Dynamic Biochemistry, Process Biotechnology and Molecular Biology ©2012 Global Science Books

Composition, Basic Features and Distribution of Cyanobacteria in Soil Crusts – A Review

Shewli Bhattacharya • Jnanendra Rath • Samit Ray[*]

Department of Botany, Visva-Bharati, Santiniketan – 731 235, West Bengal, India

Corresponding author: * ray_samit@rediffmail.com

ABSTRACT

Many of the cyanobacterial species are capable of growing on the soil and other terrestrial habitats. Soil particles form an intimate association with cyanobacteria and this results in the formation of cyanobacterial crusts that covers the surface of the soil as a coherent layer. The crusts cover the open spaces between the plantations and the soil surface remain covered by these highly specialized organisms. Crusts are found in an astonishing variety of habitats throughout the world – in desert and semi-desert plant communities ranging from shrubs and succulent desert to open woodlands, in steppe formation in both northern and southern hemisphere, in the gaps between evergreen shrubs and in the forests, on open ground or between alpine or tundra vegetation. Cyanobacteria were the major component of the blackish-brown crusts on the upper surface of the soil. Major works on cyanobacterial crusts have been reported from Africa, North and South America, Europe, Mediterranean region and Asia. Reports from India are meager. Cyanobacterial soil crusts are an important source of fixed carbon and nitrogen, which enrich the soil. They act as ecological indicator, polysaccharides produced by them prevent desiccation, presence of cyanobacteria in the soil augments mineral upake by vascular plants and seed germination is enhanced. Considering the significance of cyanobacterial soil crusts in improving the soil condition and fertility attempts are being made to develop soil crusts artificially. In this review, crust formation, types of cyanobacterial crusts, physiological and biochemical characters of crust cyanobacteria, importance of cyanobacterial crusts in ecology and their distribution in various parts of the world have been discussed in detail.

Keywords: arid and semiarid region, Biological soil crust, cyanophytes, cyanobacteria, soil crust

Abbreviations: **ARA**, acetylene reduction assay; **Chl *a***, chlorophyll *a*; **EPS**, extra cellular polysaccharide; **MAA**, mycosporine-like amino acid; **NA**, nitrogenase activity; **PET**, potential evapotranspiration; **PSI**, photosystem I; **PSII**, photosystem II; **UV**, ultraviolet

CONTENTS

INTRODUCTION

Cyanobacteria or Cyanoprokaryonta (earlier referred to as cyanophytes or blue-green algae) are oxygenic photosynthesizing prokaryotes with a wide distribution in habitat and range in morphology from unicellular to multicellular filamentous organisms capable of cellular differentiation. Cyanobacteria originated approximately 3.5 billion years ago (Schopf 1992; McClendon 1999; Schopf 2010). They were the dominant form of life on Earth for more than 1.5 billion years. They had ample time to diversify and adapt to newly evolving niches that exist on earth (Schopf *et al.* 2002; Blank 2004; Tice and Lowe 2004).

Many of the cyanobacteria are capable of growing on the soil and other terrestrial habitats. In addition, extant cyanobacteria also dominate the microbial populations of many extreme environments including soda lakes (*Spirulina*, *Cyanospira*), the nutrient-poor open ocean (*Trichodesmium*), thermal springs (*Synechococcus* and *Mastigocladus*), and the cold dry polar deserts (*Chroococcidiopsis*) (Schopf *et al.* 2002). They are present as cryptoendoliths in rocks in the cold dry deserts. The successful growth of cyanobacteria in varied habitats including extremes of environments is due to their photoautotrophic mode of nutrition, capability of switching from oxygenic to anoxygenic photosynthesis when they occur in environments where hydrogen sulfide is present at relatively high concentrations (e.g., 3 µm). Cyanobacteria have the capacity of chromatic adaptation due to change in synthesis of phycobiliproteins and composition of phycobilisomes. They can protect themselves from growth inhibiting light intensities and UV radiation with a variety of UV-absorbing pigments like Scytonemin in the sheath and other carotenoids and xanthophylls. Some cyanobacteria have the ability to grow photoheterotrophically using simple organic compounds as sole carbon sources and light as a source of energy. Many cyanobacterial species are capable of biological dinitrogen fixation by the enzyme nitrogenase and can thrive in habitats low in combined nitrogen (N).

In arid and semi-arid lands throughout the world, vegetation cover is often sparse and absent. In open spaces between the higher plants, the soil surface is generally not

Received: 23 June, 2011. Accepted: 23 March, 2012.

Invited Review

devoid of autotrophic life but covered by a community of highly specialized organisms. These communities are referred to as biological soil crusts or cryptogamic, cryptobiotic, microbiotic or microphytic soil crusts (Harper and Marble 1988; West 1990). Soil particles form an intimate association with cyanobacteria, algae, lichens, mosses, microfungi and other bacteria resulting in biological crust that covers the surface of the soil as a coherent layer (Belnap *et al.* 2001). Cyanobacteria are one of the most important components of biological soil crust. They are common colonizers among biological soil crusts, stabilizing soils and facilitating establishment of mid to late-successional mosses and lichens (Danin *et al.* 1998; Belnap and Eldridge 2003).

The biological soil-crusts are found in an wide range of habitats throughout the world – in desert and semi-desert conditions, in steppe formation in both the northern and southern hemispheres, in Mediterranean type climate, on open ground or between alpine or tundra vegetation and in temperate climatic region (Büdel 2000; Belnap *et al.* 2001). Soil crust biota also occurs in hostile environment that include extremes in temperature, light and scarcity of water (Ullman and Büdel 2001). Many species of cyanobacteria can withstand such adverse ecological conditions and respond to the onset of dry conditions by entering into a dormant resistant state and thus has been distinguished as pioneers of succession on soil. It has been stated that biodiversity of biological crusts on the topsoil surfaces is the most poorly researched habitats on earth (Moore 1998; Copley 2000). In this review we have made an attempt to discuss in detail the formation, types of cyanobacterial crusts, physiological and biochemical characters of crust cyanobacteria, distribution of the crusts in various parts of the world and importance of cyanobacterial crust in ecology.

METHODS OF STUDYING CRUSTS

Sample collection

To study general features of soil crust cyanobacteria, crust samples are collected from the upper surface of soil stored in pre-sterilised screw cap bottles for analysis. Samples can be collected by – (i) Pressing a sterile test tube into the crust, (ii) pressing a Petri dish into the crust, (iii) collecting crust with a spatula and putting into a Petri dish. The depth of sampling can be either a standard depth of 1 cm or determined by initial studies to characterize the depth of the crust (Hawkes 2001). Sarafis *et al.* (2006) reported about visualizing cyanobacteria in soil crusts from a semi-arid environment using confocal fluorescence imaging.

Study of the morphology of cyanobacteria isolated

(a) The crust samples are wetted with sterile distilled water and examined under light microscope. Within a few hours of wetting, cyanobacterial filaments can be seen but the morphological features on which identification is made are not distinct. So the crust samples are put into liquid or agar-plated media for growth. Crust samples can be collected from 25 positions in each site of interest and combined to homogenize by crushing and mixing.

(b) To quantify cyanobacteria from each composite samples one hundred fold dilutions are made by adding 1 gm of crust to 99 ml of 0.7% saline solution and aliquots of 0.1 and 0.2 ml are spread in triplicate on two agar-solidified media Z-8 (Carmichael 1986).

(c) Small fragments of soil crust may be placed in BG-11 medium (Stanier *et al.* 1971) with or without combined nitrogen. They may also be placed on agar plates (1.2% w/v agar-agar in BG-11 medium). It is incubated at 25 ± 1°C under continuous light from fluorescent tubes at an intensity 7.5 w/m^2 for up to 30 days.

The organisms that appear in the enriched culture are morphologically and morphometrically studied and identified following Desikachary (1959), Rippka *et al.* (1979), Komárek and Anagnostidis (1986, 1989) and Anagnostidis and Komárek (1988, 1990). Microphotographs are taken with a trinocular research microscope with digital camera.

Study of growth, pigments and macromolecules

To characterize crust samples physiologically and biochemically their growth, pigments and macromolecules are studied.

(a) Chlorophyll (Chl) *a* estimation is done following the methodology of Mackinney (1941).
(b) Carotenoids estimation is done following the methodology of Davis (1976).
(c) Phycobiliprotein estimation is done following the methodology of Glazer and Fang (1973).
(d) Scytonemin assay to be done by following the method of García-Pichel and Castenholz (1991).
(e) Carbohydrate estimation is done following the methodology of Herbert *et al.* (1971).
(f) Protein estimation is done following the methodology of Lowry *et al.* (1951).
(g) Amino acids are studied following the methodology of Lewis and Gonzalves (1962), Raftery and Heocha (1965).
(h) Extracellular polysaccharides, if produced by crust samples, are studied following De Phillips (1998).
(i) Stress protein – To detect various stress proteins, the methods of Hill *et al.* (1994) and Lyra *et al.* (2001) are followed.

Nitrogenase activity (acetylene reduction assay)

Methodology of Dilworth (1966) based on the fact that nitrogenase reduces C_2H_2 to C_2H_4, is employed to assess nitrogenase activity.

Dark adopted F_v/F_m measurement

F_v/F_m is a parameter widely used to indicate the maximum quantum efficiency of photosystem II (PSII). Efficiency of open reaction center in light (Φ PSII) = F_v/F_m is calculated by the formula $F_v/F_m = (F_m - F_0)/F_m$.

Here, F_0 represents emission by excited Chl *a* molecules in the antennae structure of PSII, F_m represents the maximum Chl flouorescence value obtained for a continuous light intensity, F_v represents the variable component of the recording and relates to the maximum capacity for photochemical quenching. It is calculated by subtracting the F_0 value from the F_m value.

Differentiating types of biological soil crusts in the field

Biological soil crusts are usually composed of various organisms and divided into morphological groups, unless the crust is in an early succession stage. Morphological groups consist of organisms that are similar in shape and general appearance. The crust morphology largely determines its ecological function relative to water infiltration, erosion, water retention, and resistance and resiliency to disturbance. However, one or two morphological groups will normally dominate the crust. The following are examples of morphological groupings of biological soil-crusts. Belnap (2001) classified soil crusts on the basis of surface roughness and presence of frost heave-smooth, rugose, pinnacled and rolling. Among these both smooth and rugose crusts are dominated by a thin layer of cyanobacteria and fungi. Belnap *et al.* (2004) classified cyanobacterial soil crusts on the basis of their colouration. Light cyanobacterial biological soil crusts are light coloured due to the lack of soil surface colouration. This type of crust is dominated by *Micrcoleus vaginatus* and occurs in area of low rainfall or in deserts where the disturbance level is high and prevents establishment of lichens and mosses. The second type is dark cyanobacterial biological soil crusts. When moist, organisms may be visible as black filaments on and near their soil surface. This type of crust is dominated by *Scytonema myochrous*, *Nostoc commune* and *M. vaginatus*. Dark crusts occur in hot and cool deserts where either precipitation or soil stability limits lichen development and when disturbance is low.

