Ritu Mawar · R Z Sayyed
Sushil K Sharma
Krishna Sundari Sattiraju *Editors*

Plant Growth Promoting Microorganisms of Arid Region

Springer

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Foreword

The Indian Thar Desert represents a harsh ecosystem with extreme climatic conditions having diverse life forms which require adaptive mechanisms for their survival. In addition to the critical role of plants in desert biodiversity, species of insects and microorganisms comprise the largest group of organisms, some of them are little known or rarely discussed. They are involved in various vital ecosystem services such as pollination, decomposition, recycling of nutrients, and enhancing plant immunity and act as important links in parasitoids, food chain, predators, herbivore, etc. However, in the food chain, indiscriminate use of agrochemicals or pesticides indirectly increases the toxic levels. To obviate these snags, the application of beneficial microorganisms in agriculture has increased in terms of biofertilizers and biopesticides as these provide sustainably higher economic yields. Systematic studies have been initiated to explore biocontrol potentials of microorganisms in order to develop a cost-effective and practical management strategy for plant diseases. This book discusses various aspects of microorganisms and their key role in development of healthy desert ecosystem. Additional, commercialization and regulatory issues concerning biopesticides have also been discussed in a manner that will be invaluable for academicians, scientists, researchers, and policymakers. I congratulate the editors for their useful efforts to publish such a good and informative book.

New Delhi, India
15 Feb 2022

S. C. Dubey

Preface

Deserts are characterized by scarce natural resources and an inhospitable climate. Rainfall is highly erratic and unpredictable. The region experiences extremes of temperature (−2 °C to 48 °C), high wind velocity, and sandy soil. The main problem hampering crop growth and productivity in an arid ecosystem is drought, which is further accentuated by global climate change events and is estimated to have reduced cereal, legumes, oil seeds, and spices productivity by 10–40%. Crop productivity can be increased by inoculating the plants facing drought stress with plant growth-promoting microorganisms (PGPM). The thin layer of soil immediately surrounding the plant roots is an extremely important and active area for root activity and metabolism and is known as rhizosphere. A large number of microorganisms such as bacteria, fungi, actinomycetes, protozoa, and algae coexist in the rhizosphere. The microorganisms that colonize the rhizosphere can be classified according to their effects on plants and the way they interact with roots, some being pathogens whereas others trigger beneficial effects. The microorganisms inhabiting the rhizosphere and beneficial to plants are termed PGPM. Various species of bacteria and fungi have been reported to enhance plant growth. There are several PGPM inoculants currently commercialized that seem to promote growth through at least one mechanism: suppression of plant disease (Bioprotectants), improved nutrient acquisition (Biofertilizers), or phytohormone production (Biostimulants). Hence agriculturally important microorganisms have come under focus for the management of various crop health due to their unique abilities to survive in the arid ecosystem and reducing the severity of the diseases. This book aims to gather contributions from leading scientists and researchers, with focus on microbial diversity in arid lands and deserts versus specific microbial assemblages associated with plants. The ecological drivers that shape this diversity, how plant-associated microbiomes are selected, and their biotechnological potential are discussed. Many of the chapters include PGPM-related activities of microbes from arid regions and provide novel research avenues for further exploration of potential microbial candidates for their application in plant disease management strategies aiding agricultural sustainability in arid lands. Diversity and functional redundancy of these associated PGPM makes them very active in supporting plant improvement, health, and resistance to drought, salt, and other stresses. Implementing proper biotechnological applications of the arid and desert-adapted PGPM constitutes the challenge to be raised. Further, commercialization and regulatory issues concerning biopesticides have also been discussed in a manner that will be invaluable for academicians, scientists, researchers, and policymakers. We expect that the book would be very useful for students, researchers, industrialists, entrepreneurs, academicians, and policymakers to understand the roles of plant growth-promoting microorganisms in sustainable agriculture and provide directions for the future course of action.

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"NO ONE CAN WHISTLE A SYMPHONY. IT TAKES A WHOLE ORCHESTRA TO PLAY IT." The book as you see today is the work and toil of all the participating editors operating under the stewardship of the principal editor, all sticking to the adage "*T*ogether *E*veryone *A*chieves *M*ore." As a team we realized at every step the significance of planning, execution, mutual respect to timelines, and deliverance. Writing a book is harder than we thought and more rewarding than we could have ever imagined. None of this would have been possible without the support and guidance of our mentors Prof. M.S. Reddy, Founder Chairman, Asian PGPR Society, and Prof. Satish Lodha, Principal Scientist at CAZRI. Prof. Reddy with his dynamic and enterprising nature is the emotional powerhouse to propel all such initiatives that promotes, propagates, and perpetuates research on Plant Growth-Promoting Microorganisms. Prof. Lodha was the first person whom the senior editor has met with when a proposal for the book was being made. He stood by us during this entire process. We greatly value their mentorship and sincerely acknowledge their support and encouragement.

