



Consortia of cyanobacteria/microalgae and bacteria in desert soils: an underexplored microbiota

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Abstract

Desert ecosystem is generally considered as a lifeless habitat with extreme environmental conditions although it is colonized by extremophilic microorganisms. Cyanobacteria, microalgae, and bacteria in these habitats could tolerate harsh and rapidly fluctuating environmental conditions, intense ultraviolet radiation, and lack of water, leading to cell desiccation. They possess valuable metabolites withstanding extreme environmental conditions and make them good candidates for industrial applications. Moreover, most natural microorganisms in these extreme habitats exist as consortia that provide robustness and extensive metabolic capabilities enabling them to establish important relationships in desert environments. Engineering of such consortia of cyanobacteria, microalgae, and bacteria would be functional in the sustainable development of deserts through improving soil fertility, water preservation, primary production, pollutant removal, and maintaining soil stability. Modern tools and techniques would help in constructing highly functional cyanobacterial/microalgal–bacterial consortia that are greatly useful in the establishment of vegetation in deserts as well as in biotechnological applications.

Keywords Desert soil crusts · Consortia · Cyanobacteria/microalgae and bacteria · Engineering consortia · Ecological significance

Introduction

Desert soils have been considered economically insignificant, and the study of desert microbial diversity and their characteristics has therefore been neglected. However, since last few decades, the reduction in fertile lands because of rapid urbanization and increasing the world's demand for food has necessitated the use of arid areas for agricultural purposes. Consequently, biological and environmental researchers are closely examining desert soils for microbiota useful for agricultural productivity of such lands (Moreno et

al. 2008). The 1992 Earth Summit heard that more than 40% of the earth's terrestrial area is in danger of desertification (Bhatnagar and Bhatnagar 2005). Deserts are characterized by extreme conditions such as high temperature, low moisture, and low availability of organic matter content, all influencing the composition of microbial communities and their activity in desert soil (Belnap et al. 2005; Saul-Tcherkas et al. 2013). Most studies suggest that deserts and desertified lands have scarce vegetation, but the surfaces of these landscapes are covered by microphytic communities such as microalgae, cyanobacteria, fungi, and bacteria in different combinations (Garcia-Pichel et al. 2001; Drees et al. 2006; Gómez-Silva et al. 2008; Sterflinger et al. 2012). Friedmann (1980) shows the microbial composition of desert soil and their physiology.

Cyanobacteria, microalgae, and bacteria have high potential to adapting extreme environments. Azua-Bustos et al. (2012) identified unrelated phototrophic microalgae of Cyanidiales and *Dunaliella*, and cyanobacteria such as *Chroococcidiopsis* from the coastal range of the Atacama Desert, and illustrated the convergent evolution of microalgae and cyanobacteria to survive in the desert environment. *Dunaliella* or *Chroococcidiopsis* have different survival mechanisms adapted to their respective habitats.

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On the other hand, the same mechanisms help in surviving ionic stress (caused by salt) and osmotic stress tolerance (caused by desiccation). *Dunaliella* biofilms colonize spider webs in deserts as a means of using condensed water for their survival. Very recently, Abinandan et al. (2018) critically examined the nature of mutualistic interactions established between microalgae and bacteria in biofilms of acid mine drainage for the removal of metals and consequent yield of biofuel from biomass.

In view of the fact that microalgae and bacteria have great potential for removing organic pollutants (Subashchandrabose et al. 2012; Subashchandrabose et al. 2017a) and toxic metals (Bahar et al. 2013) from contaminated soils, they serve as biomarkers for soil toxicity evaluation (Megharaj et al. 2011a; Subashchandrabose et al. 2015; Subashchandrabose et al. 2017b). Furthermore, these microorganisms could be used for agricultural purposes as nutrient sources (Megharaj et al. 1992). Studying interactions between cyanobacteria, microalgae, and bacteria even in desert soil is therefore useful in their biotechnological applications (Amin et al. 2015; Fuentes et al. 2016). This includes using consortia comprising cyanobacteria, microalgae, and bacteria, from desert habitats for bioremediation of oil-polluted desert soils since higher temperatures improve both solubility and bioavailability of hydrocarbons (Margesin and Schinner 2001). In these habitats, microbial consortia are also capable of producing high-value products with a significant impact in areas like agriculture (Moreno et al. 2008) and environmental management (Margesin and Schinner 2001). However, there is no published information on the possible implications of desert microorganisms, especially consortia of cyanobacteria/microalgae and bacteria, in bioremediation of polluted environments and use of their metabolites for industrial applications. The present review provides a detailed account on the environmental and biotechnological significance of cyanobacteria/microalgae–bacteria consortia in desert soils with a critical view as to how they could be exploited in improving the vegetation of drylands as a solution for the scarcity of usable lands.

Significance of desert soils

Deserts are characteristic in an annual rainfall lower than 254 mm. Consequently, biological activities in desert ecosystems rely on transitory water available. On the other hand, availability of water depends on abiotic factors such as temperature, declines in pan evaporation, geology, wind and interactions with precipitation inclusive of rainfall (Bhatnagar and Bhatnagar 2005). Based on the water availability, United Nations Convention to Combat Desertification (UNCCD) defined four dryland regions that include arid, semiarid, dry sub-humid, and hyper-arid deserts (Table 1). Generally, hyper-arid regions are biologically unproductive whereas the semiarid regions are well vegetated. Arid regions occur in between those two zones (Neilson et al., 2012). Deserts are broadly classified as hot and cold deserts, which are located in Arctic and Antarctic regions with limited rainfall and cold temperature (Ward 2016).

Most deserts are mainly located within two belts along the equator and the tropics of Cancer and Capricorn. Within the arid belt of Northern Hemisphere includes the Arabian, Iranian, Sahara, Gobi, Central Asian, and North American Southwest deserts while Southern Hemisphere includes with Kalahari, Namib, Peru, Chile, and Australian deserts. Flashing floods occur in deserts rarely by higher rainfall (> 250 mm). However, this water is not accessible to desert organisms because of non-absorption into the desert soil and surface run-off. Although some cold deserts obtain water as snow or ice, this water is also not available for vegetation (Ward 2016). Most of the studies indicate that the area of the desert would be increased because of the global warming resulting from fossil fuel combustion and industrial pollution (Brown et al. 1997; Rosenfeld 2000). Global warming results in higher evaporation in arid regions (Xu et al. 2016) and rapid loss of nitrogen from soil, thereby limiting microbial growth (Holmes et al. 1994).

Usually, deserts lack vegetative cover including higher plants. However, specialized microorganisms including cyanobacteria, microalgae, fungi, and many heterotrophic

Table 1 Classification of deserts according to aridity (Safriel et al. 2006) and the presence of cyanobacteria/microalgae and bacteria

Zone	Aridity index (AI)*	Global land area (%)	Cyanobacteria/microalgae (reference)	Bacteria (reference)
Hyper-arid	< 0.05	6.6	<i>Chroococcidiopsis</i> sp. (Wierzechos et al. 2006)	<i>Frankia</i> sp. (Connon et al. 2007)
Arid	0.05–0.20	10.6	<i>Chloroflexi</i> sp. (Neilson et al. 2012), <i>Microcoleus vaginatus</i> Gomont (Garcia-Pichel et al. 2001)	Actinobacteria (Neilson et al. 2012)
Semiarid	0.20–0.50	15.2	<i>Microcoleus vaginatus</i> , <i>Nostoc punctiforme</i> , and <i>Chroococcus</i> sp. (Kameli et al. 1996)	<i>Cylindrospermopsis raciborskii</i> (Marc et al. 1999)
Dry sub-humid	0.50–0.65	8.7	<i>Chloroflexus</i> sp. (Yasir et al. 2015)	Proteobacteria, Actinobacteria, and Acidobacteria (Yasir et al. 2015)

bacteria colonize few millimeters of top soil layers (Mazor et al. 1996; Garcia-Pichel et al. 2001; Nagy et al. 2005). These biological soil crusts (BSC) provide surprising capabilities for deserts to avoid desiccation and survive from extreme conditions such as high temperatures, low nutrient levels, high summer UV radiation, physical instability caused by strong winds, high pH, and high salinity (Bowker et al. 2005; Belnap et al. 2007; Chamizo et al. 2013). These organisms are essential in enhancing soil fertility and stability (Abed et al. 2010; Wierzechos et al. 2015; Ward 2016). Majority of deserts have spatial variations of their soil types and shifted habitats with unique vegetative forms creating through the dune systems and high salinity (Abed et al. 2015). Nutrient such as nitrogen limitation in the soil causes less vegetation in most deserts (Hadley and Szarek 1981; Gallardo and Schlesinger 1992). Most limiting nutrient in the Australian deserts is phosphorus, while Africa's Namib and Kalahari deserts have lower nitrogen, phosphorus, and potassium content (Grimm et al. 1981; Robinson 2001).

Soil type in the deserts could be varying according to the region or climatic conditions and affects for microbial composition. The sand deserts are not generally accounting for 15–20% of the total number of deserts (Robinson 2001). Deserts mainly with minerals and low organic matter contain saline soil (Goudie and Middleton 2006). Furthermore, Fierer and Jackson (2006) demonstrate that soil in tropical forests with acidic pH has lesser bacterial taxa compared to the desert with neutral pH. Denaturing gradient gel electrophoresis (DGGE) analysis showed that Atacama Desert has a microbial composition, which can grow in hypersaline habitats (de los Ríos et al. 2010). The imperfectly developed wide range of unidentified bacteria and fungi exists in the hyper-arid polar desert (Pointing et al. 2009). All these studies illustrate unique and extraordinary microbial diversity related to desert soil.

