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Plant Microbiomes for Sustainable Agriculture

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Foreword

The plant microbiomes play important role in plant growth, development, and soil health. The plants and rhizospheric soil are the hotspots harboring microbes playing critical roles in the maintenance of global nutrient balance and ecosystems. The diverse groups of microbes are the key components of soil–plant systems, where they are engaged in an intense network of rhizosphere/endophytic/phyllospheric interactions. The rhizospheric, endophytic, and epiphytic microbes with plant growth-promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. PGP microbes promote plant growth directly or indirectly, by releasing plant growth regulators; solubilization of phosphorus, potassium, and zinc; biological nitrogen fixation or by producing siderophores, ammonia, HCN, and other secondary metabolites which are antagonistic against pathogenic microbes. These PGP microbes could be used as biofertilizers/bioinoculants in place of chemical fertilizers for sustainable agriculture. The aim of the present book is to collect and compile the current developments in the understanding of the rhizospheric, endophytic, and epiphytic microbial diversity associated with plants. The book encompasses current knowledge of plant microbiomes and their potential biotechnological applications for plant growth, crop yield, and soil health for sustainable agriculture. The book will be highly useful to the faculty, researchers, and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects.

The present book entitled *Plant Microbiomes for Sustainable Agriculture* is a very timely publication providing state-of-the-art information in the area of microbial biotechnology focusing on microbial biodiversity, plant–microbe interaction, and their biotechnological application in plant growth and soil fertility for sustainable agriculture. The book volume comprises sixteen chapters. Chapter 1 by Subrahmanyam as the lead author describes the biodiversity of rhizospheric microbiomes and their biotechnological applications for plant growth promotion and soil health for sustainable agriculture. Chapter 2 presented by Saleem et al. highlights the culturable endophytic fungal communities associated with cereal crops and their role in plant growth promotion. Chapter 3 by Sujatha et al. describes the genetic diversity of endophytic fungi having phosphate-solubilizing attributes and their ecological significances. Chapter 4 by Berde et al. highlights the opportunities and challenges of endophytic fungi from medicinal plants and their secondary metabolites for diverse applications. Sivakumar et al. describe the biodiversity of epiphytic microbiomes and their ecological significance and biotechnological applications in agriculture and environments in Chap. 5. Chapter 6 by Kumar and Singh deals with the functional attributes of biofilms forming microbial communities, mechanisms of biofilms formation, and role in agriculture. Nalini and Prakash highlight the recent advancements in taxonomical progress in phylum Actinobacteria and biotechnological applications of actinobacterial genera in agriculture in Chap. 7. In Chap. 8, Ashok and his colleagues describe in detail the alleviation of abiotic stresses in plants by epiphytic pink-pigmented methylotrophic bacteria. Pandey et al. highlight the diversity, ecological significance, and biotechnological applications in agriculture of the potassium-solubilizing microbe in Chap. 9. Etesami et al. explain the mitigation of different abiotic stresses in plant by the use of ACC deaminase-producing microbes in Chap. 10. The roles of halophilic microbes for plant growth promotion and alleviation of saline stress in plants have been described by Enespa et al. in Chap. 11. Chapter 12 by Gontia-Mishra deals with the microbial-mediated drought tolerance in plants. Odoh et al. highlight the microbial consortium formulation for use as biofertilizers and their applications under the natural as well as abiotic stress condition in Chap. 13. Singh et al. discuss the current advancements and future challenges in plant microbiome research in Chap. 14. The biotechnological applications of microbes as bioinoculants and biopesticides have been discussed in Chap. 15 by Misra et al. Finally, the conclusion and future visions on plant microbiomes have been given by Ajar Nath Yadav in Chap. 16.

Overall, great efforts have been carried out by Dr. Ajar Nath Yadav, his editorial team, and scientists from different countries to compile this book as a unique and up-to-date source on plant microbiomes for the students, researchers, teachers, and academician. I am sure the readers will find this book highly useful and interesting during their pursuit on plant microbiomes.

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Dr. H. S. Dhaliwal is presently the Vice Chancellor of Eternal University, Baru Sahib, Himachal Pradesh, India. He holds Ph.D. in Genetics from the University of California, Riverside, USA (1975). He has 50 years of research, teaching, and administrative experience in various capacities. He is also a Professor of Biotechnology at the Eternal University, Baru Sahib from 2011 to date. He had worked as Professor of Biotechnology at IIT, Roorkee (2003–2011); Founder Director of Biotechnology Centre, Punjab Agricultural University, Ludhiana (1992–2003); Senior Scientist and wheat Breeder-cum-Director at PAU Regional Research Station, Gurdaspur (1979–1990); Research Fellow FMI, Basel, Switzerland (1976–1979); D.F. Jones Postdoctoral fellow, University of California, Riverside, USA (1975–1976). He was elected as Fellow, National Academy of Agricultural Sciences, India, (1992); worked as Visiting Professor, Department of Plant Pathology, Kansas State University, Kansas, USA, (1989) and Senior Research Fellow, CIMMYT, Mexico, (1987). He has many national and international awards such as Cash award from the Federation of Indian Chambers of Commerce and Industry (FICCI) in 1985 and Pesticide India Award from Mycology and Plant Pathology Society of India (1988). He has to his credit more than 300 publications including research papers: 250; reviews: 12; chapters contributed to books: 15; papers presented in meetings, conferences, and abstracted: 105; popular articles: 18; project report/books/bulletins/manuals. His important research contributions are: Identification of a new species of wild diploid wheat *Triticum urartu* and gathered evidences to implicate *it* as one of the parents of polyploid wheat; Team leader in the development of seven wheat varieties, *viz.*, PBW 54, PBW 120, PBW 138, PBW 175, PBW 222, PBW 226, and PBW 299 approved for cultivation in Punjab and North Western Plain Zone of India; molecular marker-assisted pyramiding of bacterial blight resistance genes *Xa5, Xa21*, and xa13 and the green revolution semi-dwarfing gene *sd*1 in Dehraduni basmati and development of elite wheat lines biofortified for grain iron and zinc through wide hybridization with related non-progenitor wild *Aegilops* species and molecular breeding. He made a significant contribution to the development of life and epidemiology cycle of *Tilletia indica* fungus, the causal organism of Karnal bunt disease of wheat and development of Karnal bunt-tolerant wheat cultivars. He has been the member/chairperson of several task forces and committees of Department of Biotechnology, Ministry of Science and Technology, Government of India, New Delhi and ICAR, New Delhi. Presently, he is a Member of an Expert Committee of DBT for DBT-UDSC Partnership Centre on Genetic Manipulation of Crop Plants at UDSC, New Delhi (2016 onwards), SAC of NABI of DBT and RAC of IIAB, Ranchi of ICAR.

Preface

The plant microbiomes (rhizospheric endophytic and epiphytic) play important role in plant growth promotion and nutrient recycling. The microbes associated with plant growth-promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. PGP microbes promote plant growth directly or indirectly, either by releasing plant growth regulators; solubilization of phosphorus, potassium, and zinc; biological nitrogen fixation or by producing siderophore, ammonia, HCN, and other secondary metabolites which are antagonistic against pathogenic microbes. The PGP microbes belonged to different phylum of archaea (Euryarchaeota); bacteria (Acidobacteria, Actinobacteria, Bacteroidetes, Deinococcus-Thermus, Firmicutes, and Proteobacteria); and fungi (Ascomycota and Basidiomycota), which include different genera, namely, *Achromobacter, Arthrobacter, Aspergillus, Azospirillum, Azotobacter, Bacillus, Erwinia, Gluconoacetobacter, Methylobacterium, Paenibacillus, Pantoea, Penicillium, Piriformospora, Planomonospora, Pseudomonas, Rhizobium, Serratia,* and *Streptomyces*. These PGP microbes could be used as biofertilizers/bioinoculants at place of chemical fertilizers for sustainable agriculture. The present book on *Plant Microbiomes for Sustainable Agriculture* covers biodiversity of plant-associated microbes and their role in plant growth promotion, mitigation of abiotic stress and soil fertility for sustainable agriculture. This book will be immensely useful to biological sciences, especially to microbiologists, microbial biotechnologists, biochemists, researchers, and scientists of microbial and plant biotechnology. We are thankful to the leading scientists who have extensive, in-depth experience and expertise in plant–microbes interaction and microbial biotechnology took the time and effort to develop these outstanding chapters. Each chapter is written by internationally recognized researchers/scientists so the reader is given an up-to-date and detailed account of our knowledge of the microbial biotechnology and innumerable agricultural applications of plant microbiomes.

We are grateful to the many people who helped to bring this book to light. Dr. Ajar Nath Yadav gives special thanks to his exquisite wife for her constant support and motivation in putting everything together. Dr. Yadav also gives special thanks to his esteemed friends, well-wishers, colleagues, and senior faculty members of Eternal University, Baru Sahib, India.

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All authors are sincerely acknowledged for contributing up-to-date information on the plant microbiomes (epiphytic, endophytic, and rhizospheric microbes), their biodiversity, and application as biofertilizers, biopesticides, and biotechnological implication for mitigation of abiotic stress in plants. The editors are thankful to all authors for their valuable contributions.

The editor, Dr. Ajar Nath Yadav is thankful to his Ph.D. research scholars Ms. Divjot Kour, Ms. Tanvir Kaur, Ms. Rubee Devi, Mrs. Kusam Lata Rana and colleagues for their support and motivation in all my efforts during this project.

All editors would like to thank their families who were very patient and supportive during this journey. Our sincere thanks to the whole Springer team who was directly or indirectly involved in the production of the book. Our special thanks to Dr. Kishan Gopal Ramawat, Dr. Valeria, and Dr. Ineke Ravesloot for the assistance and support.

We are very sure that this book will interest scientists, graduates, undergraduates, and postdocs who are investigating "plant microbiomes" microbial and plant biotechnology.

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About the Editors

Ajar Nath Yadav is an Assistant Professor (Sr. Sacle) in Department of Biotechnology, Dr. Khem Singh Gill Akal College of Agriculture, Eternal University, Baru Sahib, Himachal Pradesh, India. He has 4.5 years of teaching and 10.5 years of research experience in the field of Microbial Biotechnology, Microbial Diversity, and Plant–Microbe Interactions. He obtained doctorate degree in Microbial Biotechnology, jointly from Indian Agricultural Research Institute, New Delhi and Birla Institute of Technology, Mesra, Ranchi, India; M.Sc. (Biotechnology) from Bundelkhand University and B.Sc. (CBZ) from University of Allahabad, India. He has 150 publications, which include 75 research/review papers, 15 books, 58 book chapters, and 02 patents with h-index of 28, i10-index of 64, and 2356 citations (Google Scholar). He has published 111 research communications in different international and national conferences. He has got twelve Best Paper Presentation Awards, one Young Scientist Award (NASI-Swarna Jyanti Purskar), and three certificate of excellence in reviewing awards. He received "Outstanding Teacher Award" in 6th Annual Convocation 2018 by Eternal University, Baru Sahib, Himachal Pradesh. He has a long-standing interest in teaching at the UG, PG, and Ph.D. level and is involved in taking courses in agriculture microbiology, bacteriology, bioprocess engineering and technology, environmental microbiology, industrial microbiology, and microbial biotechnology. He is currently handling two projects, one funded by Department of Environments, Science & Technology (DEST), Shimla entitled “Development of Microbial Consortium as Bio-inoculants for Drought and Low Temperature Growing Crops for Organic Farming in Himachal Pradesh” as Principal Investigator and another funded by HP Council for Science, Technology & Environment (HIMCOSTE) on “Value-added products” as Co-PI. He also worked as an organizing committee member for 7 international conferences/symposia in the related field. Presently, he is guiding 05 scholars for Ph.D. degree and 01 for M.Sc. dissertations. In his credit, ~6700 microbes (archaea, bacteria, and fungi) isolated from diverse sources and ~550 potential and efficient microbes deposited at culture collection National Bureau of Agriculturally Important Microorganisms (NBAIM), Mau, India. He has deposited **2423** nucleotide sequences, **03** whole genome sequences (*Bacillus thuringiensis* AKS47, *Arthrobacter agilis* L77, and *Halolamina pelagica* CDK2), and **02** transcriptome to NCBI GenBank databases: in public domain. He and his group have developed method for screening of archaea for phosphorus solubilization for the first time. He has been serving as an editor/editorial board member and reviewer for more than 35 national and international peer-reviewed journals. He has lifetime membership of Association of Microbiologist in India, Indian Science Congress Council, India and National Academy of Sciences, India. Please visit https://sites.google.com/site/ajarbiotech/ for more details.

Joginder Singh is presently working as Professor at the Department of Microbiology, Lovely Professional University, Punjab, India. Previously, he has worked as Young Scientist at Microbial Biotechnology and Biofertilizer Laboratory, Department of Botany, Jai Narain Vyas University in Department of Science and Technology, Government of India. He is an active member of various scientific societies and organizations including Association of Microbiologists of India, Indian Society of Salinity Research Scientists, Indian Society for Radiation Biology, and European Federation of Biotechnology. He has more than 60 research and review articles in the peer-reviewed journals, edited four book entitled “Arbuscular Mycorrhizal Fungi” and “Microbes: In Action” published by AgroBios, India and "Microbial Bioprospecting for Sustainable Development" and "Fungi and their Role in Sustainable Development: Current Perspectives" published by Springer International Publishing, and authored/co-authored 26 chapters in edited books. He serves as reviewer for many prestigious journals, including Current Research in Engineering, Science and Technology, Science of the Total Environment, Environmental Monitoring and Assessment, Pedosphere, Soil and Sediment Contamination, Symbiosis, International Journal of Phytoremediation, Ecotoxicology and Environmental Safety, Annals of Agricultural Sciences, Annals of the Brazilian Academy of Sciences, and many more. He attended several international and national seminars, symposia, conferences, and chaired technical sessions and presented papers in them.

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Neelam Yadav is currently working on microbial diversity from diverse sources and their biotechnological applications in agriculture. She obtained her postgraduation degree from Veer Bahadur Singh Purvanchal University, Uttar Pradesh, India. She has research interest in the area of plant–microbes interaction, and beneficial soil microbiomes from diverse sources. In her credit 35 publications in different reputed international and national journals and publishers. She is editor of 14 books, 02 in Elsevier, 03 in CRC press, and 09 in Springer under the process of publication. She has published 19 research communications in different conferences/symposiums/workshops. She got 02 best paper presentations award and 02 certificates of excellence in reviewing Award. In her credit >1700 microbes (archaea, bacteria, and fungi) isolated from diverse sources and >115 potential and efficient microbes deposited at culture collection. She has deposited 295 nucleotide sequences to NCBI GenBank databases: in public domain. She is Editor/Associate Editor/Reviewer of different international and national journals. She has the lifetime membership of Association of Microbiologists in India, Indian Science Congress Council, India and National Academy of Sciences, India.

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Chapter 1
Diversity, Plant Growth Promoting Attributes, and Agricultural Applications of Rhizospheric Microbes

Gangavarapu Subrahmanyam, Amit Kumar, Sosanka Protim Sandilya, Mahananda Chutia and Ajar Nath Yadav

Abstract Rhizosphere harbors potential microbiomes which play a pivotal role in nutrient cycling, enhancing soil fertility, maintaining plant health and productivity. Specific microbiomes that are assembled near roots are considered to be some of the most complex ecosystems on the Earth. Heterogeneous microbial communities of rhizospheric microbiomes considerably vary by soil type, land use pattern, plant species, and host genotype. It is demonstrated that root exudates act as substrates and signaling molecules which are required for establishing plant–rhizobacterial interactions. The present chapter focused on the rhizosphere microbiomes of different agricultural crops, their functions, and possible biotechnological applications for increasing crop production in a sustainable manner. Further, the plant growth-promoting mechanisms of rhizobacteria were highlighted. Although much work has been done on the biocontrol characteristics of rhizospheric bacteria, it has to be considered that soil type, plant species, and the pathogen affect altogether influence the biocontrol efficiency of strain applied against a soil-borne pathogen.

Keywords Bacterial community · Biotechnological application · Microbiome · Plant growth promotion · Rhizosphere

1.1 Introduction

Soil microorganisms play a pivotal role in nutrient cycling, regulating soil fertility, maintaining plant health, and productivity (Wagg et al. 2014). Soil microbial communities are exceedingly complex and consist of various organisms such as bacteria, archaea, fungi, algae, and viruses. Most of these microorganisms largely utilize plant root-derived nutrients such as root exudates and secondary metabolites (Huang et al.

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A. N. Yadav et al. (eds.), *Plant Microbiomes for Sustainable Agriculture*, Sustainable Development and Biodiversity 25, https://doi.org/10.1007/978-3-030-38453-1_1

2014). Rhizosphere microorganisms are component of microbiomes that assemble near plant roots. Rhizospheric microbiomes are considered to be some of the most complex ecosystems on Earth. It is estimated that one gram of soil contains more than 50,000 different microbial species, but majority of them are uncultivable in nature (Roesch et al. 2007a, b). Beneficial free-living rhizospheric bacteria are generally referred to as plant growth-promoting rhizobacteria—"PGPR". Conceptually, "PGPR" represents beneficial portion of rhizospheric microbiome and can have positive effect on both growth and development of plants by direct or indirect mechanisms.

Chemical compounds that are released by roots apparently modify physical and chemical characteristics of the soil (Mukherjee et al. 2018) and subsequently regulates the diversity and composition of soil microbial community in the rhizosphere (Huang et al. 2014). Moreover, plants may also influence composition of rhizosphere microbial communities by selectively stimulating microorganisms with beneficial traits that are needed for both plant growth and health (Chaparro et al. 2014). For example, *Acidobacteria, Proteobacteria (*mainly *Alpha, Beta,* and *Deltaproteobacteria* classes*), Chloroflexi*, and *Actinobacteria* are enriched in the rhizosphere of *Oryza sativa,* whereas soybean selected a specific microbial community consists of *Bacteroidetes, Acidobacteria, Proteobacteria*, and *Actinobacteria* (Lu et al. 2018; Ding et al. 2019; Yadav et al. 2016b). These microbial populations are found to colonize in the root rhizosphere because of their functional traits and also beneficial to plant nutrient absorption, growth, and disease suppression. In turn, the plant provides root exudates to the microbes which are used as substrates and signaling molecules (Mendes et al. 2013).

Studies revealed that root microbiomes considerably vary by soil type, habitat, land use pattern, plant species, and host genotype (Bouffaud et al. 2014; Fitzpatrick et al. 2018; Lu et al. 2018; Ding et al. 2019; Yadav et al. 2019f). In recent, the relationship between rhizosphere microbial communities and plant genotypes is well studied and the results may lead to increased plant productivity (Bouffaud et al. 2014; Bulgarelli et al. 2015; Pérez-Jaramillo et al. 2017; Leff et al. 2017; Ding et al. 2019). In this chapter, we summarize recent progress made in rhizosphere microbiomes of agriculture crops. We also discuss the importance of rhizosphere microbial communities particularly PGPR and their immense biotechnological values for sustainable production and productivity of agriculture crops.

1.2 Rhizosphere and Root Exudates

The narrow zone of soil surrounding the plant roots and influenced by roots, root hair, and plant-produced exudates is referred to as rhizosphere (Dessaux et al. 2009). There are three distinct interacting systems which are reported in the plant rhizosphere, *viz.*, rhizoplane, rhizosphere, and the root itself. Rhizoplane is defined as the root surface including the strongly adhering soil particles. Group of bacteria which are inhabitants of rhizosphere and able to compete in colonizing the root system is known as "rhizobacteria" while the total microbial component (prokaryotes, eukaryotes, and viruses) of rhizosphere is termed as rhizo-microbiome or rhizosphere microbiome. The "rhizobacteria" term was first time introduced by Kloepper and Schroth (1978) to refer the soil bacterial population that competitively colonize the roots and stimulate plant growth, thereby reducing the incidence of diseases in a sustainable manner.

Specific microbiomes that are assembled near roots are proposed to be some of the most complex ecosystems on the Earth (Raaijmakers et al. 2009). Most of these microorganisms utilize diverse array of compounds/nutrients which are derived from plant roots in the rhizosphere (Lu et al. 2018; Yadav et al. 2017b). The chemicals that are released by roots in the soil are known as "root exudates." It was suggested that chemicals secreted by plant roots act as signaling molecules and recruit wide variety of heterogeneous and metabolically active soil microbial populations (Ahemad and Kibert 2014) (Table 1.1).

Most importantly, the exudation of chemical compounds by roots apparently modifies the physical and chemical characteristics of the soil and subsequently regulates the structure and composition of rhizosphere microbial community (Doornbos et al. 2012). Impact of root exudates on bacterial communities in the rhizosphere was extensively reviewed by Doornbos et al. (2012). Further, it is estimated that around five to twenty-one percent of caron (photosynthetically fixed carbon) gets transported to the rhizosphere through the process of root exudation (Doornbos et al. 2012). Therefore, the rhizosphere is redefined by Dessaux et al. (2009) as "any volume of soil selectively influenced by plant roots, root hairs and plant-produced materials."

Table 1.1 Different kinds of compounds in root exudates of plants

Chemical nature	Compounds
Carbohydrates, amino acids, and derivatives	Chlorogenic acid, caffeic acid, cinnamic acid, canavanine, strigolactone 5-deoxystrigol, arabinogalactan proteins, arabinogalactan-like glycoprotein, glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, oligosaccharides, raffinose, maltose, α-Alanine, β-alanine, asparagines, aspartate, cysteine, cystine, glutamate, glycine, isoleucine, leucine, lysine, methionine, serine, threonine, proline, valine, tryptophan, ornithine, histidine, arginine, homoserine, phenylalanine, γ-Aminobutyric acid and α-Aminoadipic acid
Secondary metabolites and hormones	Benzoxazinoids, flavonoids, strigolactones, and related compounds that mimic quorum-sensing signals
Vitamins	Biotin, thiamine, pantothenate, riboflavin, and niacin
Enzymes	Protease, amylase, acid and alkaline-phosphatase and invertase
Organic acids	Malic acid, oxalic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, erythronic acid, piscidic acid, citric acid, formic acid, aconitic acid, lactic acid, pyruvic acid, glutaric acid, malonic acid, tetronic acid, and aldonic acid

Source Huang et al. (2014), Ahemad and Kibert (2014)

The quality and quantity of the root exudates rely on type of plant species and distinct developmental/physiological status of plants (Kang et al. 2010). Furthermore, root exudates significantly enhance the plant-beneficial microbial–symbiotic interactions in the rhizosphere. These interactions, in turn, affect the rooting patterns, supply of available nutrients, thereby modifying the quantity and/or quality of root exudates. Microbial colonization in/on root tissues is known as root colonization, similarly microbial colonization of the adjoining volume of soil under the influence of the plant root system is defined as "rhizosphere colonization" (Ahemad and Kibert 2014). Compared with the bulk soil, microbial activity and biomass are relatively enhanced in the rhizosphere as a result of root exudation (Ahemad and Kibert 2014; Huang et al. 2014).

1.3 Rhizosphere Microbiome and Its Diversity

Most of the soils contain exceedingly high microbial diversity including bacteria, fungi, algae, viruses, and protozoa. It was reported that one gram of soil contains approximately 9×10^7 bacteria, 2×10^5 fungi, 4×10^6 actinomycetes, 5×10^3 protozoa, and 3×10^4 algae. The rhizosphere which is under influence of root exudates can harbor up to 10^{-11} microbial cells and around 30,000 different prokaryotic species per gram of root (Egamberdieva et al. 2008). Metagenomic analysis of tomato rhizosphere revealed that approximately 3,050 different bacterial species (OTUs at 3% distance cutoff) were associated in the rhizosphere (Tian et al. 2015). The rhizosphere microbiomes are very diverse and can actively interact with plants and mediate distinct agro-ecological process. The rhizosphere microbiome is considerably important in bridging the plant microbiomes and bulk soil and facilitates plant growth promotion by providing nutrition (Pathak et al. 2016) . The rhizobacterial microbiota also improves host plant's health by protecting from phytopathogens and promotes plant growth and fitness in different physiochemical stresses by producing phytohormones (Fig. 1.1). It is imperative to elucidate the assembly, composition, and variation among the microbial communities present in the rhizosphere for understanding the diversity and metabolic functions of the rhizosphere microbiome. This information could be beneficial for sustainable management of plant health and the underlying mechanisms that drive microbiome assembly.

It has been revealed that the rhizosphere, rhizoplane (root surface), endosphere (root interior), and of host plants harbor a distinct microbiome (Edwards et al. 2015). Diversity, distribution, and the composition of the core rhizospheric microbiomes from several plant species such as *Arabidopsis* (Bulgarelli et al. 2012; Carvalhais et al. 2013; Chaparro et al. 2014), and economically important crops, *viz.,* maize (Bouffaud et al. 2014), rice (Edwards et al. 2015; Malyan et al. 2016a, b; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019), barley (Bulgarelli et al. 2015), citrus (Xu et al. 2018), sugar beet (Chapelle et al. 2016), sunflower (Leff et al. 2017), tomato (Tian et al. 2015), French bean (Pérez-Jaramillo et al. 2017), soybean (Mendes et al. 2011, 2014), wheat (Kour et al. 2019d; Verma et al. 2015a,

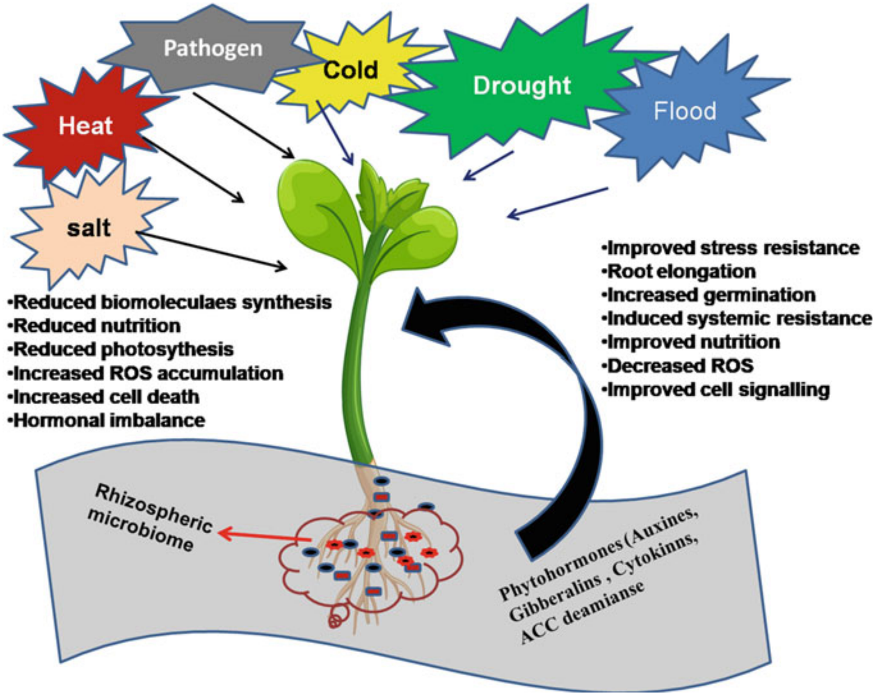

Fig. 1.1 Amelioration of abiotic and biotic stresses in plants by phytohormones produced by rhizospheric microbiome

b, 2016a, b; Yadav 2017a, 2019), and other tropical crop plants (Yadav 2017a, b; Yadav et al. 2019a; Yadav and Yadav 2018) have been established. All these studies have utilized 16S rRNA gene-based high-throughput sequencing analysis for understanding the microbial community dynamics. Although different methodologies have been suggested to explore soil microbial diversity and functions, culture-independent molecular methods are appropriate choice for deciphering diversity of microbiomes in high resolution (Fig. 1.2). Dominant microbial communities and their functions in core rhizospheric microbiomes of different agricultural crops have been extensively summarized in Table 1.2.

1.3.1 Diversity of Rhizospheric Microbiome in Wild Plants

Microorganisms represent the richest gamut of molecular and chemical diversity in nature, as they comprise the simplest yet dynamic forms of life (Yadav et al. 2015). Interest in the exploration of microbial diversity has been spurred by the fact that microbes are essential for life as they perform numerous functions integral to the

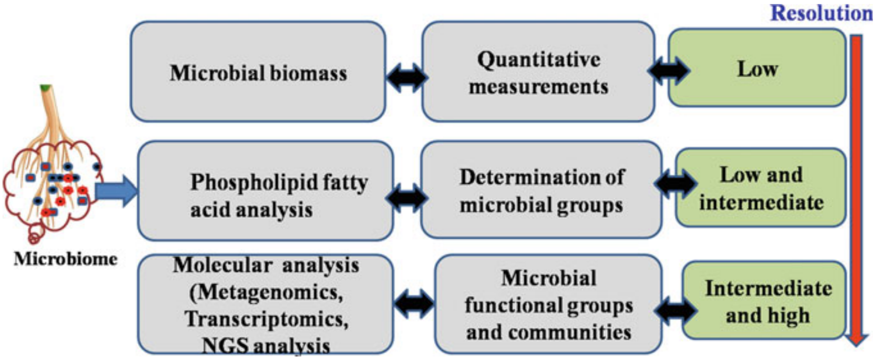

Fig. 1.2 Different methods for elucidation of rhizospheric microbiomes assembly and activity. Molecular methods are preferable choice to establish microbial communities with a higher resolution

sustenance of the biosphere, including nutrient cycling and environmental detoxification, which involve process such as augmentation, supplementation, and recycling of plant nutrients, so vital to sustainable agriculture (Kumar et al. 2019; Malyan et al. 2019; Rana et al. 2018; Yadav et al. 2017a, c, d). More recently, this largely unexplored reservoir of resources is the focus of investigations for innovative applications useful to mankind (Rastegari et al. 2019; Yadav et al. 2019c, d, e).

The distribution and diversity of bacterial community compositions in the rhizosphere microbiomes of six different wild plant species (*Bidens biternata* of the Asterales order, *Ageratum conyzoides*, *Artemisia argyi*, *Euphorbia hirta*, *Viola japonica* of the Malpighiales order, *and Erigeron annuus*) were evaluated by Lei et al. (2019). All the six different wild plant species were grown in the same experimental field. In this study, high-throughput sequencing of 16S rRNA gene targeting the hypervariable V3 and V4 regions was carried out with Illumina MiSeq platform. Comprehensive details for composition and distribution of rhizospheric microbiomes of wild plants have been shown in Fig. 1.2.

Approximately, 3000 OTUs for each rhizosphere sample were obtained. Rhizosphere microbiomes in the six wild plant species were dominated by bacterial phyla Proteobacteria (35%), Acidobacteria (12%), Actinobacteria (11%), Bacteroidetes (10%), Planctomycetes (8%), Chloroflexi (6%), and Verrucomicrobia (6%) and the details have been shown in Fig. 1.3a, b, c, d. *Rhizobiales* (8%) and *Sphingomonadales* (3.5%) orders of class Alphaproteobacteria (15%); *Nitrosomonadales* (4.28% ± 1.24%), and *Burkholderiales* (3%) orders of class Betaproteobacteria (9%); *Myxococcales* (5.5%) order of class *Deltaproteobacteria* (8%); and *Xanthomonadales* (4%) orders of class Gammaproteobacteria (7%) were found to be abundant in phylum Proteobacteria (Fig. 1.3a). Abundant members of phylum Actinobacteria were found to be Acidimicrobiales (4%). Similarly, Subgroup 4 (6%) and Subgroup 6 (4%) were abundant in Acidobacteria phylum.

The core rhizospheric microbiome of wild plant species showed a total of 1,109 operational taxonomic units (OTUs) affiliated to 113 bacterial genera accounting

Table 1.2 Diversity and functions of rhizosphere microbiomes in different agricultural crops

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Phaseolus vulgaris	Significant associations between rhizobacterial community composition, crop genotype, and specific root phenotypic traits were reported	*Bacteroidetes* and *Verrucomicrobia* in roots of wild beans; *Actinobacteria* and *Proteobacteria* were enriched on roots of modern bean accessions	Growth and health of common bean	Pérez-Jaramillo et al. (2017)
Hordeum vulgare	Host genotype has a significant effect on the diversity of root-associated bacterial communities	*Comamonadaceae, Flavobacteriaceae, Rhizobiaceae*	Traits related to pathogenesis, phage interactions, and nutrient mobilization are enriched in the barley root-associated microbiota	Bulgarelli et al. (2015)
Arabidopsis thaliana	Soil type defines the composition of root-inhabiting bacterial communities. Host genotype determines specific bacterial groups in microbiome of rhizosphere. Plant cell wall features serve as sufficient colonization (up to 40%) of root-associated microbiota	*Proteobacteria, Bacteroidetes Actinobacteria, Acidobacteria, Planctomycetes*	Growth, health, and crop domestication	Bulgarelli et al. (2012)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Arabidopsis thaliana	Jasmonic acid plant defence pathway may mediate plant–bacteria interactions in the soil and alters the composition of rhizosphere bacterial communities	*Bacillales sp.*, *Bacillus sp.*, *Planococcacea sp.*„ *Lysinibacillus sp.*, *Pseudomonas sp.*,	Induced systemic resistance (ISR)	Carvalhais et al. (2013)
Beta vulgaris	Invading pathogenic fungus and plant stress responses directly influence the shift in rhizobacterial community in microbiome composition	*Oxalobacteraceae*, *Burkholderiaceae*, *Sphingobacteriaceae* *Sphingomonadaceae*	Antagonistic traits that restrict pathogen colonization and infection	Chapelle et al. (2016)
Helianthus annuus	Plant-associated fungal communities are strongly influenced by host genetic factors than bacterial communities	*Nectriaceae, Olpidiaceae Mortierellaceae, unclassified Pleosporales, Preussia spp., unclassified Thelebolaceae, Fusarium spp., Conocybe spp.*	Native microflora may have symbiotic action	Leff et al. (2017)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Poaceae crops such as *Zea mays L; Zea mays ssp. Parviglumis; Sorghum bicolor cv. Arprim; (Triticum aestivum L. cv. Fiorina)*	Bacterial community composition in the rhizosphere is different from that in bulk soil. Rhizobacterial community composition differed according to the *Poaceae* genotype. The extent of diversification of eukaryotic hosts can be a significant factor for selection of their associated bacterial compartment	*Rhodospirillales* such as *Azospirillum, Gluconacetobacter, Rhodospirillum Sphingomonadaceae (Alphaproteobacteria); Burkholderiales* such as *Acidovorax, Alcaligenes, Burkholderia, and Hydrogenophaga (Betaproteobacteria); Francisella, Moraxella, Pantoea, Photorhabdus, Pseudomonas, and Xanthomonas (Gammaproteobacteria); Myxococcales* such as *Anaeromyxobacter (Deltaproteobacteria), (v) Megasphaera, Mogibacterium; Bacillales* such as *Bacillus* and *Peanibacillus (Firmicutes); Collinsella*; and *Actinomycetales* such as *Actinomyces, Corynebacterium, Kocuria, and Propionibacterium (Actinobacteria)*	Normal growth and plant health	Bouffaud et al. (2014)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Citrus crop	Provided a comprehensive taxonomic and functional biogeographical analysis of the citrus rhizosphere microbiome	*Pseudomonas, Agrobacterium, Cupriavidus, Bradyrhizobium, Rhizobium, Mesorhizobium, Burkholderia, Cellvibrio, Sphingomonas, Variovorax and Paraburkholderia,, Ascomycota, Fusarium* and *Hirsutella*	Nutrition acquisition and plant growth promotion	Xu et al. (2018)
Amaranthus albus, Sonchus arvensis, Sisymbrium officinale, Medicago sativa, Solanum dulcamara, and other 25 angiosperm plant species	Evolutionary divergence among host plant species affects the assembly of the endosphere and rhizosphere microbiome. This indicates that the potential role of host-associated microbial communities in mediating interactions between hosts and their biotic and abiotic environment	*Proteobacteria, Actinobacteria, Firmicutes, Verrucomicrobia, Bacteroidetes, Chloroflexi, Acidobacteria*	The root microbiome is associated with drought tolerance across host plant species	Fitzpatrick et al. (2018)
Arabidopsis thaliana	Different developmental stages of plant influence rhizosphere microbiome assemblage. Plant can select a subset of microbes at different stages of development, presumably for specific functions	*Acidobacteria, Actinobacteria, Bacteroidetes, Cyanobacteria*	Disease suppression	Chaparro et al. (2014)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Oryza sativa	Rhizosphere microbiome is shaped by soil- and plant-related conditions such as geographic location, soil type, rice genotype, oxic and anoxic interface, agricultural management and growth stages	*Proteobacteria* (mainly *Alpha-*, *Beta- and Deltaproteobacteria* classes), *Acidobacteria, Actinobacteria* and *Chloroflexi* phyla. *Archaeal* communities composed of *Crenarchaeota, Thaumarchaeota* and *Euryarchaeota* phyla	Growth promotion and disease inhibition	Ding et al. (2019), therein references
Triticum aestivum, Hordeum vulgare, Oryza sativa (indica and japonica)	*Triticum aestivum* and *Hordeum vulgare* had shown much stronger selection effects than *Oryza sativa* for the rhizosphere microbial community	*Proteobacteria, Bacteroidetes, Acidobacteria, Planctomycetes, Nitrospirae, Actinobacteria, Verrucomicrobia, Firmicutes, Cyanobacteria, Chloroflexi, Gemmatimonadetes, Ascomycota, Basidiomycota, Zygomycota, Unidentified fungi*	Glycan, limonene, and pinene degradation; Nitrogen and sulfur metabolism; Plant growth promotion	Lu et al. (2018)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Solanum lycopersicum	Nematode infections were associated with diversity and composition of rhizosphere bacterial populations in tomato plant roots. Root endophytes and rhizobacteria had significantly different community structures and species abundance	*Proteobacteria, Alphaproteobacteria. Sphingomonadales, Rhizobiales*	Degradation of plant polysaccharides; Carbohydrate and protein metabolism and biological nitrogen fixation	Tian et al. (2015)
Glycine max (L.)	Selection of the microbial community in the rhizosphere is based on niche-based processes as a result of the selection power of the plant and other environmental factors	phyla *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Cyanobacteria*, *Chlamydiae*, *Tenericutes*, *Deferribacteres*, *Chlorobi*, *Verrucomicrobia,* and *Aquificae*	Growth promotion and nutrition	Mendes et al. (2014)

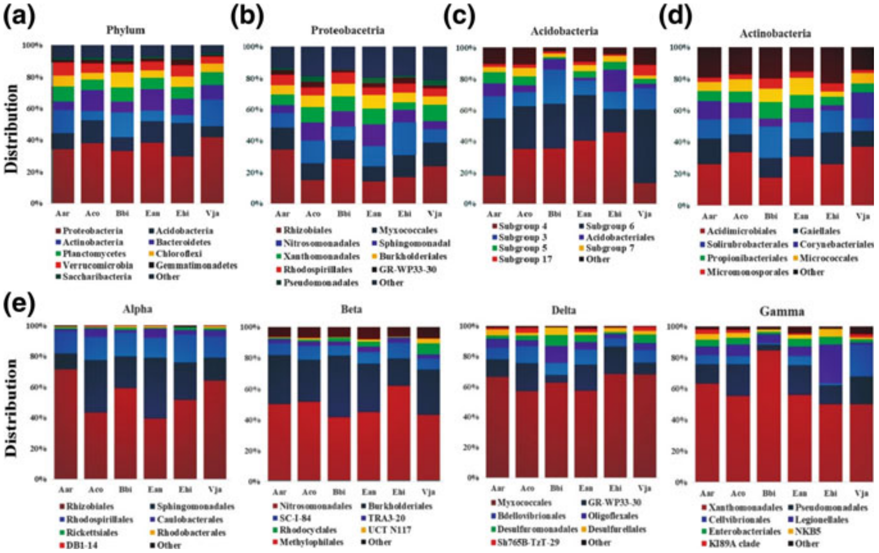

Fig. 1.3 The composition and relative abundance of major bacterial taxa in a typical rhizosphere of six different wild plant species Adapted with permission from Lie et al. (2019)

for more than 70% of the total sequencing data analyzed. The predominant bacterial genera of core OTUs are *Variovorax, Acidibacter, Ferruginibacter, Bradyrhizobium, Blastocatella, Variibacter, Sphingomonas,* and unclassified bacteria (Fig. 1.3e). The predominant bacterial orders were found to be composed of *Xanthomonadales, Rhodospirillales, Rhizobiales, Burkholderiales, Sphingomonadales, Myxococcales, Nitrosomonadales* of Proteobacteria; *Acidimicrobiales* of Actinobacteria; *Subgroup 4* and Subgroup *6* of Acidobacteria.

Variations in microbial community compositions at the order level in the rhizosphere of six different plant species were also demonstrated (Lei et al. 2019). Predominant bacterial group in *E. hirta* rhizosphere is Proteobacteria, while the same group is least represent in *V. japonica* microbiome. Highly enriched *Rhizobiale*s order of Proteobacteria was found in *V. japonica* and *A. argyi.* Predominant members of *Myxococcales* were noticed in *V. japonica* rhizosphere. Abundant members of *Nitrosomonadales* were observed in *E. hirta*. Similarly, higher abundance of Burkholderiales and *Sphingomonadales* was noticed in *E. annuus*. Members of *Xanthomonadales* were dominated in *V. japonica* rhizosphere.

1.3.2 Diversity of Rhizospheric Microbiome in Agriculture Crops

1.3.2.1 Rhizospheric Microbiome of Rice

The structure of microbial communities present in the rice rhizosphere is very complex, dynamic, and diverse (Edwards et al. 2015; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019). Recently, microbiome inhabiting rice roots and rhizosphere is extensively reviewed by Ding et al. (2019). A study taken by Edwards et al. (2015) revealed that endosphere (inside the root compartment), rhizoplane (surface of the root), and rhizosphere of rice had distinct microbiomes. Microbial communities from the rice rhizosphere are established by amplification of the 16S rRNA gene (variable regions V4-V5) followed by high-throughput sequencing using the Illumina MiSeq platform (Edwards et al. 2015). Results indicate that rice endosphere microbial communities had the lowest α-diversity, whereas rice rhizosphere had higher α-diversity. Furthermore, the mean α-diversity was found to be relatively high in the rhizosphere than in the bulk soil (Edwards et al. 2015).

The most dominant bacterial genera of rice rhizosphere is summarized in Fig. 1.4. Bacterial community profiles and their relative abundance are shown in Fig. 1.5 (Lu

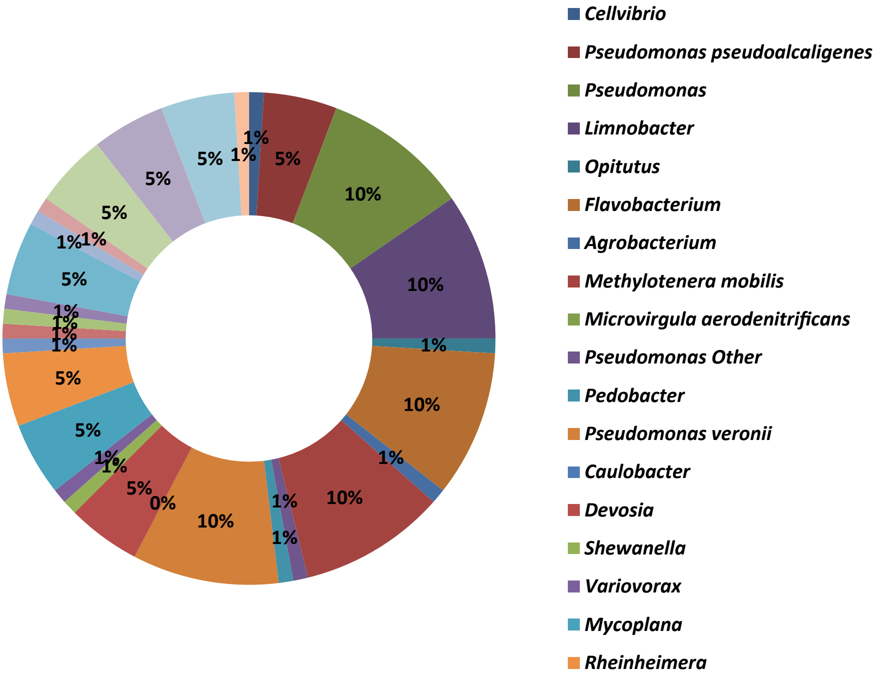

Fig. 1.4 Dominant bacterial genera in the rhizosphere microbiome of rice Adapted from Moronta-Barrios et al. (2018)

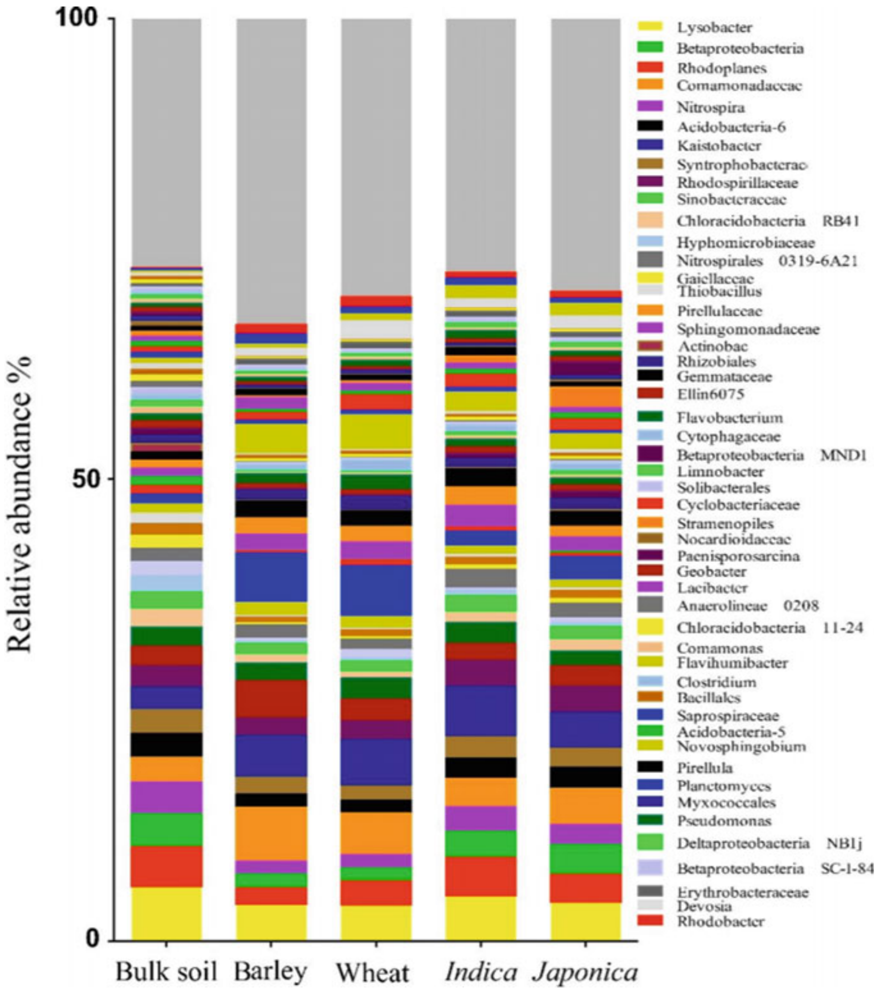

Fig. 1.5 Bacterial community profiling in the rhizospheric microbiomes of *Hordeum vulgare (Barley), Triticum aestivum (Wheat)*, *Oryza* sativa *Indica* and *Japonica* (Rice) Adapted with permission from Lu et al. (2018)

et al. 2018). Bacterial, archaeal, and fungal communities and their relative abundance in the rice rhizosphere have been studied (Ding et al. 2019). Bacterial populations were found to be abundant in the rice rhizosphere (Edwards et al. 2015). The abundance of rhizosphere microbial populations such as bacterial, fungal, and archaeal was twice those that of the bulk soil which is an indication of rhizospheric effect (Ding et al. 2019).

Proteobacteria dominated the microbiome of rice rhizosphere accounting more than 71%. Among Proteobacteria, the most abundant class was Gammaproteobacteria followed by *Betaproteobacteria, Alphaproteobacteria, Deltaproteobacteria*, and

Epsilonproteobacteria (Moronta-Barrios et al. 2018). Representatives of *Epsilonproteobacteria* and *Deltaproteobacteria* classes were not detected in the rice endorhizosphere. *Phyla Verrucomicrobia* and *Bacteroidetes* were abundant across the samples. Representative members of *Nitrospirae and Acidobacteria* were found only in rice-rhizospheric samples (Moronta-Barrios et al. 2018). Bacterial phyla *Proteobacteria, Firmicutes, Chloroflexi, Nitrospirae, Spirochaetes, Fibrobacteres, Planctomycetes, Bacteroidetes, Proteobacteria, Actinobacteria, Verrucomicrobia, Cyanobacteria*, and *Acidobacteria* are the most commonly found bacterial members of the rice rhizosphere (Edwards et al. 2015; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019). Similarly, the most common bacterial genera of rice rhizosphere are as follows: *Pseudomonas sp., Limnobacter, Devosia, Opitutus, Flavobacterium, Shewanella, Caulobacter, Agrobacterium, Pseudomonas veronii, Methylotenera mobilis, Microvirgula aerodenitrificans, Pedobacter, Rhodoferax, Variovorax, Mycoplana, Rheinheimera, Flavisolibacter, Fluviicola, Chryseobacterium, Asticcacaulis, Halothiobacillus, Pleomorphomonas, Sphingobium, Thiobacillus, Bacillus sp., Flavobacterium gelidilacus, Methylophaga,* and *Acidovorax* (Moronta-Barrios et al. 2018). Further details on dominant microbial communities and their functions in rice-rhizospheric microbiomes have been summarized in Table 1.2.

Methanogenic archaea, viz., *Methanobacterium, Methanosarcina, Methanocella*, and *Methanosaeta* were also reported in the rice rhizosphere (Malyan et al. 2016a; Edwards et al. 2015). *Firmicutes, Bacteroidetes, Betaproteobacteria*, and *Chloroflexi* were found to be differentially enriched in rice rhizosphere. The *Betaproteobacterial* OTUs that are enriched in rice rhizosphere belong to mainly *Comamonadaceae* and *Rhodocyclaceae* families (Edwards et al. 2015). Total bacterial count of rice rhizosphere is approximately 5×10^{9} cells g dw^{-1} soil, whereas as archeal members are found to be 2.5×10^{8} cell g dwt^{-1} soil.

1.3.2.2 Rhizospheric Microbiome of Wheat and Barley

Rhizosphere community of wheat was analyzed by comparative metatranscriptomics approach (Hayden et al. 2018). The rhizosphere community of wheat was predominately bacteria. Classes *Gammaproteobacteria, Alphaproteobacteria,* and *Actinobacteria* were dominant in the rhizosphere of wheat and barley. Bacterial families such as *Micrococcaceae*, *Enterobacteriaceae,* and *Pseudomonadaceae* were abundant in the rhizosphere microbiomes (Hayden et al. 2018). Predominant archaeal members in the rhizosphere are affiliated to family *Nitrososphaeraceae* under phylum Thaumarchaeota. *Ascomycota* is the dominant fungal phylum found in the rhizosphere representing more than 72% of total fungal transcripts. Other fungal phyla in the rhizosphere of wheat and barley were affiliated to Basidiomycota (>10%), which includes the genus *Rhizoctonia*, and Glomeromycota (4%) form arbuscular mycorrhizae. Interestingly, fungal families represent a smaller proportion of the total microbial transcripts analyzed in the rhizosphere (Hayden et al. 2018). Rhizosphere community of barley was reported by Lu et al. (2018). Bacterial phyla *Proteobacteria, Bacteroidetes, Acidobacteria, Planctomycetes, Nitrospirae, Actinobacteria, Verrucomicrobia, Firmicutes, Cyanobacteria, Chloroflexi*, and *Gemmatimonadetes* were associated with barley rhizosphere. Further, fungi *Ascomycota, Basidiomycota, Zygomycota*, and Unidentified fungi were distributed in the barley rhizosphere (Hayden et al. 2018).

1.3.2.3 Rhizospheric Microbiome of Soybean

Shotgun metagenomics approach was used to study functional and taxonomic diversities of microbial communities in the rhizosphere of soybean, *Glycine max* (L.) (Mendes et al. 2014). Metagenomic libraries were dominated by bacteria (>95%) followed by eukaryotes (3%) and archaea and virus (1%). *Proteobacteria* was found to be the most abundant phylum in soybean rhizosphere and represented around 47% distribution. Other dominant bacterial phyla in the rhizosphere of soybean were found to be *Actinobacteria* (23%), *Acidobacteria* (5%), and *Firmicutes* (6%) (Mendes et al. 2014). In general, 28% of total sequences found in the soybean rhizosphere were novel and were not affiliated to known bacterial taxa. Results indicate clear differences in microbial community structure among rhizosphere and bulk soil. Overrepresentation of the phyla *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Chlamydiae*, *Cyanobacteria*, *Deferribacteres, Tenericutes*, *Chlorobi*, *Aquificae,* and *Verrucomicrobia* was found in rhizosphere and the results were significant at $P < 0.01$ (Mendes et al. 2014). Similarly, abundance of class *Mollicutes*, *Bacilli*, *Clostridia*, *Epsilonproteobacteria*, *Gammaproteobacteria*, *Thermomicrobia,* and *Chlamydiae* was found in the rhizosphere of *Glycine max* (L.).

1.3.2.4 Rhizospheric Microbiome of French Bean

Microbiome of French bean was elucidated by amplification of 16S rRNA (V3–V4 region) followed by high-throughput sequencing performed at Illumina MiSeq platform (Pérez-Jaramillo et al. 2017). Phylum *Proteobacteria* was the dominant member, whereas lower abundance of *Acidobacteria* was noticed in wild bean rhizosphere. The phyla *Verrucomicrobia* and *Bacteroidetes* were predominant in the wild bean rhizosphere. Phylum *Actinobacteria* was found to be more abundant in the modern bean rhizosphere and these results were statistically significant.

Significant increase in the relative abundance of bacterial families *Sphingomonadaceae* and *Rhizobiaceae* was observed in the rhizosphere as compared to the bulk soil. Furthermore, it was noticed that there is a gradual decrease in the relative abundance of the *Chitinophagaceae* and *Cytophagaceae* of the Bacteroidetes phylum in the French bean rhizosphere. Gradual increases in relative abundance of families *Streptomycetae* and *Nocardiodaceae* of *Actinobacteria* and *Rhizobiaceae* of *Proteobacteria*.

1.3.2.5 Microbiome of Maize and Other Members of Poaceae Crops

Rhizospheric microbiome of Poaceae crops such as *Zea mays L; Zea mays ssp. Parviglumis; Sorghum bicolor cv. Arprim; Triticum aestivum L. cv. Fiorina* was established by Bouffaud et al. (2014). The dominant bacterial members of *Microbiome of Poaceae crops* were found to be *Rhodospirillales such as Gluconacetobacter, Rhodospirillum*, *Azospirillum,* and *Sphingomonadaceae of* class *Burkholderiales; Actinomycetales* such as *Corynebacterium, Actinomyces, Propionibacterium*, and *Kocuria; Acidovorax* of *Alphaproteobacteria; Xanthomonas, Francisella, Pantoea, Moraxella, Pseudomonas*, and *Photorhabdus* of class *Gammaproteobacteria; Burkholderia, Hydrogenophaga*, and *Alcaligenes* of class *Betaproteobacteria; Myxococcales* such as *Anaeromyxobacter* of class *Deltaproteobacteria; Mogibacterium, Bacillales (Firmicutes)* such as *Bacillus* and *Paenibacillus; Megasphaera* and *Collinsella* (Bouffaud et al. 2014).

1.4 Factors Influencing Rhizospheric Microbiome in Agriculture Crops

The rhizosphere microbiomes participate in very important functions suitable for plant growth promotion. The key functions mediated by rhizosphere microbiome include abiotic stress tolerance, nutrient acquisition, and protection against plant pathogen infection. Therefore, understanding the assembly of rhizosphere microbiome and their molecular mechanisms will provide us basic information. This information will be useful to develop soil management practices, designing of healthy rhizosphere microbiome, and introduction of biofertilizers and biological control agents to develop sustainable agricultural strategies. Different factors that are influencing structure, assembly, and function of rhizospheric microbiomes are depicted in Fig. 1.6.

Rhizobacterial community composition in *Phaseolus vulgaris* was influenced by specific root morphological traits and host plant genotype (Pérez-Jaramillo et al. 2017). Impact of host plant genotype on rhizosphere microbial community was mediated by qualitative and quantitative composition of root exudates (Huang et al. 2014; Ahemad and Kibert 2014). Host genotype had a tremendous effect on the composition of root-associated microbial communities in *Hordeum vulgare* (Bulgarelli et al. 2015). Bulgarelli et al. (2012) reported that host genotype and soil type define the diversity of root-inhabiting bacterial communities in *Arabidopsis thaliana*. Plant cell wall properties confer sufficient colonization (40%) of root-associated microbiota in *Arabidopsis thaliana* (Bulgarelli et al. 2012).

Invading fungal pathogens and plant stress response induces a shift in microbiome composition of sugar beet (Chapelle et al. 2016). Rhizosphere microbial community structure varied according to the Poaceae genotype (Bouffaud et al. 2014). Evolutionary divergence among host plants and type of plant species affects the assembly

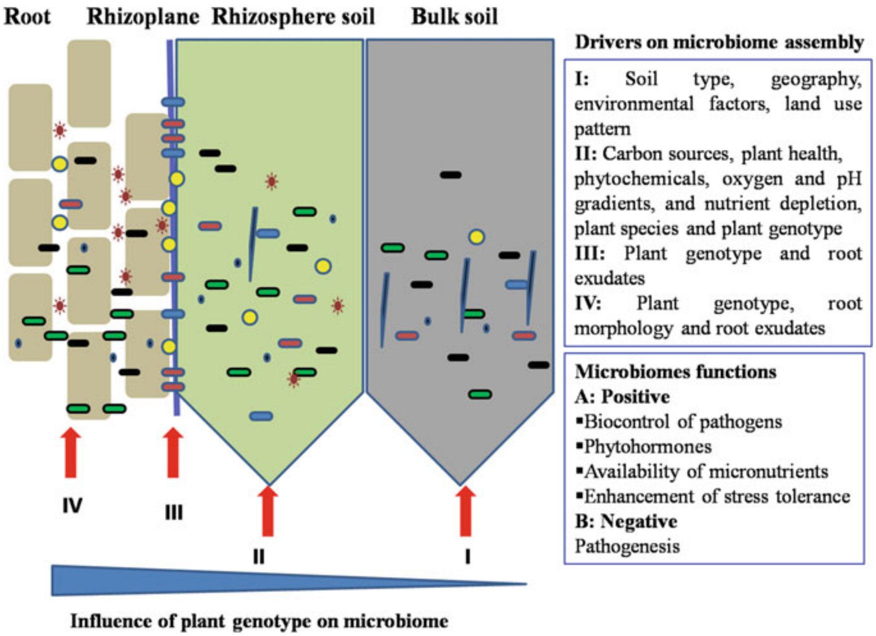

Fig. 1.6 Factors influencing assembly of microbiomes in agriculture crops. Microbial community structures in the four different compartments (I–IV) such as bulk soil, rhizosphere, rhizoplane, and root systems are distinct in nature

of the rhizosphere and endosphere and microbiome (Fitzpatrick et al. 2018). The root microbiome is also associated with drought tolerance of host plants (Fitzpatrick et al. 2018, Kour et al. 2019). Different developmental stages of plant also influence rhizosphere microbiome assemblages (Chaparro et al. 2014). Rhizosphere microbiome of *Oryza sativa* is shaped by plant and soil-related conditions such as soil type, geographic location, rice genotype, oxic–anoxic interface, agricultural management, and growth stages (Ding et al. 2019). Selection of the microbial community in the wheat rhizosphere depends on niche-based processes as a result of environmental factors and the selection power of the plant (Mendes et al. 2014). Further, agricultural management practices and growth stages of host plants exerted much influence on the rice rhizosphere microbiome (Edwards et al. 2015).

1.5 Plant Growth-Promoting Mechanisms of Rhizospheric Microbiome

Rhizobacteria plays a crucial role in growth promotion and immunity of the agricultural crops. These plant growth promoters follow certain mechanisms during the entire sequential process for nutrient mobilization, phytohormones for the growth and development, and chemical agents for defense-related issues of the crops (Suman et al. 2016; Verma et al. 2017; Yadav et al. 2018a, b). According to Mahanty et al. (2016), similar mechanisms are adopted by all bacterial genera during promotion of plant growth, although they are phylogenetically of different origins. The mechanisms behind the scene could mainly be divided into two types, direct mechanisms and indirect mechanisms. Comprehensive details of plant growth-promoting mechanisms of rhizobacteria in different agricultural crops have been summarized in Table 1.3.

1.5.1 Direct Mechanism

The direct mechanisms mainly involve the bacterial activities like phosphate solubilization, nitrogen fixation, secretion of plant hormones, ACC deaminase activities, and siderophore production.

1.5.1.1 *Phosphate Solubilization*

In spite of the large reservoir of phosphorus in soil, a very low amount of it is available to the plants (Ahemad and Kibret 2014). This is because plants utilize them in only two forms: (a) monobasic and (b) dibasic ions (Bhattacharyya and Jha 2012). It has also been reported that due to rapid conversion of phosphorus into insoluble complexes of different metal oxides most of the cultivable soils are deficit of available phosphate (Sandilya et al. 2016). Phosphate fertilizers are mostly applied to the agricultural soils in order to overcome the overall loss. But, continuous use of these chemical fertilizers is harmful to the soil and the environment in vivo. Hence, the importance of biofertilizers having plant growth-promoting traits was raised worldwide.

Native rhizobacteria pays an immense attribute to solubilize the inorganic phosphate so as to make it available for the utilization of various crops or plants (Widawati 2011). Certain bacterial genera, viz., *Bacillus*, *Pseudomonas*, *Azospirillum*, *Achromobacter*, *Acetobacter*, *Acinetobacter*, *Enterobacter*, *Klebsiella*, and *Serratia* are able to solubilize the inorganic form of phosphate to the available form (Kumar et al. 2012; Rana et al. 2019a, b). Besides, the role of bacterial organic acids for cation uptake by the plants is also worth mentioning (Sandilya et al. 2016). Researchers further stated that the bacterial genera belonging to the Proteobacteria and some of the *Firmicutes* and *Actinobacteria* are the most capable of the abovementioned conversion process.

Table 1.3 Plant growth-promoting mechanisms of plant microbiomes

Rhizobacteria	PGP traits	Crops/Plant rhizosphere	References
Bacillus sp. *Burkholderia* sp.	Phosphate solubilizer	*Zea mays*	Oliveira et al. (2009)
Pseudomonas aeruginosa strain MAJ PIA 03 *Bacillus firmus* strain MAJ PSB12	IAA, GA_3, ACC deaminase activity, HCN production, NH3 production, Siderophore production, antagonist, and phosphate solubilizer	*Ricinus communis*	Sandilya et al. (2016, 2017)
Rhodococcus sp. EC35, *Pseudomonas* sp. EAV, and *Arthrobacter nicotinovorans* EAPAA	Phosphate solubilizer	*Zea mays*	Sofia et al. (2014)
Azospirillum brasilense Az39, *Bradyrhizobium japonicum* E109	Phytostimulation	*Glycine max*	Cassan et al. (2009)
P. fluorescens Aur6, *Chryseobacterium balustinum* Aur9	Biocontrol agents	*Oryza sativa*	Lucas et al. (2009)
Bacillus, *Azotobacter*, *Pseudomonas*, and *Acinetobacter*	IAA, NH_3, HCN, Siderophore, phosphate solubilizer, antagonistic activity, nitrate reducer	*Momordica charantia*	Singh et al. (2017)
Pseudomonas putida, *Gluconacetobacter azotocaptans*, *Azospirilum lipoferum*	Phosphate solubilizer, plant hormones, siderophore	*Zea mays*	Mehnaz and Lazarovits (2006)
Sphingobacterium canadense	Phosphate solubilizer, plant hormones, siderophore	*Zea mays*	Mehnaz et al. (2007)
Chryseobacterium palustre, *Chryseobacterium humi*, *Sphingobacterium*, *Bacillus*, *Achromobacter*	IAA, HCN, NH_3, siderophore, ACC deaminase	*Zea mays*	Marques et al. (2010)
Pseudomonas fluorescens strain Psd	Zinc solubilizer, nitrate reducer	*Triticum aestivum*	Sirohi et al. (2015)
Bacillus sp. strain WG4	Antifungal metabolite pyrrolo [1, 2-a] pyrazine-1, 4-dione, hexahydro-3-(phenylmethyl)	*Zingiber officinale*	Jimtha et al. (2016)
Bacillus sp. PSB10	IAA, siderophores, HCN, ammonia	*Cicer arietinum*	Wani and Khan (2010)

(continued)

Table 1.3 (continued)

Rhizobacteria	PGP traits	Crops/Plant rhizosphere	References
Bradyrhizobium sp. 750, *Pseudomonas* sp., *Ochrobactrum cytisi*	Heavy metal mobilization	*Lupinus luteus*	Mehnaz et al. (2010)
Mesorhizobium sp. strain MRC4	IAA, siderophores, HCN, ammonia, exo-polysaccharides	*Cicer arietinum*	Ahemad and Khan (2009, 2010a, b)

1.5.1.2 *Nitrogen Fixation*

Nitrogen being the most important limiting factors, its fixation in nature is an interesting phenomena led by the plant growth-promoting rhizobacteria both in the symbiotic and non-symbiotic or free-living forms (Fagodiya et al. 2017a, b). It has been believed that the free-living nitrogen fixers provide a very lower amount of available nitrogen to the plants in comparison to the symbiotic nitrogen fixers since time immemorial (James and Olivares 1997). The *nif* genes found in the nitrogen-fixing rhizobacteria complete the nitrogenase enzyme by the means of its structural and regulatory proteins responsible for activation of the Fe protein, iron molybdenum, cofactor biosynthesis, and electron donation in case of the former and synthesis and function of the enzyme in the later (Glick 2012). Numerous PGPR genera capable of converting nitrate into nitrite by the catalysis of the nitrate reductase enzyme have also been reported. The most common among them are *Azospirillum*, *Azotobacter*, *Achromobacter*, *Bradyrhizobium*, *Beijerinckia*, and *Rhizobium* (Kour et al. 2019b, c; Yadav et al. 2019b).

1.5.1.3 Phytohormones and ACC Deaminase Enzyme Activity

Major plant hormones such as IAA and GA_3 (Marques et al. 2010; Ahmed and Hasnain 2010 and Khan et al. 2014) along with cytokinin secretion (Liu et al. 2013) by the PGPR's have often being reported by various authors. The IAA secreted by the bacterial population associated with the roots of the agricultural crops could augment the root surface area and length that could pave an easier route for absorption of the soil nutrients by the plants (Ahemad and Khan 2012). Amino acid tryptophan being a major precursor of IAA boosts the level of IAA biosynthesis. Almost five different types of IAA pathways have been reported by Spaepen and Vanderleyden (2011).

The role of GA_3 has also been explained by some authors in the context of plant growth-promoting rhizobacteria. The most important among them are the induction of seed germination and emergence and development of stem, leaf, flower, and fruits (Bottoni et al. 2004). The most common bacterial strains *Bacillus cereus*, *Sphingomonas* sp. LK11 were reported by them to enhance the growth and production of red pepper and tomato. Similarly, some other mechanisms of a plant body, viz., cytokinesis, sensitivity of vascular cambium, and their differentiation and root apical dominance are being conducted by the hormone cytokinin. Root-associated bacteria such as *Azotobacter chroococcum*, *Bacillus megaterium*, and *B. subtilis* were accounted to produce cytokinin thereby enhancing plant growth. On the other hand, synthesis of ethylene by the plant growth-promoting rhizobacteria induces ripening of fruits, opening of flowers, and leaf abscission.

Plants growing under stress are able to withstand the adverse effects of the environment with the due help of these phytohormones (de Garcia et al. 2006). Ethylenes produced in such conditions are called as "stress ethylene" that adds to the existing production of ethylene. However, excessive production of ethylene is a harmful phenomena for the longer development of the roots and in order to check such level of production, PGPR's with the help of 1-aminocyclopropane-1-carboxylate (ACC) deaminase plays a vital role in the early stages of growth which modulates the level of ethylene by hydrolyzing ACC, a precursor of ethylene, in ammonia and a-ketobutyrate (Glick et al. 1998; Marques et al. 2010). Bacteria synthesizing IAA along with endogenous plant IAA could stimulate plant growth or accelerate the amalgamation of the enzyme ACC synthase translating the compound *S*-adenosyl methionine to ACC being the immediate precursor of ethylene in higher plants (Glick 2012). Different kinds of phytohormones and their plant growth-promoting activity in agriculture crops have been summarized in Table 1.4.

1.5.1.4 Siderophore Production

Iron being one of the most important nutrients for all forms of life is found to occur as Fe^{3+} that could most likely form insoluble hydroxides and oxyhydroxides making it nearly impossible for plants and microflora for easy access (Rajkumar et al. 2010). In order to overcome such situations, bacteria secretes siderophores which are iron chelating agents with low molecular mass. According to Glick (2012), siderophores are mostly water soluble and could be divided into extracellular and intracellular siderophores. Siderophore forming Fe^{3+}-siderophore complex on the bacterial membranes gets reduced to Fe^{2+}. These ionic forms of iron are released into the cell from the complex via another mechanism linking both the membrane systems (inner and outer) which may finally lead to the destruction or recycling of the left out siderophore (Rajkumar et al. 2010). Thus, the siderophores prove to be excellent iron solubilizing agents from minerals and other inorganic sources. Pseudomonads, the bacterial genera, are the best-known secretors of siderophores playing an important role in the overall plant growth promotion activities (Sandilya et al. 2017).

Table 1.4 Phytohormones produced by microbiomes

Phytohormone produced	Plant growth-promoting rhizobacteria	Agriculture crop	References
Indole-3-acetic acid (IAA)	*Aeromonas veronii*	*Oryza sativa*	Mehnaz et al. (2001)
	Azospirillum brasilense	*Triticum aestivum* L.	Kaushik et al. (2000)
	Enterobacter sp.	*Saccharum officinarum*	Mirza et al. (2001)
	Enterobacter cloacae	*Oryza sativa*	Mehnaz et al. (2001)
	Pseudomonas sp. RJ10	*Brassica napus*	Sheng and Xia (2006)
	Bacillus sp. RJ16	*Brassica napus*	Sheng and Xia (2006)
	Enterobacter sp.	*Cicer arietinum* L.	Fierro-Coronado et al. (2014)
	Pseudomonas sp, *Bacillus* sp.	*Sulla carnosa*	Hidri et al. (2016)
	Bacillus licheniformis	*Triticum aestivum* L.	Singh and Jha (2016)
	Bacillus subtilis	*Acacia gerrardii* Benth	Hashem et al. (2016)
	Pseudomonas sp.	*Zea mays*	Mishra et al. (2017)
	Enterobacter sp. C1D	*Vigna radiata* L.	Subrahmanyam and Archana (2011)
	Proteus vulgaris JBLS202	*Arabidopsis thaliana*	Bhattacharyya et al. (2015)
Cytokinin	*Pseudomonas fluorescens*	Glycine max L.	De Salamone et al. (2001)
	Pseudomonas fluorescens	*Pinus* sp.	Bent et al. (2001)
	Paenibacillus polymyxa	*Triticum aestivum* L.	Timmusk et al. (1999)
	Micrococcus luteus	*Zea mays*	Raza and Faisal (2013)
	Bacillus subtilis	*Platycladus orientalis*	Liu et al. (2013)
	Arthrobacter sp., *Bacillus* sp., *Azospirillum* sp.	*Glycine max* L.	Naz et al. (2009)
	Proteus vulgaris JBLS202	*Arabidopsis thaliana*	Bhattacharyya et al. (2015)
Gibberellin	*Bacillus* sp.	*Alnus* sp.	Gutierrez-Manero et al. (2001)

(continued)

Table 1.4 (continued)

Phytohormone produced	Plant growth-promoting rhizobacteria	Agriculture crop	References
	Aspergillus fumigatus	*Glycine max* L.	Khan et al. (2011)
	Azospirillum lipoferum	*Triticum aestivum* L.	Creus et al. (2004)
	Phoma glomerata, Penicillium sp.	*Cucumis sativus*	Waqas et al. (2012)
	Proteus vulgaris JBLS202	*Arabidopsis thaliana*	Bhattacharyya et al. (2015)
ACC deaminase	*Enterobacter cloacae*	*Brassica napus*	Saleh and Glick (2001)
	Pseudomonas putida	*Vigna radiata* L.	Mayak et al. (1999)
	Pseudomonas sp.	*Zea mays* L.	Shaharoona et al. (2006)
	Methylobacterium fujisawaense	*Brassica* sp.	Madhaiyan et al. (2006)
	Rhizobium leguminosarum	*Pisum sativum*	Ma et al. (2003)
	Achromobacter xylosoxidans, Acidovorax facilis	*Brassica juncea* L. Czern	Belimov et al. (2005)
	Bacillus, Microbacterium, Methylophaga, Agromyces	*Oryza sativa*	Bal et al. (2013)
	Enterobacter sakazakii 8MR5, *Pseudomonas* sp. 4MKS8, *Klebsiella oxytoca* 10MKR7	*Zea mays* L.	Babalola et al. (2003)
	Methylobacterium fujisawaense	*Brassica campestri*	Madhaiyan et al. (2006)
	Enterobacter sp. C1D	*Vigna radiata* L.	Subrahmanyam et al. (2018)

1.5.2 Indirect Mechanisms

Plant growth-promoting rhizobacteria has been implemented in various crop fields for their promising capability to work both as biocontrol agents and growth promoters since last two decades. Bacteria secretes various metabolites and chemical agents that makes them wonderful candidates for controlling different crop diseases most of them being originated from fungal sources. According to Bhattacharyya and Jha (2012), PGPRs are able to synthesize different antifungal secondary metabolites such as phenazines, HCN, pyrrolnitrin, 2, 4-diacetylphloroglucinol, viscosinamide, tensin, and pyoluteorin. Availability of bacterial antagonist in the rhizosphere soil may even adapt the plant for developing induced systemic resistance against broad-spectrum bacterial, fungal, and viral pathogens (Lugtenberg and Kamilova 2009). Cyanide is the most dangerous chemical known for its high toxic properties which can well inhibit the pathogens sensitizing agricultural crops. HCN being the secondary metabolite secreted by the PGPRs does not have any pessimistic effect on the host plants, and hence they are frequently used for controlling weeds (Zeller et al. 2007). According to various reports, HCN-producing PGPRs are very helpful in controlling dreaded phytopathogens such as *Pythium ultimum*, *Fusarium oxysporum*, and pathogenic *Agrobacterium*. The mode of action mechanisms involves lysis of fungal cell walls (Maksimov et al. 2011), root colonization (Kamilova et al. 2005), reduction of stress ethylene level (Van Loon 2007), siderophore and antibiotic production (Beneduzi et al. 2012).

Certain genera like *Bacillus* have been best studied for their ability to secrete antimicrobial traits with higher rate of agricultural applicability (Compant et al. 2005). The members of this group of bacteria hold a key role in biocontrol aspects as they could reluctantly replicate at a very faster rate and are mostly resistant to environmental stress (Shafi et al. 2017). They secrete bacillomycins, iturins, and mycosubtilin very much effective against fungal pathogens, particularly *Aspergillus flavus* (Gong et al. 2015). Similarly, Lee et al. (2015) reported almost 99.1% of the antagonistic success in crops fields inoculated with *Bacillus amyloliquefaciens* strain HK34 against *Phytophthora cactorum* in *Lycopersicum esculentum*, *Sclerotium rolfsii*, *Capsicum annuum* var. acuminatum, *Colletotrichum gloeosporioides,* and *Cucumis sativus*.

Apart from that, other bacterial genera like *Pseudomonas* and *Paenibacillus* have also been reported by various authors having antimicrobial properties in both in vitro and in vivo conditions. Although laboratory results may not always be relied under field conditions, PGPR has been reported to be effective in both the conditions in different agricultural cropping systems. That is why they may be termed as multifunctional agents by controlling a wide spectrum range of phytopathogens and a spectacular replacement for chemical fertilizers by enhancing plant growth and overall yield per hectares of cultivated soil further playing a vital role in maintaining ecological balance across the globe (Ahemad and Kibret 2014).

Although much work has been done on the biocontrol characteristics of rhizospheric bacteria, it has to be considered that soil type, plant species, and pathogen affect in rhizosphere competence and/or biocontrol efficiency of applied biocontrol strain against a soil-borne pathogen.

1.6 Biotechnological Applications of Rhizosphere Microbiomes

In the recent past, sustainable technologies have gained lot of momentum to improve quality and yield of agricultural crop production. Nevertheless, still there is uncertainty about success of chemical-based formulations in plant protection management. In general, pests and diseases are mainly controlled by chemical-based pesticides which pose major health risks as well as adverse negative impacts in the ecosystem and environment. In addition to this, indiscriminate use of chemical fertilizers resulted in negative impacts on biodiversity and function of biogeochemical cycles. Most importantly, agricultural practices require novel products according to the demand of farmers and consumers. Therefore, alternative management tools have to be developed on the basis of biological solutions.

The plant rhizosphere hosts a considerable amount of microbiome. Plant growth-promoting rhizobacteria (PGPR) is an integral component of rhizosphere microbiome and is competent to promote plant growth by direct and indirect mechanisms. PGPR also promotes defense against diseases causing organisms using diverse plant-beneficial functions. Therefore, it is anticipated that crop inoculation with suitable PGPR could reduce the use of pesticides and fertilizers in agrosystems. Biotechnological applications of various PGPR inoculants for enhancing crop production were summarized in Table 1.5. Since most of the research information on PGPR comes from rhizosphere microbiome, one can further explore and exploit biotechnical prospects of rhizosphere microbiomes for sustainable agricultural production. We have specially highlighted the production of extracellular lytic enzymes, bioactive metabolites, and volatile organic compounds (VOCs) of rhizosphere bacteria in this section and the details are given extensively in Table 1.6.

1.6.1 Production of Lytic Enzymes by Rhizospheric Bacteria

Rhizosphere bacteria can benefit plant growth indirectly through biocontrol mechanisms which can inhibit the growth and colonization of phytopathogens. This potential antagonism character of biocontrol agent might occur through different mechanisms which include production of extracellular lytic enzymes, secondary metabolites, siderophores, antibiotics, and induction of systemic responses (Saraf et al. 2014, Jadhav and Sayyed 2016; Kour et al. 2019a; Yadav et al. 2016a, 2019f). One of the important mechanisms for biocontrol agent is the production of lytic enzymes which are able to degrade the membrane constituents of phytopathogens, such as proteases (Felestrino et al. 2018), acylases, and lactonases (Combes-Meynet et al. 2011). These hydrolytic enzymes degrade the structural integrity of the pathogen cell wall. Their ability to inhibit phytopathogens makes them to be the preferable choice in biological control process. The application of

Table 1.5 Biotechnological applications of bio-inoculants for sustainable agriculture

SN	Crop	Organism/Biofertilizers	Mode of action	References
1	Canola and lettuce	*Rhizobium leguminosarum*	Early development, Growth promotion	Sneha et al. (2018), Abd El-Lattief (2016)
2	Wheat, oat, barley mustard, seasum, rice, linseeds, sunflower, castor, maize, sorghum, cotton, jute, sugar beets, tobacco, tea, coffee, rubber, and coconuts	*A. chroococcum, A.vinelandii, A. beijerinckii, A. nigricans, A. armeniacus, and A. paspali.*	Nitrogen fixation, produce thiamine and riboflavin, indole acetic acid (IAA), gibberellins (GA) and cytokinins (CK), improves the plant growth by enhancing seed germination and advancing the root architecture, inhibiting pathogenic microorganisms around the root systems of crop plants	Revillas et al. (2000), Abd El-Fattah et al. (2013), Gholami et al. (2009), Mali and Bodhankar (2009), Wani et al. (2013), Bhardwaj et al. (2014)
3	Chickpea lentil, pea, alfalfa and sugar beet rhizosphere, berseem, ground nut and soybean *Cicerarietinum* and *Tigonella foenum-gracecum*	*Rhizobium* inoculants	Increase the grain yields	Patil and Medhane, (1974), Rashid et al. (2012), Ramachandran et al. (2011), Hussain et al. (2002), Grossman et al. (2011), Sharma et al. (2011, 2012a, b), Kumar et al. (2013)
4	Tomato	*Pseudomonas putida*	Early developments, Growth stimulation	Sneha et al. (2018), Abd El-Lattief (2016)
5	Wheat and maize	*Azospirillumbrasilense and A. irakense*	Growth of wheat and maize plants by secrete gibberellins, ethylene, and auxins	Abd El-Lattief (2016); Perrig et al. (2007), Bhardwaj et al. (2014), Sneha et al. (2018)

(continued)

Table 1.5 (continued)

SN	Crop	Organism/Biofertilizers	Mode of action	References
6	Banana Pearl millet	*P. flourescens*	Enhance growth, leaf nutrient contents, and yield	Sneha et al. (2018), Abd El-Lattief (2016)
7	Rice	Cylindrospermum musicola	Nitrogen fixation, liberation of growth-promoting substances and vitamins; increase the root growth	Venkataraman and Neelakantan (1967)
8	Canola	*Azotobacter* and *Azospirillum* spp.	Growth and productivity	Sneha et al. (2018), Abd El-Lattief (2016)
9	Maize crop.	*P. alcaligenes*, *Bacillus polymyxa*, and *Mycobacterium phlei*	Improves the uptake of N, P, and K	Sneha et al. (2018), Abd El-Lattief (2016)
10	Chick pea.	*Pseudomonas*, *Azotobacter*, and *Azospirillum* spp.	Stimulates growth and increases the yield	Sneha et al. (2018), Abd El-Lattief (2016)
11	Wheat	*R. leguminismarum and Pseudomonas* spp.	Enhances the yield and phosphorus uptake	Sneha et al. (2018) Abd El-Lattief (2016)
12	Maize.	*P. putida, P. fluorescens, A. brasilense,* and *A.lipoferum*	Enhances seed germination, seedling growth, and yield	Sneha et al. (2018), Abd El-Lattief (2016)
13	Wheat, maize, and rice	*Azotobacter Azotobacter Alcaligenes, Azospirillum, Bacillus, Enterobacter, Herbaspirillum, Klebsiella, Pseudomonas,* and *Rhizobium*	Improves growth and grain yield	Sridhar (2012), James (2000)
14	Wheat maize, and rice	*Azospirillum*	Synthesis of phytohormones (indole-3-acetic acid, IAA), and regulation of plant hormonal balance by deamination of the ethylene precursor	Abd El-Lattief (2016)

(continued)

Table 1.5 (continued)

SN	Crop	Organism/Biofertilizers	Mode of action	References
15	Rice	*Alcaligenes*, *Azospirillum*, *Bacillus*, *Herba spirillum*, *Klebsiella*, *Pseudomonas,* and *Rhizobium*	N-fixation	Sneha et al. (2018)
16	Chickpea	Co-inoculation (*Pseudomonas* + *Bacillus* strains + effective *Rhizobium* spp.)	Stimulate chickpea growth, nodulation, and nitrogen fixation	Sneha et al. (2018)
17	Chickpea	Co-inoculation (PSB + *Rhizobium* + *Trichoderma)*	Increase sugar, protein, starch contents, nodule weight and seed nitrogen, potassium, phosphorus	Mohammadi (2010, 2011)
18	Rice	Green manure and biofertilizer	Stimulated the growth of plants with more number of tillers and broader leaves, increased leaf area	Shanmugam and Veeraputhran (2000)

these hydrolytic enzymes from rhizospheric origin is a viae solution as they are totally natural and are eco-friendly in nature (Mishra et al. 2019).

Lytic enzymes produced by various microorganisms can hydrolyze polymeric compounds like cellulose, hemicellulose, chitin, and protein of phytopathogens. Extracellular hydrolytic enzymes like chitinases, lipases, proteases, and glucanases are involved in the lysis of fungal cell wall (Neeraja et al. 2010). These enzymes either disintegrate or digest the molecular components of cell wall of fungal phytopathogens. Therefore, this process would be considered as eco-friendly control of soil-borne pathogens in agriculture crops. These enzymes further involve in nutrient cycling by decomposition of organic matter and plant residues in the rhizosphere. It is demonstrated that extracellular lytic enzymes produced by *Myxobacteria* sp. have the ability to suppress fungal plant pathogens (Bull et al. 2002). In an another study, glucanase-producing antagonistic bacteria *Lysobacter sp.* is capable of controlling diseases of *Pythium* sp. *and Bipolaris* sp. (Palumbo 2005). These hydrolytic enzymes rescue plants from biotic stresses and directly contribute in the parasitization of phytopathogens.

Hydrolytic enzymes of rhizospheric microbes were reviewed extensively by Jadhav and Sayyed 2016. Many rhizobacterial microbial species are capable of producing extracellular enzymes and effectively hydrolyze wide variety of polymeric substances like cellulose, hemicellulose, proteins, and chitin of phytopathogens (Jadhav and Sayyed 2016). Microbial strains like *B. subtilis* strains PCL1608 PCL1612, Streptomyces cyaneofuscatus B-49, *Serratia marcescens* strain ETR17,

Table 1.6 Biotechnological prospects of different rhizobacteria suitable for enhanced production of agricultural crops

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
Hydrolytic enzymes				
β-1,3-glucanase and β-1,4-glucanase activities, Chitinase, oxalate oxidase	*Bacillus sp.*	Bean	Biocontrol	Kumar et al. (2012)
Glucanases, protease	*B. subtilis* strains, PCL1608 and PCL1612	Avocado	Biocontrol	Cazorla et al. (2007)
Chitinase	*Bacillus subtilis* BP 9	Cotton	Biocontrol	Gajbhiye et al. (2010)
Chitinase, β-1,3-glucosidase, cellulose,. Protease	*Streptomyces cyaneofuscatus* B-49, *Streptomyces kanamyceticu* X-4, *Streptomyces rochei* Z-13, *Streptomyces flavotricin*	Cotton, chili pepper, canola	Biocontrol	Xue et al. (2013)
Glucanases, proteases or chitinases,	*B. megaterium B*5, *B. cereus* sensulato *B*25, and *Bacillus* sp. *B*35	Maize	Biocontrol	Ramírez et al. (2016)
β-1,3-, β-1,4-, and β-1,6-glucanases	*Actinoplanes philippinensis*, *Microbispora rosea*, *Micromonospora chalcea*, and *Streptomyces griseoloalbus*	Cucumber	Biocontrol	El-Tarabily (2006)
Chitinase, β-1,3 glucanase (laminarinase) and β-1,4 glucanase (cellulase)	*Pseudomonas fluorescens* and *Bacillus subtilis*	Tomato	Biocontrol	El-Gamal et al. (2016)

(continued)

Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
chitinase, protease, lipase, cellulase	*Serratia marcescens* strain ETR17	Tea	Biocontrol	Purkayastha et al. (2018)
Extracellular proteases and lipases	*Lysobacter enzymogenes*	Cucumber	Biocontrol	Folman et al. (2003)
Antibiotics/secondary metabolites				
DAPG and HCN	*P. fluorescens strains CHA0, Pf-5, Q2-87,*	Tobacco	Biocontrol	Weller (2007)
DAPG and HCN	*P. fluorescens Pf-5*	Cotton	Biocontrol	Nowak-Thompson et al. (1994)
DAPG and HCN	*P. fluorescens*	Rice	Biocontrol	Reddy et al. (2007)
DAPG and HCN	*P. fluorescens Q2-87*	Wheat	Biocontrol	Harrison et al. (1993)
HCN	*Bacillus* sp. BPR7	Bean	Biocontrol	Kumar et al. (2012)
HCN	*Bacillus subtilis BP-9*	Cotton	Biocontrol	Gajbhiye et al. (2010)
Bacilysin and iturin	*Bacillus subtilis* ME488	Cucumber and pepper	Biocontrol	Chung et al. (2008)
Pyrrolnitrin and prodigiosin	*Serratia marcescens* strain ETR17	Tea	Biocontrol	Purkayastha et al. (2018)
Lipopeptides surfactin, fengycin, and/or iturin A	*B. subtilis* strains, PCL1608 and PCL1612	Avocado	Biocontrol	Cazorla et al. (2007)
Viscosinamide, cyclic lipopeptides	*P. fluorescens* DR54	Cotton	Biocontrol	Nielsen et al. (1999)
Antifungal protein	*Bacillus* sp. KM 5	Rice	Biocontrol	Majumdar et al. (2011)
polymyxin B1	*Paenibacillus* sp. strain B2	sorghum	Biocontrol	Selim et al. (2005)

(continued)

Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
Eicosane ($C_{20}H_{42}$) and dibutyl phthalate ($C_{16}H_{22}O_4$), cyclononasiloxane, octadecamethyl-($C_{18}H_{54}O_9Si_9$) and benzoic acid, 2,5-bis(trimethylsiloxy) ($C_{16}H_{30}O_4Si_3$)	*Streptomyces* strain KX852460	Tobacco	Biocontrol	Ashan et al. (2017)
Fungichromin	*Streptomyces padanus* strain PMS-702 i	Cabbage	Biocontrol	Shih et al. (2003)
Pyrrolnitrin	*P. fluorescens* BL915	Wheat	Biocontrol	Chin-A-Woeng et al. (2003)
Oomycin A	*P. fluorescens*	Cotton	Biocontrol	Howie and Suslow (1991)
Phenazine-1-carboxylic acid	*P. fluorescens*	Wheat		Pierson and Pierson (1996)
Volatile organic compounds (VOCs)				
VOCs	*Bacillus subtilis* GB03	Arabidopsis	Vegetative growth promotion, elevated photosynthetic capacity, and iron accumulation	Xie et al. (2009)
VOCs	*Bacillus subtilis* GB03	Arabidopsis	Vegetative growth promotion, plant acquisition of iron, and increased photosynthetic capacity	Zhnag et al. (2009)
2-pentylfuran, aldehydes, alkanes, ketones, and aroma components	*Bacillus megaterium*	Arabidopsis	Fresh weight	Zou et al. (2010)

(continued)

Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
4-nitroguaiacol and quinoline	*Pseudomonas simiae*	Soybean	Salt tolerance, increased shoot and root length, fresh weight and leaf surface area	Vaishnav et al. (2016)
13-Tetradecadien-1-ol, 2-butanone and 2-Methyl-n-1-tridecene	*Pseudomonas fluorescens* SS10	Tobacco	Fresh weight, dry weight	Park et al. (2015)
Dimethylhexadecylamine	*Arthrobacter agilis* UMCV2	*Sorghum*	Fresh weight, shoot length, chlorophyll concentration, and lateral root number	Castulo-Rubio et al. (2015)
Brassinosteroid	*Proteus vulgaris* JBLS202	Arabidopsis	Fresh weight	Bhattacharyya et al. (2015)
Long-chain VOC signaling molecules, acetoin 2,3-butanediol, ethanethiol, isoprene, and acetic acid-butyl ester, tridecane, a C13 hydrocarbon compound	*Pseudomonas fluorescens* 89B-61, *Bacillus amyloliqefaciens* IN937a, *Bacillus subtilis* GB03, and *Paenibacillus polymyxa* E681	*Arabidopsis*	Induced systemic resistance	Lee et al. (2012a)
β-Caryophyllene	*Fusarium oxysporum* MSA 35	Lettuce	Root length, fresh weight, chlorophyll content	Minerdi et al. (2011)
Sesquiterpenes	*Laccaria bicolor*	*Arabidopsi and Populus*	Lateral root development	Ditengou et al. (2015)
α-pinene, (-)-trans-caryophyllene, tetrahydro-2,2,5,5-tetramethylfuran, dehydroaromadendrene, and (+)-sativene	*Cladosporium cladosporioides* CL-1	Tobacco	Fresh weight	Paul and Park (2013)
2,3-butanediol	*Bacillus subtilis*	Pepper	Plant defences/resistance	Yi et al. (2016)

Table 1.7 Mode of action of different lytic enzymes produced by rhizobacteria

S.No	Extracellular lytic enzyme	Mode of action
1	Chitinase	Degradation of chitin involves breakdown of chitin polymer into monomer, random cleavage at internal sites of chitin micro-fibril or progressive release of diacetylchitobiose in a stepwise manner without releasing monosaccharide or oligosaccharides
2	Glucanase	Glucanase can hydrolyze the substrate by sequentially cleaving glucose residues from non-reducing end. The enzyme can also initiate cleaving linkages at random sites along the polysaccharide chain, releasing smaller oligosaccharides
3	Protease	Protease can hydrolyze major proteins of phytopathogenes into small peptide chains, subsequently release their constituent amino acids and thereby destroy capacity of phytopathogen's protein to act on plant cells. Some of the proteases are capable of inactivating extracellular enzymes produced by phytopathogenic fungi
4	Cellulase	Cellulases hydrolyze the β-(1,4) glucosidic linkages in cellulose polymer and play a significant role in recycling this polysaccharide in the rhizosphere. Cellulose chains are composed of complex, rigid, insoluble, crystalline microfibrils. Therefore, complete degradation of cellulose involves a complex interaction between different cellulolytic enzymes such as cellulose/endoglucanases, exo-cellobiohydrolase/exo-glucanases, and β-glucosidases act synergistically to convert cellulose into glucose molecules

Pseudomonas fluorescens, *Serratia marcescens* strain ETR17, and many other antagonistic microbes have a potential to synthesize hydrolytic enzymes for the biocontrol of fungal phytopathogens like *P. ultimum, F. oxysporum, R. solani,* and *S. rolfsii,* (Cazorla et al. 2007; Kumar et al. 2012a, b; Purkayastha et al. 2018, El-Gamal et al. 2016). The mode of actions of extracellular enzymes is given in Table 1.7.