PHYSIOLOGICAL AND BIOCHEMICAL FEATURES OF CYANOBACTERIAL CRUST

Water relation

The various types of organisms that comprise the crust share some interesting physiological traits. They are all capable of drying out and temporarily suspending respiration without negative effects, unlike vascular plants that either die or must re-grow new tissue. These types of organisms are referred to as "poikilohydric." Most of them equilibrate their water content with the atmospheric humidity or soil surface moisture content. Poikilohydric organisms generally become photosynthetically active very quickly, producing carbohydrates or sugars minutes after wetting. However, most species still require high levels of hydration for optimal physiological functioning. The moisture content threshold for activity is species specific and helps to determine the distribution of various taxa that make up the biological crust. Many of these organisms perform under a variety of light intensities and prefer to dry out rapidly. Because they lack a waxy epidermis, crustal organisms also tend to leak nutrients into the surrounding soil upon wetting and drying (Belnap *et al.* 2001). Mager (2010) studied soil crusts in the South west Kalahari, Botswana and stated that cyanobacterial soil crusts are well adapted to dry lands because EPS secretions provide stabilization of soil and resistance to desiccation. When the carbohydrate content was evaluated in the upper soil profile on Kalahari sands and pan soils, it was found that topsoil carbohydrate concentration decreased exponentially with depth. The carbohydrate content produced in cyanobacterial soil crusts in the south west Kalahari represents up to 75% of the total soil organic carbon and is thus an essential component for the fertility of Kalahari sand soil. For survival in harsh conditions the organisms in the biological soil crusts developed survival mechanisms. Most important of these is the ability to reversibly activate metabolism and grow in the short periods when water is available and to retard metabolic activity during dehydration. Potts (1994, 2000) and Billi and Potts (2002) studied the acclimation of the desiccation tolerant *Nostoc commune* to hydration dehydration cycles. It was concluded that stabilization of existing protein during dehydration must be involved to ensure rapid reappearance of growth of *Nostoc* under favourable conditions.

Belnap *et al.* (2004) reported about the response of desert biological soil crusts to alterations in precipitation frequency. According to them, biological soil crusts are a critical component of desert ecosystems. They are only metabolically active when wet. As soil surfaces dry quickly in deserts during late spring, summer, and early fall, the amount and timing of precipitation is likely to have significant impacts on the physiological functioning of these communities. Using the dominant soil crust types found in the western United States, three levels of precipitation frequency were applied (50% below-average, average and 50% above-average) while maintaining average precipitation amount. As the impact of these treatments on photosynthetic performance (dark adopted quantum yield and Chl *a* concentration), nitrogenase activity (NA- means catalysis of the reduction ("fixation") of molecular nitrogen to ammonia in diazotrophs, using reduced ferredoxin and ATP), concentration of radiation of protective pigment was measured, it was found that increased precipitation frequency had large negative impact on the above mentioned factors. Under field conditions of high air temperatures and frequent small precipitation event crust organisms appear unable to produce protective pigments in response to radiation stress as they dried more quickly. Larger and less frequent precipitation was more favourable for the crusts. Reduced activity time likely resulted in less carbon available to produce or repair Chl *a* and protective pigments.

Photosynthesis

Tirkey and Adhikary (2005) measured photosynthesis of soil crust cyanobacteria, collected from laterite soils in and around Bhubaneswar on the east coast, brown soils in the forest of Salboni, arid soils in and around Tiruchirapally and Sandy soils of old Goa in the west coast of India. Chl *a* content was also determined. According to these authors, photosynthetic oxygen evolution increased steadily and within 12 to 24 h of wetting, it nearly stabilized. Early stabilization of the rate of photosynthesis within 12 h of wetting was observed in the crust from Tiruchirapally, this also showed maximum oxygen evolution per gram of crust. Photosynthesis of the wetted crusts from sandy soils of Goa and lateritic soils of Bhubaneswar took longer time for saturation.

Ohad *et al.* (2005) reported about inactivation of photosynthetic electron flow during desiccation of desert biological sand crusts and *Microcoleus* sp. enriched isolate. Desiccation of native crusts resulted in a rapid decline of F_0 (minimum fluorescence) and complete loss of F_v (variable fluorescence). These changes were accompanied by a decrease of energy transfer from phycobilisomes to PSII. Lowering the turgor pressure through the addition of 1.5 M trehalose to natural crusts, reduced F_v/F_m (F_v/F_m used to determine how much solar energy can be converted into fixed carbon) by over 50% and was accompanied by a decrease of 77 K PSI (77 degrees K fluorescence maxima) fluorescence induced by chlorophyll excitation. Excitation of phycobilisomes resulted in a downshift of the PSI emission wavelength by 8 nm. Decline of F_v/F_min trehalose-incubated *Microcoleus* sp. isolates grown on nitrocellulose filters did not induce significant changes in 77 K fluorescence emission. These results suggest that alterations in energy transfer from antennae to reaction centers may be part of the survival strategy of *Microcoleus*.

Harel *et al.* (2004) reported about activation of photosynthesis and resistance to photoinhibition in cyanobacteria within biological desert crust. They have studied the kinetics of activation of photosynthesis during rehydration of the cyanobacteria, primarily *Microcoleus* sp. within crust samples from Nagev desert. Activation of the photosynthetic apparatus did not require *de novo* protein synthesis. Over 50% of the PSII activity, assembled phycobilisomes and PSI antennae were detected within less than 5 min. of rehydration. The cyanobacteria within the crusts are remarkably resistant to photo-inhibition even in the absence of protein synthesis. The rate of PSII repair increased with light intensity and time of exposure. Ability of the crusts organisms to rapidly activate photosynthesis up on rehydration and withstand photoinhibition under high light intensity may partly explain their ability to survive in desert ecosystem.

Tiwari *et al.* (2005) reported distribution and physiological characterization of cyanobacteria isolated from arid zones of Rajasthan. Soil samples were collected from selected arid zones of Rajasthan, namely Achrol, Jaiselmer, Manwar and Pokhran. These isolates were characterized for Chl content, specific metabolic content and N-fixing ability. *Nostoc piscinale* from Achrol showed highest Chl content and total carbohydrate content while *Phormidium* sp. from Jaiselmer and *Nostoc carneum* from Manwar produced maximum Chl and proteins. *Nostoc linckia* from Achrol showed highest Nitrogenase activity but lowest Chl accumulation and soluble proteins but was most efficient for its N-fixing ability in comparison to other isolates examined from soils of Jaiselmer. *Nostoc carneum* from Manwar exhibited lowest NA but showed highest Chl accumulation and soluble protein content. *Calothrix javanica* from Pokhran showed poorest growth in terms of Chl accumulation but was most efficient for N-fixing potential.

Mineral nutrition

Harper and Belnap (2001) reported the influence of biological soil crusts on mineral uptake by associated six vascular plants of the deserts of Utah. According to them, presence of soil crusts increases surrounding soil N by up to 200%. Crust organisms show negative influences on ion uptake by seed plants for iron (Fe), manganese (Mn), sodium (Na), phosphorus (P) and zinc (Zn). Crust organisms secrete extracellular polymers. They increase soil polysaccharides and total carbon by up to 300%. Polysaccharide production can be stimulated by soil magnesium (Mg), potassium (K) and calcium (Ca). In turn more polysaccharides result in greater availability of those nutrients. Inorganic compounds like sulphides of copper (Cu), Zn, lead (Pb), Zn dust, magnesic oxide and ferric hydroxide many bind to crustal organism and remain available to vascular plants. Cyanobacteria secrete metal chelators such as siderochromes that maintain metals in a biologically available form. They also secrete peptide N and riboflavin, which form complexes with tricalcium phosphate, Cu, Zn, nickel (Ni) and ferric iron, keeping them available to plants. Cyanobacteria secrete glycollate (a common extracellular product) which stimulates uptake of phosphate. They also secrete vitamins, auxin-like compounds that promote growth and cell division in plant tissues. The mineral content of a deeply rooted shrub was less influenced by co-occurrence of biological soil crusts.

N fixation

The N-fixing ability of the soil crust organisms in general and cyanobacteria in particular has been established. In desert ecosystems, N fixed by the cyanobacteria and cyanolichens found in the biological soil crusts can be the dominant source of N. This is especially true for regions where rainfall and anthropogenic inputs of N are low. Tirkey and Adhikary (2005) examined NA of soil crusts by using ARA. NA increased with time of wetting and maximum activity was noticed after 72 h. The crust from lateritic soils of Bhubaneswar and sandy soils of old Goa contained non-heterocystous forms of cyanobacteria that did not show ARA in light up to 72 h of incubation. The brown forest soils of Salbani and arid soil of Tiruchirapally showed NA in light as well as dark due to presence of heterocystous cyanobacteria. ARA value in dark was much lower corresponding to incubation in light.

Most cyanobacterial N fixation takes place in heterocysts. Heterocystic genera that commonly occur in soil crusts include *Anabaena*, *Calothrix*, *Cylindrospermum*, *Dicothrix*, *Hapalosiphon*, *Nodularia*, *Nostoc*, *Plectonema*, *Schizothrix* and *Scytonema* (Harper and Marble 1988). N fixation has also been measured in non-heterocystous soil genera such as *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phormidium* and *Tolypothrix* (Rogers and Gallon 1988; Belnap 1996). N fixation rates in individual species of soil cyanobacteria are controlled by species composition, moisture, temperature and light (Kershaw 1985, 1988; Nash 1996). Belnap (2002) has reported N fixation in cyanobacterial members of biological soil crusts from Southeast Utah, USA. Crusts that were used for this study contained predominantly *Microcoleus*, along with *Nostoc* and *Scytonema* and soil lichen *Collema* sp. In all observations *Collema* had higher NA activity than dark crusts, which had higher NA than light crusts, indicating that species composition is critical when estimating N inputs. Climatic conditions also had effect on NA. Without precipitation within a week of collection no NA was recorded regardless of other conditions being favourable. Low (<1°C) and high (>26°C) temperatures precluded NA, even if the soil was moist. Annual N input from dark crusts found at relatively undisturbed sites was estimated at 9 kg ha^{-1} year^{-1}. N input from light crusts, generally indicating soil surface disturbance, was estimated at 1.4 kg ha^{-1} year^{-1}. It appears that much of the N fixed by crusts is released almost immediately to the surrounding soils mainly in the form of NO_3^-, with small amounts of NH_4^+, amides, peptides and free amino acids. The released N is readily taken up by surrounding organisms, including vascular plants, fungi, actinomycetes and bacteria (Stewart 1967; Jones and Stewart 1969; Rogers and Burns 1994).

Klubek and Skujins (1980) reported that in biological soil crusts of the great Basin, *Artemisia*, *Ceratoides* and *Atriplex* plant communities contain a significant heterotrophic N-fixing microbial population in addition to the predominating filamentous cyanobacteria. Heckman *et al.* (2006) reported distribution and activity of hypolithic soil crusts in a hyper-arid desert (Baja California, Mexico). They examined physiology and potential soil N contribution of hypolithic, biological crusts in hyper-arid ecosystems of the Baja California peninsula and islands in the midriff region of the Gulf of California, Mexico. Evidence of low rates of N fixation was inferred from $\delta^{15}N$ values of crust and soil. Hypolithic crusts were found to have minimal influence on soil salinity, pH and NO_3^-, but may represent up to 14% of the biomass of primary producers on these islands and provide C and N to the below ground and possibly above ground heterotrophic communities where crusts exist.

