Arid ecosystem: future option for carbon sinks using microbial community intelligence

Leena Agarwal, Asifa Qureshi, Vipin Chandra Kalia, Atya Kapley, Hemant J. Purohit* and R. N. Singh

Desert, comprising one-third of the Earth's surface, was a synonym for 'no life' as it supports very less or no life due to nutritional stress and extreme weather. Microbial autotrophic biochemistry is the principal source of carbon in arid environment, but understanding of these processes in arid ecosystem is limited. Emerging molecular tools have identified associations of phototrophic and chemolithoautotrophic communities often termed as 'biological soil crust' or 'microbiotic crust'. They are the sole sources of carbon and nitrogen, collectively providing soil stability to support vegetation. Here the curiosity arises, whether this phenomenon could be exploited in deserts for carbon sink using microbial community intelligence. By following the precipitation event under regulated nutrient supply that promotes the soil microbial intelligence for autotrophy would enrich soil carbon and nitrogen which in turn support plant growth in desert. Additionally, bioaugmentation of rhizobacteria could enhance the process. This will enable us to refine and formulate our strategies to exploit CO₂-fixing microorganisms in such niches vis-à-vis supporting the carbon sink using microbial community intelligence.

Keywords: Arid ecosystem, biological soil crust, carbon sequestration, metagenome, microbial intelligence,

CLIMATE change is a global phenomenon shown to be related with the increase of CO₂ levels, which have been reported up to 399 ppm in May 2013 (Mauna Loa Observatoy, Hawaii). It is attracting the attention of the scientific community and correlations have shown that the increasing levels of CO₂ are directly associated with climate change effects¹. There is a need to identify CO₂ sink options that could address the issue of ever increasing atmosphere CO2 at global level. Is there an answer for this issue by increasing carbon sequestration capacity through degraded land or deserts? Deserts are a major portion of the terrestrial ecosystem, mostly considered as barren or without life due to extreme environment with unbalanced or compromised nutritional status². Soils after a precipitation event, show subsurface soil heterotrophic activity. Deserts are oligotrophic in nature, here microbial autotrophy drives CO₂ fixation and significantly contributes to associated biomass at comparatively low levels than plants. Microbial CO₂ assimilation involves photo-

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Increasing the capacity of desert and degraded land could be the next option to sequester carbon. Long-term storage of carbon in basic resources of an ecosystem is called carbon sequestration. The two major natural C sink options are ocean and terrestrial ecosystem, of which oceans can bring maximum carbon sinks since they make 71% of the Earth's surface. Terrestrial storage includes abstraction of CO₂ in both forest area as well as non-

Leena Agarwal, Asifa Qureshi, Atya Kapley and Hemant J. Purohit are in the Environmental Genomics Division, CSIR-National Environmental Engineering Research Institute, Nehru Marg, Nagpur 440 020, India; Vipin Chandra Kalia is in Microbial Biotechnology and Genomics Division, CSIR-Institute of Genomics and Integrative Biology, Delhi University Campus, Mall Road, Delhi 110 007, India; R. N. Singh is in the CSIR-National Geophysical Research Institute, Hyderabad 500 007, India.

*For correspondence. (e-mail: hj_purohit@neeri.res.in)

Forest

forest area like desert.

Forest ecosystem is a reservoir for more than 70% of the terrestrial and soil organic carbon^{4,5}. Although forest

trophs and chemolithoautotrophs, viz. iron oxidizing, sulfur oxidizing, ammonia oxidizing and nitrifying bacteria. They are the key source of soil carbon in case of arid soil, principally sequestering CO₂ by Calvin–Benson–Bassham (CBB) cycle. Beyond the CBB cycle, there are five other options, viz. reductive acetyl CoA pathway (rACoA), reductive tricarboxylic acid (rTCA) cycle, 3-hydroxypropionate bicycle (3-HP), hydroxypropionate/hydroxybutyrate cycle and dicarboxylate-hydroxybutyrate cycle³ available for the microbial community to assimilate CO₂.

floors accumulate C quickly, but being labile and available for a limited period, they are not considered as long-term solutions⁶. The potential of enhancing C sequestration rates of existing forests is not encouraging and provides a rather conflicting set of evidences⁵. Forest soils act as potential C sinks, but only a small proportion of plant-derived C becomes stabilized on the mineral soil⁷. Afforestation cannot help achieve large amounts of C sequestration than is possible by fertilization of forest, particularly on nutrient-limited sites like deserts⁸.