Chitinolytic microorganisms are heavily colonized in plant rhizosphere among which actinobacteria are the most abundant members (Yadav et al. 2018c). Actinobacteria such as *Streptomyces* flavotricini, *Streptomyces kanamyceticu, Streptomyces cyaneofuscatus*, and *Streptomyces rochei* produce chitinases and inhibit the growth of phytopathogen, viz, *Verticillium dahlia* in cotton rhizosphere (Xue et al. 2013). Chitinase-producing *Bacillus thuringiensis* spp. *colmeri* can inhibit the growth of plant pathogenic fungi, including *Rhizoctonia solani*, *Penicillium chrysogenum*, and *Physalospora piricola* (Liu et al. 2010). Biocontrol agent *Bacillus subtilis* inhibits the growth of pathogenic fungi *Fusarium oxysporum* through production of extracellular chitinase (Gajbhiye et al. 2010). Chitinases produced by *Brevibacillus laterosporus* effectively inhibit the growth of phytopathogenic fungi *Fusarium equiseti* (Prasanna et al. 2013). *Lysobacter enzymogenes* showed to inhibit *Pythium aphanidermatum* by producing extracellular protease and lipases (Folman et al. 2003)

Minimal use of chitinase-based fungicides in agriculture crops was associated with the perception that their efficacy will be slowly reduced in the soil environment. Nevertheless, Dahiya et al. (2006) extensively reviewed biotechnological prospects of chitinolytic enzymes and suggested that chitinases can be used as supplementary inputs along with other chemical-based fungicides to enhance their effectiveness against phytopathogenic fungi and reduce the required amount of chemical fungicides. In addition to this, it was shown that the application of mixed consortia containing two different chitinolytic bacteria is more effective in controlling the pathogen. Application of chitinase-producing *Streptomyces* sp. 385, *Paenibacillus* sp. 300, and both together is more effective in controlling cucumber wilt caused by *F. oxysporum* than individual strains applied (Singh et al. 1999). Similar kind of observation was reported by El-Tarabily et al. (2000) wherein growth of fungal pathogen *Sclerotinia* responsible for vegetable rot was effectively controlled by combination of *S marcescens, Streptomyces viridodiasticus,* and *Micromonospora carbonacea* strains. In recent, chitinase, protease, lipase, and cellulose-producing *Serratia marcescens* strain ETR17 showed in vitro antagonism toward nine different root and foliar pathogens of tea (Purkayastha et al. 2018).

Actinomycetes were considered to be strong biocontrol agents against fungal pathogens. This is mainly due to production of different types of antifungal compounds such as antibiotics and extracellular hydrolytic enzymes which includes chitinases and glucanases (Xue et al. 2013; Yadav et al. 2018c). *Streptomyces halstedii*, *Streptomyces cavourensis* SY224, and *Streptomyces griseus* are known to produce potential antifungal extracellular chitinases, which makes them to be used as biocontrol agents in crop protection strategies (Ki et al. 2012; Gherbawy et al. 2012). *Lysobacter* spp. was reported to be an effective biocontrol agent against soilborne pathogens through production of extracellular enzymes and other metabolites (Folman et al. 2003). *Lysobacter* spp. was abundant in the soil which is suppressive to root pathogen, viz., *Rhizoctonia solani*. Certain antagonistic strains showed in vitro biocontrol activity against *Xanthomonas campestris, R. solani*, and other important phytopathogens such as *Aspergillus niger, Fusarium oxysporum,* and *Pythium ultimum.*

These natural microbial biofungicides will be used as integrated pest management supplement for reduction of negative impact of chemical pesticides on the environment and maintain the sustainable production of agriculture.

1.6.2 Production of Antibiotics

Rhizospheric bacteria produce distinct antimicrobial products to inhibit the growth and colonization of plant pathogens to compete the nutrients present in the rhizosphere. This has become a beneficial trait to the host plant as disease development is significantly reduced by PGPR. Rhizosphere harbors diverse actinomycetes species which have been further exploited for secondary metabolites (Yadav et al. 2018b; Geetanjali and Jain 2016). Actinobacteria is known to produce wide variety of natural antimicrobial products (approximately 10,000 secondary metabolites) (Passari et al. 2015, 2017; Yadav et al. 2018a, b). Production of antibiotics by Actinobacteria was extensively reviewed by Yadav et al. (2018b, c). Application of secondary metabolites producing rhizobacterial isolates against phytopathogens is increasing over the past decade (Yilmaz et al. 2008). A variety of antimicrobial agents such as 2,4-diacetylphloroglucinol (DAPG), pyoluteorin (PRN), phenazine, cyclic lipopeptides, tensin, and pyrrolnitrin (PLT) have been screened and identified from *Pseudomonas* sp., *Arthrobacter* sp., and *Streptomyces* sp., (Weller 2007; Gupta et al. 2015). Details of antibiotics/secondary metabolites producing organisms and their application in different crops have been summarized in Table 1.6.

Rhizospheric soil isolates *Bacillus* sp. S2 and *Pseudomonas fluorescens* S5 were found to exert good antimicrobial activity against multi-drug-resistant clinical pathogens such as *Pseudomonas aeruginosa, Klebsiella pneumonia*, *Escherichia coli,* and *Staphylococcus aureus* obtained from different samples (Dhore et al. 2014). Thirty *Pseudomonas fluorescens* strains isolated from rice rhizosphere against pathogenic fungi *Sarocladium oryzae*, *Dreschelaria oryzae*, *Magnaporthe grisea*, and *Rhizoctonia solani*. Among these, *P. fluorescens* Pf 003 effectively inhibited (62–85%) the mycelial growth in all the pathogenic fungi in dual culture. The antifungal compounds extracted with ethyl acetate from *P. fluorescens* at 5% completely inhibited the pathogens (Reddy et al. 2007). Walia et al. (2013) isolated the bacteria from the tomato rhizosphere for having broad-spectrum antifungal activity against *Sclerotinia sclerotiorum, Rhizoctonia solani,* and *Fusarium oxysporum.*

DAPG, phenazines, PLT, and PRN are considered to be potent antibiotics synthesized by *Pseudomonas* biocontrol agents affiliated to gammaproteobacteria (Table 1.6). In recent, antibiotics-producing *Pseudomonas spp*. has got much attention in biocontrol research, and corresponding genes involved in the expression and regulation of these metabolites are now fully understood (Weller 2007and there in references). For the last 30 years, developments on biocontrol applications of *Pseudomonas* sp. against soil-borne pathogens have been summarized by Weller (2007). *P. fluorescens* strain CHA0 was isolated from tobacco rhizosphere which is naturally suppressive to black root rot of tobacco caused by *Thielaviopsis basicola* (Stutz et al. 1986). *P. fluorescens* CHA0 produces siderophore (pseudobactin), PLT, DAPG, PRN, HCN, salicylic acid, pyoverdine, indoleacetic acid, pyochelin, and other secondary metabolites (Voisard et al. 1994). Antagonistic bacterium *P. fluorescens* F113 isolated from sugar beet was applied in the field for suppression of damping-off of sugar beet infection caused by a pathogen *Pythium ultimum* (Cronin et al. 1997a, b).

Antibiotics such as bacilysin- and iturin-producing *Bacillus subtilis* ME488 suppressed soil-borne pathogens in pepper and cucumber crops (Chung et al. 2008). Secondary metabolites, viz., Pyrrolnitrin and prodigiosin-producing *Serratia marcescens* strain ETR17 *Serratia marcescens* strain ETR17 showed significant level of in vitro antagonistic property against different root and foliar pathogens of tea (Purkayastha et al. 2018). Antifungal lipopeptides such as surfactin-, fengycin-, and iturin-producing *B. subtilis* strains PCL1608 and PCL1612 have shown biocontrol mechanism toward soil-borne pathogen *Fusarium oxysporum* (Cazorla et al. 2007). *Paenibacillus* sp. strain B2 isolated sorghum mycorrhizosphere showed production of antibiotic polymyxin B1 and significantly inhibited the growth of fungal pathogens (Selim et al. 2005). Antifungal peptides-producing *Bacillus* sp. KM 5 isolated from rice rhizosphere showed antagonist activity toward pathogenic fungi *Gibberella fujikuroi, Sclerotium rolfsii* Saccardo, *Fusarium udum, Helminthosporium oryzae, and Rhizoctonia solani* Nees (Majumdar et al. 2011).

1.6.3 Production of Volatile Organic Compounds (VOCs)

Volatile organic compounds are lipophilic low molecular weight (<300 g mol − 1) compounds emitted from microbial metabolic pathways with high vapor pressure and low boiling point. VOCs can act as signal molecules in rhizosphere over short and long distances (Fincheira and Quiroz 2018). It is evidenced that VOCs released from diverse rhizospheric microorganisms, e.g., *Arthrobacter* sp*., Proteus* sp*., Bacillus* sp*., Fusarium* sp*., Pseudomonas* sp*., Alternaria* sp. and *Laccaria* sp., can promote plant growth on a specific "target". Detailed description about chemical nature of VOCs and their functions have been summarized in Table 1.6. Ryu et al. (2003) reported for the first time about the mechanism mediated by volatile organic compounds released by *Bacillus subtilis* GB03 which induced growth on *Arabidopsis thaliana*. This study evidenced that VOCs can modulate stress, growth, nutrition, and health processes in host plants. Some identified VOCs compounds, such as acetoin, β-Caryophyllene 2,3-butanediol, Sesquiterpenes, 2-pentylfuran, and dimethylhexadecylamine, have shown their ability to elicit plant growth at above and below ground biomass (Fincheira and Quiroz 2018; Chung et al. 2016) (Table 1.6).

Few studies indicate that VOCs act as signals and chemical messengers to regulate phytohormone synthesis, metabolic pathways, and nutrition levels. Effects of VOCs for induction of resistance and tolerance in plants are documented, wherein compounds such as 3-pentanol, dimethyl disulfide, 6-pentyl-α-pyrone, and acetoin were reported. VOCs derived by rhizospheric bacteria showed antagonistic activity toward plant pathogen *Rhizoctonia solani* and inhibit mycelial growth (Kai et al. 2007). Certain plant volatiles are proven to induce plant growth promotion through biochemical signals, eliciting local defence reactions known as induced systemic resistance (Chung et al. 2016; Kai et al. 2007). Long-chain VOCs signaling molecules, acetoin 2,3-butanediol, ethanethiol, isoprene, and acetic acid-butyl ester, and tridecane are found to be involved in induced resistance in *Arabidopsis* (Lee et al. 2012a, b). Yi et al. (2016) reported that 2,3-butanediol is produced by a *Bacillus subtilis* isolate involved in plant defense mechanisms. Root exudates of pepper inoculated with the *B. subtilis* were used to challenge various phytopathogens. For example, growth of *Trichoderma* sp (saprophytic fungus) and *Ralstonia solanacearum* (soil-borne pathogen) was inhibited by VOCs. This indicates that VOCs triggered the secretion of root exudates and subsequently acted as a plant defence inducer toward soil-borne fungal and bacterial pathogens.

Volatile organic compounds *such as* dehydroaromadendrene, α-pinene, tetrahydro-2,2,5,5-tetramethylfuran, (-)-trans-caryophyllene, and (+)-sativene-producing *Cladosporium cladosporioides* strain CL-1 showed increased growth parameters in Tobacco crop (Paul and Park 2013). In an another study, rhizospheric isolates such as *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937, *Pseudomonas fluorescens* 89B-61, and *Paenibacillus polymyxa* E681 produced Brassinosteroid **a** long-chain VOC and signaling molecules such as acetoin 2,3-butanediol, ethanethiol, acetic acid-butyl ester, and isoprene. These VOCs are involved in induced systemic resistance in *Arabidopsis (*Lee et al. 2012a, b). Fresh weight, shoot length, chlorophyll concentration, and lateral root numbers of *Sorghum were significantly increased by dimethylhexadecylamine produced by Arthrobacter agilis* UMCV2. Salt tolerance, increased shoot and root length, fresh weight, and leaf surface area were increased in soybean by VOCs, 4-nitroguaiacol, and quinoline produced by Vaishnav et al. (2016). VOCs of fungal origin also showed increased growth parameters in host plants like lettuce, Arabidopsis, and tobacco. *Fusarium oxysporum* MSA 35 showed production of β-Caryophyllene and increased fresh weight of tobacco in field experiment (Minerdi et al. 2011). Sesquiterpenes synthesized by ectomycorrhizal fungi *Laccaria bicolour* increased the lateral root of *Arabidopsis* (Ditengou et al. 2015). In the same study, it was demonstrated that other ectomycorrhizal ascomycote, *Cenococcum geophilum*, which cannot synthesize Sesquiterpenes does not promote lateral root of *Arabidopsis.* These studies indicate that volatile organic compounds emitted by microorganisms in the rhizosphere are cheaper, effective, efficient, and eco-friendly alternatives for controlling phytopathogens.

Environmentally friendly biotechnological approaches offer the development of PGPR inoculants and their potential application in metal-contaminated systems. Plant growth promotion by PGPR is a result from improved nutrient acquisition or phytohormonal stimulation (Table 1.3). Different mechanisms involved in plant growth promotion were shown in Fig. 1.6. PGPR inoculants were widely used in agriculture, forestry, horticulture, and in environmental restoration/phytoremediation sectors.

1.7 Conclusion and Future Prospects

Although studies have focused on plant microbiome structure and its function under natural and agricultural environments, there have been no significant coordinated efforts to combine and translate research results into practical solutions for farmers. According to Busby et al. (2017), integration of beneficial plant microbiome into agricultural production is one of the ways to assist in achieving these goals. However, this requires large-scale efforts from academic and industry researchers, farmers, and policy-makers to understand and manage complex plant–microbiome interactions under current challenges of the agriculture production.

For achieving this goal, five key research priorities have been identified by Busby et al. (2017). Few research priorities include development of host–microbiome model systems with associated microbial culture collections and reference genomes; characterization and refinement of a model “plant genotype–environment stress–microbiome–management interactions”; elucidation of the role core microbiome and determine functional mechanisms of plant–microbiome interactions. These research priorities may enable us to manipulate agricultural microbiomes and thereby to develop management strategies for increased production and productivity of global agriculture in a sustainable manner. One of the challenges for future research work includes protection and conservation of rhizosphere biodiversity and their potential application in agricultural soils. Sustainable agriculture production may not be possible unless integration of plant germplasm and beneficial microbial species in the current agricultural practices globally.

Exploitation and production of natural drug formulations from microbial species have gained a significant leap during last three decades. Therapeutic applications of anticancerous compounds extracted from actinobacteria have been well addressed (Busi and Pattnaik 2018). The research priority is now shifted toward rhizosphere microbial communities for developing new drugs through high-throughput screening and fermentation techniques. Exploitation of bioprospecting potential of rhizosphere microbiomes is an upcoming new avenue.

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Chapter 2
Culturable Endophytic Fungal Communities Associated with Cereal Crops and Their Role in Plant Growth Promotion

Hira Saleem, Hareem Mohsin, Rabia Tanvir and Yasir Rehman

Abstract Many microorganisms are known to live in association with plants. Endophytes are the microorganisms that live in the internal tissues of plants. Endophytic fungi hold great importance for the roles that they play in association with the host plants. Endophytes are known to promote the growth of the host plants by various activities such as detoxification of toxic compounds, protection against pathogens, and production of plant growth promoting hormones. Many biotechnologically important metabolites are also produced by endophytes such as anticancer and antimicrobial compounds. There is a rich diversity of endophytes that needs to be explored for biotechnological purposes. This chapter focuses on the endophytic fungi of cereal crops and the roles they play.

Keywords Cereal crops · Endophytic · Fungal communities · Plant growth promotion · Sustainable agriculture

2.1 Introduction

Plants play a vital role in the ecosystem. They are the producers that interact with different microbial communities and help in maintaining the biodiversity and stability of the ecosystem. There can be two types of such microbial communities with respect to the location, i.e., epiphytic fungi and endophytic fungi (Lindow and Brandl 2003). Epiphytic Fungi (epi; *upon*, phytic; plant) refers to the fungal communities propagating or adhering to the plant surface. Common examples include *Pestalotia* and

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Botryosphaeria (Santamaría and Bayman 2005). Endophytic Fungi (endo; *within*, phytic; plant) refers to the fungal communities which are present within the plant tissues asymptomatically. Common examples include *Colletotrichum*, *Xylaria,* and *Guignardia* (Schulz et al. 2002). Majority of these microbial communities comprise of endophytic fungal species.

Plants majorly depend on different kinds of associations with microbial species, especially the endophytic fungi, which play essential roles in plant growth, resistance against diseases, and tolerance against environmental stresses (Yang et al. 2018). The preliminary definition for the term endophytes was given by Hallmann et al. (1997) who stated that these are the microbial communities present within the plant tissue that cause no visible symptoms of any disease in the plant. However, this definition cannot be taken as the sole source to describe the endophytes (Hallmann et al. 1997; Lugtenberg et al. 2016). Mainly because there has been not much discussion about the unculturable endophytic species in the plant microbiome. Secondly, the latent plant pathogens are difficult to be recognized by culturable techniques and thus cause problems if they are in association with the unculturable endophytic communities. Due to these two major reasons, the endophytes, especially the endophytic fungal communities, are a challenge to study (Card et al. 2015; Hardoim et al. 2015; Lugtenberg et al. 2016).

The endophytes are most commonly associated with either roots or shoots of the plant. Such a relationship is termed as a symbiotic relationship in which two organisms are associated with each other. This can either be mutualism, commensalism, or parasitism. Furthermore, one fungal association which is in a mutualistic relation with one type of plant can be pathogenic to other types of plants (Bokati et al. 2016; Johnson et al. 1997). The root associated fungal endophytes usually have a mutualistic relation. They play a vital role in the better uptake of water and minerals and in return utilize carbohydrates from the host plant (Jumpponen 2001). In the case of shoots, most of such association has been found in the foliar regions of the plants at the point of contact of the leaves and the soil (Clement et al. 1997; Saikkonen et al. 2013). They play an important role in alleviating the stress, which can be abiotic or biotic, experienced by the host plant, thus making the host fit for survival (Bokati et al. 2016).

A research conducted by Bokati et al. (2016) demonstrated that not just the presence of fungal communities as endophytes is important, but the timing of their colonization also plays a critical role (McGonigle et al. 1999). The earlier the colonization and propagation of the endophytes, the better the absorption of nutrients and minerals from the soil with reduced effects of environmental stresses (Bokati et al. 2016). Endophytic fungal species are also reported to be promising candidates for the control of diseases (Kusari et al. 2012). Reports also state that the rice blast disease can be effectively controlled by the application of endophytic fungi (Atugala and Deshappriya 2015). Endophyte application, therefore, can limit the long term use of fertilizers and fungicides which are harmful to environment and human health (Priyadarshani et al. 2018; Tian et al. 2004).

Cereal crops, also known as grain crops, are the most commonly consumed group of plants all over the world. Approximately 50% of the total intake of food constitutes cereals and thus is considered as the staple food (Awika 2011). The word cereal is derived from the Latin word “cerealis” which means “grain”. These crops belong to the grass family Poaceae (Gramineae) characterized by thin and long stalks. The grain usually comprises of three parts, i.e., endosperm (the part present around the embryo which provides nutrition for growth), germ (the part which becomes a plant), and the bran (hard outer covering of the grain) (Sarwar et al. 2013).

In the form of whole grain, it is a rich source of a number of nutrients such as starch, fats, oils, vitamins, and proteins. But when processed and converted into a refined form, bran and germ are removed and the endosperm is left which serves as a rich source of carbohydrates in the human diet (Sarwar et al. 2013). To fulfill the need of carbohydrates in our body, cereals are included in the daily diet. In wheat, proteins comprise of about 7–22% and in rice, it is the second major nutrient. Monosaccharides and disaccharides are also present but in a lesser quantity. Different kinds of oils and triglycerides along with some other nutrients are also present.

A diversity of endophytes has been isolated from cereal crops as well and the most extensively studied crops are wheat and maize (Larran et al. 2007; Sapkota et al. 2015; Yadav 2017). These endophytic species are reported to enhance the growth of the aforementioned cereal crops in nutrient depleted areas (Bokati et al. 2016; Yadav et al. 2019a). Research has been performed to assess the effect of abiotic factors on the growth of the plants in association with fungal strains. Different factors such as the intensity of light, availability of nutrients, and pH have been studied. Variations in plant growth were observed in the presence of fungal endophytes; however, the changes were specific for specific plant–fungal association. This indicated that the influence of abiotic factors usually depends on the plant–symbiont association and interaction (Kia et al. 2017).

This chapter describes the importance of endophytic fungal association with cereal crops. These symbiotic fungal species play a significant role in enhancing the plant growth along with providing resistance and tolerance against diseases and stress factors. They have also proven themselves as promising candidates in a number of biotechnological applications. Due to the production of a plethora of substances, secondary metabolites, and enzymes, they have the potential to be used in various industries such as medicine and agriculture.

2.2 Biodiversity of Endophytic Fungal Communities

Fungal endophytes, in association with the plants, are an indispensable element of the plant microbiome. These endophytes are ubiquitously present in nature (Herrera et al. 2013) and variation is found among these endophytes in different geographical locations (Weiss et al. 2011) such as Arctic tundra, mangroves, grasslands and savannahs, tropical and temperate forests as well as hot deserts (Arnold and Lutzoni 2007). It has also been reported that there is a limited number of fungal endophytes in places at higher latitudes but the number increases in the tropical regions. Plants that are reported to possess these fungal communities include mosses, non-vascular plants, ferns, flowering plants, and conifers (Arnold 2007; Suman et al. 2016; Yadav et al. 2018b).

The diversity of these species is also marked by the host specificity. Studies show that there can be only one host plant or a particular range of host plants with which the association can be made. Through this "host specificity", fungal species are restricted to a particular plant or a group of plants. Another important term is the "host recurrence" which is defined by the frequency of occurrence of an endophyte within a particular plant host, or a range of plant hosts, in a particular habitat. The phenomenon of "host selectivity" is also there according to which the endophyte has the capability to be in relationship with a number of plants but still the endophytic species will show a preference toward one particular plant. Host selectivity is most commonly termed as "host preference" by the mycologists (Cohen 2004; Dequn 2001; Huang et al. 2008; Rana et al. 2019a, b).

It has been reported by Dreyfuss and Chapela (1994) that approximately one million endophytic species inhabit the plants. These endophytic species are said to shape the diversity and structure of the plant microbial communities (Sanders 2004). It has been reported that out of these one million species, only 80000–100000 have been studied (Ainsworth 2008). Kumar and Hyde (2004) reported that in the tropical and temperate forests, the plants contain a high number of fungal endophytes. Prior studies have demonstrated that around as many as 17 endophytic fungal species can be isolated from a single leaf of a plant. Such observations lead to the conclusion that endophytes can be present in a large number in a single part of a plant (Gamboa and Bayman 2001). Arnold et al. (2000) also reported a large number of unculturable endophytes residing in plants of tropical forests.

2.3 Importance of Cereal Crops

Cereal crops are the staple foods which hold great importance in an individual's diet. The significance of these crops are listed below (Papageorgiou and Skendi 2018):

- These crops provide energy of 10000–15000 kJ/Kg. This is almost 10–20 times more as compared to energy provided by citrus fruits.
- They provide almost 30% of the total calories in the daily diet. In Asia, the cereals fulfill around 70–80% of the daily energy requirement of the people.
- It is a rich source of minerals which include magnesium, calcium, and potassium in a combined form of sulfate and phosphates. In low quantities, zinc, manganese, and copper are also present.
- Wheat products, which are rich in phytosterols, play an important role in minimizing the chances of breast cancer as they stimulate estrogen production.
- There are fibers present in the cereals, both soluble and insoluble, such as cellulose, pectin, and hemicellulose. They are efficient in making the peristaltic movements more effective which ultimately prevents constipation.

- There is extremely low sugar content which helps in lowering the blood sugar level.

2.4 Relation of Endophytic Fungal Communities and Cereal Crops

With the rising demands of the crops, their production needs to be increased as well. However, there are certain limitations and challenges with the traditional methods of crop production. The challenges include the application of herbicides, pesticides, and fertilizers and the impact of these chemical formulations on the environment and soil. Furthermore, the crop rotation system and increased cultivation of the crops have led to a decrease in the nutrient supply from the soil, reduction of the soil fertility and to some extent reduction in the crop yield (Kour et al. 2019b; Rees et al. 2013). Due to these problems, the challenge remains on how to meet the rising demand of cereal crops while maintaining the quality of the crops and avoiding any harm to the environment.

To address these problems, scientists have been studying the symbiotic relation of fungal communities which can enhance the productivity and sustainability of the crops. These endophytic symbionts reside in the healthy tissues within the plants and propagate within asymptomatically. They have been reported to act as “biological trigger” which will switch on the response systems of the host plants more effectively and rapidly as compared to the plants without any such symbiotic associations (Bandara et al. 2006; Redman et al. 2002). Such symbiotic relations not only help in enhancing the crop growth and yield but can also be used as biofertilizers thus causing a reduction in the harmful effects on the environment caused by the use of chemical fertilizers. These fungal communities also play a vital role in recycling nutrients in the soil and in making the quality of soil better (Karthik et al. 2016; Khan et al. 2013; Kumar et al. 2019; Ripa et al. 2019; Yadav 2019b).

2.5 Role and Importance of Endophytic Fungal Communities

In recent years, the role of endophytic fungi has been extensively studied related to plants and crops from all over the world (Vandenkoornhuyse et al. 2015). A number of important roles have been found related to this symbiotic relation:

- Increased supply and recycling of nutrients
- Protection of cereal crops and plants from abiotic and biotic stresses
- Enhancement in crop growth and yield
- Improving the biodiversity of plants in the ecosystem
- Plants' protection against different predators and other plant pathogens.

2.6 Isolation of Endophytic Fungi

2.6.1 Prerequisites for Isolation of Endophytic Fungi

For the isolation of these endophytic fungal communities, some prerequisites are to be taken into consideration. These are as follows:

- The plants at the sampling site should be healthy and free of any kind of disease. But if the research is being conducted with respect to any kind of biotic stress, then the site should be having plants that are infected and facing high malady pressure.
- There should be no previous study or research work done with the respective soil.
- Minimum exposure to the contaminants whether they are from the land, air, or water pollution.
- The piece of land under study should be inhabiting plant species of the same kind.
- There should be the active growth stage of the plants.
- Sampling is to be done under normal conditions, not after a heavy rain or a cold spell or any other infrequent weather condition, without any kind of disturbance.

During sampling, all other factors such as pH, salinity, type of soil, temperature, humidity, moisture content of soil, and nutrients in the soil should be recorded (Murphy et al. 2018).

2.6.2 Method for Isolation

The protocol for isolation of endophytic fungi is followed as given by Strobel et al. (1996). Modifications can be done according to the plant species or the type of fungal community being targeted (Radji et al. 2011). Following are the common steps which are carried out for the isolation purpose:

- Collection of plant samples which include leaves, roots, stem, or branches.
- Washing of plant samples under tap water for 10 min.
- Air-drying the samples.
- Cutting of sample into small pieces of approximately 1.0 cm in length with the help of a sterile surgical blade.
- Surface sterilization by immersing the sample in 70% ethanol for 1 min.

- Immersion of samples in 5.25% sodium hypochlorite solution for 5 min.
- Immersion of samples again in 70% ethanol for 30 s.
- Lastly, the immersion of samples in autoclaved distilled water for 3–5 s.
- Placement of the sterilized sample pieces on a plate of potato dextrose agar (PDA) containing antibiotics such as chloramphenicol (50ug/ml) and streptomycin (250ug/ml). The presence of antibiotics will not allow bacterial growth.
- Incubation of plates at 28°C for almost 10–14 days. The plates should be checked within that time for the growth of fungal isolates.
- Transfer of pure cultures into agar plates of PDA and again incubation at 28°C for almost 10–14 days.

Another method for isolation of endophytic fungi has been described by Huang et al. (2001). Following steps are included:

- Removing the outer bark of the sample.
- Cutting of the outer bark into small pieces with a sterile surgical blade.
- Grinding the pieces in the form of a paste.
- Adding the paste in autoclaved PDA medium just when the medium reaches the pouring temperature, i.e., 40–45 °C.
- Pouring the media in autoclave plates under aseptic conditions.
- Incubating the poured plates at 25 °C and keep checking the plates till the growth of hyphal tips is observed.
- Removing the hyphal tips and sub-culturing in fresh PDA medium followed by incubation at 25 °C for at least 14 days.
- Purification of cultures by transferring them into a new medium plate by the hyphal tip method.
    - The hyphal tip method involves the observation of the hyphae under a dissecting microscope at high magnification. The hyphae of interest are cut (a segment of about 1 mm thick) with the help of a sterile surgical blade and then transferred to the agar plate.

2.6.3 Characterization of Endophytes

After isolation of endophytic microorganisms, identification and characterization come as the most important step. A number of methods have been adopted by researchers for this purpose. Traditional techniques such as morphological characterization, biochemical profiling, as well as sequencing of the PCR products have been extensively used for the identification of molecular markers. Advanced technologies are now being used which include terminal restriction fragment length polymorphism (T-RFLP), denaturing gradient gel electrophoresis (DGGE), and metagenomics. These methods have paved the way toward better and precise characterization of the endophytic communities (Rodriguez et al. 2009; Yang et al. 2018). Tao et al. (2008) characterized *Bletillaochracea* for endophytic diversity and phylogenetic relationship through the DGGE technique. Berg et al. (2005) characterized the microbial communities associated with potato plant using T-RFLP technique. Sessitsch et al. (2012) characterized the endophytic microbial communities associated with the roots of rice plants through shotgun clone library construction followed by Sanger sequencing.

2.6.4 Maintenance and Preservation of Endophytic Fungi

For keeping microorganisms and endophytes in a viable state for a longer time, different preservation strategies are used. The metabolic functioning and physiological properties are maintained via these techniques. The simple techniques include the sub-culturing method, storing the cultures under oil (Smith and Onions 1994), water (Burdsall and Dorworth 1994), silica gel, or soil (Smith and Onions 1994). Other methods include Lyophilization (Onions 1971) and cryopreservation (Smith 1998) of the strains.

Following are the five major strategies used for preservation (Freire et al. 2016)

i. **Continuous Sub-culturing**: This technique was devised by Lacaz et al. (1991). This technique involves continuous transferring of the cultures to new vials having fresh sterilized PDA media followed by incubation at 25 °C.
ii. **Use of Mineral Oil for Preservation**: This method of preservation was introduced by Braz et al. (2009). 20 ml glass tubes are filled with 2 ml PDA medium and microbial strain is inoculated in the tube and incubated for 7 days. Following the incubation, a thick layer of 10 ml mineral oil (autoclaved for 2 days consecutively) is used for covering the culture tubes. The tubes are then covered with stopper, sealed with aluminum foil, and stored at 25 °C.
iii. **Use of Autoclaved Water for Preservation**: This technique was introduced by Diogo et al. (2005). 10 ml autoclaved distilled water (autoclaved for 2 days consecutively) is filled in glass tubes (20 ml). Five small segments of the fungal hyphae are taken from a 7-day old culture and transferred to the tubes. The tubes are then covered with the stopper, sealed with aluminum foil, and stored at 28 °C at room temperature.
iv. **Preservation at –20 °C**: This technique was introduced by Girão et al. (2004). Glass tubes of 20 ml are prepared having 8 ml of autoclaved distilled water, 0.5 ml dimethyl sulfoxide (DMSO), and 1 ml of glycerol (DMSO and glycerol act as cryo-protectants). All the components are subjected to autoclaving for 2 days consecutively. Five small segments of the fungal hyphae are taken from a 7-day old culture and transferred to the tubes. The tubes are then covered with stopper, sealed with aluminum foil, and stored at –20 °C.
v. **Preservation at –70 °C**: For this strategy, 0.4 ml of autoclaved distilled water, 0.025 ml of DMSO, 0.05 ml of glycerol, and 10 mg of polypropylene spheres are put in a 1.5 ml eppendorf. Small segments of the fungal hyphae are taken from a 7-day old culture and transferred to the tubes. The tubes are then covered with stopper, sealed with aluminum foil, and stored at –70 °C (Freire et al. 2016).

2.7 Specific Cereal Crops and Their Associated Endophytic Fungal Communities

2.7.1 **Triticum aestivum** *(Wheat) and Its Associated Fungal Communities*

Wheat is the major cereal crop being consumed globally. It has diverse endophytic fungal communities associated with it via symbiosis. The fungal isolates *Aspergillus flavus, Cladosporium cladosporioides, Trichoderma harzianum,* and *Fusarium proliferatum* have been majorly reported with the wheat crop. It was reported by Ripa et al. (2019) that these isolates were involved in producing plant growth promoting hormones, majorly indole acetic acid and siderophores. Majority of these isolates were able to resist the high salinity pressure of up to 7.5% and showed good growth in PDA medium. Metal resistance against copper, nickel, and cadmium was also observed which makes them promising candidates for the better growth of the crops even at areas where there is heavy metal pollution (Ripa et al. 2019).

2.7.2 **Oryza sativa** *(Rice) and Its Associated Fungal Communities*

Rice is the second major cereal crop cultivated all over the world. A number of fungal communities are associated with rice as well. Naik et al. (2009) conducted a research in which it was concluded that the major endophytes associated with rice crops were *Penicillium chrysogenum*, *Fusarium oxysporum,* and *Cladosporium cladosporioides*. These species were reported to act antagonistically against pathogenic compounds by producing different bioactive compounds. These facts can be exploited for better and enhanced crop production.

There are also reports that fungal species are also residing in the roots of the plant. Most noteworthy is the presence of *Ascomycota* phylum in which the most prominent members are *Aspergillus, Penicillium, Fusarium,* and *Trichoderma* (Santos-Medellín et al. 2017; Sharma et al. 2019). The species of *Aspergillus* and *Penicillium* are reported for the production of different organic acids (Ding et al. 2019; Khan et al. 2014).

2.7.3 **Zea mays** *(Maize) and Its Associated Fungal Communities*

Maize being an important cereal crop has a high content of vital nutrients (Ngachan et al. 2011). Maize crop is reported to be in symbiotic relation with the endophytic fungi mainly in the root area (Orole and Adejumo 2009; Potshangbam et al. 2017).

It has been reported by Potshangbam et al. (2017) that major endophytic fungal communities associated with the leaves of maize plants were *Acremonium*, *Fusarium,* and *Penicillium.* The root part of the maize plant inhabited a large number of fungal communities including *Fusarium, Trichoderma, Aspergillus, Alternaria alternate,* and *Botryodiplodia*. The study reported that *Fusarium* sp. is present in different parts of the maize plant. These endophytes are also involved in the production of different biologically important molecules that help the plant to grow better. Such beneficial associations can be exploited to synthesize biofertilizers thus minimizing the use of chemical fertilizers and the associated risks (Potshangbam et al. 2017; Shweta et al. 2010).

2.7.4 **Hordeum vulgare** *(Barley) and Its Associated Fungal Communities*

Barley being an important nutritional crop has a high content of minerals including magnesium, manganese, and selenium. Furthermore, it is considered as a storehouse for dietary fibers which play a role in keeping the gut healthy (Pourkheirandish and Komatsuda 2007). Barley plant is vulnerable to attack by several pests such as *Diuraphis noxia*, *Metopolophium dirhodum* and *Mayetiola destructor.* The endophytic fungi *Neotyphodium* is reported to be anti-herbivore and proves to be a biologically controlling agent against pest attack. This can also have many biotechnological interventions to stop the accumulation of harmful substances in plants by eliminating the use of pesticides (Clement et al. 2005).

2.8 Role of Endophytic Fungi in Plant Growth Promotion

2.8.1 Growth Promotion Mechanisms

2.8.1.1 Phosphate Solubilization

Phosphate is one of the essential macronutrients needed for plant growth. Many microbial species including fungi have the ability to solubilize phosphate leading to its mineralization (Yadav et al. 2015a, b, c). Among total population of fungi, 0.1–0.5% constitute the phosphate solubilizing fungi in which the endophytic fungi contribute majorly. Important endophytic P-solubilizing fungi belong to genera *Aspergillus, Penicillium, Curvularia, Fusarium,* and *Candida* (Mehta et al. 2019). Phosphate solubilization is highly dependent on the tendency of the microorganisms to produce organic acids in the surrounding environment. These organic acids form complexes with calcium, iron, and aluminum present in the soil to convert low soluble phosphate into soluble one through chelation and exchange reactions. Low pH is required to make insoluble phosphate available to the plants in the form of soluble phosphates. Organic acids such as citric acids, gluconic, and ketogluconic acid lower the pH of the environment, thus providing the medium in which insoluble metal part of the phosphate is exchanged with sodium or magnesium resulting in soluble phosphate salt (Behera et al. 2017; Yadav et al. 2016). Organic acids also increase the accessibility of phosphate for the plants by blocking phosphate adsorption sites on soil particles or by forming complexes with cations on mineral surfaces of soil (Rodríguez and Fraga 1999). On the other hand, insoluble part of phosphate can be released with the help of enzymes such as phytase and phosphatases which are released by the microorganisms including endophytic fungi. Acid phosphatases (AcPase) are unique sets of enzymes mostly located in the cell wall of many microorganisms. They hydrolyze phosphomonoesters at acidic pH by transferring a phosphoryl group to alcohol in the presence of certain phosphate acceptors. Acid phosphatases production by *Serratia* sp. is well documented and directly related to plant growth promotion (Behera et al. 2017). With the help of this mechanism, soil fertility and plant growth are enhanced by the "phosphate solubilizing microorganisms" (Adhikari and Pandey 2019). Spagnoletti et al. (2017) described the solubilization of phosphate in the presence of iron, calcium, and aluminum by dark septate endophytic fungi and reported that phosphate solubilization was maximum in calcium phosphate ranging from 42.87 ± 5.37 to 51.33 ± 1.87 μgml^{-1}. Microbial phosphate solubilization is one of the major events that contribute to promotion of the plant growth (Tarafdar and Gharu 2006).

2.8.1.2 Synthesis of Siderophores

Siderophores are iron binding compounds of low molecular weight (500–1000 Dalton). These extracellular agents are synthesized by the many microorganisms including bacteria and fungi present in iron deficient soil (Crowley 2006). These compounds are helpful in chelating Fe(III) and its subsequent transport into cells for growth. Microbial siderophores, therefore, help the plants to scavenge iron required for their growth. Endophytic fungi *Acremonium sclerotigenum* from host tree *Terminalia bellerica* produce siderophores that not only help in the uptake of iron by the plant but also act as a biocontrol agent against many pathogens (Prathyusha et al. 2015; Wang et al. 1993). *Epichloe festucae*, a foliar endophyte of perennial ryegrass, has the ability to produce extracellular fusarinine and intracellular ferricrocin that promote the growth of the host plant by mobilizing iron (Kajula et al. 2010). *Phialocephala fortinii*, a dark septate fungi found in endophytic relationship with *Pinus sylvestris*, *Abies alba*, *Picea abies,* and *Carex curvula*, have the ability to produce three different types of siderophores such as ferricrocin, ferrirubin, and ferrichrome C in low iron conditions (Bartholdy et al. 2001). As these microorganisms contribute to the availability of iron to the host plant, these can also have the potential to serve as biofertilizers (O'Sullivan and O'Gara 1992).

Moreover, siderophores can also serve as a type of biocontrol. In this process, siderophores complement the lytic activity, antibiosis, and hormonal effect of endophytes to decrease the growth of other competing microorganisms and plant pathogens in their vicinity (Neilands and Leong 1986).

2.8.1.3 Phytohormone Production

The roots of plants which are colonized by endophytic fungi such as *Phoma glomerata*, *Porostereum spadiceum*, *Penicillium*, and *Aspergillus sp.* produce many phytohormones as compared to the plants which are not colonized (Joshi et al. 2018). Thus, one of the major contributions of the endophytic fungi is the production of plant growth promoting stimulators known as phytohormones which include abscisic acids, ethylene, auxins, cytokinins, and gibberellins. Their classes, roles, and functions are discussed in Table 2.1.

Table 2.1 PGR produced by endophytic fungi and their attributes towards plant growth promotion

PGRs	Attributes toward plant growth	Endophytic fungi producing PGPR	Reported studies
Auxins (IAA)	Positive effect on root growth, Cell division	*Phoma glomerata, Penicillium* sp.	Vessey (2003), Gravel et al. (2007), Waqas et al. (2012)
Cytokinins	Cell division, Inhibits senescence	*Fusarium* sp.	Li et al. (2012), Waqas et al. (2012), Shah et al. (2019)
Gibberellins	Cell elongation, Promote Flowering	*Porostereum spadiceum, Phoma glomerata, Penicillium* sp.	Waqas et al. (2012), Tanimoto (2005), Hamayun et al. (2017)
Abscisic acids	Abscission of leaves and fruits, Dormancy induction of buds and seeds	*Aspergillus nidulans, Glomus intraradice.*	Forchetti et al. (2007), Herrera-Medina et al. (2007), Brader et al. (2014), Xu et al. (2018)
Ethylene	Promotes senescence, epinasty, Major role in fruit ripening	*Piriformospora indica, Arabidopsis thalian, Fusarium solani.*	Camehl et al. (2010), Kavroulakis et al. (2007)

Among different types of auxin, indole-3-acetic acid (IAA) is a natural and most common auxin and its beneficial effects on the growth of plant roots enable them to absorb nutrients efficiently from the soil (Vessey 2003). It promotes the cell division and root growth leading to the differentiation of root nodules and increase in the surface area of roots. However, root tissues are sensitive to IAA concentration and when its concentration exceeds beyond the required limit, the root elongation is stopped (Gravel et al. 2007; Tanimoto 2005).

Auxin is responsible for cell elongation by increasing the turgor pressure due to the presence of dissolved solute. Here is the acid-growth hypothesis which postulates this mode of action of auxin.

- Production of IAA stimulates the H^+ pumps present in the cell membrane.
- Once H^+ pumps are activated, H^+ ions are pumped into the cell wall decreasing the pH.
- When the environment of the cell wall is acidified, it stimulates the pH dependent enzymes which cause bond breakage between the microfibrils of cellulose present in the cell wall.
- The cell wall expands due to nutrients and solutes which elongate the cell wall and ultimately enlarge the size of the cell.

Endophytic Fungi can also tolerate stress of drought and salinity and can still support the plant cells by the production of plant growth stimulators. Such stress conditions can cause plants to wilt and start senescence and can even cause the death of the plants (Iqbal and Ashraf 2013). Waqas et al. (2012) reported that endophytic fungi such as *Penicillium* sp. and *Phoma glomerata* association result in tremendous shoot growth, plant biomass, and chlorophyll ratio. These endophytes are involved in the production of phytohormones such as gibberellins with class GA_3. GA_3 helps in flowering of the plants as well as in cell elongation. Another study by Khan et al. (2012) reported endophyte *Paecilomyces variotii* LHL 10 present in cucumber roots that could produce a high amount of IAA and gibberellins.

2.8.1.4 Biological Nitrogen Fixation

Biological nitrogen fixation is one of the most important biological processes exhibited by microorganisms. The association between the host plant and the nitrogen fixing microorganisms is either symbiotic or asymbiotic. Many endophytes are also involved in this process. Plant internal environment is high in carbon and low in oxygen which is a favorable environment for the fixation of nitrogen by endophytes. This again is beneficial for the host plant (Ladha and Reddy 2003; Patle et al. 2018).

2.8.2 Endophytic Fungi as "Biocontrol" Agents

One of the major roles of endophytic fungal communities is as the biocontrolling agents which play an essential role in protecting the host plant against its predators and insects (Rana et al. 2018; Yadav et al. 2019d). It has been reported by Mirlohi et al. (2004) that the plant roots in absence of any endophytic fungi get infected with insects and pests while those which are in association with endophytic fungi are not harmed by the predators. The fungal endophytes act as biocontrol agents by the production of different fungal metabolites which include indole di-terpenes, ergot alkaloids, peramine, and the lolines which are described as follows (Malinowski and Belesky 2000):

- The class indole di-terpenes include lolitriol and paxilline. This class chiefly acts as neurotoxins. Moreover, they are tremorgenic toward small insects and mice, therefore, known for the anti-insect activity.
- Among the ergot alkaloids, the compound ergovaline is the most effective in keeping the insects away especially the stem weevil.
- The remaining two groups of metabolites, i.e., loline and peramine are less essential but are known for their activities against the insects and pests (Mirlohi et al. 2004).

2.9 Biotechnological Significance of Endophytic Fungi

2.9.1 Production of Secondary Metabolites

Secondary metabolites are the compounds that are not supporting plant growth directly but are involved in its protection. Approximately 80% of fungal endophytes produce bioactive compounds with antimicrobial and herbicidal properties. They are also a rich source for many other secondary metabolites such as antifungal, anticancer, and antiparasitic compounds (Joshi et al. 2018; Krohn et al. 2002). Many endophytic fungi have the ability to protect host plant against soil borne pathogens such as *Aspergillus fumigatus, Botrytis cinerea, Blumeria graminis, Fusarium culmorum, Globisporangium ultimum, Monilinia laxa, Moniliophthora perniciosa, Penicillium expansum, Phytophthora* sp*, Plasmopara viticola, Puccinia polygoni-amphibii,* and *Sclerotinia sclerotiorum* and thus help plant to survive (Yadav 2018; Yadav et al. 2019a, b, c). Reported mechanisms involve the mycoparasitism, antibiosis, cell wall degradation, and induction of defense response (Zhang et al. 2014). *Piriformospora indica* is a plant root endophytic fungi showing resistance against phytopathogen *Fusarium culmorum* (Waller et al. 2005; Zheng et al. 2016).

Apart from bioactivity against plant pathogens, the fungal endophytes, from the plant *Aquilaria sinensis*(agarwood),have exhibited anticancer property against different human cancer cell lines such as HL-60, 293-T, and HepG2 (Cui et al. 2011). Antimicrobial activity has been displayed by the endophytes from *Dendrobium devonianum* and *Dendrobium thyrsiflorum* which have the ability to produce inhibitory molecules against *Candida albicans, Cryptococcus neoformans, Escherichia coli, Staphylococcus aureus, Aspergillus fumigates,* and *Bacillus subtilis.* Medicinal plant *Stryphnodendron adstringens* harbors endophytic fungi that produce antimicrobial agents active against *Candida albicans* and *Cladosporium sphaerospermum*. They are also reported to inhibit the growth of the cancer cells MCF-7 and TK-10(Carvalho et al. 2012).

2.9.2 Resistance Against Heavy Metals

Heavy metals are harmful to plants as they produce oxidative stress. Plants have many mechanisms to tolerate them (Idris et al. 2004). Some plants are metal tolerant while some are hyperaccumulators. Hyperaccumulators such as *Alyssum bertolonii, Alnusfirma, Brassica napus, Nicotiana tabacum, Thlaspi caerulescens, T. goesingense,* and *Solanum nigrum* have certain endophytes associated with them that help them tolerate metal stress. Endophytes such as *Microsphaeropsis, Mucor, Phoma, Alternaria, Peyronellaea, Steganosporium, and Aspergillus* are known to help the plant in metal resistance and detoxification (Bai et al. 2012; Yadav et al. 2018a).

2.9.3 Role in Phytoremediation

Endophytic fungi are also known to facilitate the host plant in phytoremediation by protecting the plant from different contaminants present in the polluted contaminated soil. Endophytic fungi *Phomopsis liquidambari* have ability to produce the enzyme which can degrade phenolic acid allelochemicals such as 4-hydroxybenzoic acid released by the decomposing foliage. These allelochemicals have negative impacts on the plants as these slow down the growth of the plants and the bacterial population present in the soil (Chen et al. 2011; Kour et al. 2019b; Rana et al. 2019b).

2.9.4 Production of Extracellular Enzymes

Many endophytic fungi species have the ability to produce enzymes that have biotechnological and industrial importance. Many extracellular enzymes such as cellulases, chitinases, laccase, pectinases, xylanases, proteases, amylases, β-galactosidase, and other catabolic enzymes are produced by endophytic fungi. Chitinases produced by the endophytic fungi *Neotyphodium* sp. has the ability to break down the chitin which is present in the phytopathogen cell wall. Another fungal endophyte *Sarocladium zeae* isolated from maize produces hemicellulase which is an enzyme involved in bioconversion of lignocellulosic biomass into sugars which are then easily fermented (Bischoff et al. 2009; Kour et al. 2019a; Zheng et al. 2016).

2.9.5 Biotransformation and Nutrient Recycling

Biotransformation is the conversion of one chemical compound to another one with the help of a biological agent. Many endophytic fungi are also known to perform this function. Different types of transformation reactions may activate or inactivate a certain compound. Zikmundova et al. (2002) reported biotransformation of phytoanticipins 2-benzoxazolinone (BOA) to N-(2-hydroxyphenyl) malonamic acid by endophytic fungi isolated from *Aphelandra arborea* (Malyan et al. 2019).

Nutrient recycling is one of the important mechanisms exhibited by endophytic fungi. In this process, essential nutrients are balanced so that they become available for the natural ecosystem. *Phomopsis liquidambari* is one such endophytic fungi that have the ability to stimulate mineralization and facilitate the ammonium release in the environment which provokes the nitrification process by bacteria present in the soil (Chen et al. 2013; Yadav and Yadav 2018).

2.10 Ecological Significance of Endophytic Fungi in Plant Protection

Endophytic fungi have a major role in the degradation of dead host plants and thus help in the recycling of the nutrients in the environment (Boberg et al. 2011). Fungal endophytes enable the plant to tolerate stress conditions such as drought, salinity, and pH by Induced Systemic Resistance (ISR), bioremediation, and protection (Yadav 2019a). Endophytic fungi produce metabolites against insects. One of the anti-insect metabolites is anthraquinone metabolite called rugulosin discovered from the endophyte *Abies balsamea* and later from *Picea scopiformis* and *Picea glauca.* The compound was found to reduce the growth rate of *Choristoneura fumiferana*, *Lambdina fiscellaria,* and *Zeiraphera canadensis* (Joshi et al. 2018; Sumarah et al. 2008).

2.11 Conclusion and Future Prospects

It can be concluded that plant–fungal associations thrive under the principle of mutualism where both the partners are getting benefit from each other. Such endophytes play an important role in plant growth promotion as these provide resistance to plant against different environmental stresses and toxic compounds, protect host plant against several pathogens, and produce many plant growth promoting hormones. Endophytic fungi are also significantly important as biotransformers of different chemicals and help in the recycling of nutrients. These are also known to produce many metabolites that have medicinal importance such as anticancer and antimicrobial compounds. The endophytes also find many industrial usages as they are known for the production of many important enzymes and metabolites. Advance studies in genetic engineering, metagenomics, metatranscriptomics, and proteomics could be employed for better understanding of the molecular mechanisms behind these abilities, and to exploit them further for different biotechnological processes.

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Chapter 3
Current Perspectives on Phosphate-Solubilizing Endophytic Fungi: Ecological Significances and Biotechnological Applications

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Abstract Phosphorus is one of the essential nutrients for optimum plant growth after nitrogen. Their structural and chemical complexity greatly reduces their availability to the plants and is one of the major limiting macroelements to plant growth. Phosphorus is present in both organic and inorganic forms. Though abundant amount of phosphorus is present in the soil, its availability is reduced by various environmental factors that influence bio-geo-cycling of phosphorus. Current research is mainly focused on the exploitation of endophytic fungi for solubilization of phosphorus in an efficient way. Endophytic fungi including the genera *Aspergillus, Penicillium, Piriformospora, Trichoderma, Curvularia,* and other class of endophytic symbionts such as AM fungi are identified as potent Phosphate solubilizers. Endophytic fungi promote plant growth by a variety of mechanisms such as solubilization of "P"-like macronutrients by different reactions, able to produce bio-control agents, i.e., antibiotics and siderophores and plant protecting agents against pathogens, synthesis of growth hormones such as gibberellins, cytokines, and auxins. Phosphate-solubilizing endophytic fungi are promising and efficient organisms capable of increasing "P" availability and the best alternative approach to chemical fertilizers.

Keywords Endophytic fungi · Biotechnological applications · Ecological significance · Inorganic and organic phosphates solubilization

3.1 Introduction

Soil microorganisms greatly influence the nature of the soil and its health through beneficial and harmful activities. Microorganisms present in the rhizosphere mediate certain functions, for instance, decomposition, nutrient immobilization, mineralization, nitrogen fixation, and release of nutrients. In addition to these, microorganisms

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also possess phosphate-solubilizing ability by converting insoluble phosphates to soluble phosphorus (Pradhan and Sukla 2005) in soil and make them readily accessible to plants.

The father of plant pathology de Bary proposed the term endophyte to refer any organism that resides within plant tissue exclusive of any disease manifestations in host plant (Nisa et al. 2015). All types of plants harbor a wide variety of microorganisms, for instance, fungi, bacteria, and cyanobacteria that posses endophytic properties and play an imperative role in plant metabolism and physiology (Hardoim et al. 2015). During symbiotic association established between endophytes and host plants, both the organisms get mutually benefited, the plant provides nutrients to colonizing endophytes, while the endophytes accelerate biosynthetic pathways for metabolite synthesis that have many applications in agronomy. For example, management of plant growth and novel disease-resistant mechanisms against pathogens.

Endophytes can be isolated from exterior or interior part of sterilized plant tissues. Significant biochemical molecules such as Terpenoids, isoflavonoids, flavonoids, and phenolics are released from plant roots. They may attract the fungi from root region to colonize within the plant as an endophyte. However, the endophytes are depicted to be colonized in different plant tissues associated with the different ecosystems. Fungi can be classified into diverse groups derived from their role and survival, such as epiphytic, endophytic, pathogenic, and mycorrhizal fungi (Porras-Alfaro and Bayman 2011). Some endophytic fungi can find their way to either vertical or horizontal root region and penetrate to the deeper regions of plants.

Endophytic fungi colonize the tissues of host plant by particular route of transmission and this can be either vertical or horizontal method. Endophytic fungi transmit from the mother plant to offspring via seeds (true endophytes). A study carried out by Hodgson et al. (2014) in forbe species, common poppy, knapweed, cornflower, sheep's sorrel, groundsel, and ribwort plantain, and two endophyte species, *Cladosporium sphaerospermum* and *Alternaria alternata* primarily investigated the vertical transmission of species. Horizontal transmission occurs by airborne spores or through soil. Endophytes colonize forbes via leaves of the host through horizontal transmission.

According to earlier fossil records, evolutionary tendency reveals an association between a diverse group of plants and endophytic fungi. Plant endophyte communications resulted in plant growth promotion, uptake of micronutrients, and synthesis of different types of secondary metabolites and bioactive compounds with potential applications in industry, medicine, and agriculture. Endophytic fungi provide protection to plants against plant pathogens, reduce biotic and abiotic stresses, and for the reason that these organisms are considered as eco-friendly bioresources. Endophytic fungi may enhance plant growth by solubilization of potassium, phosphorus and zinc, produces phytohormones, viz., cytokines, gibberellic acids, indole acetic acids, hydrolytic enzymes and Fe-chelating compounds, ammonia and hydrogen cyanide (Rai et al. 2014). Different classes of fungi, for instance, Mucoromycota, Basidiomycota, Oomycota, and Ascomycota were depicted as plant growth promoters and protect the plants under anomalous and abiotic stress conditions. Natural products produced by endophytes were previously reported with potential anti-bacterial, anti-fungal, and anti-protozoal properties. Nonetheless, the secondary metabolites produced by endophytes are proved to have remarkable anti-cancer, anti-microbial, insecticidal properties, pharmaceutical sciences, and in other biotechnological applications (Kusari et al. 2011; Aly et al. 2010; Uzma et al. 2018; Mishra et al. 2017).

3.2 Diversity of Phosphate-Solubilizing Microorganisms

A great extent of microbial species exhibit phosphate-solubilizing ability, these include archaebacteria, bacteria, actinomycetes, and fungi. These microbes reside in the plant tissues exclusive of causing any harmful effects to the host. Generally, they prevail in tissues of the host plant with the symbiotic association. These microbes were previously isolated from different types of plants, including *Triticum* (Yadav et al. 2018a; Verma et al. 2015, 2016a, b), *Oryza sativa* (Piromyou et al. 2015), *Zea mays, Capsicum annuum L.*, *Saccharum officinarum* (Montanez et al. 2012; Thanh and Diep 2014), mustard, citrus (Kasotia and Choudhary 2014), *Solanum tuberosum* (Rado et al. 2015; Manter et al. 2010;), *Glycine max* (Mingma et al. 2014), *Pisum sativum* (Narula et al. 2013; Tariq et al. 2014), *Phaseolus vulgaris* (Suyal et al. 2015), *Helianthus* (Forchetti et al. 2010; Ambrosini et al. 2012), and *Cicer arietinum* (Saini et al. 2015). Fungal endophytes pertaining to diverse genera including *Acremonium, Aspergillus, Paecilomyces, Cryptococcus, Fusarium, Curvularia, Rhodotorula, Cladosporium, Alternaria, Phaeomoniella, Chaetomium, Colletotrichum, Berkleasmium, Rhizoctonia, Geomyces, Leptospora, Phyllosticta, Microdochium, Neotyphodium, Ophiognomonia, Glomus, Penicillium, Rhizopus, Trichoderma, Xylaria,* and *Wallemia* have been isolated from various host plants (Suman et al. 2016; Verma et al. 2017; Yadav et al. 2018a, b). Recently, a nematode fungus *Arthrobotrys oligospora* was identified to solubilize rock phosphate Togo, Tilemi rock phosphate, Kodjari phosphate rock. The fungi solubilized all three types of rock phosphates. Given these, Duponnogs and group (2006) demonstrated the phosphate solubilization ability in vivo conditions.

3.3 Biotechnological Applications of Natural Products from Endophytic Fungi

Biotechnology has opened up numerous avenues for exploitation of endophytic microorganisms in medicine, agriculture, and industry from diverse ecological niches and their applications in agriculture are aptly essential for plant growth, plant protection, and yield (Yadav et al. 2018a; Rana et al. 2019c). Because of their ability to promote plant growth and adapt under extreme abiotic stresses, the endophytic microorganisms have, in fact, captured the attention of the scientific community

(Soni et al. 2018; Yadav et al. 2019b, c, d). With the exceptional capacity to produce secondary metabolites, the endophytic fungi may perhaps unearth novel applications in pharmaceuticals, industrial processes, and horticulture (Joseph and Priya 2011). Endophytic bacterial and fungal organisms possess extensive applications as biocontrol agents, bio-inoculants, and bio-fortification of micronutrients (Yadav 2019; Yadav et al. 2019a; Yadav and Yadav 2019).

The excessive usage of chemical phosphorus (P) fertilizers to increase agricultural yield sequentially to meet the requirements of escalating global food demand potentially causes soil and water pollution, eutrophication, depletion of soil fertility, and deposition of toxic heavy metals such as arsenic (As), lead (Pb), and selenium (Se) in the soil. Abundant soil microbes together with bacteria, fungi, actinomycetes, and algae are efficient in solubilizing insoluble soil phosphate to convert into the soluble P and making it available to plants. Strikingly, these microbes promote the growth and yield of a wide variety of crops. Thus, it is essential to inoculate phosphate-solubilizing microorganisms (PSM) via the seeds, to the crop and soil, which is a potential strategy to improve the crop yield. Despite their immense significance in the improvement of soil fertility, phosphorus-solubilizing microbes are yet to replace conventional chemical fertilizers in commercial agriculture. Extensive studies are obligatory to comprehend recent approaches in a diversity of phosphate-solubilizing endophytes and their colonizing ability and application to enhance agronomic yield.

3.4 Endophytic Fungi as P-Solubilizers and Growth Promoters

Phosphate-solubilizing fungi enhance plant growth by different mechanisms and those are (Fig. 3.1): provide nutrients to plant by solubilization process, produce biological control substances, i.e., antibiotics and siderophores, provide protection against the plant pathogens, and stimulate growth hormones production (auxins, gibberellins, and cytokines). In agriculture, phosphate-solubilizing fungi play a significant role as bio-inoculants for improvement of plant growth (Khan et al. 2010; Kour et al. 2019b, c; Rana et al. 2019a, b). The competent phosphate-solubilizing fungi were tested under in vitro conditions and selected for large-scale production and eventually distributed to farmers. In addition to that, suitable carrier selection is also paramount for the development of fungal inoculants such as peat, farmyard manure, soil, cow dung, and cafe powder which are being used as suitable carriers. However, a perfect carrier is designed to possess some unique qualities like good absorption ability, sufficient level of moisture pH, aeration stability, pH buffering capacity, and porousness. In addition to these characteristics, the carrier must be eco-friendly, non-hazardous to microbes, plants, animal, and humans. In addition to this, it should be easy to handle, mix, sterilizable, and store. Keeping in view of cost–benefit ratio, the carriers ought to be cheaper and easily available. The carrier enhances the persistence of phosphorus-solubilizing activity; fungal spores after mixing with a carrier can be

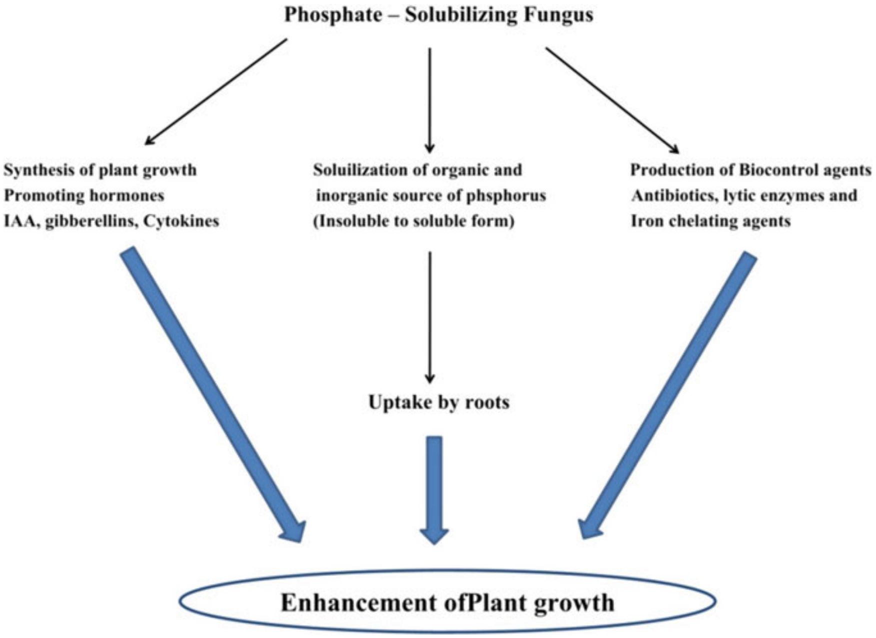

Fig. 3.1 Mechanisms of plant growth acceleration by endophytic P-solubilizing fungi

stored for about 3 months at 30 ± 2 °C. Plethora of examples of commercially available inoculants, i.e., *Penicillium radicum* and *Penicillium bilaiae* were demonstrated in large-scale production and shown to possess "P" absorption ability. Various stages involved in bulk scale production and application of P-solubilizing fungi are clearly depicted (Fig. 3.2).

Various studies indicating the effect of a single culture and/or mixed culture of phosphate-solubilizing fungus on different plant growth parameters observed the effect of mixed inoculation of P-solubilizing fungal strains (two strains of *A. awamori* and four of *P. citrinum*) on growth and seed production of chickpea in pot experiment. Notably, all the isolates were shown synergistic effect and resulted in noteworthy stimulation of root and shoot lengths of legume, height of the plant, seed weight, and number compared to the un-inoculated control.

Phosphorus is a vital nutrient and a part of structural compounds and mediates catalytic reactions in plant metabolism. Phosphorus plays a major role in capturing solar energy and is converted into useful plant compound. Phosphorus is a key component of DNA and RNA. Two phosphate-solubilizing fungi, i.e., *Penicillium oxallicum* P4 and *Aspergillus niger* P85 were isolated by Yin et al. (2015) from calcium-rich soils of China. A remarkable increase in plant fresh weight was observed in strain p24 when rock phosphate was supplemented externally. A study carried out on *Aspergillus aculeatus* P93 has also shown a significant increase in the availability of soluble phosphorus of maize grown in non-amended soil (Yin et al. 2017).

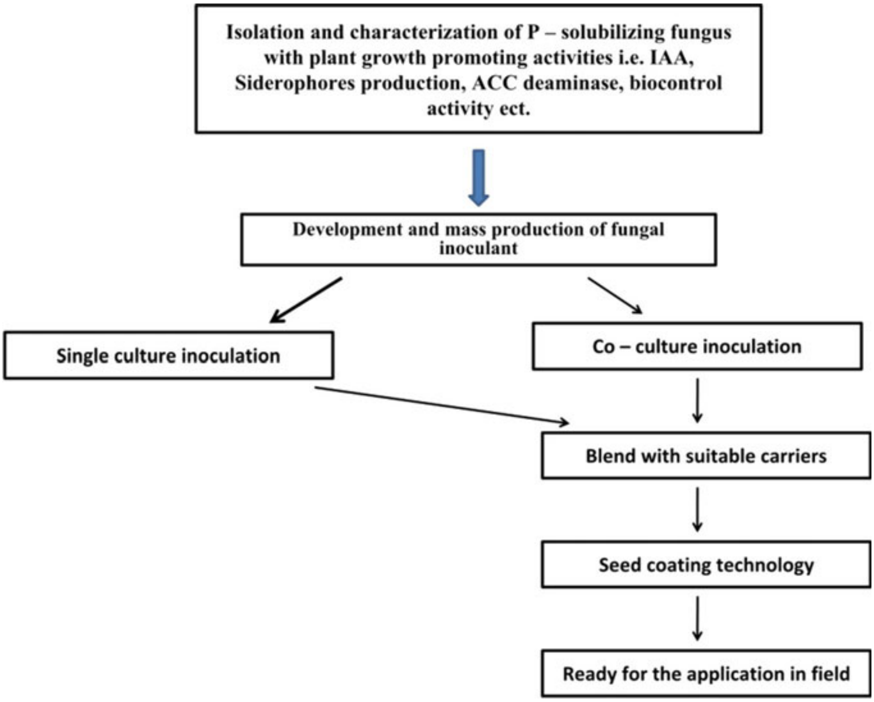

Fig. 3.2 Production and application of phosphate-solubilizing endophytic fungal inoculants

In a recent study, phosphate-solubilizing microorganisms depicted a synergistic effect on plant growth parameters and leaf chlorophyll content (Senthil kumar et al. 2018). In addition to solubilizing phosphates, some may produce potential bio-control agents against plant pathogens. PSM can produce anti-fungal compounds such as flavonoids and phenolics, siderophores, antibiotics and hydrolytic compounds. All of which inhibits growth of plant pathogens.

3.5 Phosphate Solubilization Mechanism by Endophytic Fungi

Based on the availability of type of phosphates (organic or inorganic), endophytic fungi employ suitable mechanism for solubilization of phosphates and endophytic fungi are capable to synthesize organic acids, proteins, OH^- ions, Ca^{+2} exopolysaccharides, CO, siderophores, and enzymes, those may play a significant role in phosphate solubilization (Fig. 3.3).

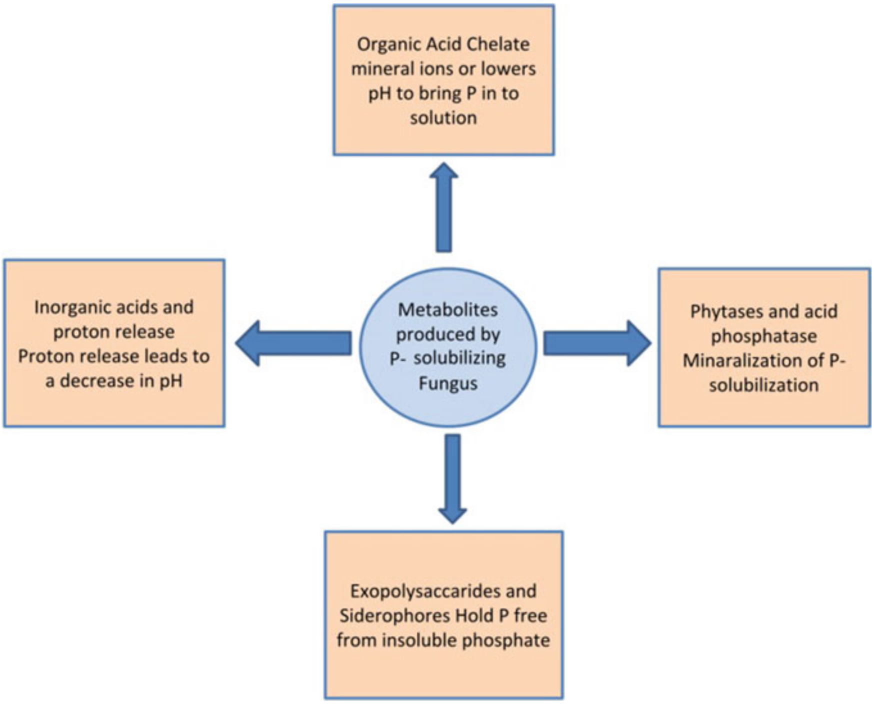

Fig. 3.3 Production of metabolites by P-solubilizing fungi

3.5.1 Inorganic P-Solubilization

Various theories explained the key mechanism underlying the inorganic phosphate solubilization. The principal mechanism is dissolving compounds such as hydroxyl ions, siderophores, organic acids, carbon monoxides, proteins, extracellular enzymes, and exopolysaccharides (Sharma et al. 2013). Secretion of organic acids by endophytic fungi into soil seems to be a most important mechanism for inorganic phosphate solubilization primarily organic acids such as glycolic, maleic, formic, lactic acid, gluconic acid, oxalic, tartaric propionic, and succinic acids. The quantity of organic acid varies with the endophytic fungal strain and also the type of organic acid produced is greatly determined by source of insoluble phosphorus. According to Mendes et al. (2013), *Aspergillus niger* FS1 primarily secrete oxalic acid in higher quantity in treatments with $FePO_4$ and $AlPO_4$, whereas gluconic acid was produced in meager quantity in $AlPO_4$. In contrast to this, *Penicillium canescens* FS23 produced citric and gluconic acids after treatment with $Ca_3\ (PO_4)_2$, $AlPO_4$, and rock phosphate. Organic matter present in soil is an excellent source of organic phosphorus. The total quantity of organic phosphorous present in soil is as high as 30–50% of total phosphorus. Organic phosphorus in the soil is principally in the form of inositol phosphate (or) soil phytates. Organic phosphorus can be mineralized with the involvement of enzymes such as phosphatases, phytases.

Many studies explained about p-solubilization based on an organic acid concept. Several genes are involved in production of organic acids. Among all organic acids, gluconic acid is more essential in P-solubilization produced by endophytic fungi. The genetic basis of P-solubilization was studied by Kusari et al. (2012). He observed upregulation of pyrroloquinoline quinine and glucose dehydrogenase genes in solubilization of phosphorous. PQQ-dependent glucose dehydrogenase present on cytoplasmic membrane stimulates oxidation of glucose to gluconic acid. Because of production of gluconic acid, the pH of the soil further decreases which make the following ions HO_4^{-2} and HPO_4^{-3} (soluble forms of phosphorus) more available. An array of genes is involved in the production of organic acids.

3.5.2 Organic P-Solubilization

Mineralization of organic phosphate carried out by involvement of various enzymes, i.e., phytases, phosphonatases, and phosphatases. Phosphatases dephosphorylation or hydrolyze and phosphoanhydride and organic phospho-ester bonds of organic matter. Among all phosphatases, predominant types of enzymes are phosphomonoesterases (Nannipieri et al. 2011). Based on pH optima they are classified as acid and alkaline phosphatase (Behera et al. 2014). Several genes encoding for alkaline and acid phosphatases with broad substrate specificity were cloned and characterized. However, a considerable amount of phosphatases was secreted by plant roots, and it has been reported that microbial phosphates possess a stronger affinity for substrate when compared to derived by plant phosphatases.

A large quantity of phosphorus is found in fruits and seeds for the reason that it is important for the development of seeds. Phytin is a significant form of "P" in seeds. Phytin is naturally degraded by phytases. This is the main source of inositol phosphate and constitutes for more than fifty percent of organic phosphorus in the soil. Phytases act upon phytate and make available free form of phosphorus. Noteworthy that the phosphonatases and carbon-phosphorus lyases hydrolyze carbon-phosphorus bond of organophosphates and release free phosphate (Rodriguez et al. 2006). Because of scarcity, organo-phosphatases do not add much to the soluble form of phosphate in the soil solution. A plethora of studies revealed that organic acids released by P-solubilizing fungi are much superior to bacteria; therefore, endophytic fungi exhibit greater P-solubilization activity. Motsara et al. (1995) revealed that solubilization of rock phosphate was much higher under in vitro conditions by *Rhizoctonia solani*, Penicillium*,* *Fusarium oxysporum,* and *Aspergillus niger*.

3.6 Development of Phosphate-Solubilizing Endophytic Fungal Inoculants

Phosphates-solubilizing endophytic fungal inoculants are used as major bio-fertilizers. These bio-inoculants are more eco-friendly when compared to chemical fertilizers. Fungi are depicted as predominant P-solubilizing inoculants when compared to other bacterial inoculants; hence, these strains hold much importance in agriculture. Nonetheless, several fungal bio-fertilizers were already developed by IARI as bio-inoculants which comprises *Aspergillus awamori, A. niger,* and *P. digitatum, P.bilaii* strains which were commercialized by Novozymes Biologicals Limited (Canada). Interestingly, the strain *P.radicum* was recently developed by Bio-Care Technology (Australia) by Gupta and Rodriguez Couto (2018). Similarly, in India, P-bio-fertilizers were produced by Ambika Biotech and Agro Services (Madhya Pradesh) (Pal et al. 2015).

For production of P-solubilizing fungal inoculums, huge amount of endophytic fungal strains are required. There are broadly three phases in development of bio-fertilizers. In the first phase, there is a selection and screening of potential phosphate solubilizers followed by a selection of fungal inoculants. The screening process can be carried but by the cultivation of fungi in modified Pikovskaya's medium. In second phase, proper endophytic fungal bio-fertilizers can be developed and the third phase includes checking the quality and persistence of P-solubilizing microorganisms and distribution to farmers (Khan et al. 2010; Kumar et al. 2017). Notably, few potent microorganisms are selected, screened, and cultivated in large scale for production of bio-fertilizers under optimized conditions in a suitable fermentation broth. For cultivation of fungi, lower pH (acidic condition) is more suitable at the same time inhibits the bacterial contamination (Nelofer et al. 2016). Once an adequate amount of growth is obtained, the biomass can be extracted and mixed with suitable pre-sterilized carrier material, purified, packed under aseptic conditions, and stored under appropriate conditions before commercialization. At every stage of bio-fertilizer production, it is mandatory to assess the level of contamination as well as for the amount of desired microorganisms.

Definite problems may also be associated with the commercial-scale synthesis of bio-fertilizers, among those sometimes microorganisms unable to survive under in vivo conditions. This may be due to the fact that the bio-inoculants are either difficult to survive under unfavorable environmental conditions or outcompeted by presented microflora (Walia et al. 2017). One of the important strategies to surmount this problem is amalgamation of bio-fertilizers with suitable carriers.

Carriers being used in production of bio-fertilizers should possess definite characteristics like it should be easily mixed with microbes to enhance the sustainability and survival of microorganisms by maintaining optimum pH, an adequate level of moisture and aeration, etc. Thus, the carrier material should possess an excellent moisture absorption ability and pH buffering capacity, nonetheless, it should also be non-toxic to microorganisms, and eco-friendly to plants, animals, and humans. In addition to there, it is easy to sterilize, and easy to mix, handle, and store. In view of the cost–benefit ratio, the carrier should be effortlessly available and cheap. Nowadays, different types of carriers are being used for the production of bio-fertilizers. Smith (1995) has classified the carriers into different categories, first category comprises different types of soils, peat and coal, waste cake powder farmyard manure, plant debris and second group comprises barnyard compost, soya bean oil, shelled nut oil, barnyard compost. The last group consists of inert materials like perlite, rock phosphate, and calcium sulfate vermiculite. These carriers have also been used in combinations. Wang et al. (2015) reported the utilization of different carriers for developing a bio-fertilizer of *A. niger* and reported a mixture of wheat husk and perlite to enhance the availability of "P" content.

Among soil microorganisms, AM fungi have been found to be a noteworthy component of soil–plant systems (Schreiner and Bethlenfalvay 2003). An AM fungus plays a major role in nutrient and water uptake by plants and provides other benefits to host, such as tolerance under adverse environmental conditions and disease resistance (Pal et al. 2014). Due to their obligatory symbiosis, it is highly difficult to produce AM-based bio-fertilizers in *in vitro* conditions.

Mass scale production AMF is highly difficult because of its specific nutritional requirements (Pal et al. 2015). The different strategies were reported by Berruti et al. (2016) for the utilization of AMF as bio-fertilizers. According to first strategy AMF-harboring rhizosphere, soil can be used as bio-inoculants; however, this method may not be reliable and may perhaps result in colonization of weeds and pathogens. In other strategies, AM spores that were isolated from root region can be used for this AM fungal organism inoculated on a host trap plant in an inert medium. The trap plant is highly susceptible for Arbuscular mycorrhizal fungal growth, and therefore it is used for production of AM fungi for bulk scale. This is frequently used inoculums for inculcation to crop plants in large scale. This consists of a set of some kind of AM spores present in soil inoculants.

In this method, trap plant should be highly amicable for inoculation of desired AM fungi and also should be ideal for large-scale production of propagates. In addition to these, the trap plant should show intense root development within a short period of time and resist to harsh environmental conditions, suitable for synthesis of fungal propagules (Sadhana 2014). An important observation came from a study of Selvakumar et al. (2016) that maize could be the suitable host trap plant when compared to the Sudan grass for the propagation of *Claroideoglomus etunicatum*. Other trap plants including *Chloris gayana, Sorghum vulgare, Zea mays*, *Sorghum bicolor var. sudanense,* and *Ipomea batatas* are most common trap plants used for mass scale culturing of Arbuscular mycorrhizal fungi (Sadhana 2014).

By wet sieving and decantation, the AM fungi is regularly isolated from soil (Singh et al. 2010) followed by microscopic observation of AM fungi. Mass multiplication is carried out by collecting a large number of spores by pot culture method. Host trap plant and AM fungi were cultured in natural solid medium containing clay, peat, sand, perlite soil, and different types of composted plant debris. Tamil Nadu Agricultural University designed a method, and according to this, a trench lined with polythene sheet is being used as plant growth pot or tub. Fifty kg of vermiculite and 5 kg of sterilized soil are filled in trench up to 20 cm height. To this 1 kg of AM spores inoculated 2–5 cm below the surface of vermiculite. Sterilized seeds of trap plant are sown in a trench along with an appropriate dosage of nitrogen source urea and superphosphate. After the period of 60 days roots of trap, plants are cut, spores, a mixture of vermiculite, hyphal fragments, and infected root pieces obtained were used as AM fungal inoculants. Without using soil also some researchers developed hydroponics and aeroponics for the cultivation of AM fungi in the presence of trap plants. The major advantage of these methods is that there is a feasibility to produce pure and clean AM spores (Ijdo et al. 2011).

3.7 Application of Phosphate-Solubilizing Endophytic Fungal Bio-Inoculants

Treatments of seed surface with suitable bio-inoculants are the most common choice of inoculation prior to seeding and reported to be the popularly used method (Walia et al. 2013b). However, there are few techniques that are widely used for the inoculation of endophytic microorganisms, viz., soil application, seed treatment, and foliar spraying. In seed treatment process, carrier-coated fungal inoculums are immersed with seeds in a liquid culture medium. In this method, a fungus adhered firmly to the seed surface. Conversely, there are some constraints in this method. Amount of viable fungi adhered on to the seed surface may not be adequate. The plant species are under cultivation at commercial scale by vegetative propagation, and the endophytic P-solubilizing bio-inoculants are usually applied to plant parts before planting in the field (Panhwar et al. 2013; Kour et al. 2019a; Kumar et al. 2019; Yadav et al. 2019e). The shoots developed from such plants are deemed to be more amenable for bacterization by endophytic microorganisms. Application of endophytes to the soil is another method of bio-inoculants application (supplementation of soil with endophytic bio-inoculants). These methods have many advantages which include the following:

- A high number of P-solubilizing fungi may disseminate per unit area.
- Less number of interactions may occur between bio-inoculants and chemically treated seeds.
- This method is more rapid in comparison with seed inoculation technique.
- These bio-inoculants are more tolerant to dry and desiccated conditions.

In view of above aspects, phosphate-solubilizing endophytic fungal inoculants can be applied by two approaches.

1. Single culture of phosphate-solubilizing fungi can be used as inoculants as single culture approach (SCA).
2. Two cultures can be used as bio-inoculants are called mixed culture approach (MCA).

3.8 Effect of Phosphate-Solubilizing Fungal Bio-Inoculants

Soil is a natural habit for wide variety of microbial communities. The interactions occurring between microbial communities basically impact a physico-chemical property of the soil, and soil fungi performs several imperative roles in the maintenance of soil biochemistry directly or indirectly. Direct endophytic fungi accelerate plant growth promotion through the production of phytohormones, mineralization of salts and ions (Guleria et al. 2014) and in the indirect mechanism; it plays an important role in bio-control agents against phytopathogenic microbe (Walia et al. 2013a). Mehta et al. (2011) studied the growth enhancement of groundnut in association with endophytic fungi. They studied two fungi, i.e., *Aspergillus niger and Penicillium notatum* supplement of soils tri-calcium phosphate (TCP) under pot culture conditions and reported that there is a remarkable improvement in dry weight and height of the plant. When a mixed culture of fungal strains was employed as inoculants, a substantial improvement was observed in plant height as 81% and plant dry weight as 105% compared to controls (Prasanna et al. 2011; Mehta et al. 2011).

It is pertinent that a number of plants and weight of seeds enhanced remarkably with single or multiple inoculations of fungal strains. Other studies carried out by Priyadharsini and Muthukumar (2017) on pigeon pea revealed that when inoculated with the fungi *Curvularia geniculata* has shown a significant impact on growth parameters. *C. geniculata* inoculated seedlings of pigeon pea were taller (26.53%) and showed increased shoot and root dry weight (16.67–33.33%) as compared to un-inoculated control seedlings. In addition to P-solubilization, endophytic fungi also play an imperative role in phytohormone production that can remarkably enhance plant growth. Thus, the exploitation of phosphate-solubilizing fungi is considered eco-friendly, profitable, and sustainable approach for enhancement of crop yield.

3.9 Application of RDNA Technology in Developing Phosphate-Solubilizing Endophytic Fungi

Interaction of endophytic fungi with host plant is relatively an intricate process. Set of genes are involved in such interaction including nitrogen, phosphorus, and other nutrient exchanges between endophytic fungi and host plant tissues were studied; nonetheless, widespread research is desirable to better comprehend the genetic aspects of such interactions. Comprehensive and enhanced knowledge is essential for the involvement of genes and their regulation to undertake genetic manifestation of fungi, which consecutively can be employed for better phosphorus uptake and improved plant growth. The molecular approaches signify a vital role in understanding the genetic aspects of host fungal interactions. Among several molecular approaches, the cloning and gene sequencing methods are most promising and consent to determine which techniques are time-consuming. Nucleic acid hybridizations and probing techniques are required to possess sufficient knowledge of microbial community. However, other molecular methods such as amplified ribosomal DNA restriction analysis or ribosomal intergenic spacer analysis can be employed for the endophytic fungal colonizations.

3.10 Future Applications of Endophytic Fungal Phosphate Solubilizers

In recent times, usage of phosphate fertilizers is highly expensive that cannot be afforded by farmers, particularly in developing countries. Scientists thus have a great responsibility toward society to find some innovative ways from biological sources to make available "P" to crop plants, by an economically efficient alternative for chemical fertilizers. Most of the soils are deficient in available phosphorus to plants and chemical fertilizers are expensive. Due to this interest has been developed in the application of rhizosphere microbes and endophytic fungi with phosphate-solubilizing capacity as bio-inoculants to solubilize phosphate from poorly available sources in soil. Although the potentiality increased for developing such inoculants, their vast applications remain incomplete by intricacy in an understanding of microbial inoculants. These endophytic fungi not only enhance the phosphate availability to the plants but also provide protection to the plants against plant pathogens and stimulate plant growth. The major challenge associated with endophytic fungi is a commercial-scale application, in fact, managing microbial communities to favor plant colonization by beneficial endophytic microorganisms. The contribution of endophytic fungal research may have environmental and economic impacts. Molecular-level research in this aspect is necessary for a better understanding of host endophytic interaction.

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Conflict of Interest We declare no Conflict of Interest.

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Chapter 4
Endophytic Microbes from Medicinal Plants and Their Secondary Metabolites for Agricultural Significances

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Abstract Endophytes constitute an important component of microbial diversity since 20 years, remarkable progress in the field revealed the significance of endophytic microorganisms. Endophytic fungi are an unexplored group of organisms that has huge potential for innovative pharmaceutical substances; they are established as anticancer, antioxidants, antifungal, and anti-inflammatory. Likewise in recent years, incredible progress was made in developing them as therapeutic molecules against diverse ailments. In recent years, more studies are warranted in bioprospecting new endophytic microorganisms and their applications. Bacterial and fungal endophytes ubiquitously reside in internal tissue of living plants. Endophytic fungi distributed out from tropical region to arctic region, possess vast potential in terms of secondary metabolite production. It is pertinent to know that the various bioactive indispensable compounds evaluated by these endophytic fungi are host-specific. They are very significant in augmenting the adaptability of the endophyte and its host plants for instance biotic and abiotic stress tolerance. The ensuing effect is to produce metabolites either primary or secondary that are obliging for fungi themselves, the host plant in addition to the human race thereof. This chapter primarily emphasizes on the ecology, colonization, biodiversity, secondary metabolites from endophytic fungal cultures.

Keywords Endophytic microbial diversity · Medicinal plants · Bioactive compounds · Secondary metabolites

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4.1 Introduction

With the human population rising, a simultaneous boost in diseases along with an increase in the incidence of reemerging diseases is noticed. The key origin of these medical emergencies being drug resistance in pathogenic bacteria, while the solution lies in the discovery of newer drugs to combat resistant bacteria. Numerous ecosystems were previously explored for the bioprospection of antibiotic producing microorganisms counting with terrestrial, marine, freshwater ecosystems. Notably, with the advent of endophytic microorganisms, a new niche is open for drug discovery (Berde 2015).

Endophyte was commonly associated with fungi initially, but now also includes bacteria as well. These microbes may perhaps exert beneficial or detrimental effects on plants and their metabolism. The endophytic microbes dwell in different tissue types within numerous plant species. The endophytic bacteria are ubiquitous in nature. An endophyte completes its life cycle colonizing inter and intracellularly contained by the healthy tissues of the host plant, with no visible symptoms of disease (Wilson 1995). And thus some endophytic microorganisms live in plant tissue without causing considerable harm to the plant.

Plant-associated microbes have been discovered in the fossilized tissues of stems and leaves (Taylor and Taylor 2000). The endophytic microorganisms are believed to have devised genetic systems and acquired as well as donated characteristics (Stierle et al. 1993). The growth, survival, and transmission of endophytic microorganisms to other plants occur vertically or via vectors and are firmly dependant on the host plants. When at least one stage of the life cycle of the endophyte is outside the host plant, it is facultative endophytes. Many substances of medicinal importance found in plants have also been extracted from their endophytes (Yadav 2017; Yadav et al. 2017; Yadav and Yadav 2018). Therefore, the attention is now on studies that are focused on the isolation and application of endophytes from medicinal plants.

Endophytic microorganisms survive inside the host plant tissues and produce novel metabolic compounds, having activity against various pathogens. Researchers have discovered new therapeutic alternatives in the form of bioactive secondary metabolites in endophytes such as antiviral, antibacterial, anticancer, and antidiabetic compounds (Kumar et al. 2015). Recently endophytes are considered as an essential source of secondary metabolites and bioactive antimicrobial natural products. The endophytic bacterial natural products, for example, munumbicins, ecomycins, pseudomycins, and xiamycins are antibacterial, antimycotic, and antiplasmodial in addition to antiviral in nature, respectively (Berde 2015).

Recent studies evidenced counts of natural products including compounds made up of terpenoids, flavonoids, alkaloids, steroids, etc. Metabolites of endophytes have been reported to hinder the growth of a number of microorganisms (Rana et al. 2019c; Yadav 2018). Microbial metabolites are considered as antifungal and antibacterial chemotherapeutic. In 2008, Moricca and Ragazzi reported that genes regulating the communication between an endophyte and a plant are strictly modulated by the environment. Hostile environment induces the production of defense chemicals.

Plants growing in extreme habitats ought to be screened for isolation of endophytes and their metabolites. Plants present in various environmental conditions including tropic, temperate, xerophytic, and aquatic, harbor the endophytic microorganisms. The endophyte associated plants produce various metabolites that induce resistance. It is notable that symbiotic plant triggers defense system more promptly than non symbiotic plants following a pathogen encounter (Jalgaonwala et al. 2011).

In the plant–microbe relationship, the endophytes supply nutrients to the plant, protect the plant from the invasion of pathogenic microorganisms, and in return, get space to colonize. The various activities of endophytes such as nitrogen fixation, solubilizing iron, and production of metabolites for plant protection enable the endophyte to help in the associate plant growth (Marx 2004; Porras-Soriano et al. 2009; Ryan et al. 2008; Rana et al. 2019a, b). The endophytes produce excess substances of impending use to modern medicine, agriculture, and industry. Endophytes were documented to produce a variety of biological activities such as antibiotic, anti-inflammatory, antiviral, anticancer, and antioxidant (Kado 1992; Kobayashi and Palumboo 2000; Yadav et al. 2019a, b, c).