We would like to express our sincere gratitude to the contributing authors whose research works and years of experience working with PGPM have played a very significant role in enriching the content of the publication. Thanks and appreciations also to our colleagues in developing the book and people who have willingly helped us out with their abilities.

We extend our sincere gratitude to Team Springer for reposing their faith in us as an Editorial team and entrusted us with this task of spreading PGPM research output across the wider scientific community.

We thankfully acknowledge our families and friends for the encouragement and motivational support rendered by them.

Finally, thanks to everyone who have been a part of this book directly or indirectly and made us realize this objective of bringing out research on contribution of PGPM with particular emphasis on dry and arid ecosystems.

Ritu Mawar
R Z Sayyed
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About the Editors

Ritu Mawar is a Principal Scientist (Plant Pathology) at the ICAR-Central Arid Zone Research Institute (CAZRI), Jodhpur, India. She worked in management of soil-borne plant pathogens such as *Macrophomina phaseolina*, *Fusarium*, and *Ganoderma* by soil solarization, use of cruciferous residues, composts, biological control, etc. She has received Best Women Scientist Fellowship from DST and Indian Society of Mycology and Plant Pathology, and Indian Patents. She has published more than 75 research papers, book chapters, and popular articles in high-impact journals, success story of management of Ganoderma in ICAR Newsletter, and has authored four books. She has presented her research at various international platforms in the county and abroad and has received a number of best presentation awards. She served as peer reviewer of foreign research journals and DST-funded projects, and External Examiner for Ph.D. thesis and viva voce of many academic universities. She is a Life Member of Indian Phytopathological Society, Range Management Society, Arid Zone Research Association, Indian Society of Mycology and Plant Pathology, and Asian PGPR Society for Sustainable Agriculture and its Advisory Board Member. She is an executive member of the editorial board of *Journal of Rainfed Farming* and Indian Phytopathological Society newsletter. She is serving as a Zonal President (CZ) of Indian Phytopathological Society, IARI, New Delhi, and Zonal Councillor (NWZ) and executive member of Range Management Society of

India for 2022–2024. She developed three bio-formulated products from native strains of bioagents viz., *Trichoderma harzianum* and *Bacillus firmus*. She received two patents on novel microbes in 2019 as Bioformulation of a biopesticide and a process for preparing the same and "Consortium of biopesticides and bioformulation comprising same." State POP was developed for managing soil-borne plant pathogens. Techniques were developed to rejuvenate *Prosopis cineraria* (*Khejri*) from Ganoderma species. IPM technologies were developed for arid legumes, oil seed, and cumin crops.

R Z Sayyed is a Professor and Head, Department of Microbiology, PSGVP Mandal's Arts, Science College, Shahada, India. Currently, he serves as the President of the India chapter of the Asian PGPR Society for Sustainable Agriculture (Estd 2019). To his credit, he has received the Best Teachers Award, Young Scientist Award (2005, 2008, and 2012), Prof M. M. Sharma Award, Springer-Society Award (2020), and Award for Excellence in PGPR Research (2017, 2018, and 2019). He is Associate Editor of Environmental Sustainability (Springer) and Guest editor of two special issues of Sustainability (MDPI, IF 3.251). He has over 25 years of teaching and 20 years of research experience in Microbiology and Biotechnology. He has authored and coauthored over 200 research papers in high IF international journal, 24 books with Springer, Wiley, CRC, and Cambridge press, and 43 book chapters in reputed edited books. He has trained several graduates, postgraduate, and research students and produced seven Ph.D.s under his guidance. He has delivered many invited talks at several Southeast Asian and European countries.

Sushil K Sharma is a Principal Scientist at ICAR-NIBSM, Raipur, India. He works in the area of microbial resource conservation and antimicrobial peptides production by bacteria for biotic stress management in crops. He has served as officer in-charge at ICAR-National Bureau of Agriculturally Important Microorganisms (NBAIM), Maunath Bhanjan, Uttar Pradesh, India. He has long experience on Soybean Research. He has delivered talks in various international conferences in the country and abroad. He has published more than 100 research articles in internationally recognized and good impact journals. His team has developed (1) a simple novel method for the detection of operation of tryptophan-independent pathway in *Micrococcus aloeverae* DCB-20 and (2) a low-cost preservation method of *Chromobacterium violaceum* using natural gums at room temperature. He received the *Best Scientist* award by PEARL Foundation, Madurai, India, and *Excellence in PGPR Research* award by Asian PGPR Society. Recently, he has been nominated as a member of *Biosafety and Biosecurity Cell* (*B2Cell*) of Indian Council of Medical Research (ICMR), New Delhi.