Yeager *et al.* (2007) reported three distinct clades of cultured heterocystous cyanobacteria which constitute the dominant N-fixing members of biological soil crusts of the Colorado plateau, USA. The identity and diversity of the dominant diazotrophs in typical biological soil crusts of the Colorado plateau were determined by combining large-scale environmental *nifH* (*nifH* is the structural gene that codes for the subunits for dinitrogenase reductase of nitrogenase enzyme complex. DNA sequences of a fragment of *nifH* from diverse cyanobacteria have been sequenced to determine the evolutionary relationship of nitrogenase within the cyanobacteria as a group and can be used as a parameter to identify uncultivated strains of cyanobacteria (Zehr *et al.* 1997) surveys with morphological and molecular analysis of cultured cyanobacteria. Of the *nifH* sequence-types detected in soil crusts of the Colorado plateau, 89% were most closely related to *nifH* signature sequences from cyanobacteria of the order Nostocales.

UV-absorbing pigment

Many members of cyanobacteria contain UV-A/B absorbing MAA (Mycosporine-like amino acids – Mycosporines comprise a diverse family of small molecular weight, colourless, water-soluble secondary metabolites) (Dunlap and Chalker 1986). It is present either in sheath or in the cytoplasm. MAA comprise the diverse family of small molecular weight, colourless, water soluble secondary metabolites. MAA synthesis is induced by osmotic and UV stress. In the firm sheaths of many colonial and filamentous cyanobacteria yellow, red and blue pigments may accumulate. The typical yellow brown pigment has been characterized as a UV-absorbing protective pigment – scytonemin (García-Pichel and Castenholz 1991). It is effective in absorbing UV-A, -B and -C. Matsunaga *et al.* (1993) reported UV-A-absorbing biopterin glucoside in a marine *Oscillatoria* sp. Chazal and Smith (1994) reported a brown pigment from a *Nostoc* sp. that was isolated from a soil sample, collected from Java, Indonesia, which was absorbing in the UV region. In addition to their resistance in white light intensity, the brown cells were also resistant to UV, particularly UV-C. Bowker *et al.* (2002) studied variation in community composition, pigmentation and quantum yield of desert cyanobacterial soil crusts. Concentrations of scytonemins, MAA, xanthophylls and carotenoids, commonly increase after exposure to UV radiation in a wide variety of cyanobacterial taxa from varying habitat types. This study shows the temporal variation of some of those pigments also occurs in desert soil crusts. Scytonemin, a proven photoprotective pigment is synthesized in desert soil crusts by the genera *Scytonema* and *Nostoc*. Terrestrial cyanobacteria take 2-3 days after exposure to UV thresholds to obtain optimal levels of UV screening. Another significant observation of this study was that the frequency of major cyanobacterial taxa was lower in fall compared to spring. The less pigmented *Microcoleus vaginatus* showed significant mortality when not in the presence of *Nostoc* or *Scytonema*, the main producers of UV protecting pigments. It is inferred that the sunscreen pigments produced by *Nostoc* and *Scytonema* in the surface crusts protect other less pigmented taxa. In the fall sample most pigments associated with UV radiation protection or repair were at their highest concentrations. The seasonal variation of pigment concentrations is induced by varying UV radiation dosage at the soil surface. Belnap *et al.* (2007) monitored among other things the concentrations of UV-protective pigments in both free-living and lichenized cyanobacteria in an undisturbed Mojave Desert shrubland. The concentrations of UV-protective pigments in free-living cyanobacteria in the Mojave Desert site were strongly and positively related to rainfall received. The predicted drop in precipitation likely caused decrease in soil lichen and moss cover and high stress or mortality in soil cyanobacteria as levels of UV-protective pigments decline. When soils are dry, the bulk of the cyanobacterial biomass is 0.2 to 0.5 mm below the soil surface, where sufficient light for net carbon gain is available but UV exposure is reduced. *Microcoleus vaginatus*, which lacks UV-screening pigments, migrates to the surface for short time periods when soils are moistened and returns to subsurface zones as they dry. On the other hand, populations of *Scytonema* and *Nostoc*, cyanobacteria containing UV-screening pigments, are more commonly found directly on the soil surface.

DISTRIBUTION OF CYANOBACTERIAL CRUST

Despite the widespread occurrence of soil crust communities a global picture of soil crust communities is not well documented. However, some significant works have been done to reveal the species composition of those cyanobacterial communities that occur aggregated with soil particles or in close contact with soil surface. These works have been conducted in Africa, North and South America, Europe, Mediterranean region and Asia including the Don and Volga region of Russia (Johansen 1993; Büdel 2001a, 2001b; Ullmanm and Büdel 2001).

Friedmann and Galun (1974) reported about desert algae, lichens and fungi. They noted that filamentous cyanobacteria such as *Lyngbya*, *Microcoleus*, *Phormidium*, *Plectonema*, *Anabaena*, *Nostoc* and *Scytonema* were most frequent on hot desert lithosole. Their studies have also indicated inter site variations and coccoid cyanobacteria such as *Synechococus* and *Synechocystis* were less common. Danin and Garty (1983) stated that more than 95% of all rock and stone surfaces of deserts were found covered by cyanobacteria and lichens in Sede Boqer. In hot deserts, endolithic organisms are nearly exclusively cyanobacteria with most commonly found *Chroococcidiopsis* and *Gloeocapsa* along with heterotrophic bacteria. *Chroococcidiopsis* is most desiccation-tolerant (Friedmann 1982; Friedmann and Ocampo-Friedmann 1985) and is found in the inner spaces of porous rocks (Friedmann and Ocampo-Paus 1976; Friedmann 1982). It is reported that endolithic algal flora in hot and cold deserts is similar (Friedmann and Ocampo-Paus 1976). Büdel and Wessel (1991) reported eleven genera of desert cyanobacteria from lithic habitats of Africa, North America, Australia and Europe.

Lange *et al.* (1992) reported taxonomic composition and photosynthetic characteristics of the "biological crusts" covering sand dunes in the western Negev Desert. They stated that the most common species of that area was *Microcoleus sociatus*. This species together with sparser *Gloeocapsa* was found within the crust, while *Nostoc* sp. and *Calothrix parietina* occurred predominantly on the crust surface. De Chazal *et al.* (1992) reported methods of using light variation for isolation of cyanobacteria. According to them, cyanobacteria dominate the micro-algal populations of hot deserts and comprise a vast majority of microflora of arid zones in soil crusts. Garcia-Pichel and Belnap (1996) reported about microenvironments and micro scale productivity of cyanobacterial desert crusts. According to them *Nostoc* sp. occur on the surface of hot deserts and may develop sunscreens such as scytonemin to survive intense radiations. Whitton (1987) while reporting about survival and dormancy of blue green alga, indicated that forms like *Chroococcidiopsis*, *Gloeocapsa*, *Gloeothece*, *Synechococcus*, *Phormidium*, *Lyngbya* and *Anabaena* were the most frequent cyanobacterial genera in hot desert. Karnieli *et al.* (1999) reported spectral characteristics of cyanobacteria soil crust in semi arid environments of Sede Hallamish dune field along the Israel/Egypt political border. Five microphytic communities were defined in this area. One community (extending over lower slopes facing south and over interdunes) consists of *Microcoleus sociatus*, *M. vaginatus* and *Phormidium* sp. Another four communities (occupying the north facing hill slopes of dunes) consist of *Nostoc microscopicum*, *Scytonema* sp., *Oscillatoria* sp., *Schizothrix friesii* and *Chroococcidiopsis* sp. along with cyanobacteria of first community.

García-Pichel *et al.* (2001) reported phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado plateau. The community structures of cyanobacteria were compared in four desert crusts. Significant differences in community structure were found among soil types. Belnap *et al.* (2001) studied the dominant biological soil crust components and forms in North American arid and semi-arid ecoregions. Important species of cyanobacteria are found in Colorado Plateau non-heterocystic cyanobacteria (*Microcoleus*), Mojave Desert non-heterocystic cyanobacteria (*Microcoleus*), Chihuahuan Desert heterocystic cyanobacteria (*Nostoc*, *Schizothrix*), Sonoran Desert heterocystic cyanobacteria (*Nostoc*, *Schizothrix*), California Chaparral heterocystic cyanobacteria (*Nostoc*, *Schizothrix*). In North America, microbiotic crusts appear to be less developed in the hottest and driest deserts, such as the Mojave Desert or Sonoran Desert, but they are typical in that they are colonized by many filamentous species of cyanobacteria (Flechtner *et al.* 1998; Johansen *et al.* 2001). In most cases, the dominant genera of filamentous cyanobacteria in hot desert soils are *Microcoleus*, *Phormidium*, *Plectonema*, *Schizothrix*, *Nostoc*, *Tolypothrix* and *Scytonema* (Cameron 1960; Durrell 1962; Shields and Drouet 1962). Belnap (2002) reported N fixation in biological soil crusts from south east Utah, USA. He collected 2 types of cyanobacterial soil crusts whose directly counted cells were >98% *Microcoleus vaginatus* (light crusts) and crusts dominated by *M. vaginatus*, but with 20% or more of the directly counted cells represented by *Nostoc commune* and *Scytonema myochrous* (dark crusts).

Büdel (2002) drew analogy of the typical structure of the crust with that of a microforest. It is composed of unicellular cyanobacteria *Chroococcidiopsis*, *Chroococcus*, *Gloecocapsa*, *Gloeothece* and few filamentous forms such as *Schizothrix* sp. are very common. The 'canopy' is formed by filamentous cyanobacteria *Scytonema* sp. and *Stigonema* sp. together with cyanolichens. Belnap *et al*. (2004) reported response of desert biological soil crusts to alterations in precipitation frequency. They used three dominant soil crust types found in the western United States. Among those crusts, the dark surface cyanobacterial crusts included *Nostoc* sp., *Scytonema* sp. and *Microcoleus* and the light cyanobacterial crusts included *Microcoleus* sp.

Heckman *et al.* (2006) reported distribution and activity of hypolithic soil crusts in a hyper-arid desert (Baja California, Mexico). Crusts were limited in distribution to areas with translucent quartz rocks less than 3 cm thick, were not found on areas of islands with seabird guano deposition, but covered as much as 1% (12,750 m^2) of the surface area of one island. The percent of available rocks colonized by crusts was similar between the mainland (38%) and islands without seabird guano (26%). Thomas and Dougill (2007) reported cyanobacterial soil crusts and N fixation in Kalahari Range lands. They concluded that cyanobacterial soil crusts are widespread (up to 95%) in the Kalahari and are inversely related to disturbance. Crusts in grazed areas form under *Acacia mellifera* and may encourage shrub encroachment and a reduction in grazing potential.

Gundlapally and García-Pichel (2006) reported the community and phylogenetic diversity of biological soil crusts in the Colorado Plateau with the help of molecular fingerprinting and intensive cultivation. They concluded that biological soil crust communities displayed less richness and Shanon diversity with apparent dominance by few members. The cyanobacterium *Microcoleus vaginatus* was dominant, with *M. steenstrupii* second among phototrophs. Bowker *et al.* (2006) reported spatial modeling of biological soil crusts to support rangeland assessment and monitoring. Samples were collected from low disturbance sites in Grand Staircase-Escalante National Monument (Utah, USA) and light and dark cyanobacterial crust types were obtained along with moss and lichen.

