surfaces variously called as desert pavements or desert crust. Soils, rocks and dead plant surfaces may have a cover of black, brown, gray, green, yellow or orange coloured crusts. Similarly rocks or desert pavements may

**Table 1.** Number of genera observed in representative groups of soil crusts (based on Büdel, 2001 and 2002)<sup>46,47</sup>

Group	Total	South America	Australia	Africa	Middle East	North America	Asia	Europe	Greenland
Cyanobacteria	35	15	10	18	14	17	17	18	Nk
Euk. Algae	68	3	5	12	13	34	9	26	Nk
Cyanolichen	13	Nk	4	4	8	8	7	5	4
Phycolichen	69	Nk	22	15	8	36	17	29	38
Mosses, liverworts	62	5	42	7	8	26	2	14	Nk

Nk: Not known.



**Figure 1 a, b.** Cryptobiotic crust (marked by arrows) on soil (a) helps binding the soil and immobilizing the dunes. Over a rock surface (b) the cyanobacteria dominated crust (black patches) largely concentrates where soil could have accumulated more, so as to provide sufficient nutrition. Such growth helps them in entering the crevices and fissures.

have films or varnishes of different colours, few of which are biogenic in nature.

### Soil crust

Crusts on soils are formed by microorganisms and microphytes. These are variously called as cryptogamic/cryptobiotic/biological/cyanobacterial/microphytic crusts<sup>42</sup>. More in vogue is the term ‘cryptobiotic crust’ and therefore we shall use it to refer to the biological crusts on soils. A consortium of green algae, cyanobacteria, lichen, fungi, bacteria, diatoms, mosses and liverworts form cryptobiotic crusts. Mosses and liverworts seem to favour the comparatively more mesic sites. Cyanobacteria favour the harshest sites, and lichens dominate in intermediate sites<sup>42</sup>. In the most extremely arid deserts of the world, Atacama<sup>43</sup> and Namib<sup>44</sup>, crusts dominated by cyanobacteria are the only plant growth present. However in others, involvement of one or more of these components in the formation of such crusts is known. Belnap<sup>45</sup> classified soil crusts on the basis of surface roughness and presence of frost heave. Accordingly, frost heave is absent in ‘smooth’ (0–1 cm roughness formed by green algae and cyanobacteria) and ‘rugose’ (1–3 cm surface roughness with lichens and mosses above ground and cyanobacteria inside the soil), but present in ‘rolling’ (1–5 cm roughness)

and ‘pinnaced’ (3–10 cm roughness) crusts. Crust with frost heave has lichens and mosses forming a canopy covering the soil surface with cyanobacteria embedded inside the soil. Table 1 shows the genera reported from the dominant groups inhabiting cryptobiotic crusts in hot and cold deserts of the world.

Thin layers of cryptobiotic crusts of soil take 5–7 years to build whereas formation of centimetres deep layers may take more than 100 years. Soil type appears to affect community structure of cryptobiotic crusts significantly, indicating that soil characteristics select for specific cyanobacteria<sup>46</sup>. Such crusts are usually absent in sandy soils subjected to aeolian sand movement. Stabilized conditions however support crusts in both tropical and subtropical deserts and also in arid temperate regions. Cyanobacterial crusts (Figure 1a) generally dominate poor sandy soils. Lichens increase proportionately with carbonates, gypsum and silt content of the substrate<sup>6,47,48</sup>. *Microcoleus chthonoplastes* is dominant in saline sand crusts<sup>48</sup>. In arid environments, specifically Central European steppe, the Mediterranean, North American, Australian and African desert and semi deserts, the most common lichens in the cryptobiotic crusts are *Catapyrenium* sp., *Collema* sp., *Diploschistes* sp., *Endocarpon* sp., *Fulgensia fulgens*, *Psora decipiens*, *Squamarina* sp. and *Toninia sedifolia*<sup>47</sup>. Cyanobacteria are more widely distributed than the eukaryotic algae. The most common genera are

*Microcoleus* (*M. chthonoplastes*, *M. paludosus*, *M. sociatus* and *M. vaginatus*) and *Nostoc* sp. Other forms are *Calothrix*, *Lyngbya*, *Oscillatoria*, *Phormidium*, *Scytonema* and *Tolypothrix*. Common green algae of soil crusts are *Chlor-ella*, *Chlorococcum*, *Coccomyxa* and *Klebsormidium*. Typical mosses belong to *Bryum* sp., *Crossidium* sp. and *Tortula* sp. *Riccia* is the most widespread genus amongst liverworts followed by *Fossombronia*<sup>47</sup>.

Cryptobiotic crusts are also associated with a wide range of bacteria and fungi. Fungal hyphae penetrating deep into the soil contribute to crust stabilization. Dominant fungal genera in crusts are *Alternaria*, *Fusarium* and *Phialomyces* whereas in non-crusts soils, *Alternaria* and *Penicillium* dominate followed by *Fusarium*. Approximately 90% of the aerobic bacterial population of cryptobiotic crusts consist of coryneform bacteria<sup>6</sup>.

Diversity studies on 32 samples of cryptobiotic crusts at Thar desert in India showed 43 morphotypes of diazotrophs in BG 11-N enrichment and 71 of algae and cyanobacteria in the same medium supplemented with nitrogen<sup>11</sup>. Most frequent form was *Phormidium tenue*. In the case of diazotrophs the most frequent forms were *Nostoc punctiforme*, *Nostoc commune* and *Nostoc pallidum*. Cyanobacterial presence was influenced by their plant partners. *Alternaria* sp. was the dominant fungus in these crusts. However lichens, mosses and liverworts were absent.

In an attempt to use molecular approaches, Garcia-Pichel *et al.*<sup>47</sup> failed to retrieve signals for otherwise conspicuous heterocystous cyanobacteria with thick sheaths suggesting that the diversity found in desert crusts was underrepresented even in currently available nucleotide sequence databases. Amongst the non-heterocystous filaments, several novel phylogenetic clusters were identified. *Microcoleus vaginatus* Gomont was dominant and frequent and a new phylogenetic cluster, named *Xeronema* grouped a series of thin filamentous *Phormidium* like cyanobacteria<sup>48</sup>.