Cyanobacteria and microalgae in desert soils

Compared to other biological species, microalgae and cyanobacteria are highly adaptive to specific environments due to their ability to survive at high temperatures, low water potential, and radiation. Also, their ability to grow as autotrophs, heterotrophs, or mixotrophs makes them as good colonizers on different ecosystems such as deserts (Subashchandrabose et al. 2013). Cyanobacteria are mainly contributing to biological crusts in deserts encouraging soil fertility regarding nitrogen and carbon fixation. The requirement of the small wet period for their metabolic functions makes them good candidates for desert soil (Belnap 2003b). Most cold deserts in Colorado Plateau are dominated by cyanobacteria, *Microcoleus vaginatus*, resulting in nitrogen fixation (Belnap 1996; Belnap 2003a).

Earlier, the scientists said that desert crusts represent a limited number of microalgae because their results mainly relied on light microscopic observations (Metting 1981). However, recent researches on different stages of zoospores and gametes along with the features on crust structure and functions show a wide range of desert algae (Lewis and Flechtner 2002; Lewis and Flechtner 2004). Phycologists use accurate methods such as nuclear 18S rDNA genes and plasmid-borne ribulose biphosphate carboxylase gene to identify and develop systematic relationships of desert algae (Cardon et al. 2008). Redfield et al. (2002) demonstrate cyanobacterial composition and their relative abundance of different soil crusts present in Colorado Plateau arid desert using terminal restriction fragment analysis (TRF) following 16S rDNA sequence. Most frequent algal species in Baja California and Mexico deserts are *Nostoc commune* and *Schizothrix calcicola* (cyanobacteria), *Myrmecia astigmatica* (chlorophyte), and diatoms such as *Hantzschia amphioxys*, *H. amphioxys* f. *capitata*, *Luticola cohnii*, *L. mutica*, and *Pinnularia borealis* var. *scalaris*, and novel strains of *Cylindrocystis brebissonii* var. *deserti* var. nov., *Elakatothrix obtusata* sp. nov., and *Fasculochloris mexicana* sp. nov. belonging to 32 genera (Flechtner et al. 1998). Lewis and Lewis (2005) demonstrate five classes of desert algae originating from freshwater ancestor using phylogenetic analysis based on 18S rDNA. Thus far, more than 400 species of microalgae have been identified from deserts throughout the world.

Some cyanobacteria exhibit specific changes in their morphology and physiology while surviving in desert habitats. For example, *Nostoc commune* var. *flagelliforme*, popularly known as a Chinese food delicacy (Gao 1998), has specific geometry in its colony and different protein pattern which makes the cyanobacterium a good survivor under desiccation. Such cyanobacteria excrete a novel protein WspA that hydrolyses the backbone of exopolysaccharides (EPS) and enhances expandability of cell wall, thereby helping in strengthening cell wall by incorporating and binding EPS molecules for the overall survival under desiccation (Liu et al. 2017). In desert environments, photosynthesis efficiency in cyanobacteria is reduced, and assimilation process limited due to decreased water availability. Therefore, the rate of nitrogen fixation under these conditions is very low in order to conserve energy because dinitrogenase utilizes more energy (Scherer and Zhong 1991). Interestingly, nitrogenase activity increases with the availability of water and starts declining after some time because the enzyme is more sensitive to temperature at this stage of wetting (Gao 1998). Some strains of cyanobacteria such as *N. flagelliforme* also develop biological soil crusts using sand particles to control desertification (Chen et al. 2011).

Biochemical components of these cyanobacteria such as secondary carotenoid complexes also change due to harsh

conditions such as excessive light, nutritional stress, oxidative stress, and UV radiations (Zakar et al. 2016). Carotenoid composition and content vary with the depth of desert layers for harvesting light conditions and surviving from above conditions (Vitek et al. 2017). These stress tolerance mechanisms in desert microorganisms produce industrially valuable products which take attention of biotechnologists (Poong et al. 2018). Thus, the valuable metabolites produced by several cyanobacteria support desert microorganisms to survive and make them serve as soil improvers and produce industrially important components (Table 2).

Bacteria in desert soils

Bacterial population in deserts could vary throughout the world from < 10 to 1.6×10^7 in deserts of Atacama and Nevada, respectively. Gram-positive bacteria are more prominent, and their population does not decline considerably even in summer. Prominent bacteria of deserts include coryneforms such as *Cystobacter*, *Archangium*, *Myxococcus*, and *Sorangium*, and other forms like *Bacillus*, *Acinetobacter*, *Micrococcus*, and *Proteus* (Bhatnagar and Bhatnagar 2005). DGGE profile of the bacterial population in an Atacama Desert is dominated by phyla of Gemmatimonadetes and Planctomycetes (Drees et al. 2006). Real-time quantitative PCR demonstrates the high abundance of *Deinococcus* and *Rubrobacter* performing tolerance against radiation and desiccation in hyper-arid polar desert in Antarctica (McMurdo Dry Valley) (Pointing et al. 2009). These desert bacteria have tolerance against gamma and UV radiations. For instance, the strength of ionization radiation affects bacterial community growing in non-arid and arid soil from Louisiana forest and Sonoran desert respectively. Bacteria dominated by *Deinococcus*, *Geodermatophilus*, and *Hymenobacter* from arid soil survive at 30 kGy whereas none of the bacteria from non-arid soil survives at the dosage greater than 13 kGy (Rainey et al. 2005). Thermostable enzymes are contributing their survival under harmful conditions. A novel esterase was found from *Escherichia coli* isolated from Antarctic desert soil, and it tolerates high pH including an optimum activity at 9.0 and broader temperature range of 7–54 °C including an optimum temperature of 40 °C (Heath et al. 2009). Thus, desert bacteria could be an excellent source of valuable enzymes and metabolites for industrial applications such as melanin using for sunscreens (Gabani and Singh 2013).

Consortia of cyanobacteria, microalgae, and bacteria in desert soil crusts

The association between cyanobacteria and microalgae with other aerobic or anaerobic microorganisms that exist as microbial flocks in a community is known as a consortium (Mouget et al. 1995; Munoz and Guieysse 2006; Megharaj

et al. 2011b; Subashchandrabose et al. 2011). This interaction could be either mutualism or parasitism (Martin et al. 2014; Fuentes et al. 2016). Under mutualism, the relationship between microalgae and bacteria facilitates the exchange of micronutrients such as vitamin B12 (Croft et al. 2005) as well as macronutrients like organic carbon, phosphorous, and nitrogen (Teplitski and Rajamani 2011; Cho et al. 2015). For instance, *Chlamydomonas reinhardtii* uses vitamin B12 supplied by heterotrophic bacteria for the exchange of photosynthate of alga (Croft et al. 2005; Kazamia et al. 2012). Bacteria enhance algal growth by excreting various hormones that change the bioactivities of both partners (Teplitski and Rajamani 2011). In the parasitism, some heterotrophic bacteria secrete chitinases, glucosidases, cellulases, and other enzymes to degrade algae within the consortium acquiring nutrients (Fergola et al. 2007; Kim et al. 2007; Xue et al. 2018). Some bacteria produce NH_2OH along the conversion of ammonium into nitrite, which inhibits the growth of *Chlorella* sp. (Baumgarten et al. 1999).

Sediment particles of ice in deserts such as McMurdo Dry Valleys in Antarctica act as a source of inorganic and organic nutrients for the enrichment of cyanobacterial/microalgal–bacterial consortia with enhanced photosynthesis, N_2 fixation, and organic matter decomposition. Microautoradiographs illustrates that heterotrophic bacteria metabolize organic substrates when they closely associated with cyanobacteria such as *Phormidium*, *Chamaesiphon*, and *Nostoc*. Cyanobacteria fix carbon and nitrogen while heterotrophs recycled CO_2 back to photoautotrophs (Priscu et al. 1998). Hypolithic microbial consortia associated with nitrogen fixers including cyanobacteria and proteobacteria play a vital role in the nutrient cycling of Antarctic desert soils. PCR amplification of metagenomic DNA using primers for *nifH*, *polF*, and *polR* shows major nitrogen fixers belonging to *Nostocales*, which contains heterocysts and proteobacteria including *Azotobacter vinelandii* (Cowan et al. 2011).