Řeháková *et al.* (2006) reported morphological and molecular characterization of selected cyanobacteria from desert soils of the western United States. They discovered four Nostocacean species. Among them three species are new to science. One is distinct from *Nostoc* by both morphological and molecular criteria and is described as *Mojavia pulchra* gen. *et* sp. nov. Two other strains are described as *Nostoc indistinguendum* sp. nov. and *Nostoc desertorum* sp. nov. The fourth one is *Nostoc lichenoides* and it is the phycobiont of lichen *Collema tenax*. Flechtner *et al.* (2008) reported about soil crusts from an isolated area, San Nicolas Island of USA, which was not studied earlier. Distinct floristic distribution was showed between this flora and that of North America. Significant biodiversity of the soil crust cyanobacteria was noted.

Johansen *et al.* (2001) conducted an extensive study of the distribution and abundance of microbiotic soil crusts in a large area of the Mojave Desert within and near the Fort Irwin National Training center, San Bernadino County, California.

Alwathnani *et al.* (2011) collected samples from six sites of Fort Irwin National Training Center in the Mojave Desert, California and isolated representatives of three orders of cyanobacteria (Pseudoanabaenales, Oscillatoriales and Nostocales). This study revealed that crusts were poorly developed even in undisturbed areas of Mojave Desert.

Thomas and Dougill (2006) reported distribution and characteristics of cyanobacterial soil crusts in the Molopo Basin, southern Africa. In Molopo Basin total average crust cover ranged from 24 to 55%. Four cyanobacterial crust types were identified. Two species of *Microcoleus* and *Scytonema* were found in all crust types.

Biological soil-crusts communities were described almost 40 years ago from Spain (Crespo 1973; Crespo and Barreno 1975). Cyanobacteria, as a component of biological soil crusts have not been well documented in Spain. Maestre *et al.* (2006) isolated more than 15 taxa of cyanobacteria which indicated diversified nature of the crust.

Yeager *et al.* (2007) reported three distinct clades of cultured heterocystous cyanobacteria that constitute the dominant N_2-fixing members of biological soil crusts of the Colorado plateau, USA. The identity and diversity of the dominant diazotrophs in biological soil crusts of this region were determined by combining *nifH* surveys, morphological and molecular analysis of cultured cyanobacteria. According to them, five major *nifH* sequence types belong to three phylogenetic groups: (i) a group of *Nostoc* strains that belong to the morphospecies *N. commune*; (ii) a phylogenetically and morphologically coherent group of strains well-represented by isolates of the morphospecies *Scytonema hyalinum*; (iii) a phylogenitically coherent but morphologically less-defined group of strains that is represented by *Tolypothrix* and *Spirirestis*. Williams *et al.* (2008) reported that grazing and drought reduce cyanobacterial soil crusts in an Australian *Acacia* woodland. They found abundance of three cyanobacteria – *Scytonema* sp., *Stigonema ocellatum* and *Porphyrosiphon notarissi* in undisturbed area.

Moghtaderi *et al.* (2009) reported cyanobacteria in biological soil crust of Chadormalu area, Bafq region in central Iran. Crust samples, collected from 14 sampling stations in northern Chadormalu desert soil (sandy soil, silt gypsum and shale) mostly included *Microcoleus vaginatus*, *Nostoc* sp., *Microcystis* sp., *Oscillatoria* sp., *Chroococcus* sp., *Chroococcidiopsis* sp.

Wu *et al.* (2009) collected soil crust samples from different sites of Gurbantunggut Desert, Northwestern China and three types of crusts were obtained: cyanobacterial crust, lichen crust and moss crust. Cyanobacterial crust was heavily dominated by *Microcoleus vaginatus*.

Zhang *et al.* (2011) collected 60 samples from Gurbantunggut desert, China and 51 cyanobacterial taxa were isolated. Results from step regression showed that species diversity was determined by total P, Mg content, soil moisture, sunlight, oxygen concentration and soil layer.

Bhatnagar *et al.* (2003) studied 32 samples of cryptobiotic crusts in the Thar Desert in India. There were 43 morphotypes of diazotrophs in BG-11 (–N) medium and 71 of algae and cyanobacteria in the same medium supplemented with N and most frequent form was *Phormidium tenue.* In case of diazotrophs, the most frequent forms were *Nostoc punctiforme*, *Nostoc commune* and *Nostoc palludosum*. Fourteen genera of diazotrophic cyanobacteria were reported with maximum morphotype variability in *Calothrix*, *Nostoc*, *Anabaena* and *Scytonema.* Tiwari *et al.* (2005) reported distribution and physiological characteristics of cyanobacteria isolated from arid zones of Rajasthan. Soil samples were collected from Achrol, Jaisalmer, Manwar and Pokhran. These were inoculated in BG-II medium under a 16-h photoperiod and identified. Cyanobacterial genera like *Phormidium*, *Oscillatoria*, *Nostoc*, *Anabaena*, *Calothrix*, *Westiellopsis* and *Chlorogleopsis* were isolated. Bhatnagar and Bhatnagar (2005) reported microbial diversity in desert ecosystems. According to them cyanobacterial crusts generally dominate poor sandy soils (Skujins 1984; García-Pichel *et al.* 2001; Budel 2002). A comprehensive account of soil crust cyanobacteria of India had been given by Tirkey and Adhikary (2006). They reported various cyanobacteria species of different regions of India. Crusts were collected from the lateritic soils in and around Bhubaneswar on the east coast, from brown soils in the forest of Salboni and Raniganj under the ancient Gondwana land in the central region, from arid soils in and around Tiruchirapalli in the southern region and from the sandy soils of Goa in the western coast of India. They described 3 spp. of *Oscillatoria*, 1 sp. of *Phormidium*, 4 spp. of *Lyngbya*, 2 spp. of *Microcoleus*, 2 spp. of *Plectonema*, 1 sp. of *Cylindrospermum*, 11 spp. of *Nostoc*, 2 spp. of *Tolypothrix*, 4 spp. of *Scytonema*, 7 spp. of *Calothrix*, 3 spp. of *Aulosira*, 5 spp. of *Hapalosiphon*, 1 sp. of *Fritscherella*, 1 sp. of *Stigonema* and 5 spp. of *Westiellopsis*. Area-wise distribution of various taxa is given in **Table 1**.

FACTORS INFLUENCING SPECIES COMPOSITION AND DISTRIBUTION

Elevation

When all crust types are combined (cyanobacterial, moss, lichen), crust cover is greatest at lower elevation inland sites (< 1,000 m) compared to mid-elevation sites (1000 to 2500 m; Hansen *et al.* 1999). Biological soil crust forms depend on temperature characteristics of the environment. In hot deserts crust form is flat or rugose and in cold deserts crust form is rolling. The positive relationship between biological crust cover and available soil surface has been amply demonstrated (Rogers 1972; Harper and Marble 1988; Eldridge 1993; Johansen 1993).

Table 1 Some important reports of distribution of soil-crust cyanobacteria.

Reference	**Organism**	**Location**	**Remarks**
Karneili *et al.* 1999	*Microcoleus sociatus*, *M. vaginatus*, *Phormidium* sp., *Nostoc microscopicum*, *Scytonema* sp., *Oscillatoria* sp., *Schizothrix friesii.*	Sede Hallamish dune fields along Egypt/Israel border.	The unique spectral features of cyanobacterial crusts growing on bare sands and those under different moist conditions, were analysed systematically throughout the visible, near-infra red and the short-wave infrared regions of the spectrum.
Garcia-Pichel *et al.* 2001	*Mircoleus vaginatus*, *Schizothrix* spp., *Phormidium* spp., *Scytonema* spp., *Nostoc* spp., *Chlorogloeopsis* sp.	Colorado plateau, USA.	Natural samples, cultures and cyanobacterial filaments or colonies (retrieved by micromanipulation) studied using microscopy, denaturing gradient gel electrophoresis and 16S rRNA genes sequencing to find the diversity in desert crusts. Gypsum crusts were most deviant from the rest while sandy silt and shale crusts were most similar among them.
Belnap 2002	Light crust (mainly *Microcoleus vaginatus)*, Dark crust (dominated by *Microcoleus vaginatus* which is mixed with *Nostoc commune* and *Scytonema myochrous)*	South east Utah, USA.	Potential nitrogen fixation rates were measured biweekly for two years, using three types of soil crusts-light crusts, dark crusts and lichen dominated crusts. The observation was –NA of lichen > NA of dark crusts > NA of light crusts.
Bowker 2002	*Microcoleus vaginatus*, *Nostoc* spp., *Scytonema myochrous.*	Colorado Plateau, USA.	This study showed variation in community composition, pigmentation and quantum yield of desert cyanobacterial soil crusts. Scytonemin, MAA and carotenoids content increased as a result of exposure to UV radiation.
Bhatnagar and Bhatnagar 2005	*Chroococcus minutus*, *Oscillatoria pseudogeminata*, *Phormidium tenue*, *Nostoc puntiforme*, *N. commune*, *N. palludosum*, *Anabaena* sp., *Calothrix* sp., *Scytonema* sp.	Thar desert, India.	Deserts are found to have a treasure of microbiota with unique flora of cyanobacteria. These cyanobacteria are responsible for the productivity, bio-geo-chemical cycling of elements and ecosystem balance and improvement of soil structure.
Tiwari *et al.* 2005	*Oscillatoria curviceps*, *Phormidium sp.*, *P. jennkelianem*, *P. molle*, *Anabaena sphaerica*, *Nostoc linckia*, *N. verrucosum*, *N. carneum*,, *N. piscinale*, *N. ellipsosprum*, *N. muscorum*, *N. calcicola*, *Calothrix membranacea*, *C. javanica*, *C. braunii*,*Chlorogloeopsis* sp., *Westiellopsis prolofica.*	Arid zones of Rajasthan, India.	These taxa were collected from arid zones. Among other features nitrogen fixing ability was determined. *Calothrix* was found to be the most predominant nitrogen fixer.
Gundlapally *et al.* 2006	*Microcoleus vaginatus*, *M. steenstrupii.*	Colorado Plateau, USA.	The cyanobacterial communities in biological soil crusts from the Colorado Plateau were studied by enrichment culture. Populations were analyzed by denaturing gradient gel electrophoresis fingerprinting of environmental 16S rRNA genes and from phylogenetic point of view.
Maestre *et al.* 2006	*Chroococcidiopsis* sp., *Microcoleus steentrupii*, *Leptolyngbya boryanum*, *L. foveolarum*, *Oscillatoria* sp., *Phormidium* sp.	A *Stipa* steppe in Alicante, Spain.	Cyanobacteria, as a component of biological soil crusts have not been well documented in Spain. But the diversity of these organisms may be high. In this study, more than 15 taxa of cyanobacteria were isolated which indicated diversified nature of the crust.
Thomas and Dougill 2006	*Microcoleus* sp., *Scytonema* sp.	The Molopo Basin, Southern Africa.	Resilient nature of South African soil was found to be due to the presence of soil-crusts. This study provided an analysis of the physical, microbiological and chemical characteristics of four morphologically distinct cyanobacterial crust types. An account of influence by soil type, livestock disturbance and vegetation cover in controlling the spatial distribution of crusts is also given.
Tirkey and Adhikari 2006	15 genera were isolated; among them followings are noteworthy-*Oscillatoria chlorine*, *Phormidium ambiguum*, *Lyngbya palmarum*, *Microcoleus. lacustris*, *Plectonema puteale*, *Cylindrospermum indicum*, *Nostoc ellipsosporum*, *Tolypothrix bouteillei*,*Calothrix parietina*, *Aulosira prolifica*, *Hapalosiphon welwitschii*, *Fritscherella muscicola Stigonema tomentosum*, *Westiellopsis prolifica.*	Different regions of India-Bhubaneswar, Salbani, Ranigaung, Tiruchirapally and Goa-different regions of India.	Cyanobacterial taxa from soil-crust samples from different regions of India have been documented.
Flechtner *et al.* 2008	19 genera were isolated, among them followings are noteworthy- *Aphanothece maritime*, *Chroococcidiopsis edaphica*, *Microcoleus vaginatus*, *Nostoc punctiforme.*	San Nicolas Island,USA.	This report was from an isolated area which was not studied earlier. Distinct floristic distribution was shown between this flora and that of North America. Significant biodiversity of the soil crust cyanobacteria was noted.
Wu *et al.* 2009	*Microcoleus vaginatus* (most dominant one).	Gurbantunggut Desert, Northwestern China.	In this work, a comparative study of nitrogenase activity in three types of crusts, collected from the desert, was represented.
Moghtaderi *et al.* 2009	*Microcoleus vaginatus*, *Nostoc* sp. *Microcystis* sp., *Oscillatoria* sp.,*Chrooccoccus* sp., *Chroococcidiopsis* sp.	Chadormalu desert, Yard Province of Iran.	In this work, the cyanobacteria of Chadormalu desert were documented. This work shows that the organisms present in Chadormalu desert are comparable with other desert in cold and warm dry conditions.
Zhang *et al.* 2011	*Cyanothece aeruginosa*, *Synechococcus parvus*, *Oscillatoria tenuis*. *Lyngbya majuscule*, *Microcoleus vaginatus*,*Nostoc commune*. *Chroococcus turgidus*, *Phormidium attenuatum*, *Microcoleus vaginatus*, *Oscillatiria subbrevis*, *Phormiodium irrigum*, *Microcoleus vaginatus*.	Gurbantunggut Desert, China.	Sixty samples were collected from sand dunes, interdune areas, leeward areas and wind ward areas and 51 cyanobacterial taxa were isolated from this desert. Results from step regression showed that species diversity was determined by total P, Mg content, soil moisture, sunlight, oxygen concentration and soil layer.