Cryptobiotic crusts in deserts are thought to play an important role in the biogeochemistry and geomorphology of arid regions<sup>50,51</sup>. They reduce soil erosion<sup>50</sup>, contribute organic carbon<sup>52</sup>, may fix nitrogen<sup>53</sup> and either promote survival of vascular plant seedlings<sup>54,55</sup> or affect them adversely<sup>56</sup>. Nitrogen fixation rates of 2 to 41 kg N ha<sup>-1</sup> year<sup>-1</sup> have been reported, however, high nitrogen fixation rates do not automatically mean that the productivity of plants is enhanced. It is so since the activity is restricted to only part of the year and the crusts also support high rates of denitrification<sup>57,58</sup> and volatilization of ammonia in some deserts<sup>59</sup> and grasslands<sup>60</sup>.

Terrestrial settings in general, and desert crusts in particular represent a habitat imposing environmental constraints that have allowed diversification of specialized cyanobacterial groups within this ecosystem. These constraints may also be responsible for simultaneous physiological resistance to desiccation, intense illumination and

temperature extremes, as exemplified in studies of *Nostoc commune*<sup>61</sup>, but most of the putative-specific adaptations remain to be explored.

## Microbiology of lithic surfaces

Most deserts have rock outcrops spread amongst sand dunes as integral feature of their topography. In arid Rajasthan, rock outcrops account for about 13,200 km<sup>2</sup> of area. Apart from rock outcrops, desert pavements and caliche are born at the surface in deserts. Such structures cover large part of the world's drylands.

Desert pavement is a dark, stony surface without sand or vegetation. It suggests that the land has been undisturbed, perhaps for thousands or hundreds of thousands of years. Desert pavements are usually dark in colour due to a thin coating of desert varnish or patina on the surface of the stones. Calcite/calcrete/caliche in desert soils is formed by the precipitation of calcite. Role of soil microorganisms in calcite precipitation in desert soils was confirmed by Monger *et al.*<sup>62</sup> who showed that soil bacteria and fungi precipitated calcite when cultured on a calcium-rich medium. Cyanobacterial-lichen crust or desert varnish and/or fungal colonies frequently cover the surfaces discussed above.

## Cyanobacterial and/or lichen crust

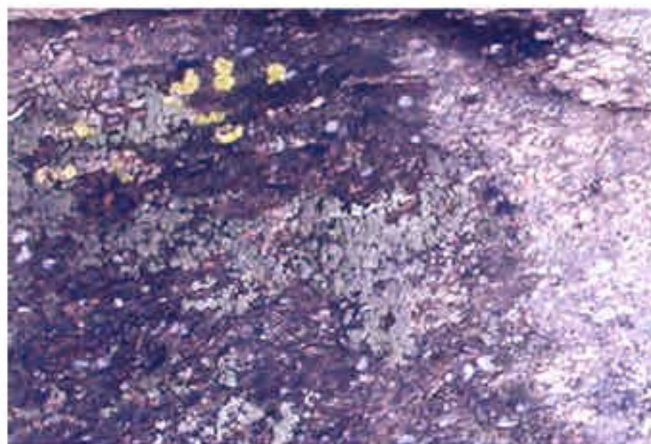
Cyanobacteria and algae are the pioneers that inhabit bare rock surfaces and make road map for further plant succession (Figure 1 b). These forms are also desiccation- and temperature-tolerant. More than 95% of all rock and stone surfaces were found covered by lithobionts like cyanobacteria and lichens in Sede Boquer<sup>63</sup>. However, lichens generally do not survive as well on the dry sun baked boulders and usually live on the lower sides of rocks or on sides with shorter sun exposure on the outcrop (Figure 2). They live in a desiccated state with a very slow annual growth rate.

Budel<sup>47</sup> drew analogy of the typical structure of the crust with that of a microforest. Accordingly, the lower story is composed of unicellular cyanobacteria (such as species of *Chroococcidiopsis*, *Chroococcus*, *Gloeocapsa*, *Gloeotheca*) and a few filamentous forms (as *Schizothrix* sp.), with the genus *Gloeocapsa* being most common. The 'canopy' is formed by filamentous cyanobacteria, *Scytonema* sp. and *Stigonema* sp., together with cyanolichens – *Paulia*, *Peltula*, *Phyliscum*, and in rare cases a few others. The unicellular cyanobacterium *Xenococcus* sp. often occurs as an epiphyte over the two filamentous cyanobacteria<sup>64,65</sup>. These organisms may form 'lithobiont forests' and totally obscure the original colour of the rock. They grow on all types of rocks including man-made rock substrates in tropical and subtropical biomes<sup>66</sup>.



Bhatnagar *et al.*<sup>11</sup> working on dry sun exposed surfaces of the Indian desert observed dominance of cyanobacterial populations contributed by the genus *Phormidium*. Fourteen genera of diazotrophic cyanobacteria were reported with maximum morphotype variability in *Calothrix*, *Nostoc*, *Anabaena* and *Scytonema*. The diversity (Shannon & Weaver Index) estimates were low ranging from 0 to 1.86 with a mean of  $1.09 \pm 0.48$  but were comparatively higher than that of the soil. In case of cyanobacteria that do not form akinetes or other spores, whole filament turns into a dormant structure within its thick sheath that germinates in presence of sufficient moisture (Figure 3).

Hypolithic algae and cyanobacteria have been found to cover the underside of many limestones and flint pebbles<sup>67,68</sup>. The hypolithic niche is favoured since this provides conserved moisture and nutrients and protects cya-



**Figure 2.** Lichen crust on rock surface on an Aravalli hill near Lohagal village, Ajmer.



**Figure 3.** On moistening the crust, new trichome of cyanobacterium emerge from dry sheaths.

nobacteria and microalgae from direct exposure to radiations and high temperature. Since these organisms do not actively permeate the substrate, only rocks of porous structure or those permeated by fissures are colonized. Such communities are dominated by cyanobacteria<sup>67,69</sup> and therefore hypoliths are mostly found below transparent/translucent stone surfaces. In some deserts however diatoms form the hypolithic crust<sup>70</sup>. *Chroococcidiopsis* is found at the lower surface of translucent stones and pebbles half embedded in the soil<sup>71</sup>. Hypolithic cyanobacteria are common in deserts around the world. Yet they are conspicuously absent in the Atacama desert in northern Chile<sup>72</sup> since the climate is more extreme, rain is practically absent, except in years of the El Nino-Southern Oscillation events, that are usually separated by intervals of ~9.9 years<sup>73</sup>.