4.2 Ecology of Endophytic Bacteria

The endophytic bacteria were perhaps isolated from monocotyledonous as well as dicotyledonous plants, including woody tree species, for example, oak (Brooks et al. 1994) and pear (Whitesides and Spotts 1991), as well as herbaceous crop plants, such as sugar beets (Jacobs et al. 1985) and maize (Gutierrez-Zamora and Martinez-Romero 2001). Diversity linked with bacterial endophytes occurs in plant species and also in colonizing bacterial taxa.

Plants can be colonized concurrently by a variety of endophytic bacteria. Plant endophytic bacteria have been classified into 82 genera within Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Actinobacteria Firmicutes, and *Bacteroidetes* and most of them fit into Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria (Lodewyckx et al. 2002; Rosenblueth and Martínez-Romero 2006). While new endophytes are being continuously reported from different plant species. Within a particular plant, in the different tissues, different bacterial and fungal species can colonize. Thus, the plant itself forms a complex microecosystem, providing niche/habitats for the endophytes as per their preferences (Kour et al. 2019b, c). These habitats are not only exemplified by plant external surfaces, where epiphytic bacteria predominate, but also by internal tissues especially in xylem and phloem, where many microorganisms penetrate and survive.

The distribution of endophytic bacteria in different parts of the plant was first observed by Gardner et al. (1982). The endophytic bacteria present in the xylem fluid of Florida citrus tree roots was identified by the authors. Among the 13 genera found, the most dominant species were *Pseudomonas* amounting to 40% while *Enterobacter* comprised of 18%. This stable biodiversity is considered to be the most important condition in the establishment of any ecosystem.

4.3 Colonization of Plant by Endophytes

In some cases, endophytic bacteria may be transferred through the seed. These endophytic bacteria can stimulate plant growth and their progress in the host tissue. Endophytic microorganisms having the ability to fix atmospheric nitrogen and solubilize phosphate, as well as the ability to eliminate soil contaminants, play a crucial role in increasing the soil fertility.

Even though bacteria are prokaryotes and fungi are eukaryotes, they share many qualities of their relationship with plant hosts. In both the cases, colonization of root tissues is internal as well as external. Mostly it is systemical. The mode of colonization, however, differs in the two. Bacteria primarily colonize intercellularly and are mostly found in the vascular tissues of host plants. This helps the endophyte in its distribution. Asymptomatic colonization of the roots by fungi may be intercellular or intracellular in nature.

4.4 Natural Products from Endophytic Bacteria as Secondary Metabolites

Knowing the importance of endophytic microbial community, the endophytic microbial composition of the medicinal plants should be studied, identity of the microorganisms should be carried out, and the endophytic microbial preservation should be given preference in research. Secondly, there is a need to bioprospect the endophytes for other industrial applications also apart from antibiotics. The relationship between the geographical distribution of plants and their endophytic composition, as well as the plant–microbe relation needs to be established.

The endophytes colonize a particular niche, i.e., the plant tissue, which helps them in their role as biocontrol agents similar to that of phytopathogens. There are numerous reports about the role of the endophytic microorganisms in controlling plant pathogens, insects, and nematodes, and also in accelerating seedling emergence, enhancing growth of plants, and helping in plant establishment under adverse conditions (Kour et al. 2019a; Suman et al. 2016). Disease development is prevented due to the de novo production of varied new compounds and antifungal metabolites.

According to Lodewyckx et al. (2002), endophytes include bacterial genera that was found in soil, such as *Pseudomonas, Burkholderia,* and *Bacillus*. A wide range of diverse range of secondary metabolic products including antibiotics, anticancer compounds, volatile organic compounds, antifungal, antiviral, insecticidal, and immunosuppressant agents are obtained from these genera. Extensive number of biologically active compounds have been isolated from endophytic microorganisms; however, there still remains a largely untapped source of novel natural products.

Guo et al. 2000 reported cytonic acids that act on viruses namely cytomegaloviruses. There are very few reports of antiviral from endophyte bacteria. Sun et al. (2006) have worked on the endophyte *B. amyloliquefaciens* (ES-2) isolated from a herb *Scutellaria baicalensis* Georgi. The endophyte produces fengycins and surfactins which have antibacterial and antifungal properties. Zhou et al. (2015) has reported an endophytic fungi *Aspergillus versicolor* producing antiviral butyrolactones. Settu et al. (2010) have worked on the endophytes of *Andrographis paniculola*. Endophytes of these plants possess activity against Gram-positive and Gram-negative bacteria. Khaled et al. (2018) have worked on endophytic fungi of Egyptian medicinal plants and have found these isolates to possess antiviral and antioxidant activities.

4.4.1 Endophytes as a Source of Antibiotics

Medicinal plants have been used in the treatment of numerous infections and diseases, with their medicinal applications described in the Ayurveda. The compounds responsible for these medical applications are present in the plants and are alo obtained from the endopytic bacteria and fungi, endophytic in these plants. These natural compounds offer a great diversity of chemical structures that can be researched and applied for betterment of mankind (Berde 2015). Research on secondary metabolites with antimicrobial activity is essential with the development of antibiotic resistance in pathogens and the problem of emerging and reemerging diseases. The potential endophytic microorganisms can be utilized to address these problems.

Numerous synthetic drugs have been developed based on the lead compounds isolated from natural products. The classical example cited is that of the prototypical taxane isolated by Wani et al. in 1971, from the bark of a yew tree *Taxus brevifolia*. In 1996, Strobel et al. reported an endophytic fungus (*Pestalotiopsis microspora*) found in Yew tree with ability to produce Taxol. Like fungal endophytic cultures, endophytic bacteria also have potential of synthesizing novel natural products. Work is being focussed in order to explore endophytic bacteria for new and unique natural products of commercial importance. Endophytes thus are a source for antibacterial, antifungal, antidiabetic, antioxidant, and immunosuppressive products. Ecomycins, Pseudomycins, Munumbicins are some examples of the unique antibiotics obtained from endophytes.

4.4.1.1 Diterpenes

A large number of compounds with cytotoxic activity have been found to be produced by endophytic fungi over the years. Paclitaxel or Taxol is an antitumor compound reported from endophytes of number of plants. *Pestalotiopsis microspora* endophytic fungal species isolated from *Taxodium distichum* (Li et al. 1996) and *Taxus wallichiana* (Strobel et al. 1996) have been reported to produce paclitaxel. The endophytic fungal isolate *Penicillium raistrickii*endophytic in *Taxus brevifolia* was found to produce paclitaxel as well as baccatin III (Stierle and Stierle 2000). Earlier, from the same plant species, an endophytic fungi *Taxomyces andreanae* was reported, producing paclitaxel and baccatin (Strobel et al. 1993). There are two more reports of Paclitaxel production by *Pestalotiopsis* species. *Pestalotiopsis pausiceta* associated with *Cardiospermum helicacabum* (Gangadevi et al. 2008) and *Pestalotiopsis terminaliae* endophytic in the plant *Terminalia arjuna* (Gangadevi and Muthamary 2009a). Scientists have reported another endophytic fungus isolated from *Terminalia arjuna*, identified as *Chaetomella raphigera*, also to produce paclitaxel (Gangadevi and Muthamary 2009b). Production of paclitaxel was reported from an endophyte, *Bartalinia robillardoides*, of the medicinal plant *Aegle marmelos* or Indian bael (Gangadevi and Muthamary 2008).

4.4.1.2 Polyketides

Curvularia geniculate, an endophytic fungus, isolated from *Catunaregam tomentosa*, is reported to produce 5 hybrid peptide–polyketides, curvularides A–E. Curvularide B showed antifungal activity against *C. albicans*in in addition to synergistic activity with a fluconazole drug. A number of polyketides have been reported from endophytic fungal strains, shown in Table 4.1.

4.4.1.3 Lignans

Podophyllotoxin is a lignin with antimitotic and tubulin polymerase inhibition activity. Its derivatives namely, etoposide, teniposide, and etoposide phosphate, are preferably used in the treatment of cancer. A number of endophytes have been reported for podophyllotoxin production. Endophytic fungi *Tramates hirsute* isolated from dried rhizomes of *Podophyllum hexandrum* produces podophyllotoxin and its derivatives (Puri et al. 2006). Another report of fungal endophyte producing podophyllotoxin from *Podophyllum peltatum* has been cited. The endophyte was identified as *Phialocephala fortinii* (Eyberger et al. 2006). *Fusarium oxysporum*, an endophyte isolated from *Juniperus recurve*, a medicinal plant found in the Himalayas, was found to produce Podophyllotoxin (Kour et al. 2008). Podophyllotoxin has also been isolated from an *Alternaria* species, an endophyte of the plant *Juniperus vulgaris*(Lu et al. 2006) and *Aspergillus fumigatus*, endophyte of *Juniperus communis* L. Horstmann (Kusari et al. 2009).

4.4.1.4 Terpenoids

Stierle and Stierle (2000) have reported the isolation of endophytic *Penicillium* species from *Taxus brevifolia* (Yew). Of these endophytes, *Penicillium brevicompactum* is reported to produce a terpenoid, mycophenolic acid. This compound is antifungal, an immune suppressant drug and used in the treatment of Dengue.

Table 4.1 Polyketides produced by endophytic fungi

Compound	Uses	Host plant	Endophytic fungi	References
Griseofulvin	Antifungal	*Abies holophylla (Manchurian fir)*	*Xylaria* sp.	Park et al. (2005)
		Pinus strobus (White pine)	*Xylaria* sp.	Richardson et al. (2014)
		Vaccinium augustifolium (Blue berry shrub)		
		Taxus brevifolia	*Penicillium* sp.	Stierle et al. (1995), Stierle and Stierle (2000)
Brefeldin A	Antifungal, antiviral, and anticancer, protein transport inhibitor	*Texus mairei* *Torruia grandis*	*Paecilomycs* sp.	Wang et al. (2002)
		Torruia grandis	*Aspergillus clavatus*	
Sequoiatones	Antitumor (Breast Cancer)	*Sequoia sempervirens*	*Aspergillus paraciticus*	Stierle et al. (2001)
Sequoiamonascins	Antitumor (Breast, lung and CNS)	*Sequoia sempervirens*	*Aspergillus paraciticus*	Stierle et al. (2003)
Torreyanic acid	Anticancer	*Torrueya taxifolia*	*Pestalotiopsis microspore*	Lee et al. (1996)
Nodulisporins A, B, C	Antifungal	*Juniperus cedrus*	*Nodulis porium* sp	Dai et al. (2006)
Nodulisporins D, E, F	Antibacterial, antifungal, antialgal	*Arica arborea*	*Nodulis porium* sp	Dai et al. (2009)
Phomopsolides	Insecticidal (antibeetle), antibacterial	*Taxus brevifolia*	*Phomopsis oblonga*	Grove (1985)
		Taxus brevifolia	*Penicillium* sp	Steirle et al. (1997)
Rugulosin	Antilarval (Sprous budworm	*Balsam fir*	*Hormonema dematioids*	Calhoun et al. (1992)
Methyl(2Z,4E)-6(acetyloxy)-5-formyl-7-oxoocta-2,4-dienoate (Macrolide pyrinopherol)	Antifungal	*Pinus strobus*	*Lophodermium* sp.	Sumarah et al. (2011)

4.4.1.5 Terpenes

Many compounds belonging to this group have been isolated from endophytic fungal cultures and have been tabulated below in Table 4.2.

4.4.2 Heterospirocyclic Compounds

Two heterospirocyclic compounds useful in the treatment of cancer have been found to be produced by endophytic fungal cultures. Pseurotin A is antibacterial in addition to being anticancer. It is produced by *Penicillium raistrickii*, an endophyte of the plant *Taxus brevifolia* (Stierle and Stierle 2000) and *Penicillium janczewskii* KM Zalessky, associated with the *Prumnopitys andina* (Schmeda-Hieschmann et al. 2008). Tauramin is an anticancer compound produced by the endophytic fungi *Phyllosticta spinarum* isolated from *Platycladus orientilis* (Wijeratne et al. 2008).

4.4.2.1 Antimicrobial Peptides

Antimicrobial Peptides (AMPs) are the new generation of native peptide molecules. These are found in all living beings. They are being referred to as natural antibiotics. The AMPs are reported to have a very wide activity against a large spectrum of pathogenic microorganisms as well as protozoan and metazoan parasites (Liu et al. 2000; Vizioli and Salzet 2002). All of these components are main elements involved directly in the innate immune response of their hosts. This activity comprises of the expression of fluid phase proteins that recognize pathogen-associated molecular patterns. The response of the antibiotic peptides is quick, highly efficient, and with broad host activity range (Hoffmann and Reichhart 2002).

4.4.2.2 Antimicrobial Peptides from Endophytes

Endophytic bacteria compete with the pathogenic organisms and prevent them from colonizing the plant tissues. Secondary metabolites produced by the endophytes prevents the growth of pathogens microorganisms, thus playing a role in the plant defense mechanisms. AMPS are molecules of choice for drug development due to specificity for their targets with higher degree of interactions. Antibacterial cyclo-(Pro-Thr) and cyclo-(Pro-Tyr) are produced by endophytic fungus *Penicillium* sp, endophytic fungi found in mangrove plant *Acrostichum aureurm*. Both peptides demonstrated activity against *Staphylococcus aureus* and *Candida albicans*.

Epichlicin, a novel cyclic peptide was reported from the endophytic fungus *Epichloe typhina*, found in plant *Phleum pretense* L. The peptide was antagonistic at low concentrations, against the *Cladosporium phlei* spores, the fungal pathogen of the timothy plant (Seto et al. 2007).

Table 4.2 Terpenes isolated from fungal endophytic isolates

Compound	Uses	Host plant	Endophytic fungi	References
5-(Hydroxymethyl)-2-(20-trimethyltetrahydro-2H-Pyran-2-yl)-Phenol	Antifungal	*Pinus strobus*	*Lophodermium* sp.	Sumarah et al. (2011)
Phomadecalin	Activity against Pseudomonas aeruginosa	*Pinus* sp.	*Microdiplodia* sp. *KS 75-1*	Hatakeyama et al. (2010)
Xylarenones	Antitumour antimicrobial	*Torreya jackii CHUN*	*Xylaria* sp. *NCYZ*	Hu et al. (2008)
Tuberculariols	Anticancer	*Taxux mairei*	*Tubercularia* sp. *TF5*	Xu et al. (2009)
Enfumafungin	Antifungal	*Juniperus communis*	*Hormonema* sp.	Pelaez et al. (2000)
Periconicins (DitStrobelerpene)	Antibacterial, antifugal against Tricophyton rubrum	*Taxus cuspidate*	*Periconia* sp.	Kim et al. (2004)
Heptelidic acid (Konigic acid)	Anticancer, antimalarial, antilarval (Spruce budworm)	*Abies balsamea*	*Phyllosticta* sp.	Calhoun et al. (1992), Kim and Choong (2009), Tanak et al. (1998)
Isopimaratriene-dione and trion analogs (diterpenoids)	Antilarval (Spruc budworm) and insect toxin	*Balsom fir*	Unidentified endophyte	Findlay et al. (1995a)
Remulosin and Mellein analogs	Antilarval (Spruce budworm)	*Picea muriana BSP*	*Canoplea elegantula (Cooke) M.B.Ellis*	Findlay et al. (1995b)

Leucinostatin A, an antitumor and antifungal peptide was isolated from extracts of *Acremonium* sp. associated with *Taxus baccata* (Strobel et al. 1997). The endophytic fungi, *Penicillium raistrickii* endophytic in *Taxus brevifolia*, produced the peptide Cycloaspeptide A, and also other nitrogen containing compounds such as Benzomalvin C (analgesic anti-inflammatory), Fiscalin B (mycotoxins), Oxaline (anticancer), and Roquefortine C (anticancer) (Stierle and Stierle 2000). Noble et al. (1991) reported the isolation of compound Echinocandin from endophytic fungal cultures *Cryptosporiosis* sp and *Pezicula* sp. endophytic in the plants *Pinus sylvestris* and *Fagus sylvatica*.

4.4.2.3 Ecomycins

The endophytic bacterium, *Pseudomonas viridiflava* was reported to produce compounds called as Ecomycins. The ecomycins, lipopeptides in nature, contain unusual amino acids such as homoserine and β-hydroxy aspartic acid. Three lipopeptides produced by *P. viridiflava* strain EB273 were identified and characterized (Harrison et al. 1991).

4.4.2.4 Pseudomycins

Pseudomycins are antifungal produced by *Pseudomonas syringae*, a plant-associated bacterium (Harrison et al. 1991). These antifungal peptides are lipopeptides containing amino acids like L-chlorothreonine, D- and L-diaminobutyric acid, and L-hydroxyl aspartic acid. Pseudomycin A shows activity against *Candida albicans,* an oppurtunistic pathogen. Pseudomycins A–C contain hydroxyaspartic acid, arginine, lysine, serine, and diaminobutyric acid. They are active against fungal plant pathogens including *C. albicans* and *C. neoformans*.

4.4.2.5 Munumbicins

The munumbicins are made up of 4 bioactive substances having a broad activity spectrum against fungal and bacterial plant pathogens as well as *Plasmodium* species. Castillo et al. (2002) have reported the production of munumbicins by *Streptomyce*s NRRL 30562, an endophytic bacterium of *Kennedia nigriscans*, a medicinal plant native to Australia. The activity of these compounds was against Gram-positive bacteria including the methicillin-resistant strain of *S.aureus* (MRSA, ATCC 33591) and a vancomycin-resistant strain of *E. faecalis* (VREF, ATCC 51299). Munumbin B is effective against multiple-drug-resistant (MDR) *Mycobacteriumtuberculosis,* an acid-fast bacterium, while munumbicins C and D are effective against the malarial parasite *Plasmodium falciparum*.

4.4.2.6 Polyhydroxy Butyrate

Polyhydroxy butyrate (PHB) and poly-3-hydroxyalkanoate (PHA) are the most widely produced microbial bioplastics. These are gaining attention due to their commercial value. Many naturally occurring species of bacteria have the ability to produce bioplastics, as proven by their genomic analysis studies (Kalia et al. 2003). *Herbaspirillum seropedicae*, a diazotrophic endophyte, is found in a variety of higher plants. Catalán et al. (2007) have shown that *H. seropedicae* produces significant levels of PHB, when grown on a range of carbon sources. Degradation of polymer in the host system takes place over the time. Hence there is a possibility of the use of these polymers in drug delivery in cases where slow release of compound is needed.

4.5 Conclusion and Future Perspectives

This chapter highlights the need for novel pharmaceutical solutions to fight emerging and reemerging infections. Endophytic microorganisms are a promising source, as these fungi and bacteria are constantly at war with pathogenic microbes to create an ecological niche for themselves. They produce secondary metabolites as a source of communication and defense. These need to be bioprospected in order to tackle the medical problems being faced presently and will appear in the future too.

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Chapter 5
Phyllospheric Microbiomes: Diversity, Ecological Significance, and Biotechnological Applications

Natesan Sivakumar, Ramamoorthy Sathishkumar, Gopal Selvakumar, Rajaram Shyamkumar and Kalimuthu Arjunekumar

Abstract The phyllosphere referred to the total aerial plant surfaces (above-ground portions), as habitat for microorganisms. Microorganisms establish compositionally complex communities on the leaf surface. The microbiome of phyllosphere is rich in diversity of bacteria, fungi, actinomycetes, cyanobacteria, and viruses. The diversity, dispersal, and community development on the leaf surface are based on the physiochemistry, environment, and also the immunity of the host plant. A colonization process is an important event where both the microbe and the host plant have been benefited. Microbes commonly established either epiphytic or endophytic mode of life cycle on phyllosphere environment, which helps the host plant and functional communication with the surrounding environment. To the scientific advancement, several molecular techniques like metagenomics and metaproteomics have been used to study and understand the physiology and functional relationship of microbes to the host and its environment. Based on the available information, this chapter describes the basic understanding of microbiome in leaf structure and physiology, microbial interactions, especially bacteria, fungi, and actinomycetes, and their adaptation in the phyllosphere environment. Further, the detailed information related to the importance of the microbiome in phyllosphere to the host plant and their environment has been analyzed. Besides, biopotentials of the phyllosphere microbiome have been reviewed.

Keywords Biotechnological applications · Diversity · Ecological significance · Phyllospheric microbiomes · Plant growth promotion

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5.1 Introduction

The term phyllosphere is referred to as "the aerial part of the plant or the parts of a plant above the ground usually surface of leaves, considered as a habitat for microorganisms." This is a place where normally a variety of microorganism (bacteria, yeasts, and fungi) colonizes. The global leaf area corresponds to both upper and lower surfaces, has approximately twice as great as the land surface area (Vorholt 2012). The phyllosphere is the ambient region for microbes to colonize and establish its association with plants usually epiphytes. Microbial communities in the phyllosphere are highly complex and consist of many cultured and uncultured microorganisms (Müller and Ruppel 2014). It has a heterogeneous group of the microbial association at the micrometer scale area due to its diverse microenvironments (habitats). The phyllospheric microbes are adapted to the insensitive environmental conditions, specifically microbial epiphytes are highly exposed to atmospheric temperature, light, UV radiation, less water, and nutrient availability. These external factors affect the composition and diversity of phyllospheric microbial communities (Vorholt 2012). However, the type of plant and invading microbial populations (pathogens) are also influencing the commensals and/or mutualistic relationship with their host plant (Lindow and Brandl 2003). Less number of studies are available for the microbiology of phyllosphere rather than plant root. Moreover, with increasing anthropogenic stresses, the diversity and community structure of phyllosphere microflora have been continually modified. In this chapter, we focused on the phyllospheric microbiome, structure and diversity, epiphytic mechanism, molecular interactions, ecological significance, and the microbial importance in biotechnology.

5.2 Basic Understanding of Leaf Structure

The leaf is a highly organized and multi-layered plant organ (Fig. 5.1), which consists of the epidermis (upper and lower) covered by a waxy cuticle that provides a physical barrier against abiotic and biotic stresses. The epidermis involves many regulatory processes of leaf physiology including gas exchange, temperature regulation, primary production, secretion of secondary metabolites, and water mobilization. Also, a specialized epidermal cell such as stomata, hydathodes (modified stomata), and trichomes (outgrowth) are there in the epidermis. The stomata are surrounded by two cupped hand cells called guard cells, which may open or close due to internal water pressure. Inside the leaf, a layer of cells called the mesophyll, is present, usually two layers, namely, palisade layer and the spongy layer. They contain chlorophyll and photosynthesis occurs in these cells. The palisade cells are more column cells and the spongy cells are more loosely packed between the palisade layer and the lower epidermis, and it allows for gas exchange. The veins of the leaf contain the vascular tissue, xylem and phloem are found in it. Veins run from tips of the roots and are extended up to the edges of the leaves. The outer layer cells are called bundle sheath

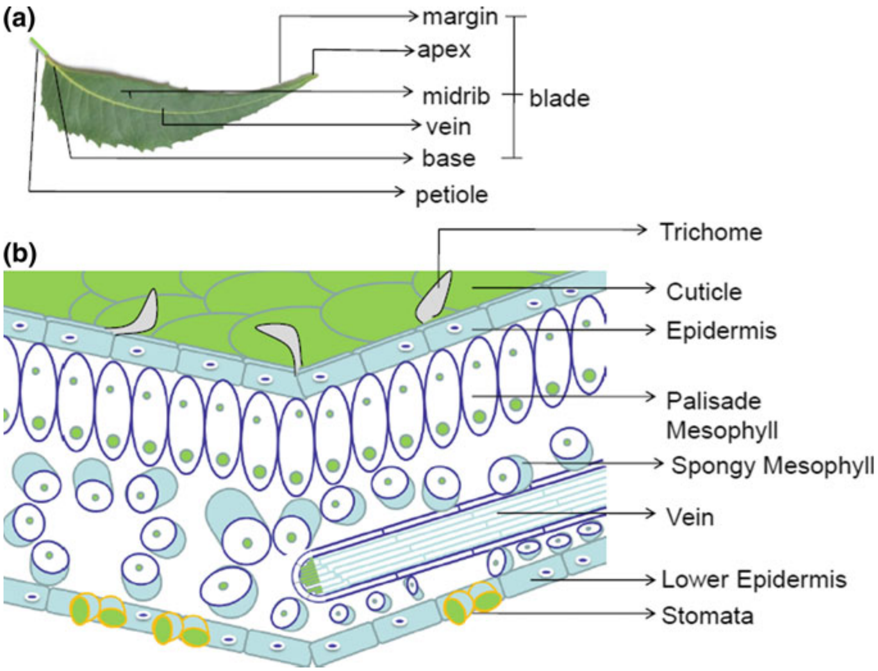


Fig. 5.1 Structural organization of a leaf

cells which circle the xylem and the phloem. The xylem transports water and phloem transports sugar (food).

Glandular trichome of the epidermis releases a wide spectrum of leaf exudates, such as polysaccharide salts, lipids, volatile compounds, and proteins, and its function is associated with plant–microbe and plant–insect interactions (Hirano and Upper 1983). But, non-glandular trichome involves regulation of water tension, light absorption, and protect the leaf from UV radiation and heat as well as drought tolerance (Hirano and Upper 1983).

5.3 Phyllosphere Habitat

The phyllosphere is a unique and dynamic habitat which constitutes irregular, and sometimes relatively large microbial community inhabitant in the ecosystem (Whipps et al. 2008). The total terrestrial phyllosphere area estimated is around 6.4×10^8 km^2 (Morris and Kinkel 2002), and it exhibits numerous microhabitat which represents a major source of microorganism. Variety of bacteria, filamentous fungi, and yeasts are naturally colonized on the phyllosphere region and less frequently, protozoa and nematodes. These microorganisms exhibit commensalism and/or mutualism (symbionts) or antagonism type of relationship on their host plants. The microbial association in phyllosphere has several advantages and importance to global processes including biogeochemical cycles (carbon and nitrogen) and environmental impact.

5.3.1 Microbial Assembly on Leaf

The arrangement of leaf epidermal cells describes the leaf physiology and the microenvironment which allow the abundance and distributions of microorganisms on the leaf surface (Shiraishi et al. 2015; Esser et al. 2015). Simply, epiphytes make biofilm-like growth, most preferably larger bacterial aggregates are on the trichomes, veins, and epidermal cell groves (Brewer et al. 1991; Morris et al. 1997), where the leaf exudates containing nutrient-rich region. The presence of outer cuticle and its physiology help the microbes to colonize this site. Presence of aliphatic compounds in the cuticle layer determines the physicochemical properties of the leaf surface and renders the permeability and wettability, which facilitate the adherence of microorganisms (Sadler et al. 2016). Water permeability of this site may play a vital role in the survival and growth of the epiphytes. Moreover, leaching the nutrients along with water makes the epiphytes to utilize and develop colonies on the phyllosphere (Burch et al. 2014). The leaf surface with higher water and nutrient penetration is heavily colonized by bacterial communities (Beattie 2011). In general, bacteria maintain the cuticular permeability by secretion of biosurfactants, for example, *Pseudomonas syringae* release syringafactin on the cuticle layer of the leaf which facilitate the availability of sugar for persistent epiphytic growth (Van der Wal and Leveau 2011). Similarly, fructose availability by *Pantoea eucalypti* 299R and *Pantoea agglomerans* (Leveau and Lindow 2001). Figure 5.2 represents the phyllosphere microbial assemblage, wherein the epiphytic microorganism exploits this microenvironment for special distribution of microbes, survival as well as blooming (colonization). At the same time, surface microorganisms change the phyllosphere chemistry, and they render the heterogeneous oligotrophic mode of epiphytic life. Besides, microorganism establishes special niches on the leaf surface with the interactive mode of life (Agler et al. 2016) in this microhabitat microbial population can be constantly maintained.

5.4 Microbial Diversity in the Phyllosphere

The phyllosphere consists of diverse numerous microbial communities including bacteria, filamentous fungi, yeasts, algae, and protozoans (Whipps et al. 2008; Verma et al. 2013, 2015, 2016a, b). The nature of various microorganisms (epiphytic and endophytic) associated with phyllosphere is given in Fig. 5.3. Among the diverse community of microbes, bacteria are the predominant community on leaves and its

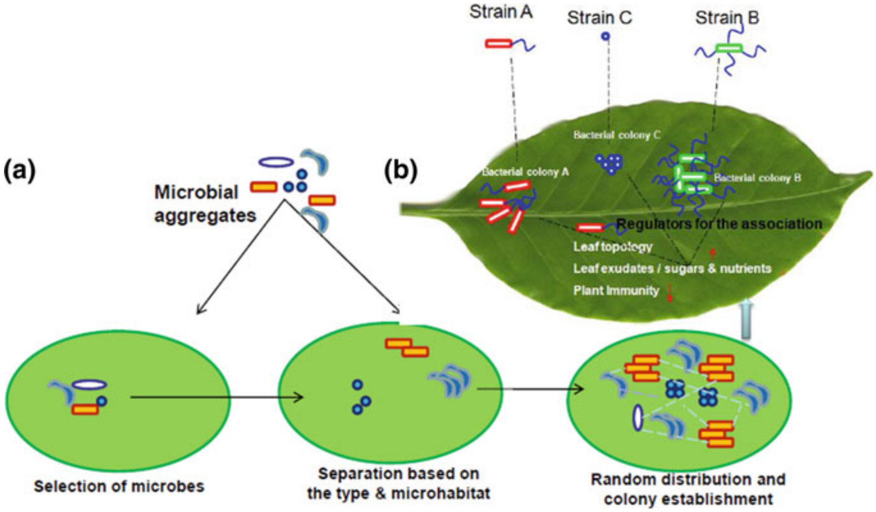
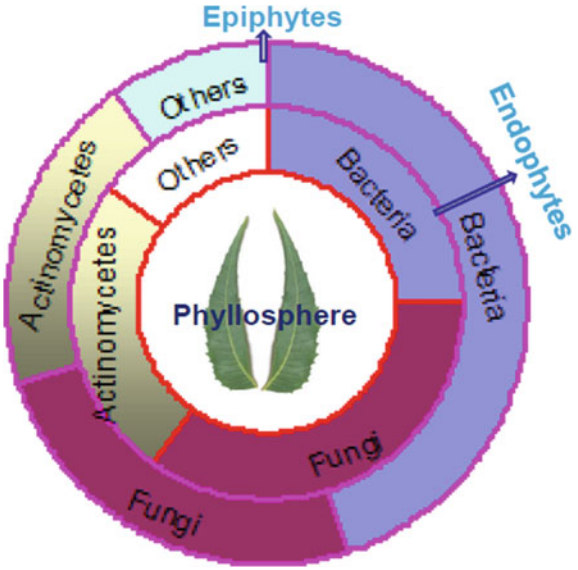


Fig. 5.2 Structure of phyllosphere microbial assemblage. **a** stages for microbial community structure development, **b** regulations for the microbial community structure in phyllosphere

Fig. 5.3 Epiphytic and endophytic microbes in phyllosphere



range is between 10^2 and 10^{12} g^{-1} of the leaf (Inacio et al. 2002). The conventional culture-based method has been used for the identification of different microbial communities of the leaves. Thompson et al. (1993) identified 78 bacterial species from the sugar beet, and Legard et al. (1994) screened 88 bacterial species from 37 genera.

However, the culture-dependent method based profiling of phyllosphere communities is likely to be incorrect and miscalculates diversity (Rasche et al. 2006). The culture-independent approaches like 16S rDNA sequences of the whole microbial mass of phyllosphere could give the complete and complex microbial community structure of the environment. Molecular studies suggested that alpha-, beta- and gammaproteobacteria and firmicutes are the dominant bacterial inhabitants of the phyllosphere. Frequently, acidobacteria, actinobacteria, and cyanobacteria are also occurring in the phyllosphere environment (Kadivar and Stapleton 2006). Lambais et al. (2006) identified that 97% of the bacterial sequences of the phyllosphere have been new and unidentified. Yang et al. (2001) reported large numbers of novel bacteria from the phyllosphere of crop plants. The number of studies confirmed the diversity of yeast in the phyllosphere environment as an epiphyte.

The cultivable yeasts genera such as *Cryptococcus, Sporobolomyces*, and *Rhodotorula* and its species have been largely inhabitant in the plant leaf (Thompson et al. 1993; Glushakova and Chernov 2004). Moreover, the culture-dependent methods have been used to study the abundance of filamentous fungi, ranging from 10^2 to 10^8 CFU g^{-1}. Genera such as *Cladosporium, Alternaria, Penicillium, Acremonium, Mucor*, and *Aspergillus* are the frequent filamentous fungi colonizing as epiphytes and endophytes (Arnold et al. 2000; Inacio et al. 2002; Rana et al. 2019a, b, c).

However, the culture-independent strategy is the best to investigate the diversity and distribution of specific bacterial groups of interest (Miyamoto et al. 2004; Sessitsch et al. 2006). Other than the 16S/18S rDNA sequences, multiplex terminal restriction fragment length polymorphism (TRFLP) has been used to analyze several phylogenetic groups or functional genes in the microenvironment (Singh et al. 2006). Soils, water, air, tree buds, and plant debris from the previous crops are the sources for microbes in phyllosphere (Manceau and Kasempour 2002). Those microorganisms may be habited in phyllosphere either transient or residual epiphytes (Suslow 2002; Zak 2002). The atmospheric microflora, rainfall, humidity, wind, etc. can directly influence the transients of microorganisms to the phyllosphere (Lighthart 1997). During the plant growth period, the epiphytic bacterial population will increase in quantity (Inacio et al. 2002). The microorganisms on the seed or roots may be established as epiphytes or endophytes (Wulff et al. 2003). Some epiphytes may be injected into the internal space of the leaf and colonize as endophytes. The distribution pattern of the phyllosphere microorganisms is not even, mostly bacteria colonize at the epidermal wall junctions, specifically in the grooves and the veins or stomata or at the base of trichomes (Melotto et al. 2008), also found in the cuticle layer, near hydathodes and stomatal pits (Aung et al. 2018). The microbial load is higher at the lower leaf surface perhaps the lower leaf surface contains thin cuticle, stomata, and/or trichomes (Beattie and Lindow 1999). Mostly, all microorganisms that appear in the phyllosphere are capable to colonize and grow (Whipps et al. 2008), and it disperses throughout the surface by rain splash, bounce-off, wash-off, water movement, or removal by insects or pest (Kinkel 1997; Yang et al. 2001; Lambais et al. 2006).

5.4.1 Bacterial Diversity in the Phyllosphere

Phyllosphere is a heterogeneous environment (Koskella 2013), bacteria are considered the most abundant inhabitants of the leaves, and its average number is being around 10^6–10^8 cells cm^{-2} (Andrews and Harris 2000; Hirano and Upper 2000). But the population of epiphytic bacteria differs depending on the plant species and its surrounding environment. The variation is mainly due to the physical and nutritional conditions of the phyllosphere. Commonly, the broad-leaf plants have the highest number of bacteria than the grasses or waxy broad-leaf plants (Kinkel et al. 2000).

Generally, the phyllosphere contains four major phyla of bacteria such as the Proteobacteria, Firmicutes, Bacteroides, and Actinobacteria (Kembel et al. 2014; Durand et al. 2018). Methylotrophic bacteria are predominant in phyllosphere which includes genera such as *Methylobacterium*, *Methylophilus*, *Methylibium, Hyphomicrobium, Methylocella*, *Methylocapsa*, and *Methylocystis* (Mizuno et al. 2013; Iguchi et al. 2013; Kwak et al. 2014; Krishnamoorthy et al. 2018). *Methylobacterium* and *Sphingomonas* are the predominant genera belonging to the class alphaproteobacteria reported in several plant phyllospheres (Delmotte et al. 2009; Kumar et al. 2019a). The bacterial community organization on phyllosphere is controlled by specific assemblage regulations (Buee et al. 2009; Reinhold-Hurek et al. 2015). Normally, soil type, plant genotype and species, immune system of the plant, age, climatic condition, and the geographic region are the factors forcing the bacterial community assembly (Leff et al. 2015; Zarraonaindia et al. 2015; Copeland et al. 2015). Extensive studies are available for the soil and rhizosphere bacterial community on phyllosphere bacterial colonization in Arabidopsis *thaliana* (Bodenhausen et al. 2013; Maignien et al. 2014; Bai et al. 2015; Muller et al. 2015) and maize (Peiffer et al. 2013). *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* are the most abundant phyla colonizing the leaf and root of *A.* thaliana (Delmotte et al. 2009; Redford et al. 2010; Bodenhausen et al. 2013). *Massilia, Flavobacterium, Pseudomonas,* and *Rathayibacter* are a prevalent bacterial genus in *A. thaliana* (Bodenhausen et al. 2013), *Deinococcus thermus* on tree phyllosphere (Redford et al. 2010), and *Bacillus* and *Pantoea dominate* the lettuce (Rastogi et al. 2012).

Kembel et al. (2014) studied the bacterial communities on tropical tree leaves, around 400 bacterial taxa the phyllosphere has been dominated with Actinobacteria, Alpha-, Beta-, and Gammaproteobacteria, and Sphingobacteria. However, Archaea is the profuse members of the plant-associated microbe, commonly Thaumarchaeota, Crenarchaeota, and Euryarchaeota make the endophytic mode of life in plants (Müller et al. 2015). Durand et al. (2018) characterized the bacterial genera such as *Methylobacterium, Kineococcus, Sphingomonas*, and *Hymenobacter* of the phylum Firmicutes from the leaf surface. The phyllosphere of the grapevine contains Acinetobacter, Bacillus, Citrobacter, Curtobacterium, Enterobacter, Erwinia, Frigoribacterium, Methylobacterium, Pantoea, Pseudomonas, and Sphingomonas as dominant genera (Kecskeméti et al. 2016). Steven et al. (2018) characterized Pseudomonas and Enterobacteriaceae as predominant taxa from apple. Several studies revealed Pseudomonas as the most abundant genus of phyllosphere region (Aleklett et al. 2014;

Kecskeméti et al. 2016; Steven et al. 2018). Seed coat associated bacteria that have been reported in phyllosphere are mainly Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria (Johnston-Monje and Raizada 2011; Rodríguez-Escobar et al. 2018).

The most notable bacterial pathogen is *Pseudomonas syringae*, it causes diseases in a wide range of economically important plant species (Mansfield et al. 2012; Morris et al. 2013; Burch et al. 2014). Hamd Elmagzob et al. (2019) identified taxa such as Rhizobiales, Clostridiales, Pseudomonadales, Burkholderiales, Bacteroidales, Enterobacteriales, Rhodocyclales, Sphingomonadales, Lactobacillales, and Bacillales from the leaves of *Cinnamomum camphora* (L.) Presl. Several studies reported diazotrophic bacteria on phyllosphere (Fürnkranz et al. 2008; Rico et al. 2014). Diazotrophic bacteria can use atmospheric dinitrogen (N_2) as nitrogen source for its metabolic activities. Bacterial diazotrophic include *Beijerinckia*, *Azotobacter*, *Klebsiella*, and Cyanobacteria (e.g., *Nostoc*, *Scytonema*, and *Stigonema*). Diazotrophic nitrogen fixation has been reported in many species which contains an enzyme nitrogenase (encoded by *nif* genes) (Rico et al. 2014). Recently, 16 s rRNA gene-based high-throughput sequencing technology has been used for the diversity analysis of phyllosphere, for example, the distribution of endophytic bacteria of *C. camphora* (L.) Presl leaves has been analyzed by 16S rRNA gene metagenomics, revealing Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, Gemmatimonadetes, Acidobacteria, Planctomycetes, Chloroflexi, and Fusobacteria are the major phyla of the polymicrobial community (Hamd Elmagzob et al. 2019).

5.4.2 Fungal Microbiota of Phyllosphere

Fungi are saprophytic and they may be associated with plants either epiphytic or endophytic, and mostly they are known for their pathogenesis on plant system (Voříšková and Baldrian 2013; Yadav et al. 2019b, c, d). There are several reports revealed that phyllosphere fungi have a profound role in the residing host. Both epiphytic and endophytic fungi inhabiting the leaf are of high species diversity with diverse metabolic functions (Yao et al. 2019), such as leaf litter decomposition and recycling the carbon and nitrogen (Kannadan and Rudgers 2008; Guerreiro et al. 2018). In general, endophytic fungi can help plant growth and also provide resistance to biotic (pathogens) and abiotic (drought and salinity) stresses, (Arnold et al. 2007; Purahong and Hyde 2011; Guerreiro et al. 2018; Yadav et al. 2018c). In culture-dependent approaches, several fungal species have been isolated from small herbs to larger woody plants. Inácio et al. (2010) reported that the density of yeast-like fungi may vary from plant to plant and approximately 5×10^4 cells cm^{-2}. *Aureobasidium pullulans* are yeast-like fungi abundant in phyllosphere (Cordier et al. 2012; Setati et al. 2012). Apart from yeast-like fungi, many filamentous fungi have been reported from health as well as infected plant leaves. Through the culture-dependent method, Ripa et al. (2019) isolated *Aspergillus niger, Fusarium oxysporum, Penicillium aurantiogriseum, Fusarium incarnatum, Alternaria alternata, Alternaria* *tenuissima, Cladosporium cladosporioides, Talaromyces funiculosus, Aspergillus flavus, Trichoderma aureoviride, Trichoderma harzianum, Penicillium janthinellum, Fusarium proliferatum, Fusarium equiseti,* and *Aspergillus stellatus* from wheat plant.

Dhayanithy et al. (2019) isolated twenty endophytic fungi from the leaves and stem of *Catharanthus roseus,* among them Colletotrichum, Alternaria, and Chaetomium were the dominant genera. Many of them make endophytic association begin with epiphytic initiation (Rodriguez et al. 2009; Porras-Alfaro and Bayman 2011), and some endophytes later turned to pathogens. The olive tree phyllosphere is found to be highly diverse having more than 149 genera and 68 families of fungi (Martins et al. 2016) in a Mediterranean ecosystem (Portugal), but Abdelfattah et al. (2015) reported only 13 endophytic fungal taxa in the leaves and twigs of olive trees. There has been a discrepancy to understand the phyllosphere fungi as endophytic or epiphytic, occasionally it is uncertain, for the reason that some can reside both epiphytic and endophytic modes of association. In general, phyllosphere endophytic fungi are the epiphytic habitats and are penetrated into the plant tissues to form an endophytic association (Kharwar et al. 2010; Porras-Alfaro and Bayman 2011). Though they are phyllospheric, the soil has acted as a reserve for these potential endophytic inoculums of the above-ground organs (Zarraonaindia et al. 2015). For example, *Ascochyta* sp. and *Fagus crenata* B1 (Osono 2006), *Colletotrichum gloeosporioides* and *Phomopsis* sp. (Rivera-Vargas et al. 2006; Twizeyimana et al. 2013), and Table 5.1 listed some examples of phyllosphere fungal endophytes.

Osono (2008) reported that endophytic *Colletotrichum gloeosporioides* and *C. acutatum*, and epiphytes *Pestalotiopsis* sp., *Aureobasidium pullulans*, *Phoma* sp., and *Ramichloridium* sp. are the phyllosphere fungi in the plant *Camellia japonica*. However, the abundance and diversity of the fungi differ in plant species as well as in different eco-climatic conditions. Moreover, seasonal and leaf age-dependent variations also occur in the epiphytic and endophytic phyllosphere fungal assembly, for example, *Geniculosporium* sp. is varied in leaf age, and *Cladosporium cladosporioides* has been varied in both season and leaf age of the plant Camellia japonica (Osona 2008). Phyllosphere fungi play an important function in mineral absorption and mineral recycling process, specifically carbon, nitrogen, and phosphorus recycling in the forest ecosystem. Therefore, the study about the phyllosphere fungi and its physiology with host plant is important.

5.4.3 Actinomycetes Diversity in Phyllosphere

In addition to bacterial diversity, actinobacteria share a considerable interest in epiphytic and endophytic life forms in the phyllosphere. They are soil-inhabiting saprophytic microbes and have been extensively studied for their therapeutic secondary metabolites. This versatile group of gram-positive bacteria has adapted to diverse environments including the phyllosphere of the plant (Singh et al. 2018). Some actinobacteria form symbiotic association residing in plant tissues have generated

Table 5.1 Phyllosphere fungal endophytes

Endophytic fungi	Host plant	Type	References
Aspergillus, Phomopsis, Wardomyces, Penicillium	*Euterpe oleracea* (palm)	Palm	Rodrigues (1994)
Ramularia spp.	*Vitis riparia* (grapevine)	Wild	Kernaghan et al. (2007)
Absidia sp., *Aspergillus* sp., *Cladosporium* sp., *Cunninghamella* sp., *Fusarium* sp., *Nigrospora* sp., *Paecilomyces* sp., *Penicillium* sp., *Rhizopus* sp.,	*Meyna spinosa Roxb.*	Medicinal plant	Bhattacharyya et al. (2017)
Penicillium chrysogenum, and *Penicillium crustosum*	*Teucrium polium*	Medicinal plant	El-Din Hassan (2017)
Alternaria alternata, Setosphaeria sp., *Cochliobolus* sp., *Alternaria* sp. *Phoma herbarum, Davidiella tassiana, Botryosphaeria dothidea, Ulocladium alternariae, Phoma macrostoma* var. incolorata, *Phoma exigua* var. exigua, *Cladosporium cladosporioides* strain, *Botryosphaeria* sp., *Guignardia mangiferae, Pyrenophora tritici-repentis, Guignardia alliacea, Rhizopus oryzae*	*Catharanthus roseus*	Medicinal plant	Sreekanth et al. (2017)

(continued)

enormous significance to the host and its environment through their novel metabolites. Diversity and distribution of endophytic actinobacteria have been largely documented, from medicinal plants, crop plants, and some other terrestrial plants (Qin et al. 2011; Masand et al. 2015; Dinesh et al. 2017; Nalini and Prakash 2017). Several species of actinobacteria have been reported from plants such as *Triticum aestivum, Lupinus termis, Lobelia clavatum, Acacia auriculiformis, Aquilaria crassna, Oryza*

Table 5.1 (continued)

Endophytic fungi	Host plant	Type	References
Ascomycetes: *Trichoderma, Penicillium, Fusarium,* and *Aspergillus*. Non-ascomycetes: *Mucor* (Mucoromycota) and *Schizophyllum* (Basidiomycota)	*Stanhopea tigrina*	Orchid	Salazar-Cerezo et al. (2018)
Trichothecium sp., *Epicoccum nigrum, Alternaria alternaria, Alternaria arborescens, Nigrospora sphaerica, Epicoccum* sp., *Alternaria* sp. *Nigrospora* sp., *Colletotrichum gloeosporioides, Fusarium oxysporum, Trichothecium roseum*	*Vitis vinifera* (Grape fruit cells)	Fruit plant	Huang et al. (2018)
Aspergillus japonicus	*Euphorbia indica* L.	Wild plant	Ismail et al. (2018)
Alternaria spp., *Trichophyton* spp., *Geotrichum* spp., *Candida* spp., *Aspergillus* spp., *Aureobasidium* spp., *Fusarium* spp., *Exserohilum* spp., *Curvularia* spp., *Coccidioides* spp., *Bipolaris* spp.	*Epipremnum aureum, Azadirachta indica, Piper betle, Catharanthus roseus, Ficus religiosa, Musa acuminate, Ficus Benghalensis, Ficus racemosa, Calotropis procera, Ocimum tenuiflorum*	Medicinal plant	Jariwala and Desai (2018)
Nigrospora sphaerica, Acremonium falciforme, Allomyces arbuscula, Penicillium chrysogenum, Acrophialophora sp, Mycelia sterilia	*Litsea cubeba*	Medicinal plant	Deka and Jha (2018)

(continued)

Table 5.1 (continued)

Endophytic fungi	Host plant	Type	References
Colletotrichum gloeosporioides f. sp. camelliae and Pleosporales sp.	*Camellia sinensis*	Tea	Win et al. (2019)
Tremellales, Davidiellaceae, Basidiomycota, Rhodotorula, Tremellales, Meria, Cryptococcus, Cladosporium, Acaromycetes, Erythrobasidium, etc.	*Aegiceras corniculatum* (*Myrsinaceae*), *Avicennia marina* (*Verbenaceae*), *Bruguiera gymnorrhiza*, *Kandelia candel* and *Rhizophora stylosa* (*Rhizophoraceae*), and *Excoecaria agallocha* (*Euphorbiaceae*)	Mangrove	Yao et al. (2019)

sativa, Xylocarpus granatum, and Elaeagnus angustifolia from various environments like arid, semiarid, and mangrove are *Actinoplane missouriensis, Actinoallomurus acacia, Actinoallomurus coprocola, Actinomadura glauciflava, Amycolatopsis tolypomycina, Actinoallomurus oryzae, Jishengella endophytica, Kribbella* sp., *Microbispora mesophila, Microbispora* sp., *Micromonospora* sp., *Nocardioides* sp., *Nocardia alba, Nonomuraea rubra, Micromonospora* sp. *Nonomuraea* sp., *Pseudonocardia* sp., *Planotetraspora* sp., *Pseudonocardia endophytica, Pseudonocardia halophobica, Streptomyces* sp.*, and Streptomyces javensis* (Coombs and Franco 2003; Thamchaipenet et al. 2010; Chen et al. 2011; Xie et al. 2011; Yadav 2017; Yadav and Yadav 2018). Reports revealed that the actinomycetes diversity in phyllosphere is high in the tropical and temperate ecosystem (Strobel and Daisy 2003; Yadav et al. 2018b; Yadav and Yadav 2019). Moreover, the physiology of the plant and the environment determines the actinobacterial association in plants and allows them to establish endophytic life (Du et al. 2013). Some important actinobacterial diversity in various plant sources is discussed in the following (Table 5.2).

5.5 Mechanism of Microbial Interaction with the Phyllosphere

The leaf physiology determines the microbial diversity and abundance on the phyllosphere. It establishes the microhabitat where the microorganisms adapt to their physiology to survive in this habitat (Staley et al. 2014; Shiraishi et al. 2015). The epiphytic microbes formed as colonial form, which gives protection to the microorganisms from this harsh microhabitat (Lindow and Brandl 2003; Remus-Emsermann

Table 5.2 Diversity of endophytic actinobacteria

Endophytic actinobacteria	Host plant	Habitat	References
Microbispora sp., *Micromonospora* sp., *Nocardioides* sp., *Streptomyces* sp.,	*Triticum aestivum*	Arid	Coombs and Franco (2003)
Actinoplane missouriensis	*Lupinus termis*	Arid	El-Tarabily (2003)
Pseudonocardia endophytica	*Lobelia clavatum*	Arid	Chen et al. (2009)
Actinoallomurus acaciae, *Streptomyces* sp., *Actinoallomurus coprocola*, *Amycolatopsis tolypomycina*, *Kribbella* sp., *Microbispora mesophila*	*Acacia auriculiformis*	Arid	Thamchaipenet et al. (2010)
Actinomadura glauciflava, Pseudonocardia halophobica, Nocardia alba, Nonomuraea rubra, Streptomyces javensis	*Aquilaria crassna*	Mangrove	Nimnoi et al. (2010)
Actinoallomurus oryzae	*Oryza sativa*	Aquatic	Indananda et al. (2011)
Jishengella endophytica	*Xylocarpus granatum*	Mangrove	Xie et al. (2011)
Micromonospora sp. *Nonomuraea* sp., *Pseudonocardia* sp., *Planotetraspora* sp.	*Elaeagnus angustifolia*	Arid	Chen et al. (2011)
Streptomyces phytohabitans	*Curcuma phaeocaulis*	Arid	Bian et al. (2012)
Nonomuraea solani	*Solanum melongena*	Arid	Wang et al. (2013b)
Actinoplanes hulinensis, Streptomyces harbinensi, Wangella harbinensis	*Glycine max*	Arid	Jia et al. (2013), Liu et al. (2013), Shen et al. (2013)
Micromonospora sonneratiae	*Sonneratia apetala*	Mangrove	Li et al. (2013)
Modestobacter roseus	*Salicornia europaea*	Saline	Qin et al. (2013)
Promicromonospora endophytica	*Eucalyptus microcarpa*	Arid	Kaewkla and Franco (2013)
Blastococcus endophyticus, *Plantactinospora endophytica*	*Camptotheca acuminate*	Arid	Zhu et al. (2013)

(continued)

Table 5.2 (continued)

Endophytic actinobacteria	Host plant	Habitat	References
Actinoplanes brasiliensis, Couchioplanes caeruleus, Gordonia otitidis, *Micrococcus aloeverae, Streptomyces zhaozhouensis*	*Aloe arborescens*	Arid	He et al. (2014)
Micromonospora schwarzwaldensis Streptomyces sp., *Wenchangensis*	*Centella asiatica*	Mangrove	Ernawati et al. (2016)
Glutamicibacter halophytocola, Kineococcus endophytica, Streptomyces sp.,	*Limonium sinense*	Saline	Feng et al. (2017)
Marmoricola endophyticus	*Thespesia populnea*	Mangrove	Jiang et al. (2017)
Allostreptomyces psammosilenae	*Psammosilene tunicoides*	Arid	Huang et al. (2017)
Micromonospora terminaliae	*Terminalia mucronata*	Mangrove	Kaewkla et al. (2017)
Nocardiopsis sp., *Pseudonocardia* sp. *Streptomyces* sp.,	*Dracaena cochinchinensis*	Semiarid	Salam et al. (2017)
Mangrovihabitans endophyticus	*Bruguiera sexangula*	Mangrove	Liu et al. (2017)
Actinoplanes sp., *Agrococcus* sp., *Amnibacterium* sp., *Brachybacterium* sp., *Brevibacterium* sp., *Citricoccus* sp., *Curtobacterium* sp., *Dermacoccus* sp., *Glutamicibacter* sp., *Gordonia* sp., *Isoptericola* sp., *Janibacter* sp., *Kocuria* sp., *Leucobacter* sp., *Mycobacterium* sp., *Micrococcus* sp., *Nocardioides* sp., *Kineococcus* sp., *Kytococcus* sp., *Marmoricola* sp., *Microbacterium* sp. *Micromonospora,* sp., *Nocardia* sp., *Nocardiopsis* sp., *Pseudokineococcus,* sp., *Sanguibacter* sp., *Streptomyces* sp., *Verrucosispora* sp.,	*Avicennia marina, Aegiceras corniculatum, Kandelia obovota, Bruguiera gymnorrhiza,* and *Thespesia populnea*	Mangrove	Jiang et al. (2018)
Glycomyces anabasis	*Anabasis aphylla*	Arid	Zhang et al. (2018)

et al. 2012). Commonly, bacteria develop larger sized colonial association on the leaf surface, especially at veins as well as the groves of epidermal cells (Morris et al. 1997; Hirano and Upper 2000). The epidermal grooves are rich in nutrients specifically sugar and water. This region is less waxy cuticle, usually the leaf surface is fully coved with waxy cuticle which prevents the permeability and wettability of the leaf surface and regulates the colonization of the microbes on phyllosphere (Lindow and Brandl 2003; Burch et al. 2014).

The leaf surface water droplets diffuse the waxy cuticle and improve the permeability by which the compounds are diffused from the apoplast to phyllosphere surface (Schreiber 2005). These leached compounds and water on the phyllosphere are making the availability of nutrients to the microorganisms. Most commonly, the flow of water from the stomata (transpiration) is increasing the permeability and wettability of guard cells and its surface cuticles (Schönherr 2006). Hence, higher permeation of the cuticle layer permits the microbes to colonize densely (Krimm et al. 2005). Moreover, the surface bacteria are able to produce certain compounds like biosurfactants (syringafactin produced by *Pseudomonas syringae*) (Krimm et al. 2005; Burch et al. 2014) which can modify the cuticle surfaces of the leaf and establish its association. This can facilitate water availability and alter sugar availability that can improve living conditions for epiphytic bacterial growth (Lindow and Brandl 2003; Van der Wal and Leveau 2011). Epiphytes such as *Pseudomonas* sp., *Stenotrophomonas* sp., and *Achromobacter* increase the water permeability of the lipophilic cuticle present in *Hedera* and *Prunus*, which increases the availability of the compounds at the phyllosphere which will improve the epiphytic fitness on the leaf surface (Schreiber et al. 2005).

It has been experimentally proved in the bean phyllosphere containing fructose facilitates the growth of *Erwinia herbicola* and *Pantoea agglomerans* (Remus-Emsermann et al. 2013; Tecon and Leveau 2016). However, irregular distribution of fructose differentially promotes the *P. eucalypti* population on bean leaves (Mercier and Lindow 2000; Leveau and Lindow 2001; Remus-Emsermann et al. 2011). These studies suggested that the permeated carbon sources on the leaf surface are merrily exploited by the epiphytic microorganisms for their growth and multiplication. At the same time, the phyllosphere microbial population can influence the modulation of the physicochemical properties of the leaf with the help of both biotic and abiotic surroundings (Bringel and Couée 2015; Ohshiro et al. 2016; Quan and Liang 2017). Soil microbial community may also influence the determination of phyllosphere microbial diversity. However, the microbes can construct the niches in the phyllosphere microhabitat wherein it can sustain and establish its population steadily (Agler et al. 2016; San Roman and Wagner 2018). Recent studies revealed the special relationships between the bacterial species in the phyllosphere community. Presence of sugars and nutrients in this environment significantly change the individual bacterial cells within the microbial aggregates (Fig. 5.2) would spatially be established with cell-to-cell interactions along with direct physical interactions (Levy et al. 2018; Tecon et al. 2018). The community structure is organized based on the driven factors such as dispersal, selection of microbes, diversification, and ecological drift. The fitness of the community is due to internal (strain types) and external determinants (environment) of the phyllosphere (Schlechter et al. 2019).

In general, the internal factors of the community are based on the microbial relationship within the aggregates. The microbes usually have either commensal or antagonistic or mutualistic or cooperative association by which the community structure can be established. Both cooperative and mutualistic microbial interactions shape the community structure as well as to develop larger colonial association containing the maximum microbial population. While commensals have weak interactive partners in the community, they are randomly distributed in the habitat. The commensals should not influence the interactive association within the structured community (Stubbendieck et al. 2016). Besides, antagonistic microbes have a negative interaction within the community, one can outcompete the other and the sensitive microbes have been eliminated from the environment. The effect of cooperative microbial interactions on the phyllosphere community structure establishment is not demonstrated (Schlechter et al. 2019).

Bacteria can ascertain the cell-to-cell communication system and establish a larger community structure with heterogeneous populations, usually with mutualistic and cooperative partners. However, some kind of mutualistic relationship may occur between rapid growing bacteria and pathogenic fungi, which leads to cause superficial infection on the host plant which increases the nutrient accessibility of the bacteria to rich its population (Suda et al. 2009; Zeilinger et al. 2016; Amine Hassani et al. 2018). Inversely, fungal–fungal interactions seem to decrease the bacterial population, for example, oomycete species *Dioszegia* sp. and *Albugo* sp. outcompete the bacterial microbiota on *A. thaliana* leaf (Chou et al. 2000; Agler et al. 2016). Moreover, competitive interactions of microbes involve negative effects on at least one species of the habitat. Some competitive microbes produce certain toxic chemical substances (antibiotics and siderophores) as secondary metabolites which pose a negative effect on its competitor microbes. The best example of such interaction is a gram-negative *Pantoea agglomerans* bacteria which inhibit the growth of *Erwinia amylovora*, a phytopathogen of apple by antibiotic activity (Wright et al. 2001; Pusey et al. 2011).

Generally, the competition of microbes is mainly for their nutrition and space. The phyllosphere is a nutrient-limited environment, wherein the competitive partner has compromised their growth by either coexisting or excluded from the site (Saleem et al. 2017). Besides, the phyllosphere is greatly colonized by both oligotrophic and competitive microbes which play an important role in community structure formation (Schlechter et al. 2019). However, the key factors of the phyllosphere community assemblage are currently vague. Hence, more studies required to find the key factors determining the phyllosphere community structure assemblage.

5.6 Factors Controlling Phyllosphere Microbiomes

Once microbes arrived at the phyllosphere, a variety of factors resolve whether microbial cells are competent to colonize the leaf and become confined. Colony establishment depends on the leaf–atmosphere environmental interaction with the residing microorganisms in the phyllosphere. At the beginning, the microbe reaches the cuticle layer, a waxy surface that protects the leaf from the pathogens. In general, cuticle restricts the microbial association due to the functions such as barrier, reducing water and solute lass, aqueous pollution, reflectance to minimize the temperature, conferring water repellent, etc. (Beattie 2002; Whipps et al. 2008). The whole-cell biosensor-based study revealed the available nutrients on the leaf surface facilitate the growth of residing microbes at a limited level (Miller et al. 2001). This was confirmed by the microscopic observation of leaf surfaces, at the low nutrient region contains less dense microbial colonization than the nutrient-rich surface (Monier and Lindow 2005). Naturally, nutrient enrichment may happen by pollen deposits and honeydew at the phyllosphere surface (Lindow and Brandl 2003), besides plant leaves release a large array of volatile organic substances into the margin layer around leaves (Jackson et al. 2006). Nutrients that include CO_2, acetone, terpenoids, aldehydes, alcohols, long-chain hydrocarbons, sesquiterpenoids, and nitrogen-containing compounds (Whipps et al. 2008) are available nutrients for microbial growth. Some of the compounds may act as growth inhibitor or toxic to microbial growth (Dingman 2000; Shepherd et al. 2005). Hence, microbes establish several adaptive mechanisms for maintaining their growth in adverse conditions.

5.6.1 Microbial Adaptations in Phyllosphere Environment

Microbes like bacteria establishing colonies at the phyllosphere are limited by various factors including both biotic and abiotic. Abiotic factors such as the available nutrient (Delmotte et al. 2009), seasonal variation, rainfall, temperature, plant immunity, and competitor microbes (Rastogi et al. 2013) are influencing surveillance of microbes in the phyllosphere. Metaproteomic studies on the leaf surface communities have been identified as microbes producing vitamins and siderophores which give adaptation to the microbes at the environment. For example, phyllosphere of soybean, clover, and Arabidopsis plants largely colonized by Sphingomonas and Methylobacterium provides vitamins and siderophores to the plant (Green 2006; Delmotte et al. 2009) and it competes for other microbes. *Methylobacterium* spp. are involved in the assimilation of methanol at the phyllosphere, a by-product of demethylated pectin during the cell wall metabolism of the plant (Galbally and Kirstine 2002; Delmotte et al. 2009), and it gives epiphytic fitness to the microbes. Proteome studies revealed that some unique properties of rhizosphere bacteria have been found in the phyllosphere microbiota. For example, genes of methanol dehydrogenase and formaldehyde-activating enzyme (of Rhizosphere *Methylobacterium* spp.) and nitrogen fixation (Rhizobium sp.) are also reported in both phyllosphere and rhizosphere samples of rice (Knief et al. 2012). Gourion et al. (2006) observed upregulation of methylotrophic proteins such as MxaF and Fae and stress-related protein PhaA during epiphytic growth of *Methylobacterium extorquens*.

Phyllosphere colonization may occur in two different habitats, (1) the surface (epiphytic) and (2) the apoplast or leaf interior (endophytic). During the epiphytic life, many of the environmental factors regulate the growth such as solar radiation, temperature, water availability, nutrient, humidity, etc., whereas the endophytes are challenged with a plant defense mechanism. A bacteria colonizing at both habitats may differentially express their genes, for example, *P. syringae* pv. syringae B728a at epiphytic growth express the genes involved in motility, chemosensing, phosphate mobilization, and utilization of tryptophan which is higher than in endophytic growth (Yu et al. 2013). However, the secondary metabolite (syringomycin, syringopeptin) production was higher in the endophytic stage. One such adaptation is the production of pigments, bacteria such as Pseudomonas, Sphingomonas, and Methylobacterium produce pigmentation by which they give protection against UV light (Lindow and Brandl 2003). Presence of extracellular polysaccharide is another protective measure of plant-bacteria against desiccation and osmotic stress (Monier and Lindow 2004). Delmotte et al. (2009) found several stress-resistant proteins (PhyR and EcfG) from the phyllosphere of soybean, clover, and Arabidopsis through metaproteogenomic survey. Flagellin-like protein is high in pseudomonas at the epiphytic growth which enables the bacteria to access the nutrition by the chemostatic model (Yu et al. 2013).

5.6.2 Plant Immunity/Responses to Control Microbial Colonization

The plant has its immune system which plays an important role in determining microbial assembly (Jacoby et al. 2017). Plants contain two layers of defense, the primary immunity is named pattern-triggered immunity (PTI), it has a conserved molecule named microbe/pathogen-associated molecular patterns (MAMPs/PAMPs). The PTI is a localized immunity mediated at the plasma membrane containing pattern recognition receptors (Monaghan and Zipfel 2012; Wang et al. 2019). The MAMP/PAMP limits the growth of bacterial pathogens. For example, the flagellin-sensitive receptor 2 (FLS2) is a pattern receptor which recognizes the *P. syringae* pathovar (pv.) bacterial flagellin (flg22) (Chinchilla et al. 2006; Newman et al. 2013; Trdá et al. 2015). However, the plant response to limits its defense against non-pathogenic bacteria is still unknown. The effector's protein-mediated destabilization of plant immunity and immune escape is also reported (Jones and Dangl 2006; Cui et al. 2009). Plant immunity is targeted with specific proteins, which involves the self-protection against the microbial association has been deactivated by the interaction of microbial effector proteins and it makes protein–protein networks (Bogdanove 2002; Snelders et al. 2018). Besides, plants have evolved with intracellular receptor molecules called nucleotide-binding leucine-rich repeat proteins (NLRs), which either openly or ultimately recognize effector proteins to give the second layer of plant immunity named effector-triggered immunity (ETI) (Jacob et al. 2013; Wu et al.

2014). Both PTI and ETI generate more specific and diverse immunity against phyllosphere microflora. Beneficial or the synergistic microbes interact with signaling pathways (MAMPs) of the plant to elevate the production of its immune response. However, if pathogen could interact by using MAMPs, the immune output will be higher and will restrict the colonial establishment of pathogens. Pathogens that live in host tissues use hemibiotrophs and necrotrophs mode of life (Table 5.3). Some chemicals of the plant tissues inhibit the microbial association either biotrophs (salicylic acid) or necrotrophs (jasmonic acid) type and also the reactive O_2 species may have an inhibitory effect on the pathogens (Lehmann et al. 2015). Plants use jasmonic acid, methyl jasmonate, ethylene, flavonoid, 12-oxo-phytodienoic acid, and salicylic acid-mediated signals for quenching pathogens on its surface (Table 5.4). Recently, pathogens with biotrophy-necrotrophy switch have been identified in fungi such as *Colletotrichum sp*, *Phytophthora capsici*, *Moniliophthora roreri,* and *Macrophomina phaseolina* in which pathogen evokes a differential response of growth in host tissues (Chowdhury et al. 2015). Some important research in the mode of immune evoke by the pathogen has been listed in Tables 5.3 and 5.4.

Phyllosphere region is usually colonized by a variety of microorganisms. Naturally, leaf epidermises are always contacted to external and internal environments and are enriched with a diverse group of bacteria, yeast, fungi, and viruses. The cuticle layer of the leaf surface plays a significant role during the contact with leaf

Table 5.3 Mode of life cycle of pathogen established against plant immunity

Organism	Life cycle	Host	References
Fusarium graminearum	Hemibiotrophic	Wheat	Ding et al. (2011)
Colletotrichum graminicola	Biotrophic and necrotrophic	Maize	Vargas et al. (2012)
Septoria tritici	Hemibiotrophic	Wheat	Yang et al. (2013)
Phytophthora capsici	Hemibiotrophic	Tomato	Jupe et al. (2013)
Colletotrichum sp.	Hemibiotrophic	Plants	Gan et al (2013)
Moniliophthora roreri	Hemibiotrophic and necrotrophic	Cacao	Meinhardt et al. (2014)
Fusarium verticillioides	Biotrophic	Maize	Lanubile et al. (2014)
Botrytis sp	Necrotrophic	Plants	Van Kan et al. (2014)
Botrytis fabae	Necrotrophic	Faba bean	El-Komy (2014)
Sclerotinia sclerotiorum	Biotrophic, hemibiotrophic, and necrotrophic	Plants	Kabbage et al. (2015)
Zymoseptoria tritici	Hemibiotrophic	Wheat	Rudd et al. (2015)
Phytophthora infestans	Hemibiotrophic	Tomato	Zuluaga et al. (2016)
Rhizoctonia solani	Necrotrophic	Wheat	Foley et al. (2016)

Note “Hemibiotrophs” - an organism that is parasitic in living tissue for some time and then continues to live in dead tissue. “Necrotrophs” - can kill the host cells and feed on the contents

Table 5.4 Signaling pathway inhibits pathogenic microbes in phyllosphere

Molecules/signals	Pathogen	Host	References
Flavonoid pathway	Bacterial pathogens	*Melampsora medusae*	Miranda et al. (2007)
Jasmonic acid, ethylene, and the flavonoid	*Phymatotrichopsis omnivora*	Medicago truncatula	Uppalapati et al. (2009)
Methyl jasmonate and ethylene	*Macrophomina phaseolina*	*Medicago truncatula*	Gaige et al. (2010)
Jasmonic acid and ethylene	*Fusarium graminearum*	Wheat	Sun et al. (2010)
Jasmonate and ethylene	*Fusarium sp*	Wheat	Gottwald et al. (2012)
Ethylene and jasmonate	*Pythium ultimum*	Apple	Shin et al. (2014)
Methyl jasmonate, 12-oxo-phytodienoic acid, salicylic acid, and flavonol	*Fusarium oxysporum* f.sp. *lycopersici*	Tomato	Krol et al. (2015)

microbiota (Vacher et al. 2016). Though some group of microorganism may not multiply after it reaches on the surface, many continue to survive and multiply, until they can attain maximum number (Schönherr 2006; Innerebner et al. 2011; Pusey et al. 2011). To multiply, microorganisms require carbon, nitrogen, inorganic, and organic energy sources. However, in the absence of such nutrients, phyllosphere is still usually colonized by a large number of bacteria (105–107 CFU/g of the leaf) in the presence of high relative humidity and free water at suitable environmental conditions (Schönherr 2006; Baldwin et al. 2017). This is due to the release of nutrients or leaf exudates which adequately supported the microbial growth. There are varieties of molecules leached from the plant leaves such as sugar, amino acids, organic acids, minerals, etc. (Beattie 2011; Remus-Emsermann et al. 2011; Meiners et al. 2017). These leaching materials may differ with plant species and the environmental condition (Beattie 2011; Remus-Emsermann et al. 2011; Mendes et al. 2013).

Nutrients such as sugar photosynthates from the leaf interior may be diffused through the cuticle reached the outer surface (Schreiber 2005), and are chiefly used by phyllosphere bacteria. Moreover, water droplets on a leaf surface facilitate the outward diffusion of these sugars (Van der Wal et al. 2013). Both non-pathogenic and pathogenic microorganisms establish colonization on the leaf surface. To survive and thrive, epiphytic microbes have several adaptive properties such as the production of antibiotics, extracellular polymeric substances (EPS), biosurfactant for increasing cuticle permeability, and availability of nutrients volatile organic compounds (VOCs) to the leaf surface. However, in order to avoid the entry of pathogens, plants develop defense reactions. The preliminary defense is activated by recognition of the chemical compounds released during the contact with microbes (Boller and Felix

2009). Pathogen-induced molecular patterns (PAMPs)-triggered immunity (PTI) is a broad spectrum of defenses against the pathogen invades. However, effectors produced by the pathogens often interfere with PTI activation and are recognized by specific proteins, which stimulate effector-triggered immunity (ETI) that induces a hypersensitive response (Craig et al. 2009).

5.7 How to Study Phyllosphere Microbiome?

The diversity and community structure of phyllosphere microbes have been intensely studied by culture-independent methods. However, this approach failed to isolate and identify the complete microbiome of the environment. Therefore, scientist used the culture-independent mass sequencing methods which have been carried out by high-throughput molecular methods, especially PCR-amplified DNA-level conserved taxonomic markers such as 16S rRNA, 18S rRNA, and internal transcribed spacer (ITS) sequences-based metagenome of phyllosphere total microbiome (Mao et al. 2012; Santhanam et al. 2014; Williams and Marco 2014; Jo et al. 2015; Copeland et al. 2015) (Fig. 5.4). The first-generation molecular techniques such as Sanger sequencing, denaturing gradient gel electrophoresis (DGGE), and terminal restriction fragment length polymorphism have been used to describe the community structure variation in plant phenotype, and geographical location (Hunter et al. 2010; Vokou et al. 2012; Izhaki et al. 2013). Those techniques are low throughput and highly expensive that can be used to detect the superficial microbial community of the environment (Rastogi and Sani 2011).

Advancements in molecular techniques, next-generation DNA sequencing is the potent method that significantly reduces the costs and allows to perform hundreds of samples in a single attempt. These techniques open up new windows of omics, specifically “environmental omics.” The 454 pyrosequencing is the first to be widely executed to study in microbial community analysis. This method comprises rRNA or ITS amplicon sequencing, whole-genome sequencing, shotgun metagenomics, and transcriptional profiling (Delmotte et al. 2009; Rastogi et al. 2012). Recently, Illumina platform has been performed better and allows ultra-high-throughput sequencing of microbial communities with high-quality reads (Degnan and Ochman 2012). Proteogenomic is another method used for the microbial community structure analysis (Delmotte et al. 2009), a combination of genomics and proteomics to a great extent makes easy the structural and functional differences of microbiota in the phyllosphere environments. Through those methods, microbial diversity of several host plants such as Arabidopsis, Apple tree, Beech, grapevine, oak, poplar, Prunus, rice, soybean, spinach, tomato wheat, etc. was documented. The metadata of the metagenomic studies helps to understand the growth behavior, colonization ability, genus-level community structure formation (or) association, low and high index of diversity, and the host genotype effects on the self-defense as well as the cell wall integrity have been reported.

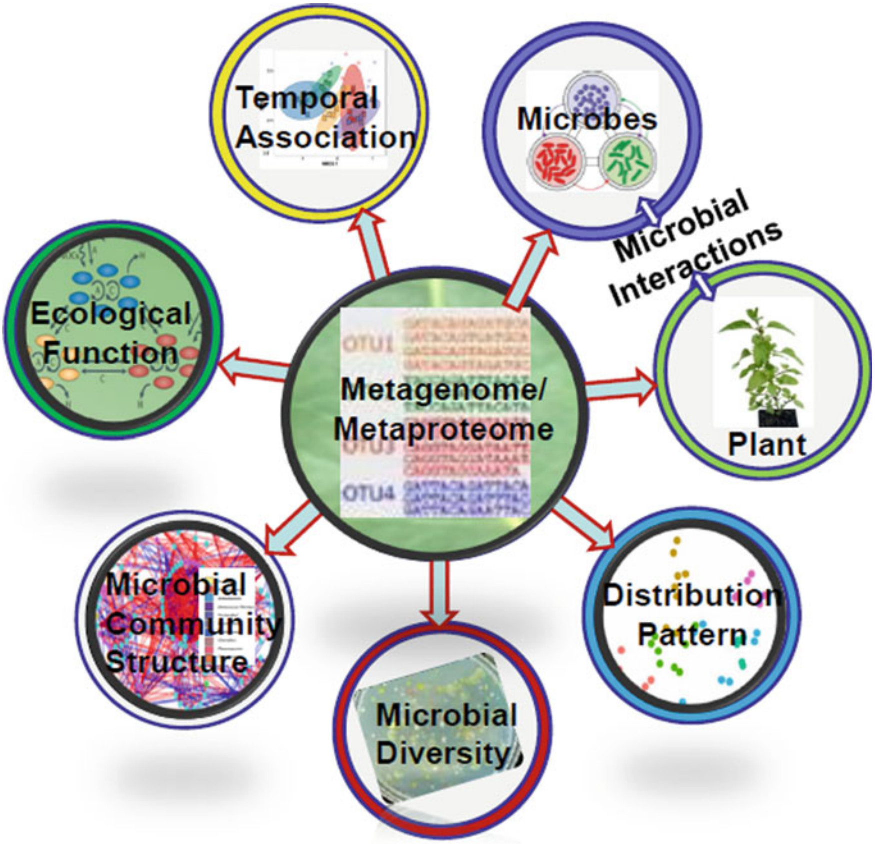


Fig. 5.4 Scope of metagenome in phyllosphere microbes and their functions

Whole microbiome analysis by environmental sequencing is popular today to explain the plant's phyllosphere containing complex microbial communities. There are many methods for mapping the diversity of microbiome which could associate with any of the living and nonliving objects. Also, the environmental sequencing approach determines the whole microbiome of the plant and it illustrates the significant association of microbes on its host under controlled conditions. Recently, studies revealed that genome-wide association (GWA) is the best method which shows potential merits for identifying the microbial communities associated with different kinds of host–microbe interactions. The high-throughput environmental sequencing approach has guided to the discoverer to find the complex microbial ecosystem of leaves. Using this strategy, many studies revealed the microbial association in the phyllosphere of different plants such as mountain shrubs (Ruiz-Pérez et al. 2016), seagrass (Fahimipour et al. 2017), subarctic grass (Uroz et al. 2016), and equatorial forest canopies (Lambais et al. 2006). The studies revealed that plant leaves are colonized by a huge and diverse group of microorganisms, including bacteria, fungi, and viruses (Rastogi et al. 2013; Morella et al. 2018; Sapp et al. 2018; Beilsmith et al. 2019). High-throughput molecular methods or culture-independent molecular techniques have interpreted the phyllosphere microbial community today (Table 5.5). Through this technique, Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria are common microbiome of plant leaves (Bulgarelli et al. 2013), and it suggests that *Pseudomonas, Sphingomonas, Methylobacterium, Bacillus, Massilia, Arthrobacter,* and *Pantoea* are predominant genera consistently firm in the phyllosphere. Findings of the studies disclose the variation of microbial community structure mainly based on the genotypic nature of the plant species and also its geographical location. For example, Finkel et al. (2011) observed similar bacterial communities from the different species of Tamarix (*T. aphylla, T. nilotica,* and *T. tetragina*) grown in the same geographical location; however, differences in community structure of microbiota have been strongly related to its geographical distances (Rastogi et al. 2012).

Moreover, the high-throughput studies revealed the special functions/metabolism of the microbes associated with leaf surfaces, specifically carbohydrate transport, leaf litter decomposition, light-driven ATP pumps, methanol metabolism, C1 metabolism (Ottesen et al. 2013; Shade et al. 2013), and the effect of ecological factors such as climate change, temperature, seasonal variation, sporadic contact to soil, and/or anthropogenic activities such as the use of agricultural chemicals and pesticides (Ikeda et al. 2011; Shade et al. 2013; Karlsson et al. 2014; Copeland et al. 2015; Glenn et al. 2015). To attain better perceptive of the phyllosphere ecosystem and understand the functional relationship among plants, microbiota, and environment, metaproteome and metagenomics have been used (Rastogi et al. 2012; Bálint et al. 2013; Dees et al. 2015).

5.8 Impact of Phyllosphere Microbiome on Ecosystem

Phyllosphere microflora significantly influences the ecological relationship of the plants. The phyllosphere usually has bacteria, fungi, lichens, algae, and viruses that have actively participated in the adaptation, growth, resistance, and infection of the plant host (Walker et al. 2017; Verma et al. 2017; Yadav et al. 2018a). The phyllosphere microbiota has not been completely studied with their ecological significance, specifically plant and ecosystem level (Remus-Emsermann and Schlechter 2018). From seed germination to plant reproduction, studies have revealed how the phyllosphere microbiome affects the leaf functions and longevity, seed mass, apical growth, flowering, and fruit development (Jones and Dangl 2006; Sawinski et al. 2013; Kembel et al. 2014); however, the net interplay of the phyllosphere ecosystem in and around the plant is scanty. Recent scientific advancements that simplify the phyllosphere microbial life become understandable. The high-throughput genomics, such as environmental genomics and metagenomics, have greatly expanded our perceptive

Table 5.5 Studies on high-throughput molecular approaches to phyllosphere communities

Method	Plant	Study	References
16S rRNA gene pyrosequencing	Soybean, clover, Arabidopsis	Epiphytic fitness of Sphingomonas and Methylobacterium	Delmotte et al. (2009)
	Pine and other trees	Phyllosphere bacteria community composition	Redford et al. (2010)
	Spinach	Genus-level communities of Proteobacteria and Firmicutes-associated spinach leaves	Lopez-Velasco et al. (2011)
	Grape	Bacterial communities on the surface of leaves and berries from grapevine	Leveau and Tech (2011)
	Lettuce	A “core” community composed of Pseudomonas, Bacillus, Massilia, Arthrobacter, and Pantoea found in lettuce foliage	Rastogi et al. (2012)
	Lettuce	Variation in phyllosphere microbiota composition. Effect of *E. coli* O157:H7 inoculation on microbiota composition	Williams et al. (2013)
	Rice	Metagenomic analysis of rice phyllospheric bacterial communities in relation to blast disease	Prasad Sahu and Kumar (2015)
	Common bean, soybean, and canola	Seasonal community succession of the phyllosphere microbiome	Copeland et al. (2015)
	Espeletia species	Microbial and functional diversity within the phyllosphere.	Ruiz-Pérez et al. (2016)
16/18S rRNA gene pyrosequencing	Oak	Fungal communities in the oak phyllosphere	Jumpponen and Jones (2009)
	Tamarix aphylla, T nilotica, T. tetragina	Geographical location is a major determinant of phyllosphere bacterial communities	Finkel et al. (2011)
	Beech	Plant genotype-based fungal communities on leaf surfaces	Cordier et al. (2012)
	Balsam poplar	Plant species-based fungal community composition	Balint et al. (2013)

(continued)

Table 5.5 (continued)

Method	Plant	Study	References
	Pine	Rapid microbial community changes during initial stages of pine litter decomposition	Gołębiewski et al. (2019)
Metaproteogenomics	Soybean, clover, Arabidopsis	Metabolic adaptations contribute to the epiphytic fitness of Sphingomonas and Methylobacterium	Delmotte et al. (2009)
	Rice	Several methylotrophic enzymes and their role in the carbon cycle by Methylobacterium	Knief et al. (2012)
	Maize	Functional genes that distinguish maize phyllosphere metagenomes in drought and well-watered conditions	Methé et al. (2017)

and understanding on the functional life of phyllosphere microbial communities in plant–environment and the impact on the ecosystem.

Environmental factors are drastically influencing the microbiome changes on phyllosphere. This is common to epiphytic microorganisms, exposed with heavy stress during the season cycle, the day/night cycle, and the growth, age, and anatomical dynamics of the plant. For instance, at drought condition, the epiphytic microbial community was notably increased on Holm oak (Rico et al. 2014). Similarly, at hot condition, bacterial endophytic communities are altered in lower leaves of paddy, but not in the epiphytes (Ren et al. 2014). However, the epiphytic fungal community responded well in worming seasons (Coince et al. 2014; Bálint et al. 2015). Besides, an increase of CO_2 at the phyllosphere region never affects the bacterial abundance (Ren et al. 2014; Vacher et al. 2016), except a few fungal genera.

Microbes have flexible metabolic adaptations, which helps them to survive in the phyllosphere microenvironment. During the metabolic functions, the plant releases carbohydrates, polyols, amino acids, amines, isoprenoids, halogenated compounds, or alcohols, as well as water and salts, which are the available nutrients for epiphytic microorganisms (Trouvelot et al. 2014). However, leaf surface commonly exhibits desolate properties such as saline or alkaline pH which generates stress in phyllosphere microbes (Finkel et al. 2012). Several alphaproteobacteria express PhyR-based stress regulation and colonization on leaf surface (Iguchi et al. 2013). Additionally, they develop multiple mode adaptation to survive in phyllosphere such as tolerance, antimicrobial, and immunity compounds against a microbial competitor (Trouvelot et al. 2014), synthesis of extracellular polysaccharides, and also synthesize phytohormonal compounds.

Besides, biotic and abiotic factors induce molecular level regulations in plants to synthesize a diverse range of phytohormones. Generally, the gaseous ethylene, jasmonate, methyl jasmonate, salicylate, and methylsalicylate are induced by bacterial pathogens (Bodenhausen et al. 2014; Horton et al. 2014). For example, many plant defense mechanisms are induced by the interaction of the biotic component of the ecosystem through signals like volatile and nonvolatile chemicals, and microbes can degrade such chemicals resulting in reduced activity (Mason et al. 2014).

The phyllosphere microbiome acts as a vital role for leaf surface environment and their surrounding ecosystem functions (Ortega et al. 2016). Phyllosphere microbes have interacted with their environment through their metabolic functions (Fig. 5.5). In general, plants release a variety of volatile organic compounds (VOCs) and its precursors on the surface of leaves (Schäfer et al. 2010), and it could regulate the microorganisms in response with the environment. Plants are the major VOCs emitter of the biosphere (>1000 Tg/year) and can release compounds such as terpenes, monoterpenes, flavones, methanol, methane, and halogenated methane (C1 compounds). The epiphytic microbes on the surface of the plant, as well as the airborne bacteria, effectively consumed the emitted VOCs through bacterial metabolism (Junker and Tholl 2013), and this effects of climate change would impact the diversity, species richness, and abundance in the phyllosphere community, and its capability on filtering of plant-emitted volatile substances.

Methane (CH_4) is the most important greenhouse gas (~1.8 ppm), and it has been detected from the leaves, roots, and stems and is released to the atmosphere (Keppler et al. 2006). Phyllosphere microbes especially methanogens use the plant-emitted methane along with leaf exudates (Lenhart et al. 2015; Bringel and Couée 2015). Phyllospheric microbes are often rich in methylotrophic bacteria and can utilize the plant-emitted C1 compounds such as methanol, formaldehyde, and chloromethane

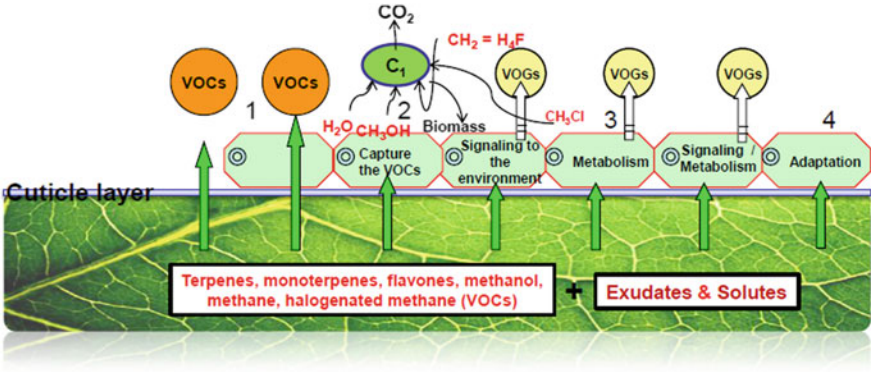


Fig. 5.5 Environmental impact of phyllosphere microbes. Utilization of plant emitting volatile organic compound (VOCs) and C1 compounds by phyllosphere microbes. (1) Free diffusion of VOCs to the atmosphere; (2) Capturing the VOCs by the surface microbes, act as filters; (3) Through specialized metabolic activities microbes metabolize the VOCs; (4) Adaptive response of microbes in the specialized environment. VOGs—Volatile organic gases

(Knief et al. 2012; Jo et al. 2015). Studies proved that the C1 metabolic epiphytic bacteria such as *Methylobacterium extorquens, Methylobacterium radiotolerans, and* Methylocystis use methanol and acetate as their carbon and energy source at the phyllosphere (Belova et al. 2011; Verginer et al. 2010; Iguchi et al. 2013; Jo et al. 2015; Iguchi et al. 2015; Krishnamoorthy et al. 2018). The *Methylobacterium extorquens* contains the methanol-dehydrogenase-like protein XoxF which is expressed during the colonization on *Arabidopsis thaliana* (Schmidt et al. 2010). Besides, chloromethane metabolism (cmu pathway) in methylotrophs has been identified from the surface leaves of *A. thaliana* harbor (Nadalig et al. 2011; Krishnamoorthy et al. 2018). Table 5.6 shows the various phyllosphere methanogenic bacteria and its metabolism.

Chloromethane (CH_3Cl) is one of the abundant chlorinated organic compounds in the atmosphere (currently ~550 ppt) and is to be responsible for the depletion of stratospheric ozone over 16% (World Meteorological Organization 2014). The fluorescence-based bacterial bioreporter study reported that phyllosphere microbes, *M. extorquens* CM4 (Roselli et al. 2013) and *Hyphomicrobium* sp. (Nadalig et al. 2011), having the genes for chloromethane utilization (*cmu*), and also volatile dimethylsulphide (DMS) and dimethylsulfoniopropionate (DMSP), considered as global climate regulator (Schäfer et al. 2010; Nevitt 2011). In the biosphere, a small number of plants like salt marsh grasses *Spartina* and sugarcanes (*Saccharum* sp.) are reported as producers of DMSP. Microbes that are associated with these plants have adaptive metabolism by which it transforms or metabolizes the DMS and DMSP (Ansede et al. 2001). Hence, the phyllosphere microbes are the major source of carbon and sulfur biogeochemical cycles, in the ecosystem and climate regulation through their active filtration or utilization of plant-related volatile compounds (DeLeon-Rodriguez et al. 2013; Šantl-Temkiv et al. 2013).

Microbial populations reside at phyllosphere as epiphytes or as endophytes, and have close contact with the rhizosphere. A microbe can be established as an epiphytic and endophytic association has the metabolic plasticity required for them to thrive. Many experimental evidences suggested that microorganisms commonly associated with plants maybe vital for nutrient accessibility and decomposition of biomass (Bernal et al. 2006; Ramírez Gómez 2011; Lizarazo-Medina and Gómez-Vásquez 2015). The functional ecology of the plant influences the composition and interaction of the phyllosphere microbes (Bodenhausen et al. 2013; Ruiz-Pérez et al. 2016). Many of the phyllosphere microbial communities share the common metabolic properties of the soil microbes. For example, the major phyllosphere bacterial communities such as Bacillus, Burkholderia, Methylobacterium, Pseudomonas, Sphingomonas, and Xanthomonas are the soil inhabitant, which have carbohydrate metabolizing genes involved in utilization of starch, hemicellulose, pectin, and cellulose, rich in humus materials (Rawat et al. 2012; Bodenhausen et al. 2013; Bulgarelli et al. 2013). The nitrogen metabolism such as ammonification, denitrification, and anammox, and the degradation of aromatic compounds are also reported in foliar microbes (Usubillaga et al. 2001; Rawat et al. 2012; Ruiz-Pérez et al. 2016).