Table 1 (Cont.)

Reference	Organism	Location	Remarks
Alwathnani *et al.* 2011	*Leptolyngbya africanum*, *L. nostocorum*, *Pseudophormidium hollerbachianum*, *Phormidium kuetzingiana*, *Microcoleus vaginatus*, *Nostoc desertorum*, *N punctiforme*, *Calothrix fusca*, *Scytonemaq javanicum*, *Tolypothrix camptylonemoides*.	Fort Irwin National Training Center in the Mojave Desert, California, USA.	Representatives of three orders of cyanobacteria (Pseudoanabaenales, Oscillatoriales and Nostocales) were isolated from six sites. This study also revealed that crusts were poorly developed even in undisturbed areas of Mojave desert.

Soils and topography

Stable or embedded rocks near or at the soil surface can increase the percent crust cover by perching water and armoring the surface from physical disturbances. Shallow soils often support a wide variety of cyanobacteria, lichens and mosses, regardless of soil texture. Different soil textures are selected by different cyanobacteria which promote different community structures (Fairchild and Wilson 1967; García-Pichel *et al.* 2001; Hawkes and Flechtner 2002). In the Gurbantunggut Desert, microenvironments, physicochemical properties and developmental levels of biological soil crusts vary depending on their position on the sand dunes (Hu *et al.* 2003; Rivera-Aguilar *et al.* 2006; Tirkey and Adhikary 2006). The more stable, fine-textural soils (such as gypsum and silty loams) support greater cover and more varied populations of cyanobacteria, lichens and mosses than less stable, coarse-textured soils (Kleiner and Harper 1977b; Hansen *et al.* 1999). Coarse-textured soils may have only large filamentous, highly mobile cyanobacteria such as *Microcoleus* sp.

Soil chemistry can also influence crust cover and composition. Calcareous and gypsiferous soils generally support high coverage of species-rich crust with some taxa being excellent indicators of soil chemistry. North and east slopes generally favor crustal development in lower elevation desert regions. Slope angle does not generally affect crust cover or species richness (Rosentreter 1986). Cyanobacteria generally dominate soils that are very sandy (>90%), very salty or have a high content of shrink-swell clays, regardless of the climatic zone (Belnap 2006).

Disturbance

Intensity and type of soil surface disturbance, along with time since disturbance, influence the composition of biological crusts. The presence, absence and abundance of early or late successional taxa can provide information regarding a site's disturbance history. Intense disturbance results in bare soil. Severely, newly or frequently disturbed soils are generally dominated by large filamentous cyanobacteria (Anderson and Rushforth 1976; Johansen *et al.* 1981, 1984; Johansen and Rushforth 1985; Harper and Marble 1988). If disturbance continues, crusts will stay in early successional stages (i.e., cyanobacteria only). Activities like grazing, off-road vehicles, recreational and commercial activities disturb soil-crust and accelerate desertification process. A reduction in trampling on the soil-surface will result in re-establishment of biological soil-crusts (Zhang *et al.* 2010).

Precipitation

Dominance of biological soil crusts is highly influenced by seasonal precipitation patterns. Ecoregions that receive summer monsoons (e.g., the Sonoran Desert) tend to have a greater diversity of heterocystic cyanobacteria (*Calothrix*, *Schizothrix*, *Nostoc*) and lower number of non-heterocystic genera. Regions with winter rainfall and/or greater rainfall are heavily dominated by *Microcoleus* (Belnap 2006).

Vascular plant community structure

The distribution, shape and height of vascular plants can either increase or decrease biological crust cover and influence crust species composition. Vascular plants reduce the overall soilcrust species composition. Vascular plants reduce the overall soil surface available for colonization especially in regions with PET. On the other hand, shading provided by plant cover enhances crust development through increased soil moisture (St. Clair *et al.* 1993). The vertical and horizontal vascular plant structure of many arid and semi-arid vegetation communities optimizes growth of biological soil crusts. In cooler regions greater structural diversity of vascular vegetation generally results in greater compositional diversity of biological crusts (Belnap *et al.* 2001).

IMPORTANCE OF CYANOBACTERIAL SOIL-CRUSTS

Carbon-fixation

Crust organisms enhance the nutrient status of soils via carbon fixation (Beymer and Kolpatek 1991). Biological soil crusts can be an important source of fixed carbon on sparsely vegetated areas. The carbon fixed by the soil crust organisms can increase the total surface soil carbon by up to 300% (Evans and Lange 2003). While vascular plants contribute organic matter to soils directly beneath them, large interspaces between plants receive little plant material input. This addition appears to benefit the soil biota, especially in the interspaces between vascular plants (Belnap 2003). Su *et al.* (2012) systematically analyzed the changes in the carbon exchange of cyanobacterial- algal soil-crusts developed in two sites (Tengger Desert - old and new crust) to dehydration, air-temperature (15-25°C) and CO_2 conc. (200-2000 ppm). The carbon exchange rate was higher at 25°C than at 15°C for both crusts. The saturation point significantly increased with the increase in the water content of the crust organisms. The water content of the crust organisms was the regulating factor for the carbon exchange rate of both the old and recent cyanobacterial-algal crusts.

N-fixation

Aside from water, N is considered the limiting resource for soil productivity in many arid and semiarid lands. Crust organisms enhance the nutrient status of soils by fixing atmospheric N (Evans and Ehleringer 1993; Houseman *et al.* 2006) and transforming it (Castrillo-Monroy *et al.* 2010). They can be the major source of N of the soil (Evans and Ehleringer 1993). Heterocystous genera that commonly occur in soil crusts include *Anabaena*, *Calothrix*, *Cylindrospermum*, *Dicothrix*, *Hapalosiphon*, *Nodularia*, *Nostoc*, *Plectonema*, *Schizothrix* and *Scytonema* (Harper and Marble 1988). From morphological and culture-based studies of crust microorganisms, it was determined that heterocystous cyanobacteria, such as *Nostoc* sp. were major suppliers of fixed N to soil crusts of the Colorado Plateau (Harper and Marble 1988; García-Pichel and Belnap 1996; Belnap 2002). N fixation has also been measured in non-heterocystous soil genera such as *Lyngbya*, *Microcolleus*, *Oscillatoria*, *Phormidium* and *Tolypothrix* (Rogers and Gallon 1988; Belnap 1996), although this may be a result of bacteria associated with the cyanobacteria (Steppe *et al.* 1996). Laboratory studies have demonstrated that N fixation rates in individual species of soil crust cyanobacteria are controlled by species composition, moisture, temperature and light (Kershaw 1985; Nash 1996). According to Zhang *et al.* (2010), the occurrence of biological soil crusts in Gurbantunggut

Desert could significantly enhance the accumulation of soil organic matter in the surface 0-5 cm. soil layer compound with areas devoid of crust cover. Biological soil crusts can contribute to nutrient cycling (Rivera-Aguilar *et al.* 2006).

Role in reduction of soil, wind and water erosion and improvement of soil quality

Cyanobacteria weave through the top few millimeters of soil, gluing loose particles together and forming a matrix that stabilizes and protects soil surfaces from erosive forces (Comeron 1966; Friedmann and Galun 1974; Friedmann and Ocampo-Paus 1976; Belnap and Gardner 1993). Loss of biological soil crusts in dryland range ecosystems is both a component of and accelerator of land degradation (Belnap 1995). Removal of soil crusts by live stock trampling accelerates soil degradation (Bowker *et al.* 2008). They can be considered ecosystem engineers in arid lands because they aggregate surface soil and reduce erosion (Mazor *et al.* 1996; Jones *et al.* 1997). They stabilize soils against water and wind erosion (Chaudhary *et al.* 2009). They also reduce wind and water erosion (Eldridge and Greene 1994; Zhang 2005; Zhang *et al.* 2006).The rate of wind erosion increases with increasing levels of crust disturbance. This indicates that biological soil-crusts are one of the factors responsible for reduced wind erosion (Zang *et al.* 2010). Cyanobacteria of Biological soil crusts play a crucial role in maintaining soil stability, improving soil structure, accumulating soil fertility and reducing salt stress (Bowker and Belnap 2004; Zhang 2005; Zhang *et al.* 2006) and influencing soil respiration (Maestre and Cortina 2003)

Retention of soil moisture, water relation and reduction of weed growth

Biological soil crusts function as living mulch by retaining soil moisture and discouraging annual weed growth. The effect of biological soil crusts on soil-water relation is highly site dependent. Research conducted under a variety of soil and climate conditions around the world shows variable and interactive effects of biological crusts and soil properties. Biological crusts influence soil hydrology because they alter soil surfaces. Aggregate stability, soil structure, organic matter content and rough microtopography are all attributes associated with superior hydrologic properties and biological soil crusts enhance these attributes in soil (Booth 1941; Fletcher and Martin 1948; Shields and Durrell 1964). Infiltration rates are controlled by the interaction of water residence time on a soil surface and the permeability of that surface (Belnap *et al.* 2001).