Two types of endolithic communities are distinguished with respect to their habitat. Chasmoendoliths live in rock fissures and cracks and cryptoendoliths inhabit structural cavities of porous rocks. In hot deserts, endolithic organisms are nearly exclusively cyanobacteria with the most common genus being *Chroococcidiopsis* and *Gloeocapsa* accompanied by heterotrophic bacteria. The former is the most desiccation-resistant cyanobacterium known<sup>74,75</sup> and is found in the inner spaces of porous rocks<sup>71,76</sup>. It is reported that the endolithic algal flora in hot and cold deserts is similar<sup>71</sup>. Such cyanobacteria possess an adaptive character that allows them to thrive on extremely low photon flux intensities<sup>77,78</sup>. *Chroococcidiopsis* is shown to fix nitrogen under strictly anaerobic conditions<sup>79</sup>.

Cryptoendolithic lichens are more predominant in sandstones of Antarctica. They form distinct zonations on the rock resembling an organized thallus of heteromerous lichen<sup>76</sup>. Dodge<sup>80</sup> lists 68 species of *Buellia*, 34 of *Lecidea* and 13 of *Acarospora* out of a total of 434 species belonging to 90 genera of the Antarctic lichen flora. *Trebouxia*, a green alga is the common phycobiont in association with these lichens.

The role of microorganisms in weathering of rocks has been well recognized<sup>81–83</sup> with bacteria and lichens breaking down the rocks both biochemically and biophysically<sup>84,85</sup>. When wetted by rain or morning dew, lichens or cyanobacteria quickly imbibe water and revive photosynthesis for a while. Microscopic rock fragments intermeshed with lichen or cyanobacteria become loosened by expansion and contraction as a result of alternate moistening and drying. This helps in the formation of soil. Lichens and cyanobacteria are also known to produce weak organic acid, but acidic etching is more consequential in calcareous rocks<sup>86</sup>. For most rock surfaces, disintegration is probably more important than dissolution. Kurtz and Netoff<sup>87</sup> showed that rock surface microorganisms can actually contribute towards stabilization of rock surfaces, protecting them from erosion. Other than cyanobacteria 39 species of lichen belonging to 24 genera have been documented from the Western Dry Region of India<sup>88</sup>.

### Patina

Within the last few years it has been widely accepted that rock surfaces and other inorganic material are common habitats for a wide variety of microorganisms such as chemoorganotrophic, chemolithotrophic and phototrophic bacteria, actinomycetes, and especially fungi and lichens. The interactions of these epi- and endo-lithic microorganisms with the rock material have been studied intensively. It has been discovered that microorganisms play an important and substantial role in all alteration processes that occur in rock, including physical and chemical alteration of the material components, material loss, the alarming deterioration of historical buildings and works of art, as well as the formation of brightly coloured patinas on material surfaces<sup>89-91</sup>. Desert varnish or patina – a dark, thin coating on rocks<sup>89</sup> is result of such interactions. It can also form on the surface of desert soil if the soil remains undisturbed for thousands of years and the underside of the rock where it is not exposed to air. Typically these depositions are ca. 20 µm (2–500 µm) thick. The term ‘patina’ internationally means ‘surface changes’. Since ‘patina’ is the oldest term for surface changes of any material that is exposed to the environment (atmosphere), Krumbein<sup>89</sup> suggested that it may be used to encompass all other terms related to surface changes such as oxalate film (pellicole ossalati), lacquer, crust, deposit, karst, rock varnish (Figure 4), micro-stromatolite, efflorescence, carbonate, gypsum, iron, manganese, oxalate and silica skins.

The varnish or patina structure eluded precise analysis as it is composed of particles too fine to be characterized by X-rays, the main diagnostic tool of mineralogical investigations. Infrared spectroscopy showed that it consists clay minerals (70%) and oxides of manganese and/or iron (30%)<sup>92</sup>. Mn or Fe oxides are black or red coloured respectively. Other minerals mixed into patina composition include hydroxides plus silica and calcium carbonate.



**Figure 4.** Patina or desert varnish over a rock at Lohagal village near Ajmer.

Exactly how patina is formed is not completely known. Mechanism of formation has been speculated to be biological, geochemical or a combination of both the processes<sup>89,92</sup>. Other than biogenic precipitation of Mn and Fe oxides, Krumbein<sup>89</sup> attributed patina formation to the pigment release by microorganisms particularly the ubiquitous microcolonial fungi on the basis that the pigments  $\alpha$ -carotene,  $\beta$ -carotene and rhodoxanthene are present both on the rock surface and in fungi isolated from the same rocks. They also showed experimental deposition of pigments on marble pieces. Microcolonial structures of fungi on desert rocks exposed above the soil and in the absence of detectable lichen or algal growth were reported by Staley *et al.*<sup>93</sup> in 1982 from desert pavements of Australia, Continental Asia, Sonoran and Mojave Desert. They found prevalence of fungi belonging to Capnodiales while most others were Hyphomycetes such as *Taeniolella subsessilis* and *Bahusakala*- and *Humicola*-like organisms. The soil fungus *Epicoccum nigrum* was also reported from rock surfaces<sup>94</sup>.

Dorn and Oberlander<sup>95</sup> isolated bacteria from patina and used scanning electron microscopy to confirm their presence *in situ*. They observed *Metallogenium*- and *Pedomicrobium*-like bacteria. They could also generate patina in laboratory by inoculating such bacteria over a period of several months. Lipid analysis of patina<sup>96</sup> showed fatty acids commonly associated with fungi and bacteria. These included 18 : 2 $\Delta$ 9, 12 and 18 : 1 $\Delta$ 9, which are often associated with fungi<sup>97</sup>. Similarly amino acid analysis also indicates possible organismal activity<sup>98</sup>. Kuhlman *et al.*<sup>99</sup> isolated three strains of bacteria from rock varnish of Death Valley, California that could resist UV-C exposure up to 5 min, while this readily killed *Escherichia coli*. One of the strains showed 98% 16S rDNA sequence similarity with multiple *Arthrobacter* strains, another showed similarity with strains of *Curtobacterium flaccumfaciens* and an unidentified glacial ice bacterium and the third one matched with *Geodermatophilus obscura* cluster I of Eppard *et al.*<sup>100</sup>

### Desert playas

Playas are characteristic desert landforms, maintained by arid climate, where a combination of tropical sun, wind and dry air evaporate many more times moisture from the land than falls in a year. These are dry, incredibly level beds of ancient lakes. Because of their extremely dynamic nature, the size, total dissolved solids concentration and relative ionic composition can fluctuate widely. Playas may be thalassic or athalassic, ranging from freshwater to hyper saline situations, and vary in the concentration of major anions. Within playas, the alternating dilution and concentration phases generate a range of chemical environments. Thousands of big and small playas exist around the world. Lakes or playas are called saline if they have



$\geq 3\%$  salt<sup>101</sup>. Arid areas are characterized by saline and hypersaline playas, for example, Great Salt lake of Utah, Lake Eyre (USA), Lake Magadi (Kenya), Owens lake, Searles lake (Sierra Nevada, USA) are the major such systems. The Sambhar lake, Nawa, Didwana (Nagaur), Lunkaransar (Bikaner), Pachpadra (Barmer), Mitha ka Rann and Kharia Rann (Jaisalmer) are the better-known saline playas of the Thar desert.