Tropospheric microbes (aerosols) play a vital function in global carbon cycles and also metabolize the organic compounds. Some airborne Gammaproteobacteria have

Table 5.6 Studies on Phyllospheric methylotrophic metabolism

Epiphyte	Host plant	Function	References
Methanotrophs and Methylobacteria	Linden, pine and blue spruce lilac, maple, and apple	Diversity of Methanotrophs in woody plant tissues within the winter period	Doronina et al. (2004)
Methylobacterium extorquens	*Medicago truncatula*	Methylotrophic metabolism is advantageous for colonization under competitive conditions	Sy et al. (2005)
Methylobacterium extorquens	–	A proteomic study of *Methylobacterium extorquens* reveals a response regulator essential for epiphytic growth	Gourion et al. (2006)
Methylobacterium extorquens AM1	–	PhyR is involved in the general stress response	Gourion et al. (2008)
Methylocystis heyeri H2(T) and *M. echinoides* IMET10491(T)	Peat	Acetate utilization metabolism as a survival strategy	Belova et al. (2011)
Methylobacterium extorquens DSM 21961	Strawberry	Monitoring the plant epiphyte *Methylobacterium extorquens* DSM 21961	Verginer et al. (2010)
Methylobacterium extorquens	Arabidopsis thaliana or Medicago truncatula	The influence of the factor site, host plant species, time and the presence of other phyllosphere bacteria on Methylobacterium community composition and population size	Knief et al. (2010)
Candida boidinii	*Arabidopsis thaliana*	Yeast methylotrophy and autophagy in a methanol-oscillating environment on growing leaves	Kawaguchi et al. (2011)

(continued)

Table 5.6 (continued)

Epiphyte	Host plant	Function	References
Methylobacterium sp. (NC4), (NC28)	Sugarcane, pigeon pea, mustard, potato, and radish	Epiphytic pink-pigmented methylotrophic bacteria enhance germination and seedling growth of wheat (*Triticum aestivum*) by producing phytohormone	Meena et al. (2012)
Methylobacterium sp. strain OR01	Perilla plants	Dominant colonization and inheritance of Methylobacterium sp.	Mizuno et al. (2013)
Methylosinus sp. B4S	–	Stress resistance and C1 metabolism involved in plant colonization of a methanotroph Arch	Iguchi et al. (2013)
Methylobacterium oryzae	Rice	plant-probiotic methylotroph in the phyllosphere	Kwak et al. (2014)
Methylobacterium radiotolerans VRI8-A4	Groundnut	Diversity of culturable methylotrophic bacteria in different genotypes of groundnut and their potential for plant growth promotion	Krishnamoorthy et al. (2018)

ice nucleation-active (INA) property and contains specific gene (*ina*) via deposition of cloud droplets (Hill et al. 2014) on the leaf surface and mineralize the carbon compounds (Vaïtilingom et al. 2013). Reports confirmed the relationship of INA bacteria and phyllosphere microbiota, combined activities of both phyllosphere microbiota and cloud microbiota actively participating carbon cycle, and strong support for climate regulation (Bringel and Couée 2015). The above information suggested that the phyllosphere microbiome not only supports the health of its host but is also beneficial to the environment, specifically it regulates plant-derived greenhouse and other gaseous pollutants.

5.9 Biotechnological Potential of Phyllosphere Microbiota

The plant beneficial microbes are agriculturally important bioresources, and it can stimulate the plant growth and enhance plant nutrient uptake through solubilization and mobilization (of P, K, and Zn), nitrogen fixation, and siderophore production (microbes-mediated bio-fortification of Fe in different crops). Beneficial microbes can play an important role in increasing yields of the crop, remove contaminants, inhibit pathogens, and produce novel substances. The growth stimulation by beneficial microbes can be a consequence of biological nitrogen fixation, production of plant growth regulators such as IAA, gibberellic acids, and cytokines, and biocontrol of phytopathogens through the production of antibiotic, antifungal, or antibacterial, Fe-chelating compounds, induction of acquired host resistance, enhancing the bioavailability of minerals (Kour et al. 2019; Kumar et al. 2019b; Yadav et al. 2019a).

In this contest, the phyllosphere microbes may positively influence the growth of host plant and produce some antagonistic compound against pathogens. Phyllosphere endophytes with properties such as nitrogen fixation (Jones 1970; Freiberg 1998; Furnkranz et al. 2008), bioremediation of harmful chemicals/pollutants, and biocontrol agents against important foliar plant pathogens (Beattie and Lindow 1995; Balint-Kurti et al. 2010; De Marco et al. 2004) have been documented. Further, the microbiome of phyllosphere is a reflection of environmental conditions; they can contribute significantly to global food webs and nutrient linkages. Many beneficial microbes such as *Achromobacter, Bacillus, Beijerinckia, Burkholderia, Flexibacterium, Methylobacterium, Micrococcus, Micromonospora, Nocardioides, Pantoea, Penicillium, Planomonospora, Pseudomonas, Streptomyces,* and *Xanthomonas* have been reported from the phyllosphere environment of different crop plants (Verma et al. 2013a, b; Mukhtar et al. 2010; Meena et al. 2012; Dobrovol'skaya et al. 2017). However, compared with most other microbial habitats, the investigation of phyllosphere microbes is quite limited. Some of its important biotechnological potentials are listed below.

5.9.1 Biocontrol Agents

Biocontrol is the measure to control pathogens and disease-causing pest including nematodes weeds, insects, and mites by other beneficial microbes or harmless living materials. In nature, plant diseases are caused by bacterial pathogens which provide a substantial decline in the development of agricultural products. For sustainable agriculture, scientific approaches use the antagonistic properties of beneficial microbes against the harmful pathogens instead of using toxic harmful chemicals as biological control (Erwin and Ribeiro 1996; Sharma et al. 2012). Biological treatment is a desirable strategy for controlling plant diseases (You et al. 2015) and there are an increasing number of biocontrol agents (BCAs), such as Bacillus spp., Pseudomonas spp., Trichoderma spp., etc. being commercialized for various crops (Trabelsi and

Mhamdi 2013; Cha et al. 2016). Most of them habitat either on phyllosphere or soil and can play a significant role in killing the number of plant pathogens on the surface of the leaves by competitive principle.

Pathogenic microbial interactions in phyllosphere decrease the fitness of plants, the productivity of crops, and question the safety of horticultural products for human consumption. Phyllosphere actinomycetes have been reported to inhibit the growth and colonization of plant pathogens (Lindow and Brandl 2003). For example, the endophytic isolate *Gordonia* sp. has been reported to produce imidazole-2-yl amino acids that have antifungal properties (Mikolasch et al. 2003) and an acidic polysaccharide called Gordon as the main component in biofilms, which is considered essential for pathogenicity against plant disease (Kondo et al. 2000). Various Streptomyces sp. including S. griseus have been reported as producing various antifungal compounds such as 1-H-pyrrole-2-carboxylic acid (PCA), cycloheximide, and streptomycin which were successfully used to control fungal and bacterial diseases in plants (Leben and Keitt 1954; Nguyen et al. 2015). Wiwiek et al. (2017) studied the rice phyllosphere actinomycetes could be used as potential biocontrol agents against fungal leaf blast disease. Wang and Ma (2011) reported that exogenous actinomycete XN-1 has the potential to act as an antagonistic agent in controlling the occurrence and development of cucumber leaf spot in the greenhouse. This also confirms that phyllosphere microorganisms play an important role in combating the infection of pathogens and have a promising future in developing biocontrol products. Table 5.7 shows the plant-associated bacteria and its biological activities.

Microbes with the production of compounds like indole acetic acid and N-acyl homoserine lactone (AHL) assist the bacteria to colonize on plant surface (Lindow and Brandl 2003). Sartori et al. (2015) studied the biocontrol potential of phyllosphere microorganisms from maize against Exserohi lumturcicum, the causal agent of leaf blight. Shrestha et al. (2016) investigated the prospects of biological control of rice-associated Bacillus against sheath blight and panicle blight of rice caused by Rhizoctonia solani and Burkholderia glumae, respectively. A variety of Bacillus isolates were observed to inhibit the sclerotial germination of the fungus, which could be attributed to the various antimicrobial secondary metabolites produced by the bacteria. Various gram-negative bacteria also show plant protection activity. For example, *Pseudomonas graminis* isolated from the apple phyllosphere showed control against fire blight caused by Erwinia amylovora (Mikiciński et al. 2016), *Pseudomonas protegens* CS1 from the lemon phyllosphere are used as a biocontrol against citrus canker (Michavila et al. 2017).

Further, microbial production of siderophores quenches the phytopathogens and protects the host plant from their infection (Scavino and Pedraza 2013; Ahmed and Holmström 2014; Harsonowati et al. 2017; Sabaté et al. 2018) as a biocontrol agent. For example, the siderophore produced by *Pseudomonas syringae* pv. *syringae* 22d/93 shows biocontrol activity against *Pseudomonas syringae* pv. *glycinea* 1a/96, a plant pathogen (Wensing et al. 2010). The siderophore pyochelin produced by the endophyte control rice blast is caused by Pyricularia oryzae (Harsonowati et al. 2017). Plant-associated *Pseudomonas* spp. has been employed efficiently as commercial biocontrol agents (Loper and Lindow 1987; Walsh et al. 2001). Cyanogenic

Table 5.7 Plant-associated microbial compounds and bioactivity

Compound	Source	Bioactivity	References
Blasticidin-S (VIII):	*Streptomyces griseochromogenes I*	Control the rice blast caused by *Pyricularia oryzae*	Fukunaga (1955)
Kasugamycin (IX)	*Streptomyces kasugaensis*	Rice blast caused by *Pyricularia oryzae*, leaf spot in sugar beet and celery by *Cercospora* spp., and scab in pears and apples caused by *Venturia* spp.	Umezawa et al. (1965)
Methoxyphenone	*Streptomyces griseolus*	Herbicides	Ito et al. (1974)
AM-toxin	*Alternaria mali*	phytotoxin	Park et al. (1977)
Milbemycin (XI):	*S. hygroscopicus* subsp. *aureolacrimosus*	Insecticidal and acaricidal	Mishima et al. (1983)
Diabroticin A	*Bacillus subtilis* and *Bacillus cereus*	Polar insecticide	Stierle et al. (1990)
Spinosad (X): spinosyn A and spinosyn D	*Saccharopolyspora spinosa*	Controls the caterpillar (*Helicoverpa zea* Boddie, *Pieris rapae* (L.), *Keiferia lycopersicella* (Walsingham), thrips (*Ceratitis capitata* (L.), *Thrips palmi* (Karny)) and beetles (*Leptinotarsa decemlineata* (Say))	Mertz and Yao (1990)
AF-toxins	*Alternaria fragariae*	Maculosin is a cyclic dipeptide—phytotoxin	Stierle et al. (1990), Uneo (1990)
Maculosin (XVI)	*Phoma lingam*	Phytotoxin	Stierle et al. (1990)
Efrapeptins	*Tolypocladium* spp.	Pesticide and insecticide	Krasnoff and Gupta (1991), Krasnoff et al. (1991)
Abamectin	*Streptomyces avermitilis*	Insecticide and acaricide	Jansson and Dybas (1996)
Nodulisporic acid	*Nodulisporium* sp.	Insecticidal activity	Ondeyka, et al. (1997)
Pyrizadocidin (VII)	*Streptomyces* #620061	Herbicides	Gerwick et al. (1997)
Syringomycin E:	*Pseudomonas syringae* ESC 10/11	Fungicide-citrus green mold *Penicillium digitatum*	Bull et al. (1998)

(continued)

Table 5.7 (continued)

Compound	Source	Bioactivity	References
Destruxin A and B	*M. anisopliae*	Insecticide	Strasser et al. (2000)
Oosporein	*Beauveria brongniartii*	Insecticide	Strasser et al. (2000)
Beauvericin A and B	*Beauveria bassiana* and *Paecilomyces* spp	Hexadepsipeptide—insecticide	Lane et al. (2000)
Borrelidin	*Streptomyces* species- neau-D50	Antifungal activity against *Phytophthora sojae*	Worapong et al. (2001)
Bialaphos (V)	*Streptomyces hygroscopicus* and *Streptomyces viridochromogenes*	Herbicide—weed control	Tachibana (2003)
Tartrolone C	*Streptomyces* sp. CP1130	Insecticidal macrodiolide	Lewer et al. (2003)
Coronatine	*Pseudomonas coronafacience*	Insecticide—herbicide	Block et al. (2005)
Macrolactin A:	*Bacillus* sp. *sunhua*	*Fungicide—Fusarium oxysporum and Streptomyces scabies*	Han et al. (2005)
Bt-Toxins	*Bacillus thuringiensis*	Bioinsecticides endotoxins	Collier et al. (2005)
Tabtoxin	*Pseudomonas syringae* var. *tabaci*	Phytotoxic—Herbicide	Hoagland et al. (2007)
Phyllostictine A	*Phyllosticta cirsii*	Mycoherbicide	Zonno et al. (2008)
Cinnacidin (XXII):	*Nectria* sp. DA60047	Phytotoxic	Irvine et al. (2008)
Beauvericin A and B	*Beauveria bassiana* and *Paecilomyces* spp.	Hexadepsipeptide—insecticide	Miller et al. (2008)
Herbimycin (VI)	*Streptomyces hygroscopicus* AM3672	Benzaquinoid ansamycin antibiotic with potential herbicidal a	Hahn et al. (2009)
Albucidin	*Streptomyces albus* subsp. *chlorinus* NRRL B-24108	Herbicides	Hahn et al. (2009)
Zinniol	*Alternaria cirsinoxia*	Phytotoxic to *Cirsium arvense* L.	Berestetskii et al. (2010)
Ascaulitoxin aglycone	*Ascochyta caulina*	Phytotoxin	Duke et al. (2011)
Antibiotic 1233A (XXIV)	*Cephalosporium* sp., *Fusarium* sp.,	Phytotoxin	Duke and Dayan (2011)

(continued)

Table 5.7 (continued)

Compound	Source	Bioactivity	References
AK-toxin (XV):	*Alternaria kikuchiana*	Phytotoxin	Saxena (2014)
Bipolaroxin (XVIII)	*Bipolaris cynodontis*	Phytotoxic to *Cynodon dactylon*	Saxena (2014)
Bt-Toxins	*Bacillus thuringiensis*	Bioinsecticides endotoxins	Radhakrishnan et al. (2017)
Phaseolotoxin (III)	*Pseudomonas* sp.	Phytotoxins—herbicide	Aguilera et al. (2017)

fluorescent *Pseudomonas* produces siderophores in the presence of a strong chelator 8-Hydroxyquinoline which inhibits pathogens such as *Rhizoctonia solani* and *Sclerotium rolfsii* (Kotasthane et al. 2017). Table 5.8 listed some important findings as endophytes as biocontrol agents. Mostly, the biocontrol agents use either nonribosomal peptide synthetase (NRPS) gene and/or type 1 polyketide synthase gene for respective compound production.

5.9.2 Plant Growth-Promoting Compounds

Plant growth is regulated by the growth hormones, available nutrient, good environmental condition, and beneficial microbial interaction. Many of the microbes are the prime producers of plant growth hormones, specifically plant-associated or phyllosphere microbial communities produce IAA, gibberellic acids, and cytokines and could fix nitrogen and mobilize nutrients (Dourado et al. 2015). There are many bacteria and fungi which produce IAA, similar to those of plants (Sun et al. 2014; Venkatachalam et al. 2016; Thapa et al. 2018. Microbes use plant tryptophan to produce IAA, which can effectively improve plant growth and enhance overall health (Hayat et al. 2010; Yadav et al. 2015a, b). The genus *Methylobacterium* is among the most commonly observed leaf epiphytes and represents an abundant and stable member of the phyllosphere microbial community of a wide range of crop plants such as sugarcane (*S. officinarum* L.), pigeon pea (*Cajanus cajan* L.), mustard (*Brassica campestris* L.), potato (*Solanum tuberosum* L.), and radish (*Raphanus sativus* L.) (Meena et al. 2012), and has produced variety of growth-promoting phytohormones. The association of plant growth-promoting bacteria (PGPB), especially *Methylobacterium* sp., with plant hosts greatly benefits plant growth by production of phytohormones like auxins and cytokinins, and increased activity of enzymes such as urease and 1-aminocyclopropane-1-carboxylate deaminase (ACCD), which promotes growth and enhances the production of siderophores, thereby enhancing the uptake of essential nutrients.

The benefits associated with plant–microbe interactions are also dependent on the variety of inoculation methods such as soil, foliar, and combination of both soil

Table 5.8 Phyllosphere endophytic fungi as biocontrol agent

Endophyte	Host	Pathogen	References
Fusarium proliferatum	Grape	*Plasmopara viticola*	Falk et al. (1996)
Acremonium zeae	Maize	*Aspergillus flavus* and *Fusarium verticillioides*	Wicklow et al (2005)
Trichoderma sp.	Apple Tobacco, bean, iris Radish, strawberry, cucumber, potato, and tomato	*Nectria galligena, Botrytis cinerea* *Sclerotium rolfsii* *Rhizoctonia solani* *Chondrostereum purpureum*	Reino et al. (2008)
Colletotrichum gloeosporioides, Clonostachys rosea, and Botryosphaeria ribis	*Theobroma cacao*	*Moniliophthora roreri (frosty pod rot), Phytophthora palmivora (black pod rot),* and *Moniliophthora perniciosa (witches broom)*	Mejía et al. (2008)
Trichoderma martiale	Cacao (*Theobroma* cacao)	*Phytophthora palmivora*	Hanada et al. (2009)
Clonostachys rosea	wheat	*Gibberella zeae*	Hue et al. (2009)
Cladosporium, Colletotrichum, Gibberella, Hypocrea, and Trichoderma	*Smallanthus sonchifolius* (Poepp.) H. Rob.	*Lecythophora* sp. *and Fusarium oxysporum*	Rosa et al. (2012)

(continued)

Table 5.8 (continued)

Endophyte	Host	Pathogen	References
Penicillium spp.	*Vitis vinifera* L.	*Botrytis cinerea*	Núñez-Trujillo et al. (2012)
Colletotrichum gloeosporioides, Flavodon flavus, Diaporthe helianthi, Diaporthe phaseolorum, Aporospora terricola	*Vitis labrusca* L.	*Fusarium oxysporum*	Brum et al. (2012)
Cladosporium cladosporioides	*Huperzia serrata*	*Colletotrichum acutatum, Colletotrichum fragariae, Colletotrichum gloeosporioides,* and *P. viticola*	Wang et al. (2013a)
Bionectria ochroleuca, Aureobasidium pullulans, Chaetomium spirochaete	*Vitis vinifera*	*Botrytis cinerea*	Cosoveanu et al. (2014)
Ramularia endophylla	Plant	*Mycosphaerella labyrinth*	Videira et al. (2015)

and foliar inoculations (Lee et al. 2011). A study has been conducted to investigate the inoculation of *Erwinia herbicola* on plant growth by IAA production. The test results showed that about 65% of the *E. herbicola* strain recovered from the leaves showed higher expression of the ipdC gene than in culture. The study indicated that physical or chemical microclimates directly influence the differential expression of ipdC (Brandl et al. 2001). Similarly, endophytic bacteria such as *Bacillus pumilus* E2S2 (Luo et al. 2012), *B. amyloliquefaciens* NBRI-SN13 (Nautiyal et al. 2013), *B. atrophaeus* EY6 and *B. sphaericus* B EY30, *B. subtilis* EY2, *S. kloosii* EY37, and *K. erythromyxa* EY43 (Karlidag et al. 2011) also produce PGPs.

Endophytic *Bacillus* produces phytohormones such as abscisic acid, auxins, brassinosteroids, cytokinins, ethylene, gibberellins, jasmonates, and strigolactones, and increases nutrient (nitrogen and phosphorous) accessibility to the host (Reinhold-Hurek and Hurek 2011; Brader et al. 2014; Santoyo et al. 2016; Shahzad et al. 2016; Ek-Ramos et al. 2019). Zeiller et al. (2015) reported that *C. botulinum* 2301 significantly produce PGPs in a field experiment of clover. A cold-tolerant bacterial strain *Exiguobacterium acetylicum* 1P promotes wheat seedlings growth (Selvakumar et al. 2010), *Brevibacillus* brevis improve the growth of cotton crop (Nehra et al. 2016) *and Bacillus* spp. induce phosphate solubilization more efficiently when present as endophytes in citrus (Giassi et al. 2016). The diazotrophic bacteria associated with phyllosphere gives benefits to the plant by fixing atmospheric nitrogen, solubilization of phosphorus (P), and utilization of available nutrients through its organic end product-mediated solubilization of rock phosphates (Mohammadi 2012; Kembel et al. 2014; Mwajita et al. 2013; Batool et al. 2016; Lambais et al. 2017).

5.9.3 Biopharmaceutical Importance

Biological activity of medicinal plants and their applications in various healing properties have been documented well. In recent years, microbes associated with plants themselves proved with high therapeutic values particularly endophytes. Endophytic microbes are known for their beneficial effects to the host, specifically phytohormones, enzymes, and stress-resistant physiology, and its biotechnological potentials (Parthasarathi et al. 2012; Singh and Dubey 2015; Gouda et al. 2016). Endophytes are known to produce bioactive metabolites, which served as a potent drug for medical and cosmetic industries (Shukla et al. 2014; Gouda et al. 2016). Secondary metabolites produced by the endophytic bacteria, actinomycetes, and fungi have economically valuable compounds such as alkaloids, flavonoids, phenolic acids, quinones, steroids, saponins, terpenoids, tetralones, xanthones, etc. (Strobel and Daisy 2003; Joseph and Priya 2011; Godstime et al. 2014; Shukla et al. 2014; Gouda et al. 2016). For example, endophytic microbes are well-known producers of taxol, a diterpene alkaloid, and lignin such as cathartics, emetics, and cholagogue used for cancer treatment (Konuklugil 1995; Zhang et al. 2009; Nair and Padmavathy 2014; Soliman

Table 5.9 Pharmaceutical valuable products from phyllosphere microbes

Producer	Compound	Activity against	References
Hypericum perforatum, Diaporthe helianthi	Hypericin, emodin, tyrosol	*Salmonella sp.*	Joseph and Priya (2011), Specian et al. (2012)
Ganoderma boninense	Rapamycin, cyclododecane, petalostemumol	*Bacillus subtilis*	Parthasarathi et al. (2012), Ismail et al. (2014)
Fusarium sp. *Cryptosporiopsis quercina*	Xularosides, munumbicins, Saadamycin, cryptocandin	*Candida albicans*	Jalgaonwala et al. (2011), Dutta et al. (2014)
Streptomyces sp., *Kennedia nigricans*	Munumbicins	*Vibrio cholerae*	Kumar et al. (2014)
Cryptosporiopsis quercina	Saadamycin	*Campylobacter jejuni*	Dutta et al. (2014)
Streptomyces sp.	Kakadumycin A, hypericin	*Shigella* sp.	Golinska et al. (2015), Joseph and Priya (2011)
Streptomyces tsusimaensis	Valinomycin	*Corona virus*	Alvin et al. (2014)
Fusarium proliferatum	Kakadumycin, beauvericin	*Listeria monocytogenes*	Golinska et al. (2015)
Boesenbergia rotunda Streptomyces coelicolor	Munumbicins	*Escherichia coli*	Golinska et al. (2015), Singh and Dubey (2015)
Grammothele lineata	Paclitaxel	*Anticancer*	Das et al. (2017), Kasaei et al. (2017), Soliman and Raizada (2018)

and Raizada 2018). There are many novel metabolites with antibacterial, antifungal, antiviral, anticancer, and antihelminthic activity isolated from plant-associated microbes (Gouda et al. 2016; Kasaei et al. 2017) (Table 5.9).

5.9.4 *Other Applications*

Besides the use of phyllosphere microbes for enhanced growth as well as biocontrol agent, some plant-associated bacteria helps the plant to improve phytoremediation of toxins. For example, hydroxamate siderophores producing bacteria compact heavy metal toxicity and improve the phytoremediation property in *A. thaliana* (Grobelak and Hiller 2017). Some endophytes provide additional functions to the host plant like drought tolerance, for example, endophytic *B. subtilis* strain B26 induces drought resistance to *Brachypodium distachyon* grass. The drought resistance mechanism is due to a specific carbohydrate metabolism, the endophytic bacteria increases stress-responsive raffinose-related family carbohydrates in the host (Gagné-Bourque et al. 2015). In another example, the endophytic association increases osmotic responses of the host plant. Endophytic strains such as Arthrobacter sp. and Bacillus spp. in pepper plant increase the proline accumulation, which gives osmotic tolerance (Sziderics et al. 2007).

Further, endophytic bacterial inoculants provide abiotic stress tolerance mechanism to the host by its extracellular enzymes. For example, the endophytic association of various *Bacillus* spp. increases the superoxide dismutase, phenylalanine lyase, catalase, and peroxidase enzymes activity in gladiolus plants under sodium high concentration conditions (Damodaran et al. 2014). Little studies reported that isolation of endophytic bacteria and their enzyme production potential vary when it colonizes in the plant tissues. Moreover, Jalgaonwala et al. (2011) observed maximum proteolytic activity in *Lactobacillus fermentum* isolated from leaves of *Vinca rosea*, which is considered greater to nonendophytic isolates. Similarly, endophytic fungi isolated from *Ocimum sanctum* and *Aloe vera* has better enzymatic activity (Yadav et al. 2015a, b). Besides these mechanisms, plant-associated microorganisms improve nutrient acquisition by supplying minerals and other micro/macronutrients from the soil (Singh et al. 2017; Singh and Singh 2017). Above all merits provide new insights in the field of phyllosphere microbiome and its essentiality of interactions to host plant growth and protection and also its significant role in the ecosystem.

5.9.5 Conclusion and Future Prospects

The phyllosphere is a unique environment colonized by a wide variety of microorganisms including epiphytes and endophytes, beneficial and pathogenic, bacteria, fungus, viruses, etc. Understanding the phyllosphere community structure, networking, and physiology is a great challenge. However, extensive research on phyllosphere microbiota gives great potential for the applications in economic plant productivity, specifically agriculture and forestry, ecosystem cleaning, and health. Hitherto, both in vitro and in vivo experiments are required to improve the understanding of microbial aggregations in the phyllosphere and dynamic play in the ecosystem. Based on the literature understanding, further and future studies should aim to (1) study the community interplay within the closely related and distanced microbial interactions and its stimulatory response on host plant and ecosystem, (2) to know the potentials of beneficial microbes and their commercial value, (3) impact on climate change on phyllosphere microbiome, and their contribution to climate change, (4) moreover, documentation of host-specific, geographic-specific, and seasonal-specific microbial interactions—guiding host–parasite and beneficial–pathogen interactions. Besides, phyllosphere microbiome research assures to understand the current challenges highlighting the terrestrial ecosystem change and the impact of global warming, especially the dominance of pathogenesis.

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Chapter 6
Biofilms Forming Microbes: Diversity and Potential Application in Plant–Microbe Interaction and Plant Growth

Ajay Kumar and Joginder Singh

Abstract Global climatic change and increasing worldwide population pose challenges for crop production. The promising sustainable solution is the integration of beneficial plant–microbes integration with microbiome to improve agriculture production. Microbial biofilms have a significant role in agriculture because they increase soil fertility and promote plant growth. Bacterial quorum sensing (QS) regulated process is biofilm formation. The plant growth promoting bacteria (PGPB) or Rhizobacteria (PGPR) has the ability to increase the crop yield. PGPR-based formulations have been commercialized to enhance agricultural productivity.

Keywords Biofilm · Quorum sensing · Phytohormones · Biocontrol · Biofertilizers · Models

6.1 Introduction

Plant and its organs in natural conditions are surrounded by microbes. Several rhizobacteria, mycorrhizal fungi, protozoa, actinomycetes, and algae are colonized around the root of plants in rhizosphere. Colonizing microorganisms are dominated by bacterial population. The role of plant growth promoting bacteria (PGPB) or Rhizobacteria (PGPR), either by a direct or indirect mechanism in plant development has been cited by many researchers (Timmusk et al. 2017). Plant growth promoting bacteria (PGPB) or Rhizobacteria (PGPR) can stimulate the production of phytohormones,1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme, and secondary metabolites for the growth and development of the plant and root system. An arbuscular mycorrhizal fungus (AMF) also triggers the root hair growth in mycorrhizal plants (Yadav et al. 2015a, b, 2016; Zhang et al. 2019). Thus, the colonization of bacteria and fungus promotes the lateral roots and hairs and reduces

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the growth of primary roots. Plant growth promoting bacteria (PGPB) or Rhizobacteria (PGPR) influences the growth of plant via nitrogen fixation to increase the crop yield, siderophores production, phosphate solubilization, osmotic stress alleviation, by effecting the auxin level in plant roots, and modify the root physiology by affecting the gene transcription (Vacheron et al. 2013; Verma et al. 2016; Yadav 2017, 2019).

PGPR such as *Bacillus amyloliquefaciens, Bacillus* megaterium, and *Bacillus subtilis* are able to produce phytohormones such as auxin (IAA) or promote growth under phosphate limitation by excreting phytase (*EC* 3.1.3.8) in the presence of phytate. The main hypothesis to explain colonization efficiency by bacterial and fungal strains is influenced by the chemotaxis effect. The proposed mechanism of root colonization by bacterial and fungal strains depends on the abilities (i) to move toward the place for root colonization, (ii) to use carbon and nitrogen sources present in the soil, (ii) provided by root exudates to shape the root microbiome, (iii) to withstand plant response reaction including reactive oxygen species (ROS), and (iv) to form a biofilm or microcolonies formation at the root surface. Bacillus sp. Strains (*Bacillus subtilis*, *Bacillus licheniformis*, *Bacillus amyloliquefaciens, Bacillus cereus*, etc.) are able to produce a set of secondary metabolites such as surfactin, fengycin, and iturin A, which belong to cyclic lipopeptides (CLPs) members and exhibit antifungal activities and inhibit the growth of several plant pathogens (Al-Ali et al. 2018). The impact of phyto stimulating PGPR on root architecture is shown in Fig. 6.1.

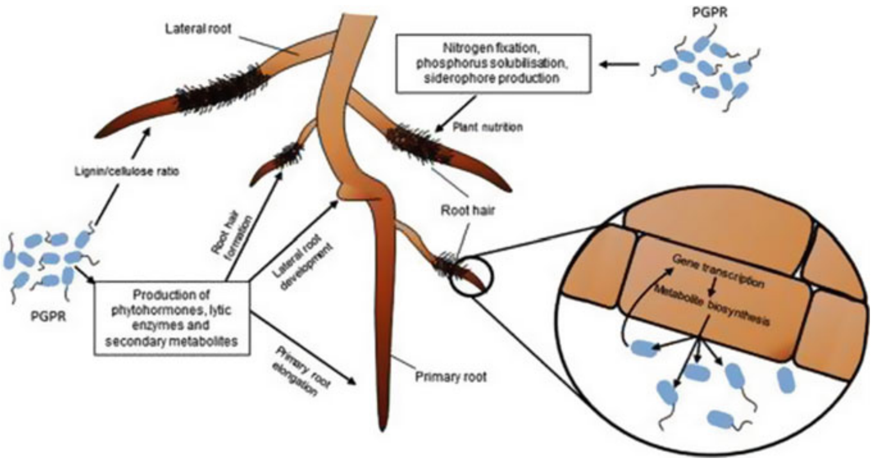


Fig. 6.1 Impact of phyto stimulating PGPR on RSA (root system architecture), nutrient acquisition, and root functioning. *Sources* Vacheron et al. (2013)

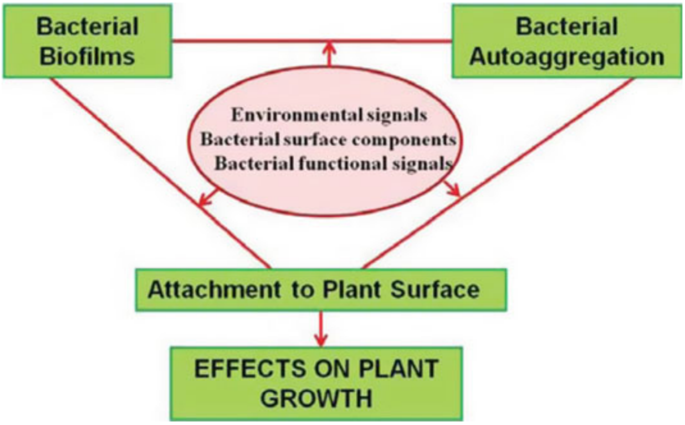


Fig. 6.2 Bacterial auto aggregation and biofilm development, and their relationship with plant colonization. *Sources* Bogino et al. (2013)

6.2 Biofilm Formation by PGPR

It has been observed that most of the bacteria develop bacterial biofilm attached to the surface. Biofilm is made up of protein, lipid, polysaccharide, and DNA in a self-produced extracellular matrix and is found on various surfaces such as soil, potable water system, and living tissues (Singh et al. 2017). It is a secreted extracellular matrix that holds cells together which is common to all bacterial biofilms and provides robustness to biofilm architecture (Molina-Santiago et al. 2019). Several factors such as environmental signals (Cyclic di-AMP act as extracellular signal), nutrient limitation of growth (Iron limitation), quorum sensing (QS) signal molecules such as acylated homoserine lactones(AHLs), exopolysaccharides (EPSs),bacterial surface components particularly flagella, lipopolysaccharides (LPSs), and other factors regulate the cell aggregation and biofilm formation in plant–bacterial associations (Primo et al. 2019; Bogino et al. 2013). Biofilm formation by PGPR and colonization with plant are demonstrated in Fig. 6. 2.

6.3 Biofilm Formation Steps by Bacteria

Biofilm formation is a complex and dynamic process (D'Acunto et al. 2017), formed by several steps (i) adhesion of planktonic cell to support surface (ii) formation of monolayer and cell proliferation (iii) microcolonies formation (iv) macrocolonies formation (v) development of matured biofilm (vi) detachment or dispersal of bacterial cells. Figure 6.3, represents the stages of the biofilm process and Table 6.1, shows some important microorganisms forming biofilms.

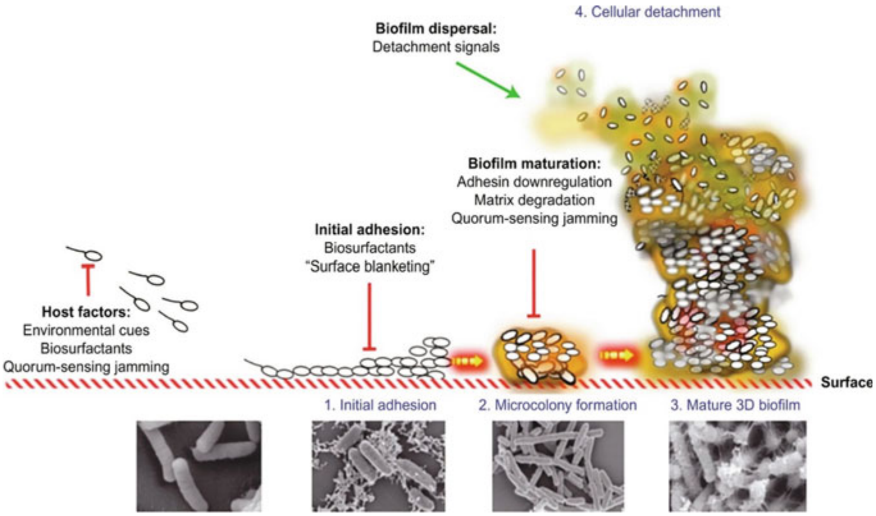


Fig. 6.3 Stages in the biofilm formation process, including scanning electron microscopy imaging of each stage. *Source* Hadla and Halabi (2018)

6.4 Factors Affecting Biofilm Formation

Several factors have been investigated which affects the biofilm formation such as temperature of the surroundings, pH of the soil, nutrient availability, minerals, flow of the fluid, plant defense compounds such as phenazine, surfactants such as cyclic lipopeptides (CLPs), bacterial strains, EPS, flagella, gene expression, Quorum sensing, surface characteristics (hydrophobicity, roughness, wettability), organic fouling, and presence of other microbes (Velmourougane et al. 2017).

Mass transport characteristics have also influenced the biofilm's density (Fysun et al. 2019). The rate of nutrient transport to the biofilm is determined by the rates of convective external mass transfer $[k_l(C_b - C_s)]$ and internal mass transfer $(D_f \frac{dC}{dZ})$ be equal at biofilm surfaces (Beyenal and Lewandowski 2002) as shown in Eq. (1).

$$N_s = k_l(C_b - C_s) = D_f \frac{dC}{dZ} \tag{1}$$

where N_s, the nutrient flux.

k_l, the external mass transfer coefficient
C_b, the substrate concentration at bulk phase
C_s, the substrate concentration at surface of the biofilm
D_f, the effective diffusivity in the biofilm.

Factors affecting biofilm formation are shown in Fig. 6.4.

Table 6.1 Biofilm formation by agriculturally important microorganisms

Microbes	Attributes	References
Trichoderma–Azotobacter	Improves soil nutrient availability and plant growth	Velmourougane et al. (2019a,b)
B. amyloliquifaciens, *B. licheniformis*, *B. megaterium*, *B. pumilus*, *B. subtilis*,	Promotes plant growth and development	Tiwari et al. (2019)
Anabaena–Azotobacter	Enhanced the availability of nitrogen, phosphorus, and micronutrients in the soil	Kanchan et al. (2019)
Azotobacter chroococcum (*Az*)—*Trichoderma viride* (*Tv*)	Plant growth promotion and biocontrol	Velmourougane et al. (2019a, b)
Agrobacteriumtumefaciens	Tumor formation	Choi et al. (2018)
Azospirillum brasilense	Fix atmospheric nitrogen and synthesize phytohormones such as indole-3-acetic acid (IAA)	Jijón-Moreno et al. (2019)
Rhizobium leguminosarum	Nitrogen fixation	Shahid et al. (2019)
Pseudomonas sp	Plant growth promotion activity, such as synthesis of phytohormones, phosphorus solubilization, production of ammonia, HCN, and siderophore	Singh et al. (2019)
Pseudomonas aeruginosa-Bradyrhizobium sp.	Improving plant growth, nutrient acquisition, and soil health	Kumawat et al. (2019)
Gluconacetobacter diazotrophicus	Plant growth and protect the plants against abiotic stresses	Filgueiras et al. (2019)
Herbaspirillum huttiense, *Enterobacter asburiae,* and *Staphylococcus sp.*	Nitrogen fixation	Andreozzi et al. 2019
Sinorhizobium meliloti	Fix atmospheric nitrogen	Primo et al. (2019)

Source Besset-Manzoni et al. (2018)

6.5 Mathematical Model of Biofilm Formation

A mathematical model of biofilm formation developed by Eberl et al. (2001) which consists of a set of nonlinear density dependent reaction–diffusion equation which is applicable for single species QS-regulated biofilm system.

$$\frac{\partial C(t)}{\partial t} = D_c \Delta C - \frac{k_1 C M}{k_2 + C} \tag{2}$$

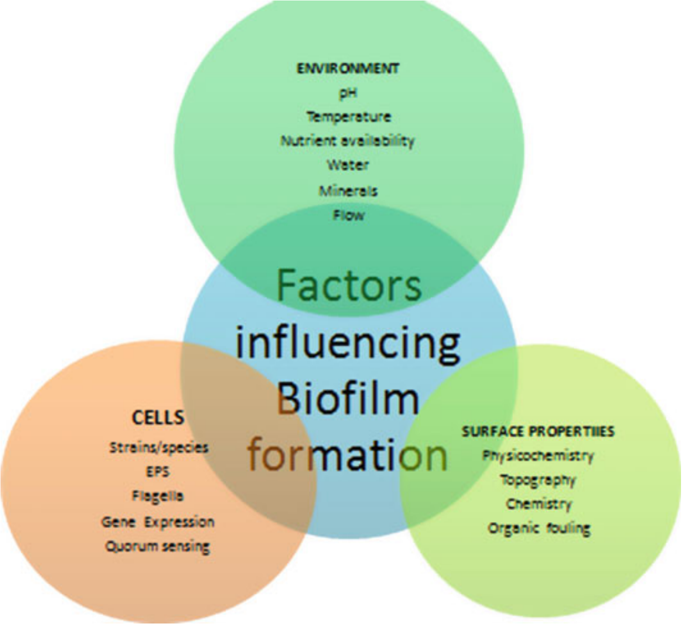


Fig. 6.4 A complex interplay of factors results in biofilm formation, architecture, and hence functionality. *Source* Whitehead and Verran (2015)

$$\frac{\partial M(t)}{\partial t} = \nabla.(D_M(M)\nabla M) + M\left(\frac{k_3 C}{k_2 + C} - k_4\right) \tag{3}$$

$$D_M(M) = \delta \frac{M^a}{(1 - M)^b} \tag{4}$$

where $D_C, D_M, k_1, k_2, k_3, k_4$ are positive constant parameters and $a > 1, b > 1$. M denotes biomass density, δ is biomass mobility coefficient, and C is the growth-limiting substrate.

Sometimes the phenomenon of floating biofilm (Fig. 6.5) is observed when a microbial aggregate does not attach to the surface. Fickian diffusion equation is used to describe the phenomenon of dispersed cell diffusion within the biofilm and bulk liquid. The growth is modeled by a hyperbolic partial differential equation and diffusion of dispersed cells by a parabolic partial differential equation. The transport of substrates from the bulk liquid to the biofilm is achieved by diffusion. The role of signaling molecule such as Nitric oxide (NO) in the regulation of dispersal in biofilm has been demonstrated by many researchers (D'Acunto et al. 2019; Zhu et al. 2019). Biofilm formation

$$\frac{\partial X_i}{\partial t} + u\frac{\partial X_i}{\partial z} = \rho_i R_{Mi}(z, t, X, S, \psi) \tag{5}$$

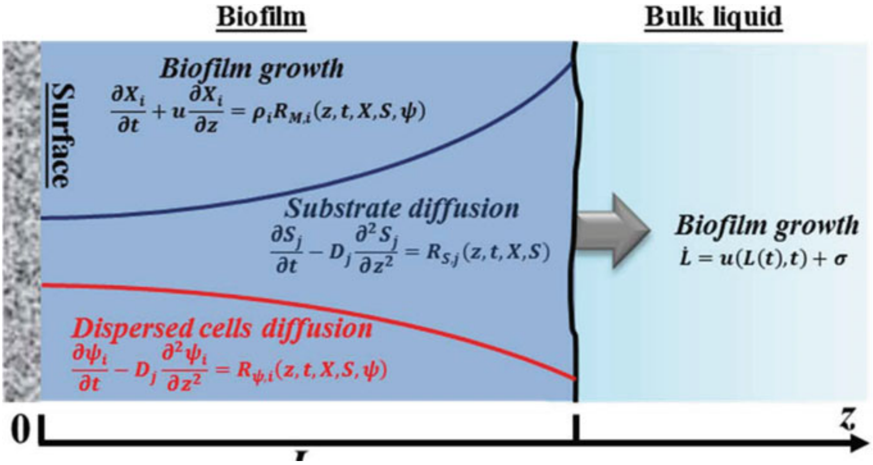


Fig. 6.5 Phenomenon of biofilm growth. *Source* D'Acunto et al. (2019)

Substrate diffusion

$$\frac{\partial S_j}{\partial t} - D_j\frac{\partial^2 S_j}{\partial z^2} = R_{S,j}(z, t, X, S) \tag{6}$$

Dispersed cell diffusion

$$\frac{\partial \psi_i}{\partial t} - D_j\frac{\partial^2 \psi_i}{\partial z^2} = R_{\psi,i}(z, t, X, S, \psi) \tag{7}$$

Biofilm Growth

$$L = u(L(t).t) + \sigma \tag{8}$$

where concentration of dispersed cells is defined by the variables $\psi_{,i}(z, t)$, X_i is biomass concentration, S_j is substrate concentration, L is biofilm thickness, ρ_i is biofilm density, D is diffusion coefficient, where $D_{M,i}$ denotes the diffusivity coefficient of planktonic species i. $R\psi$, $i(z, t, \mathbf{X}, \mathbf{S})$ is the species i conversion rate into the planktonic state, u is superficial velocity, and σ is biomass flux between biofilm and bulk solution.

6.6 Mechanism of Quorum Sensing

Quorum sensing (QS) is a bacterial communication mechanism which is achieved through diffusible signal molecules that enables biofilm formation. Small amounts of chemical signaling molecules (autoinducers) such as N-Acyl Homoserine Lactones

(AHL) are produced and released by gram-negative bacterial cells (Emerenini et al. 2015) while oligopeptides are used by gram-positive bacteria (Roy et al. 2011). High enough concentration of AHL, can bind to and activate a transcription activator, or R protein in turn induces the expression of target gene (De Kievit and Iglewski 2000; Saraf et al. 2014). The regulation of a quorum sensing in bacteria systems are represented in Fig. 6.6.

Quorum sensing (QS) in gram-negative organisms is shown in Fig. 6.7. As formation of biofilm is QS-regulated mechanism and therefore, the position in the biofilm, thickness of biofilm, boundaries of the biofilm surface are directly related to the concentration of signal molecules (Pérez-Velázquez et al. 2016). Several mathematical models for biofilm formation, maturation, and dissolution have been investigated by researchers.

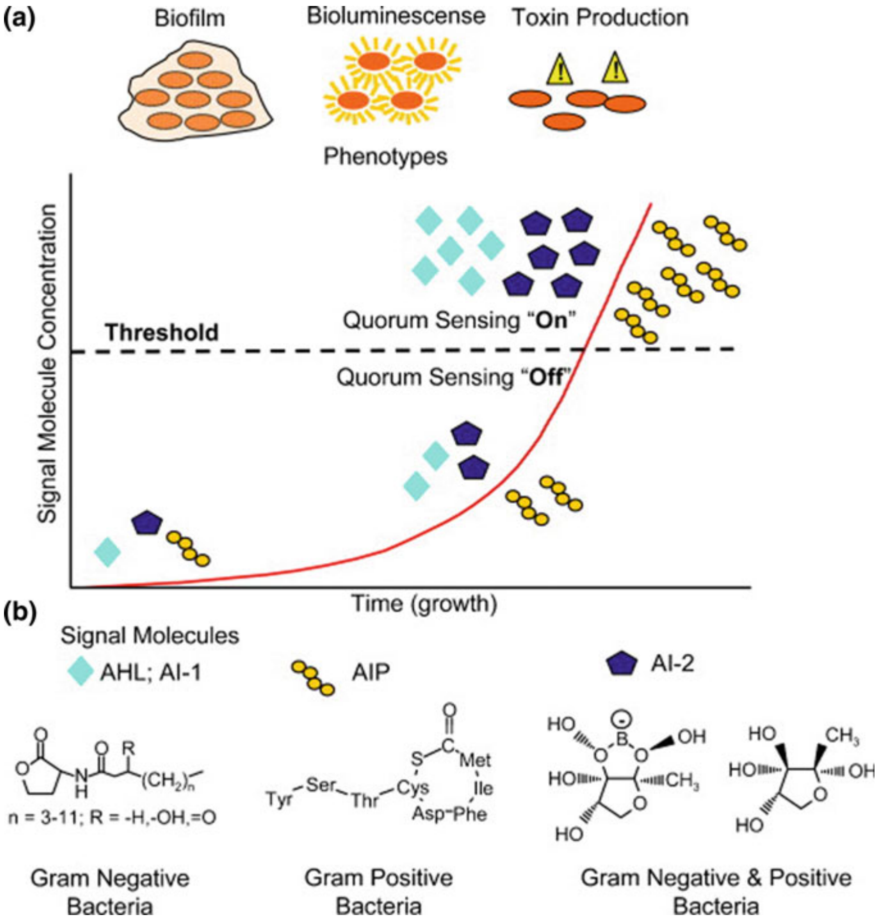


Fig. 6.6 Schematic representation of the triggering of a quorum sensing system (**a**) and the main signaling molecules involved in Gram-positive and Gram-negative bacteria (**b**). *Source* Roy et al. (2011)

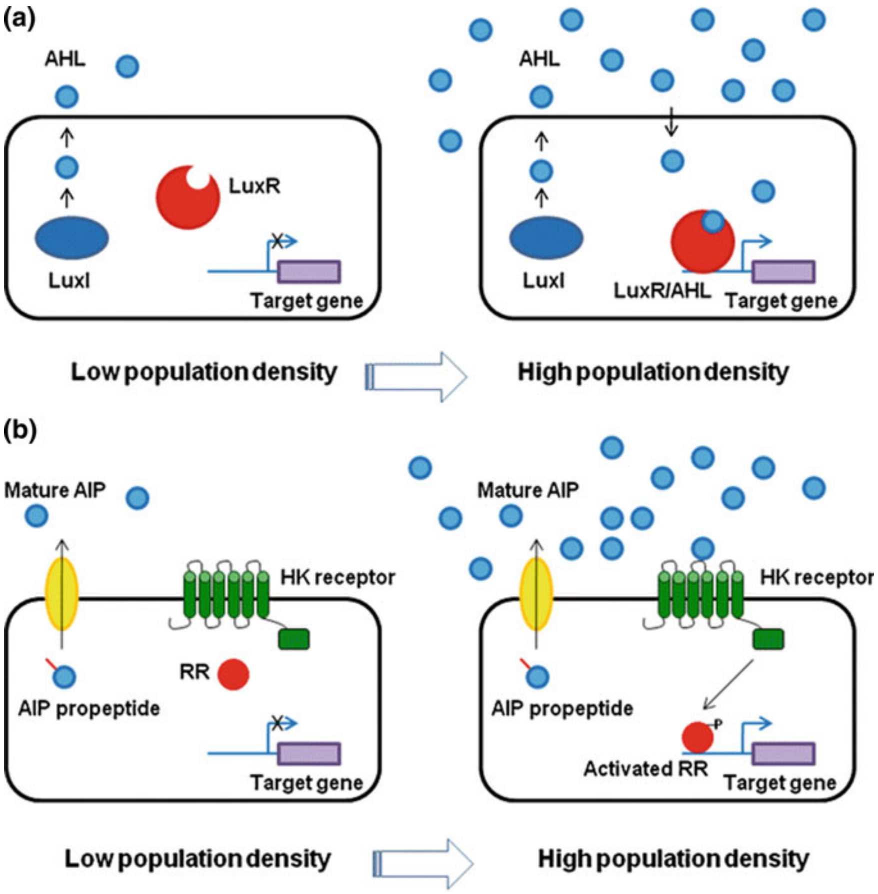


Fig. 6.7 Quorum sensing in gram-negative (**a**) and gram-positive organisms (**b**). *Source* Choudhary and Schmidt-Dannert (2010)

6.7 Applications of Biofilm

Different applications of biofilms have been investigated by investigators in plant–microbe interaction and plant growth as represented in Fig. 6.8 (Velmourougane et al. 2017).

6.7.1 Biofertilizers

Some of the plant growth promoting bacteria (PGPB) or Rhizobacteria (PGPR) are classified as biofertilizers and biocontrol agents or biopesticides. Biofertilizer is a

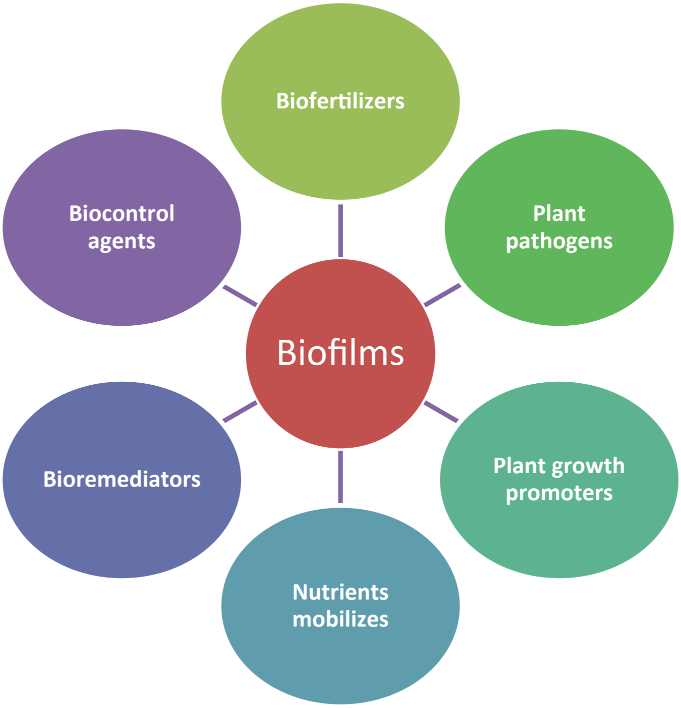


Fig. 6.8 Overview of the significance of biofilms in agriculture. *Source* Velmourougane et al. (2017)

group of beneficial bacteria such as Rhizobacteria enhancing the productivity of the soil (Olanrewaju et al. 2019; Yadav et al. 2017a, 2019a; Yadav and Yadav 2019). Microbial inoculants used in agricultural crops are shown in Fig. 6.9.

Microorganisms sre involved in the production of biofertilizer.

The following are the types of biofertilizer (Barman et al. 2019)

- Nitrogen-fixing biofertilizers (*Rhizobium, Brady rhizobium, Azospirillum, Beijerinckia*, *Clostridium*, and *Azotobacter*).
- Phosphorus-solubilizing biofertilizers (*Bacillus, Penicillium, Pseudomonas, Xanthomonas Fusarium*, and *Aspergillus*).
- Phosphate-mobilizing biofertilizer (Arbuscular Mycorrhiza, Ectomycorrhiza, Orchid Mycorrhiza).
- Plant growth promoting biofertilizer *Rhizobium, Pseudomonas*, *Azotobacter, Azospirillum*).

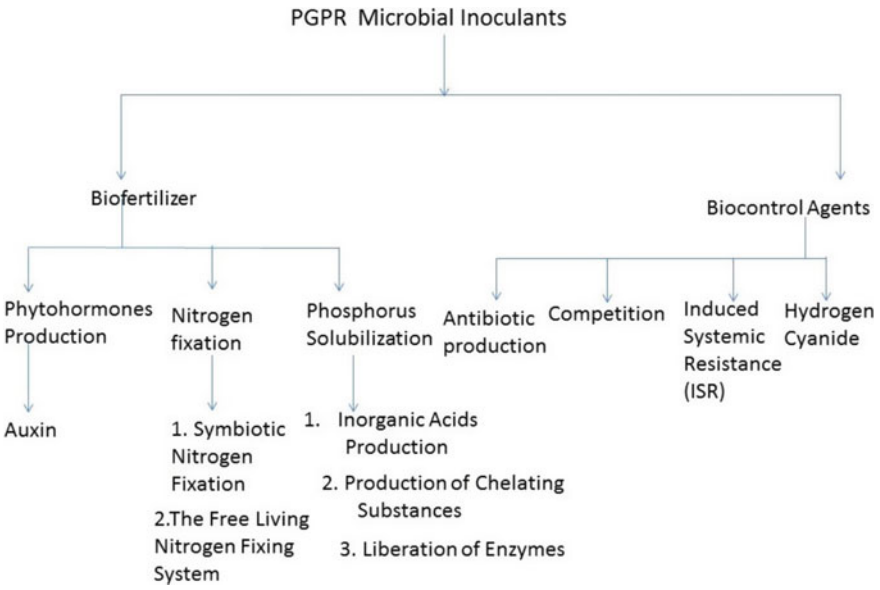


Fig. 6.9 Schematic representation of some importance of microbial inoculant in agriculture and the mechanism of actions. *Source* Alori and Babalola (2018)

6.7.2 Biocontrol Agents

The main function of biocontrol agents (BCA) or biopesticides such as *B. thuringiensis, B. popilliae, P. Fluorescens* is suppressing or controlling plant disease by acting as antifungal or antimicrobial agents (Alori and Babalola 2018; Glick 2012). *Pseudomonas* spp. produces metabolites that include 2,4-diacetylphloroglucinol (2,4-DAPG) [$C_{10}H_{10}O_5$, Molecular Weight: 210.18 g/mol], phenazine (PHZ) [$C_{12}H_8N_2$, Molecular Weight: 180.2 g/mol], pyrrolnitrin (PRN) [$C_{10}H_6Cl_2N_2O_2$, Molecular Weight: 257.07 g/mol], pyoluteorin (PLT) [$C_{11}H_7Cl_2NO_3$ Molecular Weight: 272.08 g/mol], hydrogen cyanide [HCN, Molecular Weight: 27.025 g/mol), and 2-hexyl-5-propyl resorcinol (HPR) [$C_{15}H_{24}O_2$, Molecular Weight: 236.35 g/mol]. It has been observed that 2-hexyl-5-propyl resorcinol (HPR) pay a key role in biofilm formation (Calderon et al. 2019). Structures of microbial metabolites and their interaction with plants are shown in Fig. 6.10.

6.7.3 Plant Growth Promoters

Several factors such as abiotic factors and biotic factors influence the growth and yield of the crop plants (Fig. 6.11). Abiotic factors of soil include moisture, pH, salt concentration, nutrient, temperature, humidity, heavy metals, antibiotics, etc. Biotic

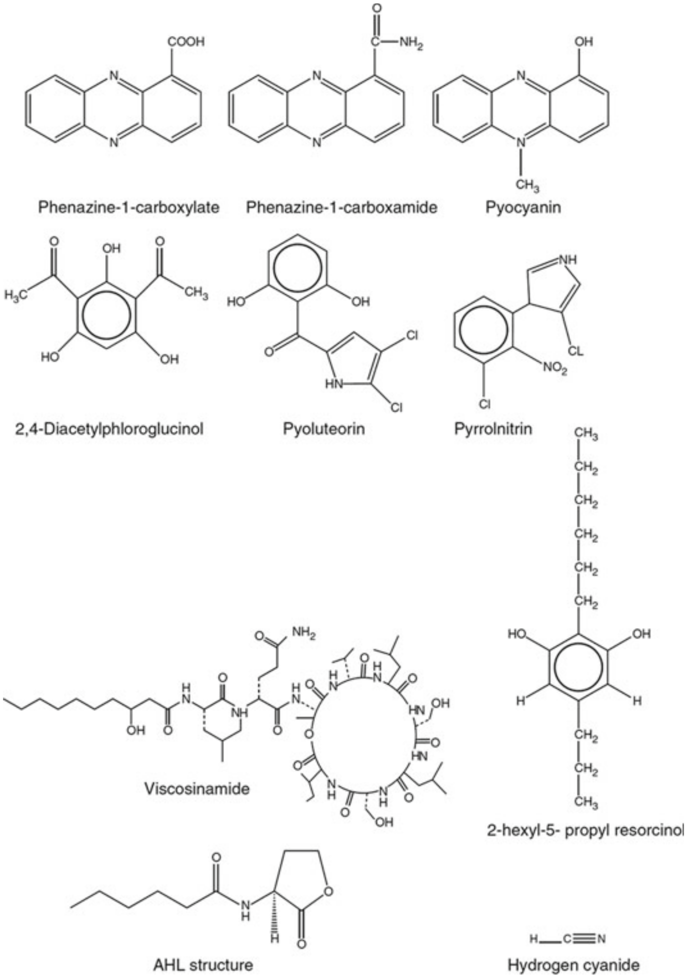


Fig. 6.10 Structures of important metabolites which play a role in the interaction between plant beneficial bacteria and plants. *Source* Pliego et al. (2011)

factors such as plant genotype and soil macro and microflora including soil bacteria, viruses, and protozoans are contributed for the regulation of bacterial populations in the rhizosphere (Ansari et al. 2017; Kumar et al. 2019a, b; Yadav 2018; Yadav et al. 2019b).

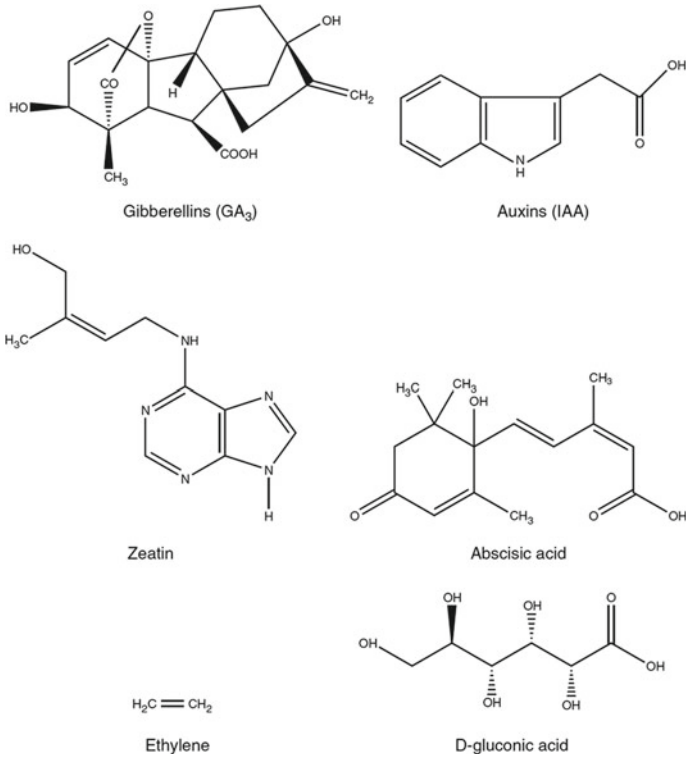


Fig. 6.10 (continued)

6.7.3.1 Direct Mechanism of Plant Growth

Nitrogen Fixation

Biofilm formation enables free living nitrogen-fixing rhizobacteria such as *Rhizobium*, *Gluconacetobacter*, *Pseudomonas*, and *Azospirillum* to fix nitrogen under aerobic conditions with the help of *nif* gene (Yadav et al. 2017a, b, c; Wang et al. 2017). The rhizospheric nitrogen-fixing bacteria have the potential to increase the productivity of the agricultural crops such as rice, wheat, and corn (Suman et al. 2016; Verma et al. 2017a, b).

The biological nitrogen fixation processes are shown in Fig. 6.12.

Phosphorus Solubilisation

Biofilm forming phosphate-solubilizing bacteria (PSB) such as *Bacillus, Erwinia, Pseudomonas, Burkholderia,* and *Rhizobium* are solubilizing the inorganic phosphorus (Pi) released by root exudates (Taktek et al. 2017). Phosphorus solubilization by bacteria is a complex mechanism (Fig. 6.13). Production of organic acid such as gluconic acid (GA) is considered as the primary mechanism of phosphate solubilization

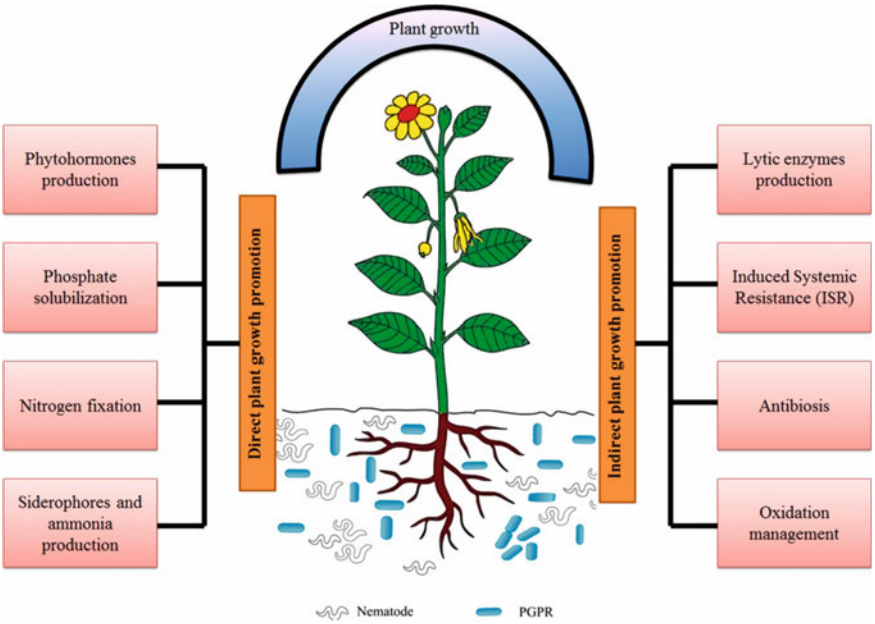
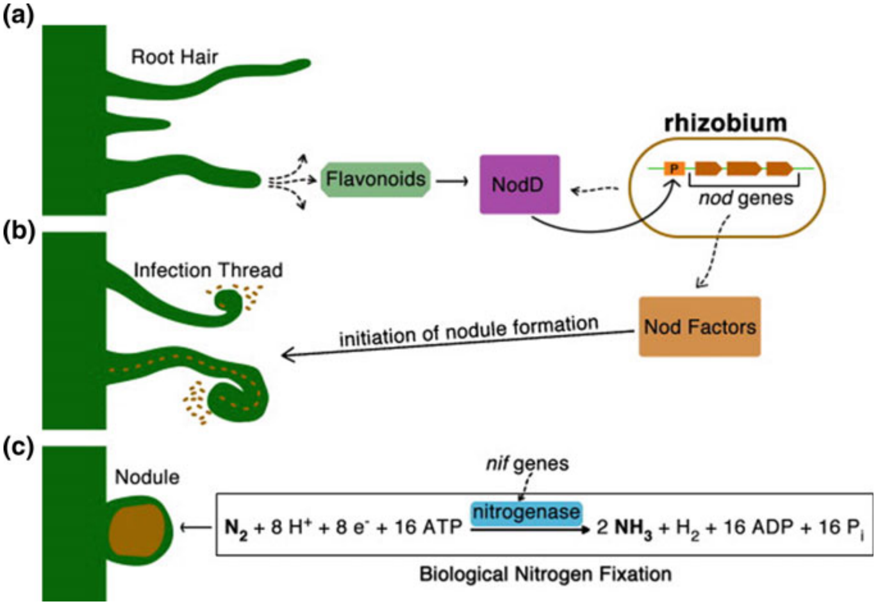


Fig. 6.11 Schematic diagram represents the plant growth promoting and nematicidal activity of PGPR. *Source* Mhatre et al. (2018)



$N_2 + 8 H^+ + 8 e^- + 16 ATP \xrightarrow{\text{nitrogenase}} 2 NH_3 + H_2 + 16 ADP + 16 P_i$

Fig. 6.12 Schematic overview of the nodulation process and biological nitrogen fixation. *Source* Laranjo et al. (2014)

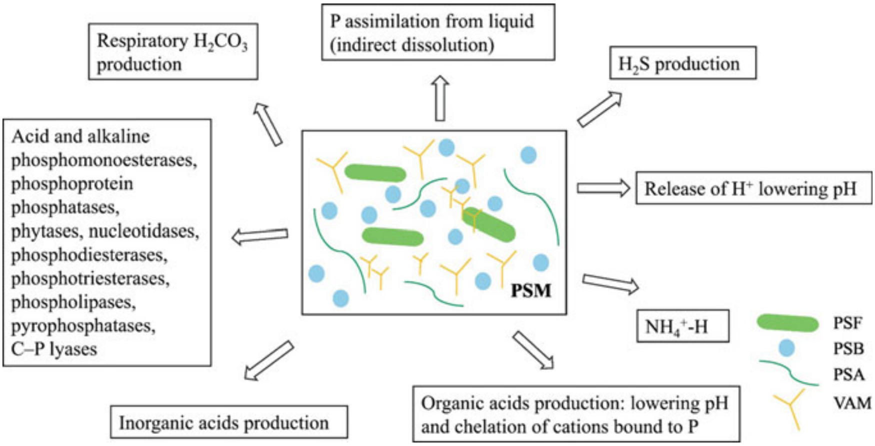


Fig. 6.13 Potential mechanisms for the solubilization of insoluble Phosphate by phosphate-solubilizing microorganisms (PSMs). PSF: phosphate-solubilizing fungi; PSB: phosphate-solubilizing bacteria; PSA: phosphate-solubilizing actinomycete; VAM: vesicular-arbuscular mycorrhizae. *Source* Zhu et al. (2018)

by lowing the pH of surroundings (Liu et al. 2019; Prabhu et al. 2019; Yadav et al. 2015c).

Siderophores Production

Siderophores are ferric ion-specific chelating organic compounds that areproduced under low iron stress conditions. Several microorganisms such as *Pseudomonas, Bacillus,* and *Beauveria* spp, are reported to secrete siderophores (Verma et al. 2016; Yadav et al. 2015a, b; Yadav et al. 2016). The primary function of siderophores is to chelate the ferric iron [Fe(III)]. Siderophore iron complex is adsorbed by plants to meet their iron demands. (Ahmed and Holmström 2014; Pedraza 2015; Rajkumar et al. 2010). Figure 6.14 shows the role of siderophores producing bacteria (SPB) in chelating the heavy metal.

Biocontrol Activity

Due to the microbial diseases and their harmful effects, about one third of the crop yields are lost every year. Harmful activity of one organism is limited by the application of other microorganisms during biocontrol (Kumar et al. 2019a, b; Rana et al. 2019; Yadav et al. 2019b). *P. fluorescens* contains toxic producing genes from *B. thuringiensis* (Bt) and is used as a biopesticide to limit the activity of black cutworms on maize. Biocontrol activity are mediated by the synthesis of bacterial allelochemicals (phenazines, pyoluteorin, 2, 4-diacetylphloroglucinol, etc.) including iron-chelating siderophores, antibiotics (Streptomycin, Cephamycin C, Tetracyclines,

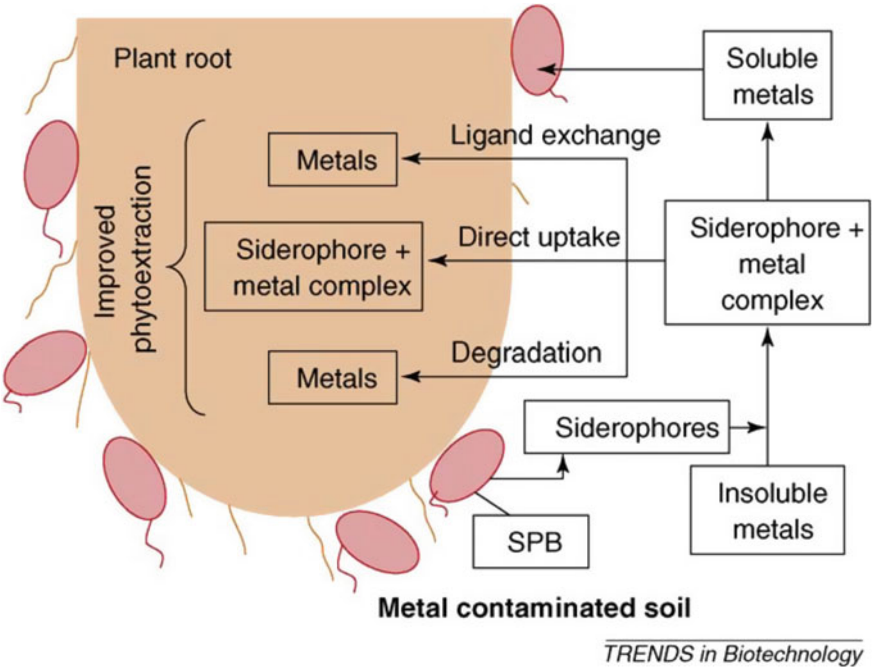


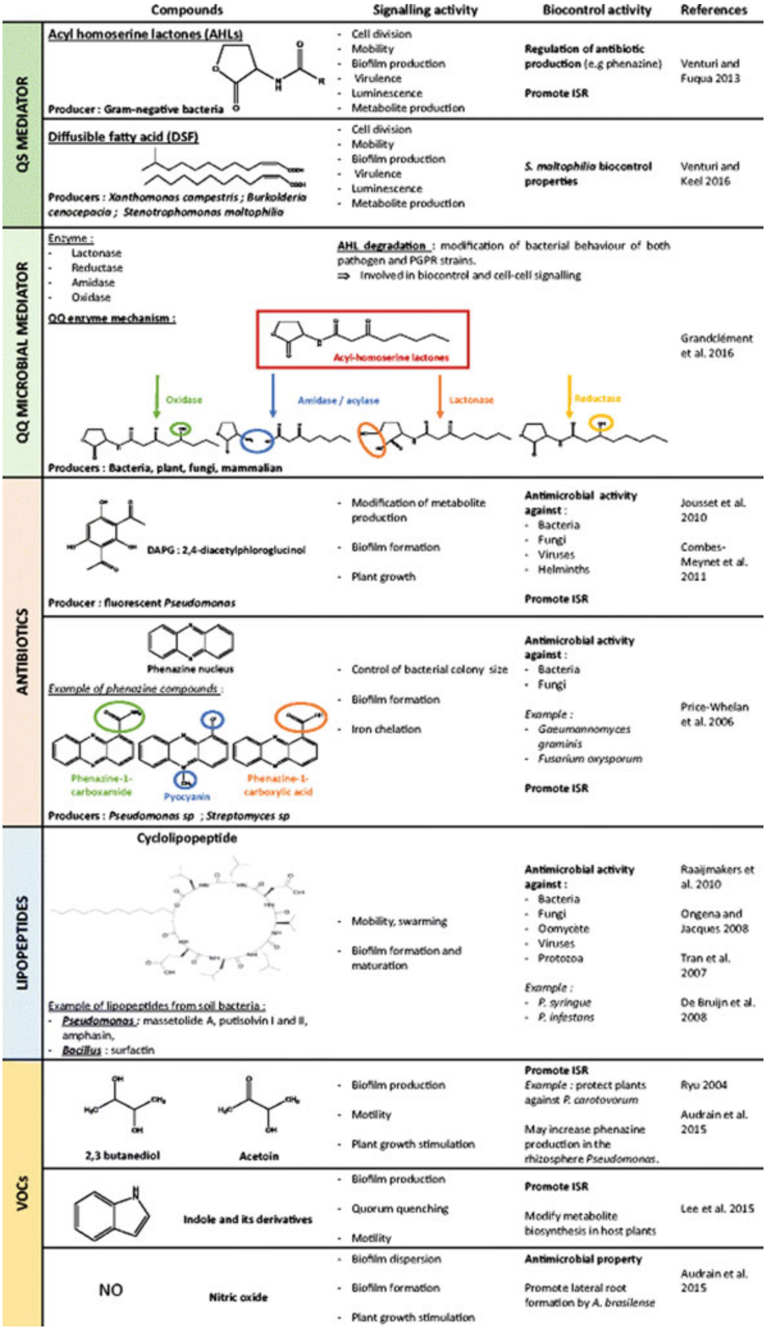
Fig. 6.14 Role of SPB in phytoextraction of heavy metal contaminated soils. *Source* Rajkumar et al. (2010)

Chloramphenicol, etc.),biocidal volatiles (Dimethyldisulfide, Furfural, Benzaldehyde, etc.) lytic enzymes (Glucanases, chitinases, pectinase, etc.), and detoxification enzymes (Pandin et al. 2017; Compant et al. 2005). Plant growth promoting bacteria (PGPB) produces hydrogen cyanide and antibiotics to control pathogens. Microbial compounds used in biocontrol activities are tabulated in Table 6.2 and mechanisms of interactions by plant growth promoting bacteria (PGPB) in the rhizosphere are demonstrated in Fig. 6.15.

6.8 Commercialization of PGPR

Gram-positive bacteria such as *Bacillus* spp. are preferred as commercially available PGPR because of inoculant stability and ease of storage of inoculant product. Other potential PGPR stains such as *Azospirillum, Pseudomonas* do not produce spores and hence difficult to formulate as a biocontrol agent. In the global market, United States, China, India, Russia, and Australia are the main players for biocontrol product as the prospects of PGPR for agricultural crop yield enhancement and disease production

Table 6.2 Example of microbial compounds implicated in biocontrol and microbial cooperation



	Compounds	Signalling activity	Biocontrol activity	References
QS MEDIATOR	**Acyl homoserine lactones (AHLs)** **Producer : Gram-negative bacteria**	- Cell division - Mobility - Biofilm production - Virulence - Luminescence - Metabolite production	**Regulation of antibiotic production** (e.g phenazine) **Promote ISR**	Venturi and Fuqua 2013
	Diffusible fatty acid (DSF) **Producers : *Xanthomonas compestris ; Burkolderia cenocepacia ; Stenotrophomonas maltophilia***	- Cell division - Mobility - Biofilm production - Virulence - Luminescence - Metabolite production	***S. maltophilia* biocontrol properties**	Venturi and Keel 2016
QQ MICROBIAL MEDIATOR	Enzyme : - Lactonase - Reductase - Amidase - Oxidase **QQ enzyme mechanism :** Acyl-homoserine lactones Oxidase Amidase / acylase Lactonase Reductase **Producers : Bacteria, plant, fungi, mammalian**	**AHL degradation** : modification of bacterial behaviour of both pathogen and PGPR strains. ⇒ Involved in biocontrol and cell-cell signalling		Grandclément et al. 2016
ANTIBIOTICS	**DAPG : 2,4-diacetylphloroglucinol** **Producer : fluorescent *Pseudomonas***	- Modification of metabolite production - Biofilm formation - Plant growth	**Antimicrobial activity against :** - Bacteria - Fungi - Viruses - Helminths **Promote ISR**	Jousset et al. 2010 Combes-Meynet et al. 2011
	Phenazine nucleus *Example of phenazine compounds :* Phenazine-1-carboxamide Pyocyanin Phenazine-1-carboxylic acid **Producers : *Pseudomonas sp ; Streptomyces sp***	- Control of bacterial colony size - Biofilm formation - Iron chelation	**Antimicrobial activity against :** - Bacteria - Fungi *Example :* - *Gaeumannomyces graminis* - *Fusarium oxysporum* **Promote ISR**	Price-Whelan et al. 2006
LIPOPEPTIDES	**Cyclolipopeptide** Example of lipopeptides from soil bacteria : - ***Pseudomonas*** : massetolide A, putisolvin I and II, amphasin, - ***Bacillus*** : surfactin	- Mobility, swarming - Biofilm formation and maturation	**Antimicrobial activity against :** - Bacteria - Fungi - Oomycète - Viruses - Protozoa *Example :* - *P. syringue* - *P. infestans*	Raaijmakers et al. 2010 Ongena and Jacques 2008 Tran et al. 2007 De Bruijn et al. 2008
VOCs	**2,3 butanediol** **Acetoin**	- Biofilm production - Motility - Plant growth stimulation	**Promote ISR** *Example : protect plants against P. carotovorum* May increase phenazine production in the rhizosphere *Pseudomonas*.	Ryu 2004 Audrain et al. 2015
	Indole and its derivatives	- Biofilm production - Quorum quenching - Motility	**Promote ISR** Modify metabolite biosynthesis in host plants	Lee et al. 2015
	NO **Nitric oxide**	- Biofilm dispersion - Biofilm formation - Plant growth stimulation	**Antimicrobial property** Promote lateral root formation by *A. brasilense*	Audrain et al. 2015

Source Besset-Manzoni et al. (2018)

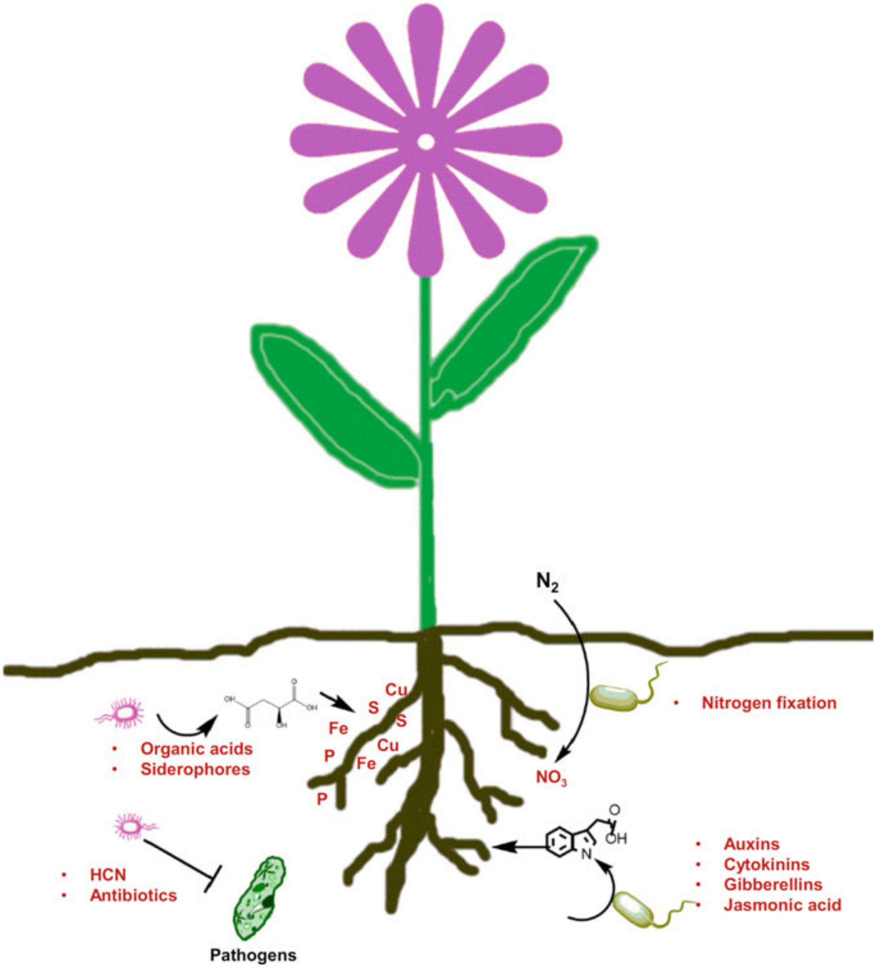


Fig. 6.15 Mechanisms used by plant growth promoting bacteria (PGPB) to enhance interactions in the rhizosphere for higher grain yield and nutrient content. PGPB produce plant hormones, siderophores, and organic acids and solubilize phosphate. They produce hydrogen cyanide and antibiotics to control pathogens. *Source* Ramakrishna et al. (2019)

can never be ignored (Tabassum et al. 2017; Kour et al. 2019a, b, c). The biopesticide formulation technology by industry is shown in Fig. 6.16 and PGPR-based commercialized bioformulation in Table 6.3.

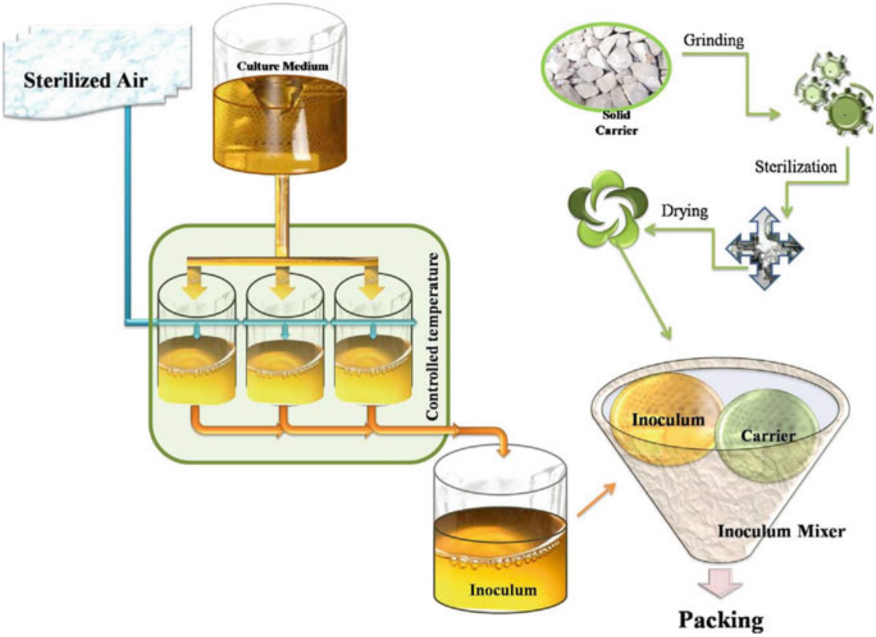


Fig. 6.16 Generalized scheme of the biopesticide formulation by industry where PGPRs are preserved in an appropriate carrier molecule and packaged for commercial application at farmer's end. Several PGPR formulations are commercially available in the market by different commercial producers and different Government institutions. *Source* Tabassum et al. (2017)

6.9 Conclusions and Future Prospects

Biofilm forming bacteria are growing on and around the plants and show the significant plant–microbes interaction to enhance the yield of the agricultural crops. Cell to cell communication and quorum sensing (QS) play a critical role in the formation of biofilm. Biofilms can provide protection from plant responses and thus promoting colonization. The Phyto microbiome offers enormous potentials for agricultural benefits. For the enhancement of the crop yield, researchers are looking for the development of mathematical model based customized inocula of PGPB/PGRP. Thus, the sustainable use of microbial inoculants is a viable alternative for enhancing crop production rather than the use of agrochemicals such as insecticides, pesticides, and inorganic fertilizers. In the coming future, the microbial inoculant technology will ensure sustainable crop production.

Table 6.3 PGPR-based commercialized bioformulation

Product Name	Composition	Country	Benefit/target pathogen/disease	Applications
Bio-phospho	*Bacillus Subtilis*	India	Phosphate solubilization	Wheat, jowar, rice, sorghum, maize, sugarcane, cotton
Rhizobium bio promotor	*Rhizobium sp.*	India	Nitrogen fixation	Leguminous plants
Symbion-P	*Bacillus megaterium var. phosphaticum*	India	Phosphate solubilization	Wheat, rice, teff, barley, maize, corn (sweet and baby corn), sorghum, pearl millets
Azospirillum Inoculant	*Azospirillum*	India	Nitrogen fixation	Crops, cereals, millets
Paddy Azospirillum	*Azospirillum*	India	Nitrogen Fixation	Paddy crops
Actinovate AG	*Streptomyces lydicus* strain WYEC 108	USA	Soil borne diseases like powdery mildew, downy	Fruit and vegetable crops
Symbion-K	*Frateuria aurantia*	India	k-solubilizing	Wheat, rice, teff, Barley, maize, corn (sweet and baby corn), sorghum, pearl millets
Symbion-N	*Rhizobium, Azospirillum, Acetobactor,* and *Azotobactor*	India	Nitrogen fixation	Legumes and pulses
TerraMax's MicroAZ-ST dry	*Azospirillum brasilense* and *lipoferum*	USA	Nitrogen fixation	Corn
NPK liquid	*Azotobacter chroocomccum, Pseudomonas*	India	Nitrogen-fixing, P-solubilizing, k-solubilizing	All crops

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Chapter 7
Actinobacteria: Diversity, Plant Interactions and Biotechnology Applications

Monnanda Somaiah Nalini and Harischandra Sripathy Prakash

Abstract Actinobacteria are Gram-positive members of the novel phylum and are present in diverse ecosystems on the earth. Basically, they are saprophytes, thriving in all soil types, litter and are one of the successful rhizocolonizers. Actinobacteria are associated with plants as litter degrading, symbiotic, endophytic or as pathogenic microorganisms. These associations often have benefited microbiologists, biotechnologists and chemists to introspect the potentials of strains and their secondary metabolites for manifold applications. Mainly, soil actinobacteria are potential producers of life-saving antibiotics or antimicrobial metabolites with myriad applications in medicine and agriculture. Actinobacteria of the soil and rhizosphere and as endophytes often have excellent plant growth-enhancing traits and function as antagonists in several important plant diseases of agriculturally prominent crops. In biotechnology, they are preferred for the production of antibiotics, drug analogues, engineered drugs, as sources of industrially important enzymes, and in the biodegradation of harmful xenobiotics.

Keywords Actinobacteria · Diversity · Bacterial associations · Biodegradation · Antibiotics · *Streptomyces*

7.1 Introduction

The actinobacteria are a group of microorganisms with high Guanine to cytosine (G + C, >55%) nucleotide content and constitute a major portion of the rhizosphere and its soil. To date, their ubiquitous nature of occurrence is well supported by their isolations from diverse habitats ranging from terrestrial to aquatic and hostile environments such as hyperthermal, hyperacidic, hypersaline, caves, coal mine, volcanic and unusual arid regions. The actinobacteria are placed in the novel phylum

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(*Actinobacteria Phyl. nov.*) comprising 16 orders, with many of them elevated to the novel orders (*Ord. nov.*) (Ludwig et al. 2012) and are as follows:

Actinomycetales	Actinopolysporales *Ord. nov.*
Bifidobacteriales	Catenulisporales *Ord. nov.*
Corynebacteriales *Ord. nov.*	Frankiales *Ord. nov.*
Glycomycetales *Ord. nov.*	Jiangellales *Ord. nov.*
Kineosporales *Ord. nov.*	Micrococcales *Ord. nov.*
Micromonosporales *Ord. nov.*	Propionibacteriales *Ord. nov.*
Pseudonocardiales *Ord. nov.*	Streptomycetales *Ord. nov.*
Streptosporangiales *Ord. nov.*	*Incertae sedis Ord. nov.*

Soil is a complex substrate varying in composition, pH, and is known to harbour microorganisms. The presence of actinobacteria in soil was documented in 1903. Since then, the use of cultivation media with antibiotics for the selective isolation and enumeration of actinomycete colonies was devised (Williams and Davies 1965). Actinobacteria are broadly classified as commonly occurring and cosmopolitan generic group, the Streptomycetes and non-streptomycetes, also known as rare actinomycetes. *Streptomyces* are primarily soil bacteria comprising 10% of the total soil microbiome (Hayakawa et al. 1996a), are identified by profuse aerial mycelia and spore chains and are recovered easily from a number of substrates and plant litter. The chalky and powdery colonies are readily visible on humic acid–vitamin agar (HV) plates (Hayakawa and Nonomura 1987), which otherwise restricts the growth of filamentous bacteria. The rare actinobacteria grow on HV agar, but require selective isolation techniques and enrichment methods such as the use of chemoattractant, i.e., vanillin for the isolation of *Catenuloplanes* and *Virgosporangium*; pollen baiting for *Actinoplanes*; and rehydration/centrifugation for the isolation of motile actinomycetes (Hayakawa 2008).

Actinobacteria exhibit diversity in plant microbiomes, with a reduction of populations documented in the spermosphere and phyllosphere microbiomes (Lopez-Velasco et al. 2013; Kembel et al. 2014; Yadav and Yadav 2019a). Nevertheless, in the rhizospheric soil and in plants, they occur widely in all tissues. As endophytes, their diversity has been documented from crop plants (Coombs and Franco 2003; Cao et al. 2005; Tian et al. 2007), native plants (Janso and Carter 2010; Kim et al. 2012; Kaewkla and Franco 2013) and medicinal plants (Qin et al. 2009; Zhao et al. 2011). Due to high species diversity, the identification of actinobacteria is challenging as well as cumbersome. In the absence of accurate methods based on morphology, the 16S rRNA as a phylogenetic marker has been reliable in the identification of species. Recently, the multilocus sequence analysis (MLSA) was applied as a molecular tool, for resolving the identification in members of Streptomycetaceae (Labeda et al. 2017), whereas for studies on the actinobacterial communities of phyllosphere and rhizosphere microbiomes, a 16S rRNA microarray technology known as PhyloChip (Mendes et al. 2011) has been designed.

Interest in actinomycete research was generated over the past decades due to the identification and production of antibiotic compounds from soil *Streptomyces* species. ~8,000 antibiotic compounds are described from streptomycetes alone (Berdy 2005) and the number of compounds described for non-streptomycetes are lesser but with anti-pathogenic and antagonistic potentials (Lazzarini et al. 2000; El-Tarabily and Sivasithamparam 2006).

Actinobacteria are useful in improving crop yields through the enhancement of plant growth traits. Rhizoactinobacterial and endophytic strains of *Streptomyces*, *Nocardia* and *Nonomuraea* function as plant growth enhancers by producing the growth regulator, Indole acetic acid (IAA), siderophores, enzymes, by phosphate solubilization or by increasing the nutrient levels (Nimnoi et al. 2014; Vurukonda et al. 2018; Verma et al. 2015; Yadav et al. 2015). Actinobacteria are useful in the degradation of polyhydrocarbons and xenobiotic compounds. Strains of *Rhodococcus* are extensively used in the biodegradation of harmful polyhydrocarbons, aromatic and plasticizer compounds due to their ability to thrive in harsh environments (Yadav et al. 2019f). The physiology and genomic diversity among *Rhodococcus* strains make them amenable to genetic manipulation and greater understanding of the pathways for functional gene (s) involved in the biodegradation processes (Zampolli et al. 2019). Actinobacteria are known sources of industrially important enzymes such as cellulases, pectinases, chitinases, xylanases and proteases (Kour et al. 2019a; Yadav et al. 2016). These enzymes are used in detergent, leather, textiles, paper and pulp and in food industries. High stability, extreme pH and temperature tolerance are some of the criteria to be employed for industrial processes (Yadav et al. 2019c, d, e).

This chapter highlights the actinobacterial diversity associated with soil and rhizosphere microbiomes, and in endophytic plant species, their interactions with plant microbiomes, association with plants and few applications in biotechnology.