Krishna Sundari Sattiraju presently serves as Professor in the Department of Biotechnology at JIIT, Noida. She has 20 years of academic and research experience, working at places of national and international repute such as TERI (The Energy and Resources Institute), New Delhi; Institute Nationale Recherche Agronomie (INRA), Champenoux, France; and brief work assignments at ENSAIA, France, Universitae Henrie Poincare, France, and University of Florida, Gainesville, USA. The educational institutes where she worked earlier include Institute of Applied Medicines and Research (IAMR), Ghaziabad, Institute of Home Economics (IHE), New Delhi, Jamia Milia Islamia, New Delhi, and TERI–SAS, New Delhi.

She harbors research interest in the area of Microbial Biotechnology with applications for Agriculture, Environment, and Industry. She has successfully taken up projects worth more than 2 crores funded by DBT, Govt. of India. She has published nearly 25 papers in international refereed journals and has more than 50 conference papers and book chapters. Prof. Krishna holds membership in various international scientific societies and presently serving as Exec. Vice President for Asian PGPR Society, Auburn, USA.

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Chapter 1
Exploring Microbial Diversity of Arid Regions of Globe for Agricultural Sustainability: A Revisit

Ritu Mawar, Madhavi Ranawat, Sushil K Sharma, and R Z Sayyed

1 Introduction

Environmental pollutions, climate changes, emergence of deadly microbial variants, scarcity of water, and food resources are the global issues of twenty-first century's world. Among the concerning issues, increasing world's population leading reduction in land available for cultivation is the biggest hurdle agriculture sustainability is in face with (Shahbaz and Ashraf 2013). A vast area of planet's land is covered by desert ecoregions which account for more than 46 million square kilometers of available land (Osborne et al. 2020). Exploring available arid land for cultivation can open various new avenues to tackle with these issues. Cultivation in dry arid zones of world is not as easy as it sounds. Brutality of environment in such land challenges the idea of successful cultivation; yet several efforts have been made to establish cultivation in unexplored arid lands. Utilizing beneficial microorganisms with exceptional potentials to not only tolerate or withstand but also thrive in extremities imposed by desert environment can aid agriculture sustainability in such land. By exploring their unique potentials, genetic diversity, biocontrol abilities, plant growth-promoting capacities, and other tendencies idea to successfully sustain agriculture in desert land can come into reality (Fig. 1.1). This chapter explores microbial diversity found in desert across of globe and provides insight to their utilization in agricultural sustainability.

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Fig. 1.1 Microbes in desert ecosystems for agri-sustainability

Deserts are significant part of world's natural and cultural heritage covering one-third of planet's surface. Deserts are home for nearly 2.1 billion people and to diverse flora, fauna, and microbial species that are unique to dry ecosystems in terms of adaptations. Deserts have been defined in several ways—biologically, they are ecoregions with well-adapted life forms; physically, they are areas with low vegetative cover and extensions of bare soils, and climatologically, they are all the arid and semiarid regions of globe. Deserts play an important role in global ecology and environment and are significant migratory corridor for several species, trade corridors, and exporters of unique agricultural and other goods to nondesert areas (Osborne et al. 2020; United Nations Environment Programme 2006). Around 33% land is actually converted into deserts, and rest is in the process of desertification. Desert ecoregions have been addressed as dry/arid land(s) or zone(s) (Laity 2009). Deserts have been classified into three different zones around the world based on Aridity Index (AI) and are hyperarid zones, semiarid zones, and arid zones (Cherlet et al. 2018; Alsharif et al. 2020). Life thrive there endure climatic conditions imposed by environment including extreme and abrupt temperature fluctuations, high soil salinity, wind velocity, radiations and scarcity of water, nutrient and organic matter. Several other abiotic and biotic factors like soil pH, composition, depth, texture, conductivity, nutrient cycling, precipitation rate and composition, diversity, and shape of functional group of communities affect and contribute to desert ecosystem at varying degree. The desert land is essentially barren with limited number of biological communities and probably dominated with microbial coteries contributing to key desert ecosystem processes. Environmental factors play key role in shaping desert microbial communities, and findings suggest that deterministic factors favor bacterial communities over any other in deserts (Wang et al. 2013).