Desert

Desert covers substantial part of terrestrial ecosystem and have been shown to absorb around 100 g C/m²/yr (ref. 9). The net CO₂ exchange data using eddy covariance method in Mojave and Gurbantunggut desert (China) suggests that deserts act as 'large carbon sink'9-11. However, the absolute size of desert makes it significantly more important for CO₂ sinks. The carbon flux between the desert soil and the atmosphere is smaller in comparison to that which takes place between organically rich soils. The carbon storage capacities of ecosystems with low organic content, viz. arid and semiarid regions are not well studied¹⁰.

Microbial community knowledge in deserts

Microbial autotrophs are closely associated with life on Earth and are distributed amongst all the three domains of life³. Microbial activity in desert soils is principally governed by soil carbon comparable to nitrogen¹². The total organic carbon of desert ecosystem has been reported between 560 and 765 µg/g soil in Atacama Desert, whereas it is 7000 and 1700 µg/g soil in Mojave and Sahara deserts respectively¹³. The same argument strongly proposes to make the desert a better sink for CO₂, since a lot of autotrophic and oligotrophic bacteria are found to exist in low organics^{14,15}. Though deprived of green cover, desert provides shelter to photoautotrophic and chemolithoautotrophic microbial communities that access carbon from the atmosphere 16,17. The unvegetated soil of Atacama Desert supports many chemolithotrophic genera which were phylogenetically affiliated to previously reported non-phototrophic genera, viz. Nitrospira, and gamma-proteobacteria¹⁸ that obtain energy for CO₂ fixation by the oxidation of nitrite, carbon monoxide, iron or sulfur. Microbial community in arid soil was also found to be rich in archaeal members affiliated to Crenarchaea^{19,20}, an indicator group for the operation of 3hydroxypropionate pathway²¹ and primordial life-forms. Freeman et al.²² report the abundance of photoautotrophic microbial community in barren soil due to light-driven CO2 influx. This CO2 influx resulted in the abundance of photoautotrophic microbial communities on surface soil compared to deeper soil. Yuan *et al.*¹⁶ determined the diversity and abundance of CO₂-fixing bacteria and algae by clone library, T-RFLP and qPCR of rubisco gene. The ¹⁴C-CO₂ incubation studies revealed the incorporation of ¹⁴C into the soil microbial biomass accounting up to 4% of the total CO₂ fixed by terrestrial ecosystems per year. Yousuf *et al.*³² studied the diversity and abundance of chemolithotrophic bacteria in coastal saline soil of Gujarat, targeting both phylogenetic and functional gene (*cbb*) marker.

Biological soil crust (BSC) is a vital C sink in the desert due to the photosynthetic community which is decisive for carbon cycling either by oxygenic or anoxygenic phototrophy²³. The association of cyanobacteria, lichens and mosses forms the principal component of BSC¹¹. It sequesters 6% of total carbon sequestered by terrestrial vegetation and fixes about 40% of biological nitrogen²⁴. The crust significantly contributes soil carbon, nitrogen, nutrients and reduces soil erosion, thereby improving soil fertility²⁵⁻²⁷. The carbon fixation capacities of BSC increase from 0.4 to 3.3 g C m⁻² yr⁻¹ with its maturity as a result of increase in crust cover, its thickness, chlorophyll content, organic carbon and nitrogen content²⁸. During the process of BSC succession, the cyanobacteria-algae-dominated crust shifts toward lichen-moss dominance. This shift causes increase in the amount of carbon sequestered from 11.36 26.75 g C m⁻² yr⁻¹, possibly due to more surface area and water-holding capacity of the later successions²⁹. The average rate of nitrogen fixed by BSC in different deserts accounts for 70 µmol m⁻² h⁻¹ of nitrogen²⁶. Establishment of BSC in desert supports plantation better compared to bare soil, but principally depends on the succession stage of BSC³⁰. The promising route for restoration of degraded land is the establishment of BSC on dry land that results in an increase in soil organic carbon and nitrogen²⁸.

In desert, microbial community intelligence for autotrophy is possessed by members of cyanobacteria, chloroflexi, bacteroidetes/chlorobi and some proteobacteria 16,31,32 along with group chemolithotroph affiliated with purple sulfur, purple non-sulfur, green sulfur and green non-sulfur bacteria. Besides the knowledge of autotrophy, understanding of nitrogen fixation by Azospirillum sp., Rhizobium sp. and Pseudomonas sp. is also present in arid ecosystem³³. It is proposed that if the intelligence for carbon, nitrogen and nutrient cycle possessed by microbial components of BSC could be harnessed for increasing the soil nutritional status, then a system with enhanced efficiency of carbon sequestration could be designed (Figure 1). So the key to account desert as a carbon sink should be to consider together the effect of precipitation event, temperature, soil process and microbial activity to support plant productivity³⁴.