Playas never last more than days or weeks, evaporating at a rapid pace to leave behind huge expanses of shiny, gooey mud flats, level as the surface of a pool table, encrusted with a new coat of calcium, sodium, gypsum and other salts from the recently-departed water. The mud surface dries into curls, pie-wedge-shapes, cylinders or shard-like plates. Polished by the ever-constant wind, it sometimes shines like glass. When the lakes return briefly, the profusion of salty water teems with tiny aquatic lives: archaea, eubacteria, algae, protozoa, yeast, freshwater shrimp and brine flies. Depending on the water chemistry and the population density, which may at times bloom, the lake gets coloured as green, orange, purple or claret (Figure 5). Although a number of studies have been carried out on playas, the uniqueness of these habitats has been considered as any other saline or hypersaline water body. Since extremely halophilic microorganisms have been dealt somewhere else in this issue, only a brief mention shall be made about the microbial diversity of saline playa.

Cyanobacteria are predominant forms observed in playas both as periphyton and benthic mats. A total of six species of cyanobacteria, two species of green algae and 22 species of diatoms were reported from Lake Carey, an ephemeral inland lake from the arid region of Western Australia. Vast majority of algae was periphyton or benthic mat made of *Schizothrix* species<sup>102</sup>. Dominance of aerial forms in diatom flora has been observed in playas from Nevada<sup>103</sup> and in South California<sup>104</sup>. *Aphanothece*

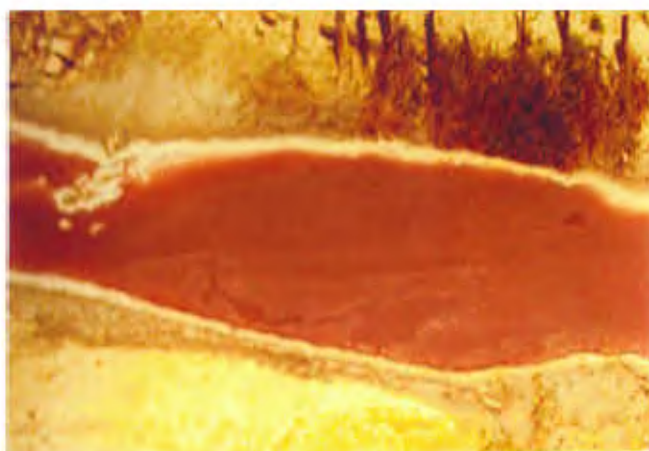
*halophytica*, *Synechocystis* sp. and *Dactylococcopsis salina* are a few cyanobacteria described from the Great salt Lake and the saline playas of the Thar desert<sup>11,105</sup>. *Cyano- spira ripkae* and *C. capsulatus* have been reported by Florenzano *et al.*<sup>106</sup> from Lake Magadi. A number of filamentous forms belonging to Oscillatoriales like *Oscillatoria limnetica*, *O. neglecta*, *O. salina* and *Phormidium ambiguum* have also been reported from these environments. While these are representative of moderate halophiles, *Asteromonas gracilis* and *Dunaliella* can grow at saturating concentrations of salt. As the lake water gets concentrated, a number of phototrophic bacteria develop beneath the cyanobacterial layer in anaerobic but lighted zones. *Ectothiorhodospira halochloris*, *E. abdelmalekii*<sup>107</sup> and *E. vacuolata*<sup>108</sup> have been described from Lake Magadi, Owens lake and Searles lake. *Chlorobium vibrioforme* has been reported from endorheic lakes of Spain. Other bacteria reported from these habitats are *Natronobacterium*<sup>109</sup>, *Natronococcus*<sup>110,111</sup>, *Sarcina littoralis*, *Flavobacterium*<sup>112</sup> and *Halomonas magadi*<sup>113</sup>.

## Epilogue

Microbiota of desert ecosystems is not only responsible for the productivity, biogeochemical cycling of elements and ecosystem balance<sup>6</sup>, but also for soil neogenesis and improvement of soil structure. Painter<sup>114</sup> and Sarig and Steinberger<sup>115</sup> accorded central significance to the capsular and sheath proteoglycans produced by edaphic cyanobacteria in soil neogenesis in deserts. Several microorganisms support authigenic activity of particularly the calcic minerals. On the other hand, they are one of the major forces in rock weathering and formation of soil. The former is also important from the point of view of soiling and reconstruction of historical monuments. Stress-tolerant diazotrophs, phosphate solubilizers and polymer-excreting algae and cyanobacteria from arid regions catalyse stabilization of sand dunes and change the barren and saline soils of dry regions into arable lands<sup>116</sup>.

Biopolymers can have uses as bioflocculants, bio-surfactants, bioadhesives and lubricants. Accumulation of organic osmotica as a strategy to tolerate water scarcity under arid and saline habitat adds biotechnological value to *Dunaliella* sp. for glycerol production. Production of sheath pigments as gloeocapsin, fuscocorhodin and fuscocochlorin is known to enhance drought resistance<sup>117</sup>. UV-sorbing pigments like scytonemin allow them survival under radiations of tropical sun. While the former may lead to search of new pigments, the latter may be of use in UV-screening creams and lenses.

Growing a particular species in outdoor ponds is always fraught with dangers of contamination. But a few microorganisms can grow in case of arid lands where salty water is often available, solar irradiation is generally plentiful and land is not utilizable for conventional crops. There-



**Figure 5.** Extreme halophiles belonging to archaea colour the water red in a ditch at the saline playa of Sambhar.

fore such systems are most suited for mass cultivation of single cell proteins, food, feed, fodder or extractable chemicals of commercial value, viz. carotene, polyunsaturated fatty acids, bioactive molecules and enzymes.

There appears no exaggeration in saying that the desert though they appear devoid of life, possess a treasure of microbiota having unique qualities that is yet to be explored to realize its full glory.