Desert microbes not always provide beneficial services, but some of the communities are notorious for very long time for their pathogenic potentials. Several soil-inhibiting microbes including bacteria, fungi, nematodes, and actinomycetes are known to cause serious diseases in plants worldwide. On the other side, several microbial consortia exhibit beneficial relationships with plants. Microbes are not only economic but also the most reliable option available since excessive use of chemical-based strategy has negative impact on agro-ecosystems. Chemicals also contribute to global pollution, climate change, and plant pathogens evolving to compete with them for developing resistance are debatable issues for the continuation of utilization for agri-sustainability. The collection of concerning disadvantages offered by other conventional physical and chemical approaches has necessitated the development of novel eco-friendly, durable, and cost-effective strategies that aid crop performance and productivity, as well as control loss caused by plant pathogens. Exploring microbial services in dry and arid terrains may provide us with rightful directions for agriculture sustainability.

Exploring microbial communities in natural ecosystems is difficult task indeed, and vast diversity of microbes is critical and challenging factor in their characterization (Torsvik et al. 1998). Traditional culture-dependent methods are easy and inexpensive but only provide information for minor fraction of microbes than of total microbes present in environment. Similarly, the biochemical and chemotaxonomic methods are fast and sensitive but again applicable on restricted fraction of communities. Recent advantages in molecular approaches have provided us with novel culture-independent tools which are based on nucleic acid analysis, including gene coding, fingerprinting, probing, and sequencing (Kirk et al. 2004; Fakruddin and Mannan 2013). Molecular genetic tool provides information about community structure, diversity, and phylogeny and is applicable for vast range of communities without restrictions. Technical demands, error-prone approaches, misleading interpretations, and high cost are disadvantages associated with new molecular strategies for microbial characterizations and still have space for regular improvisation. Combining different complementary molecular strategies is adventitious in monitoring microbial communities in natural ecosystems than individual approaches (Kirk et al. 2004; Fakruddin and Mannan 2013). More recent advancement has expanded our abilities to characterize globe-scale microbiomes with next-generation sequencing technologies and motivated initiatives like Earth Microbiome Project (Thompson et al. 2017). Several individual maneuvers solicit to describe and compare soil microbial communities in arid environment (McHugh et al. 2017; Mandakovic et al. 2018). A variety of data have been piled up but systematic collective records targeting arid zones microbial communities have not been accomplished yet and regarding their services aiding agriculture sustainability is recent emerging subject under research concerns. Environmental microbiologist exploring metagenomes will be a ‘collective nucleic acids from natural sites including of nonviable communities’ have privileged ongoing research to explore microbes with benefits in different ecosystems. Microbial symbionts are getting appreciations for their critical roles in health of plant hosts, and studies targeting their interactions and coevolution have encapsulated specific terms like “holobiont” and “hologenome” (Moran and Sloan

2015). Host plant with all its associated microbial communities is referred as holobiont (Rohwer et al. 2002), and genetic composition of a holobiont, i.e., collectively of host and its microbial residents, is termed as hologenome (Bordenstein and Theis 2015). A variety of metagenome studies in arid soils have been conducted with conclusion that desert soil encompasses lower functional diversity of microbes than nondesert soil. Further metagenomic studies revealed that the harshness imposed by environment is in linear relation with adaptability in communities; i.e., greater the cruelty, better the adaptive weapons (Fierer et al. 2012).

2 Adaptive Strategies of Dryland Flora

Lives in desert have different weapons to fight battle against atrocities of environment. With great history of evolution of plant, animals and microbes of desert lands have advanced their adaptive mechanisms and established uncountable lineages even in the extreme of desert edges. Still the harshness limits the diversity of communities and vegetation to mostly shrubs, grasses, or trees with moisture retention capabilities or short life cycles (Monson 2014). Wide range of morphological, physiological, and genetic adaptations have been seen and studied in desert flora. To cope with high radiation, temperature, and water scarcity, popular adaptations among desert plants are reduced leaf or plant size, vertical leaf orientation, leaf reflectance (Gibson 1996), thick wax layer (Holmes and Keiller 2002), accumulation and production of phenolics as UV-absorbing sunscreens and solutes to maintain tissue turgor (Caldwell et al. 1998; Julkunen-Tiitto et al. 2015), high transpiration rate and tissue elasticity (Smith et al. 1997), photorespiration, Crassulacean acid metabolism (Batanouny 2001; Ludwig 2012; Greenville 2018), high levels of heat shock proteins (Al-Whaibi and Mohamed 2011; Zhu et al. 2018), antioxidative enzymes like superoxide dismutase, catalase, and ascorbate peroxidase to scavenge reactive oxygen species, plant growth and stress hormones including auxin, cytokinin, abscisic acid, jasmonic acid, salicylic acid, and strigolactones (Munns and Tester 2008; Deinlein et al. 2014; Evelin et al. 2019), low xylem hydraulic conductance, extended seed viability, seed dormancy (Smith et al. 1997; Norton et al. 2016), long profuse, and deep fibrous roots (Smith et al. 1997).