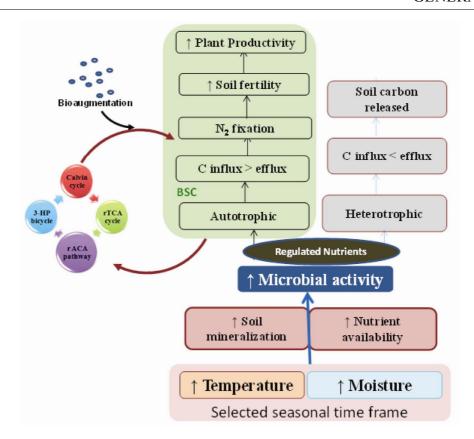


Figure 1. Conceptual strategy for carbon sequestration in arid ecosystem using microbial community intelligence: The identification of critical time-frame for precipitation event and its exploitation in favour of development of effective biological crust (BSC) has been hypothesized. It includes defining the strategy for development of microbial community intelligence for carbon sequestration by identification of community structure or by applying required microbial members to complete the desired community structure. This could be further assisted by supplementation of nutrients responsible for synthesis and stabilization of BSC under the selected climatic conditions of temperature and humidity. Establishment of such microbial knowledge would ultimately support in an increase of soil carbon, nitrogen and its fertility. The programmed scenario would support the pool of nutrients to heterotrophs and plant to further participate in sequestration process. Conversely, under non-optimal climatic conditions of increased temperature and humidity, deep subsurface heterotrophic microbial activity enhances, which further reduces soil carbon resulting in land degradation.

Molecular tools aiding mining the microbial community intelligence

Microbial community intelligence is the overall knowledge that a community has in order to adapt to the present state of stress or environmental conditions by altruistic or cooperative behaviour. Such example of microbial community intelligence is found in soil ecosystems. Soil is a complex dynamic biological system that harbours almost 4000 different bacterial species/g soil, but almost 99% could not be isolated due to unavailability of the knowledge about their culturing conditions. This 99% could be accessed by metagenomics, which provides the knowledge of total community from any environmental sample. It is an efficient technique to address the functional capacity of uncultivable microorganisms from any niche³⁵. The advancement of soil metagenomics provides a new perspective for understanding the role of soil microorgan-

isms and to unearth the hidden functional knowledge associated with the microbial community, even with the extreme environment like Atacama Desert^{2,36,37}. Earlier studies on the microbiology of desert soil have proved that life in the desert was not explored due to limitations of culturing techniques. The emerging molecular tools could be applied for the analysis of microbial wealth while considering the possible limitations^{16,38–40}. Improvement in DNA extraction efficiency and high sampling frequency is required to explore the huge microbial world, inhabiting the soil³⁹; and this could be further improved using high throughput approaches such as microarray^{41,42}.

Next-generation sequencing techniques have opened a wide spectrum of taxonomic and functional aspects of microbial community⁴³. Identification of many unculturable microbes and archaeal members of group Thermoprotei in Sonaron Desert soil highlights the magnitude of

pyrosequencing¹². Of late, metatranscriptomics and metaproteomics have been evolved to access the functional knowledge from such a vast metagenome data⁴³. The functional annotation of such datasets is based on homology search against the publicly available database and requires knowledge of bioinformatics tools and computational storage space⁴⁴. Recent advances in the field of microbiology, biotechnology, molecular biology and bioinformatics opened up the way to identify novel genes and for improving the quality of target output⁴⁵. There are many microbes reported for CO2 fixation through unknown pathways, pointing towards the scope of finding new genes, enzymes and pathways underlying CO2 fixation⁴⁶. Developing such resource and database enlightens the area of research and the understanding of new genes and pathways.

The biochemistry of CO₂ fixation by microbial communities in extreme environments could be understood by exploring the genetic information carried by the metagenomes. Metagenome analysis suggests colonization of various phototrophs and lithotrophs in Arctic, Antarctic and Atacama Desert^{2,25,37,47}. This was evidenced by the identification of *rubisco* gene in the metagenome^{32,48}. Marker genes for CO₂ fixation were observed in metagenome isolated from various niches, but little is known about the CO₂ fixing gene other than *rubisco*. Hence there is still scope for finding new genes that can fix CO₂ in arid ecosystems. In addition to the phylogenetic analysis, knowledge of functional gene diversity is more important to study climate change impact in desert and provide insight into the role of desert as a CO₂ sink.