Acting ecological indicators

Pellant *et al.* (2000) suggested the use of biological soil crusts as an optional indicator of rangeland health in regions where crusts are present, potentially providing a sensitive measure of departure from ecological health. They act as indicators of abiotic factors, such as the presence of calcareous soils. They can thus be used as indicators of ecological health.

Role in ecological rehabilitation

Biological soil crust cover is important for ecological rehabilitation due to its stabilizing function. It can re-establish to a state comparable to undisturbed reference conditions (Kidron *et al.* 2008). Theories of succession suggests that biological soil crusts are common colonizers of exposed soils and may re-establish as a permanent component of ecosystems with low vascular plant cover (Bowker 2007).

Production of extra-cellular polysaccharides

Polysaccharides are renewable resources representing an important class of polymeric materials of biotechnological interest, covering a wide variety of potentially useful products to mankind. It has been reported in some soil crust cyanobacteria that polysaccharides increase survival and activity. However there is a relationship between desiccation and production of EPS in soil crust cyanobacteria of semiarid regions.

Secretion of exopolymers and metal chelators

Biological soil crusts secrete exopolymers that help prevent nutrient losses via leaching and concentrate plant-essential nutrients such as Na, K, Mg, Ca, Mn, Fe, Ni, Cu and Zn. They secrete powerful metal chelators that maintain metals in bio-available forms; peptide N and riboflavin which help to keep P, Cu, Zn, Ni and Fe available to plants; glycollate, which stimulates P uptake; and various other factors such as B_{12} and auxin-like substances that stimulate growth (Belnap *et al.* 2004).

Influence on mineral uptake by associated vascular plants

Cyanobacterial crusts significantly alter uptake by plants of many bioessential elements. These crusts always increase the N content of associated seed plants. Uptake of Cu, K, Mg and Zn is usually (>70% of reported cases) increased in the presence of the biological soil crusts. Increases in bioessential elements in vascular plant tissue from biologically-crusted areas are greatest for short–lived herbs that are rooted primarily within the surface soil (Harper and Belnap 2001).

Creation of artificial soil crust

Considering the importance of biological soil crusts scientists have formulated methodology to develop artificial soil crusts (Bo and Yun-ge 2010). The soil was passed through a sieve with 10 mm diameter. Then the prepared soil was packed into eight boxes. Afterward, the natural biological soil crusts collected from field were crushed and mixed with some fine soil and seeded uniformly. Inoculation dose of air dry matter is 1.25 kg/m^2. The simulated rainfall experiment was started when the cultured biological soil crusts were initially formed.

Effects on germination of vascular plants

Biological soil crusts can affect vascular plant germination. They provide habitat for microfauna (Li *et al.* 2006), may facilitate recruitment of vascular plants (Langhans *et al.* 2009; Su *et al.* 2009) and influence the performance of vascular plants (Escudero *et al.* 2007). Many exotic vascular plant species lack self-burial mechanisms. Because biological crusts stabilize soils, germination of such seeds can be inhibited in sites with well-developed crusts and low plant litter, as was recently found in case of the annual exotic grass cheat grass (*Bromus tectorum*) in both field and laboratory (Kaltenecker *et al.* 1999). The biological soil crusts can affect the generation of some plants. The effect may be positive or negative and it mainly depends on both moisture condition and biological characteristics of vascular plants (Zhang *et al.* 2010). Godinez-Alvarez *et al.* (2012) analysed germination, seedling survival and growth of three vascular plants (*Agave marmorata*, *Prosopis laevigata* and *Neobuxbaumita tetetzo*) on cyanobacteria and mixed soil crust from a tropical desert region of south-central México. According to them plant species performance was qualitatively higher on biological soil crust than bare soil. The highest performance of *A. marmorata* and *P. laevigata* was observed on cyanobacteria and mixed crusts respectively. The highest performance of *N. tetetzo* was on both crust types.

Conservation of biological soil crust

It has already been established that biological soil crusts are strong indicators of multiple ecosystem functions including N fixation, carbon fixation, soil building and retention and modification of hydrological processes. Biological soil crusts are often more vulnerable to degradation than associated vascular plant. In desert regions, they respond predictably to surface degradation. Thus conservation of biological soil crusts is important. Conservation value of biological soil crusts was defined in three ways: sites with relatively high biological soil crusts biodiversity, high functional significance of biological soil crusts or a combination of both. Bowker *et al.* (2008) identified areas (arid regions of Utah) that were simultaneously high in conservation value of biological soil crusts and highly at risk of degradation.

CONCLUSION

Biological soil crusts in general and the soil-crusts whose main component is cyanobacteria form an important constituent of arid and semi-arid ecosystem. The poikilohydric nature of this crust, reverting back to normal metabolism concerning photosynthetic activity after a dry season and with the onset of prolonged precipitation, ability of the cyanobacteria to fixed N biologically and contributing the fix N along with other organic matter for the enrichment of the soil are some of the features that make the cyanobacterial soil-crusts extremely important for the arid and semi-arid regions. A review of the published works clearly indicates that the cyanobacterial soil-crusts are widely distributed in all kinds of ecological conditions on earth. The variations of physiological, biochemical characters, distribution pattern, species composition, capacity to fix N, synthesizing UV-protecting pigments show the variation of response of cyanobacterial species to different and varying ecological parameters encountered by them. Considering the significant role played by these organisms in improving the arid zones artificial development of cyanobacterial crusts are being considered seriously by the scientists. Preliminary attempts have been successful in this regard.

REFERENCES

Alwathnani H, Johansen JR (2011) Cyanobacteria in soils from a Mojave Desert ecosystem. *Monographs of the Western North American Naturalist* **5**, 71-89

Anagnostidis K, Komárek J (1988) Modern approach to the classification system of cyanophytes, 3-Oscillatoriales. *Algological Studies* **50/53**, 327-472

Anagnostidis K, Komárek J (1990) Modern approach to the classification system of cyanophytes, 5-Stigonematales. *Algological Studies* **59**, 1-73

Anderson DC, Rushforth SR (1976) The cryptogamic flora of desert soil crusts southern Utah. *Nova Hedwigia* **28**, 691-729

Belnap J (1995) Surface disturbances: Their role in accelerating desertification. *Environmental Monitoring and Assessment* **37**, 39-57

Belnap J (1996) Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. *Biology and Fertility of Soils* **23**, 362-367

Belnap J (2001) Comparative structure physical and biological soil crusts. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 177-191

Belnap J (2002) Nitrogen fixation in biological soil crusts from south east Utah, USA. *Biology and Fertility of Soils* **35**, 128-135

Belnap J (2003) Microbes and microfauna associated with biological soil crusts. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 167-174

Belnap J (2006) The potential roles of biological soil crusts in dry land hydrologic cycles. *Hydrological Process* **20**, 3159-3178

Belnap J, Eldrige DJ (2003) Disturbance and recovery of biological soil crusts. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 363-383

Belnap J, Gardner JS (1993) Soils microstructure in soils of the Colorado plateau: The role of the cyanobacterium *Microcoleus vaginatus. Great Basin Naturalist* **53**, 40-47

Belnap J, Büedel B, Lange OL (2001) Biological soil crust. Characteristics and distribution. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 3-30

Belnap J, Phillips SL, Miller ME (2004) Response of desert biological soil crusts to alterations in precipitation frequency. *Oecologia* **141**, 306-316

Belnap J, Phillips SL, Smith SD (2007) Dynamics of cover, UV-protective pigments and quantum yield in biological soil crust communities of an undisturbed Mojave Desert shrubland. *Flora* **202**, 674-686

Belnap J, Prasse R, Harper KT (2003) Influence of biological soil crusts on soil environments and vascular plants. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 281-300

Belnap J, Kaltenecker H, Rosentreter R, Williams J, Leonard S, Eldridge D (2001) Biological soil crusts: ecology and management. BLM Technical Reference 1730-2. United States Bureau of Land Management, Washington, D.C., 110 pp

Beymer RJ, Kolpatek JM (1991) Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation* **5**, 187-198

Bhatnagar A, Bhatnagar M (2005) Microbial diversity in desert ecosystems. *Current Science* **89 (1)**, 91-100

Bilger W, Björkman O (1990) Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in *Hedera Canariensis*. *Photosynthesis Research* **25**, 173-185

Bilger W, Schreiber U, Bock M (1995) Determination of the quantum efficiency of photosystem II and of non-photo chemical quenching of chlorophyll fluorescence in the field. *Oecologia* **102**, 425-432

Billi D, Potts M (2002) Life and death of dried prokaryotes. *Research in Microbiology* **153**, 7-12

Blank CE (2004) Evolutionary timing of the origins of mesophilic sulfate reduction and oxygenic photosynthesis: A phylogenomic dating approach. *Geobiology* **2**, 1-20

Blankenship RE (1992) Origin and early evolution of photosynthesis. *Photosynthesis Research* **33**, 91-111

Bo X, Yun-ge Z (2010) Artificial culture of biological soil crusts and their effects on runoff and infiltration under simulated rainfall on the Loess Plateau of China. In: *19th world Congress of Soil Science, Soil Solution for a Changing World*. 1-6 August 2010, Brisbane, Australia, pp 11-14

Booth WE (1941) Algae as pioneers in plant succession and their importance in erosion control. *Ecology* **22**, 38-46

Bowker MA (2007) Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology* **15**, 13-23

Bowker MA, Belnap J (2004) predictive modeling of biological soil crusts can be used as a tool for better range management. *Ecological Society of America Annual Meeting Abstracts* **89**, 58

Bowker MA, Belnap J, Miller ME (2006) Spatial modeling of biological soil crusts to support range land assessment and monitoring. *Range land Ecology Management* **59**, 519-529

Bowker MA, Belnap J, Chaudhary BV, Johnson NC (2008) Revisiting classic water erosion models in drylands; The strong impact of biological soil crusts. *Soil Biology and Biochemistry* **40**, 2309-2316

Bowker MA, Reed SC, Belnap J, Phillips SL (2002) Temporal variation in community composition, pigmentation, and F_v/F_m of desert cyanobacterial soil crusts. *Microbial Ecology* **43**, 13-25

Bowker MA, Miller ME, Belnap J, Sisk TD, Johnson NC (2008) Prioritizing conservation effort through the use of Biological Soil Crusts as ecosystem function indicators in an arid region. *Conservation Biology* **22 (6)**, 1533-1543

Büdel B (2001) Biological soilcrusts of Asia including the Don and Volga region. *Ecological Studies* **150**, 87-94

Büdel B (2001a) Biological soil crust of Asia including Don and Volga region. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 87-94

Büdel B (2001b) Synopsis: Comparative biography and ecology of soil crust biota and communities. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 141-152

Büdel B (2002) Diversity and ecology of biological soil crusts. In: Esser K, Luttge U, Beyschlag W, Hellwig F (Eds) *Progress in Botany*, Springer, Berlin, pp 386-404

Büdel B, Wessels DCJ (1991) Rock inhabiting blue green algae/cyanobacteria from hot arid regions. *Algological Studies* **64**, 385-398

Cameron RE (1960) Communities of soil algae occurring in the Sonoran Desert in Arizona. *Journal of the Arizona Academy of Science* **1**, 85-88

Carmichael WW (1986) Isolation, culture and toxicity testing of toxic freshwater cyanobacteria (blue-green algae). In: Shilov V (Ed) *Fundamental Research in Homogenous Catalysis* (Vol 3), Gordor and Breach, New York, pp 1249-1262