7.2 Actinobacterial Interactions with Plants

Microbial associations with plants can be described as by far the most reliable and beneficial in providing increased plant growth, in terms of seedling vigour, nutrition and productivity (Mendes et al. 2013). The 'microbiome concept', which was initially coined to describe the microbial associations in the human gut (Qin et al. 2010), has also been extended to microbial communities associated with plant species. They are dependent on plants for specific functional traits to sequester the physiologically fixed carbon into direct surroundings. Currently, five types of microbiomes are described, namely, spermosphere (Verona 1958), rhizosphere (Berendsen et al. 2012), phyllosphere (Vorholt 2012), endosphere (Hardoim et al. 2015) and mycorrhizosphere (Frey-Klett et al. 2007). Actinobacterial communities are known to exist in all the microbiomes and their interactions are documented.

7.2.1 Plant Microbiome and Actinobacteria

'Plant microbiome' is a term defined as 'the collective genomes of microorganisms living in association with plants', which has in turn led to new inputs on the evolution of plants (Rosenberg et al. 2009). For greater than 100 years, plant microbiome has been considered as significant contributors in maintaining plant health and productivity. The development in research methodologies with inputs from molecular and next-generation sequencing techniques and analytical tools (Jansson et al. 2012; Berg et al. 2013) has led to achieve important goals in understanding the plant-associated microbial communities in several plant species (Mendes et al. 2011; Bulgarelli et al. 2012) with high functional diversity.

'Spermosphere' is defined as the zone surrounding the seeds which interacts with soil, microbial communities and the germinating seed and strictly is applicable to the short timed germination process occurring in seeds (Schiltz et al. 2015). The term was first coined by Verona (1958) to describe the interplay between the soil, seed-borne microbiota and the germinating seeds. During the process, seeds exude substances that either stimulate or inhibit microbial growth and have a direct influence on plant health and growth parameters. Since the timing related to the unfolding of events is of a short duration, the spermosphere remains the less studied zone among the microbiomes. Spinach spermospheric microbial communities were analysed by Pyrosequencing at the germination stage and the actinobacterial abundance was poorly represented by the genera *Corynebacterium* (0.08%), *Sanguibacter* (0.08%) and *Micrococcus* (0.16%) (Lopez-Velasco et al. 2013).

'Rhizosphere' refers to the narrow contact zone between the roots and the soil particles. It is also the first plant environment encountered by the soil microorganisms (Dessaux et al. 2016), which in turn influences plant growth. Three zones are contained in the rhizosphere: the endorhizosphere (root cortex and endodermis; the rhizoplane (mid zone) and the ectorhizosphere (outer zone) extending from rhizoplane to the bulk soil (McNear Jr. 2013). Root exudates, mainly photosynthate secretions mainly serve as source of energy, influencing the soil microbial communities. Actinobacterial communities of rhizosphere primarily comprise of the soil dweller, *Streptomyces*, the species of which composition tends to vary among crop plants (Petrolini et al. 1996; Suarez-Moreno et al. 2019). The rhizosphere dwelling actinobacteria enhance plant growth promotion (PGP) traits by the production of siderophores, phosphate solubilization, nitrogen fixation (Berendsen et al. 2012) and antifungal compounds (Turpaulta et al. 2007). The composition of spermosphere and rhizosphere microbiomes of wild and modern bean accessions cultivated in an agricultural and a native soil from Colombia was characterized by metagenomics and cultivation-dependent approaches (Perez-Jaramillo 2019). Results indicated an increase in the abundance of actinobacteria in the rhizosphere of plants grown from cultivated bean accessions from native to agricultural fields.

'Phyllosphere' is one of the most diverse habitats on earth and a niche for the interaction of epiphytic and endophytic microorganisms. The phyllosphere spans 10^9 sq. km across the dorsal as well as the ventral leaf surfaces and has an estimate of

10^{26} bacterial cells (Vorholt 2012). It encompasses four regions of the above-ground parts: caulosphere, anthosphere, carposphere and phylloplane. The phyllosphere organisms compete for the availability of nutrients and contribute to the diverse architecture and density of the habitat. The actinobacterial diversity is estimated to be lesser than that of proteobacteria and firmicutes. The actinobacteria of the phyllosphere in spinach plants represent <1% of the total bacterial communities (Lopez-Velasco et al. 2013). The relationship between plant functional traits and bacterial communities of the phyllosphere was studied in the leaves of 57 tree species in a neotropical forest in Panama (Kembel et al. 2014). The host leaves harboured 400 bacterial taxa of which, the actinobacteria comprised 5.5% of the core microbiome taxa among the dominant phyla.

'Endosphere' is a term applied to the internal tissues of plants, forming a niche. It is applicable in various ways depending on the purpose for colonization. The microbes called endophytes as well as pathogens dwell within the endosphere, but perform different functions related to either symbioses, mutualism or pathogenic. The route of entry into the endosphere is facilitated by wounds created due to abrasion, via stomata or by the action of cell wall degrading enzymes. Microorganisms interact in the endosphere of plants parts, viz., the roots, root nodules, stem, leaves, floral parts and the fruits (Suman et al. 2016; Verma et al. 2017b; Yadav et al. 2018a, b). Actinobacterial endophytes are dominant colonizers of roots in many agricultural crops or native and medicinal species (Sardi et al. 1992; Coombs and Franco 2003; Janso and Carter 2010; Kaewkla and Franco 2013) and include *Streptomyces* as well as non-streptomycetes. Preferential colonization of *Streptomyces lydicus* WYEC108 in pea root nodules was demonstrated (Tokala et al. 2002).

Mycorhizosphere represents the zone of soil encasing the plant roots (rhizosphere) and the extraradical fungal hyphae protruding from the mycorrhizae. The mycorrhizosphere is the zone surrounded by both the root and the mycorrhizal fungus (Rambelli 1973). The actinobacteria interact with the microbiome for specific production of secondary metabolites, enzymes, plant hormones and growth inhibitors.

7.2.2 Associations of Actinobacteria with Plants

Plant and microbial interactions have often postulated to be old involving beneficial, symbiotic, harmful, mutualistic or free-living types. Actinobacteria form all these associations with plant species (Fig. 7.1). The events leading from the entry to establishment in plants is documented for many host–microbial systems. Such phenomena are well established for fungal and bacterial symbionts, pathogens and saprobes. The following are the associations exhibited by actinobacteria with plant species.

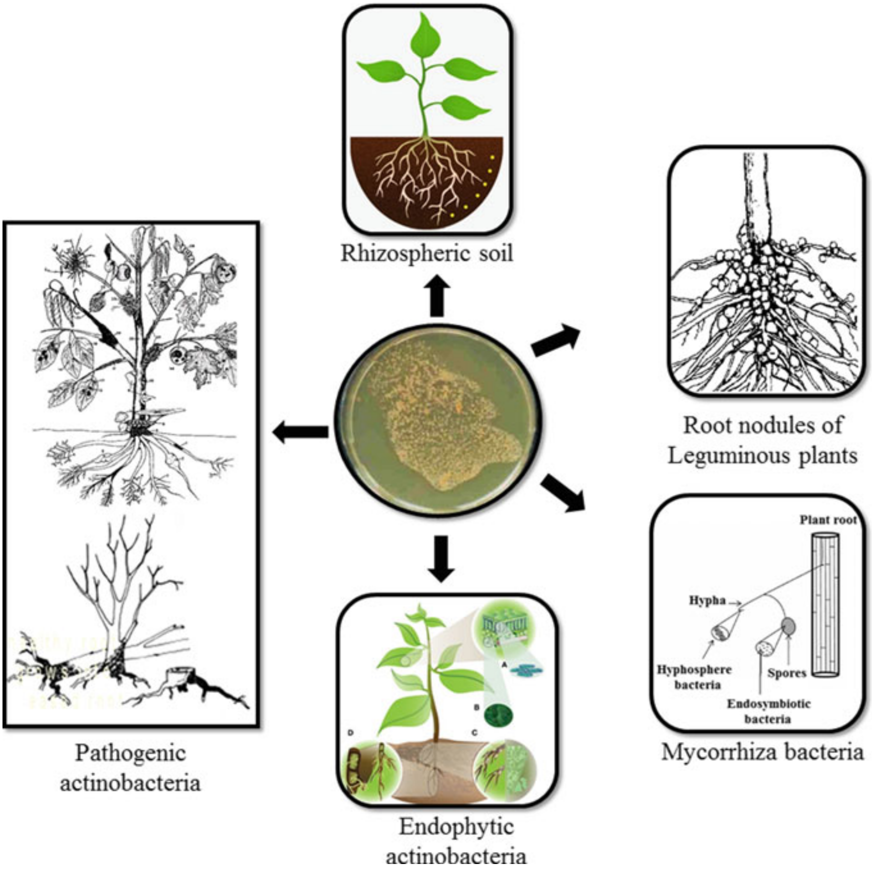

Fig. 7.1 Actinobacterial associations with plants

7.2.2.1 Saprophytic

Actinomycetes reside in the soil types of various habitats and are therefore saprophytic in nature assisting in the decomposition of various substrates into organic matter, which is utilized by other organisms in the food web, thereby balancing the nutrient cycle. One such substrate is the plant litter which serves as principal source of nitrogen (N) and carbon (C) in the soil and has significant development in the terrestrial ecosystem (Sauvadet et al. 2016). In the aquatic habitats such as streams, litter accumulated by leaf fall constitutes one of the chief sources of energy. Microorganisms, both bacteria and fungi are bestowed with the ability to degrade plant remains by secrete cell wall degrading enzymes to breakdown large molecules such as cellulose, lignin and chitin into smaller compounds, which are in turn utilized by saprophytes in the food web (Sinsabaugh and Lenskins 1990). Microbial degradation of litter is the resultant co-effort of fungi and bacteria, with the biochemical and physiological processes of the latter are well established (Das et al. 2007).

The assessment of actinobacterial diversity on the decaying senescent leaves of sugar maple and white oak in a forested stream, along northeastern Ohio (Das et al. 2007) resulted in the lesser diversity of actinobacteria than fungi by Denaturing Gradient Gel electrophoresis technique (DGGE). A study to determine the impact of C cycling on the quality of litter and the bacterial communities of soil in Oak (*Quercus wutaishanica*) secondary forest region in Fuxian Observatory in China was conducted (Zeng et al. 2017). The annual litter accumulation over a two year period due to leaf fall was estimated at 200 g m^{-2} per year. The actinobacteria formed 10–21% of the dominant groups in the primary soil types, which enhanced due to the decomposition of litter. Litter degrading actinobacterial populations are documented from fallen leaves as well as from streams. Actinobacteria such as *Streptomyces, Micromonospora, Actinomadura* and *Pseudonocardia* degrade lignocellulose in plant litter (McCarthy 1987). Fallen leaves from pine litter layers are sources for the isolation of numerous *Streptomyces* and *Microbispora* (Matsukuma et al. 1994). High frequency of *Microbispora* and *Actinokineospora* spp. were isolated from the fallen leaves of bamboo and loosestrife and other plants (Matsumoto et al. 1998; Otoguro et al. 2001).

7.2.2.2 Symbiotic

The term ‘Symbiosis’ was originally coined by de Bary in 1879 to describe a long-term interaction between two biological species meaning ‘living together’. One of the remarkable examples for the plant–microbe symbiotic relationship is that of leguminous plant roots and the bacterium of the genus *Rhizobium* in the fixation of nitrogen. Today, a number of genera, *Azorhizobium, Bradyrhizobium, Mesorhizobium, Sinorhizobium* and *Ensifer*, collectively referred to as ‘rhizobia’ are documented as nitrogen fixers (Hardoim et al. 2015). In non-leguminous plants, nitrogen fixation is achieved by the Gram-positive actinobacterium, *Frankia*. It is known to establish root nodules in 23 species of non-legumes, called ‘actinorhizal plants’ of dicotyledonous families. The phylogenetically related groups of actinorhizal plants are Fagales (Betulaceae, Casuarinaceae, Myricaceae), Cucurbitales (Datiscaceae, Coriariaceae) and Rosales (Rosaceae, Elaeagnaceae, Rhamnaceae) (Berry et al. 2011). Actinorhizal plant species are able to colonize in nutrient-poor sites and are ecologically important. Non-*Frankia* actinobacterial strains of Micromonosporaceae and Thermomonosporaceae isolated from the surface-sterilized roots of *Casuarina equisetifolia* was able to fix nitrogen, as analysed by the amplification of *nif*H genes (Valdes et al. 2005).

7.2.2.3 Pathogenic

Plant-associated actinobacteria cause diseases in plant species and are termed pathogenic. Several species of *Streptomyces* infect potato as pathogens and are common agents of potato scab, i.e., *Streptomyces acidiscabies, Streptomyces europaeiscabei, Streptomyces scabies* and *Streptomyces turgidiscabie*s (Bignell et al. 2010). *Clavibacter* is a Gram-positive actinobacteria with many subspecies and is the causal agent of bacterial spot of tomato, disease of alfalfa (*C. michiganensis* subsp. *insidiosus*), maize (*C. michiganensis* subsp. *nebraskensis*) and wheat (*C. michiganensis* subsp. *tessellarius*). The ratoon stunting of sugarcane is caused by *Leifsonia xyli* subsp. *xyli* (Young et al. 2006), while *Rathayibacter tritici* incites gumming disease in several grasses (Evtushenko and Dorofeeva 2012). Besides crop plants, garden species, beet, American holly and poinsettia are affected.

7.2.2.4 Endophytic

Endophytes are microorganisms residing inside healthy plant tissues without causing any ‘overt, negative effects’ on hosts (Bacon and White 2000). In plants, endophytic associations include those of fungi, actinobacteria, bacteria, yeasts, etc. Actinobacteria form endophytic associations in host plants. In 1886, *Frankia* was first isolated as the actinobacterial endophyte from the non-legume root nodules. The first description of an actinobacterial association from the leaves of grass was the new genus *Actinosynnema* (Hasegawa et al. 1978). Endophytic actinobacteria are described from several plants: crop plants (Coombs and Franco 2003; Cao et al. 2004, 2005; Tian et al. 2007), native plants (Janso and Carter 2010; Kim et al. 2012) and medicinal plants (Castillo et al. 2002, 2006; Akshatha et al. 2016). Native tree species do have actinobacterial associations with streptomycetes as major strains (Kaewkla and Franco 2013), while rare actinobacteria were also isolated from fewer tree species (Caruso et al. 2000; Himaman et al. 2016). They are distributed in all plant parts with high diversity in the root tissues than stems and leaves. Root endophytic strains, of *Streptomyces* spp. have excellent antagonistic potentials or as biocontrol agents to several plant pathogens.

7.3 Actinobacterial Diversity: Predictions or Reality?

Of all the microorganisms associated with plant species, the diversity estimate for the total number of fungal species has been documented to be 6,11,000 (Mora et al. 2011), which is much lower than the earlier predicted conservative estimate of 22,70,000 (Hawksworth 2001), solely based on the traditional taxonomical approaches. On a global basis, the actual number of fungal species is underestimated. Conventional techniques employed in the identification of actinobacteria have often resulted in the misidentification of closely related species. Advanced methods using molecular data with next generation technologies have emerged as a reliable tool in the accurate identification of closely related species and in enumerating diversity. Pyrosequencing and Illumina platform technologies have provided reliable methods to enumerate the number of species in microbial communities of several ecosystems (Buee et al. 2009). Recently, a high-density 16S rRNA microarray technology known as PhyloChip (Mendes et al. 2011) was designed to detect the abundance and diversity of bacterial communities in the rhizosphere and phyllosphere microbiome.

7.3.1 Diversity in Soil and Rhizosphere

Soil contains a complex mixture of microorganisms, both pathogenic and beneficial to plants. The diversity of microbes in soil as well as the rhizosphere has been underestimated. The estimate of microbial presence in soil has not been accurately measured and has often resulted in ambiguity. Studies indicate actinobacteria as important components in the rhizosphere and are known to influence plant growth and protect roots against the invasion of plant pathogens. Actinobacterial species diversity estimates predicted ca. 10,000 species per gram of boreal forest soil (Yadav 2019; Torsvik et al. 2002). Using improvised computational estimates, bacterial counts were recorded to be greater than one million per gram of soil (Gans et al. 2005). Different types of soil samples consisting of forest, greenhouse, mountain and waterfalls from the Western Ghats of India were enumerated for the actinobacteria isolated using actinomycete isolation agar (AIA) supplemented with the antibiotics, ketoconozole (30 mg/l) and nalidixic acid (100 mg/l). 12 species of *Streptomyces* were documented (Ganesan et al. 2017).

The most common actinobacteria distributed in soil are the *Streptomycetes*, which account for the total actinomycete populations, but in order to isolate rare genera, selective media and enrichment methods have been designed (Hayakawa 2008). Pretreatment methods such as physical and chemical, enrichment by rehydration and centrifugation allowed the delineation of streptomycetes and favoured the isolation of rare taxa such as the non-motile as well as the motile actinomycete genera. Actinomycetes are known to utilize humic acid as the sole source of carbon and nitrogen, which facilitated the growth of actinomycete colonies of the genera *Streptomyces, Micromonospora, Microbispora*, *Streptosporangium, Nocardia, Dactylosporangium, Microtetraspora* and *Thermomonospora* on agar medium, while restricting the development of true bacteria (Kumar et al. 2019b; Yadav et al. 2017a, b, d). The recovery of *Microtetraspora* a rare genus, and four-spored actinomycetes, with LSV-SV agar enriched with Kraft lignin as the source of carbon and nitrogen was reported (Hayakawa et al. 1996b). The distribution of actinobacteria in soil types were documented along a vertical gradient through test borings (Takahashi et al. 1990). Top layers contained actinobacteria at 10^7 g^{-1}, second layer (0.5–5.0 m) and still below (1.0 m) had reduced actinomycete populations.

Fort-five and 93 strains of actinobacteria representing streptomycetes and non-streptomycetes were isolated from the rhizospheres of carrot (El-Tarabilly et al. 1997) and cucumber (El-Tarabilly 2006). Actinobacterial strains were isolated from the rhizospheric soils of *Vitis vinifera* across four Moroccan sites (Loqman et al. 2009). The total count ranged from 16–65 $\times 10^6$ cfu/g of dry soil. The rhizospheric soil adhered to the roots of seven traditional medicinal plant species from the Panxi plateau, China was analysed for the diversity of actinobacteria (Zhao et al. 2012). 196 strains were grouped into eight suborders and 13 families. In three species, streptomycetes were dominant, while in four species, rare actinobacteria were isolated, each plant species contained unique strains. Soils sampled from ten crop plants at a depth of 5–15 cm contained 156 actinomycete isolates (Kaur et al. 2013). 382 actinobacteria were isolated from 27 rhizospheric soil samples of eucalyptus plantation (Himaman et al. 2016). The total actinomycete counts in two different media of isolation ranged from 9.4×10^4 to 3.4×10^6 and 1.0×10^5 to 2.16×10^6 cfu g^{-1} of dry soil on Starch casein agar and HV agar, respectively. The rhizospheric strains comprised mainly of non-streptomycetes. *Micromonospora* was most frequently isolated from endophytic and rhizospheric samples.

Oak rhizosphere and the surrounding soil had contrasting bacterial diversity, as studied by Pyrosequencing technology (Uroz et al. 2010). Differences in the distribution of bacterial communities of soil and rhizosphere in *Arabidopsis thaliana* were observed (Lunderberg et al. 2012). Using 454 pyrosequencing of the bacterial communities associated with leaves and roots of *A. thaliana*, Bodenhausen et al. (2013) observed abundant distribution of actinobacteria in the samples along with other bacterial communities. Therefore, owing to the contradictions arising in the estimations of actinobacteria from soil and its rhizosphere, the next-generation sequencing techniques have become handy in accurately predicting the actinobacterial populations in several rhizospheric soils of plant species. PhyloChip, a high-density 16S r RNA gene microarray technology, could detect the diversity and abundance of the bacterial communities in the rhizosphere (Mendes et al. 2011), and the results were consistent in estimating the actinobacterial communities in oat rhizosphere (De Angleis et al. 2009). Actinobacteria accounted for 11% of total bacterial populations in two distant potato fields and three cultivars in Netherlands (Weinert et al. 2011), while a study in the rhizosphere of beet seedlings, actinobacteria was recorded as the second largest taxa (Mendes et al. 2011).

Composite soil samples of wheat rhizosphere, from Idar region of Gujarat, resulted in the isolation of *Streptomyces* spp. (Jog et al. 2012) with plant growth-promoting ability. Rhizospheric soils sampled from South African plant species indicated the diversity of *Streptomyces* spp. (Adegboye et al. 2012). Soils from the rhizosphere of legume and Japanese grass species analysed for the actinobacteria contained 84% Streptomycetes, while rare actinomycetes were less (Matsumoto and Takahashi 2017). The rhizosphere is a potential site for the existence of actinobacteria, wherein the filamentous bacteria are found at a count of 10^6 cells per mm^3.

Plantation soils are a niche for microorganisms and do play a major role in the decomposition and degradation of complex organic residues formed from the crop residues and shade trees. Actinobacterial populations are present in the plantation soils and help in degrading the organic matter by producing the extracellular enzymes. Coffee plantation soils are well suited for the isolation of actinomycetes as they are rich in humus and fallen litter. In a study conducted to isolate soil actinomycetes from Coffee plantation of Chikmagalur region, Western Ghats, India, Sameera et al. (2018a) documented the presence of 24 species of actinobacteria across altitudinal gradients and two soil profiles. The physico-chemical parameters of the soil and total actinomycete counts correlated with the soil profiles. The actinobacteria consisted of 54.2% *Streptomyces* spp. and 45.8% of non-streptomycetes, comprising three novel orders.

7.3.2 Diversity in Crop Plants

Actinobacteria are associated with roots of many crop plant species, although they are major components of the rhizosphere. Their presence around the roots is necessary to evade the invasion of root pathogens. 28 healthy plant species cultivated in Northwestern Italy were subjected to actinobacterial isolations from the surface-sterilized roots (Sardi et al. 1992). Of the 499 isolates, 482 strains were *Streptomyces*, two strains were *Streptoverticillium* and four strains were *Nocardia*, while one strain each of *Micromonospora* and *Streptosporangium* were obtained. Streptomycete populations in the roots of 156 plant species were studied along the seven-year sampling period in Italy (Petrolini et al. 1996). 81% of the strains belonged to *Streptomyces*, other rare actinobacteria belonged to *Micromonospora* (215 strains), *Streptosporangium* (12), *Streptoverticillium* (2), *Saccharomonospora* and *Nocardia* (70) species. Healthy wheat plants (*Triticum aestivum* L.), growing in the major regions of southern Australia were analysed for the actinobacteria. The surface-sterilized fragments yielded 88% of *Streptomyces* and 12% of *Microbispora, Micromonospora* and *Nocardioides* (Coombs and Franco 2003). Since the actinobacteria are soil-inhabiting populations, the diversity was assessed in the surface-sterilized roots of banana plants from a plantation in China (Cao et al. 2005). Of the 131 isolates, 99 comprised of *Streptomyces*, followed by morphologically distinct genera *Streptoverticillium* (28) and *Streptosporangium.* The diversity of actinobacterial community in the internal portions of rice (*Oryza sativa* cv. Qilisimiano) stems and root tissues was determined from South China (Tian et al. 2007). 191 strains were morphologically distinguished into 33 groups by the 16S rDNA genes as *Streptomyces* and *Nocardioides.* The gene clones from the library distinguished strains from roots as belonging to nine genera; *Streptomyces* (24%), *Micromonospora* (6.6%), *Actinoplanes* (6.6%), *Frankia* (4.4%), *Dactylosporangium* (4.4%), *Amycolatopsis* (4.4%), *Corynebacterium* and *Rhodococcus* each with 2%. An uncultured actinobacterium was also detected. More diversity of actinobacteria was obtained from roots than stem portions.

619 actinobacteria were isolated from the roots of field-grown tomato cultivars in south China during 2014 (Tan et al. 2006). The isolates were grouped into *Streptomyces aureochromogenes* (30.3%), *Hygroscopicus* and *Viridis* groups in healthy tomato roots, while *Cinereus* and *Flavus* groups were characterized from the roots of *Ralstonia* wilt tomato cultivars. Healthy tomato plant roots collected from southern Australia were analysed for the actinobacteria, and *Streptomyces* spp. were the most

commonly isolated ones, and rare members included *Microbispora* and *Nonomuraea* spp. (Inderiati and Franco 2008). Ten plants comprising the crop and medicinal species were used for the isolation of actinobacteria from plant parts. 50% comprised of the root isolates, while the stem and leaf isolates were 29% and 21%, respectively (Kaur et al. 2013).

The wattle tree (*Acacia auriculiformis* A. Cunn. ex Benth.) grown for its association with rhizobacteria is used to improve the soil fertility and is native to Australia. The diversity of actinobacteria in the leaves and roots was determined from four sites in the University campuses of Thailand (Bunyoo et al. 2009). The four sites differed in the actinobacterial diversity, with *Streptomyces* from two sites, and rare genera such as *Actinoallomurus, Amycolatopsis, Microbispora and Kribbella* with two species each from three sites. 23 root samples were collected from the eucalyptus plantation in Thailand for endophytic actinobacterial analysis (Himaman et al. 2016). Overall, 95 endophytic root isolates were characterized as strains and included genera of rare actinobacteria, namely, *Micromonospora* (28.9%), *Nocardia, Actinomadura, Actinoallomurus, Cryptosporangium* and *Amycolatopsis.*

There is strong evidence that the endophytic populations have originated mainly from the rhizosphere. The rhizospheric populations of actinobacteria consist mainly of *Streptomyces* spp. and are abundant and diverse. Several species of crop plants have developed associations with these groups of microorganisms that have immense applications in agriculture and biotechnology.

7.3.3 Diversity in Medicinal Plants

Actinobacteria occur as abundant microbiota in the plants of medicinal value, as isolated from various plants across biodiverse regions. They are often referred as 'endophytes' and reside in the intercellular spaces of plant parts. Diverse actinobacterial species have yielded array of metabolites with wide applications in agriculture, pharmacy and biotechnology.

Taechowisan et al. (2003) obtained 330 actinomycetes from seven medicinal species from Chiang Mai, Thailand with *Streptomyces* ($n = 277$) as the dominant isolates followed by *Microbispora* ($n = 14$), *Nocardia* ($n = 8$) and *Microbispora* sp. ($n = 4$). Plant species (300) sampled from the Amazonian rainforest sites yielded 14 endophytes, 12 belonged to *Streptomyces*, one each of *Micromonospora* and *Amycolatopsis* spp. (Bascom-Slack et al. 2009). Three Indian medicinal species, *Aloe vera, Ocimum sanctum* and *Mentha arvensis* were selected for the actinobacterial isolations from the roots, stems and leaves. Of the 40 isolates, *Streptomyces* spp., were dominant genera and the rest were represented by *Saccharopolyspora, Micromonospora* and *Actinopolyspora* spp. (Gangwar et al. 2011).

The Sichuan Province of China has a subtropical climate and medicinal species have been used from 3000 years for human health. 13 native medicinal species were subjected to the isolation and study of actinobacterial diversity in the plant parts (Yuan et al. 2008). The actinobacteria were classified into two genera: *Streptomyces* and *Micromonospora,* of which the former showed high species diversity. The Chinese tropical rainforest is a unique region comprising the transition vegetation and is a home to 3,000 endemic plant species. At Xishuangbanna, medicinal plants were studied for the presence of diverse actinobacterial populations in the plant parts. One plant speci*es, Maytennus austroyunnanensis,* was selected for the actinobacterial isolations (Qin et al. 2012) due to the importance of maytansinoids. Culture-dependent and -independent methods were applied for the actinobacterial isolations and to study their diversity in plant parts. A total of 312 strains were detected of which, roots comprised of major isolates (40.4%) than the stems (27%) and leaves (32.6%). The actinobacteria were distributed in eight suborders. *Streptomyces* were the most frequently isolated genus with 15 species, and rare ones belonged to 20 genera.

The roots of four medicinal plant species collected from the Chinese Herbal Plant Base, Hebei, were evaluated for the presence of actinobacteria, which comprised of *Streptomyces* spp. and two species of *Glycomyces* (Zhang et al. 2012). Four medicinal plant species from the Western Ghats, namely, *Rauwolfia densiflora, Leucas ciliata, Cajanus lineata* and *Gomphostemma heyneanum,* were evaluated for the presence of actinobacteria from the stem and leaves (Akshatha et al. 2016). 68% of the strains belonged to *Streptomyces* and the rare ones included *Promicromonospora, Arthrobacter, Patulibacter, Rhodococcus* and *Nocardia* spp. The diversity of actinomycetes mentioned in the above paragraph indicates that morphological, physiological and biochemical characteristics were undertaken by Taechowisan et al. (2003) to identify the actinomycetes to the generic level, while in all other studies the identification to the species level was accomplished by the sequencing of 16S rRNA gene. A combination of techniques involving the crumbling of sterilized plant fragments, desiccation with calcium carbonate and enzymatic hydrolysis coupled with differential centrifugation were standardized for the actinobacterial species from 90 tropical rainforest plants in Southwest China (Qin et al. 2009), which facilitated the isolation of rare actinobacteria.

7.3.4 Diversity in Native Tropical Species

The Papua New Guinea along with the adjoining areas of Archipelago is home to a number of tropical plant species and is one of the biodiverse regions on the earth. A range of plant parts and habit were sampled for the isolation and identification of 123 actinobacterial strains from 113 plant species (Janso and Carter 2010). The use of different isolation techniques as well as the enrichment procedures resulted in the isolation of rare genera, viz., *Lentzea, Lechevalieria, Kitasatospora* and *Planotetraspora.* Molecular characterization of the isolates resulted in resolving the diverse actinobacterial taxa into six families: Streptomycetaceae (27%), Streptosporangiaceae (40%), Thermomonosporaceae (16%), Micromonosporaceae (8%), Pseudonocardiaceae (8%) and Actinosynnemaceae (2%). The non-streptomycetes comprised of 74% of the total actinobacterial strains. The diversity of endophytic actinobacteria from the surface-sterilized root samples of eleven native herbaceous plants from Korean Provinces was assessed (Kim et al. 2012). 61 strains identified comprised of *Streptomyces* (45.9%), *Micromonospora* (18.8%), *Rhodococcus* (6.6%), *Microbispora* (4.9%), *Micrococcus* (4.9%), and other strains included *Arthrobacter, Dietzia, Kitasatospora, Herbiconiux, Mycobacterium, Nocardia, Rathayibacter* and *Tsukamurella*.

The tropical neem tree (*Azadirachta indica* A. Juss.) yielded diverse actinobacteria (Verma et al. 2009a, b) from the stems (23.6%), roots (54.5%) and leaves (21.8%). *Streptomyces* was the dominant genus (49.09%), while rare actinobacterial genera identified were *Streptosporangium* (14.5%)*, Streptoverticillium* (5.5%)*, Microbispora* (10.9%)*, Nocardia* (3.6%) *and Saccharomonospora* (5.5%). Kaewkla and Franco (2013) reported diverse *Streptomyces* spp. (72%) from four Australian native trees such as native pine tree (*Callitris preissii*), red gum (*Eucalyptus camaldulensis*), grey box tree (*Eucalyptus microcarpa*) and apricot tree (*Pittosporum phillyraeoides*). The native pine tree and grey box tree contained 33.7% and 33.1% of the isolates, while the apricot and red gum tree isolates comprised of 26.4 and 6.4%, respectively. Rare actinobacteria: *Polymorphospora, Gordonia, Actinomycetospora* and two novel genera *Williamsia* and *Flindersia* were isolated. Of the four native trees, the apricot tree yielded 12 *Streptomyces* spp. and four genera, *Amycolatopsis, Actinopolymorpha, Polymorphospora* and *Nocardiopsis*, which were not recovered from other trees.

7.4 Applications of Actinobacteria in Biotechnology

7.4.1 Antibiotics in Medicine and Agriculture

Actinobacteria are pioneers in their ability to produce wide range of antibiotic compounds, which have immense benefits in medicine and agriculture. Since the discovery of Streptomycin from the soil isolate, *Streptomyces griseus*, soil-derived *Streptomyces* spp. are the most sought microorganisms in the industrial screening programmes. ~8,000 antibiotics are described from *Streptomyces* spp., followed by rare actinomycetes (Berdy 2005).

7.4.1.1 Antibiotics from Soil-Derived Actinobacteria

Soil-derived actinobacteria, especially *Streptomyces*, deserve a special mention as the single largest producer (80%) of life-saving antibiotic drugs. They are typically soil bacteria, with plenty of spores readily recognized for the volatile, earthly odour, geosmin. Though the first antibiotic was discovered in the fermentation product of *Streptomyces griseus*, over the subsequent decades there has been a phenomenal search for the discovery of newer antibiotics owing to the emergence of multidrug-resistant Gram-negative bacterial strains. The mercurial period from 1945 to 1950s is remarkable for the discovery of antibiotics from actinobacterial genera *Actinomyces, Streptomyces, Micromonospora, Nocardia*, etc. *Streptomyces* spp. produce a range of antibiotics with diverse chemical structures and the basic classification deals with two broader classes (Benedict 1953): pigmented antibiotics (Aureomycin, Trichomycin, Griseolutin, Actinorhodine, Rhodocidin, etc.), non-pigmented antibiotics (Antimycin, Nigericin, Cardicine, Nocardamin, Flavomycin, etc.), non-pigmented organic bases (Streptomycin, Streptolin A & B, Neomycin, Flavomycin, Viomycin, Achromycin, etc.) and miscellaneous group (Streptocin, Chromin, Ascosin, Cacaomycetin, etc.).

The selectivity of antibiotic molecules to inhibit growth of the test organism is based on their inhibition against target structures or functions related to cell wall biosynthesis, translation, RNA transcription, DNA synthesis and replication (Lo Grasso et al. 2016). Recent studies on the genes and or gene clusters involved in biosynthesis of antibiotics and their regulation have opened up newer mechanisms to incorporate tailoring steps for operating the genes of interest for a particular antibiotic synthesis. Media composition, alteration of fermentation conditions and other genetic factors are required to produce antibiotics. Since many of the antibiotic-producing actinomycetes resist the genetic manipulation, transferring the antibiotic synthesizing genes to a heterologous expression system represents a successful strategy. Shuttle vectors harbouring the gene(s) of interest expressed in model organisms such as *S. coelicolor, S. avermitilis* and *S. lividans* have been reported (Yadav et al. 2019a; Alduina et al. 2003, 2005; Giardina et al. 2010).

Therapeutic drugs from actinobacteria have wide implications as targets against cancer, immunomodulators. Drug discovery is based on high-throughput platforms to screen thousands of fermentation products of microbes to deliver a new medicine with high market value. Actinobacteria have yielded drugs with potential value in clinical trials (Table 7.1). Rare actinobacteria, namely, *Micromonospora, Actinoplanes, Actinomadura* and *Streptosporangium* produce antibiotic classes such as macrolides, polysaccharides, aminocyclitols (Lancini and Lorenzetti 1993). The years 1966–1998 have provided literature on the antibiotics belonging to macrolides, quinones, diterpenes, anthracyclines and ansa-macrolactams in these rare genera (Lazzarini et al. 2000).

7.4.1.2 Antibiotics from Endophytic Actinobacteria

Antibiotics are important drugs preferred for health care due to their potent therapeutic applications for the clinical use (Farnet and Zazopoulos 2005). Plant-associated endophytic actinomycetes produce wide range of antibiotics (Matsumoto and Takahashi 2017). *Streptomyces* and *Micromonospora* are the potential producers of antibiotics. Munumbicins, the novel peptide antibiotics are produced by the endophytic *Streptomyces* spp., from the ethnomedicinal plants of the Upper Amazon and Northern Territory of Australia and were effective against Gram-positive bacteria *Bacillus anthracis* and *Mycobacterium tuberculosis* (Castillo et al. 2002, 2006). *Streptomyces* sp. 30566 produced Kakadumycins active against *B. anthracis* (MIC 0.2

Table 7.1 Antibiotics as drug targets from actinobacteria and their clinical applications

Drug	Analogue	Producer strain	Target	Mechanism	References
Approved drugs					
Everolimus	Rapamycin	*Streptomyces hygroscopicus*	Interleukin (IL)-2 and IL-15, T-cells and B-cells, Vascular smooth muscles	Arrest of cell cycle at the G1/S phase	Chapman and Perry (2004)
Telithromycin	Erythromycin A	*Saccharopolyspora erythraea*	Peptidyltransferase	Inhibits protein synthesis Antibacterial effect	Zhanel et al. (2002)
Miglustat	Nojirimycin	*Streptomyces lavendulae*	NK	Inhibits glucosylceramide synthase	Pastores et al. (2005)
Daptomycin		*Streptomyces roseosporus*	Bacterial cell membranes	Antibacterial	Fenton et al. (2004)
Amrubicin	Doxorubicin	*Streptomyces peucetius* var. *caesius*	Human tumor xenografts of breast lung and gastric cancer	Antitumour activity	Sugiura et al. (2005)
Biapenem	Thienamycin	*Streptomyces cattaleya*	Gram-positive and -negative bacteria	Antibacterial	Perry and Ibbotson (2002)
Ertapenem	Thienamycin	*Streptomyces cattaleya*	*Escherichia coli*, *Klebsiella* sp., *Citrobacter* sp., *Enterobacter* sp., *Morganella morganii*, *Proteus* sp. and *Serratia marcescens*	Antibacterial	Sader and Gales (2001)

(continued)

Table 7.1 (continued)

Drug	Analogue	Producer strain	Target	Mechanism	References
Pimercolimus	Ascomycin	*Streptomyces hygroscopicus* var. *ascomyceticus*	T-cell	Blocking T-cell activation	Gupta and Chow (2003)
Ozogamycin	Calichemicin	*Micromonospora echinospora Calichensis* sp.	Acute myeloid lymphoma	DNA cleaving antibiotics	Lee et al. (1987)
Drugs in clinical trials					
Elsamitrucin	Chartreusin	*Streptomyces chartreusis*	Topoisomerase II	Antitumour effect	Portugal (2003)
Brostallicin	Distamycin A	*Streptomyces distallicus*	DNA minor groove	Anticancer agent	Broggini et al. (2004)
Geldanamycin		*Streptomyces hygroscopicus*	NK	Inhibition of the protein chaperone heat shock protein (HSP)	Bisht et al. (2003)
Fidaxomicin	Lipiarmycin	*Actinoplanes deccanensis*	Gram-positive aerobes, anaerobes, Gram-negative anaerobes	RNA-polymerase inhibitor	Srivastava et al. (2011)
Lantibiotics	Carbacyclic lantibiotics	*Actinomadura namibiensis*	*Streptococcus aureus, Streptococcus pyogenes* and *Streptococcus faecium*	Antimicrobial activity	Boakes et al. (2011)

(continued)

Table 7.1 (continued)

Drug	Analogue	Producer strain	Target	Mechanism	References
Lantibiotics NAI-107	NK	*Microbispora* sp.	*S. aureus*	NK	Seibert et al. (2009) Meindl et al. (2010) Donadio et al. (2010) Genilloud and Vincente (2013)
Lucensimycins and okilactomycins	NK	*Streptomyces lucensis* MA7349	Lucensimycins A–B bind weakly to the S4 protein	NK	Singh et al. (2006, 2008a, b)
Delaminomycins A–C	NK	*Streptomyces albulus*	*S. aureus*, *Streptococcus pneumoniae*	Antibiotic activity	Ueno et al. (1993)
Okilactomycin A, B, C and D	NK	*Streptomyces scabrisporus* *Streptomyces griseoflavus* subsp. *zamamiensis*	*S. pneumoniae* *Enterococcus faecalis* and *Bacillus subtilis*	Inhibition for RNA synthesis	Imai et al. (1987)
Philipimycin	Thiazolyl peptides	*Actinoplanes philippinensis* MA7347	*S. pneumoniae*, *E. faecalis*, *E. faecium, S. aureus*	Inhibitor of protein synthesis	Singh et al. (2013)
NOVO3 and NOVO4	NK	*Streptosporangium* P1532, *Amycolatopsis* Z0363	*S. aureus* and *Enterococci*		Peoples et al. (2011, 2012)
Tetracycline	NK	*Streptomyces aureofaciens*	Inhibits aminoacyl-tRNA binding	Blocks protein synthesis	Van Bambeke (2004)

(continued)

Table 7.1 (continued)

Drug	Analogue	Producer strain	Target	Mechanism	References
Chloramphenicol	NK	NK	*Streptomyces orchidaceus*	Anti peptidoglycan synthesis	Lo Grasso et al. (2016)
Erythromycin	NK	*Saccharopolyspora erythraea*	50S subunit	Blocking the peptidyltransferase activity	
Kanamycin	NK	*Streptomyces kanamyceticus*	Binds to 30S subunit	NK	
Thiostrepton	NK	*Streptomyces laurentii*	NK	Inhibits ribosome-dependent EF-Tu and EF-G GTPase	
Streptomycin	NK	*S. griseus*	NK	Prevents formation of initiation complex	
Rifampicin	NK	*Amycolatopsis mediterranei*	NK	Anti-tuberculosis and inhibits the bacterial RNA polymerase	Schulz and Zillig (1981)
Novobiocin	Albamycin or cathomycin	*Streptomyces niveus*	GyrB subunit of the enzyme	Aminocoumarin antibiotic, inhibitor of bacterial DNA gyrase	Walsh et al. (1993), Maxwell (1999)

NK = not known

to 0.3 μg ml^{-1}) (Castillo et al. 2003). The antimycotic Coronamycin produced by *Streptomyces* NRRL 30562 at 2 μg ml^{-1} (MIC) is effective against pythiaceous fungi and the human pathogen *Cryptococcus neoformans* (MIC 4 μg ml^{-1}) (Ezra et al. 2004). It was tested against agriculturally important plant pathogens along with *S. griseoviridis* formulation (Mycostop) and considered as a potential agricultural agent. Maklamicin, an antibacterial polyketide from *Micromonospora* isolated from Maklam Phueak (*Abrus pulchellus*) has shown activity against Gram-positive bacteria at 0.2–13 μg ml^{-1} (Igarashi et al. 2011). The peptide antibiotic coronamycin from *Streptomyces* sp. (MSU-2110) showed cytotoxic potentials by inhibiting the HMEC and BT20 cell lines (IC$_{50}$ 5–10 μg ml^{-1}) (Ezra et al. 2004). A trehalose-derived antibiotic and a novel inhibitor of metastasis, Brartemicin is produced by *Micromonospora* sp., isolated from *Artemisia vulgaris,* the Brazilian medicinal plant (Igarashi et al. 2009). The compound indicated anti-invasive property in murine colon carcinoma cells (IC$_{50}$ 0.39 μM) without toxicity (Table 7.2).

7.4.2 Anti-pathogenic Potentials of Actinobacteria

Actinobacterial metabolites either produced by soil or endophytic organisms have strong antimicrobial potentials. 70% of these novel metabolites are produced by actinomycetes (Miyadoh 1993). Of all actinobacteria, *Streptomyces* spp., have contributed phenomenally for the production of the life-saving drugs such as the novel antibiotics, enzyme inhibitors, antiviral, antitumor targets and immunomodulators. Rare actinobacteria have contributed to antibiotic database as target drugs. A number of papers have published the anti-pathogenic potentials of soil, rhizospheric and endophytic actinobacteria, which is related to their antagonistic potentials (Table 7.3). Some of the mechanisms of antagonistic nature of these organisms and their metabolites include antibiosis, hyperparasitism and secretion of cell wall degrading enzymes resulting in hyphal lysis (El-Tarabily and Sivasithamparam 2006).

7.4.2.1 Anti-pathogenic Potentials of Soil and Rhizospheric Actinobacteria

The actinomycetes, of the genus *Streptomyces,* are saprophytic bacteria that decompose organic matter, such as lignocellulose, starch and chitin, in soil. Actinomycetes are important in the rhizosphere, where they influence plant growth and protect plant roots against the invasion of root pathogenic fungi (Crawford et al. 1993). A number of diseases of crop plants are caused by the root invading pathogens, panicle and sheath blight and grapevine trunk diseases (Loqman et al. 2009; Harikrishnan et al. 2014; Suarez-Moreno et al. 2019). The potential biocontrol agents from actinobacteria are summarized in Table 7.3. The anti-pathogenic activity against root rot pathogens is by hyperparasitism and well documented in the strains *A. philippinensis, M. carbonacea* against cavity spot disease of carrots (El-Tarabily et al. 1997) and

Table 7.2 Bioactive novel antibiotics produced by endophytic actinobacteria of medicinal plants

Actinobacterial strain	Medicinal species	Antibiotics	Chemical group	Bioactivity	References
Streptomyces NRRL 30562 *Streptomyces* NRRL 3052	*Kennedia nigriscans*	Mumumbicins A–D Munumbicins E-4 & E-5	Peptide antibiotics	Antibacterial; antimalarial	Castillo et al. (2002, 2006)
Streptomyces NRRL 30566	*Grevillea pteridifolia*	Kakadumycin A	Peptide antibiotics	Antibacterial; antimalarial	Castillo et al. (2003)
Streptomyces (MSU-2110)	*Monstera* sp.	Coronamycin	Peptide antibiotics	Antifungal; antimalarial	Ezra et al. (2004)
Micromonospora sp.	*Artemisia vulgaris*	Brartemicin	Trehalose-derived antibiotic	Anti-metastatic/anti-invasive	Igarashi et al. (2009)
Micromonospora sp.	*Abrus pulchellus* subsp. *puchellus*	Maklamicin	Polyketide	Antibacterial	Igarashi et al. (2011)

Table 7.3 Anti-pathogenic activity of actinobacterial strains from rhizosphere and selected plant species

Host plant	Pathogen	Disease	Anti-pathogenic Strain(s)	Mechanism	References
Rhizospheric soil strains					
Taraxacum officinale	*P. ultimum*	Damping off	*Streptomyces* sp.	Antagonism	Crawford et al. (1993)
Raspberry	*Phytophthora fragariae* var. *rubi*	Root rot	Actinomycete strains	Cell wall degradation by β-glucanases	Valois et al. (1996)
Daucus carota L.	*Pythium coloratum*	Cavity spot	*Actinoplanes philippinensis* *Micromonospora carbonacea*	Hyperparasitism	El-Tarabily et al. (1997)
Cucumis sativus L.	*Pythium aphanidermatum*	Root rot	*A. philippinensis* *Microbispora rosea* *Micromonospora chalcea* *Streptomyces griseoflavus* *Actinoplanes campanulatus* *Streptomyces spiralis*	Cell wall degradation by β-glucanases	El-Tarabily (2006), El-Tarabily et al. (2009)
Piper sp.	*Phytophthora capsici*	Root rot	*Streptomyces rochei*	Co-antagonistic with *Trichoderma harzianum*	Ezziyyani et al. (2007)
Traditional medicinal plants	Plant pathogenic Test bacteria	–	*Streptomyces* spp.	Antagonism	Zhao et al. (2012)
O. sativa L.	*R. solani*	Sheath blight of paddy	*Streptomyces aurantiogriseus* VSMGT1014	Antagonism	Harikrishnan et al. (2014)

(continued)

Table 7.3 (continued)

Host plant	Pathogen	Disease	Anti-pathogenic Strain(s)	Mechanism	References
Eucalyptus camaldulensis	*Cylindrocladium* sp.	Leaf and shoot blight	*Streptomyces ramulosus* *Streptomyces himastatinicus*	Antagonism	Himaman et al. (2016)
Vitis vinifera L.		GTD YGD	*Streptomyces* spp.	Antagonism	Alvarez-Perez et al. (2017)
Capsicum annuum L.	*Colletotrichum capsici*	Chilli anthracnose	*Streptomyces violaceoruber*	Antagonism	Thilagam and Hemalatha (2019)
Oryza sativa L.	*Burkholderia glumae*	Panicle blight	*Streptomyces* spp. A20	Antibiotic production	Suarez-Moreno et al. (2019)
Soil strains					
Soil/compost	*Fusarium oxysporum* f. sp. *cucumerinum*	Wilt of cucumber	*Streptomyces* sp. 385	Cell wall degradation by chitinolytic enzymes	Singh et al. (1999)
Culture collection (Malaya)	*Fusarium oxysporum* f. sp. *cubense*	Wilt of Cavendish banana	*Streptomyces* sp. g10	Antagonism	Getha et al. (2005)
Pond soil	*Fusarium oxysporum* f. sp. *lycopersici*	Wilt of tomato	*Streptomyces griseus*	Chitinase production	Anitha and Rabeeth (2009)
Loktak lake area (Manipur)	Rice fungal pathogens	Rice fungal diseases	*Streptomyces vinaceusdrappus*	Antagonism	Ningthoujam et al. (2009)
Soil, Northwest Iran	*Bacterial strains*	–	*Streptomyces* sp.	Antibacterial	Dehnad et al. (2010)

(continued)

Table 7.3 (continued)

Host plant	Pathogen	Disease	Anti-pathogenic Strain(s)	Mechanism	References
Herbal compost	*Fusarium oxysporum* f. sp. *ciceri*	Wilt of chickpea	*Streptomyces tsusimaensis*, *Streptomyces caviscabies*, *Streptomyces setonii*, *Streptomyces africanus*	Antagonism	Gopalakrishnan et al. (2011a)
Herbal vermicompost	*Macrophomina phaseolina*	Charcoal rot of Sorghum	*Streptomyces* sp.	Antagonism	Gopalakrishnan et al. (2011b)
Culture collection (Thailand)	*Fusarium oxysporum* f. sp. *capsici*	Wilt of chilli	*Streptomyces* sp.	Inhibition of conidial germination	Saengnak et al. (2013)
Crop plants	Plant pathogenic fungi	–	*Streptomyces* sp.	Antagonism	Kaur et al. (2013)
Field soil	*Sclerotinia sclerotiorum*	Stem rot of oilseed rape	*Streptomyces felleus* YJ1	Antagonism	Cheng et al. (2014)
Agricultural field	Test bacteria	–	*Streptomyces* sp. SCA 7	Antagonism	Kumar et al. (2014)
Mountain forest soil	*Alternaria alternata*	Brown spot of tobacco	*Streptomyces microflavus*	Pathogen inhibition	Gao et al. (2014)
Soil sample (Korea)	*Colletotrichum gloeosporioides*	Tomato and pepper anthracnose	*Streptomyces* sp. A 1022	Antagonism	Kim et al. (2014)
Vitis vinifera L.	*Botrytis cinerea*	Grey mold Grapevine trunk disease Young grapevine decline	*Micromonospora* sp. *Streptomyces* sp. *Streptomyces* spp.	Hyphal colonization Antagonism	Loqman et al. (2009), Alvarez-Perez et al. (2017)
Soil samples (Malaysia)	*Colletotrichum gloeosporioides*	Chilli anthracnose	*Streptomyces ambofaciens* S2	Antifungal compound	Heng et al. (2015)

(continued)

Table 7.3 (continued)

Host plant	Pathogen	Disease	Anti-pathogenic Strain(s)	Mechanism	References
Soil samples	Test microorganisms	–	*Streptomyces* sp. T-4	Antibiotic production	Atta (2015)
Soils, Western Ghats	Pathogenic fungal/bacterial strains	Human pathogenic	*Streptomyces rimosus*	Growth inhibition	Ganesan et al. (2017)
Endophytic strains					
Native plant species (Italy)	*Micrococcus luteus* *Escherichia coli* *Fusarium oxysporum* f. sp *cyclaminis*	–	*Streptomyces* spp.	Growth inhibition	Petrolini et al. (1996)
Lycopersicon esculentum	*Rhizoctonia solani*	Damping off	*Streptomyces* sp. S30		Cao et al. (2004)
Musa sp. AAA Cavendish	*Fusarium oxysporum* f. sp. *cubense*	*Fusarium* wilt	*Streptomyces griseorubiginous*	Antagonism	Cao et al. (2005)
L. esculentum	*Ralstonia solanacearum*	Bacterial wilt of tomato	*Streptomyces* spp.	Antagonism	Tan et al. 2006
Thottea grandiflora *Polyalthia* sp. *Mapania* sp.	Plant pathogenic fungi Test bacteria	–	*Streptomyces coelicolor* *Streptomyces caelestis* *Streptomyces fulvoviolaceus*	Antagonism	Zin et al. (2007)
L. esculentum	*R. solani* *Alternaria solani* *Phytophthora* sp. *Pythium irregulare*	–	*Streptomyces* spp. *Microbispora* spp.	Antagonism	Inderiati and Franco (2008)

(continued)

Table 7.3 (continued)

Host plant	Pathogen	Disease	Anti-pathogenic Strain(s)	Mechanism	References
Cucumis sativus *Cucumis moschata*	*Colletotrichum orbiculare*	Anthracnose	*Streptomyces* sp.	Hyphal colonization	Shimizu et al. (2009)
A. indica	*Pythium* spp. *Phytophthora* spp.	Damping off; late blight; root rot	*Streptosporangium* sp. *Streptoverticillium* sp. *Nocardia* sp.	Antagonism	Verma et al. (2009a, b)
Traditional medicinal plants	Plant pathogenic Test bacteria	–	*Streptomyces* spp. *Nonomuraea roseola* *Micromonospora chokoriensis*	Antagonism	Zhao et al. (2011)
Ocimum sanctum *Mentha arvensis* *Aloe vera*	Plant pathogenic fungi	–	*Saccharopolyspora* sp.	Antagonism	Gangwar et al. (2011)
Artemisia argyi *Paeonia lactifolia* *Radis platycodi* *Achyranthes bidentata*	*Staphylococcus aureus* MRSA	–	*Streptomyces* spp. *Glycomyces* sp.	Antibacterial inhibition	Zhang et al. (2012)
Crop plants	Plant pathogenic fungi	–	*Streptomyces* sp.	Antagonism	Kaur et al. (2013)
Native Algerian plants	*Rhizoctonia solani*	Damping off	*Streptomyces mutabilis* *Streptomyces cyaneofuscatus*	Antagonism	Goudjal et al. (2014)
Eucalyptus camaldulensis	*Cylindrocladium* sp.	Leaf and shoot blight	*Streptomyces ramulosus* *Streptomyces himastatinicus* *Streptomyces malaysiensis*	Antagonism	Himaman et al. (2016)

by the action of cell wall degrading enzymes in the hyphal lysis of plant pathogens such as glucanases and chitinases (El-Tarabily 2006; El-Tarabily et al. 2009).

In a previous study (El-Tarabily et al. 1996), 352 out of 817 streptomycete and non-streptomycete actinomycete isolates produced inhibitory compounds active against *Pythium coloratum* in vitro using the dual culture agar method. 45 inhibitory isolates were identified as *Streptomyces* spp., *Streptoverticillium* spp., *Actinoplanes* spp., *Micromonospora* spp., *Actinomadura* spp., *Microbispora* spp. and *Streptosporangium* spp. These isolates were chosen for further in vitro and in vivo studies. Non-streptomycete actinobacteria are excellent antagonists of several plant pathogens (El-Tarabily and Sivasithamparam 2006).

7.4.2.2 Anti-pathogenic Potential of Endophytic Actinobacteria

Some actinomycetes form associations with plants and colonize the internal tissues. *Streptomyces scabies* and *Frankia* species can penetrate host plant tissues and form pathogenic or endophytic associations between plants and actinomycetes, respectively (Hasegawa et al. 2006). Until reports of Sardi et al. (1992), work on endophytic actinomycetes other than *Streptomyces* were rare. *Streptomyces* spp., *Microbispora* spp. and *Streptosporangium* spp. were isolated from roots of different plant species in Italy and Brazil that showed antagonistic activities against Gram-positive bacteria and fungi (Sardi et al. 1992; Coombs and Franco 2003) and as biocontrol agents (Verma et al. 2011). The use of actinomycetes as biological control agents of soil-borne root disease of several crop plants is of interest. The endophytic presence of *Streptomyces* spp. may play important roles in plant development and health.

7.4.3 Actinobacteria as Plant Growth Promoters

Sustainable agriculture is a key player for boosting the food productivity. The increasing demand for food production with the use of conventional methods by the application of fungicides, herbicides, insecticides and chemical fertilizers adversely affects human health (Kour et al. 2019c; Rana et al. 2019a, b; Verma et al. 2017a). As an alternative, environment-friendly approach using beneficial microorganisms to improve plant traits for high yields is an efficient strategy (Glick 2012). Soil is a habitat for the multiplication of various microorganisms. The concentration of actinobacteria is greater in the soil attached to the roots, i.e., the rhizosphere and is facilitated by the secretion of amino acids, sugars and micromolecules from the root exudates (Badri et al. 2009). Therefore, actinobacteria are capable of promoting plant growth by a number of ways involving the uptake of nitrogen, phosphorus and iron (Kour et al. 2019b; Kumar et al. 2019b; Yadav et al. 2019b, f; Yadav and Saxena 2018). Plant rhizosphere contains growth-promoting rhizobacteria termed PGPR. The most abundant rhizosphere colonizing actinobacteria are the *Streptomyces* spp. with high species diversity. Rare actinobacteria are documented from these plant species. They are the important components of rhizospheric soils of crop plants, medicinal plants and trees.

Actinobacteria augment plant growth by direct or indirect mechanisms involving the (1) fixation of nitrogen, (2) phosphate solubilization, (3) sequestering of iron, (4) production of growth regulators and (5) ethylene. The genera *Streptomyces, Frankia, Nocardia, Kitasatospora and Thermobifida* are IAA producers (Rana et al. 2019c; Yadav 2018; Yadav et al. 2017c; Yadav and Yadav 2018; Franco-Correa and Chavarro-Anzola 2016). Rhizosphere soil samples collected from three-month-old wheat plants contained 15 morphologically distinct actinobacteria (Jog et al. 2012), while three strains: *S. rochei, S. carpinensis* and *thermolilacinus* with PGP traits were tested positive for the production of Indole acetic acid (IAA, 2.6–19.22 mg l^{-1}), siderophores (1.3–34.17 mg l^{-1}) and high phosphate solubilization (911.6 mg l^{-1}). Rice rhizosphere actinobacterial strain *Streptomyces* A20 showed PGP traits by solubilizing phosphate (79.5 mg l^{-1}), siderophore production, IAA production (4.0 mg l^{-1}) and extracellular enzymes cellulases and proteases (Suarez-Moreno et al. 2019). *Streptomyces violaceolatus,* from the coffee plantation soils, produced 109.24 mg ml^{-1} of IAA and enhanced seedling growth parameters in bean and sorghum as evaluated by the roll towel method (Sameera et al. 2018b). *Streptomyces* spp. isolated from the rhizospheres of plant species including crop plants was able to promote PGP traits.

One of the strategies to enhance plant growth is by adopting co-inoculation of the nodule-inducing species with the actinobacterial strains. Under greenhouse trials, co-inoculation of soybean (*Glycine max*) with *Bradyrhizobium japonicum* and the actinobacterial strains *Nocardia alba*, *Nonomuraea rubra* and *Actinomadura glauciflava* increased acetylene reduction activity ~1.7 to 2.7-fold with increased levels of potassium, N, calcium, iron, magnesium and zinc in the plants (Nimnoi et al. 2014). The association of actinomycetes is known to confer advantages to host plants with the production of IAA, siderophores and nutrient uptake.

Streptomycetes have demonstrated their ability as plant growth enhancers and as biocontrol agents and their products have high commercial value in controlling several plant–pathogenic diseases of agricultural species (Vurukonda et al. 2018). Some of the commercial products are registered as microbial pesticides in European Union, Canada, South Korea, USA in the targeted soil-borne, powder/downy mildews, sheath blight, grey molds, leaf spots of fruits and vegetables, bacterial rots, cankers, basal rots, fire blight etc.

7.4.4 Production of Industrially Important Enzymes

Actinomycetes are abundant taxa in the soil and act as decomposers of complex organic matter helpful for the nutrient cycling in the terrestrial and the aquatic ecosystems. Over the past few decades, considerable interest has been generated in the enzymatic degradation of complex polymers or substrates by microorganisms.

Their abundance, renewable and as inexpensive nature often ensures them as potential candidates in the industrial applications, viz., in food processing, oxychemicals production, and in textiles for the biopolishing of fabrics, and pulp and paper industry (Kasana et al. 2008).

Lignocellulolytic enzymes, one of the potent enzymes produced by actinomycetes, and exploited widely in various lignocelluloses based industries. They are hydrolytic enzymes capable of degrading tough lignocellulose in the plant biomass. Hydrolysis of lignocellulosic biomass by lignocellulolytic enzymes is used in the production of bioethanol and biomethane, textile industry, pulp and paper making, detergents industry, animal feed and food. Hemicellulases are used in biobleaching, deinking of paper waste, clarification of fruit juices, upgradation of feed, fodder and fibres, and saccharification of hemicelluloses to xylose sugars. Actinobacterial cellulases are inducible extracellular enzymes produced on wide variety of substrates. Jeffery et al. (2007) isolated a *Streptomyces griseus* strain from Malaysian soil that produced cellulase with carboxymethyl cellulose property (4.5 mg ml^{-1}). *Streptomyces* spp., *Cellulomonas fimi, Microbispora bispora* and *Thermobifida fusca* are cellulase producing actinomycetes (Saini et al. 2015). Proteases have applications in the bioremediation and degradation of gelatinous wastes generated by food and pharmaceutical industries. *Streptomyces* spp., isolated from Indian soil has protease producing property (Jain et al. 2009). Industrial production of enzymes on large scale is associated mainly with substrate. The use of agriculture residues as low-cost substrates for the production of industrial enzymes is a significant way to reduce production cost.

Xylan is the abundant source of noncellulosic polysaccharide present in hardwoods and annual plants, and comprises 20–35% of the total dry weight in tropical plant biomass (Elegir et al. 1994). Xylanase degrades β-1, 4 xylan, by cleaving the β-1, 4 glycosidic linkages randomly, and the products are xylose and xylo-oligosaccharides like xylobiose (Ninawe et al. 2008). Xylanases are important industrially, which is used in paper manufacturing to bleach paper pulp, increase the brightness of pulp and to improve the digestibility of animal feed and for clarification of fruit juices. Microorganisms are the rich sources of xylanases and are produced by diverse species of actinobacteria. *Streptomyces* sp. strain B-12-2 and *Streptomyces cyaneus* SN32 secrete high amounts of extracellular xylanases (Elegir et al. 1994; Ninawe et al. 2008).

7.4.5 Biodegradation Potentials of Actinobacteria

7.4.5.1 Pesticides

Pesticides are the chemicals employed to kill pests and are known to persist in soils over time. They are pollutants and accumulate in the body parts of plants, animals and humans. Soil microbes are known for their efficiency to degrade pesticidal compounds. Actinobacteria are dominant colonizers of soil types. The process of breakdown of chemical pesticides such as Carbofuran by soil actinobacteria has been documented (Jayabarath et al. 2010). *Streptomyces abnosinicus, Streptomyces atratus, Streptoverticillium album, Nocardia farcinia, Nocardia vaccine, Nocardia amarae* and *Micromonospora chalcea* have shown the ability to resist carbofuran under culture conditions (Kumar et al. 2019a). A soil *Streptomyces* sp. has shown the ability to degrade Chlorpyrifos, the insecticide into a less toxic form by hydrolysis (Briceno et al. 2012).

7.4.5.2 Hydrocarbons

The actinobacterial genus *Rhodococcus* is bestowed with the ability to degrade a wide range of organic and xenobiotic compounds, which poses severe health hazards. Besides, it is able to produce metabolites of biotechnological significance such as carotenoids, wax esters, oils, biosurfactants and bioflocculation agents (Yadav and Yadav 2019b; Jones and Goodfellow 2010). Progress related to the biosynthetic pathway and functional genomics have led to its immense applications in biotechnology. Hydrocarbons are released into the environment by the anthropogenic activities and by natural sources. *Rhodococcus* strains, *Rhodococcus jostii, Rhodococcus opacus, Rhodococcus ruber,* are able to oxidize n-alkanes due to the presence of the enzyme, alkane 1-monooxygenase (Tiancsics et al. 2014), alkane hydroxylases and cytochrome for the oxidation of xenobiotics. Some species are able to degrade highly classified aromatic hydrocarbons exemplified by benzene, toluene, ethylene and *o*-xylene (BTEX). *Rhodococcus* sp. strain DK17 has the ability to degrade Toluene and *o*-Xylene (Kim et al. 2002, 2010), whereas *R. jostii* RHA1 efficiently assimilates ethylbenzene, isopropyl benzene and biphenyl (Seto et al. 1995). Genetic analysis of this strain has identified 203 oxygenases, 86 dioxygenases, 88 flavoprotein monooxygenes and 50 hydroxylases in the conversion of steroids and aromatic compounds (McLeod et al. 2006). Phenols are degraded by *Rhodococcus* strains due to the presence of phenol hydroxylase. *R. erythropolis* UPV-1 efficiently degrades Polyaromatic hydrocarbons (PAH), phenol and a mixture of cresols (Irvine et al. 2000). PAH degradation is by the action of intercellular dioxygenases. Naphthalene is degraded by *R. opacus* R7 via this mechanism followed by the oxidation into salicylate and gentisate (Di Gennaro et al. 2010).

7.4.5.3 Plasticizer Compounds

Plasticizer compounds are released into nature by the industrial processes, which have deleterious effects. *Rhodococcus* strains efficiently degrade toxicants such as phthalates and terephthalates via the protocatechuate ortho-cleavage pathway (Patrauchan et al. 2005). Another noted synthetic polymer generated as plastic wastes is polyethylene and has a complex degradation process involving the oxidation of hydrocarbon chains into aliphatic fragments and subsequently requires specific microbial strains for their mineralization in nature (Koutny et al. 2006). *R. ruber* C208 efficiently degrades polyethylene. *R.* strain AD45 consumes Polyisoprene, the synthetic rubber used in seedlings by oxidation to epoxide and conjugation with glutathione and by dehydrogenation steps (Van Hylckama Vlieg et al. 2000). Gene coding for latex clearing protein (*lcp*) was identified in *Rhodococcus rhodochrous* strain RPK1 (Watcharakul et al. 2016) (Table 7.4).

7.4.6 Bioemulsifiers

Microorganisms produce bioemulsifiers during their growth phase. They contain surface active agents such as proteins and find applications in the form of biofilms as well are used as biomediators (Doshi et al. 2010). Biosurfactants have a hydrophilic moiety, comprising an acid, peptide cations, or anions, mono-, di- or polysaccharides and a hydrophobic moiety of unsaturated or saturated hydrocarbon chains or fatty acids (Lang 2002). These structures confer the ability to lower surface and interfacial tension of liquids and to form micelles and microemulsions between two different phases. These compounds are divided into two classes: low-molecular-weight compounds termed biosurfactants, such as lipopeptides, glycolipids, proteins and high-molecular-weight polymers of polysaccharides, lipopolysaccharide proteins or lipoproteins that are collectively called bioemulsans or bioemulsifiers (Banat et al. 2010). Many microorganisms are producers of bioemulsifiers. The hydrocarbon-degrading actinobacterial strains, *R. ruber and R. erythropolis* were earlier identified to produce bioemulsifiers (Bicca et al. 1999). *Actinopolyspora* sp. A18 isolated from garden soil exhibited emulsification activity and a partially purified glycopeptide (68% protein, 5% lipids, 22.2% non-reducing sugars) bioemulsifier was identified (Doshi et al. 2010). Five strains of *Streptomyces* isolated from the hydrocarbon-contaminated soil of Baghdad, Iraq showed biosurfactant properties, and strain SS20 produced maximum bioemulsifier property (E24% = 100%), and stability of 75% for two weeks (Hayder et al. 2014).

7.4.7 Conclusion and Future Prospects

Actinobacteria are ubiquitous in soil types, plant litter, plant rhizospheres and are associated with plant microbiomes as microbial communities. With plants, they form diverging modes of lifestyles ranging from saprophytic to endophytic associations. Actinobacterial diversity among crops, medicinal and native plant species have focused them as soil or rhizospheric and as endophytic colonizers. Actinobacteria comprising both streptomycetes and non-streptomycetes are producers of antibiotics and antimicrobial metabolites of high therapeutic applications. They are also used often as potential biocontrol agents in several crop diseases and as plant growth promoters. Besides, actinobacteria are known producers of important extracellular

Table 7.4 Biodegradation potentials of hydrocarbons and plasticizer compounds by *Rhodococcus* spp

Hydrocarbon class	Strain	Genes	Mechanism	Enzymes identified	References
Aliphatic hydrocarbons	*R. erythropolis, R. ruber, R. opacus, R. equi* and *R. jostii*	alk B	Oxidation	Alkane 1-monooxygenase	Tiancsics et al. (2014)
	R. jostii RHA 1	Cyp125	–	–	RosÅoniec et al. (2009)
	R. rhodochrous	Cytochrome P450	Hydroxylate octane	–	Cardini and Jurtshuk (1970)
	R. aetherivorans BCP1	prm A, C, B, D genes smo A, B, D, C genes	Degradation of short-chain n-alkanes	(soluble di-iron monooxygenase)	Cappelletti et al. (2015)
Aromatic hydrocarbons					
BTEX	*Rhodococcus* sp. strain DK17,	akb gene	Hydroxylation	Oxygenase, Reductase, a ferredoxin component and a dehydrogenase	Kim et al. (2002, 2010)
	R. jostii RHA1	bph, etb1, and etb2,	–	–	Seto et al. (1995)
	R. opacus R7	Monooxygenases/phenol hydroxylases	o-Xylene degradation pathway	Dioxygenase	Di Canito et al. (2018)
Phenols	*R. erythropolis* CCM2595	pheA1 and pheA2	–	Phenol hydroxylase enzyme	Zídková et al. (2013)
	R. erythropolis UPV-1	–	–	Degrading PAHs, phenol, and a mixture of o-, m-, and p-cresols	Irvine et al. (2000)
	R. opacus 1CP		Ortho-pathway	Catechol−1,2 dioxygenase	Kolomytseva et al. (2007)

(continued)

Table 7.4 (continued)

Hydrocarbon class	Strain	Genes	Mechanism	Enzymes identified	References
Polyaromatic hydrocarbons	*R. opacus* R7	narAa and narAb,	Dioxygenation of the aromatic ring	Naphthalene dioxygenase	Di Gennaro et al. (2010)
Plasticizer compounds					
Phthalate	*R. jostii* RHA1	–	Protocatechuate ortho-cleavage pathway 3-oxoadipate pathway	–	Hara et al. (2007, 2010); Patrauchan et al. (2005)
Polyethylene	*R. ruber* C208	–	Polyethylene degradation	–	Gravouil et al. (2017)
Polyisoprene	*Rhodococcus* sp. AD45	10 genes	Oxidation and dehydrogenation	Glutathione S-transferase and a 1-hydroxy-2-glutathionyl-2-methyl-3-butene dehydrogenase	Van HylckamaVlieg et al. (2000)
	R. rhodochrous RPK1	lcp	Oxidation	–	Watcharakul et al. (2016)
4,4-Dithiodibutyric acid (DTDB)	*R. erythropolis* MI2	MI2	4 MB catabolism pathway	Monooxygenase	Khairy et al. (2016)

enzymes which find applications in the industrial processes. They are also degraders of harmful substances known to be environmental and health hazardous. New insights in the actinobacterial genomics have deciphered the mystery behind antibiotic production, engineered drugs for clinical applications and their efficiency in biodegradation. A thorough understanding of these strategies combined with metagenomic approaches may unravel the true potentials of many more actinobacterial taxa for future applications.

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Chapter 8
Phylogenetic Diversity of Epiphytic Pink-Pigmented Methylotrophic Bacteria and Role in Alleviation of Abiotic Stress in Plants

**Ganapathy Ashok, Guruvu Nambirajan, Krishnan Baskaran,
Chandran Viswanathan and Xavier Alexander**

Abstract Plant and methylotrophic bacterial interactions that improve plant growth and plant fitness are becoming a topic of very important considerable interest. Methylotropic bacteria are distributed in various diverse environments/colonize different habitats and utilize reduced one-carbon compounds as source of energy and play an important role in the biogeochemical cycle. Methylotrophic bacteria colonize in different parts of the plants like endophytes, epiphytes and in roots of plant rhizosphere. Pink-pigmented facultative methylotrophic (PPFM) bacteria present in the phyllosphere enhance plant growth by producing phytohormones such as IAA, Zeatin, Cytokinins, ACC deaminase and diverse secondary metabolites to overcome abiotic stress. Biological interactions of Methylotrophic bacteria enhance plant growth indirectly by increasing the nutrients uptake and beneficial in reduction of greenhouse effects to the environments. Pink-pigmented facultative methylotrophic bacteria colonize in phyllosphere of plants as epiphytes and utilize methanol as a sole carbon source of energy. In plant colonization, the occurrence and distribution of Methylotrophic bacteria may be influenced by various factors like plant genotype, geographical conditions or by interactions with associated microorganisms and phytohormones production which may result and lead to increased plant fitness.

Keywords Methylotrophic bacteria · PPFM · Plant growth promotion · Phyllosphere · Sustainable agriculture

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8.1 Introduction

Prolonged biological and chemical research have expanded our agricultural knowledge. Chemical fertilizer contains the most important elements of modern agriculture that provide the required nutrients, which are not present in the soil or other organic sources for crop improvement. The utilization and overexploitation of chemical fertilizers have an ‘ecological footprint’. It reduces productivity and disturbs nutrients level in the soil, which further leads to a deterioration in quality of the soil and causes various plant diseases. The excessive use of chemical fertilizers in the field depletes non-renewable resources and dangerous to soil fertility and environments (Dubey et al. 2012). In general, the association of *Methylobacterium* spp. and host plants may be or epiphytic or endophytic in nature (Kumar et al. 2019b; Jourand et al. 2004; Omer et al. 2004b; Lacava et al. 2004). *M. nodulans* and *M. radiotolerans* interact with host plants and fix nitrogen fixation and nodule formation (Sy et al. 2001; Menna et al. 2006), whereas some *Methylobacterium* species are involved in the production of phytohormones (Meena et al. 2006) or interact with plant pathogens (Lacava et al. 2004), promoting plant growth (Madhaiyan et al. 2006b; Tani et al. 2012) and higher rate of photosynthetic activity (Cervantes et al. 2004).

Methylobacterium spp. are in connection with more than 70 plant species that actively colonize in different parts of the plants like branches, roots and leaves. Several studies have reported earlier that *Methylobacterium* spp. are identified as endophytes of various plants, such as citrus fruits, pine, cotton, eucalyptus, strawberries, peanuts, hemp, Catharanthus roseus, mangroves and tobacco.

Methylobacterium spp. are well known to be not phytopathogenic bacteria and reported that few *Methylobacterium* spp. produce enzyme pectinase and cellulose, which may cause systemic resistance during plant colonization of methylotrophs strains. In addition to phytohormone production*, Methylobacterium* spp. are capable of producing valuable biotechnological potential product like bioplastic, which are biodegradable and ecofriendly in nature. Polyhydroxyalkanoate (PHA) and polyhydroxybutyric acid (PHB) are biopolymers that are genetically modified strains like *M. extorquens* to increase higher amount of PHB and PHA production by utilizing methanol as substrate (Hofer et al. 2011).

Methylotropic bacteria colonize in different parts of the host plant as endophytes, epiphytes in the phyllosphere and produce diverse secondary metabolites as biocontrol agents to defense against phytopathogens. This chapter mainly deals with *Methylobacterium* spp. diversity, biotechnological importance of pink-pigmented facultative methylotrophic (PPFM) bacteria and various potential applications in agriculture as biofertilizers, co-inoculants and its role in biogeochemical cycle. This chapter also covers diversity of methylotrophs, genomics, metabolic potential of pink-pigmented facultative methylotrophic bacteria in the plant phyllosphere and role in alleviation of abiotic stress to the host plants.

8.2 Diversity and Metabolism of Methyotrophs

Methylotrophs are classified and subdivided into three subgroups on the basis of their metabolic activity like carbon-substrate utilization: (1) Obligate methylotrophs utilize single carbon compounds as sole source of energy (2) Restricted facultative methylotrophs utilize a limited range of complex carbon compounds apart from C1 compounds and (3) methylotrophs utilize and grow in medium with complex carbon compounds are called less-restricted facultative (Jenkins et al. 1987). Three distinct genera such as *Methylophilus* (Jenkins et al. 1987), *Methylobacillus* (Urakami and Komagata 1986; Yordy and Weaver 1977), and *Methylovorus* (Govorukhina and Trotsenko 1991) of betaproteobacteria are classified and considered as restricted facultative methylotrophs, whereas genus *Methylobacterium* is considered and well known as less-restricted facultative methylotrophs in the Alphaproteobacteria. Recently, Taubert et al. (2016) identified and reported an additional active group of the methylotrophic community. A common one-carbon (C1) substrate for many methylotrophic bacteria is methanol, whereas subgroups of these bacteria have the ability to use methane, methanesulfonate, other methylated sulphur species, methylated amines and the halogenated hydrocarbons chloromethane, bromomethane and dichloromethane, either in addition to methanol or exclusively methane, methanesulfonate, other methylated sulphur species, methylated amines and the halogenated hydrocarbons chloromethane, bromomethane, and dichloromethane as sole source or in addition with methanol as source of energy. The association of Methylobacterium spp. and host plants may be or epiphytic, phlylosphere, rhizosphere or endophytic in nature and produce phtohormones, nitrogen fixation, abiotic stress tolerance and maintain biogeochemical cycles (Kumar et al. 2019b) (Figs. 8.1 and 8.2).

8.3 Methylotrophic Community in the Phyllosphere

The distribution and diversity of phyllosphere microorganisms are influenced by various factors like nutrient availability, stress resistance, motility, growth, bacterial traits and metabolic activity (Bulgarelli et al. 2013; Yadav 2018; Yadav et al. 2017c, 2019). In addition, climate, plant genotype and geography are the major driving forces for methylotrophic bacterial population in the phyllosphere region of plants (Redford et al. 2010; Siefert et al. 2014 and Knief et al. 2010). Knief et al. (2010) reported efficient methylotrophic bacterial colonization, competitiveness and survival are closely linked to bacterial phylogeny and metabolic diversity of microorganisms of *Arabidopsis thaliana* in the phyllosphere. Knief et al. (2010) studied and reported that *Methylobacterium* community composition had strong effects and it varies based on culture-independent metagenome sequencing

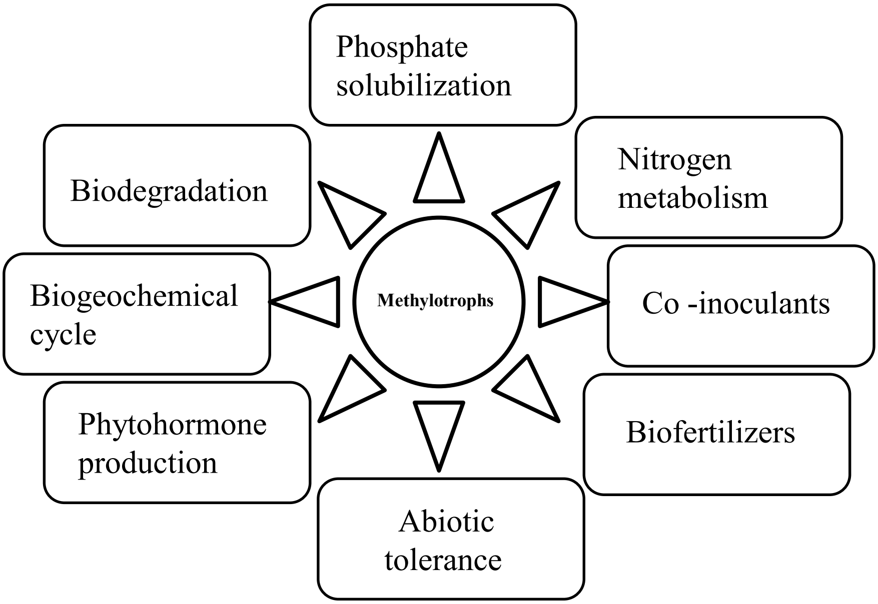

Fig. 8.1 Diverse role of methylotrophic bacteria application

analysis of leaves from *Medicago truncatula, Arabidopsis thaliana* and surrounding plant species at different locations. In *Medicago truncatula*, efficient colonization of phyllosphere Methylotrophs was observed due to the advantage of utilizing methanol as a source of energy and as a solitary carbon substrate (Sy et al. 2005). The association and interactions of different methylotrophic species like *M. mesophilicum, M. radiotolerans* and *M. fujisawaense* reported as strong colonizers with plant species were observed (Mizuno et al. 2013). In phyllosphere, methylotrophic microbes are present in huge numbers and under competitive conditions or during plant colonization, methylotrophic bacteria use plant-derived methanol as a substrate for energy and used for efficient colonization in the phyllosphere region (Abanda-Nkpwatt et al. 2006; Fall and Benson 1996; Sy et al. 2005). Colonization pattern of plant root and leaf surfaces was observed by using of green-fluorescent-marked strain of *Methylobacterium suomiense* (Poonguzhali et al. 2008) (Fig. 8.3).

8.4 Epiphytic PPFM Methylotrophs in the Phyllosphere

Epiphytic Pink-Pigmented Facultative Methylotrophs (PPFMs) are phylogenetically diverse and belong to the genus *Methylobacterium.* PPFMs utilize one-carbon compounds such as methanol, formate, formaldehyde and other multicarbon substrates as a sole source of energy. Pink-Pigmented Facultative Methylotrophs (PPFMs) belong

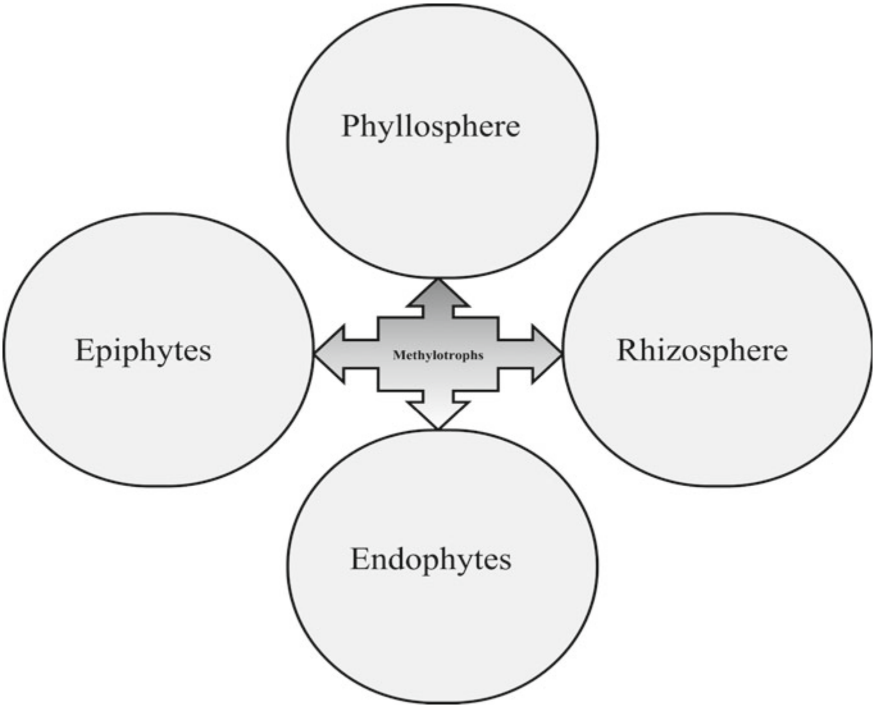

Fig. 8.2 Distribution role of methylotrops associated with different parts of the plants

to *Proteobacteria*, order Rhizobiales and Methylobacteriaceae family (Green and Bousifield 1982). PPFM is found in diverse habitats ubiquitous in nature including phyllosphere, rhizosphere, dust, freshwater, sediments and Lakes (Corpe and Rheem 1989; Green and Bousifield 1982). *Methylobacterium* spp. are generally distributed as epiphytes representing a significant bacterial population on plant leaves and in phyllosphere region of numerous plants (Hirano and Upper 1991; Holland and Polacco 1994). The colonization of *Methylobacterium* in a mucilaginous layer of plant tissues is the first step in colonization of microbes in the plant phyllosphere region (Andreote et al. 2006; Rossetto et al. 2011; Verma et al. 2017; Yadav et al. 2018c). The presence of methanol dehydrogenase (*mxaF*) gene in the genome of Pink-Pigmented Facultative Methylotrophic bacteria oxidizes methanol as an energy source (Anthony et al. 1994). In phyllosphere region of some plants, methane and methanol are emitted in the aerial part and serve as a habitat for distribution of methylotrophic bacterial population were reported earlier (Corpe and Basile 1982). Pink-Pigmented Facultative Methylotrophs were isolated using methanol-based mineral medium using methanol as an exclusive carbon and energy source (Corpe 1985).

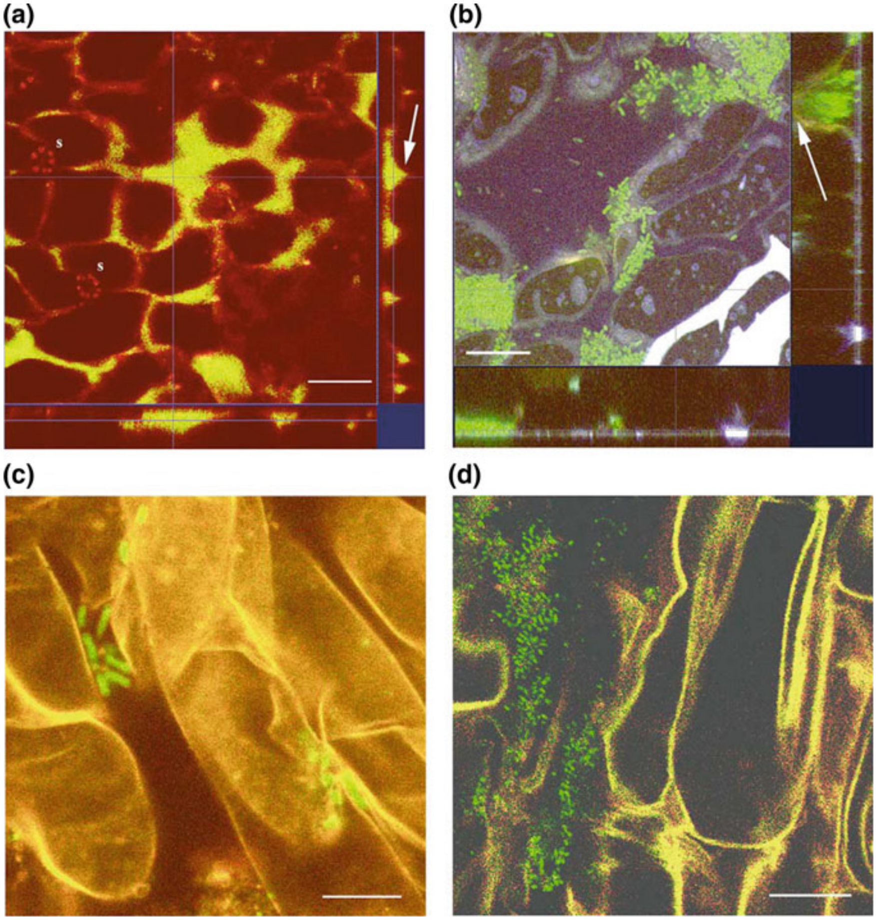

Fig. 8.3 Colonization of methylotrophic bacteria using green-fluorescent-marked strain of *Methylobacterium suomiense*

8.5 Genomics of PPFM Bacteria

The genotype of PPFM bacteria or interactions of associated microorganisms influence bacterial colonization and distribution in the host plant either directly or indirectly (Dourado et al. 2012).

8.6 Genetic Diversity of Methylotrophs

In general, Methylotrophic bacteria appears pink-pigmented in colours due to biosynthetic potential of carotenoids in the bacterium (VanDien et al. 2003). Methylotrophs are rod shaped aerobic in nature and able to grow in medium containing methanol and methylamine as carbon(C1) source for its metabolic activity (Toyama et al. 1998). The most significant characteristic feature of this group is the ability to oxidize and utilize methanol as a substrate by using the enzyme methanol dehydrogenase enzyme (MDH). PPFMs strains were isolated through leaf impression technique from phyllosphere of three different crops, which were further confirmed based on genomic DNA isolation of the isolates and PCR amplification of partial *mxaF* gene (550 bp sized partial *mxaF* gene). In metabolism of methylotrophic bacteria, the enzyme methanol dehydrogenase (MDH), the *mxa*F gene encode for encodes the large subunit, which helps to understand *Methylobacterium* niche-specific plant association (Dourado et al. 2012).

The enzyme methanol dehydrogenase (MDH) oxidizes methanol into formaldehyde metabolism, which starts in the periplasm of methylotrophic bacterium (Zang et a 2003). *The mxa*F and *mxa*I genes encodes for large, small subunits and cytochrome C primary electron acceptor for methanol dehydrogenase are encoded by *mxa*G gene (Mcdonald and Murrell 1997). Methanol dehydrogenase enzyme is mainly composed of two small (8.5 kDa) and two large (66 kDa) subunits. The large subunit (MxaF) is important for the functional activity of methanol dehydrogenase (Skovran et al. 2011). Random amplified polymorphic DNA (RAPD) is a unique molecular fingerprinting technique which was commonly used to distinguish between closely related bacterial strains at species level (Mazurier et al. 1992; Williams et al. 1990).

Van Aken et al. (2004) investigated and reported metabolic and genetic diversity of PPFM bacteria in the phyllosphere region of maize, cotton and sunflower to understand the PPFMs diversity within a particular plant species and different plant species using RAPD molecular fingerprinting and profiling carbon-substrate utilization pattern. Vuilleumier et al. (2009) reported variations in the numbers of insertion elements (IS) and in the organization of the genes have been identified in two different *Methylobacterium* (AM1 and DM4) strains associated with methanol metabolism. *Methylobacterium* bacterial strains have been sequenced and reported *M. extorquens PA1 as an* as a competitive colonizer of the phyllosphere region of *Arabidopsis thaliana* plants (Knief et al. 2010).

8.7 Methylotrophic as Plant Growth Promoters

Methylotrophs promote plant growth through beneficial interactions with plants by producing phytohormones and indirectly by increasing the availability of nutrients (Lidstram and chistordava 2002; Koenig et al. 2002). Methylotrophs colonize in various parts of the plant and produce phytohormones like auxins, cytokinin and zeatin. Plant growth substance promotes growth of both shoot and root system (Verma et al. 2013, 2014, 2015, 2016; Yadav et al. 2016). Doronina et al. (2001) reported aerobic methylotrophic bacteria produce auxins range from 20 mg/ml in the culture medium. In methylotrophic bacteria, biosynthesis of IAA was initiated from tryptophan as precursor and addition of tryphtophan enhances the synthesis of IAA (Schneider and

Wightman 1974). The biosynthesis of IAA through IPA pathway, which involves the transfer of amino group from tryphtophan to IPS, which is catalyzed by aromatic aminotransferases and then to IAA in methylotrophic bacteria. The enzyme aminotransferase activity was observed and identified in several methylotrophic bacteria (Ivanova et al. 2001).

The genes responsible for enzymes such as amine oxidase, aldehyde dehydrogense, N-acyl transferase and amidase were related to auxins biosynthesis and identified in methylotrophic bacteria (Kwak 2014; Madhaiyan et al. 2006c; Tani et al. 2012). Schauer and Kutschera (2011) reported a novel *Methylobacterium funariae* produced phytohormone like auxin and cytokinin were isolated from phyllosphere region of common mosses. In phyllosphere region, inoculation with *Methylobacterium* produced phytohormone IAA, which indirectly alter IAA concentrations in the plant and stimulate the plant growth (Lee et al. 2006). Pink-pigmented facultative bacteria were widely distributed and colonize in the phyllosphere of medicinal, agricultural crops and wild plants in Ukraine region (Romanovskaya et al. 1998). Lee et al. (2004) reported phytohormone IAA from methylotrophic isolates such as *Methylotrophic extorquens* and *Methylotrophic fujisawaense* isolated from the phyllosphere region of rice.