- Meigs, P., Arid and semiarid climatic types of the world. In Proceedings, Eighth General Assembly and Seventeenth International Congress, International Geographic Union, Washington, 1952, pp. 135–138.
- Goodall, D. W. and Perry, R. A., *Arid Land Ecosystems: Structure, Functioning and Management*, IBP Program 16, Cambridge University Press, Cambridge, 1978, pp. 5–20.
- Buyanovsky, G., Dicke, M. and Berwick, P., Soil environment and activity of soil microflora in the Negev desert. *J. Arid Environ.*, 1982, **5**, 13–28.
- Parker, L. W., Miller, J., Steinberger, Y. and Whitford, W. G., Soil respiration in a Chihuahuan desert rangeland. *Soil Biol. Biochem.*, 1983, **15**, 303–309.
- Parker, L. W., Freckman, D. W., Steinberger, Y., Driggers, L. and Whitford, W. G., Effects of simulated rainfall and litter quantities on desert soil biota: soil respiration, microflora and protozoa. *Pedobiologia*, 1984, **27**, 185–195.
- Skujinš, J., Microbial ecology of desert soils. *Adv. Microbial Ecol.*, 1984, **7**, 49–91.
- Venkateswarulu, B. and Rao, A. V., Distribution of microorganisms in stabilised and unstabilised sand dunes of Indian desert. *J. Arid Environ.*, 1981, **4**, 203–208.
- Khathuria, N., *Rhizosphere microbiology of desert*, M.Sc. dissertation, Department of Microbiology, Maharshi Dayanand Saraswati University, Ajmer (Rajasthan), 1998, p. 52.
- Rao, A. V. and Venkateswarlu, B., Microbial ecology of the soils of Indian desert. *Agric. Ecosyst. Environ.*, 1983, **10**, 361–369.
- Hethener, P., Activite microbiologique des sols a *Cupressus dupreziana*. A Camus au Tasali N'ajjer (Sahara central). *Bull. Soc. Hist. Nat. Afr. Nord.*, 1967, **58**, 39–100.
- Bhatnagar, A., Bhatnagar, M., Makandar, Md. B. and Garg, M. K., Satellite Centre for Microalgal Biodiversity in Arid Zones of Rajasthan. Project completion Report, Funded by Department of Biotechnology, New Delhi, 2003.
- Lobova, E. V., Pochvy pustynnoi zony SSSR, Akademiya Nauk, Moscow (translation Lobova, E.V., Soils of the desert zone of USSR. US department of Commerce, Springfield, Virginia, 1967).
- Cameron, R. E., Cold desert characteristics and problems related to other arid lands. In *Arid Lands in Perspective* (eds McGinnies, W. G. and Goldman, B. J.) University of Arizona Press, Tucson, 1969, pp. 167–205.
- Trappe, J. M., Mycorrhizae and productivity of arid and semi arid range lands. In *Advances in Food Production System for Arid and Semi Arid Lands* (eds Manassah, J. J. and Briskey, E. J.), Academic Press, New York, 1981, pp. 581–599.
- Yechieli, A., Oren, A. and Yair, A., The effect of water distribution on bacterial numbers and microbial activity along a hill slope, northern Negev, Israel. *Adv. Geocol.*, 1995, **28**, 193–207.
- Mahmoud, S. A. Z., Abou-Al-Fadl, M. and El-Mofty, M. K., Studies on the rhizosphere microflora of a desert plant. *Folia Microbiol.*, 1964, **9**, 1–8.
- Elwan, S. H. and Diab, A., Studies in desert microbiology. III. Certain aspects of the rhizosphere effect of *Rhazya stricta* Decn in relation to environment. *UARJ Bot.*, 1970, **13**, 109–119.
- Elwan, S. H. and Diab, A., Studies in desert microbiology. IV. Bacteriology of the root region of a fodder xerophyte in relation to environment. *UARJ Bot.*, 1970, **13**, 159–169.
- Hamdi, Y. and Yousef, A. N., Nitrogen fixers in the rhizosphere of certain desert plants. *Zentralbl. Bakteriell. Naturwiss.*, 1979, **134**, 19–24.
- Steinberger, Y., Degani, R. and Barnen, G., Decomposition of root litter and related microbial population dynamics of a Negev desert shrub, *Zygophyllum dumosum*. *J. Arid Environ.*, 1995, **31**, 383–389.
- McCully, M. E., Roots in soil: Unearthing the complexities of roots and their rhizosphere. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1999, **50**, 695–718.
- Watt, M., McCully, M. E. and Canny, M. J., Formation and stabilization of rhizosheaths of *Zea mays* L. (Effect of soil water content). *Plant Physiol.*, 1994, **106**, 179–186.
- Young, I. M., Variation in moisture contents between bulk soil and the rhizosheath of *Triticum aestivum* L. cv. *New Phytol.*, 1995, **130**, 135–139.
- McCully, M. E. and Boyer, J. S., The expansion of maize root cap mucilage during hydration 3. Changes in water potential and water content. *Physiol. Plant.*, 1997, **99**, 169–177.
- Wullstein, L. H. and Pratt, S., Scanning electron microscopy of rhizosheaths of *Oryzopsis hymenoides*. *Am. J. Bot.*, 1981, **68**, 408–419.
- Wullstein, L. H., Nitrogen fixation (acetylene reduction) associated with rhizosheaths of Indian ricegrass (*Oryzopsis hymenoides*), used in stabilization of Slick Rock, Colorado Tailings pile. *J. Range Mgmt.*, 1980, **33**, 204–206.
- Bristow, C. E., Campbell, G. S., Wullstein, L. H. and Neilson, R., Water uptake and storage by rhizosheaths of *Oryzopsis hymenoides*: A numerical simulation. *Physiol. Plant.*, 1985, **65**, 228–232.
- Jacobson, K. M., Macrofungal ecology in the Namib desert: a fruitful or futile study? *McIlvainea*, 1996, **12**, 21–32.
- Kiran Bala, Rao, A. V. and Tarafdar, J. C., Occurrence of VAM associations in different plant species of the Indian desert. *Arid Soil Res. Rehab.*, 1989, **3**, 391–396.
- Mathur, N. and Vyas, A., Mycorrhizal dependency of *Prosopis cineraria* in Indian Thar desert. *Indian J. For.*, 1995, **18**, 263–266.
- Staffeldt, E. E. and Vogt, K. B., Mycorrhizae of desert plants. *US/IRP Desert Biome Res. Memo*. Utah State University, Logan, 1975, pp. 75–87.
- Hirrell, M. C., Mehravaran, H. and Gerdemann, J. W., Vesicular–arbuscular mycorrhizae in the Chenopodiaceae and Cruciferae: Do they occur? *Can. J. Bot.*, 1978, **56**, 2813–2817.
- Reeves, F. B., Wagner, D., Moorman, T. and Kiel, J., The role of endomycorrhizae in revegetation practices in the semi arid West. I. A comparison of incidence of mycorrhizae in severely disturbed vs natural environments. *Am. J. Bot.*, 1979, **66**, 6–13.
- Cul, M. and Nobel, P. S., Nutrient status, water uptake and gas exchange for 3 desert succulents infected with mycorrhizal fungi. *New Phytol.*, 1992, **122**, 643–649.
- Morte, M. A., Cano, A., Honrubia, M. and Torres, P., *In vitro* mycorrhization of micropropagated *Helianthemum almeriense* plantlets with *Terfezia clavayii* (Desert Truffle). *Agric. Sci. Fin.*, 1994, **3**, 309–314.
- Roth-Bejerano, N., Livne, D. and Kagan-Zur, V., *Helianthemum–Terfezia* relations in different growth media. *New Phytol.*, 1990, **114**, 235–238.
- Trappe, J. M., Use of truffles and false truffles around the world. In Proceedings, Atti del Secondo Congresso Internazionale sul Tartufo. Spoleto 1988 (eds Bencivenga, M. and Granetti, B.), Spoleto, Italy, Comunita Montana dei Monti Martini e del Serano, 1990, pp. 19–30.
- Kiraly, B. C. and Bratek, Z., *Terfezia terfezioides*, a common truffle in Hungary. *Micol. Veget. Medit.*, 1992, **7**, 303–304.