In addition to these, plant–microbe interactions as adaptation to dry stresses are common among desert flora and have been studied in detail to understand mechanisms of such interactions. Plants interact with microbial communities colonizing and inhabiting in surrounding soil by forming plant rhizosheaths, i.e., soil aggregates firmly attached to root surface (Brown et al. 2017; Pang et al. 2017). Formation of rhizosheath has been correlated with increase number and length of root hair and thus provides drought tolerance and with enhanced nutrient uptake (Delhaize et al. 2012; James et al. 2016; Pang et al. 2017 Khan et al. 2020; Najafi et al. 2021; Kour and Sayyed 2019). Plant rhizosheaths are ideal niche for several nitrogen-fixing and plant growth-promoting bacteria (Othman et al. 2004; Tahir et al. 2015). Besides superficial interactions on root surface, i.e., in rhizoplane and in the zones around the roots (rhizosphere and rhizosheath), plants internally accommodate microbial communities in phyllosphere, i.e., aerial parts of plant and endosphere, i.e., inside of plant. Different factors involved in recruitment, selection, enrichment, and dynamic interactions between plant and associated microbes are location and climatic factors; host plant-dependent factors that include host genotype, selection of communities based on host immunity and defense abilities and diversity of compounds secreted by host to attract microbial communities and finally soil properties, i.e., its nature, composition, conductivity, pH, and moisture (Saad et al. 2020). Microbial communities inhabiting in rich niche provided by desert plants as rhizosphere, rhizosheath, endosphere, and phyllosphere are unexploited reservoir for biofertilizers and biocontrol agents that enhance plant health, increase plant tolerance to variety of biotic and abiotic stresses, and enhance crop productivity in eco-friendly way (Alsharif et al. 2020). Groups of beneficial soil microbes are being called as plant growth-promoting microorganisms (PGPM) that are capable of alleviating plant immunity and growth through indirect means via inducing plant defense against phytopathogens or directly promote growth by nutrient solubilization, by assimilation, by modulating phytohormones, and by secreting specific solutes and enzymes (Ma et al. 2016). Some common PGPM and their specific mechanism through which they promote plant health are listed in Table 1.1.

2.1 Structure of Desert Microcommunities

2.1.1 Bacterial Communities

Desert biomes have been inspected by researchers to understand diversity, distribution, composition, and functions of soil microbial communities. Frequently reported bacterial phyla in desert soil across the globe include Proteobacteria, Actinobacteria, and Bacteroidetes (Chanal et al. 2006; Connon et al. 2007; Lester et al. 2007; Fierer et al. 2009). An effort with bacterial communities in rhizosphere of widely distributed perennial shrub Caragana in arid and semiarid regions of north China revealed dominance of bacterial phyla including Proteobacteria, Gemmatimonadetes, Firmicutes, Actinobacteria, Bacteroidetes, Acidobacteria, and Cyanobacteria, where on genus-level abundance of *Pseudomonas, Acinetobacter, Bacillus, Stenotrophomonas, Burkholderia, Paenibacillus, Sphingobacterium*, *Chitinophaga, Arthrobacter,* and *Chryseobacterium* reported (Na et al. 2018).

Proteobacteria prosper well in nutrient-deficient arid soil by performing bacteriochlorophyll-dependent photosynthesis and are most prominent in desert soil. Data retrieved through 16S rRNA gene amplicon pyrosequencing have suggested almost twice abundance of Proteobacteria in desert soil than that of in agriculture soil type, with richness of genus *Ochrobactrum*, a kind of Alphaproteobacteria (Köberl et al. 2011). A Proteobacteria isolated from Gobi Desert reported to horizontally transfer their photosynthetic ability to other phyla