Community response to climatic drivers

The Southeast Asian region is observing the shift in the geographical distribution of rainfall pattern. The trend shows that it is moving towards the western plains and feeding the precipitation to deserts and also moving towards the Middle East⁴⁹. Desert is highly responsive to climatic variability since bacteria-inhabiting deserts are under various stresses, viz. temperature, salinity, precipitation, carbon, etc. The bacteria that survive in desert cope with these stresses. The presence of carbon dioxidefixing bacteria in deserts counteracts the carbon stress by fixing the inorganic carbon and hence increases soil organics and supports other lifeforms. The member of genus Azospirillum, a known plant growth promoting bacteria (PGPB), exerts its growth-promoting effect on plants under various desert stresses of salinity⁵⁰, drought⁵¹ and extreme pH⁵². The soil microbial community alters with change in precipitation, atmospheric CO2 concentration and temperature^{53,54}. In arid ecosystems, precipitation is the key driver controlling carbon, nitrogen and nutrients due to change in microbial response⁵⁵. The nature of episodic precipitation events in arid ecosystem increases carbon influx due to increased surface microbial autotrophic activity. The soil of Kalahari (Botswana) Desert harbours cyanobacteria, which fix atmospheric CO₂ to add significant quantity of organic matter⁵⁶. The gains and losses of CO₂ through the sands of Kalahari Desert after light rainfall are the same as grassland soil, but after the heavy rainfall, large amount of CO₂ is released due to increased degradation of organic matter by heterotrophic bacteria, which masks the activity of cyanobacteria. The heterotrophic microbial respiration operates at a very low level in the desert ecosystem and for short durations, particularly after rains, when the availability of nutrients enables CO₂ efflux⁵⁵. In response to the increased precipitation in desert soil, the rate of carbon efflux is observed in the range 65.6-339.2 mg C $\text{m}^2 \text{h}^{-1}$ compared to 2.8–14.8 mg C $\text{m}^2 \text{h}^{-1}$ in dry soil⁵⁶. CO₂ efflux increases with an increase in soil temperature due to more heterotrophic microbial activity⁵⁷. As increase in soil temperature limits moisture and results in reduced CO₂ fixation capacity of desert due to declined phototrophic activity. Here the microbial intelligence and natural selection favours the temperature-tolerating phototrophic members in order to provide soil stability⁵⁸.

Another climatic driver is atmospheric CO₂ concentration, which is ever-increasing since 1988. Elevated CO₂ concentration causes an increase in soil carbon sequestration due to increased plant productivity⁵⁹. The soil enzyme activity alters in response to elevated CO2 that affects the quantity and quality of soil organic matter and microbial processes⁶⁰. Microbial response to such an elevated CO₂ was studied in different ecosystems, but the observation suggests the need for more extensive analysis to reveal the microbial response to these changes⁶¹. An integrated approach of pyrosequencing and GeoChip has suggested that the functional structure of soil community alters under elevated CO₂ (ref. 42). There was an increased abundance of genes responsible for carbon fixation, nitrogen fixation and phosphorus release under elevated CO₂ (ref. 42). A variety of carbon sources and their metabolites support the network of different genomes, which collectively decide the way a biological process evolves under the stress conditions prevailing in such a system⁶².

Instances of microbial community intelligence exploitation

Increasing the capacity of desert and degraded lands could be the option to sequester carbon vis-à-vis CO_2 mitigation. Integrating various approaches of carbon sequestration and energy generation, exploiting microbial intelligence could serve as a better option in the near future. One such paradigm is a Sahara forest project, which aims at integrating different technologies where processes feed each other and provide environmental as