Castillo-Monroy AP, Maestre FT, Delgado-Baquerizo M, Gallardo A (2010) Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. *Plant and Soil* **333**, 21-34

Chaudhary VB, Bowker MA, O'Dell TE, Grace JB, Redman AE, Rillig MC, Johnson NC (2009) Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications* **19**, 110-122

Chazal NM, Smith GD (1994) Characterization of a brown *Nostoc* sp. from Java that is resistant to high light intensity and UV. *Microbiology* **140**, 3183-3189

Comeron RE (1966) Microbiological characteristics of Hilgard soils. In: Mclaren AD, Skujins JJ (Eds) *Enzyme Activity in Terrestrial Soil in Relation to Exploration of the Martian Surface*, Space Sciences Laboratory, NASA, University of California, Berkley, 108 pp

Copley J (2000) Ecology goes underground. *Nature* **406**, 452-454

Crespo A (1973) Composición florística de la costar de líquenes del Herniario-Teucrietum pumili de la provincial de Madrid. *Anales del Instituto Botánico Antonio José Cavanilles* **30**, 57-68

Crespo A, Barreno E (1975) Ensayo Florístico y ecológiuco de la vegetación Liquénica de los yesos del centro de España (*Fulgensietalia desertori* ord. nov). *Anales del Instuto Botanic Antonio José Cavanilles* **32**, 873-908

Danin A, Garty J (1983) Distribution of cyanobacteria and lichens on hill sides of the Negev highlands and their impact on biogenic weathering. *Zeitschrift Geomorphologie* **27**, 423-444

Danin A, Dor I, Sandler A, Amit R (1998) Desert crust morphology and its relations to microbiotic succession at Mt. Sedom, Israel. *Journal of Arid Environments* **38**, 161-174

Davis BH (1976) Carotenoids. In: Goodwin TW (Ed) *Chemistry and Biochemistry of Plant Pigments*, Academic Press, London, pp 38-155

De Chazal NM, Smaglinski S, Smith GD (1992) Methods of involving light variation for isolation of cyanobacteria: Characterization of isolates from central Australia. *Applied and Environmental Microbiology* **58**, 3561-3566

De Phillips R, Vincenzini M (1998) Extracellular polysaccharides from cyanobacteria and their possible applications. *FEMS Microbiology Review* **22**, 151-175

Desikachary TV (1959) *Cyanophyta*, Indian Council of Agricultural Research, New Delhi, 686 pp

Dilworth MJ (1966) Acetylene reduction by nitrogen fixing preparations from *Clostridium pasteuriamum. Biochimica et Biophisica Acta* **127**, 285-294

Dunlap WC, Chalker BE (1986) Identification and quantification of near-UV absorbing compounds (SW-320) in a hermatypic scleractinian. *Coral Reefs* **5**, 155-159

Durrell LW (1962) Algae of Death Valley. *Transactions of the American Microscopical Society* **81**, 267-278

Eldridge DJ (1993) Cryptogams, vascular plants and soil hydrological relations: Some preliminary results from the semiarid woodlands of eastern Australia. *Great Basin Naturalist* **53**, 48-58

Eldridge DJ, Greene RSB (1994) Microbiotic soil crusts: A review of their roles in soil and ecological processes in the range lands of Australia. *Australian Journal of Soil Research* **32**, 389-415

Eldridge DJ, Rosentreter RR (2000) Morphological groups: A frame work for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments* **42**, 11-25

Escudero A, Martínez I, de la Cruz A, Otálora MAG, Maestre FT (2007) Soil lichens have Species-specific effects on the seedling emergence of three gypsophile plant species. *Journal of Arid Environments* **70**, 18-28

Evans RD, Ehleringer JR (1993) A break in the nitrogen cycle of arid lands. Evidence from δ^{15}N of soils. *Oecologia* **94**, 314-317

Evans RD, Lange OL (2003) Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 263-279

Fairchild ED, Wilson DL (1967) The algal flora of two Washington soils. *Ecology* **48**, 1053-1055

Fletcher JE, Martin WP (1948) Some effects of algae and moulds in the rain crust of desert soils. *Ecology* **29**, 95-100

Flechtner VR, Johansen JR, Clark WH (1998) Algal composition of microboitic crusts from the central desert of Baja California, Mexico. *Great Basin Naturalist* **58**, 295-311

Flechtner VR, Johansen JR, Belnap J (2008) The biological soil crusts of the San Nicolas Island: Enigmatic algae from a geographically isolated ecosystem. *Western North American Naturalist* **68 (4)**, 405-436

Friedmann EI (1982) Endolithic microorganisms in the Antarctic cold desert. *Science* **215**, 1045-1053

Friedmann EI, Galun M (1974) Desert algae, lichens and fungi. In: Brown GWJ (Ed) *Desert Biology*, Academic Press, New York, pp 165-212

Friedmann EI, Ocampo-Paus R (1976) Endolithic blue-green algae in the dry valley: Primary producers in the Antarctic desert ecosystem. *Science* **193**, 1247-1249

Friedmann EI, Ocampo-Friedmann R (1985) Blue-green algae in arid cryptolithic habitats. *Archiv für Hydobiologie (Suppl.)* **71**, 349-350

Garcia-Pichel F, Belnap J (1996) Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology* **32**, 774-782

Garcia-Pichel F, Castenholz RW (1991) Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. *Journal of Phycology* **27**, 395-409

Garcia-Pichel F, Lopez-Cortés A, Nübel U (2001) Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado plateau. *Applied and Environmental Microbiology* **67**, 1902-1910

Glazer AN, Fang S (1973) Formation of hybrid proteins from the α and β subunits of phycocyanins of unicellular and filamentous blue-green algae. *Journal of Biological Chemistry* **248**, 663-671

Godinez-Alvarez H, Morin C, Rivera-Aguilar V (2012) Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. *Plant Biology* **14 (1)**, 157-162

Gundlapally SR, Garcia-Pichel F (2006) The community and phylogenetic diversity of biological soil crusts in the Colorado plateau studied by Molecular fingerprinting and intensive cultivation. *Microbial Ecology* **52**, 345-357

Harbert D, Phipps PJ, Strange RE (1971) Chemical analysis of microbial cells. *Methods in Microbiology* **5B**, 209-344

Harel Y, Ohad I, Kaplan A (2004) Activation of photosynthesis and resistance to photoinhibition in cyanobacteria within biological desert crust. *Plant Physiology* **136**, 3070-3079

Harper KT, Belnap J (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments* **47**, 347-357

Harper KT, Marble JR (1988) A role for non-vascular plants in management of arid and semiarid rangeland. In: Tueller PT (Ed) *Vegetation Science Applications for Rangeland Analysis and Management*, Kluwer Academic Publishers, Dordrecht, pp 135-169

Hausen DJ, Ostler WK, Hall DB (1999) The transition from Mojave Desert to Great Basin Desert on the Nevada Test Site. In: McArthur ED, Ostler WK, Wambolt CL (Eds) *Proceedings: Shrubland Ecotones. Proceeding RMRS-P-11*, USDA Forset Service, Rocky Mountain Research Station, Ogden, pp 148-158

Hawkes CV (2001) *Methodology Paper Series of the 4th International Conference on ILTER in East Asia and Pacific Region*, Ulaanbaatar-Hatgal, Mongolia, pp 36-45

Hawkes CV, Flechtner VR (2002) Biological soil crusts in a xeric Florida shrubland: Composition, abundance and spatial heterogeneity of crusts with different disturbance histories. *Microbial Ecology* **43**, 1-12

Heckman KA, Anderson WB, Wait DA (2006) Distribution and activity of hypolithic soil crusts in a hyper arid desert (Baja California, Mexico). *Biology and Fertility of Soils* **43**, 263-266

Herbert D, Phipps PJ, Strange RE (1971) Chemical analysis of microbial cells. *Methods in Microbiology* **5B**, 209-344

Hill DR, Peet A, Potts M (1994) Biochemistry and structure of the glycan secreted by desiccation-tolerant *Nostoc commune* (Cyanobacteria). *Protoplasma* **182**, 126-148

Hill DR, Hladun SL, Scherer S, Potts M (1994) Water stress proteins of *Nostoc commune* (Cyanobacteria) are secreted with U.V.-A/B absorbing pigments and associated with 1, 4-b-d-xylanxylanohydrolase activity. *Biological Chemistry* **269**, 7726-7734

Housman DC, Powers HH, Collins AD, Belnap J (2006) Carbon and nitrogen fixation differ between successional stages of biological soil crusts in Colorado Plateau and Chihuahuan desert. *Journal of Arid Environments* **66**, 620-634

Hu CX, Zhang DL, Huang ZP, Liu YD (2003) The vertical microdistribution of cyanobacteria and green algae within desert crusts and the development of the algal crusts. *Plant and Soil* **257**, 97-111

Johansen JR (1993) Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* **29**, 140-147

Johansen JR, Rushforth SR (1985) Cryptogamic crusts: Seasonal variation in algae populations in the Tinctic Mountains, Juale Country, Utah, USA. *Great Basin Naturalist* **45**, 14-21

Johansen JR, Rushforth SR, Brotherson JD (1981) Sub-aerial algae of Navajo National Monument, Arizona. *Great Basin Naturalist* **41**, 433-439

Johansen JR, St Clair LL, Webb BL, Nebeker GT (1984) Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbances. *The Bryologist* **87**, 238-243

Johansen JR, Britton C, Rosati TC, Xuesong L, St. Clair LL, Webb BL, Kennedy AJ, Yanko KS (2001) Microbiotic crusts of the Mojave Desert: factors influencing distribution and abundance. *Nova Hedwigia* **123**, 339-369

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946-1957

Jones K, Stewart WDP (1969) Nitrogen turnover in marine and brackish habitats III. Production of extracellular N by *Calothrix*. *Journal of Marine Biology Association of the United Kingdom* **49**, 475-488

Kaltenecker JH, Wicklow-Howard M, Pellant M (1999) Boilogical soil crusts: Natural barriers to *Bromus Tectorum* L. establishment in the northern Great Basin, USA. In: Eldridge D, Freudenberger D (Eds) *Proceedings of the VI International Rangeland Congress*, Aitenvale, Queensland, Australia, pp 109-111

Karnieli A, Kidron GJ, Glaesser C, Ben-Dor E (1999) Spectral characteristics of cyanobacteria soil crust in semiarid environments. *Remote Sensing of Environment* **69**, 67-75

Kershaw KA (1985) *Physiological Ecology of Lichens*, Cambridge University Press, Cambridge, 293 pp

Kidron GJ, Vonshak A, Abeliovich A (2008) Recovery rates of microbiotic crusts within a dune ecosystem in the Negev Desert. *Geomorphology* **100**, 444-452

Kleiner EF, Harper KT (1977) Soil properties in relation to crytogamic ground cover in Canyolands National park. *Journal of Range Management* **30**, 203-205

Klubek B, Skujins J (1980) Heterotrophic N_2-fixation in arid soil crusts. *Soil Biology and Biochemistry* **12 (3)**, 229-236

Komárek J, Anagnostidis K (1986) Modern approach to the classification system of cyanophytes 2. Chroococcales. *Algological Studies* **43**, 157-226

Komárek J, Anagnostidis K (1989) Modern approach to the classification system of cyanophytes 4. Nostocales. *Algological Studies* **56**, 247-345