Table 1.1 Plant growth-promoting microorganisms and their mechanism of action

Plant growth-promoting microorganism (PGPM)	Growth promotion mechanism	References
Nutrient assimilation		
Azospirillum, Azotobacter, Achromobacter, Bradyrhizobium, Beijerinckia, Rhizobium, Clostridium, Klebsiella, Anabaena, Nostoc, Frankia	*Nitrogen fixation*: through reduction of nitrogen gas (N_2) to ammonia (NH_3)	Souza et al. (2015), Bhat et al. (2019)
Bacillus, Pseudomonas, Rhizobium, Achromobacter, Burkholderia, Micrococcus, Agrobacterium, Erwinia sp., Penicillium sp., and *Aspergillus sp.*	*Phosphate solubilization*: transformation and solubilization of inorganic phosphorus into forms capable of being absorbed by plants, such as monobasic (H2PO − 4H2PO4-) or dibasic phosphate ($HPO4^{-2}$)	Martínez-Viveros et al. (2010)
Burkholderia, Enterobacter, Grimontella, and *Pseudomonas*	*Siderophore production*: improves plant nutrition and inhibits phytopathogens through iron sequestration from the environment.	Souza et al. (2015), Varma et al. (2019)
Bacillus and *Aspergillus*	*Potassium solubilization*: produces organic and inorganic acids, acidolysis, chelation, and exchange reactions which are capable of solubilizing potassium	Varma et al. (2019)
Rhizophagus irregularis and Funneliformis mosseae	*Phytoextraction and stabilization*: fungi that extract Cd and enhanced phytostabilization of Cd and Zn, respectively.	Hassan et al. (2013)
Phytohormone production		
Pseudomonas sp. and *Bacillus*	*Auxin secretion*: promote plant growth by increasing auxin and ACC (amino-cyclopropane carboxylate) deaminase	Samaddar et al. (2019), Danish et al. (2020), Khoshru et al. (2020)
Sphingomonas SaMR12, *Phyllobacterium myrsinacearum* RC6b	*IAA:* indole acetic acid production and root promotion	Chen et al. (2014), Ma et al. (2013)
Exopolysaccharide secretion		
Bacillus spp.	*Exopolysaccharides*: forms a protective biofilm on root surface	Hashem et al. (2019)
Proteus penneri, *P. aeruginosa*, and *Alcaligenes faecalis*	*Exopolysaccharides*: Alleviate water stress and improve plant biomass under drought stress	Naseem and Bano (2014)
Osmoregulants		
Burkholderia sp.	*Metabolism*: Increases plant tolerance against low temperature by modifying carbohydrate metabolism	Fernandez et al. (2012)

(continued)

Table 1.1 (continued)

Plant growth-promoting microorganism (PGPM)	Growth promotion mechanism	References
Pseudomonas fluorescens	*Osmoprotectants solutes and enzymes*: promote plant tolerance by increasing the activity of catalase and peroxidase and the accumulation of proline	Saravanakumar et al. (2011)

like Gemmatimonadetes. Gemmatimonadetes are among other most common desert bacterial phyla including Firmicutes and Cyanobacteria (Makhalanyane et al. 2015). Abundance of Gemmatimonadetes in desert soil has been found interlinked with low moisture content of arid soil, i.e., around Pearson coefficient (r) of 0.409. Not much regarding their physiology and ecology is known, and only six isolates of arid soil Gemmatimonadetes are known till date. Firmicutes are among most frequently isolated microbes from arid soil with extraordinary adaptive mechanisms such as rapid spore germination, nonfastidious growth patterns, and rapid doubling frequencies other than these Firmicutes spp. including *Bacillus, Paenibacillus,* and others which are known to form endospores to cope with dryness of desert environment. A 16 S rRNA gene pyrosequencing data reported more than 30% members of Firmicutes, majorly of class Clostridia dominating among Antarctic vascular plant's rhizospheric bacterial communities suggesting their significance in arid zones (Teixeira et al. 2010).