well as commercial benefits. This serves turning an arid land into green oasis⁶³. Another project 'Biodesert program' enables unearthing of microbial resources in deserts, which serve as a knowledge pool to develop approaches to mitigate climate change. Carbon cycling is one of the thrust research areas of the Genomic Science Program funded by US Department of Energy (DOE) (http://genomicscience.energy.gov/). It is aimed at developing biosequestration strategies for ocean and terrestrial ecosystem. The DOE Joint Genome Institute has generated genome sequences of many microbes and plants, which provide knowledge of microbial/microbial community intelligence. Genomic science researchers are developing advanced methods to translate microbial intelligence into an understanding of function to provide insights into plant-microbe and microbe-microbe interactions that increase carbon fixation in soils. Synthetic biology has come up to explore microbial intelligence of stress survival for smart assembly of genome 'parts' to find key solutions to carbon sequestration and climate change⁶⁴. Such resources fulfil the DOE mission of synthesizing a microbial system that was otherwise unculturable, to improve carbon fixation capacities in soil and sediments. Application of bioaugmentation strategy could also enhance the process of carbon fixation in arid systems. Rhizospheric plant-microbe interaction serves as one of the options to enhance carbon sequestration⁶⁵. It enhances nutrient uptake capacity of the plant due to increase in surface area of roots, nitrogen and phosphorus availability. Researches targeting the development of microbial consortia involving microbial members responsible for nitrogen fixation, phosphorus solubilization, siderophore production, phytohormone synthesis, biological crust formation that would finally support plant growth in symbiotic or non-symbiotic manner could help develop microbe-based strategies for carbon sequestration. Restoration of Sonoran Desert has been demonstrated by bioaugmentation of PGPB formulation consisting of Azospirillum brasilense and Bacillus pumilus, along with arbuscular mycorrhizal fungi and compost^{66,67}. However, the plant growth response depends on the varying degrees of bio-formulation application. A bio-formulation of immobilized A. brasilense and microalgae Chlorella sorokiniana was also used to increase the organic content of desert soil to support sorghum plantation⁶⁸. By integrating the knowledge-based research of application of PGPB with the development of application-based technology would promote desert farming. This basically relies on the detailed knowledge in terms of soil characteristics, climatic factors and microbial intelligence present in that niche that has to be reclaimed. This enables us to understand the missing knowledge that could be offered externally favouring the natural entropy. The microbial community reserves of an arid ecosystem may offer insight into finding new solutions to global environmental issues and adding up to the existing natural capacities.

Conclusion

Deserts can be equated as dry 'oceans', but the vision of converting deserts into green oasis could address the problem of climate change. A biological approach for carbon capture through the microbial process in deserts is the establishment of BSC. Researches targeting to identify the factors promoting BSC formation and their effect on plant establishment offer a way to develop desert as a carbon sink. Additionally, bioaugmentation of PGPB could also address soil fertility. The genetic potential to fix CO₂ is widespread in soils; their capacity to fix CO₂ has yet to be fully investigated. The knowledge of key functions related to climatic drivers, their effect and microbial responses within the desert ecosystem would be useful for developing better solutions for carbon sequestration in the desert.

- Solomon, S., Plattner, G. K., Knutti, R. and Friedlingstein, P., Irreversible climate change due to carbon dioxide emissions. *Proc. Natl. Acad. Sci. USA*, 2009, 106(6), 1704–1709.
- Warren-Rhodes, K. A. et al., Hypolithic cyanobacteria, dry limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. Microb. Ecol., 2006, 52(3), 389–398.
- Berg, I. A., Ecological aspects of the distribution of different autotrophic CO₂ fixation pathways. *Appl. Environ. Microbiol.*, 2011, 77(6), 1925–1936.
- Jobbagy, E. G. and Jackson, R. B., The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.*, 2000, 10(2), 423–436.
- Six, J. et al., Measuring and understanding carbon storage in afforested soils by physical fractionation. Soil Sci. Soc. Am. J., 2002, 66(6), 1981–1987.
- Jandl, R. et al., How strongly can forest management influence soil carbon sequestration? Geoderma, 2007, 137(3-4), 253-268.
- Giardina, C. P. et al., The response of belowground carbon allocation in forests to global change. In *Tree Species Effects on Soils: Implications for Global Change* (eds Binkley, D. and Menyailo, O.), NATO Science Series IV: Earth and Environmental Sciences, Springer, 2005, vol. 55, pp. 119–154.
- Köberl, M., Müller, H., Ramadan, E. M. and Berg, G., Desert farming benefits from microbial potential in arid soils and promotes diversity and plant health. *PLoS One*, 2011, 6(9), e24452.
- Stone, R., Ecosystems: have desert researchers discovered a hidden loop in the carbon cycle? Science, 2008, 320(5882), 1409– 1410
- Liu, R., Li, Y. and Wang, Q-X., Variations in water and CO₂ fluxes over a saline desert in western China. *Hydrol. Process.*, 2012, 26, 513–522.
- Wohlfahrt, G., Fenstermaker, L. F. and Arnone III, J. A., Large annual net ecosystem CO₂ uptake of a Mojave Desert ecosystem. Global Change Biol., 2008, 14(7), 1475–1487.
- Andrew, D. R., Fitak, R. R., Munguia-Vega, A., Racolta, A., Martinson, V. G. and Dontsova, K., Abiotic factors shape microbial diversity in Sonoran desert soils. *Appl. Environ. Microbiol.*, 2012, 78(21), 7527–7537.
- 13. Lester, E. D., Satomi, M. and Ponce, A., Microflora of extreme arid Atacama desert soil. *Soil Biol. Biochem.*, 2007, **39**(2), 704–708.
- Yoshida, N., Ohhata, N., Yoshino, Y., Katsuragi, T., Tani, Y. and Takagi, H., Screening of carbon dioxide-requiring extreme oligotrophs from soil. *Biosci. Biotechnol. Biochem.*, 2007, 71(11), 2830–2832.