Lange OL, Kidron GJ, Büdel B, Meyer A, Kilian E, Abelovich A (1992) Taxonomic composition and photosynthetic characteristics of the "biological crusts" covering sand dunes in the western Negev Desert. *Functional Ecology* **6**, 519-527

Langhans TM, Storm C, Chwabe A (2009) Biological soil crusts and their microenvironment; impact on emergence, survival and establishment of seedlings. *Flora - Morphology, Distribution, Functional Ecology of Plants* **204**, 157-168

Lewis EJ, Gonzalves EA (1962) The protein, peptide and free amino acid contents of some species of marine algae from Bombay. *Annals of Botany* **26**, 301-315

Li XR, Chen YW, Su YG, Tan HJ (2006) Effects of biological soil crust on desert insect diversity: Evidence from the Tengger desert of Northern China. *Arid land Research and Management* **20**, 263-280

Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Protein measurement with the folin phenol reagent. *Journal of Biological Chemistry* **193**, 256

Lyra C, Suomalainen S, Gugger M, Vezie C, Sundman P, Paulin L, Sivonen K (2001) Molecular characterization of planktic cyanobacteria of *Anabaena*, *Aphanizomenon*, *Microcystis* and *Planktothrix* genera. *International Journal of Systematic and Evolutionary Microbiology* **51**, 513-526

Mackinney G (1941) Absorption of light by chlorophyll solutions. *Journal of Biological Chem*istry **140**, 315-322

Maestre FT, Cortina J (2003) Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. *Applied Soil Ecology* **23**, 199-209

Maestre FT, Martín N, Beatriz Díet B, López-Poma R, Santos F, Luque I, Cortina J (2006) Watering, fertilization and slurry inoculation promote recovery of biological crust function in degraded soils. *Microbial Ecology* **52**, 365-377

Mager DM (2010) Carbohydrates in cyanobacterial soil crusts as a source of carbon in the South West Kalahari, Botswana. *Soil Biology and Biochemistry* **42**, 313-318

Matsunaga T, Burgess JG, Yamada N, Komatsu K, Yosida S, Wachi Y (1993) An ultraviolet (UV-a) absorbing biopterin glucoside from the marine planktonic cyanobacterium *Oscillatoria* sp. *Applied Microbiology and Biotechnology* **39**, 250-253

Mazor G, Kidron GJ, Vanshak A, Abeniovich A (1996) The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiology Ecology* **21**, 121-130

McClendon JH (1999) The origin of life. *Earth-science Reviews* **47**, 71-93

Moghtaderi A, Taghavi M, Rezaei R (2009) Cyanobacteria in biological soil crust of Chadormalu area, Bafq region in Central Iran. *Pakistan Journal of Nutrition* **8 (7)**, 1083-1092

Moore DD (1998) Life in the upper crust. *Nature* **393**, 419-420

Nash TH (1996) *Lichen Biology*, Cambridge University Press, Cambridge, 320 pp

Ohad I, Nevo R, Brumfeld V, Reich Z, Tsur T, Yair M, Kaplan A (2005) Inactivation of photosynthetic electron flow during desiccation of desert microbiological sand crusts and *Microcoleus* sp.- enriched isolates. *Photochemical and Photobiological Science* **4**, 977-982

Paerl H (1990) Physiological ecology and regulation of N_2 fixation in natural water. *Advances in Microbial Ecology* **11**, 305-344

Pellant M, Shaver P, Pyke DA, Herrick JE (2000) *Interpreting Indicators of Rangeland Health, Version 3. Technical Reference 1734-6*, USDI, BLM, National Science and Technology centre, Denver, USA

Potts M (1994) Desiccation tolerance of prokaryotes. *Microbiological Review* **58**, 755-805

Potts M (2000) *Nostoc*. In: Whitton BA, Potts M (Eds) *The Ecology of Cyanobacteria*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 465-504

Raftery MA, Heocha CÓ (1965) Amino acid composition and C-terminal residues of algal billiproteins. *Biochemical Journal* **94**, 166-170

Řeháková K, Johansen JK, Casamatta DA, Xuesong L, Vincent J (2006) Morphological and molecular characterization of selected desert soil cyanobacteria: Three species new to science including *Mojavia pulchera* gen. et. sp. Nov. *Journal of Arid Environments* **64 (2)**, 270-283

Rippka R, Deruelles J, Waterbury JR, Herdman M, Stanier RY (1979) Deneric assignments, strain histories and properties of pure cultures of cyanobacteria. *Journal of General Microbiology* **(III)**, 1-61

Rivera-Aguilar V, Montejano G, Rodriguez-Zaragoza S, Duran-Diaz A (2006) Distribution and composition of cyanobacteria, mosses and lichens of the biological soil crusts of the Tehuacan Valley, Puebla, Mexico. *Journal of Arid Environments* **67**, 208-225

Rogers RW (1972) Soil surface lichens in arid and subarid South-Eastern Australia. *Australian Journal of Botany* **20**, 301-316

Rogers SL, Burns RG (1994) Changes in aggregate stability, nutrient status, indigenous microbial populations and seedling emergence following inoculation of soil with *Nostoc muscorum*. *Biology and Fertility of Soils* **18**, 209-215

Rogers L, Gallon J (1988) *Biochemistry of the Algae and Cyanobacteria*, Clarendon Press, Oxford, 374 pp

Rosentreter R (1986) Compositional patterns within a rabbit brush (*Chrysothamnus*) community of the Idaho Snake River plain. In: McArthur ED, Welch BL (Eds) *Proceedings-Symposium on the Biology of Artemisia and Chrysothamnus*, General Technical Report INT-200, USDA Forest Service, Intermountain Research Station, Oyden, U.T., pp 273-277

Sarafis V, Heintzmann R, Karnieli A (2006) Visualizing cyanobacteria in soil crusts from a semi-arid environment using confocal fluorescence imaging. *Phytomorphology* **56 (1&2)**, 65-68

Schopf JW (1992) The oldest fossils and what they mean. In: Schopf JW (Ed) *Major Events in the History of Life*, Jones and Bartlett, Boston, MA, USA, pp 29-63

Schopf JW (2009) Organismal evolution and radiation before the Cambrian. In: Ruse M, Travis J, Zinser J (Eds) *Evolution: The First 4 Billion Years*, Harvard University Press, Cambridge, MA, pp 775-786

Schopf JW (2010) The paleobiologic record of photosynthesis. *Photosynthesis Research* **107**, 87-101

Schopf JW, Hudryavtsev AB, Agresti DG, Wdowiak T, Czaja AD (2002) Laser-Raman imagery of Earth's earliest fossils. *Nature* **416**, 73-76

Shields LM, Drouet F (1962) Distribution of terrestrial algae within the Nevada Test Site. *American Journal of Botany* **49**, 547-554

Shields LM, Durrell LW (1964) Algae in relation to soil fertility. *The Botanical Review* **30**, 92-128

Stanier RY, Kunisawa R, Mandel M, Cohen-Bazire G (1971) Purification and properties of unicellular blue-green algae (order Chroococcales). *Bacteriological Review* **35**, 171-205

Steppe TF, Olson JB, Paerl HW, Litaker KW, Belnap J (1996) Consortial N_2 fixation: A strategy for meeting nitrogen requirements of marine and terrestrial cyanobacterial mats. *FEMS Microbiol*ogy *Ecology* **21**, 149-156

Stewart WDP (1967) Transfer of biologically fixed nitrogen in a sand dune slack region. *Nature* **214**, 603-604

St. Clair LL, Johansen JR, Rushforth SR (1993) Lichens of soil-crust communities in the intermountain area of Western United States. *Great Basin Naturalist* **53**, 5-12

Su YG, Li XR, Qi P, Chen YW (2012) Carbon exchange responses of cyanobacterial - algal crusts to dehydration, air temperature and CO_2 concentration. *Arid Land Research and Management* **26 (1)**, 44-58

Su YG, Li XR, Zheng JG, Huang G (2009) The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants. *Journal of Arid Environments* **73**, 931-936

Thomas AD, Dougill AJ (2006) Distribution and characteristics of cyanobacterial soil crusts in the Molopo basin, southern Africa. *Journal of Arid Environment* **64**, 270-283

Thomas AD, Dougill AJ (2007) Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: implications for soil surface properties. *Geomorphology* **85**, 17-29

Tice MM, Lowe DR (2004) Photosynthetic microbial mats in the 3416-Myr-old ocean. *Nature* **431**, 549-552

Tirkey J, Adhikary SP (2005) Cyanobacteria in biological soil crusts of India. *Current Science* **89 (3)**, 515-521

Tirkey J, Adhikary SP (2006) Blue green algae in the biological soil crusts of different regions of India. *Feddes Repertorium* **117 (3-4)**, 280-306

Tiwari ON, Singh BV, Mishra U, Singh AK, Wattaldhar D, Singh AK (2005) Distribution and physiological characterization of cyanobacteria isolated form arid zones of Rajasthan. *Tropical Ecology* **46 (2)**, 165-171

Ullmann I, Büdel B (2001) Ecological determinants of species composition of biological soil crusts on landscape scale. In: Belnap J, Lange OL (Eds) *Biological Soil Crusts: Structure, Function and Management*, Springer-Verlag, Berlin, pp 202-213

West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid and semiarid regions. *Advances in Ecological Research* **20**, 179-223

Whitton BA (1987) Survival and dormancy of blue green alga. In: Henis Y (Ed) *Survival and Dormancy of Microorganism*, Wiley, New York, pp 109-167

Williams WJ, Eldridge DJ, Alchis BM (2008) Grazing and drought reduce Cyanobacteria soil crusts in Australian *Acacia* woodland. *Journal of Environments* **72 (6)**, 1064-1075

Wu N, Zhang YM, Downing A (2009) Comparative study of nitrogenase activity in different types of biological soil crusts in the Gurbantunggut Desert, North Western China. *Journal of Arid Environments* **73**, 828-833

Yeager CM, Kornosky JL, Morgan RE, Cain EC, Garcia-Pichel F, Housman DC, Belnap J, Kuske CR (2007) Three distinct clades of cultured heterocystous cyanobacteria constitute the dominant N_2-fixing members of biological soil crusts of the Colorado plateau, USA. *FEMS Microbiology Ecology* **60**, 85-97

Zehr JP, Mellon MT, Hiorns WD (1997) Phylogeny of cyanobacterial *nifH* genes: Evolutionary implications and potential applications to natural assemblages. *Microbiology* **143**, 1443-1450

Zhang YM, WU N, Zhang BC, Zhang J (2010) Species composition, distribution pattern and ecological functions of biological soil crusts in the Gurbantunggut Desert. *Journal of Arid Land* **2 (3)**, 180-189

Zhang B, Zhang Y, Downing A, Niu Y (2011) Distribution and composition of Cyanobacteria and microalgae associated with biological soil crusts in the Gurbantunggut Desert, China. *Arid Land Research and Management* **25**, 275-293

Zhang YM (2005) The microstructure and formation of biological soil crust in their early developmental stage. *Chinese Science Bulletin* **50 (2)**, 117-121

Zhang YM, Wang HL, Wang XQ (2006) The microstructure of biological soil crust and its influence on wind erosion for a sandy soil surface in the Gurbantunggut Desert of Northwestern China. *Geoderma* **132**, 441-449