39. Mao, X. L., *The Macrofungi of China*, Henan Science and Technology Press, Beijing, 2000, pp. 719 (available at www.hceis.com).
40. Bratek, Z., Jakucs, E., Bóka, K. and Szedlay, G., Mycorrhizae between black locust (*Robinia pseudoacacia*) and *Terfezia terfezioides*. *Mycorrhiza*, 1996, **6**, 271–274.
41. Panwar, J. and Vyas, A., AM fungi: A biological approach towards conservation of endangered plants in Thar desert, India. *Curr. Sci.*, 2002, **82**, 576–578.
42. West, N. E., Structure and function of microphytic soil crusts in wild wind ecosystems of arid to semi-arid regions. *Adv. Ecol. Res.*, 1990, **20**, 179–223.
43. Rauh, W., The Peruvian-Chilean deserts. In *Hot deserts and Arid Shrub lands, 12A: Ecosystems of the World* (eds Evenari, M., Noy-Meir, I. and Goodall, D. W.), Elsevier, Amsterdam, 1985, pp. 239–268.
44. Walter, H., The Namib Desert. In *Hot Deserts and Arid Shrub lands, 12A: Ecosystems of the World* (eds Evenari, M., Noy-Meir, I. and Goodall, D. W.), Elsevier, Amsterdam, 1985, pp. 245–282.
45. Belnap, J., Comparative structure of physical and biological soil crusts. In *Biological Soil Crusts. Ecological Studies* (eds Lange, O. L. and Belnap, J.), Springer, Berlin, 2001, pp. 177–191.
46. Büdel, B., Synopsis: Comparative biogeography and ecology of soil crust biota and communities. In: *Biological Soil Crusts. Ecological Studies* (eds Lange, O. L. and Belnap, J.), Springer, Berlin, 2001, pp. 141–152.
47. Büdel, B., Diversity and ecology of biological crusts. In *Progress in Botany* (eds Esser, K., Lüttge, U., Beyschlag, W. and Hellwig, F.), Springer-Verlag, Berlin, 2002, pp. 386–404.
48. Garcia-Pichel, F., Lopez-Cortes, A. and Nubel, U., Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado plateau. *Appl. Env. Microbiol.*, 2001, **67**, 1902–1910.
49. Ullmann, I. and Büdel, B., Ecological determinants of species composition of biological soil crusts on a landscape scale. In *Biological Soil Crusts. Ecological Studies* (eds Lange, O. L. and Belnap, J.), Springer, Berlin, 2001, pp. 203–213.
50. Eldridge, D. J. and Greene, R. S. B., Microbiotic soil crusts – a review of their roles in soil and ecological processes in the rangelands of Australia. *Austr. J. Soil Res.*, 1994, **32**, 389–415.
51. Evans, R. D. and Johansen, J. R., Microbiotic crusts and ecosystem processes. *Crit. Rev. Plant Sci.*, 1999, **18**, 183–225.
52. Beymer, R. J. and Klopatek, J. M., Potential contribution of carbon by microphytic crusts in Pinyon–Juniper woodlands. *Arid Soil Res. Rehabil.*, 1991, **5**, 187–198.
53. Cameron, R. E. and Fuller, R. H., Nitrogen fixation by some soil algae in Arizona. *Soil Sci. Soc. Am. Proc.*, 1960, **24**, 353–356.
54. Harper, K. T. and St. Clair, L. L., Cryptogamic soil crusts on arid and semi arid rangelands in Utah: Effects on seedling establishment and soil stability. Final Report to the Bureau of Land Management, Utah State Office, Salt Lake City, Utah, 1985.
55. Malam Issa, O., Trichet, J., Défarge, C., Couté, A. and Valentin, C., Morphology and microstructure of microbiotic soil crusts on a tiger bush sequence (Niger, Sahel). *Catena*, 1999, **37**, 175–196.
56. Prasse, R., *Experimentelle Untersuchungen an Gefäßpflanzenpopulationen auf verschiedenen Geländeoberflächen in einem Sandwüstengebiet*, Universitätsverlag Rasch Osnabrück, 1999.
57. Westerman, R. L. and Tucker, T. C., Denitrification in desert soils. In *Nitrogen in Desert Ecosystems* (eds West, N. E. and Skujinš, J.), IBP Synthesis, Dowden, Hutchinson & Ross, Stoudsberg, Penn. 1978, vol. 9, pp. 75–106.
58. Burns, S. J., Nitrogen fixation and transformations in cryptogamic soil crusts as affected by disturbance, M.S. thesis, Brigham Young University, Provo, Utah, 1983, 93 pp.