Hypolithic communities including culturable bacteria like *Bacillus* sp., *Streptomyces* sp., and a cyanobacterium, *Chroococcidiopsis* sp., are in Atacama Desert experiencing an annual rainfall < 5 mm per year (Gómez-Silva et al. 2008). It suggests that microbial consortia with cyanobacteria have longer survival under the sunlight of 16–300 kJ m^{-2} in Atacama Desert since cyanobacterial species produce exopolysaccharides (EPS) that provide residence for other cyanobacteria and bacteria besides protecting bacteria from desiccation. These EPS enhance stabilization of sediments and cohesion of the mat which provides surface and growth substrate for the consortium and assists detoxification by binding to potential toxins and heavy metals (Decho 1990). Longer exposure to desiccation induces production of scytonemin, a stable and passive sunscreen in *Chroococcidiopsis* sp. used for its

Table 2 Metabolites produced by desert cyanobacteria

Site location	Cyanobacterial strain found in desert	Valuable metabolites	Applications	Reference
Cold desert in Himachal Pradesh, India	<i>Nodularia sphaerocarpa</i> PUPCCC 420.1	Phycobiliprotein pigment	More stable at alkaline conditions and food colorant production	(Kaushal et al. 2017)
Desert of Shapotou, Zhongwei County, China	<i>Phormidium tenue</i>	Polysaccharide composed of 12 monosaccharides	Increases seed germination rate, has nitrate reductase activity of desert shrubs, and serves as a biofertilizer	(Xu et al. 2013)
Hyper-arid zone of Atacama Desert	<i>Chroococcidiopsis</i> sp.	Scytonemin pigment	UV-screening pigment used for sunscreen	(Vítek et al. 2014)
Tengger Desert, China	<i>Nostoc</i> sp., <i>Microcoleus vaginatus</i> , <i>Desmococcus olivaceus</i> , <i>Phormidium tenue</i> , and <i>Scytonema javanicum</i>	Extracellular polysaccharides	Soil conditioner, sandy soil stabilizer	(Hokputsa et al. 2003; Hu et al. 2003)
The eastern edge of the Qubqi Desert	<i>Scytonema javanicum</i>	Exopolysaccharides	Antioxidant and antitumor activities	(Wu et al. 2018)
Negev desert, Israel	<i>Chroococcidiopsis</i> sp.	<i>Carotenoids</i>	UV-C resistance through activity against oxidative stress	(Baque et al. 2013)
Wadi Al-Khoud in Muscat, northern Oman	<i>Calothrix</i> and <i>Scytonema</i>	Scytonemin Lipids Phytols	UV-screening pigment used for sunscreen Biofuel industry Organic matter supplier for higher plants	(Abed et al. 2018)
Tengger Desert, China	<i>Nostoc</i> sp.	<i>N</i> -acetylcysteine and sodium nitroprusside	Antioxidant precursors of other antioxidant molecules that act against reactive oxygen species caused by UV-B radiations	(Wang et al. 2008)
Canyonlands National Park, USA	<i>Microcoleus vaginatus</i>	Exopolysaccharides	Protection against DNA breakages, peroxidation of lipids via blocking reactive oxygen species caused by UV-B radiations	(Lan-Zhou et al. 2009)
Gurbantunggut Desert, China	<i>Microcoleus vaginatus</i>	Polysaccharides and other organic matter	Increase nitrogenase activity of bacteria in soil, enhance the microalgal activity, and increase invertase activity	(Zhang et al. 2013)

survival in desert soil (Mazor et al. 1996; Gómez-Silva et al. 2008; Abed et al. 2010).

Consortia of heterotrophic bacteria with microalgae contribute to the production of water-stable aggregates needing for nitrogen cycle, water retention, primary production, mineralization, and soil stability (Evans and Johansen

1999). Furthermore, this biological interaction could be used for mitigation of climatic changes, stabilizing desert soil from wind and water erosion, and fertilizing arid soils. Certain aerobic heterotrophic bacteria exhibit hydrocarbon degradation while cyanobacteria in the consortia provide oxygen to oil degraders for oxidative degradation of

hydrocarbon (Abed and Köster 2005). Desert soils with hydrocarbon-degrading rhizospheric consortia enhance the plant growth and these organisms support for bioremediation of oil-polluted area (Radwan et al. 1998). Activity of nitrogen-fixing bacteria in Tengger Desert in China enhances soil fertility and algal diversity including *Chlamydomonas* sp., *Chlorococcum humicola*, and *Chlorella vulgaris* which increases soil texture, nutrient availability, and organic matter content in the desert, thus providing favorable environment for establishing desert soil and propagating cryptogams that supports restoration of biodiversity in deserts (Li et al. 2003).

In Atacama Desert, endolithic microbial communities exhibit higher water availability due to less exposure to harmful UV and photosynthetic active radiation (PAR) through gypsum rocks containing sepiolite inclusions. However, intensive PAR enhances colonization of cyanobacteria and microalgae in the cryptoendolithic environment resulting in the production of carotenoids within the topmost algal layer. Simultaneously, hypoendolithic cyanobacteria produce scytonemin pigment as a defense mechanism against damages of photoinhibition and photo-oxidation, which could use for drugs preventing skin from UV damages. This could apply for sunscreen due to its broad absorption spectrum of UV radiations (Gabani and Singh 2013). Orange-colored algal cells produced larger quantities of carotenoids just below the gypsum to provide protection to green algae from intense solar radiation and allow them to grow in little deeper layers until maturation. Meanwhile, scytonemin in the hypoendolithic environment protect colonized cyanobacteria beneath the green microalgal cell layer (Wierzchos et al. 2015).

Ecological significance of consortia in soil crusts on desert plants

The presence of consortia dominated by cyanobacteria enhances uptake of essential nutrients. They increase the nitrogen content of soil while enhancing the plant uptake of Na, Cu, Zn, and K (Harper and Belnap 2001). In contrast, they cause negative impacts on the uptake of P and Fe by the associated seed plants as depicted in Fig. 1. The dense growth of these microorganisms on the soil surfaces is most influencing on essential elements for short-lived herbs, which are rooted on soil surface instead of deeply rooted herbs. The rhizosphere bacteria of desert plants such as *Opuntia cholla*, *Stenocereus thurberi*, and *Pachycereus pringlei* fix atmospheric nitrogen and produce organic acids which reduce pH of the soil and rock medium for enhancing bacterial growth and consequently dissolving insoluble phosphates, limestone, and rocks. The desert bacteria are thus able to discharge minerals such as Mg, K, Cu, Fe, and Zn from the rocks and

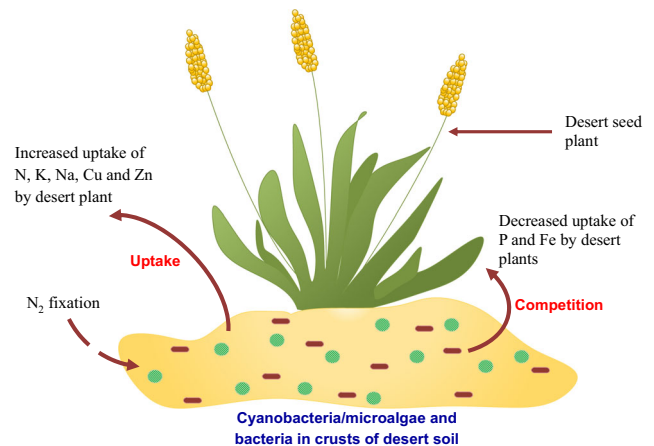


Fig. 1 Nutrient uptake by desert seed plant in the presence of cyanobacteria/microalgae and bacteria in soil crusts

subsequently help the growth of plants and other microorganisms. These results indicate that rhizosphere bacteria on cacti root support chemical weathering in hot and subtropical deserts and enhance the growth of desert plants (Puente et al. 2008).

Cyanobacteria first colonize and stabilize topmost layers of soil, and form biological soil crusts with bacteria and microalgae stabilizing the topsoil. Therefore, cyanobacterial amendments to soils can effectively control the desertification process by increasing nutrient availability and promoting growth of vegetation. Lan et al. (2014) used cyanobacteria, *Microcoleus vaginatus* and *Scytonema javanicum*, as an inoculum, for soil stabilization because they produce exopolysaccharides that help in the aggregation of soil particles and formation of biological crusts which leads to soil stability. These cyanobacterial soil crusts, in turn, increase soil carbon content and nitrogen thereby provide necessary nutrients for vascular plants.

The fine roots of plants penetrate the desert soil and hold together by mucilage to provide a “rhizosheath.” Bacteria such as *Bacillus polymyxa*, *Ancalomicrobium* sp., and *Hyphomicrobium* sp. are associated with desert rhizosheaths and stimulate water retention and plant uptake of nutrients (Watt et al. 1994). Thus, desert soil crusts dominated by heterotrophic bacteria, microalgae, and cyanobacteria play a major role in the biogeochemistry of arid zone. They also contribute organic carbon for plant growth (Belnap et al. 2003; Bashan and de-Bashan 2010), fix atmospheric nitrogen (Malam Issa et al. 2001; Pointing and Belnap 2012), and promote survival of vascular plant seedlings (Godinez-Alvarez et al. 2012). Consortia of *Chlorella* sp. and *Azotobacter* sp. that are isolated in desert rhizosphere were used as a biostimulator and biofertilizer for enhancing germination and growth of rice plants (Zayadan et al. 2014). Bacteria, *Acinetobacter rhizosphaerae*, isolated from the cold desert in Himalaya

have high phosphorus solubilization and indole acetic acid (IAA) production supporting for plant growth (Gulati et al. 2009). This IAA supports the growth of resident microorganisms including microalgae within rhizosphere and non-rhizosphere and root elongation of plants (Vassilev et al. 2012; Amin et al. 2015). These microalgae subsequently serve as a source of carbon for plant growth (Trejo et al. 2012). Therefore, these organisms play the major role in the vegetation of deserts, and subsequently, they can be used for agricultural purposes. The presence of consortia of photosynthetic organisms and bacteria on the desert surface or within the soil supports water retention, reduction of soil erosion, soil stability maintenance, and nutrient availability enhancement for plants (Subashchandrabose et al. 2013).