- Agarwal, L. and Purohit, H. J., Genome sequence of *Rhizobium lupini* HPC(L) isolated from saline desert soil, Kutch (Gujarat). *Genome Announc.*, 2012, 1(1), e00071–12.
- Yuan, H., Ge, T., Chen, C., O'Donnell, A. G. and Wu, J., Significant role for microbial autotrophy in the sequestration of soil carbon. *Appl. Environ. Microbiol.*, 2012, 78(7), 2328–2336.
- 17. Wood, S. A., Rueckert, A., Cowan, D. A. and Cary, S. C., Sources of edaphic cyanobacterial diversity in the dry valleys of eastern Antarctica. *ISME J.*, 2008, **2**, 308–320.
- 18. Neilson, J. W. *et al.*, Life at the hyperarid margin: novel bacterial diversity in arid soils of the Atacama Desert, Chile. *Extremophiles*, 2012, **16**(3), 553–566.
- Soule, T., Anderson, I. J., Johnson, S. L., Bates, S. T. and Garcia-Pichel, F., Archaeal populations in biological soil crusts from arid lands in North America. Soil Biol. Biochem., 2009, 41(10), 2069– 2074
- Wong, F. K. Y., Lau, M. C. Y., Lacap, D. C., Aitchison, J. C., Cowan, D. A. and Pointing, S. B., Endolithic microbial colonization of limestone in a high-altitude arid environment. *Microb. Ecol.*, 2010, 59(4), 689–699.
- Hügler, M., Huber, H., Stetter, K. O. and Fuchs, G., Autotrophic CO₂ fixation pathways in archaea (Crenarchaeota). *Arch. Microbiol.*, 2003, 179(3), 160–173.
- Freeman, R., Pescador, M. Y., Reed, S. C., Costello, E. K., Robeson, M. S. and Schmidt, S. K., Soil CO₂ flux and photoautotrophic community composition in high-elevation, 'barren' soil. *Environ. Microbiol.*, 2009, 11(3), 674–686.
- Belnap, J. and Lange, O. L. (eds), Biological Soil Crusts: Structure, Function, and Management, Ecological Studies Series 150 (Series edited by Baldwin, I. T. et al.), Springer, Berlin, 2003.
- Elbert, W., Weber, B., Büdel, B., Andreae, M. O. and Pöschl, U., Microbiotic crusts on soil, rock and plants: neglected major players in the global cycles of carbon and nitrogen? *Biogeosci. Discuss.*, 2009. 6, 6983-7015.
- 25. Borin, S. *et al.*, Rock weathering creates oases of life in a High Arctic desert. *Environ. Microbiol.*, 2010, **12**(2), 293–303.
- Strauss, S. L., Day, T. A. and Garcia-Pichel, F., Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. *Biogeochemistry*, 2012, 108, 171– 182
- Zhang, B., Zhang, Y., Zhao, J., Wu, N., Chen, R. and Zhang, J., Microalgal species variation at different successional stages in biological soil crusts of the Gurbantunggut Desert, northwestern China. *Biol. Fertil. Soils*, 2009, 45(5), 539–547.
- Yan-Gui, S., Xin-Rong, L., Ying-Wu, C., Zhi-Shan, Z. and Yan, L., Carbon fixation of cyanobacterial—algal crusts after desert fixation and its implication to soil organic carbon accumulation in desert. *Land Degrad. Dev.*, 2011, doi: 10.1002/ldr.1131.
- Li, X. R., Zhang, P., Su, Y. G. and Jia, R. L., Carbon fixation by biological soil crusts following revegetation of sand dunes in arid desert regions of China: a four-year field study. *Catena*, 2012, 97, 119–126.
- Godínez-Alvarez, H., Morín, C. and Rivera-Aguilar, V., Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. *Plant Biol.*, 2012, 14(1), 157-162.
- 31. Atomi, H., Microbial enzymes involved in carbon dioxide fixation. *J. Biosci. Bioeng.*, 2002, **94**(6), 497–505.
- 32. Yousuf, B., Sanadhya, P., Keshri, J. and Jha, B., Comparative molecular analysis of chemolithotrophic bacterial diversity and community structure from coastal saline soils, Gujarat, India. *BMC Microbiol.*, 2012, **12**, 150.
- Chowdhury, S. P., Schmid, M., Hartmann, A. and Tripathi, A. K., Identification of diazotrophs in the culturable bacterial community associated with roots of *Lasiurus sindicus*, a perennial grass of Thar Desert, India. *Microb. Ecol.*, 2007, 54(1), 82–90.