59. Klubeck, B., Eberhardt, P. J. and Skujinš, J., Ammonia volatilization from Great Basin Desert soils. In *Nitrogen in Desert Ecosystems* (eds West, N. E. and Skujinš, J.), IBP Synthesis, Dowden, Hutchinson & Ross, Stoudsberg, Penn. 1978, vol. 9, pp. 107–129.
60. Woodmansee, R. G., Vallis, J. and Mott, J. J., Grassland nitrogen. In *Terrestrial Nitrogen Cycles* (eds Clark, F. E. and Rosswall, T.), Ecol. Bull. (Stockholm), 1981, vol. 33, pp. 443–462.
61. Potts, M., Desiccation tolerance of prokaryotes. *Microbiol. Rev.*, 1994, **58**, 755–805.
62. Monger, H. C., Dougherty, L. A., Lindermann, W. C. and Liddell, C. M., Microbial precipitation of pedogenic calcite. *Geology*, 1991, **19**, 997–1000.
63. Danin, A. and Garty, J., Distribution of cyanobacteria and lichens on hill sides of the Negev highlands and their impact on biogenic weathering. *Z. Geomorph.*, 1983, **27**, 423–444.
64. Büdel, B., Becker, U., Follmann, G. and Sterflinger, K., Algae, fungi and lichens on Inselbergs. In *Inselbergs – Biotic Diversity of Isolated Outcrops in Tropical and Temperate Regions. Ecological Studies 146* (eds Porembski, S. and Barthlott, W.), Springer, Berlin, 2000, pp. 69–90.
65. Weber, H. M., *Ein Biofilm auf freiem Fels: Cyanobakterien der Inselberge Brasiliens*, Diploma Thesis, Universities of Bonn and Rostock, 1997.
66. Garty, J., Influence of epilithic microorganisms on the surface temperature of building walls. *Can. J. Bot.*, 1989, **68**, 1349–1353.
67. Friedmann, E. I. and Galun, M., Desert algae, lichens and fungi. In *Desert Biology* (ed. Brown, G. W.), Academic Press, London, 1974, vol. II, pp. 165–212.
68. Berner, T. and Evenari, M., The influence of temperature and light penetration on the abundance of the hypolithic algae in the Negev desert of Israel. *Oecologia*, 1978, **33**, 255–260.
69. Büdel, B. and Wessels, D. C. J., Rock inhabiting blue–green algae/cyanobacteria from hot arid regions. *Arch. Hydrobiol. Suppl.*, 1991, **92** (Algol. Stud. 64), 385–398.
70. Rummrich, U. and Rummrich, M., Lange-Bertalot, H., Diatmeen als ‘Fensteralgen’ in der Namib-Wüste und anderen ariden Gebieten von SWA/Namibia. *Dinteria*, 1989, **20**, 23–29.
71. Friedmann, E. I. and Ocampo, R., Endolithic blue–green algae in the dry valleys: Primary producers in the antarctic desert ecosystem. *Science*, 1976, **193**, 1247–1249.
72. Friedmann, E. I., Extreme environments, limits of adaptation and extinction. In *Trends in Microbial Ecology. Proceedings of the Sixth International Symposium on Microbial Ecology* (eds Guerrero, R. and Pedros-Alio, C.), Spanish Society for Microbiology, Barcelona, 1993, pp. 9–12.
73. Quinn, W. H. and Neal, V. T., Antunez de Mayolo, S.E., El Nino occurrences over the past four and half centuries. *J. Geophys. Res.*, 1987, **92**, 14,449–14,461.
74. Friedmann, E. I. and Ocampo-Friedmann, R., Blue–green algae in arid cryptoendolithic habitats. *Archiv. Hydrobiol. Suppl.*, 1985, **71**, 349–350.
75. Potts, M. and Friedmann, E. I., Effects of water stress on cryptoendolithic cyanobacteria from hot desert rocks. *Arch. Microbiol.*, 1981, **130**, 267–271.
76. Friedmann, E. I., Endolithic microorganisms in the Antarctic cold desert. *Science*, 1982, **215**, 1045–1053.
77. Albertono, P., Epilithic algal communities in hypogean environments. *Giorn Bot. Ital.*, 1993, **127**, 372–386.
78. Albertono, P., Pigment ratios in sciphilous terrestrial cyanophytes. *Giorn Bot Ital.*, 1994, **128**, 784–785.
79. Friedmann, E. I. and Kibler, A. P., Nitrogen economy of endolithic microbial communities in hot and cold deserts. *Microb. Ecol.*, 1980, **6**, 95–108.
80. Dodge, C. W., *Lichen Flora of the Antarctic Continent and Adjacent Islands*, Phoenix, Canaan, NH, 1973, pp. 399.
81. Barker, W. W. and Banfield, J. F., Biologically versus inorganically mediated weathering reactions: relationships between min-