Industrial potential of enzymes from desert microalgae, cyanobacteria, and bacteria

Desert soil is a good source for exploration of thermostable enzymes for biotechnological applications because desert isolates of microalgae, cyanobacteria, and bacteria have great potential in degrading materials rich in carbohydrates (Herbert 1992; Varshney et al. 2015). Biological crusts formed in desert soils predominantly by *Nostoc* spp. and *Microcoleus* spp. were shown to have increased enzymatic activities compared to those of bare lands. For instance, the activities of invertase, cellulases, and proteases in the desert soil layers were $21.70 \mu\text{mol glucose g}^{-1} \text{h}^{-1}$, $0.13 \mu\text{mol glucose g}^{-1} \text{h}^{-1}$, and $21.12 \mu\text{mol NH}_3 \text{g}^{-1} \text{h}^{-1}$, respectively, and the corresponding enzyme activities in barren soils were $0.08 \mu\text{mol glucose g}^{-1} \text{h}^{-1}$, $0.03 \mu\text{mol glucose g}^{-1} \text{h}^{-1}$, and $0.03 \mu\text{mol NH}_3 \text{g}^{-1} \text{h}^{-1}$, respectively (Miralles et al. 2012). Interestingly, cyanobacteria showed increased degradation of low molecular weight substrates compared to high molecular weight substrates. Indeed, such an activity supports cyanobacteria for their survival under conditions of desiccation and developing symbiosis, leading to increased soil nutrient availability for vegetation (Miralles et al. 2012).

Of the total bacteria isolated from a hot desert environment, the percent occurrence for amylolytic, proteolytic, and cellulolytic bacteria was 70.83, 50.41, and 5.41, respectively (Aanniz et al. 2015). These enzymes help in decomposing limited organic matter available in desert soils and increase nutrient uptake by seed plants. Moreover, the thermostability of the enzymes in desert isolates has greater industrial applications in starch industry (Prakash and Jaiswal 2010), production of food additives (Demirjian et al. 2001), and synthesis of pharmaceutical intermediates (Niehaus et al. 1999). Nithya et al. (2017) reported thermostable α -amylase activity in an actinobacterium, *Streptomyces fragilis* DA7-7, isolated from desert soil samples from Saudi Arabia. They demonstrated the potential of the enzyme in starch liquefaction and pharmaceutical and

food industries, and as an additive in detergent production, since it has tolerance to high temperatures, pH, salt, and detergents. Although microalgae, cyanobacteria, and bacteria present in desert soils are rich sources of thermostable enzymes, very limited investigations explored their potential as such studies require development of high-throughput screening based on advanced omics tools and mass culturing of these organisms present in desert consortia (Varshney et al. 2015).

Engineering consortia of cyanobacteria/microalgae and bacteria for desert soils

Using cyanobacterial/microalgal–bacterial consortia as a sustainable engineered system to restore desert ecosystems for agricultural purposes has become a growing trend in the recent past. Alginate beads with different shapes and arrangements are used in various industries as suitable carriers of inoculants. *Chlorella vulgaris* and *Azospirillum brasilense* (PGPB) within rhizosphere co-immobilize on small alginate beads to build-up the close relationship and it shows considerable growth and proliferation of microalgae (Gonzalez-Bashan et al. 2000). Light microscopic observations reveal colonization of the microalga at the periphery of the beads because of high oxygen concentration while the bacteria colonized throughout the whole bead. *A. brasilense* produce phytohormones such as indole-3-acetic acid (IAA) increasing the growth of the microalga *C. vulgaris*. The alginate beads with co-cultures compared to those containing sole organisms increased soil quality along with root and shoot development resulting in higher organic matter content and microbial activity in desert soils as represented in Fig. 2. They also showed an increase in soil microbial carbon by the co-cultures in the beads within 60 days (Table 3) as when compared with the individual microorganisms immobilized in beads (Trejo et al. 2012).

Sears and Prithiviraj (2012) suggest cyanobacteria-based consortial inoculant called TerraDerm for fertilizing the desert soil. In the preparation of a particular consortium, the selected microorganisms are initially mass cultured in a liquid medium using both light and sugar-fed photobioreactors. The cultivated microorganisms strain using capillary belt arrangement onto a thin damp mat without damaging the living biomass. These damp mats are composed of the following: antioxidants such as beta carotene, xeriprotectants as layers to avoid cell damage of microorganisms by desiccation, micronutrients and sugars for initial establishment of non-photosynthetic organisms, quartz and clay to support granulation of mats and to avoid cell damage, unique gene sequence for tracing the growth and proliferation, and vascular plant seeds for germination and survival in harmony with cyanobacteria and other microorganisms. The wet mat is then dried into thin granules using low-temperature belt without harming microorganisms. Finally, processed granules of consortia feed into the fluidized

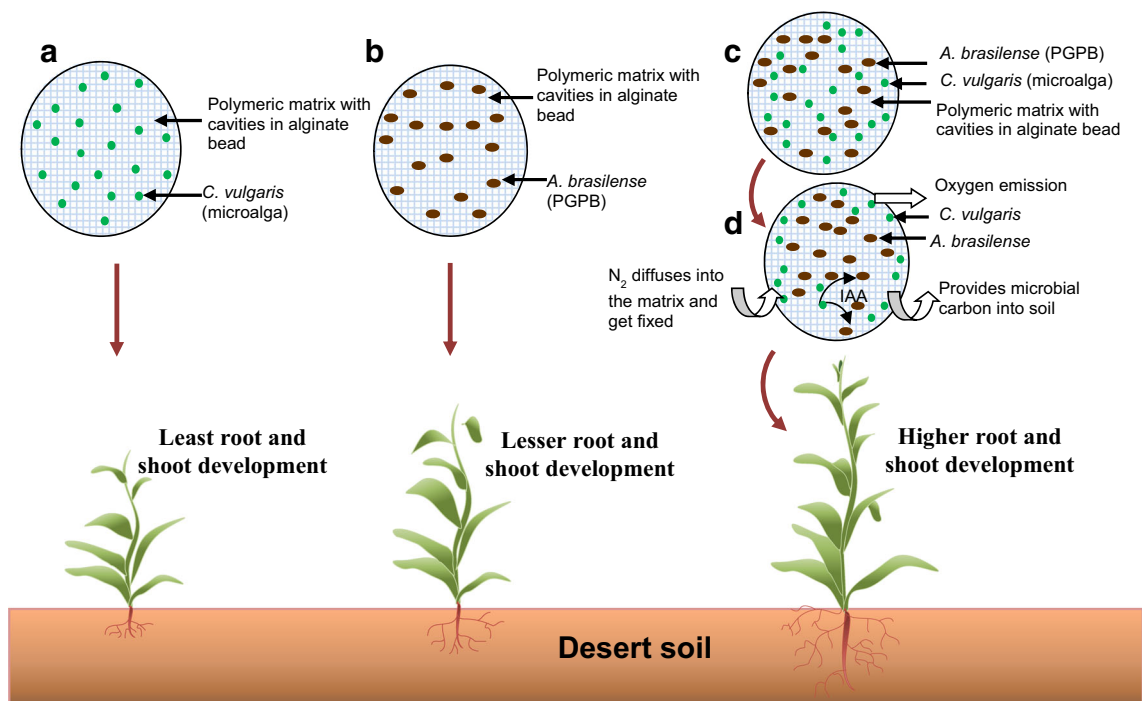


Fig. 2 Impact of a microalga and a plant growth-promoting bacterium (PGPB) immobilized in alginate beads on plant growth in desert soil. (A) Immobilization of *Chlorella vulgaris* in an alginate bead. (B) Immobilization of *Azospirillum brasilense* in an alginate bead. (C) Co-

immobilization of both the microorganisms in alginate matrix randomly. (D) PGPB excretes IAA that stimulates microalgal growth, and consequently, alginate beads release more microbial carbon and oxygen into the soil

bed bioreactors. Cost-effective agricultural aircrafts use for the distribution of these inoculants in the desert region improving the soil fertility and stability against soil erosion.

Increasing the indigenous microbial consortia supports efficient hydrocarbon degradation and vegetation of desert soil. Wang et al. (2009) demonstrate improving microbial consortia within desert through isolated cyanobacterial strains, *Microcoleus vaginatus* Gom and *Scytonema javanicum* Born et Flah from algal soil crusts from a desert area of Inner Mongolia. Liquid medium inoculating with both organisms was placed in a greenhouse and subsequently transferred to a tank and into previously setup moving dunes with sand barriers and erecting straw checkerboards. *M. vaginatus* and *S. javanicum* were mixed in a ratio of 10:1 and sprayed

uniformly over the sand surface. The automated sprinkler system is watering for 15–18 days until the cyanobacterial consortia emerged. This soil medium can be introduced to desert soil facilitating vegetation and establishing stable soil.

Zambrano et al. (2016) introduced a simple lab-scale photobioreactor to obtain cyanobacterial/microalgal–bacterial consortia. These bioreactors are made of glass, and either side is covered by steel. All the contents including biomass of algae and bacteria and dissolved substrates of ammonium and nitrate are stirred uniformly at 350 rpm and temperature under 23 °C. The reactors are supplied with oxygen and carbon dioxide and placed under fluorescent light. The dominant bacteria and microalgae are genus *Rhodobacter* and *Scenedesmus*, respectively. While constructing such models for developing consortia for deserts with high light irradiation, light attenuation (light gradient from top to bottom) must be considered since these light intensities could affect the algal growth under real situations. Also, culture conditions such as medium temperature, species and inoculum densities of bacteria and algae, and the quantity of incident light to be provided are the major criteria for engineering the consortia, and it should include advanced approaches for controlling their physical and chemical environmental conditions.