- King, G. M., Enhancing soil carbon storage for carbon remediation: potential contributions and constraints by microbes. *Trends Microbiol.*, 2011, 19(2), 75–84.
- Sagarkar, S., Mukherjee, S., Nousiainen, A., Björklöf, K., Purohit, H. J., Jørgensen, K. S. and Kapley, A., Monitoring bioremediation of atrazine in soil microcosms using molecular tools. *Environ. Pollut.*, 2013, 172, 108–115.
- Cary, S. C., McDonald, I. R., Barrett, J. E. and Cowan, D. A., On the rocks: the microbiology of Antarctic Dry Valley soils. *Nature Rev. Microbiol.*, 2010, 8(2), 129–138.
- Smith, J. J., Tow, L. A., Stafford, W., Cary, C. and Cowan, D. A., Bacterial diversity in three different Antarctic Cold Desert mineral soils. *Microb. Ecol.*, 2006, 51(4), 413–421.
- 38. Campbell, J. H., Clark, J. S. and Zak, J. C., PCR-DGGE comparison of bacterial community structure in fresh and archived soils sampled along a Chihuahuan desert elevational gradient. *Microb. Ecol.*, 2009, **57**(2), 261–266.
- Direito, S. O. L., Ehrenfreund, P., Marees, A., Staats, M., Foing, B. and Röling, W. F. M., A wide variety of putative extremophiles and large beta-diversity at the Mars Desert Research Station (Utah). *Int. J. Astrobiol.*, 2011, 10(3), 191–207.
- Dafale, N., Agrawal, L., Kapley, A., Meshram, S., Purohit, H. and Wate, S., Selection of indicator bacteria based on screening of 16S rDNA metagenomic library from a two-stage anoxic-oxic bioreactor system degrading azo dyes. *Bioresour. Technol.*, 2010, 101(2), 476-484.
- 41. Yergeau, E. *et al.*, Environmental microarray analyses of Antarctic soil microbial communities. *ISME J.*, 2009, **3**(3), 340–351.
- He, Z. et al., Metagenomic analysis reveals a marked divergence in the structure of belowground microbial communities at elevated CO₂. Ecol. Lett., 2010, 13, 564–575.
- 43. Simon, C. and Daniel, R., Metagenomic analyses: past and future trends. *Appl. Environ. Microbiol.*, 2011, 77(4), 1153–1161.
- 44. Prakash, T. and Taylor, T. D., Functional assignment of metagenomic data: challenges and applications. *Brief. Bioinform.*, 2012, **13**(6), 711–727.
- Xing, M. N., Zhang, X. Z. and Huang, H., Application of metagenomic techniques in mining enzymes from microbial communities for biofuel synthesis. *Biotechnol. Adv.*, 2012, 30(4), 920-929
- Yoshida, N., Hayasaki, T. and Takagi, H., Gene expression analysis of methylotrophic oxidoreductases involved in the oligotrophic growth of *Rhodococcus erythropolis* N9T-4. *Biosci. Biotechnol. Biochem.*, 2011, 75(1), 123–127.
- Varin, T., Lovejoy, C., Jungblut, A. D., Vincent, W. F. and Corbeil, J., Metagenomic analysis of stress genes in microbial mat communities from Antarctica and the High Arctic. *Appl. Environ. Microbiol.*, 2012, 78(2), 549–559.
- Kong, W., Dolhi, J. M., Chiuchiolo, A., Priscu, J. and Morgan-Kiss, R. M., Evidence of form II RubisCO (cbbM) in a perennially ice-covered Antarctic lake. *FEMS Microbiol. Ecol.*, 2012; doi: 10.1111/j.1574-6941.2012.01431.x
- 49. Singh, N., Sontakke, N. A., Singh, H. N. and Pandey, A. K., Recent trend in spatiotemporal variation of rainfall over India an investigation into basin-scale rainfall fluctuations. Regional hydrological impacts of climatic change: hydroclimatic variability. IAHS Publication, 296, 2005, pp. 273–282.
- Bacilio, M., Rodriguez, H., Moreno, M., Hernandez, J.-P. and Bashan, Y., Mitigation of salt stress in wheat seedlings by a gfptagged Azospirillum lipoferum. Biol. Fertil. Soils, 2004, 40, 188– 193
- Creus, C. M., Sueldo, R. J. and Barassi, C. A., Water relations in *Azospirillum* inoculated wheat seedlings under osmotic stress. *Can. J. Bot.*, 1998, 76, 238–244.
- 52. de-Bashan, L. E., Antoun, H. and Bashan, Y., Cultivation factors and population size control uptake of nitrogen by the microalgae *Chlorella vulgaris* when interacting with the microalgae growth-