8.7.1 Production of Phytohormones by PPFM

Anitha (2010) reported Pink Pigmented Facultative Methylotrophic bacteria (PPFMs) was isolated from phyllosphere of soybean and groundnut producing phytohormone IAA and enhance plant growth. Keerthi et al. (2015) reported PPFM were used as biofertilizers in green grams isolated from phyllosphere environment. Tani et al. (2015) reported methylotrophic sp. producing both IAA and cytokinin associated with red pepper. Cytokinins are plant growth hormones, which regulate many physiological processes in plants such as to stimulate plant cell division, activate dormant buds, remove apical domination and induce seed germination. Ivanova et al. (2000) reported *M. mosophilicum* isolated from phyllosphere of rye grass lium perenne were able to synthesize cytokinins using biotest with the *Amaranthus candatus* L. seedlings. Holland (1997) reported application of exogenous methanol to the host plant, which stimulates the growth of PPFM bacteria by producing phytohormone cytokinins. In addition to the cytokinin PPFM bacteria isolated from different crops like soybean, barley, maize and Arabidopsis plant contain phytohormone zeatin and zeatin rhiboside (Long et al. 1996). The presence of phytohormone cytokinins and zeatin in the culture liquids of methylotropic bacteria is confirmed through chromotagraphic and enzyme immuno assay analysis (Ivanova et al. 2000). Epiphytic pink-pigmented methylotrophic bacteria produce cytokinin, stimulate germination and growth of wheat (*Triticum aestivum*) seedling was reported Meena et al. (2012). Phytohormone production by methylotrophic bacteria associated with different crops (Table 8.1).

Table 8.1 Phytohormone production by methylotrophic bacteria associated with different crops

Crop plants	Crop associated Methylotrophs	Biofertilizer/Phytohormones production	References
Groundnut	Pink-pigmented facultative methylotroph	IAA production	Anitha (2010)
Green Gram	Pink-pigmented facultative methylotroph	Biofertilizer	Keerthi et al. (2015)
Soybean	Pink-pigmented facultative methylotroph	IAA production	Anitha 2010)
Red Pepper	*Methylobacterium* sp.	IAA and cytokinin production	Tani et al. (2015)
Rice	*Methylobacterium extorquens, Methylobacterium fujisawaense*	IAA production	Lee et al. (2004)
Wheat	*Methylobacterium* sp.	Cytokinin production	Meena et al. (2012)

8.8 PPFM as Biofertilizers

The spraying of PPFM on plants with 20% methanol leads to twofold increase in the PPFM population and increase in soybean plants, when compared to control plants (Nishio et al. 1977; Kumar et al. 2019a; Yadav et al. 2018a, b). Jayajyothi et al. (2014) reported foliar spray of pink-pigmented methylotrophic bacteria and Pseudomonas strains, in addition with biofertilizer enhance the microbial population and increase the nutrient uptake to the plants. Abd El Gawad et al. (2015) studied and reported enhanced growth, antioxidant activities and increased yield in snap bean crops based in field experiments in different seasons using PPFM bacterial isolates. Foliar spray or irrigation of PPFM bacteria along with methanol, ethanol or even both showed improvement in plant growth of cotton, sugarcane and strawberry plants (Madhaiyan et al. 2005; Yavarpanah et al. 2015). Ivanova et al. (2001) reported application of methanol spray on leaf surfaces to promote the growth of plants by producing phytohormones like cytokinin and auxin by PPFM bacteria. Madhaiyan et al. (2006a, b) investigated and reported higher yields of sugarcane (Saccharum officinarum L.), cotton (Gossypium hirsutum L.) were observed through foliar spray of PPFM along with methanol, which increases phytohormone production. Chauhan et al. (2010) also reported that the application of fertilizers with PPFM as foliar spray leads to higher crop yields. ICAR (2013) advocated application of PPFMs as biofertilizers can protect crops from drought stress conditions.

8.9 PPFM in the Nitrogen Metabolism

Nitrogen is considered as one of the essential nutrients required for plant growth, but the availability of nitrogen from the atmosphere was limited for the metabolism of plants (Kour et al. 2019a, b). In nitrogen fixation, the conversion of atmospheric nitrogen into ammonia takes place for the nutrient availability to the plants. The nitrogenase enzyme was involved in the biological reduction of nitrogen to ammonia which was carried out by a few prokaryotic organisms (Menna et al. 2006). PPFM are involved in the nitrogen metabolism of colonized plants indirectly. Soybean plants have several urease isoenzymes: the Eu1 urease located in beans, the Eu4 urease located in all plant tissues and the Eu2 and Eu3 ureases, which are necessary for the normal urease activity of soybean plants. In the soybean plants with the mutant *eu3-e1/eu3-e1* gene, urea was accumulated in the plant tissues because of impaired urease activity. The colonization of such plants by PPFM did not restore their urease activity. At the same time, the colonization of the double *eu1-sun/eu1-sun, eu4/eu4* soybean mutants by PPFM led to the restoration of their urease activity to a level of 20–40% of that of the wildtype plants, due to the PPFM urease (Holland and Polacco 1992).

8.10 PPFM as Bio-inoculants and Co-inoculants

Meena et al. (2012) reported application of methylotrophs as bio-inoculants for seed coating or as seed inoculation enhances seed germination. Methylotrophs are capable of promoting plant growth with different groups of bacteria as co-inoculants, which results in higher yield in pot and crop field conditions Poonguzhali et al. (2008). Meena et al. (2012) suggested development of bio-inoculants and co-inoculation of methylotrophic bacteria results in increased production of cytokinins and higher crop yield. Meenakshi and Savalgi (2009) reported co-inoculation of methylotrophs with *B. japonicum* as foliar spray consequences raise in number of nodules, when compared to seeds with single *B. japonicum* as control. In addition, foliar spray of bio-inoculants with methylotrophs leads to increase in chlorophyll content to the host plants. Nalayani et al. 2014 reported foliar application of different types of microbial consortia strains Pseudomonas, Bacillus and Azospirillum with PPFM results in higher yield of cotton plants.

8.11 PPFM in Abiotic Stress Tolerance

The phyllosphere methylobacteria are highly resistant to UV dehydration, freezing on hygroscopic carriers and ionizing radiation and elevated temperatures. The phyllosphere epiphytic methylotrophic PPFM may remain viable after UV irradiation with higher doses that are lethal to bacterial strains like *Pseudomonas, Enterococci* and *Methanotrophs* (Romanovskaya et al. 1998; Yadav et al. 2017a, b, d; Yadav and Saxena 2018). Plants can regulate phytohormones production during unfavourable conditions and in stressed environments to overcome from biotic or abiotic stresses (Salamone et al. 2005). Ethylene is a plant growth hormone essential for plants, which is produced during various physiological changes in plants and endogenously by plants (Khalid et al. 2006). Saleem et al. (2007) reported earlier ethylene as a plant growth regulator and identified as a stress-related hormone. Saleem et al. (2007) also reported the production of ethylene during unfavourable conditions or stress conditions, the invivo accumulation of ethylene is drastically increased, which negatively alters the overall growth of plant. The overall increased concentration of ethylene may lead to reduced performance of the crop.

Ethylene is a stress associated hormone related to auxin biosynthetic pathway and an increased level of ethylene in plants leads to deleterious effects like plant growth, accelerating abscission, ageing, inhibiting root elongation and senescence. In ethylene biosynthetic pathway, aminocyclopropane-1-carboxylic acid (ACC) is the precursor of the ethylene hormone converted from S-adenosylmethionine (SAM) and to ethylene by ACC synthase (ACS) and ACC oxidase (ACO), enzymes that are transcriptionally regulated separately by both biotic and abiotic factors. ICAR et al. (2013) reported the beneficial application of *Methylobacterium* (PPFMs) as biofertilizer helps the crops to protect and overcome crops drought stress and during high-temperature conditions. PPFMs synthesize phytohormones, 1-aminocyclopropane-1-carboxylate (ACC) to overcome abiotic stress conditions by utilizing methanol produced from plant leaves as a source of carbon and energy (ICAR 2013).

Plant growth-promoting methylotrophic bacteria produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which indirectly stimulate growth by decreasing ethylene concentrations in plants (Glick 1995). Chinnadurai et al. (2009) revealed that phyllosphere methylobacteria distributed in the rice leaves produce the enzyme ACC deaminase, which control the ethylene concentrations level in the rice plant. In earlier investigations, *Methylobacterium* strains were identified and reported to have ACC deaminase activity and tested for their potential in plant growth-promoting traits in various crops. *Methylobacterium* spp. are not phytopathogenic in nature which help in plant growth promotion by decreasing environmental stress, immobilizing heavy metals, degrading toxic organic compounds and even inhibiting plant pathogens. *Methylobacterium* spp able to synthesize polymer degrading pectinase and cellulase, suggesting that they can indirectly induce systemic resistance during plant colonization.

8.12 Conclusion and Future Prospects

PPFMs isolates and other methylotrophs improve plant growth by controlling or by inhibiting phytopathogens. PPFMs inhibit several phytopathogens including *Fusarium oxysporum, Sclerotium rolfsii, Colletotrichum capsici, Xanthomonas campestris and Cercospora capsici* and serve as biocontrol agents. Methylotrophs are widely used as bio-inoculants as a foliar spray on plants and serve as an alternative to chemical fertilizers to enhance crop yield. The application of methylotrophs as foliar spray regulates plant growth directly or indirectly. Methylotrophs regulate and play a key role in biogeochemical cycle of soil ecosystem, making the soil more suitable for higher crop yield. In addition, several characteristic features of methylotrophs like nitrogen fixation, phytohormone production, nodulation and nutrient acquisition as a promising substitute for synthetic or chemical fertilizers. In conclusion, methylotrophic bacteria serve as an alternative of biological control, plant growth promotion by nitrogen fixation, phosphate solubilization, phytohormone production and ACC deaminase production, along with balanced carbon cycling. Beneficial methylotrophic can be used for effective organic farming in sustainable agriculture in the future.

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Chapter 9
Potassium Solubilizing Microbes: Diversity, Ecological Significances and Biotechnological Applications

Dheeraj Pandey, Harbans Kaur Kehri, Ifra Zoomi, Uma Singh, Kanhaiya L. Chaudhri and Ovaid Akhtar

Abstract Potassium (K) is seventh abundant element on earth and considered as third most significant macronutrient after nitrogen and phosphorus for plants. K plays an important role in metabolism, activation of enzyme, osmoregulation, balancing of charge and preventing unnecessary water loss, and regulating the stomatal movement in plants. The deficiency of K results in poor growth and development which intensely related to crop yield and resistance to disease. In soils, the fixation of K is comparatively fast; however, its release is a slow process. Many potassium solubilizing microbes (KSMs), such as fungi, bacteria and some arbuscular mycorrhizal (AM) fungi assist in mobilization of K from soil/mineral to plants. Microbes secrete various organic acids, which release K from the minerals and make it bioavailable to the plants. Fixation of K in soil, its uptake by the plant and leaching reduce the availability of K content in the soils. Application of microbial inoculants improve the growth and yield by converting the K in available form. KSMs work as biofertilizer in agriculture; improve the productivity, nutrient availability and reduce the use of agrochemicals in an economic, eco-friendly and sustainable manner. Future studies should focus on isolation and inoculation of indigenous K solubilizers to the plants from different environmental conditions such as cold, drought, nutrient-deficient soils, etc., to improve the availability of K for plants.

Keywords Potassium (K) · Potassium fertilizers · Potassium solubilizing microbes (KSMs) · AM fungi · Quality nutrient · Biofertilizer · H^+-ATPase · K cycling

9.1 Introduction

Potassium (K), with atomic number 19, is situated in alkali metal group with density 0.862 grams per cubic centimetre. It is a soft and silvery-white metal which rapidly

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reacts with oxygen and forms dull-white potassium peroxides. K has single valence electron which is easily ionized as K^+. In 1807, Sir Humphry Davy was first isolated K from plant ashes (caustic potash) by electrolysis method (Thomas et al. 2008). K is seventh abundant element on earth which comprises 2.4% of the earth crust (NCBI Pubchem, 2019) and never found as elemental form in nature because of its very reactive nature. K comprises with different compounds to form ores such as langbeinite (K_2Mg_2 $(SO_4)_3$), carnallite ($KCl{\cdot}MgCl_2{\cdot}6H_2O$), polyhalite ($K_2Ca_2Mg$ $(SO_4)_4{\cdot}2H_2O$) and sylvite (KCl). There are many substitutes of K such as Potassium chloride (KCl) utilized as fertilizers, Potassium hydroxide (KOH) utilized in soaps, detergents and drain cleaners, Potassium carbonate ($KHCO_3$), also known as pearl ash and Potassium nitrate (KNO_3) or saltpeter/saltpetre or nitre, utilized in fertilizers etc. K is third most significant macronutrient after nitrogen and phosphorus, which is also considered as the “quality nutrient”. K is indispensable macronutrient for plant and is required in large quantity after N and P for proper growth and development. It plays a key role in metabolism and activates important enzymes, osmotic regulation and charge balance in plants. The deficiency of K results in poor growth and development which intensely related to crop yield and resistance to disease (Ahmad et al. 2016; White and Karley 2010; Armengaud et al. 2010).

K exists in soils in different forms of minerals such as mica, orthoclase and also found in seawater. The rock trapped K are nonexchangeable, whereas exchangeable K in ionic form (K^+) held in soil colloids, which is available to the plant. In present scenario where agricultural lands are decreasing rapidly and instance agriculture is in practice that requires important chemical fertilizers including K fertilizers (Zhang et al. 2013). These chemical fertilizers not only increase cost input but also making the soil barren day by day. Because of the limited resources, increasing world population, urbanization and salinization are alarming for challenge of quality feeding in upcoming future.

About 98% of the total K present in soil is unavailable (Mengel and Kirkby 2001). Available K is also slowly solubilizing (Ahmad et al. 2016) by soil microbes such as bacteria, actinomycetes, fungi, AM fungi, etc., and these microbes have developed different modes for energy and nutrients. Some of them inhabit in rhizospheric soil of growing plants. This plant–microbe interaction provides a solution for sustainable agriculture and helps to increase agricultural productivity in sustainable manner. There are many bacteria (K solubilizing bacteria) and fungi (K solubilizing fungi) solubilize K with their enzymatic activities. The microbes make the K available to plants. Bacteria release acids for the solubilization of K minerals, and these microbes become very important in plant rhizosphere. Such bacteria also act as plant growth promoter and in plant pathogens protection (Zoomi et al. 2017). Some soil fungi, e.g. *Aspergillus* sp., *Fomitopsis meliae,* etc. (Anjanadevi et al. 2016; Kasana et al. 2017) are capable to solubilize K and make them available. In the rhizosphere, AM fungi symbiosis with plant roots becomes very beneficial for their growth and development (Pandey et al. 2019). These microbes solubilize different minerals such as phosphorus (P), nitrogen (N), K, etc. There are a number of studies about the role of AM fungi in K uptake (Garcia and Zimmermann 2014; Perner et al. 2007; Veresoglou et al. 2011). AM fungi solubilize K, store and transport to plant

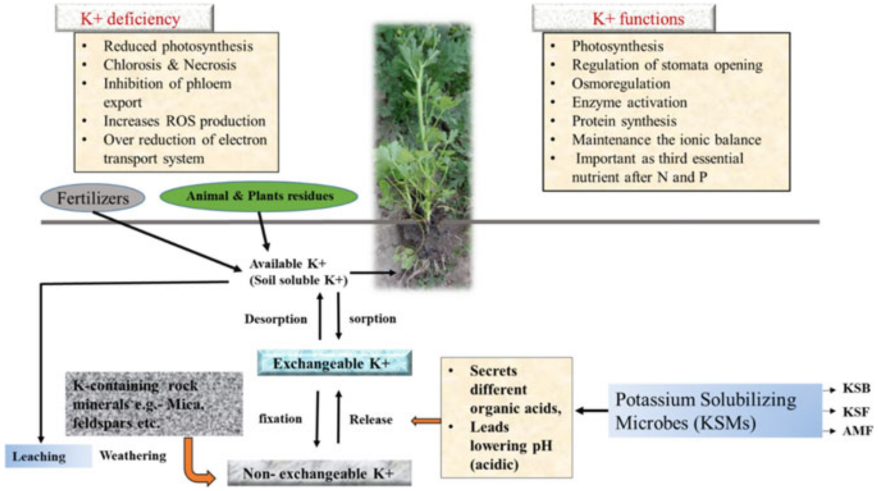

Fig. 9.1 Potassium (K) as a plant nutrient, importance and role of potassium solubilizing microbes (KSMs) in its mineral cycling

(Fig. 9.1). AM fungi accumulate K in different fungal structures like hyphae, vesicles and spores (Johansson and Campbell 1988). Vast applications of chemical fertilizers adversely affect not only the environment and soil but also our economy. There is a need to promote sustainable agriculture and application of beneficial native microbes in modern agriculture.

9.2 Potassium in Soils

9.2.1 *Potassium Availability*

Insoluble K constitutes about 90–98% in soil. Its concentration varies from 0.04 to 3.0% of total lithospheric K minerals (Mengel and Kirkby 2001; Sparks and Huang 1985). Type of soil and mineral constituents greatly influence the process of release and fixation of K (Braunschweigh 1980). So far to fulfil the requirements of crops, farmers applied synthetic K fertilizers but most of this is fixed with other elements and become inaccessible to crops (Prajapati et al. 2013). Hence, K fertilizer is applied on regular basis, but K unavailability to plants is continued for upcoming crops (Kang et al. 2002). So that unavailable K increases in large amount in soil. This condition interferes with soil physiology and ecology. To overcome this problem, there is a need for enhancement of K cycling soil microbes. K deficiency occurs in agricultural land of 75% of the paddy soils of China, 66% of the wheat belt of Southern Australia and 21% Indian soils (Hasan 2002; Meena et al. 2014a, 2016). In the year 2009–10, Indian farmers applied 42.38 lakh tonnes of muriate of potash fertilizer, and the demand by 2020 would be 9.52 metric tonnes (Kinekar 2011; Pathak et al. 2010).

9.2.2 Fixation of Potassium in Soil

Minerals found in the soil can also fix K and considerably affects the K availability. K fixation in soil comprises the adsorption of K^+ onto weathered sheet of montmorillonite, illite and vermiculite (silicate). Additionally, fixation of K in soils depends on the clay mineral, wetness, opposite ions, pH of the soil and K concentration in soil solution (Schneider et al. 2013). It has also been observed by Oborn et al. (2005) that fixation of K is comparatively fast; however, its release is a slow process. It has been reported by several author that organic acids play a crucial role in the release of fixed K from the clay minerals. Hence, management of the soil pH may be a mean of improving the release of K.

9.3 Role of Potassium

9.3.1 Function of Potassium as a Nutrient

K is very important macronutrient for plants (Hafsi et al. 2014). In plants, it is very important for physiological and biochemical functions (Zhang and Kong 2014). K^+ is absorbed from dissolved soil solution, clay and organic colloids by roots; translocated inside the plants through the xylem and phloem; and then converted into complex compounds (Zandonadi et al. 2010). K is highly mobile macronutrient and has very significant role in regulation of water status in plant cells. K^+ prevents unnecessary water loss and regulates the activity of stomatal cells. It promotes water absorption, maintains osmotic pressor and turgor in cells, and regulates stomatal movement (Meena et al. 2016). K is an important part for the development of chlorophyll and process of photosynthesis such as reduction of CO_2 into carbohydrate (White and Karley 2010). K does not play structural role but help in production of carbohydrate and its translocation in different sites of growth, development and storage and associated with sugar and starch accumulation (Cakmak 2005); however, it plays important roles in cellular organization and membrane permeability, which are important aspects for keeping the appropriate protoplasm hydration. K is transported through K^+ channels, maintains membrane transport and helps in the regulation of 60 different stress enzymes (Meena et al. 2016). K activates necessary enzymes essential for the ATP production as a source of energy, and it is also important in activation of essential enzymes of protein metabolism, amino acid synthesis, progress of cell division and growth-related enzymes of plants, which is also associated with disease resistance against bacteria and fungi.

9.3.2 Potassium Deficiency

Deficiency of K is associated with decrease in crop and food production called hidden hunger. In initial phase, deficiency does not show any specific symptoms. In scarce condition, the K is relocated from older leaves to new growing leaves. Hence, the deficiency symptoms of K appear in older leaves, beginning from tip to base. Leaves start yellowing and eventually develop necrosis at the border of the leaves. K deficiency reduces the strength, slows down the photosynthesis, shortens the internodes, slows down the photosynthate transport and reduces the resistance toward the diseases in plants (Meena et al. 2016) (Fig. 9.1). Blackening of potato tubers and margin of older leaves in cotton, maize, legumes and tobacco is due to K deficiency (Ashley et al. 2005). The accessibility of K in the soil influences root morphology (Thaler and Pages 1998). K-efficient rice had developed better roots as compared to the rice grown under deficient K condition (Yang et al. 2003). *Hordeum maritimum* and *Catapodium rigidum* increase their root length and root surface for uptake of more K (Hafsi et al. 2011). Lateral root number and growth was reduced in barley (Drew 1975) and *Arabidopsis thaliana* (Shin and Schachtman 2004) when raised under low K condition. K deficiency stress affects the dry mass partitioning in root and shoot. This may vary with species and culture conditions (Andrews et al. 1999). There are many studies regarding root shoot dry weight which reported increment in dry weight in *Brassica oleracea* (Singh and Blanke 2000), *H. maritimum* (Hafsi et al. 2011) and *Triticum aestivum* (Andrews et al. 1999).

9.4 Mechanism of K^+ Uptake and Regulation in Plant

In plants, there are various K transport mechanisms, which have important role in K absorption and its relocation (Véry and Sentenac 2003). K absorption is done by H^+-ATPase pump and different K^+ transporter proteins channels of cellular membrane (Hafsi et al. 2014). Absorption of K^+ nutrient is connected with net K^+ influx and low pH (Minjian et al. 2007; Chen and Gabelman 2000). Chen et al. (2008) identified 71 K^+ transporters and channels. K^+ and Na^+ transport system named high-affinity K^+ transporter 1 (HKT1) was reported in *Triticum aestivum* and cloned for the first time by Schachtman and Schroeder (1994). The HKT1 was also identified in *Eucalyptus camaldulensis* by Fairbairn et al. (2000). High-affinity K^+ transporter 5 (AtHAK5) and K^+ channel arabidopsis K^+ transporter 1 (AtAKT1) are two K^+ transporter system identified in *Arabidopsis* (Gierth et al. 2005; Pyo et al. 2010). In plant, K^+ channel is Shaker-type efflux channel, outward-rectifying K^+ channel (SKOR) type which is associated with K^+ transporter from root to xylem. Lack of this SKORK$^+$ channel affects the plant shoot biomass production. SKOR mutant *Arabidopsis thaliana* showed fifty percent decrease in shoot K$^+$; however, root K$^+$ content was not changed (Gaymard et al. 1998). Another Shaker-type efflux channel AKT2 is also found in phloem which is associated with recirculation of K$^+$ (Chérel et al. 2002; Gajdanowicz et al. 2011). KAT1 and KAT2 are inward-directed channels in guard cell that facilitate K$^+$ uptake (Schachtman et al. 1992; Pilot et al. 2001) while GORK is outward-directed K$^+$ channel associated with releasing K$^+$ from guard cell during stomatal movement regulation (Hosy et al. 2003). Many studies at the level of transcriptome and genetic analysis in rice have observed several genes of transporter families, which have significant roles in responses to K$^+$ deficit (Ma et al. 2012). Ma et al. (2012) identified three families of OsHAK genes in an up-regulation to increase K$^+$ uptake by increasing genes expression encoding K$^+$ transporters during K$^+$ deficiency. Buschmann et al. (2000) also identified TaAKT1 gene in *Triticum aestivum* in K deficient condition. Transcription level K regulating factors are also identified, which bind to transport promoter and activate the expression genes such as DDF2, JLO, bHLH121 and TFII-A involved in upregulating with HAK5 promoter (Hong et al. 2013). Du et al. (2019) investigated the role of transcription factor MYB59 in *Arabidopsis*, which regulates NRT1.5/NPF7.3 transporter in K deficit conditions.

9.5 Microbes-Mediated Potassium Solubilization

Different groups of soil microflora are reported which solubilize inaccessible fixed form of K to soluble and make them available to the plants. The potent K solubilizers microbial inoculants enhanced the plant growth and development, which increases the crop yields in eco-friendly way (Meena et al. 2016). Muentz (1890) was first reported the microbial role in rock K solubilization. In present scenario, there are many microbes discovered with K solubilizing potency, and many researches are still going on for their application at large scale. Many potassium solubilizing microbes (KSMs) are discovered till date. Several fungi, bacteria, actinomycetes and some AM fungi (especially rhizospheric microbes) assist in mobilization of K from soil/mineral to plants (Gundala et al. 2013; Verma et al. 2015, 2016a, b). KSM may differ in number and species from soil to soil. Some microbes reported for solubilizing K from silicate mineral (Sheng et al. 2002) such as *B. mucilaginosus* sub spp. *siliceous* can solubilize K from aluminosilicates and feldspar (Aleksandrov et al. 1967; Groudev 1987; Gundala et al. 2013). Various bacterial genera such as *Bacillus*, *Enterobacter*, *Acidithiobacillus*, *Pseudomonas*, *Burkholderia, Paenibacillus*, *Cladosporium* and *Arthrobacter* are reported for K solubilizing (Muralikannan 1996; Wu et al. 2005; Sheng 2005; Liu et al. 2012; Singh et al. 2010; Meena et al. 2016). *Bacillus mucilaginosus* strain CS1 is reported as solubilizer of silicate from both rhizospheric and non-rhizospheric soil (Lin et al. 2002; Liu 2001). Mikhailouskaya and Tcherhysh (2005) also isolated the above bacteria from K and silicate-amended soil. AM fungi can increase the solubility of K by the mechanism in which they secrete different organic acids and protons. K solubilization and uptake depends on the soil environment as well as nature of plant and other growth conditions (Clark and Zeto 2000). *Aspergillus terreus* and *Aspergillus niger* were reported for K solubilization from feldspar and potassium aluminium silicate sources (Prajapati and Modi 2012). Sangeeth et al. (2012) reported the role of *Penicillium* sp. in K solubilization from rocks and minerals. KSMs enhanced germination rate, seedling vigour, plant growth and their production (Sangeeth et al. 2012). Similar results were also obtained from some horticultural plants, vegetables and cereals with KSMs (Singh et al. 2010; Prajapati et al. 2013). Under the field test, Xie (1998) concluded that KSMs application in maize, wheat, sudan grass and forage crop significantly reduced the need of chemical fertilizers.

9.6 Diversity of Potassium Solubilizing Microorganisms

The various groups of KSMs including fungi and bacteria have been recovered minerals rocks, soils, industrial area and rhizosphere of a number of plants. These microorganisms have central role in ecosystem functioning and could be utilized as a bioinoculants (Kour et al. 2019a, b, c; Yadav et al. 2019a). These beneficial microorganisms have been cultured from rhizosphere of cotton (Sheng and He 2006), potato–soybean cropping sequence (Biswas 2011), rice (Muralikannan 1996), common bean (Kumar et al. 2012), peanut and sesame (Youssef et al. 2010), black pepper (Sangeeth et al. 2012), sugarcane (Rosa- Magri et al. 2012) rhizospheric soil of different other plants (Zhao et al. 2008; Zhang and Kong 2014; Meena et al. 2014b; Kumar et al. 2015) and from diverse extreme environments (Yadav et al. 2015a, b, c; Yadav et al. 2016). Diep and Hieu (2013) isolated 20 KSB strains from soils/weathered rocks. The microorganisms were also isolated from ceramic industry soil (Prajapati and Modi 2012) and mica core (Gundala et al. 2013). Leaungvutiviroj et al. (2010) isolated these organisms from rhizospheric soil in Thailand and were capable to release K. Based on the above data, it could be concluded that most of the KSMs belong to the bacteria domain.

9.6.1 Bacteria

KSB has been isolated from various habitats including plant microbiomes (Yadav 2017a, b; Yadav et al. 2017b) as well as microbiomes of extreme habitats (Yadav 2019a, b; Yadav and Yadav 2018). Raj (2004) isolated *Bacillus* sp. from the granite crusher yard, Hu et al. (2006) isolated *Bacillus mucilaginosus* from Tianmu mountain, Prajapati and Modi (2012) isolated *Enterobacter hormaechei* from ceramic industry soil, Syed and Patel (2014) isolated *Pseudomonas* spp. and *Bacillus* sp. from loamy sand soil, and Diep and Hieu (2013) isolated *Bacillus megaterium* and *Bacillus coagulans* from soils/weathered rocks. Potassium solubilizing bacteria (KSB) reported to improve the morphogenesis in plants (Lian et al. 2002; Singh et al. 2010). Several bacterial genera such as *Bacillus, Enterobacter, Pseudomonas* and *Azotobacter* were also reported to provide benefit to the plant (Kloepper et al. 1991; Han and Lee 2005; Singh et al. 2010). Sangeeth et al. (2012) reported to enhanced K uptake and biomass in inoculated black pepper. Similarly, Valencia orange trees inoculated with *Bacillus circulans* considerably enhanced K uptake, fruit biomass and yield (Shaaban et al. 2012). Yield of tomato plant was reported to improve when inoculated with *Pseudomonas* sp. (Lynn et al. 2013). Maize plant inoculated with *B. megaterium, B. mucilaginosus* and *A. chroococcum* improved K uptake along with nitrogen and phosphorus and growth of the plant (Wu et al. 2005). Furthermore, KSB also shows resistance towards various stresses such as chilling drought stress (Cakmak 2005; Ramarethinam and Chandra 2006). KSB belongs to different phylum including actinobacteria, firmicutes, proteobacteria and bacteroidetes (Kumar et al. 2019; Rana et al. 2019c; Yadav et al. 2017a, 2019e; Yadav and Saxena 2018).

9.6.2 Fungi

Fungi play paramount role in the release of mineral such as phosphates, silicate (Banfield et al. 1999) and carbonate (Verrecchia and Dumont 1996). Additionally, numerous studies have also been concluded the roles of fungi in releasing the K from minerals (Wallander and Wickman 1999; Yuan et al. 2000, 2004; Glowa et al. 2003; Yadav 2018; Yadav et al. 2019b, c, d). According to Lopes-Assad et al. (2010), filamentous saprophytic fungi of the genera *Aspergillus, Penicillium* and *Fusarium* are well-recognized K solubilizers. Several fungi, e.g. *Aspergillus fumigatus* (Lian et al. 2008), *Aspergillus niger* (Prajapati and Modi 2012), *Penicillium* spp. (Sangeeth et al. 2012), *Aspergillus* spp. and *Aspergillus terreus* (Prajapati et al. 2013), have been reported to mobilize organic and inorganic K and enhance the release of K from minerals and rock. Potassium solubilizing fungi (KSF) enhanced the biomass, yield and nutrient uptake in plants (Badr et al. 2006). Utilization of these beneficial fungi can be an emerging aspect concerning the sustainable development in the preparation of biofertilizer (Priyadharsini and Muthukumar 2016; Raghavendra et al. 2016; Yadav and Sidhu 2016).

Arbuscular mycorrhizal (AM) fungi belonging to the phylum Glomeromycota (Kehri, et al. 2018a) form mutualistic symbiotic association with roots of the plants and are ubiquitous in distribution (natural and agroecosystems) (Kehri et al. 2018b; Akhtar et al. 2019). These fungi provide several benefits to the plant including nutrition and increased the tolerance of plant towards various stresses. AM symbiosis can positively affect the plant growth by solubilizing fixed form of minerals (Verma et al. 2017a, b; Yadav et al. 2018a, b, c, d). AM fungi produce structures such as vesicles, spores, intra- and intercellular hyphae, auxiliary cells and extraradical mycelium (Kehri et al. 2018a). Particle-induced X-ray emission (PIXE) experiments including the *Rhizophagus intraradices* suggested that AM fungi accumulated K in hyphae, vesicles and spores (Olsson et al. 2008, 2011). Moreover, Casieri et al. (2013) identified four sequences in *Rhizophagus irregularis* in which three sequence coding for Shaker-like channels and one for KT/KUP/HAK transporter are reported to involve in K^+ transport from an ETS library.

9.7 Mechanism of Potassium Solubilization

There are various mechanisms used by KSB to release the K from the minerals. These bacteria produced low molecular weight organic acids which decrease the pH (Goldstein 1994) and produce the chelated compounds that form complexes with K, thereby enhancing the availability to the plant (Uroz et al. 2009; Keshavarz et al. 2013; Parmar and Sindhu 2013). The production of different types of organic acids is the foremost mechanism used by the bacteria to release the K from the minerals and make it bioavailable to the plant (Sheng et al. 2003). There are various types of organic acids produced by the bacteria such as propionic acid, lactic acid, 2-ketogluconic acid, citric acid, tartaric acid, acetic acid, oxalic acid, glycolic acid, succinic acid, malonic acid and fumaric acid (Table 9.1) (Wu et al. 2005; Sheng and He 2006). The production of organic acids decreases the pH (acidification) of soil thereby solubilizing K (Keshavarz et al. 2013; Parmar and Sindhu 2013). Römheld and Kirkby (2010) also reported that the bacterial-mediated acidification stimulates the production of chelates that ultimately enhance the crop growth and productivity. In addition to this, KSB also known to solubilize the K by the production of siderophores and lipo-chitooligosaccharides (Calvaruso et al. 2006).

Fungi adopt several mechanisms to solubilize K from minerals, thereby making it bioavailable to the plant. The known and the potential mechanisms used by fungi to solubilize the K comprise the production of organic acids (gluconic, oxalic and citric acid), protons and chelating agents such as siderophores and organic ligands. Lian et al. (2008) have been reported that *Cladosporium, Aspergillus* and *Penicillium* spp. excrete large quantity of citric, gluconic and oxalic acids that solubilize the silicates, mica and feldspar. Lian et al. (2007) also reported that *Aspergillus fumigatus* improved K solubilization when inoculated onto minerals containing K. Besides this, fungi also apply direct biophysical forces that can break the K mineral, thereby reducing the particle sizes (Xiaoxi et al. 2012). Fungi decrease soil pH and enhance the K solubilization in the soil. Lopes-Assad et al. (2006) studied the K solubilizing capacity of two strains of *Aspergillus niger* (CCT4355 and CCT911) and found that the studied fungi significantly decreased the pH of the soil. Similar to this finding, Rosa-Magri et al. (2012) found that the acids released by *Torulaspora globosa* solubilized the alkaline ultramafic rock and solubilized K in the medium within two weeks. Some of the PSF has been listed in Table 9.1.

There are very few reports on the mechanisms of AM fungi for K solubilizing. AM fungi do so by redox redaction, acidification, complexation and metal accumulation (Burgstaller and Schinner 1993; Adeleke et al. 2010). Most of these mechanisms are related to production of various low molecular weight organic acids (oxalate, malate

Table 9.1 Mechanism of potassium solubilizing microorganisms

Microorganisms	Mechanisms	References
Bacteria		
Sphingomonas, Burkholderia	Acidification, complexation	Uroz et al. (2007)
Pseudomonas spp.	Tartaric, citric acids	Krishnamurthy (1989)
Bacillus circulans GY92	Lipo-chitooligosaccharides production	Lian et al. (2001)
Bacillus glathei	Siderophores, organic ligands	Calvaruso et al. (2006)
E. hormaechei	Organic acids	Prajapati et al. (2013)
Pseudomonas spp.	Organic acids	Sheng and Huang (2002)
Pseudomonas aeruginosa	Acetate, citrate, oxalate	Sheng et al. (2003), Badr et al. (2006)
Paenibacillus mucilaginosus	Tartaric, citric, oxalic acids	Liu et al. (2012), Hu et al. (2006)
Bacillus mucilaginosus	Organic acids	Han and Supanjani (2006)
Fungi		
Penicillium frequentans, Cladosporium	Oxalic, citric, gluconic acids	Argelis et al. (1993)
Aspergillus niger, Penicillium sp.	Citric, glycolic, succinic acids	Sperberg (1958)
Aspergillus fumigatus, Aspergillus candidus	Oxalic, tartaric, citric, oxalic acids	Banik and Dey (1982)
Aspergillus fumigatus	Acidification	Lian et al. (2007)
AM fungi		
Arbuscular mycorrhiza	Released protons (H^+) or CO_2 and many different types of organic acids or compounds	Meena et al. (2014b)

and citrate) and ligands (Burgstaller and Schinner 1993; Jain and Sharma 2004). AM fungi can increase the solubility of K from minerals by discharging protons, H^+ or CO_2. Some of the mechanism of AM fungi has been listed in Table 9.1.

9.8 Role of Potassium Solubilizers in Sustainable Agriculture

Fixation of K in soil, its uptake by the plant and leaching reduced the availability of K in the soils (Sheng and Huang 2002). Application of microbial inoculants improved the growth and yield by releasing fix form of K from the soil (Rana et al. 2019a, b). It has been reported that crops inoculated with K solubilizers enhanced the productivity of crops (Yadav et al. 2017c, d; Yadav and Yadav 2019) (Table 9.2)

Table 9.2 Effect of potassium solubilizing microorganisms on the crops

Microbes	Crops	Effect on crops	References
Bacillus sp.	Wheat	Increased yield and disease resistances	Kloepper et al. (1991)
Paenibacillus glucanolyticus	Black pepper	Enhanced potassium uptake and dry weight	Sangeeth et al. (2012)
Bacillus mucilaginosus KCTC 3870	Eggplant	Increased P and K uptake	Han and Lee (2005)
Pseudomonas putida and *P. fluorescens*	Lettuce/tomato	Increased root and shoot growth	Hall et al. (1996), Glick et al. (1997)
Pseudomonas putida	Tea	Theaflavin, thearubigin, highly polymerized substances, total liquor colour, were improved	Bagyalakshmi et al. (2012)
Bacillus circulans	Valencia orange trees	Inoculation significantly improved leaf K content, fruit weight and yield	Shaaban et al. (2012)
Azotobacter and silicate bacteria	Cotton	Yield	Ciobanu (1961)
Bacillus pasteurii	Peanut/sesame	Significant increase in K availability	Youssef et al. (2010)
Aspergillus and *Bacillus*	Sorghum	Increased dry matter yield and uptake	Badr et al. (2006)
Bacillus edaphicus	Cotton rape	Growth, uptake	Sheng (2005)
Azospirillum chroococcum	Wheat	Increased crop productivity and nutrient uptake	Kapulnik et al. (1985, 1987), Kloepper et al. (1989, 1991)
Enterobacter hormaechei, Aspergillus terreus	Okra	Increased root, shoot growth and K uptake in Okra	Prajapati et al. (2013)
AM fungi	Switch grass	Increased plant height, root and shoot weight, root length and P, N contents	Clark et al. (1999)
Bacillus spp.	Chilly	Increased the uptake	Supanjani et al. (2006)
Frateuria aurantia	Brinjal	Improved the growth and yield	Ramarethinam and Chandra (2005)

(continued)

Table 9.2 (continued)

Microbes	Crops	Effect on crops	References
Bacillus spp.	Rice	Improved the yield	Muralikannan (1996)
Bacillus spp.	Rice	Improved the yield	Raj (2004)
Bacillus mucilaginosus, Azotobacter chroococcum	Maize-wheat	Improved growth and yield	Singh et al. (2010)
Bacillus mucilaginosus MCRCp1	Groundnut	Improved the growth and yield	Sugumaran and Janarthanam (2007)
Bacillus mucilaginous	Sorghum	Increased the uptake	Basak and Biswas (2009)
A. brasilense, A. chorococcum, Burkholderia cepacia, Rhizophagus clarus and *R. fasciculatus*	*Lycopersicon esculentum*	Increased the uptake in shoot	Pulido et al. (2003)
Bacillus mucilaginosus, *B. subtilis* and phosphate solubilizer (*Bacillus megaterium*)	Maize (*Zea mays*)	Co-inoculation increased the availability and uptake of P and K in maize. The shoot and root growth enhanced significantly grown on P- and K-limited soils	Abou-el-Seoud and Abdel-Megeed (2012)
Glomus mosseae and *Glomus intraradices*	*Zea mays*	Enhanced K uptake in plant	Wu et al. (2005)
Glomus etunicatum and *Glomus mosseae*	Corn and wheat	Enhanced the uptake of K, Mg and Ca and alleviated the negative effects of soil compaction	Miransari et al. (2009a, b)
Glomus intraradices	*Lycopersicon esculentum*	Enhanced the acquisition of K, Mg and Ca.	Cimen et al. (2010)

Lin et al. (2002) reported considerable increase in the uptake of K and P in *B. mucilaginosus* inoculated. Similar to this, Basak and Biswas (2009) and Meena et al. (2015) reported that the inoculation of bacteria improved the biomass over non-inoculated plants. Ramarethinam and Chandra (2006) reported that *Frateuria aurantia* improved the crop yield. Additionally, these microorganisms also produce vitamins, amino acids, auxins and gibberellic acids that improve the performance of the plant (Ponmurugan and Gopi 2006). Ai-min et al. (2013) reported that the enhancement of K also enhanced the enzymatic activities. In the same year, Prajapati et al. (2013) stated that inoculation of okra with *Enterobacter hormaechei* improved the root and shoot length by K mobilizing.

Pindi and Satyanarayana (2012) concluded from their experiment that these microorganisms could be used with other microorganisms such as *Rhizobium, Azospirillum, Azotobacter,* PSM, etc. The plant growth was also reported to increase by the co-inoculation of beneficial microorganisms. Singh et al. (2010) reported that maize and wheat plants inoculated with *Bacillus mucilaginosus*, *Azotobacter chroococcum* and *Rhizobium* show maximum K mobilization from waste mica and sequentially translocate it to the plant, thereby improving the growth (Singh et al. 2010). A field study was conducted by Han et al. (2006) on cucumber and pepper inoculated with *Bacillus mucilaginosus*, and the authors reported that inoculation of *B. mucilaginosus* mobilized the K from minerals. Thus, application of KSMs as a biofertilizer in agriculture improves the productivity, nutrient availability and reduces the use of agrochemicals in an economic, eco-friendly and sustainable manner (Sheng et al. 2003; Sindhu et al. 2010).

AM fungi play a pivotal role in uptake of mineral nutrient (especially K) and its subsequent translocation to the plants (Perner et al. 2007; Baslam et al. 2013). In the year 1999, Clark et al. reported that, under AM fungi conditions, the acquisition of K^+ was enhanced more in switchgrass grown in acid soil as compared to calcium and magnesium. Similar to this, Kaldorf et al. (1999) reported the acquisition of K^+ in *Zea mays* roots inoculated with the *Glomus* Br1 isolate. Furthermore, *Glomus mosseae* and *Glomus intraradices* enhanced K uptake by *Zea mays* (Wu et al. 2005). Miransari et al. (2009a, b) studied the influence of *Glomus etunicatum* and *Glomus mosseae* on nutrient uptake and concluded that AM fungi enhanced the uptake of K, Mg and Ca and alleviated the negative effects of soil compaction on corn and wheat. Study conducted on tomato (*Lycopersicon esculentum* L.) by Cimen et al. (2010) reported that inoculation of *Glomus intraradices* enhanced the acquisition of K, Mg and Ca. Similar study was conducted and reported that the fungus improved the uptake of K, Ca and Mg in tomato plant (Meena et al. 2015b; Singh et al. 2015). Moreover, Zaefarian et al. (2011) studied the single and combined effects of *Glomus intraradices, Glomus etunicatum, Glomus mosseae, Glomus fasciculatum* and *Gigaspora hartiga* on the uptake of N, K, Fe, Zn, Cu, etc. The role of AM fungi in K nutrition to the plant has been extensively reviewed by Garcia and Zimmermann (2014).

9.9 Conclusion and Future Perspectives

K^+ plays a key role in the metabolism of plant and triggers enzymes, osmotic regulation and charge balance in plants. The deficiency of K results in poor growth and development which intensely related to crop yield. Application of K as a fertilizer and less awareness of the farmers about K aggravates the situation. Therefore, utilization of naturally present K in the soil (fix form or not bioavailable form) is important for sustainable agriculture. Soil microorganisms (bacteria, fungi and AM fungi) are the integral component of soil and play a key role in K solubilization from the minerals. These microorganisms have various mechanism to solubilize the unavailable K and make it available to the plants. Results from various studies specified that soil inoculated with KSMs had positively influence the availability of K to the soil and plants. Additionally, KSMs also increase the availability of other nutrients (Ca, Mg, P) to the plants and also release siderophores, growth hormones and ammonia (NH^{3+}). Application of biological agents such as bacteria, fungi and AM fungi could offer an earlier and never-ending source of K for plant uptake. Therefore, there is a need to design experiments including different types of soil and microbial inoculants to find the best combination. There is also a need to commercialize the KSMs as an inoculum and make them available to the farmers. Future studies should also require focusing on the factors affecting availability of K and isolation of indigenous K solubilizers and inoculation of indigenous K solubilizers to the different environmental conditions such as cold, drought and nutrient-deficient soils.

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Chapter 10

Alleviation of Stress-Induced Ethylene-Mediated Negative Impact on Crop Plants by Bacterial ACC Deaminase: Perspectives and Applications in Stressed Agriculture Management

Hassan Etesami, Fatemeh Noori, Ali Ebadi and Narges Reiahi Samani

Abstract The environmental stresses such as heavy metal toxicity, salinity, water deficit, flooding, extreme temperatures, nutrient deficiency, and pathogenicity, which are considered to be the most important limiting factors for agricultural production, are rising all over the world. The occurrence and magnitude of environmental (abiotic and biotic) stresses might augment in the near future because of global climate change. These stresses lead to a significant reduction in yield and growth of stressed plants. It is well known that a sizable portion of the damage that occurs in stress-sensitive crop varieties as a consequence of abiotic and biotic stresses is due to the deleterious action of "stress ethylene" and not necessarily from the direct effects of the stress. In order to reduce the negative effects of "stress ethylene" on growth and yield of stressed plants, application of ecologically compatible and environmentally friendly methods is needed. An alternative approach to reducing stress-induced ethylene production in growing plants in stress-affected soils involves

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employing 1-aminocyclopropane-1-carboxylate (ACC) deaminase-generating bacterial endophytes. These bacteria may promote stressed plant's growth as a consequence of expressing the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase which cleaves 1-aminocyclopropane-1-carboxylate (ACC) (prerequisite of ethylene production) to α-ketobutyrate and ammonia and thereby diminishes ethylene levels in stressed host plants. In this review, the role of bacterial endophytes equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in mitigating stress-induced ethylene-mediated negative impact on stressed plants under various environmental stresses (heavy metal toxicity, salinity, water deficit (drought), flooding, extreme temperatures, and nutrient deficiency) is described. In addition, some suggestions that are needed for future research in this context are also presented.

Keywords Bacterial endophytes · Bio-fertilizer · Environmental stress · Drought stress · Heavy metal stress · Salinity stress · Stress ethylene

10.1 Introduction

Food security is one of the most important issues in the world that cannot ever be overlooked by any society. The excessive increase in environmental degradation (due to inappropriate agricultural operations) and the pressure of human population are unpleasant consequences that will soon cause global food production to be inadequate for all people in the world. In this context, the global population, which currently has seven billion people, is projected to augment to 10 billion over the next fifty years (Etesami and Maheshwari 2018; Glick 2014), thus necessitating 70% more food production (FAO 2008). To fulfill the food supply requirements for the projected population by the next 50 years, we must culture a significant expansion of the existing land (increased crop yield through intensification) and significantly increase (an estimated fifty percent) grain yield of major crop plants such as *Oryza sativa* L., *Triticum aestivum* L., and *Zea mays* L. (Godfray et al. 2010). But the excessive use of agricultural arable land and marginal areas (areas where stress factors can be more prevalent) is problematic and may be resulted in degradation of the land (Alexandratos and Bruinsma 2012; Glick 2014; Zahir et al. 2008). On the other hand, nonbiotic stresses such as increased carbon dioxide, UV, extreme temperatures, water deficit, flooding, salinity, heavy metals toxicity, nutrient deficiency, severe winds, etc., are the most limiting factors to plant productivity in the world (Etesami 2018; Etesami and Maheshwari 2018) and result in reduced land available for cultivation (Etesami and Maheshwari 2018; Shahbaz and Ashraf 2013). In addition, climate change has affected the frequency and severity of these stresses, mainly drought and high temperatures stresses, and increased the proportion of agricultural land affected from multiple stresses (Ahuja et al. 2010), resulting in a significant decline in yield in main cereals (Carmen and Roberto 2011) and augmenting the productivity and sustainability of the agricultural production systems (Hussain et al. 2015). Across the globe, it is estimated that roughly 70% reduction in crop yields results from direct non-biological stresses (Acquaah 2009). Therefore, due to the urgency of feeding the world's growing human population under different environmental stressful conditions, research on soil and crop productivity (i.e., enhancing tolerance of plants to a wide range of stress factors) to optimize plant growth and secure our future food and feed supply is now in the top priority (Etesami and Maheshwari 2018; Etesami and Beattie 2017).

To attenuate the effects of the biological and non-biological stresses and to augment crop productivity, fitting crop management modifications are necessary. Numerous management system modifications, such as crop rotation, intercropping, row skipping (diminishing planting density by omitting rows), mulching, sheltered cropping (i.e., crops grown under glass, plastic or nets), plant genetic engineering, and bio-fertilization, could be employed to augment crop productivity and decrease the undesirable effects caused by environmental stresses on plant growth (Davies et al. 2011; Wang et al. 2003; Dimkpa et al. 2009). In recent years, sizable attention has been directed toward genetically engineering stress-sensitive crop varieties to be more tolerant to a variety of abiotic stresses and biotic ones (i.e., pathogens including viruses, bacteria, and fungi) (Ahanger et al. 2017). The evolvement of stress-tolerant crop varieties via genetic engineering and plant breeding is absolutely necessary but a long drawn and expensive process. In addition, owing to many hindrances (i.e., proprietary rights and international trade accords on genetically changed crops and restrictions in technology of DNA recombinant in some parts of the world), genetic modification of all plant species is not possible. In addition, it is not sensible to try to engineer crop plants versus all of the biological and non-biological stresses that they might meet within the environment.

There has been a supreme interest in sustainable agriculture with an underscore on the application of useful soil microorganisms. Microbial inoculation to palliate biological and non-biological stresses in plants could be a more economical environmental amiable option which could be attainable in a shorter time frame (Saleem et al. 2007; Etesami and Maheshwari 2018; Etesami and Beattie 2017; Lugtenberg et al. 2002) and helped to achieve sustainable agricultural goals faster (Etesami and Maheshwari 2018). By both extracellular and intracellular microorganisms, plants are colonized in their natural environment (Gray and Smith 2005). Due to the presence of root exudates, a large population of microorganisms is found around plant roots whose populations are more than the population of non-rhizospheric microorganisms. Plant-associated microorganisms can either attach to the outer surface of the plant, such as the roots (rhizosphere microorganisms) or leaves (phyllosphere microorganisms), or they can be located within the plant and form an endophytic relationship (endophytic microorganisms). Among the microorganisms associated with the roots of plants, bacteria have a significant population density. Interactions between plant-associated bacteria and plant roots can be classified as useful, harmful or neutral to the plant (Glick 2014). The bacteria that have mutually beneficial effects with plants can augment plant growth and health either directly through various mechanisms such as N_2 fixation, solubilization of insoluble inorganic phosphates, mineralization of organic phosphates, facilitating the micro- and macronutrient uptake via phytohormone production (e.g., auxin, cytokinin, and gibberellins) or by production of some metabolites (i.e., siderophores, organic acids, etc.), and changing the internal level of plant growth-regulating substances, or indirectly by augmenting the natural resistance of the host against pathogens (Etesami and Maheshwari 2018; Etesami and Beattie 2017; Glick 2012; Hayat et al. 2012; Kloepper et al. 1989; Glick 1995; Patten and Glick 2002; Persello-Cartieaux et al. 2003; Kohler et al. 2006).

The role of these bacteria in plant nutrient management, plant growth promotion, and plant disease control is well known and well established (Etesami and Maheshwari 2018; Compant et al. 2005). In addition to these beneficial effects, the plant growth-promoting bacteria (PGPB) can also impart some degree of tolerance to stress-sensitive crop varieties toward environmental stresses. The term IST (Induced Systemic Tolerance) has been offered for PGPB-induced physical and chemical variations that lead to augmented tolerance to non-biological stress (Yang et al. 2009). In the last ten years, PGPB possessing by distinctive genera including *Methylobacterium*, *Azospirillum*, *Achromobacter*, *Rhizobium*, *Bacillus*, *Variovorax*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Klebsiella* sp., *Kosakonia cowanii*, *Microbacterium*, and *Enterobacter* have been reported to provide tolerance to host plants under distinctive biological and non-biological stress environments (Grover et al. 2011; Etesami and Alikhani 2016, 2018; Etesami and Maheshwari 2018; Noori et al. 2018; Yadav et al. 2015a; Yadav et al. 2016; Yadav et al. 2015b). Preceding studies suggest that application of PGPB has become an encouraging alternative to relieve plant stress and the role of these bacteria in managing biological and non-biological stresses is gaining importance. The subject of PGPB elicited tolerance to biotic and non-biological stresses has been reviewed (Etesami 2018; Etesami and Beattie 2017; Etesami and Maheshwari 2018; Glick 2014; Sharma et al. 2013; Kaushal and Wani 2016; Yang et al. 2009; Etesami and Alikhani 2016; Compant et al. 2005; Glick 2012; Vurukonda et al. 2016; Dodd and Pérez-Alfocea 2012; Yao et al. 2010).

To barricade the trauma and ensure survival, crop plants bring out a convoluted and unanimous molecular and cellular responses in response to various biological and non-biological stresses (Fahad et al. 2015). Phytohormones have a vital function in mediating plant's responses to these stresses, by which the plant may try to outlive the stressed conditions (Skirycz and Inzé 2010). One of the phytohormones entangled in stress response is ethylene, which is also considered as a stress hormone in addition to its roles in regulating plant growth and development and in bringing about multifarious physiological alterations in plants at molecular level (Abeles et al. 2012). Under abiotic and biological stress conditions (i.e., nutrient deficiency, salinity, water deficit, waterlogging/flooding, heavy metal toxicity, and pathogenicity), the internal production of ethylene and its direct precursor ACC are quickened considerably which unfavorably affects the root growth, and they finally result in decreasing the growth of the stress-sensitive crop varieties in a general sense (i.e., suppression of root elongation, nodulation and auxin transport, induction of hypertrophies, increase in speed of aging, and promotion of senescence and abscission) (Sun et al. 2006; Abeles 1992; Morgan and Drew 1997).

A number of PGPB are equipped with a pivotal enzyme, ACC (1-Aminocyclopropane-1-Carboxylic Acid) deaminase, which regulates ethylene generation via metabolizing ACC (an instantaneous precursor of ethylene production in higher plants) into alpha-ketobutyrate ($C_4H_6O_3$) and ammonia (NH_3) (Yadav 2017a; Yadav et al. 2017a, b). Inoculation of crop plants with the ACC deaminase-generating PGPB could be beneficial in supporting growth and enlargement of stress-sensitive crop varieties under stressful conditions by diminishing stress-mediated ethylene generation (Glick 2014; Etesami and Maheshwari 2018; Etesami 2018; Etesami and Beattie 2018). The ability to produce this enzyme has been reported in a variety of rhizosphere and endophytic bacterial genera (Glick 2014). One of the leading drawbacks in the large-scale employment of PGPB including ACC deaminase-producing microorganisms is that these bacteria may not always outlive rough environmental conditions such as extremes of pH and temperature, high concentrations of environmental contaminants, salinity, drought, and the presence of other microorganisms that either consume or outcompete these bacteria. A feasible solution to this problem may lie in the application of EPGPB (endophytic plant growth-promoting bacteria) (Sturz and Nowak 2000). Bacteria that are isolated from plant tissues after their surface disinfection and show no symptoms of disease on the plant are known as endophytic bacteria. It seems that the contribution of endophytic bacteria to the production of 1-aminocyclopropane-1-carboxylate deaminase and the abatement of stress ethylene production relative to the contribution of rhizosphere bacteria is much wider (Etesami and Maheshwari 2018). The internal tissues of plants provide a more uniform and safer environment for bacteria than plant surfaces. Considering the important role of 1-aminocyclopropane-1-carboxylate deaminase-producing bacteria in reducing stresses caused by ethylene, aim of this review is to describe the role of bacterial endophytes equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in lessening of impact of biological and abiotic stresses onto plants. In addition, some suggestions needed for future research in this field are also presented.

10.2 Abiotic and Biotic Stresses

Apart from physiological and environmental factors such as availability of macro- and micronutrients (i.e., N, P, K, S, Mg, Ca, Fe, Mn, Cu, Zn, etc.), physical and chemical characteristics of soil (EC, soil texture, organic matter, pH, etc.), plant genotype and growth conditions, the growth of stress-sensitive crop varieties in the field may be repressed via a large number of both biological and non-biological stresses. These stresses include temperature extremes (high and low temperatures), high light, waterlogging, global scarcity of water resources (water deficit), the presence of toxic metals (i.e., Cd, Ni, Co, As, etc.), and environmental organic contaminants (i.e., phenols, colorants, alcohols, aldehydes, DDT and metabolites, Dieldrin, PCP, PAHs, RDX, TNT, etc.), radiation, wounding, insect predation, increased salinization of soil and water, mechanical stress, nutritional stress, and damage done to stress-sensitive crop varieties by living organisms, such as bacteria, viruses, fungi, parasites, harmful insects, weeds, and cultivated or native plants (Abeles et al. 2012; Stearns and Glick 2003; Morgan and Drew 1997). These stress factors cause widespread crop losses throughout the world. In the plant grown under the stressed conditions, immense amounts of ROS (reactive oxygen species) are generated that can bring about peroxidation, leading to detriment to cell membranes, protein oxidation, enzyme deterrence, and strand fracture in nucleic acids (Allen 1995).

One of the principal concerns bringing about some of the distinctive ecological and environmental problems is heavy metal pollution of agricultural soils. Due to industrial applications, use of metal-contaminated fertilizers, types of pesticides (i.e., insecticides, herbicides, rodenticides, bactericides, fungicides, and larvicides), and sewage sludge in agricultural land, toxic metals and metalloids accumulate in the environment (Etesami 2018). Some heavy metals such as Fe, Mn, Zn, Cu, etc., are essential or beneficial micronutrients needed by plants for growth and development. But, when present in superfluous, they may act as toxicants and repress the plants growth (Etesami 2018). In addition, high metal amounts in the soil have also been indicated to bring about augmented ethylene synthesis (Rodecap et al. 1981; Safronova et al. 2006) and inhibition of root and shoot development and interfere with numerous biochemical and physiological processes such as CO_2 fixation, respiration, photosynthesis, sugar translocation, N and protein metabolism, and micro- and macronutrients absorption (Zhang et al. 2009; Prasad and Strzalka 2013).

Organic pollutants (i.e., DDT, lindane, polychlorinated biphenyls, dioxins, etc.) in the soil environment, if present above permissible limits, hinder plant growth via many mechanisms such as unusual growth of stress-sensitive crop varieties (Adam and Duncan 1999). This irregular growth of the plant root system might be partly owing to hastened ethylene generation (stress ethylene) in plants grown in soil environment treated with organic contaminants (Coupland and Jackson 1991; De Prado et al. 1999; Jackson 1997).

During periods of flooding/waterlogging, which occur several times in a growing season and may last for periods of from one or two days to several weeks, the root environment (rhizosphere) speedily becomes anaerobic bringing about an inauguration in the expression of 1-aminocyclopropane-1-carboxylate (ACC) synthase, leading to the cumulation of 1-aminocyclopropane-1-carboxylate (ACC) in tissues of root (Cattelan et al. 1999; Olson et al. 1995; Jackson 1997; Else and Jackson 1998; Bradford and Yang 1980; Else et al. 1995). The amassed 1-aminocyclopropane-1-carboxylate (ACC) is transported to the shoots (stem + leaf) where there is an aerobic environment and the ACC may be converted to ethylene via the enzyme 1-aminocyclopropane-1-carboxylate (ACC) oxidase, which has need for oxygen for catalyzing this reaction. Lower diffusion of ethylene in water leads to cumulation of ethylene in waterlogged and/or flooded plants and soil (Steffens et al. 2012). Cumulation of stress ethylene can also bring about epinasty, leaf chlorosis, necrosis, and diminished fruit yield (Grichko and Glick 2001a, b).

Drought affects, in essence, all climatic regions of the world, particularly in arid and semi-arid areas, and more than one-half of the earth is vulnerable to drought every year (Wilhite 2000; Kogan 1997; Grichko et al. 2000; Kour et al. 2019a; Verma et al. 2017b). Drought stress (water deficit), as one of the major non-biological stresses, restricts the growth and productivity of crops (i.e., diminution in germination rates, inhibition of photosynthesis, loss of membrane integrity, decline in leaf water potential and stomatal opening, decrease in leaf size, decrease in water uptake (osmotic stress), suppressed root growth, diminished seed number, size and viability, delayed flowering and fruiting, and increased generation of ROS) (Xu et al. 2016; Bray 1997; Ingram and Bartels 1996; Shinozaki and Yamaguchi-Shinozaki 1998; Kramer and Boyer 1995; Greenberg et al. 2008). Like many other environmental factors, water deficit stress also induces augmented ethylene production in tissues of stress-sensitive crop varieties which inhibiting root growth and development, shoot/leaf expansion, and photosynthesis (Mattoo 2017; Sharp 2002) and causes membrane leakage, eventually brings about senescence in stress-sensitive crop varieties (Hipkins and Hillman 1986).

In fact, plants are sensitive to variations in temperature, and react both to seasonal variations and more so to quotidian alterations in the season. The heat stress with regard to the aspect known as global warming is a critical intimidation to world agriculture (Moeder et al. 2002; Robertson et al. 2000). A vacillation in temperature results in hormonal unbalances in stress-sensitive crop varieties and thus their growth is considerably affected (Cheikh and Jones 1994). Following temperature stress (high and chilling temperatures), the ethylene level is swiftly augmented both in tissues of stress-sensitive crop varieties and microbial species in the rhizosphere of stressed plant (Strzelczyk et al. 1994; Arshad and Frankenberger Jr 2012; Shi et al. 2012).

Microbial pathogens are a leading and serious intimidation to food production and ecosystem stability throughout the world (Etesami and Alikhani 2018). Mostly, like abiotic stresses, plant ethylene production is augmented with severity of pathogenic infection (Bashan 1994; Elad 1988). Among abiotic and biotic stresses, salinity stress is one of the most damaging abiotic stresses (Etesami and Beattie 2017), barricading the attainment of sustainable agriculture (Paul 2013; Greenway and Munns 1980; Zhu 2002; Roy et al. 2014). Soil salinity in arid regions is frequently an important delimiting factor for cultivating agricultural crops because salinity converts arable land into non-arable land and diminishes crop productivity and quality (Shahbaz and Ashraf 2013; Yamaguchi and Blumwald 2005). Soil salinization reduces 1–2% of the area that could be used for agriculture every year. Approximately seven percent of the world's land and 20% of the total arable land throughout the world are negatively influenced by salinity (Munns 2005) with a resultant monetary loss of twelve billion US$ in agricultural production (Shabala 2013). Additionally, the salinized areas are augmenting at a rate of ten percent annually, specifically on agricultural land where growth of stress-sensitive crop varieties is contingent upon irrigation, for various reasons, such as weathering of native rocks, low precipitation, high surface evaporation, irrigation with saline water, and poor cultural practices. It has been calculated approximately that more than fifty percent of the arable land would be salinized by the year 2050 (Jamil et al. 2011).

Salinity stress has been reported to limit growth and development of stress-sensitive crop varieties (i.e., by ion toxicity stress, osmotic stress, oxidative stress, and nutrient deficiency), which brings about variations in physiology, morphology, and biochemical characteristics of stressed plants, probably all occurring simultaneously

(Tao et al. 2015; Chinnusamy et al. 2006; Munns 2002, 2005; Gorham et al. 1985; Ruiz et al. 1997; Arbona et al. 2005; Zhu 2001). Almost all of the most consequential crop plants are salinity-sensitive plants (glycophytes) and are and so susceptible to salt stress (Munns and Tester 2008; Cheeseman 2015). Intermediate levels of environmental salinity (e.g., 100 mM NaCl) are adequate to bring about dramatic decrements in the yield of most crop plants (Frommer et al. 1999; Munns and Tester 2008). It is well known that shortage of nutrients such as N, P, K, Ca, and Fe, which occurs in salt-affected soil, promotes the expressions of many genes connected to ethylene biosynthesis and signaling in the roots and enhances plant sensitivity to ethylene (Blumwald 2000; Cuartero and Fernández-Muñoz 1998; Feng and Barker 1992; O'Donnell et al. 1996; Zheng et al. 2013; Rai and Sharma 2006; He et al. 1992; Borch et al. 1999; Rabhi et al. 2007; Yousfi et al. 2007; García et al. 2015; García et al. 2010; Achard et al. 2006; Dong et al. 2011; Xu et al. 2008). According to the studies mentioned above, during periods of all environmental stresses, stressed plants in response to these stresses produce high levels of endogenous ethylene, called "**stress ethylene**", which increases sensitivity of the plants to various environmental stresses and finally leads to abnormal growth of the plants (inhibitory effect on root growth).

10.3 Ethylene as a Stress Hormone

Stress-sensitive crop varieties employ many strategies in answer to environmental stresses (i.e., variation in developmental and morphological motif and in physiological and biochemical processes) that eventually augment the stressed plant's growth and productivity in stressful agricultural lands (Tuteja 2007; Saud et al. 2014). By accumulating organic solutes such as sugars, polyols (sugar alcohols), betaines and proteinogenic amino (i.e., proline, $C_5H_9NO_2$), protecting cellular machinery, maintaining ionic homeostasis, cleansing free radicals or reactive oxygen species (ROS), expressing certain proteins and upregulating their genes and inducing phytohormones, plant increase your tolerance to the environmental stresses (Parida and Das 2005; Tuteja 2007; Munns and Tester 2008).

It is known that phytohormones are involved in regulating the interaction between stress-sensitive crop varieties and environments (i.e., plant responses to environmental stresses) throughout the life cycles of plants (Bartoli et al. 2013; Baxter et al. 2013; Skirycz and Inzé 2010). Phytohormones are thought to be the most influential internal substances that are crucial in adjusting physiological responses that ultimately result in adjustment to an undesirable environment (Khan and Khan 2013). Ethylene, known as a stress hormone, is an important growth phytohormone synthesized by almost all plants and serves as a key modulator between a wide range of plant responses to environmental stresses and normal growth (Abeles 1992). This phytohormone plays multifarious roles in regulating growth and development of stress-sensitive crop varieties (Abeles 1992). Production of ethylene occurs in all higher plants via a methionine ($C_5H_{11}NO_2S$) relying on pathway. Ethylene in plant is synthesized via 3 enzymatic reaction steps: methionine ($C_5H_{11}NO_2S$) is converted to S-adenosyl-methionine (S-AdoMet) by S-AdoMet synthetase; then the direct substrate of ethylene 1-aminocyclopropane-1-carboxylate (ACC) is generated from S-AdoMet by ACC synthase; and ultimately ethylene (carbon dioxide and hydrogen cyanide) is produced via the oxidation of 1-aminocyclopropane-1-carboxylate (ACC) by 1-aminocyclopropane-1-carboxylate (ACC) oxidase (Lin et al. 2009). Concentrations of ethylene and its direct precursor 1-aminocyclopropane-1-carboxylate (ACC) could be plainly mediated by stresses in numerous stress-sensitive crop varieties (Morgan and Drew 1997; Ellouzi et al. 2014; Ma et al. 2012). Apart from its positive effects (at levels of as low as 10 $\mu g\ L^{-1}$) on plant growth (i.e., role in root initiation, nodule formation, root extension, seed germination, xylem formation, biosynthesis of other phytohormones, and ripening as well as in stress signaling) (Mattoo 2017; Abeles 1992; Arshad and Frankenberger 1990), overproduction of ethylene (at levels of as high as 25 $\mu g\ L^{-1}$) in plant roots in answer to both biological and non-biological processes represses root elongation, nodulation and auxin transport, brings about hypertrophies, speeds aging, advances senescence and abscission, and leads to untypical root growth, which imparts an ostensible dent on plant growth and outreach (Abeles 1992; Pech 2002; Arshad and Frankenberger 1990; Frankenberger Jr and Muhammad 1995; Prayitno et al. 2006; Sun et al. 2006). This implies that no extra ethylene is mandatory for the process of stress adjustment in the early stage of plant self-adjustment (Tao et al. 2015; Peng et al. 2014), and if the ethylene concentration (increase in 1-aminocyclopropane-1-carboxylate content and 1-aminocyclopropane-1-carboxylate oxidase activity) augments above a threshold level, it becomes deleterious for plant growth and hinders growth and development of stress-sensitive crop varieties, which is disadvantageous for plants to outlive under sever stressful conditions (Kukreja et al. 2005; Glick 2014; Tittabutr et al. 2013; Albacete et al. 2009; Ghanem et al. 2008; Tao et al. 2015). Since higher amounts of ethylene ("stress ethylene") have prohibitive impacts on root growth and may lead to abnormal growth of the plants, it is crucial to govern the generation of ethylene in the close environs of stressed plant's roots (rhizosphere) for regular growth and development of stress-sensitive crop varieties (Saleem et al. 2007).

Stress tolerance in plants depends mainly on the capability of root to diminish the endogenous ethylene level. It is well known that bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase can diminish the negative effects of this hormone (stress ethylene) via diminishing the level of ACC (precursor of ethylene production). Undoubtedly, the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase by the bacteria is a major mechanism in promoting plant growth under environmental stresses. In addition to reducing "stress ethylene" level in plants, it is well known that the bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase may also provide other many benefits to stress-sensitive crop varieties (Glick 1995; Holguin and Patten 1999; Etesami and Maheshwari 2018). These characteristics make the choice of 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing PGPB more trustworthy than any other alternative.

10.4 Amelioration of "Stress Ethylene" Using Bacterial ACC Deaminase

As described previously, the surplus production of ethylene in answer to biological and non-biological stresses brings about holding back root growth and accordingly growth of the stress-sensitive crop varieties as a whole. Through certain specific enzymes, the bacteria stimulate some physiological changes in stress-sensitive crop varieties at molecular level. Amid these enzymes, bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase plays a well-understood role in regulating the plant hormone ethylene and thus, growth and evolvement of stress-sensitive crop varieties are modulated (Glick 2014). It has been well known that ACC deaminase-generating PGPB can regulate and palliate the stress-induced ethylene-mediated negative effect on plants by metabolizing 1-aminocyclopropane-1-carboxylate (ACC); a precursor of plant produced ethylene. Compared to ethylene synthesis inhibitors such as AVG (aminoethoxyvinylglycine), AOA (aminooxyacetic acid), and 1-MCP (1-methylcyclopropene), which are costly, less workable, or potentially causing damage to the environment, the use of bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase is more economical, environmental amicable, and workable in a stressed natural soil and plant system.

The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Enzyme Commission number: 4.1.99.4), which catalyzes the breaking of 1-aminocyclopropane-1-carboxylate to NH_3 and alpha-ketobutyrate ($CH_3CH_2CCO_2H$), was first found in forty years ago (in 1978) (Honma and Shimomura 1978). The 1-aminocyclopropane-1-carboxylate (ACC) activity has been known to be associated with a large number of assorted soil microbial community (free-living soil microorganisms), plant-associated bacteria (both Gram-negative bacteria and Gram-positive bacteria), including symbionts like rhizobia (diazotrophic bacteria fixing molecular nitrogen inside the root nodules of legumes), general rhizospheric and endophytic PGPB (*Agrobacterium*, *Burkholderia*, *Enterobacter*, *Methylobacterium*, *Azospirillum*, *Alcaligenes*, *Ralstonia*, *Rhodococcus*, *Rhizobium*, *Pseudomonas*, *Sinorhizobium*, *Variovorax*, and *Bacillus*), some plant pathogens, Eukarya, and fungi (Arshad et al. 2007; Etesami and Maheshwari 2018; Etesami and Beattie 2018; Glick 2014; Nascimento et al. 2014; Babalola et al. 2003; Wang et al. 2000; Belimov et al. 2001; Ghosh et al. 2003; Honma and Shimomura 1978; El-Tarabily 2008; Minami et al. 1998; Viterbo et al. 2010; Singh and Kashyap 2012; Verma et al. 2016a, b; Verma et al. 2015; Yadav et al. 2016).

The 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme is encoded by a single gene, denominated *acdS*. It was found that the genes might be come into horizontally (laterally) instead of vertically (Hontzeas et al. 2005). As a matter of fact, there are some proofs that 1-aminocyclopropane-1-carboxylate (ACC) deaminase genes may not constantly be an integral part of the chromosomal DNA of a microorganism, but rather exist on large comparatively steady plasmids (Glick et al.

2007b). On top of that, on the foundation of sequence similarity, the presence of putative 1-aminocyclopropane-1-carboxylate (ACC) deaminase genes in the genomes of several plants (*Arabidopsis*, *Populus*, and *Lycopersicon esculentum* Mill.) was exhibited (McDonnell et al. 2009; Plett et al. 2009; Singh et al. 2015).

The action mechanism of 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing bacteria to reduce "stress ethylene" level is based on a model previously tendered by Glick et al. (1998). A diagrammatic delineation of this model is shown in Fig. 10.1. It is well known that the population of microorganisms is high in the rhizosphere region due to specific conditions different from the non-rhizosphere region. In this area, because of root exudates, the bacteria including the ACC deaminase-generating bacteria attach to the surface of the seed (spermosphere) or root (rhizoplane bacteria) of the plant and some of these bacteria enter the root (bacterial endophytes). Plant growth-promoting bacteria attached to the root of the plant by various mechanisms lead to increased plant root growth. As the root of plant increases, the amount of root exudates also augments. Root exudates contain easily degradable compounds, including organic acids, amino acids, and other small molecules. L-tryptophan (L-Trp) is one of the amino acids found in root secretions. This amino acid is a precursor to the production of auxin. Some bacteria having auxin-producing genes (i.e., *ipdC* and *iaaM* gene*)* can convert this amino acid to indole-3-acetic acid (IAA). Part of this bacterial IAA is absorbed by the plant. This bacterial IAA together with the plant IAA (IAA produced inside the plant by the plant itself) can lead to the proliferation and elongation of plant cells. These IAAs can also promote the synthesis of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) synthase. The enzyme 1-aminocyclopropane-1-carboxylate (ACC) synthase catalyzes the formation of ACC.

The synthesized 1-aminocyclopropane-1-carboxylate (ACC) exits the plant along with root exudates, and the bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in the rhizosphere/rhizoplane can use some of the ACC as a nitrogen source by breaking it down into NH_3 and $C_4H_6O_3$ (α-ketobutyrate). As a result of the uptake and consumption of 1-aminocyclopropane-1-carboxylate (ACC) by bacteria equipped with the enzyme ACC deaminase, its content is reduced outside the stress-affected plant. Additionally, in order to establish a balance between the amount of ACC produced inside the plant and the ACC removed from the plant, the plant discharges a greater amount of the stress-induced ACC produced inside the plant into the rhizosphere of host plant. On the other hand, more ACC excretion from the plant provides the carbon and nitrogen requirement of the 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing microorganisms, which results in a greater activity and population of these microorganisms around the plant root. The end result is ACC depletion inside the plant and consequently ethylene depletion within the plant. Decreased ethylene levels, in turn, leads to increased plant root system and consequently plant growth (Glick et al. 1998). Thus, the net outcome of the interaction of ACC deaminase-generating microorganisms with plant cells is

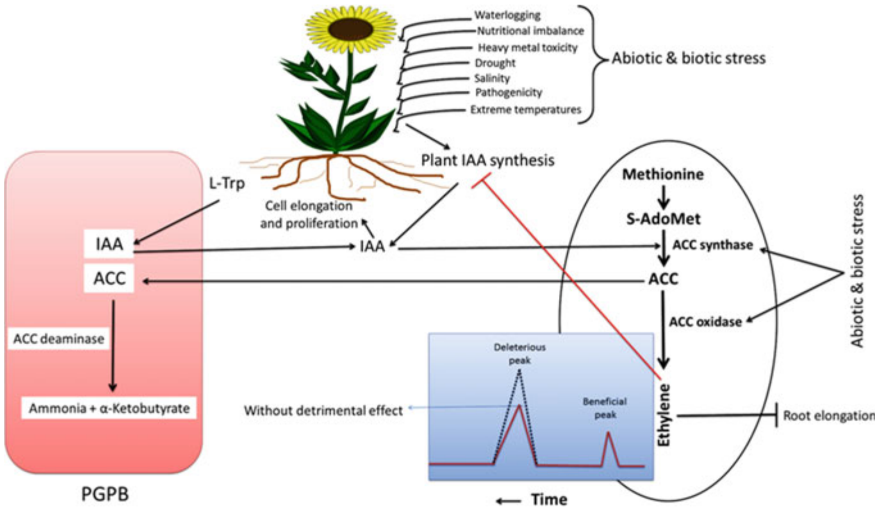

Fig. 10.1 A diagrammatic representation of how plant growth-promoting bacteria (PGPB) having 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity can alleviate the stress-induced ethylene-mediated negative impact on stressed plants. Stressed plants often respond to stressful conditions by producing what is known as "stress ethylene". In the pathway of ethylene biosynthesis, S-AdoMet (S-adenosylmethionine) is converted by ACC synthase to ACC, the immediate precursor of ethylene, and ACC is also converted to ethylene by ACC oxidase. Following the beginning of the stress, a small peak of ethylene is produced after a short time. This small peak of ethylene uses up the existent pool of ACC within plant tissues and likely activates the synthesis of defensive genes within the plant. Afterward, a second much larger peak of ethylene, which is generally detrimental to plant growth, is typically observed following the synthesis of additional ACC within the plant. Due to enhancing transcription of ACC synthase genes, the second peak of ethylene, which mostly is triggered by environmental cues, occurs and acts as a signal to initiate the inhibitory processes to plant growth and survival. The ACC deaminase-producing bacteria can sequester and degrade the stressed plant's ACC (to ammonia and α-ketobutyrate) to supply nitrogen and energy, which reduce the deleterious effect of ethylene and subsequently ameliorate plant stress and promote plant growth. It is expected that ACC deaminase-producing bacteria decrease the magnitude of the second ethylene peak. It has been reported that IAA can also activate the transcription of ACC synthase and ultimately result in the production of relatively high concentrations of ACC and subsequently inhibitory levels of ethylene. However, it was found that with PGPB that both secrete IAA and synthesize ACC deaminase, plant ethylene levels do not become elevated to the same extent as when plants interact with bacteria that secrete IAA but do not synthesize ACC deaminase. In general, when plant ethylene levels increase, the ethylene that is produced feedback inhibits IAA signal transduction thereby limiting the extent that IAA can activate ACC synthase transcription. For more details, see Glick (2014). Abbreviations: L-Trp, Tryptophan; IAA, Indole-3-acetic acid

that the bacteria act as a sink for 1-aminocyclopropane-1-carboxylic acid (Glick et al. 2007a; Glick 2014).

Since the hormone ethylene has been known to be needed for the inspiration in plants of systemic resistance triggered by PGPB (Van Loon et al. 1997), the query arises whether inoculating stress-sensitive crop varieties with ethylene-diminishing bacteria (bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate deaminase) might barricade this induction. But, practically, “diminishing ethylene levels by bacterial ACC deaminase does not seem to be irreconcilable with the instigation of systemic resistance. Indeed, some bacterial strains possessing ACC deaminase also incite systemic resistance” (van Loon and Glick 2004). In a general manner, the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase exists in bacteria at a low level until it is incited, and the inspiration of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity is a comparatively slow and intricate process. Shortly following an abiotic or biotic stress, the pool of 1-aminocyclopropane-1-carboxylate (ACC) in the plant is low as is the level of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in the collaborated bacterium. Following the proportionately rapid inspiration of a low level of 1-aminocyclopropane-1-carboxylate (ACC) oxidase in the plant, it is likely that there is augmented flux via this enzyme causing the first small peak of ethylene which is of adequate magnitude to trigger a protective/defensive reaction in the plant (Fig. 10.1). With time, bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase is motivated (by the augmenting amounts of 1-aminocyclopropane-1-carboxylate (ACC) that ensue from the inspiration of 1-aminocyclopropane-1-carboxylate (ACC) synthase in the plant) so that the dimensions of the second, detrimental, ethylene peak is diminished expressively (Fig. 10.1). The second ethylene peak may be diminished dramatically, but it is not ever entirely abrogated since 1-aminocyclopropane-1-carboxylate (ACC) oxidase has a much higher affinity for 1-aminocyclopropane-1-carboxylate (ACC) than does 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Therefore, when bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase are present, ethylene levels are eventually contingent upon the ratio of 1-aminocyclopropane-1-carboxylate (ACC) oxidase to 1-aminocyclopropane-1-carboxylate (ACC) deaminase. For PGPB to be able to diminish plant ethylene levels, level of the 1-aminocyclopropane-1-carboxylate (ACC) deaminase should be at least one hundred- to one thousand-fold greater than level of the 1-aminocyclopropane-1-carboxylate (ACC) oxidase (Glick et al. 1998).

In previous studies (Prayitno et al. 2006; Morgan and Gausman 1966), ethylene stress-induced inhibition of IAA transport and signal transduction has been reported. Whereas bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) diminish the ethylene amount in roots of stress-sensitive crop varieties, this assuages the ethylene repression of auxin (i.e., indole-3-acetic acid) response factor generation, and indirectly augments growth of development of stress-sensitive crop varieties (Fig. 10.1) (Dharmasiri and Estelle 2004). Therefore, IAA-producing bacteria, despite activating of the transcription of ACC synthase, cannot ultimately bring about the generation of comparatively high concentrations of ACC and afterward repressive levels of ethylene. In general, by diminishing ethylene deterrence of assorted plant processes, and permitting IAA motivation of cell rapid multiplication and extension without the damaging impacts of augmenting 1-aminocyclopropane-1-carboxylate (ACC) synthase and plant ethylene levels, plant growth-promoting bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase assist forward the growth and development of stress-sensitive crop varieties (Glick 2014).

The role of bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in diminishing stress-induced ethylene-mediated negative impact on plants is well known and well established (Glick et al. 2007b; Glick 2014). According to antecedent studies (Noori et al. 2018; Ali et al. 2014; Zhao et al. 2015; Zhang et al. 2011; Qin et al. 2014; Nascimento et al. 2012; Palaniyandi et al. 2014; Karthikeyan et al. 2012; Sgroy et al. 2009; Sziderics et al. 2007; Saravanakumar and Samiyappan 2007; Win et al. 2018; Afridi et al. 2019; Yoolong et al. 2019; Barnawal et al. 2016; Gamalero et al. 2017), stress-sensitive crop varieties inoculated with various bacterial strains equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase could cope with the stressful conditions by lowering ethylene level (Table 10.1). There are some reports that endophytic and rhizosphere ACC deaminase-producing bacteria (i.e., *Burkholderia* sp., and *Pseudomonas fluorescens*) have antagonistic impacts toward pathogenic microorganisms such as *Fusarium oxysporum* (Yuquan et al. 1999; Donate-Correa et al. 2005), *Pythium ultimum* (Wang et al. 2000), *Fusarium proliferatum* (Donate-Correa et al. 2005), *Rhizoctonia solani* (Pandey et al. 2005; Rasche et al. 2006b), *Sclerotinia sclerotiorum* (Pandey et al. 2005), *Erwinia carotovora* sp. *atrospetica* (Eca) (Rasche et al. 2006a), and *Ralstonia solanacearum* (Rasche et al. 2006b). The results of the research revealed that bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase were more effective in biocontrol of these pathogens than those without this enzyme. It is also very likely that bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, besides straightly antagonizing pathogenic microorganisms, play a potential role in motivating disease tolerance in stress-sensitive crop varieties (augmented the plant's resistance against pathogen attack) (Saleem et al. 2007; Belimov et al. 2007). But, doing more research in this area is needed for further understanding of this mechanism in the future (Saleem et al. 2007).

It was found that diminished salinity-induced ethylene by bacteria could diminish the detrimental impact of salinity onto growth of stress-sensitive crop varieties (Glick 2014). Previous researches have revealed that plants treated with PGPB equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (i.e., *Achromobacter piechaudii*, *Enterobacter* sp., *Pseudomonas* spp., *Mesorhizobium*, *Kocuria rhizophila*, *Cronobacter sakazakii*, *Leclercia adecarboxylata*, *Streptomyces venezuelae*, *Brachybacterium paraconglomeratum*, *Brevibacterium epidermidis*, *Variovorax paradoxus*, *Bacillus mojavensis*, *Serratia* sp., *Klebsiella* sp., *Kosakonia cowanii*, and *P. fluorescens*) were better able to thrive through the salt stress while manifesting a normal pattern of growth (Mayak et al. 2004a, b; Saravanakumar and Samiyappan 2007; Cheng et al. 2007; Nadeem et al. 2006; Noori et al. 2018; Sarkar et al. 2018; Win et al. 2018; Chaudhary and Sindhu 2017; Afridi et al. 2019; Orozco-Mosqueda et al. 2019; Kang et al. 2019; Yoolong et al.

Table 10.1 Alleviation of the stress-induced ethylene-mediated negative impact on plants by 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing endophytic bacteria

Bacterial strains	Experimental plant	Type of stress	Reference
Pseudomonas fluorescens YsS6 and *P. migulae* 8R6	Tomato	Salinity	Ali et al. (2014)
Bacillus endophyticus	*Salicornia europaea*	Salinity	Zhao et al. (2015)
Bacillus sp. and *Acinetobacter* sp.	*Commelina communis*	Heavy metal	Zhang et al. (2011)
Bacillus flexus and *Streptomyces pactum*	*Limonium sinense*	Salinity	Qin et al. (2014)
Streptomyces sp. PGPA39	Tomato	Salinity	Palaniyandi et al. (2014)
Achromobacter xylosoxidans AUM54	*Catharanthus roseus*	Salinity	Karthikeyan et al. (2012)
Bacillus licheniformis Ps14	*Prosopis strombulifera*	Salinity	Sgroy et al. (2009)
Bacillus sp. TW4	Sweet pepper	Osmotic stress	Sziderics et al. (2007)
P. fluorescens	*Arachis hypogea*	Salinity	Saravanakumar and Samiyappan (2007)
Pseudomonas spp. OFT2	Tomato	Salinity	Win et al. (2018)
Kocuria rhizophila and *Cronobacter sakazakii*	Wheat	Salinity	Afridi et al. (2019)
Streptomyces venezuelae ATCC 10712	Rice	Salinity	Yoolon et al. (2019)
Brachybacterium paraconglomeratum	*Chlorophytum borivilianum*	Salinity	Barnawal et al. (2016)
Pseudomonas migulae 8R6	*Catharanthus roseus*	*Flavescence dorée* Yellows disease	Gamalero et al. (2017)
Paenibacillus and *Bacillus*	Wheat	Pathogenic fungi	Zhao et al. (2015)

2019; Barnawal et al. 2016; Siddikee et al. 2015; Habib et al. 2016; Singh and Jha 2016). These bacteria reduced the production of ethylene by stressed plants.

Under drought stress, PGPB equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (i.e., *Variovorax paradoxus* 5C-2, *Achromobacter piechaudii* ARV8, and *Paenibacillus polymyxa*) also diminished the production of ethylene by stressed plant (Mayak et al. 2004c; Dodd et al. 2004; Arshad et al. 2008; Timmusk and Wagner 1999; Glick et al. 2007a; Kumar et al. 2019; Yadav 2017a, b;

Yadav et al. 2019b). According to previous studies, lower 1-aminocyclopropane-1-carboxylate (ACC) content was observed in plants inoculated with ACC deaminase-producing PGPB and in plants genetically engineered to express ACC deaminase than in non-inoculated plants and non-engineered plants under flooded conditions, indicating that the enzyme had a significant role in ACC depletion (Grichko and Glick 2001a, b). Plants inoculated with bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (i.e., *Pseudomonas putida*, *Enterobacter cloacae*, and *P. putida*) showed remarkable tolerance to flooding stress implying that bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase diminished the negative impacts of stress-mediated ethylene (Saleem et al. 2007; Grichko and Glick 2001a; Farwell et al. 2006; Rana et al. 2019; Verma et al. 2017a, b).

ACC deaminase-producing bacteria could also mediate heavy metal (i.e., nickel, Ni; lead, Pb; zinc, Zn; copper, Cu; cadmium, Cd; cobalt, Co; and arsenic, As) stress-induced ethylene negative effect in various plants (Arshad et al. 2007; Etesami 2018; Farwell et al. 2006; Safronova et al. 2006; Dell'Amico et al. 2005; Reed and Glick 2005; Belimov et al. 2001). It has studied the significance of PGPB equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase in augmenting the growth of stress-sensitive crop varieties in the presence of organic contaminants (Saleem et al. 2007; Arshad et al. 2007; Greenberg et al. 2006; Saleh et al. 2004; Huang et al. 2004; Reed and Glick 2005; Yadav et al. 2018a, b, c). The ACC deaminase-producing bacteria (i.e., *Burkholderia phytofirmans* and *P. putida*) helped stressed plants in maintaining normal growth under low and high temperature stress by diminishing "stress ethylene" concentration similar to that under other abiotic and biotic stresses (Bensalim et al. 1998; Barka et al. 2006; Cheng et al. 2007; Kour et al. 2019a, b, c; Yadav et al. 2019a). The results obtained from these few studies indicate that the bacteria equipped with the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase were able to diminish the stress induced in temperature extremes-affected plants. According to studies mentioned above, it can be concluded that use of the bacterial endophytes with 1-aminocyclopropane-1-carboxylate (ACC) deaminase trait can be a useful strategy to recuperate growth and yield of the stressed plant. It seems that these bacteria may be good candidates for bio-fertilizer formulation in stress-based agriculture.

10.5 Conclusions and Future Perspectives

One of the most prominent restrictions to crop production in the world is both biological and non-biological stress conditions dominating in the agricultural land, which are also intensifying with climate change. Under normal conditions, when the plant is not exposed to any stress, the plant produces a small amount of ethylene, which is necessary for the growth and development of the plant, although the amount of ethylene required during fruit ripening is much higher (Abeles 1992). But plants under either biological or non-biological stresses produce augmented levels of ethylene, known as "stress ethylene", which is capable of inhibiting overall plant growth. To mitigate negative effects of high levels of "stress ethylene" on plants and to augment crop productivity, fitting crop management techniques is indispensable. In this context, one of the suggested ways to reduce the negative effects of stress resulting from ethylene production is genetic modification of stress-sensitive crop varieties, but this method, although successful in some cases, is a long and costly process. On the other hand, making a plant resistant to all the stresses that are present in the environment is not an easy task. Bacteria's ability to increase plant resistance to environmental stresses and consequently to plant growth in stress conditions has been well established. In addition, due to their manifold PGP properties, these bacteria are able to reduce most of the stresses imposed on the plant. Because of this bacterial characteristic, it is no longer necessary genetically engineer all stress-sensitive crop varieties to be tolerant to a large number of biological and non-biological stresses. In the present storyline, the use of plant-associated PGPB containing 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity along with other innovations to alleviate ethylene-induced stresses in stress-sensitive crop varieties could be a more cost-efficient environmental amicable option, which could be attainable in a shorter time frame and ensure sustainable agriculture. One of the limitations of using such bacteria (ACC deaminase-producing PGPB) to diminish the effect of stress imposed on plant under natural conditions (i.e., field conditions) is the reduction in their ability and survival under natural conditions (i.e., high concentrations of heavy metals, high salinity and temperature, water deficit, competition with other native microorganisms for water and nutrients, and adverse soil physical and chemical conditions). A possible solution to this problem may lie in the utilization of ACC deaminase-producing bacterial endophytes (Sturz and Nowak 2000).