Genetically engineering of algae and bacteria consortia with favorable characteristics such as stability, robustness, and scalability would be supportive for applying them into desert vegetation (Goers et al. 2014; Ramanan et al. 2016).

Table 3 Total microbial carbon content in desert soil after 60 days of inoculation with a microalga and/or bacterium immobilized in alginate beads (Trejo et al. 2012)

Soil treatment	Microbial carbon (mg kg ⁻¹ soil)
Untreated soil	1.12 ± 0.005
Alginate alone	1.17 ± 0.003
<i>Chlorella sorokiniana</i>	1.30 ± 0.004
<i>Azospirillum brasilense</i>	1.81 ± 0.006
<i>C. sorokiniana</i> + <i>A. brasilense</i>	1.95 ± 0.011

However, *in vitro* studies would be required before they are applied into deserts. Microfluidic devices fabricated with accurate micron-scale environments could be used for studying their interactions, development, communication, and establishment such as biofilm formation of these synthetic cocultures (Hong et al. 2012). Usually, microorganisms in natural environments cooperatively live with different types of organisms that perform very complex functions. Therefore, synthetic biologists engineer clonal communities containing unique characters like cellular memory, cell division, differentiation, and adaptation presenting in complex multicellular forms. This would be supportive for various biotechnological applications and study how new functions within artificial or natural consortia useful in cellular signaling and communication pathways between diverse organisms that help to construct the consortia for the extreme environmental conditions in the deserts (Brune and Bayer 2012). A better understanding of associations such as competition and the cooperation of both algae and bacteria for different types of nutrients available in ecosystems would be the significant factors for engineering of consortia for a particular environment such as deserts. Furthermore, engineering of the consortium would be achievable in view of the existing biotechnological tools, for instance, metabolic profiling and functional genomics (Subashchandrabose et al. 2011).

Conclusions

Desert soils are characteristic of having harsh and rapidly fluctuating environmental circumstances, intense ultraviolet radiation, and lack of water, and are colonized by extremophilic microorganisms that include cyanobacteria, microalgae, and bacteria. Most of these naturally occurring microorganisms in the extreme habitats exist as consortia by developing extensive metabolic capabilities. Cyanobacterial/microalgal–bacterial consortia have superior performance compared to individual organisms, and engineering of such consortia would be very useful in water retention, mineralization and maintaining the stability of desert soils, primary production, and establishment of vegetation on desert surfaces, as well as in biotechnological applications such as pollutant removal from contaminated deserts and production of industrially important enzymes. Currently, there are growing trends towards the use of genetically modified microbial populations in synthetic biology for designing and studying efficient consortia with ecological functions for desert restoration. By studying the relationships such as adaptations of desert cyanobacteria, microalgae, and bacteria within a consortium would support for engineering beneficial, comprehensive, and controllable cyanobacterial/microalgal–bacterial consortia for the desert ecosystem.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

- Aanniz T, Ouadghiri M, Melloul M, Swings J, Elfahime E, Ibjibijen J, Ismaili M, Amar M (2015) Thermophilic bacteria in Moroccan hot springs, salt marshes and desert soils. *Braz J Microbiol* 46(2):443–453. <https://doi.org/10.1590/S1517-838246220140219>
- Abed RMM, Köster J (2005) The direct role of aerobic heterotrophic bacteria associated with cyanobacteria in the degradation of oil compounds. *Int Biodet Biodegrad* 55(1):29–37. <https://doi.org/10.1016/j.ibiod.2004.07.001>
- Abed RMM, Al Kharusi S, Schramm A, Robinson MD (2010) Bacterial diversity, pigments and nitrogen fixation of biological desert crusts from the Sultanate of Oman. *FEMS Microbiol Ecol* 72(3):418–428. <https://doi.org/10.1111/j.1574-6941.2010.00854.x>
- Abed RMM, Al-Kharusi S, Al-Hinai M (2015) Effect of biostimulation, temperature and salinity on respiration activities and bacterial community composition in an oil polluted desert soil. *Int Biodet Biodegrad* 98:43–52. <https://doi.org/10.1016/j.ibiod.2014.11.018>
- Abed RMM, Palinska KA, Köster J (2018) Characterization of microbial mats from a desert Wadi ecosystem in the Sultanate of Oman. *Geomicrobiol J* 35(7):601–611. <https://doi.org/10.1080/01490451.2018.1435755>
- Abinandan S, Subashchandrabose SR, Venkateswarlu K, Megharaj M (2018) Microalgae–bacteria biofilms: a sustainable synergistic approach in remediation of acid mine drainage. *Appl Microbiol Biotechnol* 102:1131–1144. <https://doi.org/10.1007/s00253-017-8693-7>
- Amin SA, Hmelo LR, van Tol HM, Durham BP, Carlson LT, Heal KR, Morales RL, Berthiaume CT, Parker MS, Djunaedi B, Ingalls AE, Parsek MR, Moran MA, Armburst EV (2015) Interaction and signalling between a cosmopolitan phytoplankton and associated bacteria. *Nature* 522:98. <https://doi.org/10.1038/nature14488>
- Azua-Bustos A, González-Silva C, Arenas-Fajardo C, Vicuña R (2012) Extreme environments as potential drivers of convergent evolution by exaptation: the Atacama desert coastal range case. *Front Microbiol* 3:426. <https://doi.org/10.3389/fmicb.2012.00426>
- Bahar MM, Megharaj M, Naidu R (2013) Toxicity, transformation and accumulation of inorganic arsenic species in a microalga *Scenedesmus* sp. isolated from soil. *J Appl Phycol* 25(3):913–917. <https://doi.org/10.1007/s10811-012-9923-0>
- Baqué M, Viaggiu E, Scalzi G, Billi D (2013) Endurance of the endolithic desert cyanobacterium *Chroococcidiopsis* under UVC radiation. *Extremophiles* 17(1):161–169. <https://doi.org/10.1007/s00792-012-0505-5>
- Bashan Y, de-Bashan LE (2010) Microbial populations of arid lands and their potential for restoration of deserts. In: Dion P (ed) *Soil biology and agriculture in the tropics*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 109–137
- Baumgarten E, Nagel M, Tischner R (1999) Reduction of the nitrogen and carbon content in swine waste with algae and bacteria. *Appl*