Members of Actinobacteria are common in desert soil and withstand extremities of desert habitats and mainly attribute to their capacity of sporulation, greater degradative tendency, wider metabolic range, and other competitive advantages including synthesis of secondary metabolites and error resisting or repairing mechanisms against effect of UV radiations (Ensign 1978; McCarthy and Williams 1992; Chater and Chandra 2006; Gao and Garcia-Pichel 2011). Wide spectrum of Actinobacteria has been recovered from extreme ecosystems and such includes acid-tolerant, alkaliphilic, psychrotolerant, thermotolerant, halotolerant, alkalitolerant, halo-alkalitolerant, and xerophilous Actinobacteria (Lubsanova et al. 2014). A report from Atacama desert suggested 72–88% dominance of members of Actinobacteria in desert soil, while in other arid regions they are among three most abundant arid bacterial phyla besides Firmicutes and Proteobacteria (Crits-Christoph et al. 2013; Mohammadipanah and Wink 2016). Members from phylum Bacteroidetes were unexpectedly common in desert soil for their known copiotrophic members, but then obviously not all members of phylum can only belong to same ecological category (Fierer et al. 2007). Desert soil from the Taklamakan Desert (China) found rich with *Pontibacter* spp. of family Cytophagaceae which is first of kind form this genus to have nitrogen fixation capability mediated through nifH gene (Xu et al. 2014). Various isolates from this phylum have shown their optimum growth at high pH supporting their habitation in alkaline character of desert soil (Lauber et al. 2009). Acidobacteria are underrepresented soil microbes distributed in almost all ecosystems and contribute dynamically in vital ecological processes including regulation of biogeochemical cycles, decomposition of biopolymers, and as plant growth promoters (Kalam et al. 2020). A deep diversity analysis of bacterial communities in unvegetated arid soils of the Atacama Desert reported presence of Acidobacteria along with Proteobacteria and Actinobacteria (Neilson et al. 2012). Cyanobacteria are well-known photosynthetic taxa with exceptional adaptations to desert desiccations, salt stresses, and high radiations and are functional participants in desert biogeochemical cycling processes (Chan et al. 2013). They contribute to soil nutrient profile by enhancing soil fertility through nitrogen fixation and stabilize soil by retaining moisture (Belnap and Gardner 1993). Accumulations of osmoprotectants like trehalose, sucrose, and glucosylglycerol; synthesis of UV screening lower reactive oxygen species; efficient repair mechanisms and moisture-induced chemotactic ability to migrate for survival of cynobacteria against desert stresses (Garcia-Pichel and Pringault 2001; Singh et al. 2002; Sorrels et al. 2009).

2.1.2 Fungal Communities

Arid zones have been found populated with greater diversity of fungi emphasizing their versatility as one of the most stress-tolerant life form on earth (Waller et al. 2005; Sterflinger et al. 2012). Fungi are economically versatile microbes of desert ecosystems and are crucial deciding factor for plant-associated soil microbial communities (Oren and Steinberger 2008). Evidently, it has been reported that without specific physiological adaptations fungi survive the extreme environment through spore-forming abilities and are belonging to heterogeneous group of saprophytes, parasites, pathogen, and symbionts or endophytes (Gadd 2007; Sterflinger et al. 2012). Various fungal groups including yeast, filamentous, terricolous, microcolonial, and mycorrhizal have been reported from dry soils (Sterflinger et al. 2012).

Soil studies from Negev and Sonoran deserts reported high taxonomic diversity of both Basidiomycota and Ascomycota (Ranzoni 1968; Taylor-George et al. 1983). A study conducted to collect information on biodiversity of fungi in hot and dry regions through culture-independent next-generation sequencing of 18S rRNA genes along with traditional culture-dependent methods reported fungal occurrence range from 3.5% to 82.7% in different soil sample from Saudi Arabia and Jordan deserts. Similar to former report, this also suggested greater abundance of Ascomycota and Basidiomycota phyla in deserts and major fungal classes were Dothideomycetes, Pezizomycetes, and Sordariomycetes (Murgia et al. 2019).

Fungal groups like mutualistic arbuscular mycorrhiza (AM) are significant plant root symbionts in desert ecosystems and known to provide resistance toward drought stresses through penetrating deep soil pores for water accessibility. A molecular assessment of AM fungi from six different desert areas, viz. northwestern Argentina, central Australia, southern Israel, southeastern Kazakhstan, central Saudi Arabia, and the southwestern USA, reported most common AM family Glomeraceae from different desert soils and other less frequently found families, Claroideoglomeraceae, Diversisporaceae, and Acaulosporaceae (Vasar et al. 2021). The report further emphasized on potentials of AM fungi in ecosystem restoration.

2.1.3 Archaeal Communities

Archaeal members are known for their resilience toward environmental stresses and extreme conditions of energy starvations (Maupin-Furlow et al. 2012). The communities are rare in usual biomes but extremes, including arid provinces. Principal desert archaeal phylotypes are chemolithoautotrophs and play significant roles in biogeochemical cycling processes. A common representative of dessert archaeal communities was found Thaumarchaeota (Brochier-Armanet et al. 2008). Arid microbial studies have revealed dominance of euryarchaeal Halobacteria from the orders Halobacteriales, Haloferacales, and Natrialbales and about 40% yet uncharacterized and unclassified members of community. Further potentially novel genera *Halorubrum* and *Haloparvum* were isolated (Bachran et al. 2019). Principal archaeal representative isolated from Tataouine Desert was Crenarchaeota (Chanal et al. 2006). Available data on arid archaeal dwellers are limited and advocate the need of explorations and evaluations.