Since the ability of PGPB including ACC deaminase-producing bacteria to augment plant tolerance to environmental stresses is impacted by environmental stressful conditions (Etesami and Beattie 2018) (i.e., loss in ACC deaminase activity by bacteria with increasing salinity) (Upadhyay et al. 2009), it is suggested testing the production ability of ACC deaminase of isolated bacteria in the presence of various stresses such as salinity, water deficit, heavy metals, etc. In other words, the use of ACC deaminase-producing PGPB that are picked out established upon both high stress tolerance and efficiency in expressing PGP characteristics would outstandingly advance our ability to grow crops in stressed agricultural environments.

In most of the previous studies, the effect of 1-aminocyclopropane-1-carboxylate deaminase-containing bacteria on alleviating a stress has been evaluated. Since most of the environmental stresses, for instance, water deficit, salinity, heavy metals, and imbalanced nutrition, exist in most agricultural land concurrently, it is recommended that the efficacy of ACC deaminase-producing PGPB be investigated concurrently in the presence of these stresses to pick out and introduce the best 1-aminocyclopropane-1-carboxylate deaminase-containing bacteria.

Relative to 1-aminocyclopropane-1-carboxylate (ACC) deaminase-containing rhizobacteria, some beneficial aspects of 1-aminocyclopropane-1-carboxylate (ACC) deaminase-containing bacterial endophytes, i.e., their function in alleviating salinity, water deficit, excess of water, biocontrol, temperature and imbalanced nutrition stresses, nodulation in legumes and field appraisal and use of potential of these bacteria as bio-fertilizers in stressed soil have not been thoroughly exploited. On a commercial scale, application of these bacteria in stressed agriculture might prove effective and could be a sound step in the direction of producing and conserving sustainable crop plants.

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Chapter 11
Halophilic Microbes from Plant Growing Under the Hypersaline Habitats and Their Application for Plant Growth and Mitigation of Salt Stress

Enespa, Jai Prakash and Prem Chandra

Abstract Salinity of the agriculture soil is the serious issue all over the world, and it is also an important environmental factor for reduction of growth and yield of agricultural crops. The density of more salt available in soil may alter the physiological and metabolic activities in the agricultural crops and reduce the growth and production of crops both qualitative and quantitative ways. For combating against soil salinity, many transgenic salt-tolerant crops have been developed but far too little is success. For solution, in the soils the use of plant growth-promoting rhizobacteria (PGPR) can reduce soil salinity, load of chemical fertilizers, and pesticide in the agricultural field, and improve soil health, seed germination, crop growth, and productivity under saline condition PGPR accepted as potential microbes that can tolerate various atmospheric circumstances like more temperature, pH, and saline soils. In the saline environment, many halophilic/halotolerant bacteria and plants/halophytes are observed/adapted and perform a significant role in saline soil ecosystem. Innumerable microfloral communities and halophytes contain salt-tolerant gene, and they perform as an essential protagonist in subsistence for extreme environmental condition especially salt. It can be concluded that PGPR can be used as a supportable, manageable, sustainable, and economical tool for salinity tolerance and productivity of crops/plants.

Keywords Halophile · Hypersaline habitats · PGPR · Soil salinity · Sustainable agriculture · Salt mitigation

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11.1 Introduction

The population of human will be expected to reach 9.8 billion until 2050 (Magallon and Dinneny 2019). In addition, the demand for food also be increased with the enhancing population, but this demand cannot be fulfilled without soil fertility, beneficial microorganisms, and essential nutrients of the soil (Poeplau et al. 2019; Chandra and Enespa 2017). Currently, many chemical fertilizers and pesticides are used in the soil for production of food; however, these ingredients can be increased for crop growth and productivity (Chandra and Enespa 2017), but simultaneously it increases soil salinity and also reduces soil fertility and beneficial microorganisms present in the soils (Rashid et al. 2016; Yang et al. 2019). The salinity in soil ecosystem is a major agrochemical/abiotic stress problem mainly in the semi-barren and waterless areas (Gu et al. 2016). Approximately, 65% of crop's productivity is adversely affected by saline soil (Machado and Serralheiro 2017).

A significant role is played by microorganisms in the improvement of productive soil and crop production and yield. In addition, some ions (e.g., sodium (Na^+) and potassium (K^+)) also affect the growth of plant and microorganisms and ultimately increase the soil salinity (Yan et al. 2015). Besides these, the climate changes such as drought, shortage of water, low rainfall, and abrupt changes in temperature also increase the soil salinity (Chandra and Enespa 2016). Reactive oxygen species (ROS), hydrogen peroxide (H_2O_2), superoxide (O_2), hydroxyl radicals (OH^-), lipid peroxidation, and the integrity of the membrane are other parameters of soil salinity which are produced by the cellular response (Choudhury et al. 2017; Chakraborty et al. 2018; Singh et al. 2018). In the presence of soil salinity, organic matter, essential nutrients, and beneficial microorganisms are reduced and ultimately it negatively affects the crop's productivity (Egamberdieva et al. 2017). Soil salinity reduces the root and shoots growth and finally decreases the crop's productivity (Glick 2014). For the management of soil salinity, plants used various types of mechanisms (Schmidt et al. 2018). Among all mechanisms, osmolyte is a common mechanism used by the plant. Osmolytes provide protection to the plant cell organelles and also build up compatible solutes (Chakraborty et al. 2018; El-Esawi et al. 2019). Besides, the formation of free radicals stabilizes DNA, stress protein, and prolines during salt stress condition are other factors for survival and growth of the plant (Teh et al. 2016; Chandra and Enespa 2016). Moreover, antioxidant enzymes such as peroxidases (POX), superoxide dismutase (SOD), and catalase (CAT) also protect against salinity and toxicity (Joseph and Jini 2010; Caverzan et al. 2016).

However, these mechanisms are not good for a long time in the reduction of soil salinity; currently, it needs a viable method for reduction of soil salinity and improves the soil fertility and increases microbial population, plant growth, and yield at high saline condition (Ladeiro 2012; Shrivastava and Kumar 2015). Microorganisms play a significant role in the improvement of soil fertility, crop's growth, and yield (Yan et al. 2015; Biswas and Paul 2017). Among all microbial group, plant growth-promoting rhizobacteria (PGPR) is an eco-friendly method for plant growth and sustainable agriculture by various ways such as the production of phytohormones, solubilization of minerals such as potassium, zinc, phosphate, and chelation of iron under saline condition (Verma et al. 2015; Yadav et al. 2015a, b, c; Habib et al. 2016; Ilangumaran and Smith 2017; Numan et al. 2018). This chapter describes the role of PGPR in the improvement of soil fertility and reduction of soil salinity and crop's yield under saline condition. In addition, how halotolerant microbes and plants survive under saline condition has been also explained.

11.2 Halophiles, Classification, and Hypersaline Environments

Those microorganisms can propagate and maintain their spore cycle at more saline concentrations ($\geq$150 g L^{-1}/15%) known as halophile (Ollivier et al. 1994; Oren 2008). The halophile is categorized into three dissimilar groups on the beginning of different salt concentrations: 1) less (1–6% NaCl), temperate (7–15%), and more salt concentrated halophile (15–30%) (de Lourdes Moreno et al. 2013; Chandra and Singh 2014; Yadav et al. 2019a, 2015d). Different concentrations of salt occur in the soil, and these are found at various depths in the soil habitats. According to Or et al. (2007), salt concentration and their variability are found much more than water. In the saline environment, different plants are growing known as halotolerant (halophytes) at different concentrations of salts and recorded well adaptability and perform a key character in the biogeochemical cycles (Nabti et al. 2015; Etesami and Beattie 2018). Microbes play a major character in enhancement of herb adaptation at various saline habitats (Bringel and Couée 2015; Bang et al. 2018; Yadav et al. 2019a). However, a limited microbial diversity is found in the extreme soil habitats/hypersaline environments due to various environmental factors and high salt concentrations (Ulukanli and Digrak 2002; Chandra and Singh 2016; Yadav and Saxena 2018). Besides soil salinity, the saline environment is mainly found in the aquatic water such as lakes, river, pond, and sea (Sánchez-Porro et al. 2003). From saline environments, the food or food-based products, plants, and animals contain salts (Maturrano et al. 2006; Ventosa et al. 2015).

11.3 Halophilic/Halotolerant Microbial Diversity in Soil

Soil salinity affects the structure, composition of microbial species, and also bacteriological populations present in the rhizospheric regions of crops. These communities have different groups, which show modified structural and physiological properties under hypersaline condition (Bever et al. 2012; Mendes et al. 2013). However, bacterial communities are dominant as compared to other microbial communities (e.g., virus, fungi, protozoa, and algae), and it is found in the rhizospheric region of the plant under saline condition (Mukhtar et al. 2017; Yamamoto et al. 2018; Chandra and Enespa 2019b). Besides rhizosphere, bacterial communities are also recorded endophytic region, in salt lakes, river water, and root nodules (Albaggar 2014; Leite et al. 2017). But in the saline soil, bacterial communities do not define a similar group of phylogeny but signify a assemblage which has progressed in altered types of microorganisms that belong to the genera *Actinopolyspora*, *Bacillus, Halomonas Micrococcus, Marinococcus, Pseudomonas, Salinicoccus,* and *Vibrio* which are mainly found in the hypersaline region (Ventosa et al. 1998; Soto-Padilla et al. 2014; Chandra et al. 2014; Verma et al. 2017b; Yadav et al. 2018a, b, d). These genera belong to both Gram-positive and Gram-negative bacteria showing rod-, comma-, and cocci-shaped cell. However, Gram-negative bacteria appear to be dominant in saline environments (Ventosa et al. 1998; Canfora et al. 2014). In Gram-negative bacteria, root-nodulating bacteria showing root-colonizing property are considered to be a halotolerant group (Zahran 1997). These bacteria have capable of nitrogen fixation and improve soil fertility at high concentration. A halotolerant bacterium *Swaminathania salitolerans* gen. nov., sp. nov. was isolated from the rhizosphere, roots, and stems of mangrove-associated wild rice (Loganathan and Nair 2004). Another bacteria belonging to the genus of *Azospirillum*, *Bacillus, Enterobacter,* and *Azotobacter* were isolated from the different agricultural under saline soils (Alamri and Mostafa 2009; Fendrihan et al. 2017). The popular nitrogen-fixing bacterium *Rhizobium* is linked with marsh grass *Spartina alterniflora* as a halotolerant plant has also been isolated and identified from hypersaline condition (Bedre et al. 2016).

Besides, another nitrogen-fixing bacterium *Bacillus* was screened from salty soils of Egypt, and it showed acetylene reduction activity at 5% NaCl concentration (Zahran et al. 1995). The genus *Azotobacter* is the free-living nitrogen-fixing bacterium showing a significant role in different environmental conditions such as soil, water, and sediments at the high salt concentration (Akhter et al. 2012; Sahoo et al. 2014). *Azotobacter* strain isolated from agricultural crops showed high nitrogen-fixing ability at 30% NaCl. The nitrogen fixation efficiency of a bacterium *A. vinellandii* was decreased from nonsaline to saline condition as reported by Sahoo et al. (2014). *Azospirillum halopraeferens* was isolated and enhanced the growth of mangrove plant by root colonization irrigated with seawater (Bashan et al. 2000). A little information is available on the halotolerant microbial diversity isolated from saline soils as compared with hypersaline aquatic locales (Oren 2008; Yang et al. 2016).

11.4 Effect of Soil Salinity in the Soil Environment

The salinity soil is considered mainly as a major problem in the ecosystem because these problems increase continuously, disturbing biotic and abiotic soil constituents (Vandegehuchte et al. 2010; Bünemann et al. 2018). It also affects natural circumstances in the barren and semi-barren regions of an ecosystem. Excess of saline soils affects seriously on the micro- and macro-floral structure and on space where it lives

(Getu 2009). Excess salt in the soils known as sodic soils contains sodium and chloride ions in the earthen constituent part (Bianco and Defez 2010). Due to insufficient discharge and drainage of irrigation water, salts accumulated in the soil (Cuevas et al. 2019). However, the chlorides, bicarbonates of calcium, sulfates, carbonates, magnesium, sodium, and potassium salts are present in the irrigation water (Warrence et al. 2002). The soil structure growth and the production of crops adversely are affected by salt concentration (Ondrasek et al. 2011; Shrivastava and Kumar 2015). On the bases of soil and groundwater practices generally, the salinity is of three types: transient, groundwater associated, and irrigation salinities (Greene et al. 2016; Chandra et al. 2020). Salinity affects both soil system and living organisms that are known as most severe abiotic environmental stress (Gupta and Huang 2014). The immediate consequences of soil are found for biological activity or conservation occurs within the pore space or on the surfaces of the particles that forms the pores (Indoria et al. 2017; Totsche et al. 2018). High salinity leads to negative effects on soil structure which is well known.

Soil dispersion and clay platelets to swell and aggregate are caused by elevated sodium concentrations (Warrence et al. 2002). Thus, in the binding of clay particles, the forces involved are dislocated under the stimulus of sodium ions. Clay particles to plug soil pores are caused due to the dispersion of soil (Arora and Dagar 2019). Therefore, the permeability of soil for water and air is reduced and forms apparent crusting (Kooistra and Tovey 1994; Greene and Hairsine 2004).

It is documented that the presence of water in the soil leads to the swelling of the soil particles with high smectite clay content, and the hydration of some minerals as a result of the reduction of the cross-sectional area of soil pores is documented (Mahrous et al. 2018). Under high sodium or low salt concentrations, this process is completed and it causes the mobilization of fine particles and diffusion within the pores (Mahrous et al. 2018; Chandra et al. 2020). The water and air will be obstructed within the soil structure and particles by the particles stored in the small pores (Schjønning et al. 2002).

11.5 Mechanisms for Adaptation of Microorganisms in the Hypersaline Environment

Phylogenetically, the microbial life is very diverse at high concentrations, and the salinity environments are occupied by halophilic and halotolerant microflora of all domains of life, such as archaea, bacteria, and eukarya (Oren 2008; Ma et al. 2010). Using this mechanisms these halophile microorganisms to tolerate the high salt concentrations, and in various cases to acclimatize their structure to alterations in high salinity in their environments, are miscellaneous as well (Oren 2008).

The basic mechanisms for adaptation of microorganisms in the hypersaline environment are given below:

- Biological membranes of the microorganism are absorptive to water containing salt. Consequently, the movement of water inside and outside of microbial cells is possessed by changes in ionic activity between cytoplasm and external medium (Murínová and Dercová 2014; Watson 2015).
- The bacterial cell maintains high osmotic pressure under saline condition; therefore, it is another strategy for adaptation mechanism (Weinisch et al. 2018).
- The high concentrations of inorganic salts inside the microbial cell are accumulated and achieved the osmotic balance. The sodium ions are left out from cells in all three domains of life, and inside the cell the salt strategy is based on KCl rather than NaCl as a main salt of intracellular organism (Oren 2002).
- Di-myoinositol-1, 1-phosphate, cyclic 2,3-diphosphoglycerate, α-diglycerol phosphate, mannosylglycerate, and mannosylglyceramide are compatible solutes which are very strong water structure formers and are excepted from the hydration shell of proteins, thus alleviating the hydration shell and decreasing the water activity coefficients (Gunde-Cimerman et al. 2018).
- In many extremophiles, such low-molecular weight compounds are accumulated to increase the concentrations of salts but also as a reply to other ecological alterations such as temperature stress.
- Di-myoinositol-1, 1-phosphate, cyclic 2, 3-diphosphoglycerate, α-diglycerol phosphate, mannosylglycerate, and mannosylglyceramide are the examples of organic compatible solutes in thermophiles and in psychrophiles (da Costa and Santos 2009).
- Mostly, at low salt concentration, the microorganisms are endured and also accumulate salts inside the cell in the form of solutes from outside medium (Shrivastava and Kumar 2015).

11.5.1 Mechanism of Salt Tolerance

The microbial population in the rhizosphere decreases severely due to increase in pH and salinity (Ibekwe et al. 2010). In hypersaline atmosphere the microbes inhabits using “compatible solute strategy” having capability to strong osmotic pressure to resist the salt stress (Pikuta et al. 2007; Chandra and Singh 2017). Choline, betaine, proline, glutamic acid, and other amino acids are the compatible solutes stored by various halophilic bacteria at high concentrations without interfering with cellular processes (Poolman and Glaasker 1998).

11.5.2 Characteristics and Function of Compatible Solutes

The HPLC and NMR methods are followed for the determination and production of compatible solutes in various archaea and bacteria (Roberts 2005a, b). The compounds in limited numbers comprise the bacteria such as sugars (trehalose), polyols (glycerol and glucosyl glycerol), free amino acids (proline and glutamate), offshoots thereof (proline, betaine, and ectoine), quaternary amines and their sulfonium analogs (glycine betaine, carnitine, and dimethylsulfoniopropionate), sulfate esters (choline-O-sulfate), and N-acetylated diamino acids and small peptides (N-acetylornithine and N-acetylglutaminylglutamine amide) (Kempf and Bremer 1998). Generally, the compatible solutes do not carry a net charge at physiological pH due to their high molecular solubility (Galinski 1993). The vital cellular functions such as DNA replication, DNA–protein interactions, and the cellular metabolic machinery without disturbing the solutes can reach high intracellular concentrations in disparity to mineral salts (Wang and Levin 2009; Long et al. 2018). Compatible solutes such as glycine, betaine, and proline increase the cytoplasmic volume and water content freely of the cells at high osmolality, and their accumulation uninterruptedly permitted proliferation of cells under unfavorable conditions (Kohler et al. 2015).

Various halotolerant nitrogen-fixing bacteria accumulate electrolytes such as K^+ glutamate, as enzymes, ribosomes, and transport proteins of these bacteria require high level of potassium for stability and activity using salt in strategy mechanism (Da Costa et al. 1998a, b). But within the cell physiology, organic solute accumulations are more compatible (Ventosa et al. 1998; Wood et al. 2001). The organic solutes have two mechanisms under saline conditions for their mode of actions: firstly to increase the intracellular osmotic strength and secondly to stabilization; the cellular macromolecules are proposed (Yancey et al. 1982; Csonka 1989; Chandra and Enespa 2019a). After adding these solutes in bacterial culture, the drastic stimulation in growth rate is observed in cells in high osmolality media (Gouffi et al. 1998). Higher internal concentrations of solutes accumulated in the alleviation of osmolality (Patchett et al. 1992). The glucose is oxidized in Entner–Doudoroff pathway modifications by the mostly halotolerant organisms (Fig. 11.1), the synthesis of compatible solutes after formation of pyruvate, and its further oxidation by pyruvate oxidoreductase in tricarboxylic acid cycle (TCA) (Kindzierski et al. 2017).

In salt-tolerant bacteria, the accumulation of organic solutes has been found to require genetic initiation (Roberts 2005a, b). In response to osmotic stress in *Bacillus* sp., intracellular proline to increase rapidly has been observed and the corresponding genes were detected, respectively, proB, proA, and proC encoding γ-glutamyl kinase (γ-GK), γ-glutamyl-phosphate reductase (γ-GPR), and pyrroline-5-carboxylate (P5C) reductase (Pérez-Arellano et al. 2010). L-aspartokinase (Ask), L-2,4-diaminobutyric acid transaminase (EctB), L-2,4-diaminobutyric acid acetyltransferase (EctA), and L-ectoine synthase (EctC) encoding the structural gene and detected for biosynthesis of major harmonious solute like ectoine in *Halobacillus dabanensis* (Reshetnikov et al. 2006; Czech et al. 2019). Choline or choline-O-sulfate oxidized enzymatically into glycine betaine due to involvement of four genes *betI,*

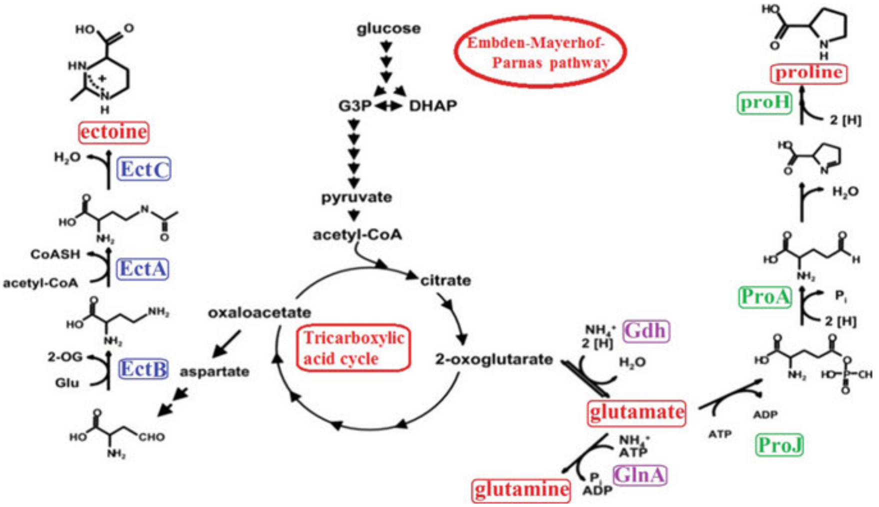

Fig. 11.1 Synthesis of compatible solutes: Proline, ectoine, and glutamine under stress conditions (Figure adopted by Saum and Müller 2008)

betC, betB, and *betA* well characterized at molecular level and organized into one operon (Osteras et al. 1998; Stöveken et al. 2011). Various halotolerant nitrogen-fixing bacteria are also observed in the cell for the maintaining of the balance of Na^+ and K^+ ions (Hanin et al. 2016; Thomas and Apte 1984). A cytoplasmic KCL concentration is maintained by bacteria similar to that of the surrounding medium in order to attain an osmotic equilibrium (Kraegeloh et al. 2005). The Na^+/H^+ antiporter performance is a major character in homeostasis of pH and Na^+ in cells that interchange Na^+ for H^+ (Suárez et al. 2008). The genes that are proved to be involved in halotolerance in nitrogen-fixing bacteria either through knockout studies or through overexpression studies are framed in Table 11.1.

11.5.3 Exchange of Solutes/Ions

Many solutes/ions are present in the soils and perform an important character in the existence of microorganisms in the presence of soil salinity (Shrivastava and Kumar 2015). However, more solutes or ions containing soils can decrease microbial population in the rhizospheric region of plants (Aung et al. 2018). Several microbes reside in hypersaline environment condition proficient passionate osmotic pressure, and thus use compatible solute strategy or salt-in strategy to resist salt stress (Oren 2011). Choline, betaine, proline, glutamic acid, and other amino acids compatible solutes accumulated in most of the bacteria at high salinity without interfering with cellular procedures (Wood et al. 2001).

Table 11.1 Genes conferring salt tolerance response in selected nitrogen-fixing bacteria

Strains	Products	Genes	References
Rahnella aquatilis HX2	1-aminocyclopropane-1-carboxylic acid deaminase	acdS gene	Peng et al. (2019)
Sinorhizobium meliloti B401	Na^+/H^+ antiporter	AtNHX1 gene	Stritzler et al. (2018)
Azospirillum lipoferum FK1	Proline and glycine betaine levels	*PAL, PPO, CHS, CHI, REB2A,* and *IFS*	El-Esawi et al. (2019)
Klebsiella sp. SBP-8	K^+/Na^+ transporters	AcdS gene	Singh et al. (2015)
Pseudomonas aeruginosa	Na^+/H^+ antiporter	nhaP	Inaba et al. (2001)
Sinorhizobium meliloti	(p) pp Gpp synthetase	relA	Wei et al. (2004)
	Glycine betaine/proline	bet genes	Mandon et al. (2003)
	Betaine transporter	betS gene	
	Transcription cleavage factor	greA	
	Potassium-uptake protein	Kup	Nogales et al. (2002)
Rhizobium tropici	Histidine kinase Na^+/H^+ antiporter	ntrY, ndvA and ndvB (synthetic gene), nhaA, nhaB, nhaC	Wai Liew et al. (2007)
Azotobacter vinelandii	Glucosyl glycerol biosynthesis	ggpPS	Klähn et al. (2009)
Enterobacter cloacae	Na^+/H^+ antiporter	nhaA	Lentes et al. (2014)
Synechocystis sp.	Na^+/H^+ antiporter	nhaS1, nhaS2, nhaS3, nhaS4, and nhaS5	Mitschke et al. (2011)
Aphanothece halophytica	Na^+/H^+ antiporter	napA	Laloknam et al. (2006)
Bacillus subtilis	γ-glutamyl kinase	proA, proBproC	Zhao et al. (2011)

11.5.4 Mechanism of Salt-Dependent Lipid Changes

The lipid content present in the microbial plasma membrane shows special character for the survival of stress environmental condition. The phospholipids of *Pseudomonas halosaccharolytica* contain glucosyl phosphatidylglycerol, phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine which are responsible for growth under high saline condition (Li et al. 2016), and this result indicates increase of phosphatidylglycerol and reduction in phosphatidylethanolamine (Hiramatsu et al. 1980). Later, Hara and Masui (1985) observed that pulse-chase labeling of lipids with several radioactive originators showed that the rate of synthesis of phosphatidylethanolamine was inhibited by an increase in salt concentration, but the rate of phosphatidylglycerol synthesis was unaffected. The deficiency of motivation of phosphatidylglycerol creation by salt does not settle with compositional data. The radiolabeling experimentations were performed with nongrowing, starved cells, whereas the compositions of lipids were resolute directly on cells collected from culture media (Hara and Masui 1985). The inhibition of phosphatidylethanolamine creation leads to an upsurge in phosphatidylglycerol comfortable in the microbial cell because of the bifurcated phospholipid biosynthetic pathway going inside the cell (Sohlenkamp and Geiger 2016). A similar type of study was performed by Ohno et al. (1979); the little amount of NaCl did not affect the growing bacteria due to the presence of glucosyl phosphatidylglycerol. However, survival mechanisms of halophilic bacteria due to membrane lipid composition cannot judge very easily; this is a very difficult process (Oren 2008). The lots of chemicals, labor, and time may be taken to well understand the interaction between bacterial lipid membrane and salt medium (Pichler and Emmerstorfer-Augustin 2018).

11.5.5 Salt-Tolerant Genes of Bacteria

Many microorganisms contain salt-tolerant gene and perform an important character in survival for extreme environmental condition especially salt (Holmberg and Bülow 1998). The bacterial spores of *Bacillus thuringiensis israelensis, B. sphaericus,* and *B. subtilis* contain osmotolerant protein, i.e., small acid-soluble spore protein (SASP) coded by an ssp gene and this gene can survive at the high salt concentration (Cucchi and Rivas 1995). Cucchi and Rivas (1995) reported a sspE gene from *B. subtilis* and is introduced into another host bacterium *B. thuringiensis israelensis* strain 4Q2 and observed 65–650 times higher level of salt-tolerant property as compared to natural *B. thuringiensis israelensis.* In addition, this bacterium does not cause any side effects in living organisms as well as environments. Some other genes such as ectA (diaminobutyric acid acetyltransferase), ectB (diaminobutyric acid aminotransferase), and ectC (ectoine synthase) genes are reported in *B. halodurans* and showed in the survival of stress tolerance (Reshetnikov et al. 2011).

There are two genes, namely, GspM and EchM have recognized from a metagenomic collection organized from water sample of pond (Kapardar et al. 2010). GspM gene displays comparison with stress proteins, and another gene EchM showed similarity with enoyl-CoA hydratases and both genes were identified to be responsible for halotolerant at high concentration and have latent solicitation in generating halotolerant recombinant bacteria or transgenic crops (Kapardar et al. 2010). The two genes were further isolated from *Rhizobium* sp. BL3 and showed hyper-salt-tolerant ability (Payakapong et al. 2006). Hence, many microbes from rhizosphere can be exploited to isolate novel gene for salt tolerance and their potential application in the plant genetic engineering or plant growth under saline environment condition.

11.5.6 Salt-Tolerant Genes of Yeast

The two genes HAL1 and HAL3 were isolated and showed overexpressed gene from yeast (*Saccharomyces cerevisiae)* and also increased the halotolerant capability by a decreasing intracellular Na^+ and enhanced internal K^+ concentration during salt stress (Ferrando et al. 1995; Locascio et al. 2019). Further, the gene HAL1 has been introduced into tomato crop by *Agrobacterium tumefaciens*-mediated transformation which improves salt tolerance of the transgenic tomato and enhances the growth and productivity (Gisbert et al. 2000). An enzyme mitogen-activated protein kinase (MAPK) coded by a gene HOG1 shows an important role in the osmoregulatory pathway in *S. cerevisiae* (O'Rourke and Herskowitz 1998). This gene is also responsible for salt tolerance in *Torulopsis versatilis* (Wang et al. 2014). A delightful mutant strain *Torulopsis versatilis* T5 showing salt-tolerant ability was fashioned from wild-type *T. versatilis* (T) consuming genome trundling and further isolated two genes T5HOG1 and THOG1, demonstrating upturn of salt tolerance in *T. versatilis* (Cao et al. 2011). Moreover, overexpression of T5HOG1 and THOG1 enhanced the acceptance of salt in *S. cerevisiae* (Cao et al. 2011).

11.5.7 Salt-Tolerant Genes of Plants

A wide range of cruel ecological circumstances such as salinity, heat, cold, drought, and insect attack are normally exposed in plants. Plants have established altered methods being in sessile nature to survive grow and develop under speedily altering environmental conditions (Hayat et al. 2012). For these mechanisms, plants regulate genes for transcription which are known as transcriptomics under stress conditions (Shu et al. 2018). The genes for regulation of transcription play different roles under stressful environmental conditions. However, during the reproductive and seedling stages, plants have more sessile to stress and the stress response studies express novel genes or proteins with imperative roles in plant anxiety reworking during these growth stages (Verma et al. 2016a, b). However, the word salinity acceptance comes from one or more genes that reduce the uptake of the salt content from the soil and the conveyance of salt through the plant (Munns 2005, 1993).

Salinity tolerance is a very complex process that is recycled by plants to regulate (up-regulation or down-regulation) the manufacture of specific gene products in the form of RNA or proteins (Gupta and Huang 2014). This process has been accepted at different stages of central dogma technologies like from initiation of RNA processing, post-transcriptional modification, and initiation translation to post-translational modification of proteins in living organisms especially plants (Zhao et al. 2017). Understanding the transcription or translation of plants delivers thorough knowledge about the gene expression at the mRNA level. The summary of transcriptional or translational level is widely used for isolation and identification of candidate genes involved in stress responses (Xiao et al. 2017).

Transcriptome profiling is the screening processes which down-regulated or up-regulated the transcription processes that are enormous evidence about salt-tolerant genes till now. Further, a genomic method gives an important role in cloning, encoding, screening, and identifying these genes (Lodish et al. 2000). Under salt stress condition, the expression of gene is altered by transcript issues and those up- or down-regulated the expression of the gene in plants or microorganisms by these are most important switches (Lodish et al. 2000).

A gene bZIP was identified and showed up-regulation gene expression in wheat crop under insistent salt stress disorder and gene expression of down-regulation in salt-tolerant variety of wheat crop (Hayano-Kanashiro et al. 2009). The osmotic regulating and ROS-scavenging genes mostly are salt tolerance genes and also up-regulated in salinity toleant species (Amirbakhtiar et al. 2019). According to study, more than 10 genes showed up-regulated genes in halophytes plant species *Spartina alterniflora* under saline condition. Under saline condition, more than 10 genes showed up-regulated genes in *Spartina alterniflora* halophytes plant species, and most of the genes were found to osmotic regulation process among them (Bedre et al. 2016).

11.6 Mechanisms of Plant Growth Promotion of Halophilic Bacteria

11.6.1 Nitrogen Fixation Under Salt Stress Condition

At global level in arid and semi-arid regions, salinity is a serious issue for agriculture. Growth promotion and photosynthesis rate at various stages of plants affected by salinity stress (Magallon and Dinneny 2019). The production of salt-sensitive crops such as legumes is affected by salt stress particularly since these plants depend on nitrogen requirement for symbiotic N_2 fixation (Hussain et al. 2010; Kour et al. 2019b, c, d). The crop productivity mainly depends on the deprived mutual association of nodulation in bacteria and ultimately decreases in nitrogen fixation capacity (Mengel et al. 2001). *Vicia faba, Phaseolus vulgaris,* and *Glycine max* legume plants are more salt-tolerant species than another leguminous plant *Pisum sativum* (Mengel et al. 2001). *V. faba* crop fixed more nitrogen under saline condition due to the presence of rhizobia inside the root nodules and it has been seen (Mengel et al. 2001). *Prosopis*, *Acacia*, and *Medicago sativa* are the other salt-tolerant leguminous plants but these are less halotolerant than the leguminous plants (Joseph et al. 2015). *Rhizobium* sp. performs a very significant character in symbiosis with plants and nodulation process but, in the presence of salt, inhibits the initial process of rhizobium–legume symbiosis (Maróti and Kondorosi 2014). However, in several reports, the effect of salt stress on nodulation and nitrogen fixation of legumes have been observed (Maróti and Kondorosi 2014). In the presence of salt, the capability of N_2-fixation reduces and is documented to a decrease in the respiration of the nodules and minimize in cytosolic production protein, especially leghaemoglobin by nodulation (Zahran 1999). Saline stress negatively affected on N_2 fixation by legumes is related to the salt-induced decline directly in dry weight and nitrogen content in plant shoot (Delgado et al. 1994).

Glycine betaine is the osmoprotective substances which perform an imperative character in the maintenance of nitrogenase activity in bacteroides under salinity stress (Normand et al. 2015). The halotolerant *Rhizobium* sp. enhanced the growth, nodulation, and fixed N_2 content in *Acacia ampliceps* plant containing 200 mM NaCl concentration in the sand culture medium (Egamberdieva et al. 2013) and one more halotolerant *Rhizobium* sp. designed N_2 fixing symbiosis more effective with soybean than other salt-sensitive strain of bacteria (Egamberdieva et al. 2013). Further, the isolated rhizobial strains from *Acacia nilotica* showed tolerance to 850 mM NaCl concentration formed effective N_2-fixing nodules on *Acacia* trees grown at 150 mM NaCl (Zahran 1999). The salt-tolerant *Rhizobium* strains produce nodulation in legumes and form effective N_2 fixing symbiosis capability in the soil under moderate halophile environment observed in the result (Zahran 1999). Therefore, the booster of salt-tolerant rhizobia strains in the rhizosphere of leguminous crop can enhance the N_2 fixation ability under saline condition. However, host tolerance legume to NaCl is a very key element in influencing the achievement of harmonious *Rhizobium* strains to form symbiosis successfully under the halophilic environment (Egamberdieva et al. 2013).

11.6.2 Phytohormone Production Under Saline Condition

Phytohormones are natural organic compounds which enhance the growth and productivity of cultivars at very less concentrations. These phytohormones support the distinction and improvement of plant growth by the regulation of various progressions. Generally, the phytohormones at plants root locality are the microbial origin recommended for a functional reply in the host crop (Verma et al. 2016a, b; Enespa and Chandra 2019). Indole-3 acetic acid (IAA), gibberellic acid, abscisic acid (ABA), cytokinins, and other plant growth regulators produced by NaCl-tolerant rhizobacteria outwardly maintain the rooting with augmented number of roots, increase root length, shoot length, and number of root tips, and finally lead to increase in the uptake of nutrients and thus progress plant fitness under saline environmental circumstances (Verma et al. 2016a, b). *Bacillus* and *Pseudomonas* strains belong to IAA production that improved the growth of soybean crop at 100 mM NaCl concentration by the increasing antioxidant activity and decreasing the lipid peroxidation (Kumari et al. 2015). Furthermore, an isolated bacterium produced osmotolerant IAA displayed to increase the sprouting of rice seeds in salinity stress are reported (Jha and Subramanian 2013).

11.6.3 ACC Deaminase Production Under Saline Condition

A volatile phytohormone known as ethylene has capacity for growth promotion of plant at very less quantity like nodulations and improvement of various asexual plant parts, rooting, cuttings, and also twisted in the transduction of a signal for the appreciation of saline stress ecosystem (Saravanakumar and Samiyappan 2007). However, a large amount of ethylene is produced under abiotic environmental ecosystem and in the presence of this substrate can inhibit the root growth, shoot growth, and productivity of plants (Morgan and Drew 1997). Some chemical substrates such as aminoethoxyvinylglycine and cobalt ions act as an inhibitor of ethylene synthesis (Arora et al. 2017).

However, these chemical substrates are too much expensive and also can harm plants and environment. Halotolerant rhizobacteria showing plant growth-promoting characters contain aminocyclopropane-1-carboxylate (ACC) deaminase which splits ACC into ammonia and α-ketobutyrate, thereby reducing the near of ethylene in stressed plants (Habib et al. 2016). In the presence of ACC deaminase-producing bacteria, plant 1-aminocyclopropane-1-carboxylate is sequestrated and ruined by the cells of bacteria to fund energy and nitrogen, enhancing the plant growth under saline ecosystem (Tiwari et al. 2018).

The rhizospheric bacteria which belong to Gram-positive and Gram-negative genera such as *Arthrobacter, Bacillus, Brevibacterium, Corynebacterium, Exiguobacterium, Halomonas, Micrococcus, Oceanimonas, Planococcus,* and *Zhihengliuella* have been widely reported for ACC deaminase activity under saline conditions and have recognized as a potential role in enhancement of growth under saline ecosystem through ACC deaminase activity (Siddikee et al. 2015; Yadav et al. 2019c, d, e). *Pseudomonas simiae* strain AU5 is the mutant bacterium overproduced ACC deaminase documented to alleviate salt stress in mung bean plants as compared to wild strain *P. simiae* AU5 and observed decrease the concentration of ethylene and salt-induced membrane (bacteria and plants) damage (Kumari et al. 2016).

11.6.4 Under Salt Condition Phosphate Solubilization

Phosphorus (P) is an indispensable mineral after nitrogen for the growth of plant promotion as it and essential of dissimilar biomolecules such as nucleic acids, nucleotides, phospholipids, and phosphoproteins (Sharma et al. 2013). In the presence of salinity, uptake of P in plants is reduced and deficiency of P is appeared in the form of symptoms such as dark bluish-green in color with leaves and stem becoming purplish, etc. (Sharma et al. 2013). Mostly, insoluble forms of phosphorus in soils, i.e., organic and inorganic phosphate, have less mobilization in the soils (Sharma et al. 2013). Insoluble organic and inorganic phosphate conversion can be possible due to species of rhizobacteria and also helps in the translocation of P from soil to roots. For the solubilization of insoluble phosphates, many rhizobacteria show one of the several mechanisms such as reactions of ion-exchange, chelation, acidification, and the production organic acids of low molecular weight such as gluconic acids (Kalayu 2019; Rana et al. 2019a, b; Verma et al. 2017a). The halotolerant rhizobacteria to be vital for the mobilization of plant nutrients in several types and reduced the acceptability of inorganic fertilizers (Jiang et al. 2019).

However, phosphate solubilization is a common process in the rhizosphere by rhizobacteria that upsurge the mineral accessibility to crop (Jiang et al. 2019). An important role played by the rhizospheric bacteria to the regulation of P from less available forms and are essential for sustaining P is voluntarily available pools. Upadhyay et al. (2011) reported rhizobacterial strains to have well-organized solubilizing ability of phosphate even up to high saline (6% NaCl concentration) condition and enhanced plant growth under similar condition. For example, *Pseudomonas* inoculated in the rhizosphere of *Zea mays* crop showed salt tolerance under 6% NaCl stress condition and increased the crop growth at same salt condition (Bano and Fatima 2009). Additionally, *Herbaspirillum seropedicae* and *Burkholderia* sp. are the phosphate dissolving bacteria; treated plants recorded 1.5–21% dry weight as a compared to control plant under saline condition. Afterward, the better germination of root and shoot growth as compared with control plant after being exposed to NaCl inoculated *Azospirillum* in lettuce seeds (Carrozzi et al. 2012). *P. simiae* solubilizes phosphate by producing acid phosphatase activity along with volatile compounds that enhanced plant storage protein and uptake of P in soybean plants under 100 mM NaCl saline ecosystem (Vaishnav et al. 2015).

11.6.5 Antioxidative Response Under Salt Condition

The compounds inhibit oxidation reaction known as an antioxidant, and this is a chemical/biochemical process that can produce free radicals (Lü et al. 2010). The oxidative stress is caused by the abiotic environmental factor like drought and saline soil and resulted in the formation of reactive oxygen species (ROS) such as singlet oxygen (O_2), hydrogen peroxide (H_2O_2), and hydroxyl radical (^-OH) that damage cellular membranes, proteins, and DNA (Nita and Grzybowski 2016). When the level of ROS increases, this causes oxidative damage to biomolecules such as lipoproteins and at last leads to the death of plants (Sharma et al. 2012). However, some major antioxidative enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) are produced by rhizospheric bacteria such as *Streptococcus. Proteamaculans*, and *Rhizobium leguminosarum,* and non-antioxidant enzymes/compounds like ascorbic acid, tocopherols, and glutathione contribute in ROS-scavenging mechanism (Sharma et al. 2012). Mycorrhizal-inoculated lettuce plants showed higher superoxide dismutase (SOD) activity and protect the plant in the presence of antioxidant under drought stress condition (Ruiz-Lozano 2003).

Salt resistance plants have been associated to more effective antioxidant schemes, and a salt-tolerant bacterium *P. simiae* strain AU enriched antioxidants (peroxidase and catalase) and gene expression in soybean plants when treated with 100 mM NaCl stress disorder (Vaishnav et al. 2016; Chandra and Enespa 2019c). Drought stress effects in maize plants are alleviated by *Pseudomonas* spp. drought-tolerant rhizobacteria due to decrease in the antioxidant enzyme activity (Afridi et al. 2019). The catalase and peroxidase activity boosted the non-inoculated crops during saline soil, whereas *Azospirillum brasilense* inoculated plants showed lower enzyme activity and expressively ameliorated the deleterious effects of salinity (Omar et al. 2009).

11.6.6 Siderophore Production Under Salt Condition

In the chelation of micronutrients, siderophore plays an imperative character such as iron even under limiting conditions and with the redox activity it serves as a cofactor of many enzymes (Ahmed and Holmström 2014; Chandra and Enespa 2016). Several studies are reported on *Bacillus* to be a good siderophore producer (Kesaulya et al. 2018). Production of siderophores in the rhizosphere by bacteria also helps in dissolving of other ingredients, for example, P, zinc, potassium, and the availability of various ionic ingredients to the plant through chelation of iron from precipitated form (Sharma et al. 2013; Ahmed and Holmström 2014). In the soils, a huge amount of iron is existent, but in an extremely unsolvable ferric hydroxide form, hence the performances of iron as a limiting factor for promotion of plants growth even in ironic soil. However, ferrous (Fe^{++}) iron is oxidized into ferric (Fe^{+++}) form by oxidation process (Kesaulya et al. 2018). Under the biological ecosystem, the ferric ions are inexplicable which forms its achievement by microorganisms, a considerable challenge in the soils (Colombo et al. 2014). Siderophores play important roles in the development of plant growth by rhizospheric microorganisms (Ahmed and Holmström 2014). Plants and bacteria mediate competition using existence of siderophore that results in exclusions of fungal pathogens and other microbial competitors in the rhizosphere by a reduction in the availability of iron for their survival (Ahmed and Holmström 2014).

11.6.7 Halophilic Microbes as Biocontrol Agents

The production of crop yield potentially increased, and its diseases controlled biologically from rhizospheric microflora. Inhibition of phytopathogens using rhizobacteria compromises a more sustainable method to control infection as compared to harmful chemical-based methods (Compant et al. 2010; Etesami and Alikhani 2018). Under the saline condition, a halophilic microbe plays an important role in maintaining morphology, physiology, and reduction in soil salinity and also increases plant susceptibility against phytopathogens (Table 11.2) (Etesami and Beattie 2018).

Halophilic microbes use to hostage the injurious properties of plant pathogens through different mechanisms. Halophilic microbes produce one or more antimicrobial metabolites that act as antifungal, antibacterial, antiviral, antioxidant, cytotoxic,

Table 11.2 Plant growth promotion of plants by halotolerant rhizobacterial inoculation

Microbes	Host Plants	Effect of host plants under saline condition	Salt concentration	References
Bacillus pumilus ST2	*Oryza sativa*	Controlling caspase-like activity, programmed cell death, antioxidative activity	25 mM NaCl	Jha et al. (2011)
B. pumilus STR2, *Exiguobacterium oxidotolerens* STR36	*Bacopa monnieri* L.	High proline content/lipid peroxidation	4 g NaCl/Kg of soil	Bharti et al. (2013)
Burkholderia phytofirmans PsJN, *Enterobacter* sp. FD 17	*Zea Mays*	Decreasing xylem Na^+ concentration/maintain nutrient balance within the plants	25 mM NaCl	Akhtar et al. (2015)
B. pumilus STR2, *Halomonas desiderata* STR8	*Zea mays*	Preventing major shifts indigenous microbial community	50 mM NaCl	Bharti et al. (2015)
P. simiae strain AU-M4	*Glycine Max L.*	Inoculated reduced Na^+ and enhanced K^+ uptake	100 mM NaCl	Vaishnav et al. (2015)
Acinetobacter sp. ACMS25, *Bacillus* sp. PVMX4	*Phyllanthus amarus*	Improved antioxidative defense system	160 mM NaCl	Joe et al. (2016)
P. fluorescens 002	*Zea Mays*	Improved root growth and root formation under salt stress	150 mM NaCl	Zerrouk et al. (2016)
Azotobacter chroococcum AZ6	*Zea mays*	Improved chlorophyll a and total content, reduced proline and amino-acid content	20 mM NaCl	Silini et al. (2016)
Bacillus aquimaris DY-3	*Zea mays* L	Chlorophyll content, leaf relative water content, accumulation of proline, soluble sugar and total phenolic compound, and activities of superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase were enhanced	1% NaCl	Li and Jiang (2017)

(continued)

Table 11.2 (continued)

Microbes	Host Plants	Effect of host plants under saline condition	Salt concentration	References
Bacillus sp., *Actinomycetes* sp., *Rhizobium* sp., *Oceanospirillum* sp.	Paddy crop	Improve rice germination, energy or germination capacity	3–12 g/L NaCl	Shi-Ying et al. (2018)
Bacillus subtilis (BERA 71)	Chickpea crop	Enhanced plant biomass and the synthesis of photosynthetic pigments and reduced the levels of reactive oxygen species (ROS) and lipid peroxidation in plants under conditions of stress.	200 mM NaCl	Abd_Allah et al. (2018)
Pseudomonas PS01	*Arabidopsis thaliana*	Improve the germination rate, transcriptional levels of genes	150 mM NaCl	Chu et al. (2019)
Enterobacter aerogenes LJL-5 and *Pseudomonas aeruginosa* LJL-13	alfalfa plants	Increased the shoot height, fresh and dry weights, yield and crude protein content	150 mM NaCl	Liu et al. (2019)

phytotoxic, and/or antitumor mediators (Olanrewaju et al. 2017). *Bacillus* and *Pseudomonas* bacterial genera secreted this type of metabolites. Halophilic microbes are also able to produce enzymes such as lipase, cellulase, β-1, 3-glucanase, chitinase, and protease which can degrade cell wall and fungal growth (Husson et al. 2017; Vaddepalli et al. 2017). Halophilic microbes compete for nutritive ingredients or for sites binding on roots of plants, and this type of antagonism reduces the growth of phytopathogen or mandatory destroyed proliferation of plant–pathogen (Olanrewaju et al. 2017). Halophilic microbes such as *Alcaligenes*, *Aeromonas, Bacillus, Rhizobium,* and *Pseudomonas* can produce hydrogen cyanide production, and the presence of this chemical substance may control phytopathogens (El-Rahman et al. 2019; Suman et al. 2016; Verma et al. 2018; Yadav et al. 2018c).

Halophilic microbes activate induced systemic resistance and enhance immunity against phytopathogens (Olanrewaju et al. 2017). Halophilic microbes disrupt signaling pathways of phytopathogens by quorum quenching approach. For interference of signal pathways to minimize pathogen virulence, some specific degrading enzymes, such as lactonase, are responsible (Olanrewaju et al. 2017). Halophilic microbes synthesized siderophore and inhibited the proliferation phytopathogens due to decrease in the iron availability to phytopathogens (Ahmed and Holmström 2014). The halophilic microbes provide biocontrol of phytopathogens by the production of antibiotics and antifungal metabolic substances. *Fusarium sambucinum*, *F. roseum* var. *sambucinum, F. oxysporum, F. moniliforme, F. graminearum, Penicillium citrinum*, *Aspergillus flavus*, and *Botrytis cinerea* are phytopathogenic fungi that are controlled by halophilic rhizospheric bacteria *B. subtilis, B. cereus*, *B. pumilus*, *B. licheniformis, C. alkalitolerans, Halomonas elongate*, and *Halobacillus halophilus*, *Halobacillus faecis*, *Salinicoccus roseus* (Ahmed and Holmström 2014; Olanrewaju et al. 2017; El-Rahman et al. 2019).

11.7 Role of Halophilic Microbes in Sustainable Agriculture

Chemical fertilizers and pesticides are commonly used by the farmers for improvement of soil fertility, growth, and productivity of crops under salt-based and non-salt-based ecosystem (Ju et al. 2018). But their regular use causes an adverse effect on living organism and soils (Bernardes et al. 2015). Apart from these, chemical fertilizers remediate in the crop which feed by the organisms and ultimately reach to top consumers and cause numerous diseases (Gonçalves et al. 2014). However, many transgenic salt-tolerant crops have been developed but far too little is successful (Bharti et al. 2016). An alternative method is available which could replace chemical fertilizers and pesticides and also improve soil health, seed germination, crop growth, and productivity by rhizospheric bacteria (Vejan et al. 2016). These rhizospheric bacteria enhance the growth and improvement of plants either straight or circuitously by colonizing the plant root (Vejan et al. 2016; Kour et al. 2019b; Yadav et al. 2019b).

The uninterrupted character of PGPRs involves the fixation of nitrogen (N_2) secretion of metabolites, for instance, the indole-acetic acid (IAA) production, ammonia, solubilization of phosphate, siderophore, and zinc (Ahemad and Kibret 2014; Chandra and Enespa 2016). Indirect growth promotion can be observed in the prevention and reduction of phytopathogens in plants through biocontrol mechanism. In this mechanism, PGPRs produce some lytic enzymes for fungal pathogens (cellulase, β-1, 3 glucanase, chitinase, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase), reduction of iron (Fe) from the soil/rhizosphere and hydrogen cyanide (HCN), salicylic acid, antibiotics, or antifungal compounds (Odoh 2017; Chandra and Enespa 2019a, b, c). Besides, PGPRs also accepted as capable rhizobacteria that can tolerant environmental stresses such as high salt, high temperature, and pH (Ahemad and Kibret 2014).

The plant growth-promoting rhizobacteria enhance nutrient availability that includes nitrogen fixation and phosphate-solubilizing microorganisms. In indirect means, it reduces the deleterious effect of plant pathogens on crop yield (Ahemad and Kibret 2014). It shows antagonism against phytopathogenic microorganisms by producing siderophore (Vejan et al. 2016). PGPR have been developed and used as biofertilizers. Biofertilizers containing these PGPRs are economical, environment-friendly, and potentially renewable source of necessary enriched plant nutrients that makes it an excellent substitute of harmful fertilizers and chemical (Vejan et al. 2016).

The mechanism-based action can be differentiated into three dissimilar groups, i.e, (1) Biofertilizer, containing PGPR having N_2 fixation and P solubilization capability, (2) biopesticide, containing PGPR that inhibits the growth of phytopathogenic microorganisms, and (3) phytostimulator, containing PGPR that have ability to produce phytohormones (Vejan et al. 2016). Various agronomically imperative PGPR include the species, such as *Alcaligenes* sp., *Caulobacter*, *Serratia*, *Erwinia*, *Bacillus, Enterobacte*r, *Phyllobacterium* sp., and *Bacillus thuringiensis*, *Hyphomicrobium*, *Azotobacter*, *Azospirillum,* and *Acetobacter* (Sharma et al. 2013; Ahemad and Kibret 2014; Vejan et al. 2016; Kour et al. 2019a; Verma et al. 2016a, b). The PGPR used as bio-pesticides and biofertilizers for supportable farming have augmented enormously all over the world. The useful properties of PGPR on the improvement and the production of crops have been studied and reported by worldwide on a wide variety of crops such as pulses, vegetables, cereals, and oilseed crops (Gouda et al. 2018). Numerous PGPRs belonging to genera *Pseudomonas*, *Bacillus*, *Azospirillum,* and *Enterobacter* have been screened from the rhizospheric habitat of various economically important crops and were reported for their synergistic effect on plant growth promotion (Egamberdiyeva et al. 2001).

11.8 Conclusions and Future Prospects

Halophilic microbes are isolated from saline soils or rhizosphere of halophytic plants and shows plant growth-promoting characters directly like the production of IAA, solubilization of phosphate, production of siderophore, fixation of N_2, deaminase ACC activity, or indirect ways by controlling phytopathogens under saline condition. However, the habitats of halophilic microbes may be rhizosphere, endophytic, or phyllosphere, and these microbes can augment the biomass and productivity of crops using the halophytic and halotolerant crops. The inoculation of halotolerant microbes in the rhizosphere of crops is a viable strategy for eco-friendly approach and supportable improvement of crop in salt-related farming, which consist of cultivation of crops in dry and semidry regions. Several possibilities of study would move us earlier to accepting these approaches for salt-related cultivation. Knowledge of plant–microbe interactions facilitates policies for the protection of crops and saline soil remediation, and this type of interactions is also observed in the area for ecological appreciative of microbes, which promotes halophyte to adaptability in salinity-rich environment.

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Chapter 12
Microbe-Mediated Drought Tolerance in Plants: Current Developments and Future Challenges

Iti Gontia-Mishra, Swapnil Sapre, Reena Deshmukh, Sumana Sikdar and Sharad Tiwari

Abstract Drought is a conspicuous stress-causing deleterious effect on plant growth and productivity. In order to compensate the yield loss due to drought, efficient and sustainable strategies are required for its management. Drought stress tolerance is complex trait involving clusters of genes; hence, genetic engineering to generate drought-resistant varieties is a challenging task. In this context, the application of plant growth-promoting microbes (PGPM) to mitigate drought stress is gaining attention as an attractive and cost-effective alternative strategy. PGPM have envisaged a plethora of mechanisms to overcome drought stress in plants which encompasses ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, production of exopolysaccharide (EPS) and volatile organic compounds (VOCs), osmolyte and antioxidant production, enhanced uptake of mineral nutrients, phytohormones production, and modulation. These mechanisms either individually or collectively bestow the PGPRs to combat drought stress in plants. The association of arbuscular mycorrhizal fungi (AMF) with the roots of crop plants can significantly promote water and nutrient uptake by host plants and induce tolerance to drought stress. The inoculation of PGPM in crop plants is also capable of modulating host transcriptome for induced drought tolerance. Further, efforts are needed to develop proficient microbial consortia for enhancing plant growth under drought stress. Thus, the application of PGPM/AMF represents a promising approach to increase nutrient availability and expedite the development of sustainable agriculture.

Keywords Drought · Plant growth-promoting rhizobacteria · Arbuscular mycorrhizal fungi · Sustainable agriculture

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12.1 Introduction

Plants being sessile are subjected to a wide array of environmental stresses such as salinity, drought, heavy metals, waterlogging, chilling, and high temperature. Furthermore, climate change is influencing the austerity of abiotic stresses, particularly high temperature and drought. Intense drought is mostly associated with the global climate change which is having a major impact of crop productivity (Etesami and Maheshwari 2018). It is being projected that drought will affect more than 50% of the arable lands worldwide by the year 2050 (Vurukonda et al. 2016). Among these stresses, drought is a conspicuous stress-causing deleterious effect on plant growth and productivity. This stress adversely affects many physiological and biochemical processes of plants such as phytosynthesis, respiration, transpiration, carbohydrates metabolism and nutrient uptake, translocation, and assimilation (Khan et al. 2018). In order to compensate the yield loss due to drought, efficient and sustainable strategies are required for its management. From past years, mainly two strategies are mostly focused to combat the drought stress in plants such as traditional breeding methods and genetic engineering of crop for drought-resistant (Naveed et al. 2014). The major constraint for application of these techniques is time taking, tedious, and expensive. Furthermore, the acceptance of a transgenic crop is uncertain in the market regarding the consumer response to genetically modified plant products which varies from country to country (Ullah et al. 2019a).

In addition to several ethical issues, genetic engineering of all crops is not feasible (Etesami and Maheshwari 2018). Besides, drought stress tolerance is complex trait involving clusters of genes; hence, genetic engineering to generate drought-resistant varieties is a challenging task (Nautiyal et al. 2013; Saikia et al. 2018). Another sustainable strategy to limit drought stress is soil resource management by application of mulching, crop residues, crop cover, non-crop mulch material (plastic foil, geotextile), etc. These methods tend to reduce runoff and evaporation from soil surfaces. Besides, use of crop residue as mulch can increase the soil organic matter which in turn increases the soil water storage capacity and its availability to crops during drought conditions (Bodner et al. 2015).

In this context, the use of plant growth-promoting microbes (PGPM) to mitigate drought stress is gaining attention as an attractive and cost-effective alternative strategy. There are various studies which suggest the beneficial role of plant growth-promoting rhizobacteria (PGPR), actinomycetes, and mycorrhiza in boosting plant growth and endurance toward drought stress (Gontia-Mishra et al. 2016; Saikia et al. 2018; Zade et al. 2019). This chapter summarizes the present understanding toward drought stress and their physiological and molecular responses in plants. The later section of the chapter highlights the imperative mechanisms of PGPM for mitigation of drought stress in plants. In the present chapter, we have also attempted to comprehend the perceptive use of PGPM to alleviate the drought stress in crop plant by fine-tuning the metabolic, signaling, and molecular pathways, thereby enhancing crop productivity.

12.2 Impact of Drought on Crop Plants

Similar to other abiotic stresses, drought is also multidimensional in its effects and has various deleterious impacts on plant. The plants respond to drought stress at physiological, biochemical, and molecular levels, from seed germination to maturity and senescence (Tiwari et al. 2017). Nonetheless, adaptability of plants to drought is determined by the severity and time of exposure to stress, plant species as well as the developmental stages (Kaur and Asthir 2017). Under water scarcity, plant exhibits various events to acclimatize such as morphological (reduced biomass and altered root structure), physiological (reduced photosynthesis and altered transpiration and stomatal activity), and biochemical changes (accumulation of osmolytes, increased oxidative enzyme activity) (Conesa et al. 2016).

Excessive loss of water in drought condition leads to closed stomata and controlled gas exchange and desiccation which lead to complete metabolism and cellular structure disruption; this gradually ends in interruption in enzymatic reactions (Jaleel et al. 2007). Aboveground parts of plant are more susceptible to drought stress than their counterparts. During water-deficit conditions, plants respond by shrinking leaf area, spiraling, and in some cases by shedding their leaves. Leaf size reduction is an important strategy to drought stress as it can directly influence the rate of transpiration. However, reduction in leaf size leads to marked decline in the photosynthetic activity of plants. Drought stress in plants is noted by declined leaf water potential, stomatal closure, and marked reduction in cell growth (Farooq et al. 2009). The first plant organs to feel and react to water deficiency are the roots. Under moderate drought stress, the root length is increased which is attributed to the plants need to utilize the groundwater (Forni et al. 2017), but severe drought conditions can retard root growth. Characteristics related to root traits like biomass, root length, root density, and depths of roots have been identified as the major drought avoidance traits under drought environment (Kashiwagi et al. 2006). A decrease in growth is the most obvious plant response to water stress, which results from decrease in water uptake by roots.

Plant growth and morphology are proportional to enlargement, division, and differentiation of cell. Drought is also reported to inhibit mitotic division of cells along with elongation and expansion which results in growth retardation of plants (Hussain et al. 2008). Various physiological changes occur in plants to overcome drought stress as the early response of plant to stress can make the plant to survive. The basic mechanism to show drought response is to decrease the osmotic potential of plant cells; as a result, the turgor potential gets maintained for routine metabolic processes (Levitt 1980). Drought stress leads to an imbalance between antioxidant defenses and the amount of Reactive Oxygen Species (ROS) resulting in oxidative stress. ROS are required to trigger the signaling but eventually at high concentration can cause impairment of plant organelles especially chloroplasts (Smirnoff 1993). Later on, ROS can initiate lipid peroxidation and degradation of vital proteins, lipids, and nucleic acids (Kaushal and Wani 2016).

Plants under drought stress starts synthesis of new metabolites for their proper functioning. Plants can accumulate biomolecules such as dehydrins (DHNs), heat shock proteins (HSPs), late embryogenesis abundant (LEA) proteins (Lipiec et al. 2013), osmolytes like proline, trehalose, and sugars (Ilhan et al. 2015), glycine, and betaine (Chen and Murata 2011). Changes in membrane fluidity, fatty acid, and protein composition of membranes help to maintain the cellular integrity of plants under drought stress (Bohnert et al. 1995). The osmolytes like ectoine, glycine, and betaine interplay in protein solubilization, and the uncharged solutes like mannitol, trehalose, and pinitol play an important role as scavengers of ROS (Ashraf and Foolad 2007). Plants have envisaged several enzymatic mechanisms including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR) and non-enzymatic components such as cysteine, glutathione, and ascorbic acid, to aid them fight against the oxidative damage caused by ROS (Kaushal and Wani 2016).

Nitric oxide also protects plants under water-deficit condition from oxidative stress. Most of these processes are regulated through a complex network governed by abscisic acid (ABA), ion transport system, and various transcription factors. Water stress in the root tips results in release of a stress-signaling hormone ABA, which is transported from root zone to the aerial parts of plants. It is directly involved in regulation of stomatal aperture closure. Various reports argued that early interaction of drought signals is mediated by transmembrane protein like histidine kinase which functions like osmosensor (Posas et al. 1996; Urao et al. 1999). Other membrane proteins like aquaporins also involved in regulation of cell volume and turgor homeostasis. In addition, some genes are also identified which regulates the synthesis of osmolytes in the cytoplasm in order to maintain the osmotic potential at water stress condition. Other mechanism involved in sensing of drought stress is changed in the fluidity of membrane lipids (Knight and Knight 2001). Phospholipase C and D along with phosphatidyl-4,5-phosphate 5-kinase are found to be involved in this mechanism which leads to control ion and water channels (Mikami et al. 1998).

12.3 PGPM with Special Context to Drought Stress Management

Almost every parts of the plant are colonized by microbes, but the rhizosphere (soil in the proximity of roots) represents the main source of bacteria with plant-beneficial activities. The microbial community residing in the rhizosphere is comparatively different than its surroundings due to the presence of root exudates (Vejan et al. 2016). These bacteria largely utilize root exudates a source of nutrients for their growth and survival, hence termed as PGPR (Kolepper and Schroth 1978; Verma et al. 2015a, b; Yadav et al. 2015). They interact with the plant roots and influence plant growth and yield as well as enhance soil fertility. Besides PGPR, association of arbuscular mycorrhizal fungi (AMF) with the roots of crop plants can significantly promote water and nutrient uptake by host plants and induce tolerance to drought stress (Xu et al. 2018; Hashem et al. 2019; Yadav et al. 2019b, c, d). Many researchers have advocated the positive impact of PGPR and AMF to promote plant growth under drought stress; hence, it is an effective developing technology (Compant et al. 2010; Carmen et al. 2016; Wu et al. 2019; Verma et al. 2017; Yadav et al. 2018a, b). Crop plants in association with PGPRs persuade morphological and biochemical adjustments leading to increased tolerance to drought by eliciting induced systemic tolerance (IST) (Naveed et al. 2014).

It is determined that PGPR can intercede the drought stress in host plant by increasing accumulation of osmolytes (compatible solutes like proline, glycine betaine, polyamines, sugars like trehalose and polyols), improved uptake of nutrients and modulating the activities of antioxidant enzymes (Barnawal et al. 2019; Kour et al. 2019c; d). Phytohormones are known to control signaling of many abiotic and biotic stresses in plants. It is an established fact that phytohormone synthesis and signaling have a great significance in response to extreme environmental conditions (Tiwari et al. 2017; Kour et al. 2019b; Yadav et al. 2019a). Interestingly, this approach is adopted by PGPR to induce drought tolerance in host plant by regulating the level of phytohormones, like ABA, salicylic acid (SA), and ethylene, therefore directly affecting plant signaling networks and altering drought-responsive genes (Lu et al. 2018). Similarly, inoculation of AMF in host plants can accelerate plant growth and yield under drought stress by increased water and nutrient uptake, modulating stress-responsive genes and cell membrane fatty acid composition and degree of unsaturation (Xu et al. 2018; Wu et al. 2019). The use of various PGPR and AMF for alleviation of drought stress and their positive impact on host plants is presented in Tables 12.1 and 12.2.

12.4 Ways Out by Which PGPM Handle Drought Stress

PGPM have envisaged a plethora of mechanisms to overcome drought stress in plants which encompasses ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, production of exopolysaccharide (EPS) and volatile organic compounds (VOCs), osmolyte production, uptake of mineral nutrients (N, P, and K), phytohormones production/modulation [auxin/indole acetic acid (IAA), cytokinins, abscisic acid (ABA), salicylic acid (SA) and jasmonic acid (JA)], and eliciting the activity antioxidant enzymes in host plants. These mechanisms either individually or collectively bestow the PGPRs to combat drought stress in plants.

12.4.1 ACC Deaminase Activity

Ethylene is a crucial plant hormone which controls a number of plant processes ranging from seed germination, fruit ripening, abscission of leaves, and plant senescence

Table 12.1 The role of PGPR in mitigating drought stress in plants

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus spp.	Rhizosphere of *Pennisetum glaucum*, *Helianthus annuus*, *Zea mays*	*Z. mays*	EPS and IAA, gibberellins, cytokinin production, and P-solubilization	Inoculated maize seedlings showed improved physiological response to drought	Vardharajula et al. (2011)
Bacillus licheniformis	Field soil	*Capsicum annuum*	ACC deaminase activity	PGPR-inoculated pepper plants tolerate the drought stress and showed differentially expressed stress proteins	Lim and Kim (2013)
Burkholderia phytofirmans	Roots of onion	*Triticum aestivum*	IAA production and ACC deaminase activity	PGPR inoculation improved grain yield and nutrients in grains	Naveed et al. (2014)
Pseudomonas aeruginosa	Rhizosphere of *Vigna radiata*	*V. radiata*	IAA, ACC deaminase, P-solubilization, and endogenous proline and glycine betaine accumulation	Increased the levels of antioxidant enzymes, proline, and subsequently modulated the regulation of stress-responsive genes in PGPR-treated plants under water stress conditions	Sarma and Saikia (2014)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus thuringiensis and *Paenibacillus polymyxa*	*Pinus ponderosa* and *Oryza sativa*	*T. aestivum*	ACC deaminase activity and P-solubilization	Greater plant biomass and fivefold higher survivorship under severe drought; reduced emissions of stress volatiles	Timmusk et al. (2014)
Pseudomonas spp., *Bacillus cereus,* and *Arthrobacter* sp.	Rhizosphere soil	*O. sativa*	IAA production	Improved plant growth and antioxidant defense systems and stability of membranes in plant	Gusain et al. (2015)
Bacillus subtilis	Roots of *Panicum virgatum*	*Brachypodium distachyon*	Phytohormone production and P-solubilization	Amelioration of phenotypic effect of drought and up-regulation of drought-responsive genes	Gagné-Bourque et al. (2015)
Klebsiella sp, *Enterobacter ludwigii,* and *Flavobacterium* sp.	Rhizosphere of *T. aestivum*	*T. aestivum*	IAA and siderophore production, ACC deaminase, P and Zn solubilization	Affected various growth parameters, water status, membrane integrity, osmolyte accumulation, and stress-responsive gene expressions, which were positively altered by PGPR inoculation in wheat under drought	Gontia-Mishra et al. (2016)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Pseudomonas putida and *Bacillus amyloliquefaciens*	–	*Cicer arietinum*	ACC deaminase activity, minerals solubilization, biofilm formation	PGPR inoculation improved the biomass and antioxidant enzymes in plants under drought stress	Kumar et al. (2016)
Pseudomonas putida	Desert regions of Rajasthan	*C. arietinum*	IAA production and P-solubilization	Altered various physiological and biochemical parameters as well as regulation of stress-responsive genes	Tiwari et al. (2016)
Bacillus subtilis	Rhizosphere soil of lemongrass	*T. aestivum*	IAA production and ACC deaminase activity	PGPR inoculation improved the physiological parameters such as net CO_2 assimilation, stomatal conductance, and transpiration rate as well as increased the endogenous IAA and ABA content under drought stress	Barnawal et al. (2017)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Azospirillum spp.	Roots of wheat and maize	*Z. mays*	N_2 fixation, IAA and siderophore production, ACC deaminase activity, P-solubilization	Significant biomass gain and better osmotic balance were noted in PGPR-inoculated plants under drought stress	García et al. (2017)
Enterobacter cloacae and *Citrobacter* sp.	Rhizosphere of *T. aestivum*	*T. aestivum*	IAA and siderophore production, ACC deaminase, P, K, and Zn solubilization	Bio-inoculants showed growth enhancement of wheat seedlings under drought stress	Gontia-Mishra et al. (2017)
Bacillus amyloliquefaciens	Alkaline soil	*O. sativa*	IAA production, ACC deaminase activity, P-solubilization, and proline accumulation	PGPR inoculation positively stimulated membrane integrity and osmolyte accumulation as well as modulated the drought-responsive genes under water-deficit condition	Tiwari et al. (2017)
Pseudomonas fluorescens, *Enterobacter hormaechei*, and *Pseudomonas migulae*	*Setaria italica*	*S. italica*	ACC deaminase activity and EPS production	PGPR inoculation caused a significant increase in dry biomass	Niu et al. (2018)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus amyloliquefaciens	–	*Arabidopsis thaliana*	EPS and IAA production	Increased the survival rate of plants, biomass, osmolytes, antioxidant enzyme activities, and modulated stress-responsive genes	Lu et al. (2018)
Ochrobactrum pseudogrignonense, *Pseudomonas* sp, and *Bacillus subtilis*	Rhizosphere soil	*Vigna mungo* and *Pisum sativum*	ACC deaminase activity, IAA production, and P-solubilization	Better plant growth and biomass, increase activity of antioxidant enzymes, down-regulation of ACC-oxidase gene under drought stress	Saikia et al. (2018)
Enterobacter sp. and *Bacillus* sp.	*Mucuna pruriens*	*M. pruriens*	ACC deaminase activity and IAA production	Improved photosynthetic performance and biomass and increased leaf isoprene content	Saleem et al. (2018)
Bacillus licheniformis	Compost	*A. thaliana*	IAA production and P-solubilization	Exposure to PGPR increased the tolerance toward water deficits and positive-modulated stress-responsive genes	Sukkasem et al. (2018)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Bacillus subtilis and *Paenibacillus illinoisensis*	–	*Capsicuum annuum*	Synthesis of nitric oxide and volatile organic compounds	Increase in root length and photosynthetic activity as well as enhanced expression and activity of vacuolar proton pumps	Vigani et al. (2018)
Variovorax paradoxus, Pseudomonas spp., *Achromobacter* spp, and *Ochrobactrum anthropi*	*T. aestivum*	*T. aestivum*	ACC deaminase activity	Improved plant growth and foliar nutrient concentrations and significant changes in antioxidant properties in treated with PGPR under drought stress	Chandra et al. (2019)
Pseudomonas spp., *Bacillus* spp.	–	*A. thaliana*	EPS and phytohormone production	Bio-inoculation remarkably increased the biomass and plant water content under drought stress	Ghosh et al. 2019

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Paenibacillus beijingensis and *Bacillus* sp.	–	*T. aestivum* and *Cucumis sativus*	–	Bio-inoculation significantly increased seed germination, whereas decreased free proline and soluble sugar in the plants. The modulation of stress-responsive and ROS scavenging genes in PGPR-treated plants under drought stress was noted	Li et al. (2019b)
Streptomyces pactum		*T. aestivum*	Biocontrol agent against antagonists	Enhanced osmotic adjustment and antioxidant capacity of plants via induction of abscisic acid accumulation and up-regulation of drought resistance-related gene expression	Li et al. (2019c)

(continued)

Table 12.1 (continued)

PGPR strain	Source of isolation	Crop	PGPR traits	Effect on plants	References
Pseudomonas simiae	Rhizosphere of *Glycine max*	*G. max*	ACC deaminase activity	PGPR inoculation increased the accumulation of osmolytes and sugars as well as down-regulated the drought stress-responsive genes	Vaishnav and Choudhary (2019)
Bacillus pumilus	Roots of *Glycyrrhiza uralensis*	*G. uralensis*	–	PGPR inoculation increased the total biomass, oxygen species, and antioxidants in plants. It also enhanced the flavonoids, total polysaccharide, and glycyrrhizic acid contents in plants under drought conditions	Xie et al. (2019)
Streptomyces rimosus and *S. monomycini*	–	*Mentha piperita*	Auxin and siderophore production, biocontrol activity against *Phytophthora drechsleri*	PGPR inoculation increased the biomass and growth and essential oils as well as menthol content under drought stress	Zade et al. (2019)

Table 12.2 The role of AMF in mitigating drought stress in plants

Crop/plant	Effect of AMF inoculation on plant	References
Strawberry	AMF inoculation plants had greater water-use efficiency under the regulated deficit irrigation (RDI) regime in comparison to non-mycorrhizal inoculated plants	Boyer et al. (2015)
Phaseolus vulgaris	AMF inoculation and methyl jasmonate prevented inhibition of root hydraulic conductivity under drought conditions, by causing reduction in root salicylic acid contents	Sanchez-Romera et al. (2016)
Zea mays	AMF symbiosis induced an improvement in physiological parameters in drought-sensitive plants including efficiency of photosystem II, membrane stability, accumulation of soluble sugars and plant biomass production. In addition, the drought-responsive genes were down-regulated by the AMF inoculation	Quiroga et al. (2017)
Sorghum bicolor	AMF inoculation alleviated plant growth retardation and prolonged plant lifespan under drought. The improved biomass and the specific leaf area were noted in inoculated plants under drought stress conditions	Sun et al. (2017)
Poncirus trifoliate	AMF inoculation significantly increased leaf sucrose, glucose, and fructose concentration under drought stress, accompanied with a significant increase of leaf sucrose phosphate synthase, neutral invertase, and net activity of sucrose-metabolized enzymes	Wu et al. (2017)
Damask rose	AMF colonization can enhance growth, flower quality, and adaptation of rose plants under drought stress levels, particularly at high level of drought stress via improving their water relations and photosynthetic status	Abdel-Salam et al. (2018)
Poncirus trifoliate	AMF inoculates seedlings showed significantly higher root density, length, and diameter and root IAA level under stress. Mycorrhization caused the up-regulation in IAA biosynthesis. The inoculation also down-regulated the transcript level of root auxin efflux under drought stress	Liu et al. (2018)
Zea mays	AMF association modifies root hydraulic responses to drought. AMF plants showed increased hydrostatic root hydraulic conductivity and osmotic root hydraulic conductivity	Quiroga et al. (2018)
Sorghum bicolor	AMF inoculation improved their transpiration efficiency and increased the nitrogen and phosphorus content of sorghum, especially under water was limiting conditions	Symanczik et al. (2018)
Glycyrrhiza uralensis	The inoculation of AMF to the plants demonstrated improved growth and physiological status such as stomatal conductance, photosynthesis rate, and water-use efficiency compared with non-AM plants. The AMF association also up-regulated the expression of an aquaporin gene PIP and decreased root abscisic acid concentrations	Xie et al. (2018)
Leymus chinensis and *Hemarthria altissima*	AMF inoculation to plants enhanced plant biomass, photosynthetic rate, stomatal conductance, intrinsic water-use efficiency, and SOD activity of the *L.chinensis* and reduced levels of malondialdehyde. The inoculation also demonstrated increased shoot growth in *H.altissima*	Li et al. (2019a)

(Sapre et al. 2019). It is also produced in plant in response to several environmental stresses including drought stress (Gontia-Mishra et al. 2014). Consequently, the ethylene generated under stressful condition is often termed as "stress ethylene" (Glick 2014). The ethylene produced during stress can subsequently induce the defoliation, retarded root, and stem growth along with the expression of genes leading to plant senescence, leading to inferior crop performance (Vejan et al. 2016). Interestingly, it is noted that ACC works as precursor for ethylene biosynthesis (Shaharoona et al. 2006). Among the different suggested strategies for improvement in plant growth under drought stress, the most plausible one is alteration in the endogenous levels of ethylene caused by the PGPR (Kumar et al. 2019a, b).

Furthermore, many PGPR possessing the enzyme ACC deaminase catalyze the conversion of ACC to ammonia and α-ketobutyrate, which indirectly decrease the ethylene concentration in plants under drought stress (Glick et al. 1998). By facilitating the development of longer roots, these PGPR may enhance the survival of seedlings, which help in combating the effect of stress ethylene. The root elongation plants under drought stress can allow a better access to water and uptake of nutrients. Ethylene is also known to compromise the nodule formation and nitrogen fixation in legume (Sapre et al. 2019). *Rhizobium* with ACC deaminase activity can diminish the deleterious effect of ethylene under drought stress by increasing the nodulation and nitrogen fixation in its symbiotic legume partner (Belimov et al. 2009). In this regard, numerous researchers have documented the application of ACC deaminase-producing PGPR in ameliorating drought stress in crop plant such as chickpea (Tiwari et al. 2016), mung bean (Sarma and Saikia 2014), wheat (Gontia-Mishra et al. 2016; Barnawal et al. 2017), rice (Tiwari et al. 2017), foxtail millet (Niu et al. 2018), and other tropical crop plants (Kumar et al. 2019a, b; Kour et al. 2019a; Yadav et al. 2017a; b; Yadav and Yadav 2018).

12.4.2 EPS Production

PGPR have the unique ability to produce exopolysaccharide (EPS)/extracellular polymeric substances. The biofilm formation and EPS production by PGPR are important mechanisms to tolerate drought stress in the environment. The EPS has multifarious function in bacterial cells ranging from quorum-sensing signals, development, survival, and host colonization (Nocelli et al. 2016). The EPS largely constitutes of high-molecular-weight macromolecules like polysaccharide along with smaller proportions of protein, lipids, and uronic acid (Naseem et al. 2018). The EPS-producing PGPR can better clamp and colonize the root surface under adverse conditions (Ali et al. 2014).

It can protect PGPR and its host plant under drought stress by enhancing water retention than the surrounding environment (Hepper 1975; Vurukonda et al. 2016). The EPS secreted by PGPR into the soil can be absorbed by soil particle due to their different anionic functional groups (e.g., sulfhydryl, carboxyl, hydroxyl, sulfonate, amine, and amide) and increase the water-holding capacity of soil and improve physicochemical properties of soil under prolong desiccation conditions (Sandhya et al. 2009). Hence, plants inoculated with EPS-producing PGPR can maintain the higher water potential, boost root-adhering soil/root tissue ratio, and accelerate the uptake of nutrients by plant, thereby enhancing plant growth and yield under drought stress (Selvakumar et al. 2012; Rolli et al. 2014; Kaushal 2019). Many researchers have suggested the use of EPS-producing rhizobacteria in alleviating drought stress in important crop plants such as maize (Vardharajula et al. 2011), sunflower (Sandhya et al. 2009), wheat (Timmusk et al. 2014), and foxtail millet (Niu et al. 2018).

12.4.3 Production of VOCs

Unlike plants, soil bacteria produce a range of volatile compounds, which have specific function in their life cycles as well as interplay with other microbes and plants (Sharifi and Ryu 2018). The bacterial VOCs are chemically characterized as alkenes, ketones, and alcohols. PGPR can stimulate plant growth by synthesizing and releasing volatile compounds, which is now known as an essential mechanism of plant–microorganism interactions (Froni et al. 2017). The role of these VOCs is largely associated as activator against plant pathogens, leading to induced systemic resistance in plants (Ruzzi and Aroca 2015). Remarkably, it is noted that besides their role in biotic stress tolerance, these compounds can actively alleviate several abiotic stresses including drought (Timmusk et al. 2014). The VOCs produced by PGPRs can promote plant growth by increasing photosynthesis, carbon assimilation, enhancing mineral uptake, altering root structure, and intensive phytohormone signaling under abiotic stress conditions (Sharifi and Ryu 2018).

It was demonstrated that a PGPR *Pseudomonas chlororaphis* releases characterized as 2R, 3R-butanediol, can induce drought tolerance in *Arabidopsis thaliana* (Cho et al. 2008). Moreover, few studies suggest the role of VOCs (produced by PGPR) in modulation of the transcript levels in plants, resulting in enhanced biosynthesis of choline and glycine betaine which in turn to shielded *A. thaliana* plants from drought stress (Cho et al. 2008; Zhang et al. 2010). It was noted that VOCs produced by soil bacteria such as acetic acid can stimulate the formation of biofilms/EPS, which can indirectly influence drought stress in plants (Chen et al. 2015). Another study of bacterial inoculation with *Bacillus thuringiensis* in wheat seedlings under drought stress markedly decreased the stress-induced volatile compounds emitted by plants and increased plant biomass and photosynthesis (Timmusk et al. 2014). VOCs producing PGPR are potential for application as bio-stimulants to improve plant health under drought stress. The mechanism of PGPR-induced VOCs in ameliorating drought stress in crop plants is limited and requires to be explored extensively.

12.4.4 Phytohormones Production

The production of phytohormones in plants is essential because of their physiological effects on its growth. The phytohormones such as auxins, cytokinins, gibberellins and ethylene, and abscisic acid (ABA) have a particular function in the regulation of plant growth and development (Vurukonda et al. 2016). PGPR have been widely known to produce these phytohormones which can help in promoting plant growth under stressed conditions by stimulating cell growth and division (Kaushal 2019). One of the important aspects of the bacterial–plant interaction that has received worldwide attention is the bacterial production of IAA/auxins. Production of IAA, a plant hormone that does not any apparent function as a hormone in bacterial cells, may have evolved in bacteria because of its significance in the bacterium–plant relationship (Patten and Glick 2002). A positive correlation is noted between the in vitro production of auxins by PGPR strains and their growth promotion effects (Jha et al. 2012). The auxin-producing PGPR can influence root proliferation and formation of lateral and adventitious roots, which results in an increased mineral and water uptake by the plants rotoscoping them against drought stress (Gontia-Mishra et al. 2016). Besides, some of the PGPR have known to modulate the expression of auxin-responsive genes in host–plant roots (Lakshmanan et al. 2013) resulting in stress tolerance in plants. Several authors have suggested the IAA production by PGPR as a mechanism to drought tolerance enhancement in crop plants such as maize, wheat, mung bean, etc. (Naveed et al. 2014; Sarma and Saikia 2014; García et al. 2017).

Gibberellins have a crucial function in plant growth such as stem elongation, germination, flowering, and senescence (Kaushal 2019). In contrast, cytokinins play a vital role in regulation of cell division and nutrient allocation, and maintain photosynthetic activity under drought stress (Ullah et al. 2019b). The application of cytokinin-producing PGPR, *Bacillus subtilis* in *Platycladus orientalis,* conferred drought stress tolerance by increasing shoot growth (Liu et al. 2013). Similarly, maize and soybean plants inoculated with gibberellin-producing PGPRs (*Pseudomonas putida* and *Azospirillum lipoferum*) registered improved plant growth under drought stress (Cohen et al. 2009; Kang et al. 2014). Consequently, there are evidences from many studies which advocate that PGPM have the ability to positively alter phytohormone levels of plant, leading to drought stress tolerance (Saakre et al. 2017; Ali et al. 2018).

12.4.5 Osmolytes Production and Alteration in Antioxidant Enzyme Activities

Water-deficit conditions result in altered osmotic balance in plants; hence, the water-absorbing capacity of plants get reduced and plant tries to change various physiological and biochemical processes for adaptation under stressed environment. Under these conditions, plants tend to produce a wide range of osmolytes or commonly known as osmoprotectants. Some cellular events like protein and membrane stabilization are supported by osmoprotectants (Nahar et al. 2016). Due to their diverse chemical properties, osmolytes also protect plant cells from oxidative stress by attacking on ROS (Zhu 2002). There are several osmoregulators like proteins, sugars, and free amino acids reported to play a key role in balancing osmotic pressure in plant cells (Hasegawa et al. 2000). It is reported in various studies that microbes residing in soil also produce and secrete osmolytes when encounter to drought stress. These osmolytes function as produced by plants. Maize inoculated with *Pseudomonas fluorescence* growing under drought has potential for accumulating proline and resulted in increased water content and plant biomass (Ansary et al. 2012). Soil microbes also reported to alter the amount of osmoprotectants and antioxidant enzyme in plants (Kaushal 2019).

Plants in response to drought also generate various types of ROS oxidative damage by reacting with importing biomolecules like protein and lipids of cell. To protect from this oxidative damage, cell has developed antioxidant defense system which includes enzymatic as well as non-enzymatic pathway (Miller et al. 2010). Inoculation of plants with beneficial microbes suppresses the activity of antioxidant enzyme activity to alleviate the drought stress. Various species of *Pseudomonas* and *Bacillus* inoculated with maize are reported to reduce the activity of antioxidant enzymes when compared to un-inoculated plants under drought (Sandhya et al. 2010; Vardharajula et al. 2011).

12.4.6 Nutrient Availability

Water deficit can reduce the uptake of nutrients in the soil due to poor soil structure. PGPR and AMF have the capability to increase the accessibility of nutrient in the rhizosphere either by fixing nutrients (N_2) or by solubilizing insoluble minerals such as P, K, and Zn into the soluble form (Vejan et al. 2016). The explanation for enhanced nutrient status in AMF inoculation in plant has increased absorption surface of extraradical hyphae for extensive acquisition of nutrients from soil. The extraradical hyphae of AMF have a deep network into the soil readily absorption of nutrients which in turn is transported to arbuscules in cortical cells and are finally released into the apoplast to ameliorate nutrient deficiency caused by stress (Zhao et al. 2015; Kaushal 2019). Several reports suggest that PGPR inoculation can improve uptake of nutrients especially P under drought stress (Sandhya et al. 2010; Timmusk et al. 2014). In addition, there are evidences of increased mobility of nutrients (P, N, K, Ca, and Zn) in plants inoculated with AMF during drought stress (Gholamhoseini et al. 2013; Zhao et al. 2015; Abdel-Salam et al. 2018).

12.5 Modulation of Host Transcriptome by PGPR Inoculation

The PGPRs have been efficiently utilized in crops to alleviate disease stress. Nevertheless, they can also be used as potential targets for inducing drought tolerance in crop species. Physiological studies in few crop species suggest an efficient application of PGPRs to reduce drought stress (Khan et al. 2018; Niu et al. 2018) (Fig. 12.1). Drought stress is a complex trait which influences various cross-linked signaling between biotic and abiotic stresses. Hence, the beneficial effects of PGPRs in biotic stress can indirectly induce tolerance to drought stress. This mode of genetic improvement comprises understanding the PGPR-induced biochemical differential regulation. These biochemical changes are governed by differential expression of genes involved in induced systemic response (ISR), which are ultimately triggered through salicylic acid (SA)-signaling pathway (Zhang et al. 2002). The PGPR inoculation greatly modifies the transcriptome of the plant species, regulating expression of several genes (Rekha et al. 2018). Microarrays and RNA-seq studies have been employed in certain crop species to understand the molecular mechanism of PGPR-induced drought tolerance.

PGPRs often colonize the root surface and may induce production of several phytochemicals that regulate phytohormone signaling like auxins and ABA (Srivastava

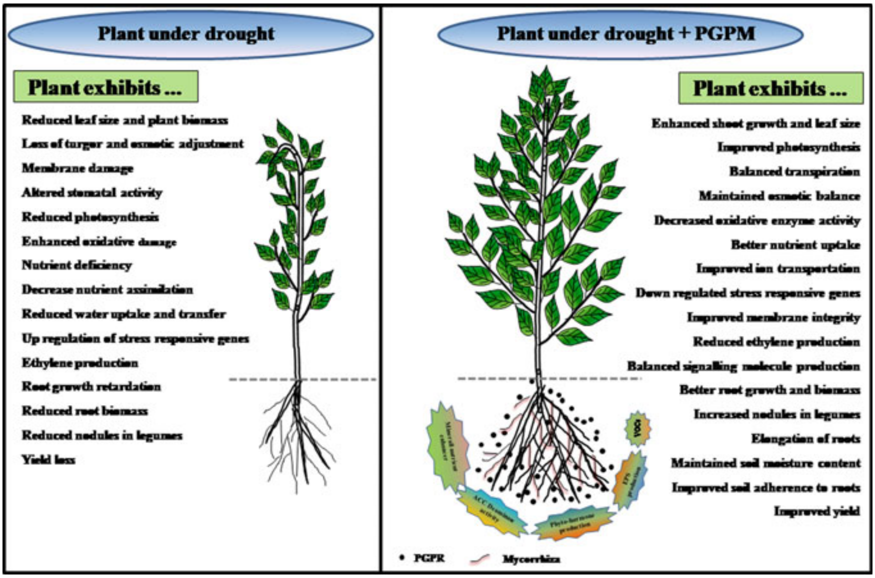

Fig. 12.1 Comparative account of effect of drought stress on plants without PGPM inoculation and with PGPR and AMF inoculation. The PGPR and AMF have envisaged diverse mechanisms for alleviation of drought stress in plants

et al. 2012). Systemic acquired resistance (SAR) is strongly regulated by phytohormones and their *in planta* levels. The inoculation of PGPR *Pseudomonas* sp. in rice plants induced the expression of LEA (late embryogenesis abundant) genes, which encodes IAA amido synthetases resulting in drought stress tolerance (Yasmin et al. 2017). Similarly, the inoculation of *A. thaliana* with PGPR *Paenibacillus polymyxa* induced drought tolerance through enhanced transcription of Early Responsive to Dehydration 15 (ERD15) gene (Timmusk and Wagner 1999). The drought alleviation by PGPR is mediated primarily through differential regulation of ABA-responsive pathway. The ABA-responsive signaling pathway transcription factor genes bZIP1, COC1, and Hsp20 proteins were overexpressed in susceptible rice cultivar upon PGPR *Pseudomonas fluorescens* inoculation, conferring drought tolerance (Saakre et al. 2017).

DHNs are a class of proteins of group 2 LEA proteins and proportionately related to their active accumulation during water stress tolerance. Microarray studies of barley seedlings overexpressing DHNs genes were drought-tolerant (Rodriguez et al. 2005). Plants expressing drought-tolerant CaDHN gene were highly expressed in pepper plant inoculated with PGPR *Bacillus licheniformis* (Lim and Kim 2013). DHN genes are interacting members of the SA-induced SAR response (Jing et al. 2016), commonly observed in PGPR-associated stress alleviation. The inoculation of water-stressed *A. thaliana* roots with *Pseudomonas chlororaphis* O6 induced an overexpression of LEA and dehydrin genes to over 100-folds (Cho et al. 2013). Trehalose is a nonreducing disaccharide, which is actively synthesized in bacteroids of *Rhizobium* sp. (Streeter 1985). It is an osmoprotectant and plays an essential role as a signaling molecule (Paul et al. 2008) during water stress management. The transformed *Rhizobium etli* and *Azospirillum brasilense* mutant with an overexpressing trehalose-6-phosphate synthase gene inoculated to *Phaseolus vulgaris* and maize, respectively, resulted in the enhanced expression of drought tolerance genes (Suárez et al. 2008; Rodríguez-Salazar et al. 2009).