- Microbiol Biotechnol 52(2):281–284. <https://doi.org/10.1007/s002530051522>
- Belnap J (1996) Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. *Biol Fert Soils* 23(4):362–367. <https://doi.org/10.1007/BF00335908>
- Belnap J (2003a) Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap J, Lange OL (eds) *Biological soil crusts: structure, function, and management*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 241–261
- Belnap J (2003b) The world at your feet: desert biological soil crusts. *Front Ecol Environ* 1(4):181–185. <https://doi.org/10.2307/3868062>
- 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 Berlin Heidelberg, Berlin, Heidelberg, pp 281–300
- Belnap J, Welter JR, Grimm NB, Barger N, Ludwig JA (2005) Linkages between microbial and hydrologic processes in arid and semiarid watersheds. *Ecology* 86(2):298–307. <https://doi.org/10.1890/03-0567>
- 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 Morphol Distrib Funct Ecol Plants* 202(8):674–686. <https://doi.org/10.1016/j.flora.2007.05.007>
- Bhatnagar A, Bhatnagar M (2005) Microbial diversity in desert ecosystems. *Curr Sci* 89(1):91–100
- Bowker MA, Belnap J, Davidson DW, Phillips SL (2005) Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. *Ecol Appl* 15(6):1941–1951
- Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc Nat Acad Sci USA* 94(18):9729–9733. <https://doi.org/10.1073/pnas.94.18.9729>
- Brune KD, Bayer TS (2012) Engineering microbial consortia to enhance biomineralization and bioremediation. *Front Microbiol* 3:203. <https://doi.org/10.3389/fmicb.2012.00203>
- Cardon ZG, Gray DW, Lewis LA (2008) The green algal underground: evolutionary secrets of desert cells. *BioScience* 58(2):114–122. <https://doi.org/10.1641/B580206>
- Chamizo S, Cantón Y, Domingo F, Belnap J (2013) Evaporative losses from soils covered by physical and different types of biological soil crusts. *Hydrol Process* 27(3):324–332. <https://doi.org/10.1002/hyp.8421>
- Chen X, Jia S, Wang Y, Wang N (2011) Biological crust of *Nostoc flagelliforme* (cyanobacteria) on sand bed materials. *J Appl Phycol* 23(1):67–71. <https://doi.org/10.1007/s10811-010-9538-2>
- Cho DH, Ramanan R, Heo J, Lee J, Kim BH, Oh HM, Kim HS (2015) Enhancing microalgal biomass productivity by engineering a microalgal-bacterial community. *Bioresour Technol* 175:578–585. <https://doi.org/10.1016/j.biortech.2014.10.159>
- Connon SA, Lester ED, Shafaat HS, Obenhuber DC, Ponce A (2007) Bacterial diversity in hyperarid Atacama Desert soils. *J Geophys Res Biogeosci* 112(G4):1–9. <https://doi.org/10.1029/2006JG000311>
- Cowan DA, Sohm JA, Makhalanyane TP, Capone DG, Green TGA, Cary SC, Tuffin IM (2011) Hypolithic communities: important nitrogen sources in Antarctic desert soils. *Environ Microbiol Rep* 3(5):581–586. <https://doi.org/10.1111/j.1758-2229.2011.00266.x>
- Croft MT, Lawrence AD, Raux-Deery E, Warren MJ, Smith AG (2005) Algae acquire vitamin B12 through a symbiotic relationship with bacteria. *Nature* 438(7064):90–93. <https://doi.org/10.1038/nature04056>
- de los Ríos A, Valea S, Ascaso C, Davila A, Kastovsky J, McKay CP, Gómez-Silva B, Wierzbos J (2010) Comparative analysis of the microbial communities inhabiting halite evaporites of the Atacama Desert. *Int Microbiol: Span Soc Microbiol* 13:79–89
- Decho AW (1990) Microbial exopolymer secretions in ocean environments: their role (s) in food webs and marine processes. *Oceanogr Mar Biol Annu Rev* 28(7):73–153
- Demirjian DC, Moris-Varas F, Cassidy CS (2001) Enzymes from extremophiles. *Curr Opin Chem Biol* 5(2):144–151. [https://doi.org/10.1016/S1367-5931\(00\)00183-6](https://doi.org/10.1016/S1367-5931(00)00183-6)
- Drees KP, Neilson JW, Betancourt JL, Quade J, Henderson DA, Pryor BM, Maier RM (2006) Bacterial community structure in the hyperarid core of the Atacama desert, Chile. *Appl Environ Microbiol* 72(12):7902–7908. <https://doi.org/10.1128/aem.01305-06>
- Evans R, Johansen J (1999) Microbiotic crusts and ecosystem processes. *Crit Rev Plant Sci* 18(2):183–225. <https://doi.org/10.1080/07352689991309199>
- Fergola P, Cerasuolo M, Pollio A, Pinto G, DellaGreca M (2007) Allelopathy and competition between *Chlorella vulgaris* and *Pseudokirchneriella subcapitata*: experiments and mathematical model. *Ecol Model* 208(2–4):205–214
- Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. *Proc Nat Acad Sci USA* 103(3):626–631. <https://doi.org/10.1073/pnas.0507535103>
- Flechner VR, Johansen JR, Clark WH (1998) Algal composition of microbiotic crusts from the central desert of Baja California, Mexico. *Great Basin Naturalist* 58(4):295–311
- Friedmann EI (1980) Endolithic microbial life in hot and cold deserts. In: Ponnampertuma C, Margulis L (eds) *Limits of life*. Springer Netherlands, Dordrecht, pp 33–45
- Fuentes JL, Garbayo I, Cuaresma M, Montero Z, González-del-Valle M, Vélchez C (2016) Impact of microalgae-bacteria interactions on the production of algal biomass and associated compounds. *Marine Drugs* 14(5):100. <https://doi.org/10.3390/md14050100>
- Gabani P, Singh OV (2013) Radiation-resistant extremophiles and their potential in biotechnology and therapeutics. *Appl Microbiol Biotechnol* 97(3):993–1004. <https://doi.org/10.1007/s00253-012-4642-7>
- Gallardo A, Schlesinger WH (1992) Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry* 18(1):1–17
- Gao K (1998) Chinese studies on the edible blue-green alga, *Nostoc flagelliforme*: a review. *J Appl Phycol* 10(1):37–49. <https://doi.org/10.1023/A:1008014424247>
- García-Pichel F, López-Cortés A, Nübel U (2001) Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau. *Appl Environ Microbiol* 67(4):1902–1910. <https://doi.org/10.1128/AEM.67.4.1902-1910.2001>
- Godínez-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 Biol (Stuttgart, Germany)* 14(1):157–162. <https://doi.org/10.1111/j.1438-8677.2011.00495.x>
- Goers L, Freemont P, Polizzi KM (2014) Co-culture systems and technologies: taking synthetic biology to the next level. *J Royal Soc Interface* 11(96). <https://doi.org/10.1098/rsif.2014.0065>
- Gómez-Silva B, Rainey FA, Warren-Rhodes KA, McKay CP, Navarro-González R (2008) Atacama desert soil microbiology. In: Dion P, Nautiyal CS (eds) *Microbiology of extreme soils*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 117–132
- Gonzalez-Bashan LE, Lebsky VK, Hernandez JP, Bustillos JJ, Bashan Y (2000) Changes in the metabolism of the microalga *Chlorella vulgaris* when coimmobilized in alginate with the nitrogen-fixing *Phyllobacterium myrsinacearum*. *Canad J Microbiol* 46(7):653–659
- Goudie AS, Middleton NJ (2006) Desert dust in the global system. *Springer Science & Business Media*. p 288. ISBN 978-3-540-32355-6
- Grimm NB, Fisher SG, Minckley WL (1981) Nitrogen and phosphorus dynamics in hot desert streams of Southwestern U.S.A.