2.1.4 Viral Communities

Desert ecosystems are known to driven by microbial communities and viruses are among most prevalent entities of such microbially driven systems with significant ecological roles; however been rarely evaluated. Pioneer studies on viruses in such ecosystems reveal higher diversity than expected and found high number of phage-like morphotypes that include Myoviridae, Siphoviridae, and Podoviridae, three major families of tailed phages. Namib Desert hypolith phylotypic survey reported most prevalent bacteriophages belonging to the order Caudovirales, in particular the family Siphoviridae (Adriaenssens et al. 2015). Exploration of cold Antarctic soil revealed combinatorial driving factors, such as soil factors, pH, calcium content, and site altitude. Besides they claim abundance of viral families including Myoviridae and Siphoviridae and high diversity families like *Phycodnaviridae* and *Mimiviridae* (Adriaenssens et al. 2017). Comparative studies disclosed low extracellular virus counts in hyperarid desert soils contrasting higher extracellular virus titers in colds deserts. These studies encounter fewer identity values to virus genomes of concern in public databases evince occurrence of widely distinct or not so yet characterized phylotypes in hyperarid deserts and advocate for frequent metavirome analysis to populate available sequence databases (Zablocki et al. 2015).

Limited or almost negligible information is available on plant–virus associations in arid ecosystems. Studies have yet only explored diversity, driving factor, and some of phylogenic data on viral communities of extreme ecosystems and their virulence being the major concerns. Plant–viral associations are still untouched subject and majorly due to their relative lower occurrence than other microbial communities and because of greater encounters with phage-like morphotypes than other types. Recent epidemiological research has identified several pathogenic plant infecting viral strains from some of common desert plants that include wilt and mosaic viruses affecting tomato, cucurbits, watermelons, and cultivation of significant crops (Brown et al. 2007; Adkins and Baker 2005).

3 Microbial Communities in Deserts Across the Globe

So far, we have learned of desert biology with specific focus on microbial communities and plant microbial associations in general, and we know desert systems are microbially driven one for they cooperate with limited number of higher life forms. Further sections more specifically describe some major deserts across the globe and their microbial communities.

3.1 Deserts of South and North America

Deserts of North America are climatically divided into two groups as cold and warm deserts and spread over 1,277,000 square kilometers in USA and Mexico (MacMahon 1988). Chihuahuan Desert is largest hot desert of North America which occupies nearly 35,000 square kilometers and considered one among the most biologically diverse arid desert of the world (Schmidt Jr 1979; Hoyt 2002). A Mars analogue gypsum desert soils of the Cuatro Cie'negas Basin (CCB) from Chihuahuan Desert, Mexico was explored for bacterial communities and have reported phyla including – Actinobacteria, Acidobacteria, Bacteroidetes, Firmicutes, Gemmatimonadetes, Chloroflexi, Cyanobacteria, Alpha/Gammaproteobacteria and other nitrogen fixing communities (López-Lozano et al. 2012). Several entomopathogens isolated from Chihuahuan Desert include fungi, nematodes, rickettsia, and viruses—*Beauveria bassiana*, *Entomophaga calopteni*, *Entomophthora muscae*, *Entomophthora planchoniana*, *Furia vomitoriae*, *Nomuraea rileyi*, *Metarhizium anisopliae* var. *anisopliae*, *Zoophthora radicans*, *Paecilomyces fumosoroseus, Paecilomyces farinosus*, *Nosema weiseri*, *Rickettsiella popilliae,* and the nuclear polyhedrosis viruses (Sanchez-Peña 2000). Further, cactus-associated microbiome exploration reveals endo-/epi-seminal plant growth-promoting capabilities of bacterial groups such as *Kluyvera, Bacillus, Paenibacillus*, *Stenotrophomonas*, and fungal classes like *Tremellomycetes, Dothideomycetes, Eurotiomycetes, Leotiomycetes,* and *Sordariomycetes* colonizing four cactus species—*Echinocactus platyacanthus, Ferocactus latispinus, Ferocactus pilosus*, and *Stenocereus queretaroensis* (Mascot-Gómez et al. 2021). The second largest hot-arid desert of North America is the Sonoran Desert, which rambles over 320,000 square kilometers (Dimmitt et al. 2015). A study conducted to examine soil- and