- promoting bacterium Azospirillum brasilense. FEMS Microbiol. Ecol., 2005, **54**, 197–203.
- Castro, H. F., Classen, A. T., Austin, E. E., Norby, R. J. and Schadt, C. W., Soil microbial community responses to multiple experimental climate change drivers. *Appl. Environ. Microbiol.*, 2010, 76(4), 999–1007.
- Davidson, E. A. and Janssens, I. A., Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 2006, 440(7081), 165–173.
- Sponseller, R. A., Precipitation pulses and soil CO₂ flux in a Sonoran desert ecosystem. Global Change Biol., 2007, 13(2), 426–436.
- Thomas, A. D. and Hoon, S. R., Carbon dioxide fluxes from biologically-crusted Kalahari sands after simulated wetting. *J. Arid Environ.*, 2010, 74(1), 131–139.
- 57. Cable, J. M. *et al.*, The temperature responses of soil respiration in deserts: a seven desert synthesis. *Biogeochemistry*, 2011, **103**, 71–90
- Garcia-Pichel, F., Loza, V., Marusenko, Y., Mateo, P. and Potrafka, R. M., Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science*, 2013, 340(6140), 1574–1577.
- Blagodatskaya, E., Blagodatsky, S., Dorodnikov, M. and Kuzyakov, Y., Elevated atmospheric CO₂ increases microbial growth rates in soil: results of three CO₂ enrichment experiments. *Global Change Biol.*, 2010, 16, 836-848.
- Kelley, A. M., Fay, P. A., Polley, H. W., Gill, R. A. and Jackson, R. B., Atmospheric CO₂ and soil extracellular enzyme activity: a meta-analysis and CO₂ gradient experiment. *Ecosphere*, 2011, 2(8), art96.
- Dunbar, J. et al., Common bacterial responses in six ecosystems exposed to 10 years of elevated atmospheric carbon dioxide. Environ. Microbiol., 2012, 14(5), 1145–1158.
- Paliwal, V., Puranik, S. and Purohit, H. J., Integrated perspective for effective bioremediation. *Appl. Biochem. Biotechnol.*, 2012, 166(4), 903–924.

- Clery, D., Environmental technology. Greenhouse-power plant hybrid set to make Jordan's desert bloom. *Science*, 2011, 331(6014), 136.
- Lee, S. J., Lee, S. J. and Lee, D. W., Design and development of synthetic microbial platform cells for bioenergy. *Front. Microbiol.*, 2013, 4, 92.
- Wu, C. H., Bernard, S. M., Andersen, G. L. and Chen, W., Developing microbe-plant interactions for applications in plant-growth promotion and disease control, production of useful compounds, remediation and carbon sequestration. *Microb. Biotechnol.*, 2009, 2(4), 428-440.
- 66. Bashan, Y., Salazar, B. and Puente, M. E., Responses of native legume desert trees used for reforestation in the Sonoran Desert to plant growth-promoting microorganisms in screen house. *Biol. Fertil. Soils*, 2009, 45, 655–662.
- 67. de-Bashana, L. E., Hernandeza, J.-P. and Bashan, Y., The potential contribution of plant growth-promoting bacteria to reduce environmental degradation a comprehensive evaluation. *Appl. Soil Ecol.*, 2012, **61**, 171–189.
- 68. Trejo, A., de-Bashan, L. E., Hartmann, A., Hernandez, J.-P., Rothballer, M., Schmid, M. and Bashan, Y., 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. Exp. Bot.*, 2012, 75, 65–73.

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