- Hydrobiologia 83(2):303–312. <https://doi.org/10.1007/BF0008281>
- Gulati A, Vyas P, Rahi P, Kasana RC (2009) Plant growth-promoting and rhizosphere-competent *Acinetobacter rhizosphaerae* strain BIHB 723 from the cold deserts of the Himalayas. *Curr Microbiol* 58(4):371–377. <https://doi.org/10.1007/s00284-008-9339-x>
- Hadley NF, Szarek SR (1981) Productivity of desert ecosystems. *BioScience* 31(10):747–753. <https://doi.org/10.2307/1308782>
- Harper KT, Belnap J (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. *J Arid Environ* 47(3):347–357. <https://doi.org/10.1006/jare.2000.0713>
- Heath C, Hu XP, Cary SC, Cowan D (2009) Identification of a novel alkaliphilic esterase active at low temperatures by screening a metagenomic library from Antarctic desert soil. *Appl Environ Microbiol* 75(13):4657–4659. <https://doi.org/10.1128/aem.02597-08>
- Herbert RA (1992) A perspective on the biotechnological potential of extremophiles. *Trends Biotechnol* 10:395–402. [https://doi.org/10.1016/0167-7799\(92\)90282-Z](https://doi.org/10.1016/0167-7799(92)90282-Z)
- Holmes RM, Fisher SG, Grimm NB (1994) Parafluvial nitrogen dynamics in a desert stream ecosystem. *J North Amer Benthol Soc* 13(4):468–478. <https://doi.org/10.2307/1467844>
- Hong SH, Hegde M, Kim J, Wang X, Jayaraman A, Wood TK (2012) Synthetic quorum-sensing circuit to control consortial biofilm formation and dispersal in a microfluidic device. *Nat Commun* 3:613. <https://doi.org/10.1038/ncomms1616>
- Hokputsa S, Hu C, Paulsen BS, Harding SE (2003) A physico-chemical comparative study on extracellular carbohydrate polymers from five desert algae. *Carbohydr Polym* 54(1):27–32. [https://doi.org/10.1016/S0144-8617\(03\)00136-X](https://doi.org/10.1016/S0144-8617(03)00136-X)
- Hu C, Liu Y, Paulsen BS, Petersen D, Klaveness D (2003) Extracellular carbohydrate polymers from five desert soil algae with different cohesion in the stabilization of fine sand grain. *Carbohydr Polym* 54(1):33–42. [https://doi.org/10.1016/S0144-8617\(03\)00135-8](https://doi.org/10.1016/S0144-8617(03)00135-8)
- Karnieli A, Shachak M, Tsoar H, Zaady E, Kaufman Y, Danin A, Porter W (1996) The effect of microphytes on the spectral reflectance of vegetation in semiarid regions. *Remote Sens Environ* 57(2):88–96. [https://doi.org/10.1016/0034-4257\(95\)00209-X](https://doi.org/10.1016/0034-4257(95)00209-X)
- Kaushal S, Singh Y, Khattar JIS, Singh DP (2017) Phycobiliprotein production by a novel cold desert cyanobacterium *Nodularia sphaerocarpa* PUPCCC 420.1. *J Appl Phycol* 29(4):1819–1827. <https://doi.org/10.1007/s10811-017-1093-7>
- Kazamia E, Czesnick H, Nguyen TTV, Croft MT, Sherwood E, Sasso S, Hodson SJ, Warren MJ, Smith AG (2012) Mutualistic interactions between vitamin B12-dependent algae and heterotrophic bacteria exhibit regulation. *Environ Microbiol* 14(6):1466–1476. <https://doi.org/10.1111/j.1462-2920.2012.02733.x>
- Kim J-D, Kim B, Lee C-G (2007) Alga-lytic activity of *Pseudomonas fluorescens* against the red tide causing marine alga *Heterosigma akashiwo* (Raphidophyceae). *Biol Control* 41(3):296–303
- Lan S, Zhang Q, Wu L, Liu Y, Zhang D, Hu C (2014) Artificially accelerating the reversal of desertification: cyanobacterial inoculation facilitates the succession of vegetation communities. *Environ Sci Technol* 48(1):307–315. <https://doi.org/10.1021/es403785j>
- Lan-Zhou C, Gao-Hong W, Song H, An L, Cheng L, Yong-Ding L (2009) UV-B-induced oxidative damage and protective role of exopolysaccharides in desert cyanobacterium *Microcoleus vaginatus*. *J Integr Plant Biol* 51(2):194–200. <https://doi.org/10.1111/j.1744-7909.2008.00784.x>
- Lewis LA, Flechtner VR (2004) Cryptic species of *Scenedesmus* (Chlorophyta) from desert soil communities of Western North America. *J Phycol* 40(6):1127–1137. <https://doi.org/10.1111/j.1529-8817.2004.03235.x>
- Lewis LA, Flechtner VR (2002) Green algae (Chlorophyta) of desert microbiotic crusts: diversity of North American taxa. *Taxon* 51(3):443–451. <https://doi.org/10.2307/1554857>
- Lewis LA, Lewis PO (2005) Unearthing the molecular phylodiversity of desert soil green algae (Chlorophyta). *Syst Biol* 54(6):936–947. <https://doi.org/10.1080/10635150500354852>
- Li XR, Zhou HY, Wang XP, Zhu YG, O'Conner PJ (2003) The effects of sand stabilization and revegetation on cryptogam species diversity and soil fertility in the Tengger desert. *Northern China Plant Soil* 251(2):237–245. <https://doi.org/10.1023/A:1023023702248>
- Liu W, Cui L, Xu H, Zhu Z, Gao X (2017) Flexibility-rigidity coordination of the dense exopolysaccharide matrix in terrestrial cyanobacteria acclimated to periodic desiccation. *Appl Environ Microbiol* 83(22):e01619-17. <https://doi.org/10.1128/aem.01619-17>
- Malam Issa O, Stal LJ, Défarge C, Couté A, Trichet J (2001) Nitrogen fixation by microbial crusts from desiccated Sahelian soils (Niger). *Soil Biol Biochem* 33(10):1425–1428. [https://doi.org/10.1016/S0038-0717\(01\)00046-3](https://doi.org/10.1016/S0038-0717(01)00046-3)
- Marc B, Renato M, Simone De O, Mauro M, Beatriz B (1999) Dynamics of a toxic cyanobacterial bloom (*Cylindrospermopsis raciborskii*) in a shallow reservoir in the semi-arid region of northeast Brazil. *Aquat Microb Ecol* 20(3):285–297
- Margesin R, Schinner F (2001) Biodegradation and bioremediation of hydrocarbons in extreme environments. *Appl Microbiol Biotechnol* 56(5–6):650–663. <https://doi.org/10.1007/s002530100701>
- Martin M, Portetelle D, Michel G, Vandenberg M (2014) Microorganisms living on macroalgae: diversity, interactions, and biotechnological applications. *Appl Microbiol Biotechnol* 98(7):2917–2935. <https://doi.org/10.1007/s00253-014-5557-2>
- Mazor G, Kidron GJ, Vonshak A, Abeliovich A (1996) The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiol Ecol* 21(2):121–130. <https://doi.org/10.1111/j.1574-6941.1996.tb00339.x>
- Megharaj M, Pearson HW, Venkateswarlu K (1992) Removal of nitrogen and phosphorus by immobilized cells of *Chlorella vulgaris* and *Scenedesmus bijugatus* isolated from soil. *Enz Microb Technol* 14(8):656–658. [https://doi.org/10.1016/0141-0229\(92\)90042-M](https://doi.org/10.1016/0141-0229(92)90042-M)
- Megharaj M, Venkateswarlu K, Naidu R (2011a) Effects of carbaryl and 1-naphthol on soil population of cyanobacteria and microalgae and select cultures of diazotrophic cyanobacteria. *Bull Environ Contam Toxicol* 87(3):324–329. <https://doi.org/10.1007/s00128-011-0347-3>
- Megharaj M, Ramakrishnan B, Venkateswarlu K, Sethunathan N, Naidu R (2011b) Bioremediation approaches for organic pollutants: a critical perspective. *Environ Internat* 37(8):1362–1375. <https://doi.org/10.1016/j.envint.2011.06.003>
- Metting B (1981) The systematics and ecology of soil algae. *Bot Rev* 47(2):195–312
- Miralles I, Domingo F, Cantón Y, Trasar-Cepeda C, Leirós MC, Gil-Sotres F (2012) Hydrolase enzyme activities in a successional gradient of biological soil crusts in arid and semi-arid zones. *Soil Biol Biochem* 53:124–132. <https://doi.org/10.1016/j.soilbio.2012.05.016>
- Moreno J, Bastida F, Hernández T, García C (2008) Relationship between agricultural management of a semi-arid soil and microbiological quality. *Commun Soil Sci Plant Anal* 39:421–439. <https://doi.org/10.1080/00103620701826548>
- Mouget J-L, Dakhama A, Lavoie MC, de la Noüe J (1995) Algal growth enhancement by bacteria: is consumption of photosynthetic oxygen involved? *FEMS Microbiol Ecol* 18(1):35–43. [https://doi.org/10.1016/0168-6496\(95\)00038-C](https://doi.org/10.1016/0168-6496(95)00038-C)
- Munoz R, Guieysse B (2006) Algal-bacterial processes for the treatment of hazardous contaminants: a review. *Water Res* 40(15):2799–2815. <https://doi.org/10.1016/j.watres.2006.06.011>
- Nagy ML, Pérez A, García-Pichel F (2005) The prokaryotic diversity of biological soil crusts in the Sonoran desert (Organ Pipe Cactus National Monument, AZ). *FEMS Microbiol Ecol* 54(2):233–245. <https://doi.org/10.1016/j.femsec.2005.03.011>
- Neilson JW, Quade J, Ortiz M, Nelson WM, Legatzki A, Tian F, LaComb M, Betancourt JL, Wing RA, Soderlund CA (2012) Life at the