- erals and extracellular microbial polymers in lithobiontic communities. *Chem. Geol.*, 1996, **132**, 55–69.
82. Barker, W. W., Welch, S. A. and Banfield, J. F., Biogeochemical weathering of silicate minerals. In *Geomicrobiology: Interactions between Microbes and Minerals* (eds Banfield, J. F. and Nealson, K. H.), pp. 81–117, Mineralogical Society of America, Washington DC, 1997, pp. 448
  83. Bloom, A. L., *Geomorphology: A Systematic Study of Late Cenozoic Landforms*, Prentice Hall, New Jersey, 1998, pp. 482.
  84. Piervittori, R., Salvadori, O. and Laccisalgia, A., Literature on lichens and biodeterioration of stonework. *Lichenologist*, 1994, **26**, 171–192.
  85. Bland, W. and Rolls, D., *Weathering: An Introduction to Scientific Principles*, Arnold, London, 1998, pp. 271.
  86. Bhatnagar, A. and Roychoudhury, P., Dissolution of limestone by cyanobacteria. In Proceedings of the National Symposium on Cyanobacterial Nitrogen Fixation, IARI, New Delhi (ed. Kaushik, B. D.), Today & Tomorrow's Printers and Publishers, Delhi, 1992, pp. 331–335.
  87. Kurtz, H. D. and Netoff, D. I., Stabilization of friable sandstone surfaces in a desiccating, wind-abraded environment of south central Utah by rock surface microorganisms. *J. Arid Environ.*, 2001, **48**, 89–100.
  88. Singh, K. P. and Sinha, G. P., Lichens. In *Floristic Diversity and Conservation Strategies in India. Vol. I. Cryptogams and Gymnosperms* (eds Mudgal, V. and Hajra, P. K.), Botanical Survey of India, New Delhi, 1997, pp. 195–234.
  89. Krumbein, W. E. Zum Begriff Patina, seiner Beziehung zu Krusten und Verfärbungen und deren Auswirkungen auf den Zustand von Monumenten. In *Jahresberichte aus dem Forschungsprogramm Steinzerfall–Steinkonservierung* (ed. Snethlage, R.), Ernst und Sohn, Berlin, 1993, pp. 215–229.
  90. Gorbushina, A. A. and Krumbein, W. E., Life on and in rocks. In *Microbial Sediments* (eds Riding, R. E. and Awramik, S. M.), Springer, Berlin, 2000, pp. 161–170.
  91. Sterflinger, K., Krumbein, W. E. and Rullkötter, J., Patination of marble, sandstone and granite by microbial communities. *Z. Dt. Geol. Ges.*, 1999, **150**, 299–311.
  92. Potter, R. M. and Rossman, G. R., The manganese and iron oxide mineralogy of desert varnish. *Chem. Geol.*, 1979, **25**, 79–94.
  93. Staley, J. T., Palmer, F. and Admas, J. B., Microcolonial fungi: Common inhabitants of desert rocks? *Science*, 1982, **214**, 603–604.
  94. Braams, J., Ecological study on the fungal microflora inhabiting sandstone monuments, Ph D thesis, Universität Oldenburg, 1992.
  95. Dorn, R. I. and Oberlander, T. M., Microbial origin of desert varnish. *Science*, 1981, **213**, 1245–1247.
  96. Schelble, R. T., McDonald, G. D. and Nealson, K. H., Comparison of Mojave Desert Varnish and Soil using Fatty Acid Analysis, Geological Society of America, Seattle Annual Meeting, Nov. 2–5, 2003, Washington State Convention and Trade Centre, Abstracts. 2003, **35** (6), p.151.
  97. Böh, E., The use of neutral lipid fatty acids to indicate the physiological conditions of soil fungi. *Microb. Ecol.*, 2003, **45**, 373–383.
  98. Perry, R. S., Engel, M. H., Botta, O. and Staley, J. T., Amino acid analyses of desert varnish from the Sonoran and Mojave deserts. *Geomicrobiol. J.*, 2003, **20**, 427–438.
  99. Kuhlman, K. R. *et al.*, Preliminary characterization of a microbial community of rock varnish from death valley, California, Third Mars Polar Science Conference, 13th October 2003, Poster Session I, # 8057.
  100. Eppard, M., Krumbein, W. E., Koch, C., Rhiel, E., Staley, J. T. and Stackebrandt, E., Morphological, physiological, and molecular characterization of actinomycetes isolated from dry soil, rocks, and monument surfaces. *Arch. Microbiol.*, 1996, **166**, 12–22.
  101. Hammer, U. T., Shames, J. and Haynes, R. C., The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. *Hydrobiologia*, 1983, **105**, 1–26.
  102. Jacob, J., Limnology of lake Carey, an inland ephemeral hypersaline system in the arid region of western Australia. Abstracts 7th International Conference on Salt Lake Research, Death Valley, September, 1999.
  103. Van Ledingham, S. L., Diatoms from dry lakes in Nye and Esmeralda, Nevada, USA. *Nova Hedwigia*, 1966, **11**, 221–241.
  104. Busch, D. E. and Kubly, D. M., Diatoms from desert playas in Southern California. *J. Arid Environ.*, 1980, **3**, 55–62.
  105. Ulukanli, Z. and DİRAK, M., Alkaliphilic microorganisms and habitats. *Turkish J. Biol.*, 2002, **26**, 181–191.
  106. Florenzano, G., Sili, C., Pelosi, E. and Vicenzini, M., *Cyanospira ripkae* and *Cyanospira capsulatus* (gen. nov. sp. nov.) a new filamentous heterocystous cyanobacterium from lake Magadi (Kenya). *Arch. Microbiol.*, 1985, **140**, 301–307.
  107. Imhoff, J. F., Halophilic phototrophic bacteria. In *Halophilic Bacteria* (ed. Rodriguez-Valera, F.), CRC Press, Boca Raton, 1988, vol. 1, pp. 85–108.
  108. Imhoff, J. F., Tindall, B. J., Grant, W. D. and Truper, H. G., *Ectothiorhodospira vacuolata* sp. nov., new phototrophic bacterium from soda lakes. *Arch. Microbiol.*, 1981, **130**, 238–242.
  109. Mwatha, W. E. and Grant, W. D., *Natronobacterium vacuolata* sp. nov., a haloalkaliphilic archaeon isolated from lake Magadi, Kenya. *Int. J. Syst. Bacteriol.*, 1993, **43**, 401–406.
  110. Tindall, B. J., Ross, H. N. M. and Grant, W. D., An alkaliphilic, red halophilic bacterium with a low magnesium requirement from Kenyan soda lake. *J. Gen. Microbiol.*, 1980, **116**, 257–260.
  111. Tindall, B. J., Ross, H. N. M. and Grant, W. D., *Natronobacterium* gen. nov. and *Natronococcus* gen. nov., two genera of haloalkaliphilic archaeobacteria. *Syst. Appl. Microbiol.*, 1984, **5**, 41–57.
  112. Nehr Korn, A. and Schwartz, W., Untersuchungen über Lebensgemeinschaften halophiler organismen. I. Mikroorganismen aus Salzeen der Californischen Wustengebeite und aus einer Natriumchlorid Sole. *Zeitsschr. Allgemeine Mikrobiol.*, 1961, **1**, 121–141.
  113. Duckworth, A. W., Grant, W. D., Jones, B. E., Meijer, D., Marquez, M. C. and Ventosa, A., *Halomonas magadii* sp. nov. a new member of the genus *Halomonas* isolated from a soda lake of the east African valley. *Extremophiles*, 2000, **4**, 53–60.
  114. Painter, T. J., Carbohydrate polymers in desert reclamation: the potential of microbial biofertilizers. *Carbohydr. Poly.*, 1993, **20**, 77–86.
  115. Sarig, S. and Steinberger, Y., Immediate effect of wetting event on microbial biomass and carbohydrate production-mediated aggregation in desert soil. *Geoderma*, 1993, **56**, 599–607.
  116. Bhatnagar, M. and Bhatnagar, A., Biotechnological potential of desert algae. In *Algal Biotechnology* (ed. Trivedi, P. C.), Pointer Publ., Jaipur, 2001, pp. 338–356.
  117. Bewly, J. D., Physiological aspects of desiccation tolerance. *Annu. Rev. Plant Physiol.*, 1979, **30**, 195–238.