- hyperarid margin: novel bacterial diversity in arid soils of the Atacama Desert. *Chile Extremophiles* 16(3):553–566
- Niehaus F, Bertoldo C, Kähler M, Antranikian G (1999) Extremophiles as a source of novel enzymes for industrial application. *Appl Microbiol Biotechnol* 51(6):711–729. <https://doi.org/10.1007/s002530051456>
- Nithya K, Muthukumar C, Kadaikunnan S, Alharbi NS, Khaled JM, Dhanasekaran D (2017) Purification, characterization, and statistical optimization of a thermostable α -amylase from desert actinobacterium *Streptomyces fragilis* DA7-7. *3 Biotech* 7(5):350. <https://doi.org/10.1007/s13205-017-0981-5>
- Pointing SB, Belnap J (2012) Microbial colonization and controls in dryland systems. *Nat Rev Microbiol* 10(8):551–562. <https://doi.org/10.1038/nrmicro2831>
- Pointing SB, Chan Y, Lacap DC, Lau MCY, Jurgens JA, Farrell RL (2009) Highly specialized microbial diversity in hyper-arid polar desert. *Proc Natl Acad Sci USA* 106(47):19964–19969. <https://doi.org/10.1073/pnas.0908274106>
- Poong S-W, Lim P-E, Phang S-M, Wong C-Y, Pai T-W, Chen C-M, Yang C-H, Liu C-C (2018) Transcriptome sequencing of an Antarctic microalga, *Chlorella* sp. (Trebouxiophyceae, Chlorophyta) subjected to short-term ultraviolet radiation stress. *J Appl Phycol* 30(1):87–99. <https://doi.org/10.1007/s10811-017-1124-4>
- Priscu JC, Fritsen CH, Adams EE, Giovannoni SJ, Paerl HW, McKay CP, Doran PT, Gordon DA, Lanoil BD, Pinckney JL (1998) Perennial Antarctic lake ice: an oasis for life in a polar desert. *Science* 280(5372):2095–2098
- Prakash O, Jaiswal N (2010) α -Amylase: an ideal representative of thermostable enzymes. *Appl Biochem Biotechnol* 160(8):2401–2414. <https://doi.org/10.1007/s12010-009-8735-4>
- Puente ME, Bashan Y, Li CY, Lebsky VK (2008) Microbial populations and activities in the rhizoplane of rock-weathering desert plants. I. Root colonization and weathering of igneous rocks. *Plant Biol* 6(5):629–642. <https://doi.org/10.1055/s-2004-821100>
- Radwan SS, Al-Awadhi H, Sorkhoh NA, El-Nemr IM (1998) Rhizospheric hydrocarbon-utilizing microorganisms as potential contributors to phytoremediation for the oil Kuwaiti desert. *Microbiol Res* 153(3):247–251. [https://doi.org/10.1016/S0944-5013\(98\)80007-4](https://doi.org/10.1016/S0944-5013(98)80007-4)
- Rainey FA, Ray K, Ferreira M, Gatz BZ, Nobre MF, Bagaley D, Rash BA, Park M-J, Earl AM, Shank NC, Small AM, Henk MC, Battista JR, Kämpfer P, da Costa MS (2005) Extensive diversity of ionizing-radiation-resistant bacteria recovered from Sonoran desert soil and description of nine new species of the genus *Deinococcus* obtained from a single soil sample. *Appl Environ Microbiol* 71(9):5225–5235. <https://doi.org/10.1128/aem.71.9.5225-5235.2005>
- Ramanan R, Kim BH, Cho DH, Oh HM, Kim HS (2016) Algae-bacteria interactions: evolution, ecology and emerging applications. *Biotechnol Adv* 34(1):14–29. <https://doi.org/10.1016/j.biotechadv.2015.12.003>
- Redfield E, Barns SM, Belnap J, Daane LL, Kuske CR (2002) Comparative diversity and composition of cyanobacteria in three predominant soil crusts of the Colorado Plateau. *FEMS Microbiol Ecol* 40(1):55–63. <https://doi.org/10.1111/j.1574-6941.2002.tb00936.x>
- Robinson CH (2001) Cold adaptation in Arctic and Antarctic fungi. *New Phytol* 151(2):341–353. <https://doi.org/10.1046/j.1469-8137.2001.00177.x>
- Rosenfeld D (2000) Suppression of rain and snow by urban and industrial air pollution. *Science* 287(5459):1793–1796. <https://doi.org/10.1126/science.287.5459.1793>
- Safrieli U, Adeel Z, Niemeijer D, Puigdefabregas J, White R, Lal R, Winsolow M, Ziedler J, Prince S, Archer E (2006) Dryland systems ecosystems and human well-being current state and trends, vol Vol 1. Island Press, pp 625–656
- Saul-Tcherkas V, Unc A, Steinberger Y (2013) Soil microbial diversity in the vicinity of desert shrubs. *Microb Ecol* 65(3):689–699. <https://doi.org/10.1007/s00248-012-0141-8>
- Sears J, Prithiviraj B (2012) Seeding of large areas with biological soil crust starter culture formulations using an aircraft dispersible granulate to increase stability, fertility and CO₂ sequestration on a landscape scale. 2012 IEEE Green Technologies Conference. pp. 1–3. <https://doi.org/10.1109/GREEN.2012.6200934>
- Scherer S, Zhong Z-P (1991) Desiccation independence of terrestrial *Nostoc commune* ecotypes (cyanobacteria). *Microb Ecol* 22(1):271–283. <https://doi.org/10.1007/BF02540229>
- Sterflinger K, Tesei D, Zakharova K (2012) Fungi in hot and cold deserts with particular reference to microcolonial fungi. *Fungal Ecol* 5(4):453–462. <https://doi.org/10.1016/j.funeco.2011.12.007>
- Subashchandrabose SR, Ramakrishnan B, Megharaj M, Naidu R (2011) Consortia of cyanobacteria/microalgae and bacteria: biotechnological potential. *Biotechnol Adv* 29:896–907. <https://doi.org/10.1016/j.biotechadv.2011.07.009>
- Subashchandrabose SR, Megharaj M, Venkateswarlu K, Naidu R (2012) *p*-Nitrophenol toxicity to and its removal by three select soil isolates of microalgae: the role of antioxidants. *Environ Toxicol Chem* 31(9):1980–1988. <https://doi.org/10.1002/etc.1931>
- Subashchandrabose SR, Ramakrishnan B, Megharaj M, Venkateswarlu K, Naidu R (2013) Mixotrophic cyanobacteria and microalgae as distinctive biological agents for organic pollutant degradation. *Environ Internat* 51:59–72. <https://doi.org/10.1016/j.envint.2012.10.007>
- Subashchandrabose SR, Megharaj M, Venkateswarlu K, Naidu R (2015) Interaction effects of polycyclic aromatic hydrocarbons and heavy metals on a soil microalga, *Chlorococcum* sp. MM11. *Environ Sci Pollut Res* 22(12):8876–8889. <https://doi.org/10.1007/s11356-013-1679-9>
- Subashchandrabose SR, Logeshwaran P, Venkateswarlu K, Naidu R, Megharaj M (2017a) Pyrene degradation by *Chlorella* sp. MM3 in liquid medium and soil slurry: possible role of dihydroliipoamide acetyltransferase in pyrene biodegradation. *Algal Res* 23:223–232. <https://doi.org/10.1016/j.algal.2017.02.010>
- Subashchandrabose SR, Wang L, Venkateswarlu K, Naidu R, Megharaj M (2017b) Interactive effects of PAHs and heavy metal mixtures on oxidative stress in *Chlorella* sp. MM3 as determined by artificial neural network and genetic algorithm. *Algal Res* 21:203–212. <https://doi.org/10.1016/j.algal.2016.11.018>
- Teplitski M, Rajamani S (2011) Signal and nutrient exchange in the interactions between soil algae and bacteria. In: Witzany G (ed) *Biocommunication in soil microorganisms*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 413–426
- Trejo A, de-Bashan LE, Hartmann A, Hernandez J-P, Rothballer M, Schmid M, Bashan Y (2012) Recycling waste debris of immobilized microalgae and plant growth-promoting bacteria from wastewater treatment as a resource to improve fertility of eroded desert soil. *Environ Exper Bot* 75:65–73. <https://doi.org/10.1016/j.envexpbot.2011.08.007>
- Varshney P, Mikulic P, Vonshak A, Beardall J, Wangikar PP (2015) Extremophilic micro-algae and their potential contribution in biotechnology. *Bioresour Technol* 184:363–372. <https://doi.org/10.1016/j.biortech.2014.11.040>
- Vassilev N, Eichler-Löbermann B, Vassileva M (2012) Stress-tolerant *P*-solubilizing microorganisms. *Appl Microbiol Biotechnol* 95(4):851–859. <https://doi.org/10.1007/s00253-012-4224-8>
- Vítek P, Jehlička J, Ascaso C, Mašek V, Gómez-Silva B, Olivares H, Wierzechos J (2014) Distribution of scytonemin in endolithic microbial communities from halite crusts in the hyperarid zone of the Atacama Desert, Chile. *FEMS Microbiol Ecol* 90(2):351–366. <https://doi.org/10.1111/1574-6941.12387>
- Vítek P, Ascaso C, Artieda O, Casero MC, Wierzechos J (2017) Discovery of carotenoid red-shift in endolithic cyanobacteria

- from the Atacama desert. *Sci Rep* 7(1):11116. <https://doi.org/10.1038/s41598-017-11581-7>
- Wang G, Chen K, Chen L, Hu C, Zhang D, Liu Y (2008) The involvement of the antioxidant system in protection of desert cyanobacterium *Nostoc* sp. against UV-B radiation and the effects of exogenous antioxidants. *Ecotoxicol Environ Saf* 69(1):150–157. <https://doi.org/10.1016/j.ecoenv.2006.03.014>
- Wang W, Liu Y, Li D, Hu C, Rao B (2009) Feasibility of cyanobacterial inoculation for biological soil crusts formation in desert area. *Soil Biol Biochem* 41(5):926–929. <https://doi.org/10.1016/j.soilbio.2008.07.001>
- Ward D (2016) *The biology of deserts (biology of habitats series)*, 2nd Edn. Oxford University Press, p 461. ISBN 978-0-19-873275-4
- Watt M, McCully ME, Canny MJ (1994) Formation and stabilization of rhizosheaths of *Zea mays* L. (effect of soil water content). *Plant Physiol* 106(1):179–186
- Wierzchos J, Ascaso C, McKay CP (2006) Endolithic cyanobacteria in halite rocks from the hyperarid core of the Atacama Desert. *Astrobiology* 6(3):415–422
- Wierzchos J, DiRuggiero J, Vitek P, Artieda O, Souza-Egipsy V, Skaloud P, Tisza M, Davila AF, Vilchez C, Garbayo I, Ascaso C (2015) Adaptation strategies of endolithic chlorophototrophs to survive the hyperarid and extreme solar radiation environment of the Atacama desert. *Front Microbiol* 6:934. <https://doi.org/10.3389/fmicb.2015.00934>
- Wu L, Zhu Q, Yang L, Li B, Hu C, Lan S (2018) Nutrient transferring from wastewater to desert through artificial cultivation of desert cyanobacteria. *Bioresour Technol* 247:947–953. <https://doi.org/10.1016/j.biortech.2017.09.127>
- Xu Y, Rossi F, Colica G, Deng S, De Philippis R, Chen L (2013) Use of cyanobacterial polysaccharides to promote shrub performances in desert soils: a potential approach for the restoration of desertified areas. *Biol Fertil Soils* 49(2):143–152. <https://doi.org/10.1007/s00374-012-0707-0>
- Xu Z, Hou Y, Zhang L, Liu T, Zhou G (2016) Ecosystem responses to warming and watering in typical and desert steppes. *Sci Rep* 6: 34801. <https://doi.org/10.1038/srep34801>
- Xue L, Shang H, Ma P, Wang X, He X, Niu J, Wu J (2018) Analysis of growth and lipid production characteristics of *Chlorella vulgaris* in artificially constructed consortia with symbiotic bacteria. *J Basic Microbiol* 58(4):358–367. <https://doi.org/10.1002/jobm.201700594>
- Yasir M, Azhar EI, Khan I, Bibi F, Baabdullah R, Al-Zahrani IA, Al-Ghamdi AK (2015) Composition of soil microbiome along elevation gradients in southwestern highlands of Saudi Arabia. *BMC Microbiol* 15(1):65. <https://doi.org/10.1186/s12866-015-0398-4>
- Zakar T, Laczko-Dobos H, Toth TN, Gombos Z (2016) Carotenoids assist in cyanobacterial photosystem II assembly and function. *Front Plant Sci* 7(295). <https://doi.org/10.3389/fpls.2016.00295>
- Zambrano J, Krustok I, Nehrenheim E, Carlsson B (2016) A simple model for algae-bacteria interaction in photo-bioreactors. *Algal Res* 19:155–161. <https://doi.org/10.1016/j.algal.2016.07.022>
- Zayadan BK, Matorin DN, Baimakhanova GB, Bolathan K, Oraz GD, Sadanov AK (2014) Promising microbial consortia for producing biofertilizers for rice fields. *Microbiology* 83(4):391–397. <https://doi.org/10.1134/s0026261714040171>
- Zhang B, Zhang Y, Su Y, Wang J, Zhang J (2013) Responses of microalgal-microbial biomass and enzyme activities of biological soil crusts to moisture and inoculated *Microcoleus vaginatus* gradients. *Arid Land Res Manag* 27(3):216–230. <https://doi.org/10.1080/15324982.2012.754514>