To identify the transcriptional regulation of plants with drought stress in the presence of PGPRs, few transcriptomic studies have been undertaken. The PGPR inoculation improves drought stress tolerance by repressing the enhanced expression of abiotic stress response genes, viz., ABA and ethylene. The transcriptome study of sugarcane plants colonizing *Gluconacetobacter diazotrophicus* identified a reverse regulation of drought stress genes to that of stressed non-inoculated roots. The DREB1A/CBF3, DREB1B/CBF1, and NCED3 homologs were down-regulated in water-stressed plants treated with *G. diazotrophicus*. Although the auxin metabolism and ABA pathway were equally enriched in both the inoculated and non-inoculated plants, cytokinin hormone pathway up-regulation was observed only in the inoculated plants. However, the auxin, ABA, and ethylene-mediated stress-responsive signaling were mainly down-regulated (Vargas et al. 2014). Similar results have been demonstrated through transcriptome analysis of maize plants inoculated with *Pseudomonas putida* strain FBKV2 displayed drought stress alleviation, by Ali et al. (2018).

The expressions of ABA and ethylene signaling pathway genes were down-regulated, including down-regulation of bZIP transcription factor (TFs), and 1-aminocyclopropane-1-carboxylate synthase2 and ethylene-responsive TFs, respectively. The transcriptome of *A. thaliana* treated with PGPR *P. chlororaphis* O6 identified remarkable up-regulation of calmodulin and calcium-binding proteins. These genes play important role in cell-to-cell communication. The stress-responsive down-regulated genes in PGPR inoculation also include class of MYB and AP2 domain transcription factors (Cho et al. 2013). This clearly presents that plant growth-promoting bacteria reduce the drought stress by reducing the expression of stress-induced molecules, keeping optimum environment to plants. It is evident from several studies that PGPRs prime the stress-responsive pathway and following subjection of plants to drought stress reduces the production or biosynthesis of stress molecules.

12.6 Concluding Remarks and Future Prospects

Agricultural productivity is largely dependent on climatic conditions. Climate change is expected to reduce water accessibility for agriculture in coming years. Drought has the noxious effects on growth and development of plant. Hence, it is the need of the hour to search for the effectual solution to overcome the problem of drought stress in plants. Moreover, drought is a complex trait, so developing transgenic plants resistant to drought stress is also a challenging task. Under such stressful conditions, the interaction of plant and beneficial microorganisms is of great importance. The application of drought-tolerant PGPM has gained abundant attention as an alternative and eco-friendly option to mitigate drought stress in crop plants. Another effective option to combat drought stress in plant is the exogenous application of PGPM in combination with either the plant growth regulators (SA, JA, Trinexapacethyl, and ABA), polyamine-like putrescine, biochar (organic carbon), silicon nanoparticles, or seaweed extracts (Ali et al. 2017; Khan et al. 2019; Hashem et al. 2019).

In the current scenario, research must be concentrated to increase the number and diversity of effective and competitive drought-tolerant PGPM from drought-stricken agricultural ecosystems. The drought-tolerant PGPM could be useful to design new bio-inoculants/biofertilizers, especially for arid regions. Additionally, the performance of potential PGPR strains should be essentially assessed under field conditions, as plants usually face cyclic drought conditions rather than continuous drought. Further efforts are needed to develop proficient microbial consortia for enhancing plant growth under drought stress. Regardless of several findings, on the adaptation of plants under drought stress and their association with PGPM for mitigation of stress, substantial efforts are required to explore the underlying molecular mechanisms of interplay between plant and PGPM in soil to hasten the process of stress amelioration in crops. Thus, it could be concluded that the use of PGPM represents a promising approach to increase nutrient availability and expedite the development of sustainable agriculture under drought stress.

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Chapter 13
Microbial Consortium as Biofertilizers for Crops Growing Under the Extreme Habitats

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Abstract Biofertilizers are typically microbial formulations in organic carrier materials that improve soil health and crop growth and development. Of late the use of biofertilizers has gained much acceptance and research interest especially in the developed countries due to ecological impacts associated with the use of synthetic inorganic fertilizers in farming. Microbial formulations could be organism-specific or a consortium of organisms. Microbial consortium biofertilizers, the main focus of this chapter, have been reported as contributing significantly to plant adaptation to various abiotic stressors in "extreme" habitats. Many soil microorganisms are endowed with an array of capabilities ranging from production of growth-enhancing substances to the release of substances which ameliorate the effects of various abiotic stress conditions such as drought, salinity, pH stress, heat stress, pollutants, and nutrient deficiency. Besides exploring the MC biofertilizer operations and mechanisms (neutral and niche), it also relies on a network of intraspecific and interspecific

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interactions for sustainable growth and development of crops in challenged environments. Among these organisms are plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), mycorrhizal-helping bacteria (MHB), and a host of others that work together in consortium biofertilizer formulations.

Keywords Biofertilizers · Microbial consortium · Extreme habitat · Plant growth-promoting rhizobacteria (PGPR)

13.1 Introduction

The role of soil microorganisms in sustainable agriculture has gained prominence over the last decades. Soil microorganisms and their activities have contributed to all spheres of biotechnological advances such as molecular understudy of litter decomposition (Tamayo-Vélez and Nelson 2018), ecosystem processes and planetary earth systems (Lladó et al. 2017), and sustainable development-driven studies (Timmis et al. 2017). Among practitioners, policy-makers, academia, and international organizations, there has been increased calls for research to unravel more benefits of soil microbes particularly in food and agriculture (Compant et al. 2010; Clark et al. 2009; Odoh et al. 2019a), environmental remediation (Sam et al. 2017; Zabbey et al. 2017; Eze et al. 2018), and industrial applications (Odoh 2017; Zuroff and Curtis 2012).

Sustainable agriculture is a unique modern farming practice that promotes soil health, wholesome agricultural yield, and reduced pollution of cultivable soils. In addition, it is a strategic agrobiotechnology approach where the present societal food demands are met without compromising future generation's food security.

As the quest to feed the ever-growing human populations (7.7 billion) gets global momentum and the push to curb food insecurity intensifies (Glick 2012), there has been an un-quenching desire for increased yield per unit area production capacity. This is paramount so as to meet the growing demand for food, while also subverting pressures arising from the natural ecosystem (Pindi and Satyanarayana 2012; Chatzipavlidis et al. 2013). According to Food and Agriculture Organization (FAO) 2010 report, 60% increase in agricultural commodities demand is expected by 2030. More fascinating is the fact that more than 85% of this estimated yield will be emanating from developing countries whose economic growth is mainly dependent on agriculture (Mia and Shamsuddin 2010).

Microorganisms constitute one of the most diverse biological communities in the soil ecosystem. The interactions and activities of soil microbes aid increase in food production, earth geochemical stability, climatic, and biogeochemical cycles (Tringe et al. 2005; Hansel, et al. 2008). According to Odoh et al. (2019a), they live in complex biological settings within which exist interactions and influence of living and nonliving parameters. Advanced studies have, however, demonstrated the applicability of engineered species in medicine such as antibiotic resistance genes (Cycon et al. 2019) and microbial pigments in food industry (Sen et al. 2019) through understanding their behavioral pattern, complexity and mechanisms of actions (Kumar 2016; Ahmad et al. 2011).

In agriculture (Table 13.1), microbial consortium (MC) involves the symbiotic interactions of two or more microbial groups (Clark et al. 2009), for improved crop growth. Association of microbial groups enhances turnover of soil organic matters and mobilizes nutrients for plants growth and fixation of nitrogen (N) in leguminous crops (Nuti and Giovannetti 2015). As a result of the intrinsic advantages, MC acceptability and applicability by practitioners have increased unlike the use of a single strain, as demonstrated by Sarkar et al. (2011) who exploited metabolic versatility of microbial community for the treatment of organic wastes. In the bulk soil, MC lives in close interaction in the plant root canopy as phyllosphere bacillus, endophytes, and as members of a complex microbiota (Hacquard et al. 2015), thus justifying their seldom existence as a single strain. In spite of the individualistic characterization of the single cells, MC often responds to environmental stress as a unique organism. This is because they have more chances than any single strain among the population to adapt and take advantage of their internal beneficial interactions (Nuti and Giovannetti 2015). On regular intervals, their activities consist of a continuous shift between viable and culturable, and viable but non-culturable cells of the diverse components of the total population. Also, via unique chemical signaling mechanism ("quorum sensing"), MC detects and responds to cell population density and nutrient gradient through gene regulation. This mechanism thus helps in expressing appealing biochemical properties that enable their stability, functionality, robustness, and capacity to perform complex biochemical tasks.

With the increase in the global use of chemical fertilizer often beyond crop and soil's requirement thresholds (Sun et al. 2015; Liu et al. 2017), researchers and agriculturists are finding ways to limit the intense applications of agrochemicals and to significantly reduce their impacts on the soil ecosystem. Consequently, integration of natural biotechnological advantages of soil microbes in crop production systems would undoubtedly mitigate plants growth challenges, while also brightening the global desire for sustainable agriculture (Manindra et al. 2013; Odoh 2017). The process of co-metabolism is another interactive advantage of MC over single inoculum. This usually manifests when a specific microbial group gratuitously produces a specific metabolite which often serves as a potential limiting nutrient for another population within the consortium. This essentially helps to ensure complete mineralization of by-products which could constitute environmental nuisance to both plants and microbiota while optimizing soil arable functions.

Table 13.1 Microbial alleviation of extreme conditions associated with crop growth

Organisms	Stress conditions	Crop	Outcome	Mode and tolerant strategies	References
Rhizobium etli	Drought	*Phaseolus vulgaris*	Reduces the sensitivity of drought in plant and nodule dry weight, nitrogen content, and nodule functionality	Overexpressing this oxidase in bacteroides	Talbi et al. (2012)
Azospirillum brasilense	Drought	*Glycine max*	Improves plant traits that can help tolerance of water deficiency	Indole-3-acetic acid synthesis and nitrogen fixation	Hungria et al. (2015)
Azospirillum brasilense	Salinity	*Zea mays*	Enhance plant growth promotion and reduction in proline content	Alteration of the selectivity of Na^+, K^+, and Ca^{++} ions	*Fukami* et al. (2017) Fukami et al. (2018)
Achromobacter piechaudii	Heavy metal and salt stress	*Populus* Species *Lycopersicon esculentum*	Increase shoot and root growth and enhance root hair formation	IAA biosynthesis and overexpression of abiotic stress response gene	Fahad et al. (2015) Carmen and Roberto (2011)
Sinorhizobium arboris	Heat stress	Acacia Senegal Cajanus cajan	Maintain basal metabolic activity under adverse heat conditions	Enzymatic activity (Esterase, Chitinase, and glucanase production)	Leena et al. (2001) Kumar et al. (2010)
Bacillus megaterium *B. subtilis* *Bacillus thuringiensis*	Drought, pH, temperature	Triticum aestivum L Cicer arietinum	Enhanced leaf relative water content (RWC), greater biomass of shoot and root, and higher accumulation of protein, sugar, and phenolic compounds	Production of phytohormones	Khan et al. (2019)

(continued)

Table 13.1 (continued)

Organisms	Stress conditions	Crop	Outcome	Mode and tolerant strategies	References
Pantoea agglomerans	Heavy metals	Avena sativa	Ameliorate heavy metals stress on plant development		Pishchik et al. (2009)
Brevibacillus Brevis	Heat stress	Cotton crop	Enhance development of various plant growth parameters	Production of plant growth promoters such as IAA, ARA, antifungal activity, and ammonia synthesis	Nehra, et al. (2016)
Curvularia protuberata	Heat and drought	Dichanthelium lanuginosum		Colonization of roots	de Zelicourt et al. (2013)
Pseudomonas aeruginosa	Zn toxicity	Triticum aestivum		Improved biomass, N and P uptake, and total soluble protein	Islam et al. (2014)
Pseudomonas koreensis AGB-1	Cd, AS, Cu, Pb toxicity	Miscanthus sinensis		ACC deaminase, IAA production	Babu et al. (2015)
Photobacterium spp.	Hg toxicity	Phragmites australis		IAA, mercury reductase activity	Mathew et al. (2015)
Bacillus thuringiensis AZP2	Drought	Triticum aestivum		Production of volatile organic compounds	Timmusk et al. (2014)
Burkholderia sp., *Streptomyces platensis*	Nutrient deficiency	*Zea mays*			Oliveira et al. (2009)
Phyllobacterium		Strawberries	Aid in phosphate solubilization, plants protection against pathogens	Potassium and phosphate solubilization	Flores-Felix et al. (2015)
Rhizobium		*lettuce*	Increase plants biomass due to enhanced nutrient uptake	Indole acetic acid synthesis	Flores-Felix et al. (2013)
Penicillium janthinellum LK5		Solanum lycopersicum		Gibberellin synthesis	Khan et al. (2015)

(continued)

Table 13.1 (continued)

Organisms	Stress conditions	Crop	Outcome	Mode and tolerant strategies	References
Chryseobacterium		Solanum lycopersicum	Increase soil microbial biomass vis-à-vis soil nutrient.	Siderophore production	Radzki et al. (2013)
Rhizobium and Root-associated plant growth-promoting rhizobacteria (PGPR)	Salinity	Oryza sativa		Expression of salt stress-related RAB18 plant gene	Jha et al. (2014)
Pseudomonas koreensis strain AK-1	Salt	*Glycine max*		Reduction in Na + level and increase in K + level	Kasotia et al. (2015)
Rhizofungal flora	Hydrocarbon pollution	*Zea mays* and *Sorghum bicolor*	Enhanced germination, shoot growth		Eze et al. (2014)
Rhizobacteria	Chromium toxicity	*Vigna unguiculata* and *Arachis hypogea*	General growth performance		Eze et al. (2018)
PGPR and AMF	Hydrocarbon pollution and saline–alkali soil	Avena sativa	Improves the soil quality and degradation of total petroleum hydrocarbon	Augment the activities of essential enzymes, e.g., urease, sucrase, and dehydrogenase	Xun et al. (2015)
AMF	Drought	Leymus chinensis, Hemarthria altissima	Enhanced plant biomass photosynthetic rate, stomatal conductance	Enhance antioxidant enzyme activities	Li et al. (2019)

13.2 Microbial Consortium: Interactions, Operations, and Mechanism

Bacteria account for over 95% of the total microbial activities in the soil. It is primarily supported by their fast proliferation and ability to utilize wide range of nutrients (Odoh et al. 2019a). In the rhizosphere, rhizobacterial concentration in the soil is estimated to be 10^{12} CFU/g, while the rhizobacterial flora of the bulk soil is 10^8–10^9 CFU/g (Compant et al. 2010; Foster 1988). During stress conditions, these rhizobacterial population structures get altered, thus affecting activities of the general soil ecosystem. These bacteria constantly interact with fungi and other associated organisms, thereby gaining adaptive capacity for complex mechanisms.

Arbuscular mycorrhizal fungi (AMF) also have developed aptitude to fix nitrogen, obtain iron using siderophores, and increase bioavailability of phosphorus via solubilization by its organic acid (Hardoim et al. 2015; Yadav et al. 2019a, b, c). According to Kim et al. (2008), MC biotechnology involves the use of more than two microbial species that are exposed to same environmental conditions be it nutrients, temperature, pH, or oxygen.

Ecological research has unveiled fascinating groups of microorganisms that live in close interactions. In the rhizosphere, diverse microbial populations acquire their nutrient via the root exudates (Philippot et al. 2013), which aid in regulating rhizospheric biotic and abiotic functions such as propagation, space competition, and soil physicochemical properties (Igiehon and Babalola 2018). This compound is made up of monosaccharides (glucose), disaccharides (sucrose), polysaccharides (arginine and benzoic acids), higher molecular-weight compounds (fatty acids, nucleotides, tannins), and vitamins (Rasmann and Turlings 2016). Technically, MC aggregation is driven by biofilm-mediated process, a biologically active body formed on/in surfaces in contact with water consisting of organic and inorganic minerals and microorganisms held together by matrix of organic polymers often produced and secreted by the microorganisms themselves (Nwankwegu and Onwosi 2017). Igiehon and Babalola (2018) suggest that these exudates play a huge role in facilitating symbiotic interactions particularly those involving rhizobacteria and arbuscular mycorrhizal fungi (AMF). This MC communicates and utilizes pheromone, a unique signaling molecule, for effective selection of partners, monitoring and maintaining integrity of their population densities (Sivasakthi et al. 2014). In addition, these signaling/sensing molecules coordinate microbial activities, which are essential for accomplishment of complex exploration of biological processes (Bernstein and Carlson 2012; Hays et al. 2015).

Harnessing this biotechnology advances in agriculture is of essence. This is because it improves crop growth and food production. Recent omics studies have thrown light on microorganisms in their natural habit, e.g., (rhizosphere), leading to the understanding of plant–microbial cooperation. In addition to providing clarity on the complexity of microbial structures in their natural environment, multiomics research also reveals weakness of genetically engineered pure cultures or single strain in biotechnological applications (Jagmann and Philipp 2014; Igiehon and Babalola 2018; Kumar et al. 2019b; Rana et al. 2019; Yadav 2017b; Yadav et al. 2019d). There are two mechanisms that explain microbial coexistence in soil, namely, neutral/equalizing and niche/stabilizing mechanisms.

13.2.1 Neutral or Equalizing Mechanism

Neutralization theory also called equalizing mechanism involves minimizing differences among varying species in a growing population while considering other demographic parameters (Zhang et al. 2009; Ale et al. 2019). It is a mathematical tool and model program, which captures epiphenomena and broad-scale patterns of ecological communities. This theory predicts that changes in species composition are related to geographic distance between samples as a result of dispersal limitation. It also suggests that species abundance follows a zero-sum multinomial (ZSM) distribution (McGill et al. 2006), a unique species abundance distribution (Hubbell 2001; Fisher and Mehta 2014). This theory suggests that microbial community structure comes solely from stochastic processes and dispersal limitation, ensuring equalizing biodiversity of all species and a uniform population growth rate at an identical ecological zone. Integral microbial biodiversity characterizations such as birth, death, colonization, immigration, speciation, and dispersal limitations are linked to neutral mechanism.

According to Rosindell et al. (2011), organisms at the same trophic level are equivalent with respect to fitness in a specific environment; as illustrated in the Vellend's processes of microbial community assembly (Nemergut et al. 2013). Through heritable genetic barcodes, community compositions are tracked in a repeatedly subculture samples. In a study carried out by Cira et al. (2018), they revealed a transition between neutral and selective regimes, with a crossover point that is dependent on the fraction of immigrants and the magnitude of fitness differences. During exclusive competition, this intrinsic mechanism regulates activities via reduction of competitive speeds resulting in decrease in population growth usually at rare conditions. Zhang et al. (2009) observed a discrepancy between stabilizing (niche mechanism) and equalizing (neutral mechanisms) and identified that the former presumes negative frequency dependence in population growth of species while the latter does not. Their result, however, justifies Zhou and Zhang (2008), who earlier opined that neutral theory presupposes that all species are functionally equivalent with diversity having a little or no effect on the ecosystem.

13.2.2 *Niche or Stabilizing Mechanisms*

This mechanism suggests increasing importance of deterministic processes. Fundamentally, it explains the ecological traits differentiation among species within a community. Ale et al. (2019) argued that the niche-based mechanism characterized a robust and progressive activity, which deals with disconfirming data by generating new testable predictions. It is regarded as a negative intraspecific interaction relative to negative interspecific interactions in the soil ecosystem. Niche theories predict that a change in species composition is related to changes in environmental variables, and that species abundance follows a log-normal distribution (Leibold and McPeek 2006). Unlike in neutral theory where only random processes, such as birth, death, colonization, immigration, speciation, and dispersal limitations (Vanwonterghem et al. 2014), are considered, niche stabilizing mechanism utilizes environmental condition (abiotic and biotic factors), habitat heterogeneity, species interactions, and species relative abundances in shaping bacterial community structure (Dumbrell et al. 2010; Gilbert et al. 2012).

Literature in microbial ecology support the eminent contributions of niche-based and neutral processes in microbial community assembly (Burke et al. 2011; Logares et al. 2013). Worthy of note is that stabilizing mechanisms result in negative frequency-dependent selection where each species enjoys an advantage in population growth at rare condition. This bio-technique is paramount for long-term stable coexistence among species through resource partitioning, frequency-dependent predation (Chase et al. 2011), and fluctuations in population density and environmental factors (Letten et al. 2017). Aside from niche partitioning primarily regulating the composition and diversity of natural arbuscular mycorrhizal (AM), stochastic-neutral processes (Dumbrell et al. 2010) also influence them. Liao et al. (2016) suggest that habitat specialists (niche process) were significantly strongly shaped by environment selection, whereas habitat generalists (neutral process) were strongly assembled via neutral bioprocesses. They identified salinity, dissolved oxygen, water transparency, total phosphorus, ammonium nitrogen, temperature, and total nitrogen as the significant habitat specialists, whereas habitat generalists are driven by natural processes. The theory also suggest that organisms do not just come to existence all at once, rather through typically assemble and sequential species colonization events (Jiang and Patel 2008; Nemergut et al. 2013; Verbruggen et al. 2012). This ultimately gives rise to ecological succession.

13.3 Microbial Consortium as Biofertilizer

Belowground microbial interactions in soil ecology are dynamic and complex. It is a determinant of the increase in yield and productivity of the aboveground crop parts (Philippot et al. 2013). This occurs through a process called biofertilization—a phenomenon where microbial inoculants are seeded on plant surfaces, seeds, and/or soil to colonize root rhizosphere. This condition enhances growth through the supply and availability of primary nutrients to the plant (Odoh et al. 2019a; Odoh 2017). Biofertilizer (Table 13.2) is a culture of bacteria, fungi, and algae either alone or in combination that is packed in carrier materials to enhance plant growth. Several support materials preferably of organic origin (notably chitosan, gelatin, sawdust, k-carrageenan, zeolite, activated carbon, etc.) are stable bio-carriers used to immobilize these biofertilizers while substantially eliminating environmental perturbations (Nwankwegu and Onwosi 2017). In a comparative research evaluating microbial consortia versus single-strain inoculants, Bradáčová et al. (2019) suggest that microbial consortia increase the efficiency of crop production, particularly under challenging environmental conditions. Microbial fertilizer plays a critical role in atmospheric nitrogen fixation and mineralization of organic compounds. In arable agricultural application, it is considered an essential component for long-term soil fertility and sustainability. Nuti and Giovannetti (2015) in their view suggested that biofertilizers act by nourishing and fortifying the host plant, and inducing general pathogenic resistance, irrespective of its origin and nature.

Table 13.2 Biofertilizer and their formulating microbial strain

Product name	Organismal consortium	Target crops	Manufacturers
Amnite A 100®	Azotobacter, Bacillus, Rhizobium, Cheatonium, Pseudomonas	Cucumber, lettuce tomato, pepper	Cleveland biotech, United Kingdom (UK)
Armour-Zen®	Chitosan. An elicitor against Botrytis cinerea (gray mold), Sclerotinia scherofiorum (white rot)	Grapevine, ornamentals	Borty-Zen 2010 Ltd., New Zealand
Bioativo®	PGPR consortia, organic matters	Bean, maize, sugarcane, rice, carrot, cotton	Embrafos Ltd., Brazil
BactofilA10®	*A. brasilense, A. vinelandii,* *B. megaterium, P. fluorescens*	Cereals	Agro bio Hungary kft, Hungary
Biomix®, Biozink®, Biodine®	Azotobacter, *P. fluorescens*, phosphobacteria	Wide range of plant varieties, e.g., field crops	GreenMax Agrotech, India
Ceres®	P. fluorescens	Horticultural crop	Biovitis, France
Complete® plus	*B. pumilus, B subtilis, B. licheniformis,*	Nursery trees and field crop	Plant Health Care, United States of America (USA)
FZB 24® fl	B. amyloliquefaciens sp, planetarium	Vegetables	AbiTEP GmbH, Germany
Gmax PGPR	PGPR consortia	Field crops	GreenMax Agrotech, India
Galtrol®	*Agrobacterium radiobacter* strain 84	Ornamentals, Fruits, Nuts	AgBioChem, USA
Hyper Coating Seeds®	Rhizobium and legume seed	Legume	Tokachi Federation of Agricultural Cooperatives (TFAC), Japan
Inomix® biostimulant	B. polymyxa (LAB/BP/01), B. subtilis (LAB/BS/F1)	Cereals	LAB (Labiotech), Spain
Mycostop®	Streptomycin griseoviridis	Ornamentals, Tree Seedlings	Kemira Agro Oy, Finland

(continued)

Table 13.2 (continued)

Product name	Organismal consortium	Target crops	Manufacturers
Micosat F® cereal	B. subtilis BR62, Paenibacillus durus PD74, Streptomyces sp ST60	Tomato, soybean	CCS Aosta Srl, Italy
Mamezo®	Rhizobium-based formulation in peat	Legumes	TFAC, Japan
Nodulator®	Bradyrhizobium japonicum	Cereals and **horticultural plants**	Lallen and plant care BASF Inc. Canada
Nitrofix®	Azospirillum sp	Wheat, barley, carrot, maize, cabbage	Labiafam S.A, Cuba
Processing Seeds®	Rhizobium	Legumes	TFAC, Japan

Modified from Odoh et al. (2019a)

Due to excessive application of chemical fertilizers, leaching and runoff of essential minerals "phosphorus (P) and nitrogen (N)" occur leading to loss of soil nutrient. With the overwhelming importance of biofertilization in modern agriculture, research has focused on halting the overdependence on synthetic fertilizers coupled with the rising depletion of soil functionality (Bhardwaj et al. 2014). Chatzipavlidis et al. (2013) is of the view that biofertilizing system requires adequate preparation of the inoculants, selection of carrier, and designing of accurate delivery system. This bioprocess, however, requires optimization to support increased yield and economic viability of small and marginal farmers. MC, apart from being able to mobilize nutritionally important elements from non-usable form through biological process (Mazid et al. 2012), secretes fascinating bioactive ligands (Myc and Nod factors) using a transduction pathway (Roberts et al. 2013) for the release of Ca^{2+} in the cytosol (Sieberer et al. 2009).

13.3.1 *Nitrogen Fixation as a Form of Biofertilizer*

Nitrogen (N) is one of the major limiting nutrients constantly required for crop growth. It is a common and essential element occurring in all organisms. As a precursor of amino acid and a major constituent of protein and nucleic acid (DNA and RNA), it constitutes 3% of body mass index and fourth most important plants dry mass. Besides circulating the atmosphere, lithosphere, and biosphere through biogeochemical cycle, it serves as a nourishing nutrient and mineral for agricultural services. In plants, this element is fixed through nitrogen fixation. Here, atmospheric nitrogen gets converted into ammonia (NH_3) and/or nitrogenous compound. The conversion of dinitrogen (N_2) into NH_3 also called biological nitrogen fixation is important as it enables broad utilization by a number of microorganisms. During this process, soil free-living symbiotic diazotrophs, e.g., *Azotobacter, rhizobium,* and *spirilla*, as well as cyanobacteria (blue-green algae such as species of *Aphanizomenon, Anabaena, Nostoc,* etc. in aquatic ecosystems) produce a highly complex oxygen labile enzyme called nitrogenase (Verma et al. 2015; Franche et al. 2009; Simone et al. 2018). This enzyme aids the reduction of nitrogen (N_2) to ammonia (NH_3).

A combination of recent nitrogenase engineering biotechnology using advances in synthetic biology to broaden understanding of the enzyme biosynthesis and biochemistry by plant scientists has been innovated (Burén and Rubio 2018). This technology enables the engineering of plants to express their own specific nitrogenase enzymes, thus overcoming negative natural pressures (increased use and availability of reactive nitrogen) and apparent economic benefits and opportunities it presents. During biological process of nitrogen fixation, a two-form (symbiotic and nonsymbiotic) process occurs owing to their associated plants and group of microorganisms. It has, however, been established that nonsymbiotic processes fix less amount of nitrogen when compared to the rhizobia association with root nodule (symbiotic) (Sippel et al. 2018). Considering the overarching importance of this event and the role played by nitrogen in agriculture cum food production, PGPR have intrinsically developed capacity in augmenting this process through diverse strategies that would improvise and support availability of the nitrogen nutrient (Odoh et al. 2019a). Elsewhere, nitrogen fixation as a biofertilizer has been documented and demonstrated with a major contribution of PGPR and AMF as seen in the suppression of major biotic and abiotic stresses and threat (Majeed et al. 2018).

13.4 Plants–Microbial Interactions

Soil is the loose material of the earth's surface consisting of a mixture of organic matter, minerals, gases, liquids, and organisms that jointly support life. It is the natural component of the earth crust with proven biological, chemical, and physical properties. One of its rich nutritional components essential for plant crop growth is "soil organic matter" (SOM). It consists largely of residue of plants and animals usually at various stages of decomposition. These substances help in sustaining soil fauna and floras. Soil microorganism contributes over "8%" of the total SOM, while the nonliving remains, and humic substances in the soil account for about 60% of SOM (Varanini and Pinton 2001; Liste 2003; Htwe et al. 2019). SOM besides being an important portion of soil with pool of nutrient supporting the propagation of soil organisms and plants, it is also vital for cation exchange and sorption of contaminants (Eze et al. 2018). Its roles in erosion control, water, and air circulation as well as soil aggregation have also been documented (Guo et al. 2019a). However, with the dominance of SOM in soil due to plant derivatives, it thus supports the premise that accumulation of organic matter in soil profile (horizon A) occurs most where the number of plant roots is greatest.

Owing to the inability to physically understudy soil–plant–microbial mechanisms, omics molecular tool has revealed levels of interaction in the soil ecosystem. This advanced technique has helped to identify and quantify the microbial diversity associated with specific plants while giving clarity to their immense interactions to which plants are exposed. Schirawski and Perlin (2018) disclosed that plants constantly relate with microorganisms via a diverse number of mechanisms necessary for their survival. Through this association, plant benefits directly or by indirect effects of the associated microbes which composition around the root zones includes rhizobacteria and mycorrhizal fungi (Nadeem et al. 2014; Hamilton et al. 2016; Yadav et al. 2015a, b). Since multidimensional interactions occur in all plant organs, total microbiomes' evaluation could help provide evidence of plants' part specificity and its identifiable organism for agrobiology. Notably, plant root, apart from serving as a host for organisms, releases compounds and also serves as nutrient upon their death. These molecules induce more resistance to abiotic or biotic stress and defend species against malignant microbes.

Due to the rich microbial diversity and low nutrient composition in the soil, competition for dominance, adaptation to stress, and capacity to enhance crop growth are prevalent (Ngumbi and Kloepper 2016). Consequently, beneficial microorganisms interact with plant roots, thus supporting plant health via a myriad of mechanisms, e.g., biocontrol, biofertilization, and biostimulation (Glick 2014; Rashid et al. 2016; Odoh et al. 2019a; Yadav et al. 2016, c). Fungal network, according to Fabbro and Prati (2014), also gives protection to plants root zones against various phytopathogens, while helping in phosphorus acquisition and water availability during drought (Barnawal et al. 2014).

13.4.1 Forms of Interactions Among Microbial Consortium

13.4.1.1 Bacterial–Bacterial Interaction

Plant growth-promoting rhizobacteria (PGPR) includes all rhizobacteria capable of directly or indirectly enhancing crop growth. Example of these organisms includes *Alcaligenes, Pseudomonas, Azospirillum, Bacillus, Klebsiella, Azotobacter, Enterobacter, Burkholderia, Arthrobacter, and Serratia*—they facilitate crop development through a number of mechanisms (Saharan and Nehra 2011; Jambon et al. 2018; Odoh et al. 2019a). Bacteria–bacteria associations in plants are often exploited to enhance efficiency of pollutants sequestration (Eze et al. 2018; Odoh et al. 2019a). Owing to high nutrient availability in the rhizosphere, unlike in the rhizoplane (surface of the roots) and phyllosphere (surface of leaves), there tend to be heightened microbial and biochemical activity in the rhizoenvironment (Venturi and Keel 2016). PGPR also exhibit special role by hindering plant infections, increasing nutrient absorption, root and shoot formation, and improving seed germination and tolerance to environmental stress (Lugtenberg and Kamilova 2009; Odoh 2015). These functions are dependent on the recruitment of rhizospheric and rhizoplane microbes by plants from the bulk soil. Bulgarelli et al. (2012) noted that PGPR recruitment is dependent on the community structure of the bulk soil. Lundberg et al. (2012) opined that different plant genotypes select different rhizospheric communities, thus implying that genetic variation across plant species drives differential recruitment of beneficial microbes. These employed bacterial consortiums engage in fascinating roles such as nitrogen fixation, solubilization of phosphates, phytohormones production, and plant development (Ma et al. 2009; Odoh 2017; Htwe et al. 2019).

During cell–cell interaction in bacteria, members of associated community converse via signaling chemical process. Notable among these sensing mechanisms is *quorum sensing.* Quorum sensing is a microbial communication and regulation of gene expression mediated by small diffusible molecules called autoinducers or quorum-sensing molecules (QSM) (Barriuso 2015). It is described as a regulatory response for transcription of specific genes in response to the detected compound (Venturi and Keel 2016). As a self-regulatory innate mechanism, the accumulation of quorum-sensing molecules occurs throughout microbial growth. When microbial concentration reaches a threshold, regulatory response control by gene expression is initiated to control cell density and population outburst (Albuquerque and Casadevall 2012). This cell-to-cell communication signal is always specific and coordinate pathogenic activities by helping bacteria acclimatize to the disadvantages in the environment when activated (Qian et al. 2019). The QS signals in bacteria consist of acyl-homoserine lactone, autoinducing peptide, and autoinducer-2. They also regulate biochemical processes such as motility, biofilm formation, sporulation, and antibiotic production and play significant role in the secretion of virulence factors (Barriuso 2015; Fleitas-Martínez et al. 2019). Through this efficient cell–cell interaction, energetically cost-effective activities are only undertaken when bacteria population size is high enough to successfully accomplish a specific task (Clinton and Rumbaugh 2016).

In addition, volatile organic compounds (VOCs) and nodulation (Nod) factors of rhizobia have also been identified with properties aiding bacterial interactions (Jambon et al. 2018; Hung et al. 2015). VOCs aid long-distance interactions between microbes, microbes and plants, control symbiotic associations, and the distribution of saprophytic, mycorrhizal, and pathogenic organisms (Hung et al. 2015; Tyc et al. 2017; Brilli et al. 2019). Through this bio-technique, plant health is guaranteed as they act as biocide against plant pathogenic bacteria and fungi. Furthermore, bacterial VOCs promote plant growth through the use of acetoin, a chemical compound that induces systemic resistance and interference with plant gene expression (Bennett et al. 2012). However, responses to flavonoids and strigolactones from plant roots are recognized as host plant symbiosis and signaling molecules (Venturi and Keel 2016). Unlike the Myc factors produced by a specific mycorrhizal fungus, Nod factors by nodulation rhizobia and VOC are cell signaling secondary compounds found in root exudates aiding specificity of rhizobial interactions with their host plant (Oldroyd 2013).

13.4.1.2 Bacteria–Fungi Interaction

Historical ecological studies have revealed that bacteria and fungi often cohabit and share common ancestral origin where assemblage and dynamic co-evolving communities occur. Due to long years of microbiological research that distinguish bacteriology and mycology as two separate disciplines, many scientists and literatures have overlooked in reality, the coexistence of these organisms in the same ecosystem. This, however, has hampered the understanding of the interactions and biochemical processes exerted by the combination of their mutual partnership. Deveau et al. (2018) disclosed that bacteria–fungi interaction (BFI) is intrinsically modulated by behavioral properties of either or both of the interacting partners. Usually, during their coexistence, there exist intimate biophysical and metabolic associations leading to the development of bacterial–fungi interdependency. BFI research has in the last decade metamorphosed into interdisciplinary studies integrating molecular biology, genomics, chemical and microbial ecology, biophysics, and ecological modeling. Through the characterization of BFI, understanding of microbiomes (e.g., arabidopsis root microbiome) has been unraveled (Bergelson et al. 2019). This is primarily through the application of molecular tools where description of biomes and ecological habitat highlight the diversity of the microbes (Thompson et al. 2017). Considering the physical complexities that exist between bacteria and fungi and their applicability in agriculture and ecological studies, Frey-klett et al. (2011) suggested a transit from disordered poly-microbial communities to highly specific symbiotic associations of fungal hyphae and bacterial cells.

Arbuscular mycorrhizal fungi (AMF) and bacteria (PGPR) association have been reported to promote crop growth (Pathak et al. 2017). Besides this association having positive influence on crop yield, it also enhances soil nutritional status and soil microbial biodata. According to Pathak et al. (2017) and Franco et al. (2011), PGPR and AMF are major bio-inoculants with potential for halting dependence on agrochemicals, thus aiding in sustainable agricultural practices when serving as biofertilizer and biocontrol agents. PGPR are classified according to host and intra- and extracellular plant growth-promoting rhizobacteria, and boost plants through direct (growth-promoting hormones) and indirect (antimicrobial substances) mechanisms (Deshwal and Kumar 2013; Zheng et al. 2018). As aid to the process of mycorrhization, mycorrhizal-helping bacteria (MHB) and PGPR symbiotically interact with mycorrhizal fungi and mycorrhizal roots for nutrient uptake. Studies have revealed that rhizospheric AMF and PGPR elicit systemic host immune responses for plant resistance (Zamioudis and Pieterse 2012; Singh 2018). Experimental evidence has shown that co-inoculants of AMF and PGPR offer synergistic advantage to crop especially in nutrient-limited agricultural soil (Gouda et al. 2018). *Bacillus* sp., *Pseudomonas* sp. (PGPR), and AMF interaction proffer viability (Philippot et al. 2013) and show significant improvement in various field applications when used singly or in combined application (Pathak et al. 2017).

13.5 Microbial Consortium as Biofertilizers in Extreme Habitat

Microbial association and adaptation in extreme environments involve progressions characterized by genetic variations and distributions in the population through natural selection or drift. Changes in microbial community composition due to any implication aid shift in the behavioral occupation of organisms inhabiting an ecological niche. These implicating conditions are either newly introduced species, fluctuating environmental conditions or low fitness genotype variants within the host's microbiota (Yadav 2017a; Yadav et al. 2017). In ecological biotic or abiotic variation, tendency of adjustments of microbial physiology and metabolic homeostasis occurs. Liu et al. (2016) in their submission suggest that rapid adaptation of microbes occurs through genetic fluctuations at the level of individual bacterial cells. They further illustrated that intra-genomic recombination processes and epigenetic switches are precise phenomena in phase variation. Furthermore, integration of beneficial plant–microbes and microbiome interactions through agricultural microbial biotechnology has proven to be a sustainable solution for species adaptation and crop production in extreme habitat (Timmusk et al. 2017). In understanding this section, we focused and laid much emphasis on habitat under abiotic stress (heat, pH, salinity, and drought) and key environmental disturbances such as heavy metal and crude oil pollutants.

13.5.1 Heat Stress

Heat stress implies increase or decrease in a temperature more than the critical edge, at a particular time. Usually, this condition is adequate enough to cause irretrievable damage to plant growth and development (Ripa et al. 2019). Temperature stress also leads to soil fertility loss, microbial diversity, loss of nutrient resources, and a series of morphological, physiological, biochemical, and molecular changes with adverse effects on plant growth (Hayat et al. 2013; Chodak et al. 2015). Documented evidence has shown that temperature-related stress either high or low severely restricts crop production and most importantly, with the upset in the global earth temperature and upsurge in human activities. In the tropics, this abiotic stress has hindered agricultural developments particularly in climate-impacted community leading to weather change and alteration of farming seasons. Besides crop productivity being tempered by change in the plant metabolism during high temperature stress, there also occur cellular changes such as reactive oxygen species (ROS) (Hasanuzzaman et al. 2013). According to Akter and Islam (2017), heat stress significantly reduces seed germination and seedling growth, cell turgidity, and plant water-use efficiency. They further explained its role in the disturbance of cellular functions, enhancement of leaf senescence, deactivation of photosynthetic enzymes, and generation of oxidative damages to the chloroplasts.

In contrast, cold and frost (low temperatures) cause decreased kinetics of biomolecules leading to reduced cell membrane fluidity and a decreased rate of enzymatic reactions. It results in cell division, impairment of water transport, photosynthesis default, alteration of crop development, and growth in arctic environment (cold). This condition leads to the formation of ice crystals in soil due to reduction in water uptake by roots resulting in cellular dehydration. As a response to this stress condition, plants over the years have developed strategies to induce accumulation of several osmolytes and hydrophilic proteins such as dehydrins. According to Kosová et al. (2018), heat and cold temperature stress exacerbate imbalance between photosynthetic electron transport processes and carbon assimilation processes, thus resulting in enhanced photo-inhibition and thermal energy dissipation.

Different researches have reported the ability of some beneficial heat- and cold-tolerant bacteria to induce stability in plants (Chang et al. 2007; Chakraborty et al. 2018; Lamaoui et al. 2018; Yadav et al. 2015a, b). This microbial-tolerant synthesis often depends on the plant genus, stress type, microbial species, and the plants' microbial relationship. An example of this is seen in phyllosphere bacteria with ice-nucleating activity that damage plant in temperate region. This can be harnessed for onward application as foliar spray to suppress the ice nucleation effect in temperate region (Selvakumar et al. 2012). Consequently, these abiotic effects even at mildest state affect the smooth growth and development of plant at all states. With several independent researches, it has also been demonstrated that increase or decrease in temperature has the propensity of reducing crop yields by over 50% (Lamaoui et al. 2018). Through advances in biotechnology such as genomics and information technology, mitigation of these abiotic stresses through the use of agronomic management practices would be sound if integrated with tolerant MC, so as to aid the development of crop varieties while boosting harvest amidst rising stress (Fig. 13.1).

13.5.2 Drought Stress

One of the documented stresses that affect crop health and growth is drought. It is an abiotic condition where plants experience deficit supply of their water needs. When rate of transpiration exceeds rate of root water uptake, drought is said to occur—this leads to reduction in the cells' relative water content and development (Utsumi et al. 2019). Research on drought tolerance has become an important field of study owing to rising global climatic state. This, however, has cut the interest of most agriculturists and scientists to probe drought challenge and its related consequences on crop breeding (De Oliveira et al. 2017). The impact of this drought condition has necessitated the exploration of belowground microbial potentials and interactions to proffer ways of curtailing the rising menace (Igiehon and Babalola 2018). Characterized by cellular water deficiency, drought is a severe condition where plants get dehydrated and ultimately die off (plant dieback) due to limited water supply. This could lead to shedding leaves, breaking branches, weak root formation, and color alteration. According to Odoh et al. (2019b), this plant dieback occurs as a result

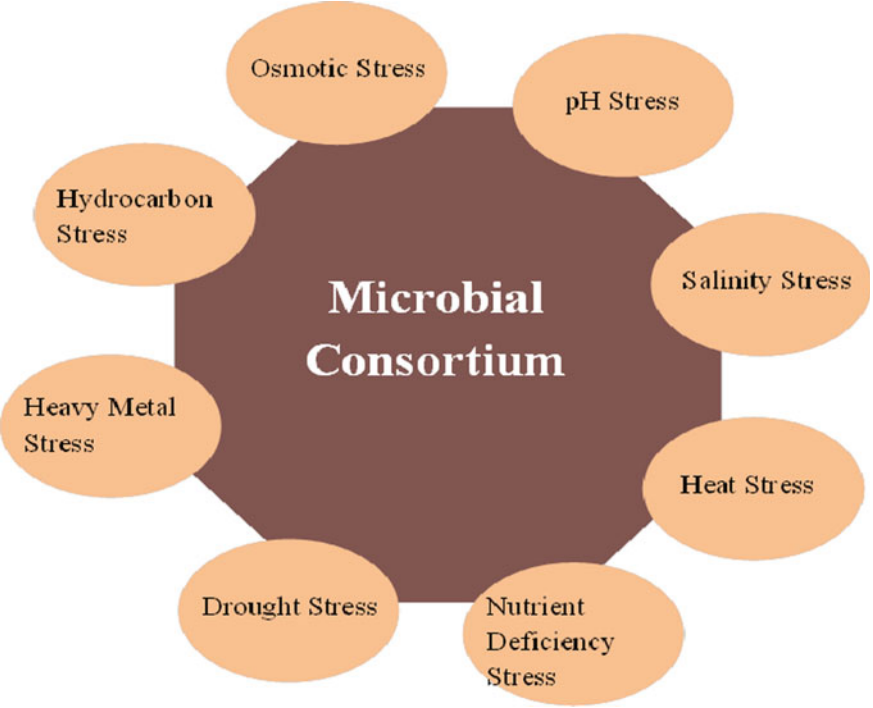

Fig. 13.1 Schematic representations of extreme conditions upturned by activities of microbial consortium

of drought, pathogens, parasite, soil acidity, and soil pollution. In general, drought stress reduces cell size, membrane integrity, produce reactive oxygen species, and promotion of leaves senescence, thus leading to decreased crop production (Tiwari et al. 2016). However, seed germination, seedling development, and morphological and molecular changes are all related developmental challenges impeded by crop exposure to drought (Nezhadahmadi et al. 2013; Varshney et al. 2018; Utsumi et al. 2019; Kour et al. 2019a, b; Rana et al. 2019; Verma et al. 2016, 2017; Yadav and Yadav 2018).

With the recent advances in omics studies, plant–microbial processes and species have showcased promising character in ameliorating agrobiotechnology-related stress (drought). At the transcriptomic level, bacterium *Paenibacillus polymyxa* B2 enhances drought tolerance in *Arabidopsis thaliana*. When PGPR (*A. thaliana*) is inoculated, it expresses genes for the overexpression of drought tolerance unlike when compared to the uninoculated plants (Glick et al. 2012; Alavilli et al. 2017). Lim and Kim (2013) in their studies using 2-D polyacrylamide gel electrophoresis and differential display polymerase chain reaction identified drought stress gene expressed in plants amended with *Bacillus licheniformis* in affected soils. Also through quantitative polymerase chain reaction (qPCR) *Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense* have shown priming effects on the expression of drought-responsive genes. Some of the genes usually expressed for drought abiotic stress include ascorbate peroxidase (APX1), S-adenosyl-methionine synthetase (SAMS1), heat shock protein (HSP17), and enzyme-enhancing drought stress in wheat leaves (Kasim et al. 2013). PGPR produce phytohormones or induce plants to synthesize molecules such as indole acetic acid, cytokinins, gibberellins, and abscisic acid (Hayat et al. 2010; Spaepen et al. 2008; Odoh et al. 2019a). These molecules trigger adaptation of plant in stress habitat through varying mechanisms (Spaepen and Vanderleyden 2011), thus influencing changes such as increase in root growth, length, surface area, and formation of lateral roots and root hairs for the acquisition of water (Egamberdieva and Kucharova 2009; Paul and Lade 2014; Manaf and Zayed 2015).

During flooding stress, anaerobiosis occurs due to excessive accumulation of water in the root; this leads to induced fermentation processes in the root region. It also results in enhanced accumulation of organic acids resulting in acidity of the cell cytoplasm affecting cellular enzymes (Kosová et al. 2018). Also using cellular organelles (nucleus, nucleolus, mitochondria, endoplasmic reticulum, plasma membrane, cell wall), a novel protein biosynthesis was found in nuclear proteome of soybean root tips (Yin and Komatsu 2016), suggesting expression of adaptive capacity in stress-driven environment.

13.5.3 Salt Stress

Salinity stress is a major abiotic factor commonly seen in most agricultural soil. It causes inhibition and impairment of crop growth and development via water stress and cytotoxicity by excessive uptake of ions (Isayenkov and Maathuis 2019). Salt stress has been reported to be detrimental on nitrogenase—an enzyme responsible for the fixation of nitrogen. Some of these ions causing salinity are responsible for changes in the ratio of ion homeostasis of plant system. This, however, leads to undue uptake of Na^+ and Cl^-, and reduction in K^+ and Ca^{2+} transport in the growing plant (Giri et al. 2007; Paul and Lade 2014). One of the significant effects of salt stress is low water budding; this leads to inability of plant to take up nutrients and water from the soil due to osmotic pressure. Álvarez-Aragón et al. (2016) in their studies revealed that overaccumulation of Na^+ and K^+ might be responsible for triggering growth reduction in NaCl-treated Arabidopsis plants. In their work, they demonstrated how stomatal regulation and/or systemic stress responses occur owing to salt concentrations. Typically, salinity stress is accompanied by oxidative stress caused by reactive oxygen species (ROS) (Isayenkov 2012). During soil salinity, electrically charged ions accumulate due to insufficient water distribution, hindering germination and uptake of nutrients. During this condition, growth responses in plant occur either as ion-independent growth reduction or by cytotoxic ion build-up. In the former, crop growth takes place within minutes to days—causing stomatal closure and inhibition of cell expansion (Rajendran et al. 2009; Isayenkov and Maathuis 2019), while the latter takes days or even weeks for development leading to slow metabolic processes, premature senescence, and cell death (Munns and Tester 2008; Roy et al. 2014).

However, harnessing PGPR potentials could directly and indirectly influence the promotion of plant growth under increased salinity concentration. Studies by Kasim et al. (2016) have it that when PGPR and endophytic microbes are inoculated, they mitigate effects of soil salt on plants using various mechanisms. In a related experiment, Bacilio et al. (2016) in their work revealed that plants inoculated with salt-tolerant bacteria (*Pseudomonas stutzeri*) reduce in high extent the negative impact of soil salinity on crop growth. Rhizobacteria sp. with capacity at reducing salt toxicity in several plants through the reduction of Na^+ concentration and increasing the K^+ and Ca^{2+} are reported (Bano and Fatima 2009; Hamdia et al. 2004; Kohler et al. 2009). This is achieved principally by altering host physiology, reducing foliar accumulation of ions (Na^+ and Cl^-) and improving the nutritional condition of macro (P and K), and micronutrients (Zn, Fe, Cu, and Mn) (Bano and Fatima 2009). In plant roots, endophytic fungi *Piriformospora indica and* AMF show ability in ameliorating ions toxicity by inducing host defense against salt stress (Ansari et al. 2013).

Cell homeostasis is the ability of a living cell to maintain internal ions concentration or remain nearly constant even in environmental stresses (Rombola-Caldentey 2019; Chérel et al. 2019). Under this ionic homeostasis stress, beneficial rhizobacteria are harnessed, e.g., *Pseudomonas* (Fu et al. 2010), *Azospirillum* (Ashraf et al. 2004), and *Bacillus subtilis* GB03 with *Arabidopsis* (Zhang et al. 2008) to maintain intracellular ionic homeostasis balance in crops such as eggplant and maize. These PGPRs have shown capacity to trigger all round physiological functions and development through the accumulation of osmolytes and several low-molecular-weight compounds such as methylated tertiary N compounds and amino acids (Guo et al. 2019). Primarily, these osmolytes operate through the modulation of osmotic pressure in the cytoplasm and cell membrane, thus stabilizing plant growth when water, salt, and/or temperatures seem unfavorable (Tiwari et al. 2010; Sze and Chanroj 2018; Chérel et al. 2019).

13.5.4 Soil Reaction (Acidity and Alkalinity)

Soil pH is an important abiotic condition that determines the growth, survival, and productivity of any given plant. In considering physicochemical properties, pH is a fundamental determinant of soil health. Some of the most important bioprocesses and microbial activities include nutrient solubility and availability to the host plant (Gentili et al. 2018). Many plant genetic traits, such as height, lateral spread, biomass, flower size and number, pollen production, etc., are influenced by soil pH (Jiang et al. 2013). Elsewhere, studies have shown that most micronutrients are more available to plants in acid soils compared to neutral–alkaline soils (Lončarić et al. 2008). In alkaline soils also, availability of most macronutrients increase with concomitant reduction of phosphorus, thus generally affecting crop growth. However, as these micronutrient accumulations increase along with other nonessential elements, they become poisonous to plants.

Alien invasive plants have usually been documented to have tolerance to environmental stress, including pH (Dassonville et al. 2008; Hao et al. 2017). They are species that upon introduction spread outside their natural habitat and threaten biological diversity. Unlike the cultivated or native plants whose optimum performing pH mostly ranges from 5.5 to 6.5 (Köpp et al. 2011), they propagate at extreme conditions. This characteristic allows them to adapt to a great variety of soil types and thus spread vigorously, while also colonizing environments not suitable for native species (Sărăteanu et al. 2010). In a study done by Gentili et al. (2018) on the effects of pH on germination, growth-related traits, reproduction, pollen production, and allergenicity of *Ambrosia artemisiifolia,* they reported that soil pH greatly affects the growth and development of *A. artemisiifolia* and may have contributed in limiting the distribution and growth of the plant. Despite the impact of this abiotic stress on plants, there has been relatively rare studies of its role in modern agro practices (Caplan and Yeakley 2006; Zeng and Clark 2013).

Some important plants' biosynthetic molecules and compounds such as proline, glycine betaine, and soluble sugars have proven to possess the capacity of ameliorating these abiotic stresses (Ranganayakulu et al. 2013; Goswami et al. 2015). Using PGPRs Zea mays exposed to pH stress showed increment in proline production upon inoculation with *Rhizobium* sp. and *Pseudomonas* sp. (Bano and Fatima 2009; Grover et al. 2011). Endomycorrhizal fungi have also shown capacity in inducing biosynthesis of glycine betaine and proline accumulation in plants subjected to abiotic stress (e.g., salt and pH) when compared to non-inoculated plants (Al-Garni 2006; Manaf and Zayed 2015). Different microorganisms have the ability to support accumulation of soluble sugar (trehalose) in plants. These organisms such as endomycorrhizal fungi, symbiotic bacteria such as Rhizobium spp., and free-living PGPRs suppress plant abiotic stresses (Grover et al. 2011 Suárez et al. 2008). Through genetic engineering, PGPRs could be designed for the overproduction of trehalose as biofertilizer, just as *Rhizobium etli* are used to overcome drought stress (Suárez et al. 2008). Similarly, genetically engineered *Azospirillum brasilense* when inoculated on maize plants overproduce trehalose which induce more resistance to varying abiotic conditions (Rodríguez-Salazar et al. 2009).

13.5.5 Heavy Metals and Hydrocarbon Stress

Heavy metals and crude oil hydrocarbon are both environmental pollutants with deleterious effects on crop food production. They are classified as environmental pollutants of major global concern due to inherent challenges associated with natural resource mining (Odoh et al. 2019b; Kumar et al. 2019a). Basically, hydrocarbon pollutants exist in the environment as total petroleum hydrocarbons (TPHs) and this according to Nwankwegu et al. (2018) are hydrocarbon derivatives/congeners, which bioaccumulate and bio-concentrate in food chain through soil ecosystem. Their presence in the ecosystem is attributed to industrialization, urbanization, and civilization (Odoh et al. 2017; Sam et al. 2017). In the developing economy, illegal activities such as artisanal refining and exploration are the basic routes of entering the soil ecosystem. It also has been traced to practices such as excessive fertilizer application, indiscriminate disposal of sewage, power plants/fossil fuel, municipal waste, and pesticides/insecticide usage among others. Examples of some heavy metal species commonly found in the soil are copper (Cu), zinc (Zn), nickel (Ni), lead (Pb), cadmium (Cd), cobalt (Co), mercury (Hg), chromium (Cr), and arsenic (As). Because they are nondegradable, they consistently bioaccumulate in the environment (Walker et al. 2003; Eze et al. 2018), thus impairìng food production and posing health threat to man and animals. In agriculture, these heavy metal pollutants lead to decrease in crop yields and further economic loss.

In hydrocarbon stress, soil toxicity occurs leading to distorted microbial population. It causes severe ecological damage, loss of biodiversity structure, and climatic impact. In Nigeria Niger Delta region, hydrocarbon spills have left footprints with devastating impact on farming activities. This significantly alters the health indices in the region with huge ecological imbalance (Ite et al. 2013). Across the tropics, crude oil exploration has threatened food security leading to loss in soil fertility status owing to technical failures, sabotage and artisanal activities (Zabbey et al. 2017; Sam et al. 2017; Odoh et al. 2019b). Ajai (2010) stated that hydrocarbon stress has a direct impact on the total environment especially the food chain and other life-supporting entities.

In the rhizosphere, bacteria, fungi, protozoa, and algae coexist and exert multifunctional strategies in the utilization of mineral and organic wastes. These organisms mostly plant growth-promoting rhizobacteria (PGPR), phosphorus solubilizing bacteria, mycorrhizal-helping bacteria (MHB), and arbuscular mycorrhizal fungi (AMF) play a critical role through bioremediation and phytoremediation technology (Ahemad 2015; Stambulaka et al. 2018; Yadav and Yadav 2019a, b). These microorganisms alleviate the pollutants' noxious effects on plants through secretion of acids, proteins, phytoantibiotics, and other chemical molecules (Denton 2007; Wei et al. 2017; Pettit et al. 2019). Microorganisms, namely, bacteria, fungi, protozoa, and algae coexist in the soil especially within the rhizosphere region and serve as effective metal sequestering and growth-promoting bio-inoculants for plants in metal-stressed soils (Rajkumar and Freitas 2008; Stambulaka et al. 2018).

13.5.6 Osmotic Stress

Reactive oxygen species (ROS) are a bioproduct of metabolic activities and pathways localized in different cellular compartments (Apel and Hirt 2004). They are a group of very reactive, short-lived chemicals often produced during metabolic processes or after an oxidative reaction. Examples of ROS include superoxide ($\cdot O2^-$), hydroxyl radical ($\cdot OH$), hydrogen peroxide (H_2O_2), and singlet oxygen ($1O_2$) (Iqbal 2018).

These chemical molecules have the capacity to impair a number of physiological developments such as proliferation, differentiation, senescence, and apoptosis when found in minimal concentrations (Lai et al. 2007; Iqbal et al. 2016; Iqbal 2018). This occurs owing to their involvement in oxidative damage on proteins, DNA, and lipids (Carmen and Roberto 2011). Studies have shown that accumulation of ROS occurs most during stress condition unlike in normal growth conditions. This is a result of the disparity in the production and the number of scavenging molecules of ROS. According to Apel and Hirt (2004), ROS-scavenged molecules are antioxidative defense components that act to restore the physiological growth conditions. Intrinsically, this antioxidant defense system is synthesized in aerobic cells to offset the damaging effects of ROS (Ishizawa et al. 2017; Utami et al. 2018).

In plants, enzymatic and non-enzymatic components such as superoxide dismutase (SOD), catalases (CAT), ascorbate peroxidase (APX), and low-molecular-mass antioxidants play a key role in mopping up different types of ROS (Akram et al. 2017; Utami et al. 2018). Also, in the chloroplast and other cellular compartments, ascorbic acid and glutathione, which are found in high concentrations, play crucial roles in plant defense against oxidative stress (Miller et al. 2010). A combination and synergistic role of MC containing fungi and bacteria can be explored to improve plant growth and ecophysiological responses in extreme conditions. Here, the interactive effects of phytohormones-producing endophytic fungal and bacterial symbionts in plant growth and stress tolerance are harnessed. According to Bilalet al. (2018), phytohormones-producing endophytic *Paecilomyces formosus* LHL10 and *Sphingomonas* sp. modulated the stress state through reduced hydrogen peroxide, lipid peroxidation, and antioxidant enzymes (catalase and superoxide dismutase) when compared to the non-inoculated plants. Inoculation of PGPR strains has been attributed to the reduction of osmotic-related conditions in lettuce plants (Kohler et al. 2010). Apart from plant inoculated with *Pseudomonas mendocina* having the capacity to alleviate salt-related stress, it also reduces oxidative damage (reduced chlorosis, necrosis, and drying) in plants, thus enhancing activity related to antioxidant enzymes such as SOD, APX, GR, and POX (Bianco and Defez 2009). *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli* are some of the promising MC with significant capacity in osmotic and oxidative activity, drought, and salinity stress (Sandhya et al. 2010; Carmen and Roberto 2011).

13.5.7 Nutrient Deficiency

One of the fundamental targets of crop especially when exposed to harsh environmental condition is to survive its present threat. It does this through the activation of tolerant traits and adaptations using a number of mechanisms. It has been established that nutritional status of plants greatly affects their ability to adapt to adverse environmental conditions especially abiotic stress. A plethora of literature have reported exacerbated adverse effects of abiotic stresses on plants cultivated in nutrient-deficient agricultural soil (Munns and Tester 2008; García-Martí et al. 2019), which are alleviated by exogenous addition of macronutrients (Khoshgoftarmanesh et al. 2010; Turan et al. 2016; Meena et al. 2017). In a study investigating N deficiency and compensation with focus on its uptake, utilization, and the physiological characteristics in rice, Xiong et al. (2018) reported double-cropping super hybrid late rice and N compensation at young panicle differentiation stage after N deficiency at tillering stage. This according to their submission resulted in yield compensation in plants. Its deficiency in plants owing to rise in soil salinity has been reported to be detrimental (Carstensen et al. 2018). P deficiency has also been shown to limit plant productivity. Recent advances have shown that P deficiency affects electron transport to photosystem I (PSI), but the underlying mechanisms are still unknown (Mehra et al. 2018; Carstensen et al. 2018). Invariably, P reduction in saline soils has been linked to ionic strength effects which reduce the activity of phosphate and the tight control of P concentrations by sorption processes, and by low solubility of Ca-P minerals (Carmen and Roberto et al. 2011). With the concentration of these essential minerals (nitrogen and phosphorus), usually very low and insufficient for optimum crop growth, some PGPR have shown promising effects in augmenting this process by making the scarce nutrient readily available to plants (Odoh et al. 2019a). They exhibit this property by taking up several P forms, while the remaining part is adsorbed in the forms of HPO4-2 or H2PO4-1. PGPR play a leading role in mobilizing these nutrients through their participation in biogeochemical cycle (nitrogen and phosphorus cycle) where rhizobia species directly solubilize and mineralize inorganic phosphorus and facilitate the mobility of the organic forms (Richardson and Simpson 2011).

The conversion of some phosphate compounds, e.g., tricalcium phosphate, dicalcium phosphate, hydroxyapatite, and rock phosphate, is predominantly carried out by phosphate-solubilizing bacteria (PSB) such as *Arthrobacter, Pseudomonas, Alcaligenes, Bacillus, Burkholderia, Serratia, Enterobacter, Acinetobacter, Azospirillum, Azotobacter, Flavobacterium, Rhizobium,* and *Erwinia* (Zaidi et al. 2009, Odoh et al. 2019a). They exert this by the secretion of organic acids, e.g., carboxylic acid, formic acid, propionic acid, lactic acid, glycolytic acid, succinic, and fumaric acid. These acids, however, lower the pH of the rhizosphere, thus causing the release of the bound forms of phosphate like Ca_3 $(PO4)_2$ in the calcareous soils (Kaur et al. 2016). Phosphate-solubilizing bacteria (PSB) also contribute to the mineralization of insoluble organic phosphate via the excretion of enzymes such as phytases, C-P lyases, and phosphatases (Weyens et al. 2010, Daur et al. 2018). *Medicago sativa L, Zea mays*, *Glycine max*, and a number of plants have been reported with increased yield through the inoculated PSB either singly or in combination with a number of rhizobacteria (Daur et al. 2018; Tagele et al. 2019).

13.6 Production and Commercialization Biofertilizer

With recent advances in agrobiotechnology, a wider coverage, application, production, and commercialization of MC biofertilizers holds promises. This is, however, welcoming as the world over is driving toward smart and sustainable agriculture. Consortium of PGPR is currently the most sought-after strain with multifunctional potentials. Their formulation and application in agriculture are currently advocated to reduce the overreliance on synthetic fertilizers and other agrochemicals. Backer et al. (2018) in their latest studies agree that members of phytomicrobiome (PGPR) offer huge potential in sustainable crop production, thus necessitating the need for more studies to unravel their potentials and challenges. Although the use of MC as an inoculant has been on for centuries, it has mainly focused on legumes and cereals in the past years (Sessitsch and Mitter 2015). As the world human population continuously gets on the rise in geometric fashion, there is an increasing need to meet the growing food demand through development of new agro technologies such as species engineering and screening for biomolecules production to enhance crop growth. PGPR, for instance, is designed to improve nitrogen fixation, ACC deaminase activity, auxin synthesis, and calcium phosphate solubilization when inoculated (Backer et al. 2018). In situ research approach should be adopted in carrying out research using PGPR MC to ascertain the most suitable strain and appropriate biotic condition needed for their growth, while paying attention on the soil quality and season of optimum performance (Odoh et al. 2019a).

For effective long shelf-life microbial inoculant to be developed and commercialized, field trial and conditions must be properly ascertained and approved. This is vital to curtail the release of strain in the environment. Here, PGPR are inoculated in plant material without an appropriate carrier or in quantities that do not allow for efficient rhizosphere colonization under field conditions (Backer et al. 2018). This is primarily due to competition with resident soil micro- and macro-fauna. Also, in the case of soils cultivated with value, they are often fumigated with broad-spectrum biocidal fumigants that alter the bio-community structure of the soil (Dangi et al. 2017). This fumigation system (short-term) is carefully done not to upset soil microbes and their interactions which help in nutrient acquisition and mobilization. In designing microbial consortia, their role specificity (e.g., bioremediation and plant growth potential) must be clearly defined (Macouzet 2016; Baez-Rogelio et al. 2017), as their bioprocess when inoculated will be based on the specific soil conditions. Combining effects of bioremediation and related abiotic condition ameliorations along with plant growth promotion would be essential in addressing some of the global agricultural problems. This, however, must be accompanied with training of staff, farmers, and associate users on efficient application of the bio-inoculants bearing in mind their soil specificity, environmental condition, and complexity or constraints for optimum impact (Bashan 2016; Parnell et al. 2016; Itelima et al. 2018). To develop a MC inoculant (Table 13.2), the following basic steps must be followed (Backer et al. 2018):

- Isolation of the bacterial strain.
- Screening in laboratory and controlled growth environment.
- Field assessment for a range of crops, geographic locations, planting dates, and soil types.
- Evaluation of the possible combinations of strains.

- Consideration of the management practices (e.g., agrochemical use and rotation).
- Refinement of the product.
- Experiments confirming absence of eco-toxicological effects.
- Product delivery formulation—e.g., peat, granular, liquid, or wettable powder.
- Registration and regulatory approval of the product.
- Product available on the market.

13.7 Regulation of MC Biofertilizer

In the developed economy, there are strict regulations and guidelines moderating the use and application of microbial-based nutrient (bio-inoculant). The first point of call of this product after its due formulation and successful testing is registration where the product must meet specific regulatory requirements. Prior to this, the product must be established in a carrier such as alginate (Bashan 2016) or biochar (Głodowska et al. 2016) through which the cells or inoculants are adhered to seeds using sticking agent at the time of sowing. In the case of liquid inoculants, they are spread on seeds prior to sowing or dripped into the seed furrow at the time of sowing. Importantly also are the storage and product lifespan so as to ensure microbial viability, survival, and/or bioactivity of the strain. There should also be clarity on acute versus chronic application of the biomolecule. In most cases, acute application occurs in a limited number of times during a growing season; it can also be on a target stage of crop development, or in response to environmental and abiotic conditions (drought), while in chronic application, the product could be applied at regular time sprays interval or as a slow-release seed treatment (Backer et al. 2018). With ambiguity on a clear-cut regulatory definition of plant biostimulants (MC), there has been complexity in the regulatory procedure and registration cum commercialization of these products across Europe and America. This, however, necessitates the need for unified standard, characterization and regulation of MC, genetically modified species (GMO), and other biostimulants across the globe especially in Africa and Asia which have huge agricultural potentials and high uneducated local engage in agropractices.

13.8 Prospects and Challenges of Biofertilizer Application

MC has recently been gaining public acceptance and recommendation for applicability in agrifood production. Even though its prominence has been in Asia, America, and Europe, there is still laxity of its growth in other regions especially in Africa. This is because of a number of factors ranging from lack of awareness, skilled manpower, and infrastructures to supportive regulatory framework. These identifiable constraints have militated against sustainable agricultural practices in the regions, thereby missing the benefits accruing to biofertilizer application "yield increase, biological nitrogen fixation, cost saving, nutrient uptake" unlike in some Asian countries (e.g., India, Thailand, and China).

13.8.1 Policy Definition and Enforcement

For any nation to produce, commercialize, and use her formulated MC biofertilizer successfully, she must have instituted a sound regulatory framework. This is necessary to curtail excesses that could emanate from application of engineered species into her environment. In Europe, United States, Canada, Argentina, Brazil, and India, for instance, there seems to be an existing policy and guideline governing application of biological products (biofertilizer, biostimulants, and biocontrol). There have also been discussions on science-based standards and policies that will clearly state the definitions and regulations of these bioproducts in India, European Union, Latin America, and USA. According to International Biocontrol Management Association (IBMA), these products are currently regulated by state governments in USA, thus necessitating discussions by the US Environmental Protection Agency (EPA), to establish unified federal regulations. The food and agricultural organization (FOA) should initiate and enforce these policies among existing member states so that they can harness the gains associated with MC. Also, governments in the developing regions in Africa should improve research in the agricultural sector as biofertilizers' application is still at the infant stage. This is primarily derailed by lack of awareness, human capacity, and infrastructure, thus not tapped the potentials of biofertilizers. A regional and national policy regulatory framework that will boost establishment of indigenous manufacturing firms bearing in mind the regions' specificity in terms of her inherent bioagents (microbes and plants), climatic conditions, soil quality, and complexity is also encouraged.

13.8.2 Global Action on Sustainable Agriculture

With the rising environmental stresses which have become unprecedented in recent time and impediment to agricultural productivity across the globe, a clear-cut global action is necessary to curtail possible monumental impact (food insecurity). In the 2014, the food and agricultural organization (FAO) and the world health organization jointly released the International Code of Conduct on Pesticide Management following series of death recorded from users of agrochemicals across the globe. In India, death associated with chemical pesticides used by farmers has continued to rise following flouting of the global norm and best practices, and also due to ill-informed users (farmers). These agrochemicals which are mostly classified as Class 1 are consistently released into the market by merchants and giant multinationals with no recourse to the harmful effects they have on the end users. These practices flout international regulations guiding a number of these products (e.g., monocrotophos and oxydemetonmethyl).

In Nigeria also, there is an upsurge in the use of agrochemicals in the last decades. The situation is indeed worrisome as citizens whose knowledge on the hazardous effects and impacts of these products (minimal concentration) have embraced in totality the use of agrochemicals (pesticides and herbicides) in every farming exercise. The government push to diversify the economy through agriculture has also worsened the situation owing to the sporadic campaign on the quest to rejuvenate the agricultural sector. Available statistics has shown that over 25% of the globally produced pesticides are used in Nigeria with 99% of the death associated with pesticide occurring in developing countries (Ojo 2016). These are linked to factors such as lack of education, non-use of safety procedures, use of cheaper but lethal chemicals, poor legislation and enforcement, and improper handling.

Also, in China, its water body (Lake Taihu) has been polluted by years of continuous seepage of runoff pesticides, herbicides, and fertilizers from nearby agricultural farms. Despite the prohibition of organochlorine pesticides by Chinese government in 1983, traces of HCH and DDT residues are still easily detected in its sediments (Feng et al. 2003). These happenings across the globe, however, pose serious threat not just to human health but to our ecosystem and biodiversity structures. It therefore calls for a global framework most importantly from FOA and WHO alongside regional and national governments to prohibit classified chemicals and properly regulate hazardous products, while also sensitizing the public especially in developing countries on the advantages of microbial-based formulated bioproducts and the need to hold onto green technology. This move will ultimately help in preventing and controlling the associated environmental problems such as air, water (eutrophication and fertilizer seepage), and soil pollutions linked to synthetic agrochemicals application.

13.8.3 Clarity of the Benefit of MC

It has become clear that the benefit associated with MC application is so enormous. This in comparison with single strain has recorded positive milestone in areas such as food production in industries, use in agricultural application, medicine, and environmental remediation. Through metabolic modeling and reconstruction of individual strains, a formidable and complex community of model microbial agents are formed for optimum performance and production of needed biochemical agents and biomass (Faust 2018). More metabolic research needs to be done on plants and microbial species for more understanding of genetic characters and genes needed to perform complex functions. There is need for farmers and practitioners in agricultural sectors to be abreast of this biotechnology owing to the growing abiotic conditions and alteration of climatic conditions. Proteomics and transcriptomic approaches and genetic engineering of species provide suitable alternatives to these challenges.

13.8.4 Lack of Skilled Manpower and Innovative Research

The thin line between successful utilization of biofertilizer in some Asian countries, Europe, America, and Africa is technical knowhow. The developed regions have sound research-based biotechnological approach for the formulation of bioproducts, increased awareness on their usage while fighting for corresponding decline on the use of chemical fertilizers. Developing countries in Africa are yet to pay adequate attention on the advantages of biofertilizer in agricultural system. This is evident in the skeletal application of biofertilizers by very few farmers across the region. This is in contrast to what is obtainable in Brazil, where almost all the crop protein produced is through BNF; in east and southern Africa, not up to 1% use any form of bio-inoculant. Most often these imported biofertilizers are formulated in conformity or tailored to the countries of origin's standard bearing in mind their local conditions (e.g., climatic conditions, storage condition). These parameters play a huge role in determining their shelf life and viability. With improved manpower development through training, and increased awareness, research, and innovations, locally influencing conditions will become a considerable factor when producing biofertilizer that will be indigenous to a particular region (African climatic conditions). It will also help limit loss of viability observed in some biofertilizers in the market across Africa (Jefwa et al. 2014) where storage conditions and handling play a major role. Through adequate training, knowledge gap usually witnessed in developing economy could be upturned as their trained agriculturists and scientists will see the need to localize their products for the overarching need of the populace. However, with the lack of far-reaching research to develop formulations that could cater for the spatial crop responses, Africa will not be able to benefit from the full potential of biofertilizers. It will also help improve qualitative product delivery in countries such as India, where significant government support has boosted biofertilizers production.

13.9 Conclusion and Future Prospects

Many arable lands are in urgent need of natural and eco-friendly alternatives to synthetic fertilizers for crop production and also to help cushion the shock emanating from abiotic stresses on crops growing in extreme habitats. Microbial consortium biofertilizers have been developed as dependable solution to this mayhem, and some parts of the developed world are already harnessing the benefits of the green technology. However, as appealing and promising as this agrotechnology can be, it is still replete with challenges especially in the undeveloped world where illiteracy and lack of skilled manpower impede proper implementation of its use in crop production.

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Chapter 14
Global Scenario of Plant–Microbiome for Sustainable Agriculture: Current Advancements and Future Challenges

Simranjeet Singh, Vijay Kumar, Satyender Singh, Daljeet Singh Dhanjal, Shivika Datta and Joginder Singh

Abstract Phyto-microbiome are the microorganisms (fungi and bacteria) associated with all major plant components such as flowers, stems, roots, leaves, and fruits. They form symbiotic association with the plant, inhabit the intra- and intercellular positions without harming the host and frequently profit the host plant. They indicate the complex connections within the host plants involving the symbiotic, mutualistic relationship, and rarely the parasitism relationship. They are omnipresent and are known to improve the nutrient enrichment and growth of the plant. They not only produce root exudates but also release signal molecules which regulate various biochemical and genetic activities. They provide the immunity to plants from pests and insects and enhance the ability of plants to tolerate the impacts of abiotic and biotic stress and also produce bioactive compounds and phytohormones of biotechnological interest. In this book chapter, we will review the advent role of microbiome in plant growth and development. Efforts have been made to summarize the utilization of various hormones to mitigate the effects of various environmental stresses on cultivated plant communities. The final sections of the book chapter describe the applications of phyto-microbiome in twenty-first century and the clear out cut to commercialize of a phyto-microbiome-based technology.

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14.1 Introduction

Soil is considered to be the reservoir for various microbes and organisms like ants, moles, and nematode (Dhanjal et al. 2017). Recent advances in sequencing techniques and elevation in number of microbial libraries have expanded the aura of the tree of life, as it is dominated by microbes (Anand et al. 2019). The horizontal gene transfer and mutation events have evolved wide array of variation among the microbial community. This significantly increases the diversity within species and endows them their functional characteristic (Bengtsson-Palme et al. 2017a). Here, soil plays the major role in recycling the nutrients (phosphorus and nitrogen) and imparting protection against abiotic and biotic stress (Dhanjal et al. 2018). Although the agricultural activities have increased the yield of crop, simultaneously it has also deteriorated the biological and physical properties of the soil (Gomiero 2017). Even usage of fertilizer aids in maintaining the soil fertility, but on tillage microbial communities get disrupted (Dong et al. 2012). The degradation of soil due to anthropogenic activities has emerged as a global concern and sustainable agriculture has become the need of the time for sustaining the life of humans on this earth. Thus, to sustain the life, plant–microbiome plays significant role in improving soil quality and plant growth, and providing resistance from stress (Rashid et al. 2016; Kumar et al. 2019a).

Plant–microbiome is essential as they contain distinct properties like production of secondary metabolites as well as phytohormone and nitrogen fixation and many more. Therefore, it represents the microbial community which is directly or indirectly associated with plants. Hence, they have been generally characterized into epiphytic, endophytic, and rhizosphere microbiome (Igiehon and Babalola 2018a; Kour et al. 2019; Kumar et al. 2019b; Rana et al. 2019a; Rana et al. 2019b). The soil contains both types of microbes, i.e., pathogenic and nonpathogenic in nature (Finkel et al. 2017). Nonpathogenic involves the symbiotic and neutral microbes which plays variety of roles in diverse fields like biodegradation, biofuel production, biocontrol, biotransformation, seed production, phytoremediation, and many more (Dwibedi and Saxena 2019). These potentials of microbes prompt us to understand the hyperdiversity of these unexplored plant microbial communities, not only for sustaining the ecosystem but also to preserve these biodiverse microbial communities beneficial for mankind (Braga et al. 2016). Hence, untapping and deep understanding of these plant microbes as whole have become important to explore the positive interactions for sustainable agriculture, especially during microbiome-dependent cropping approach (Busby et al. 2017). In this chapter, we will discuss the challenges and efforts put forward to advance our knowledge about different properties of microbes and how these properties affect plants. Further, we will also discuss about the soil microbiome improving the crop production.

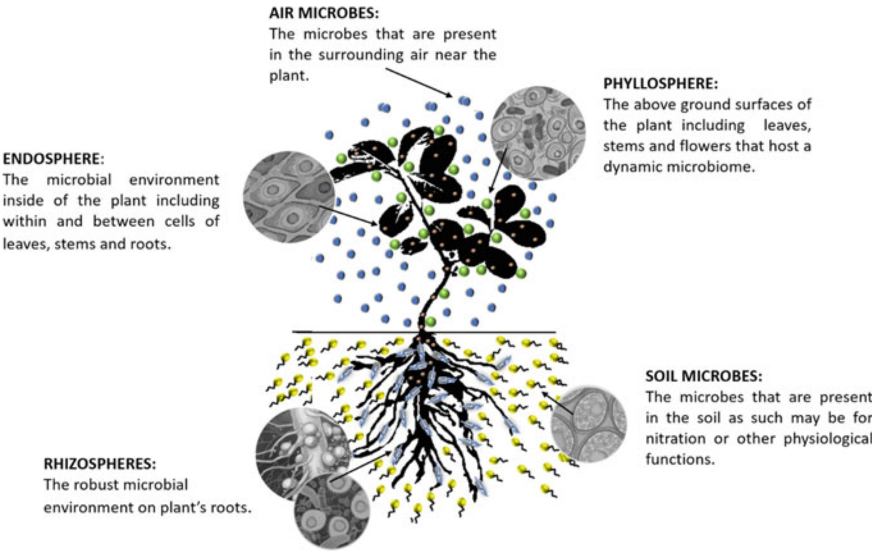

Fig. 14.1 Compartmentalization of plant microbiome

14.2 Composition and Function of Plant Microbiome

Plants are surrounded by a variety of microbes and vary according to their location like anthosphere, carposphere, phyllosphere, rhizosphere, and spermosphere (Shade et al. 2017) (Fig. 14.1). Here, we categorized the bacteria into three broad categories as follows.

14.3 Plant Microflora Below the Ground

Root microflora generally get horizontally transferred as they are predominantly present in soil (Lareen et al. 2016). Most dominating microbes belong to the family of *Acidobacteria, Actinobacteria, Bacteroidetes, Planctomycetes, Proteobacteria,* and *Verrucomicrobia* (Mendes et al. 2013; Kour et al. 2019; Suman et al. 2016; Verma et al. 2017b). There is a possibility of vertical transmission through seeds. Seeds also serve as reservoir for microbes, which allows them to multiply in the roots during plant development (Shahzad et al. 2018). Root system of plant provides distinctive niche to soil microbes residing in the rhizosphere (roots and certain portion above the ground) (Raaijmakers et al. 2009). Recently, Donn with his colleagues reported about the changes in bacterial community surrounding the roots of wheat and found 10-fold increase in population of actinobacteria, copiotrophs, oligotrophs, and pseudomonads at rhizosphere. Moreover, they also reported that over time, variation takes place in rhizoplane and rhizosphere community but there is no variation in soil microbial population (Donn et al. 2015). Similar results were also seen for *Brachypodium distachyon* rhizosphere which reported about the predominance of species of *Burkholderiales, Sphingobacteriales,* and *Xanthomonadales* family (Kawasaki et al. 2016). There have been reports which claimed that root exudates like amino acids, fatty acids, organic acids, plant growth regulators, phenolics, putrescine, sterols, sugars, and vitamins also affect microbes present in the rhizosphere, proclaimed as rhizosphere effect (Hunter et al. 2014). For example, secondary metabolite benzoxazinoids (BXs) synthesized by the roots of maize amends the composition of root-associated microbes, out of which members of *Actinobacteria* and *Proteobacteria* family were highly affected (Neal et al. 2012; Kudjordjie et al. 2019). Moreover, other researchers are investigating the mechanisms responsible for the assembly of microbial community and effects of substrate and root exudation on microbial community. Hence, this confirms that composition of rhizosphere microbes gets influenced by plants species and root exudates (Jacoby et al. 2017; Yadav et al. 2015a; Yadav et al. 2015b).

Various bacterial endophytes have colonized the roots of plants internally (Santoyo et al. 2016). These bacterial endophytes enter the root tissues via passive processes or root abrasion and active mechanisms (Santos et al. 2018). The transmission and colonization of these bacterial endophytes inside the plant depend on various factors like ability of endophytes to colonize plant and distribution of plant resources (Kandel et al. 2017). Various microbes have gained access to root tissues, for instance, *Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Firmicutes, Gemmatimonadetes, Planctomycetes, Proteobacteria*, and *Verrucomicrobia* are the bacterial taxa which have gained access to grapevine roots (Morgan et al. 2017; Verma et al. 2016; Yadav et al. 2016). On the other hand, members of *Bradyrhizobiaceae, Comamonadaceae, Rhizobiaceae,* and *Streptomycetaceae* family are the one predominantly found in rice roots (Edwards et al. 2015).

14.4 Plant Microflora Above the Ground

Floral parts, leaves, and vegetative parts present above the ground provides distinctive environment for epiphyte and endophyte microbes (Frank et al. 2017). The endophytes predominantly translocate themselves through xylem to different parts of plants, which can either be fruit, leaves, or stem (Hardoim et al. 2015). With respect to location on the plant, aboveground microbes distribute themselves with other members of endophytic community (Nair and Padmavathy 2014). It has been observed that phyllosphere microbes obtained from the soil get influenced by external stimuli and later shows the profound effect (Carvalho and Castillo 2018). Subsequently, various microbes have been found in the phyllosphere and endosphere up to species level (Schlaeppi and Bulgarelli 2015). For example, on analyzing the carposphere and phyllosphere microbes of grapevine uncovered the presence of *Acinetobacter, Bacillus, Citrobacter, Curtobacterium, Enterobacter, Erwinia, Frigoribacterium, Methylobacterium, Pantoea*, and *Pseudomonas* species (Kecskeméti et al. 2016; Verma et al. 2017a; Verma et al. 2017b; Yadav et al. 2019; Yadav et al. 2018a; Yadav et al. 2018b; Yadav et al. 2018c). On the other hand, endophyte analysis of grape berries uncovered that *Bacillus, Burkholderia, Dyella, Mesorhizobium, Propionibacterium, Pseudomonas,* and *Ralstonia* species are the dominant (Campisano et al. 2014).

There is a study conducted on 300 different varieties of maize to analyze the leaf microbiome that revealed the predominance of *methylobacteria* and *sphingomonads* taxa (Wagner et al. 2019), whereas in apple flowers there is predominance of *Enterobacteriaceae* and *Pseudomonas* species (Steven et al. 2018). Various other studies conducted on almond, apple, grapefruit, pumpkin flower, and pumpkin also revealed the abundance of *Pseudomonas* species (Aleklett et al. 2014). Lately, seed-associated microbes have highlighted the abundance of *Actinobacteria, Bacteroidetes, Firmicutes,* and *Proteobacteria* (Qiao et al. 2017). Usually, microbes found on aboveground have originated from air, seed, and soil and adapted themselves to sustain their life on or inside the tissue of plant, where various factors like environmental condition, soil, and management influence microbial composition (Raaijmakers et al. 2009). Compartment-specific assembly with the host illustrates the strong relationship among the aboveground microbes and plant on the basis of functionality, but still there is a need to understand this association deeply (Garcia and Kao-Kniffin 2018). Aboveground microbes and endophytes are recognized for their ability to alleviate stress tolerance, increase disease resistance, and promote plant growth (Kumar and Verma 2018).

14.5 Satellite and Core Microflora

Core microflora or core plant–microbiome (CPM) refers to those microbes that closely linked with particular type of plant and are independent of soil and environmental conditions (Lakshmanan et al. 2014). *Bradyrhizobium, Microvirga,* and *Sphingobium* were found to be the core microbiome of *Solanum tuberosum* (potato) (Pfeiffer et al. 2016). Another study revealed that *Hyphomicrobiaceae*, *Micrococcaceae*, and *Pseudomonadaceae* sps. are the core microbes found in grapevine (Zarraonaindia et al. 2015). The CPM contains those microbial taxa that are essential for plant and have established themselves in plant during the course of evolution (Jacoby et al. 2017). The enhancement of microbial taxa through evolutionary selection process contains the genes responsible for survival and holobiont of the plant (Rosenberg and Zilber-Rosenberg 2018).

Distinctively, the microbial taxa found in less affluence and fewer locations are referred to as satellite taxa. They are described based on their habitat, geography of habitat, and their regional population. These taxa are perceived as the regulators of important mechanisms in an ecosystem (Banerjee et al. 2018). Few researchers found that microbial taxa having the scarce population play a crucial role in obstructing the entrance of undesirable microbial taxa in soil. Parallelly, the scarce bacterial population produces different antifungal chemicals which guard the plants against soil-induced infectious organisms (Ciancio et al. 2016). Various researches demonstrate that forfeiture of scarce microbial population compromises with plants' efficiency (Garcia and Kao-Kniffin 2018). Researchers also found that microbial taxa regulate vital mechanisms that can be unequal to their population number (Pineda et al. 2017). Numerous ecological factors should be taken into account to comprehend mechanisms of plant–microbiome taken in response to certain environmental tensions (Braga et al. 2016).

14.6 Factors Affecting Plant Microbiota

The microbial organization in plant's tissues is linked with various organic and inorganic constituents. These constituents can be type, pH, salinity, structure, moisture, organic matter, and exudates of soil, respectively (Jacoby et al. 2017; Yadav et al. 2015c; Yadav and Yadav 2018). These constituents above are important for parts of the plants which are present beneath the ground level. Other constituents such as infectious agents, environmental conditions, and human activities affect the microbial community of above- and belowground plant parts (Mendes et al. 2013). Using high-throughput approaches like a shotgun and 16S rRNA sequencing, Bulgarelli with his colleagues examined the root microbial community of various barley species and concluded that root exudates and innate immune system determine the organization of root microbiota (Bulgarelli et al. 2015). Various host-influence factors such as growth stage, age, and wellness of plants affect organization of plant microbiota by the formulation of root exudates and plant signaling processes (like induced and acquired systemic resistance, respectively) (Ortíz-Castro et al. 2009).

14.7 Function and Role of Plant Microbiome

Plant–microbiome consists of all neutral, beneficial as well as pathogenic microbes. There are few plant growth-promoting (PGP) bacteria which promote the growth of plant by synthesizing different phytohormones such as gibberellin, cytokinin, and auxin (Egamberdieva et al. 2017; Yadav 2017a, b; Yadav 2019; Yadav et al. 2017a). However, few PGPB produce ACC deaminase (1-aminocyclopropane-1-carboxylate deaminase) which regulate the level of ethylene (stress hormone) in plant (Glick 2014). Literature survey revealed that *Arthrobacter* spp., *Bacillus* spp., and *Pseudomonas* spp. are the ACC deaminase producer, which enables them to enhance the growth of plant (Souza et al. 2015). On analyzing the root microflora of soybean and wheat, it showed the dominance of *Pantoea* spp., *Paraburkholderia* spp., and *Pseudomonas* spp. These species promote the plant growth because of the properties like phytohormones (ACC deaminase, indole acetic acid), nitrogen fixation, and phosphate solubilization mechanism to enhance the stress tolerance

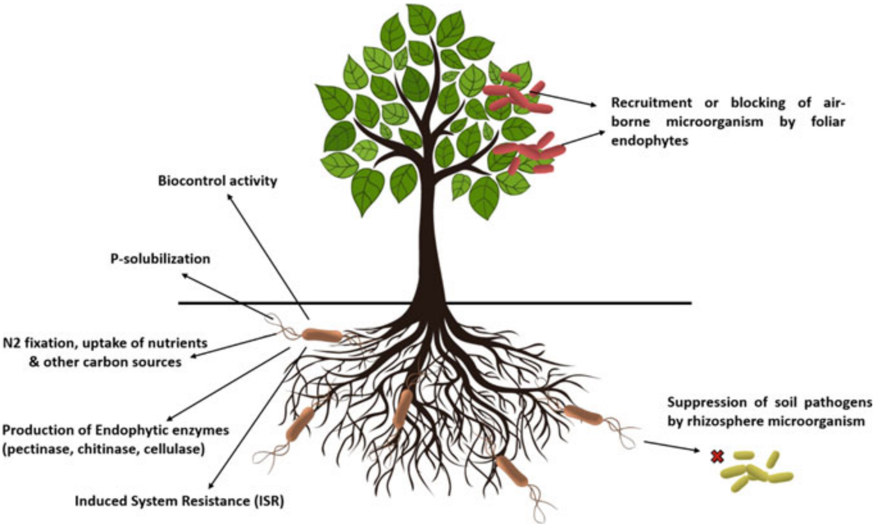

Fig. 14.2 Schematic overview of function and impact of plant–microbiome on the host plant

and improve nutrient uptake (Rascovan et al. 2016). Schematic representation of the function performed by microbiome is illustrated in Fig. 14.2.

On the other hand, there are few bacteria which show disease symptoms because of the production of phytohormones and phytotoxic compounds (Olanrewaju et al. 2017). For instance, *Pseudomonas syringae* is a plant pathogen which affects various plants like green bean, olive, tobacco, and tomato (Hirano and Upper 2000). *Erwinia amylovora*, another pathogenic bacterium, causes fire blight disease in ornamental plants. *Ralstonia solanacearum, Xylella fastidiosa,* and *Xanthomonas* sps. are the bacterial species that are associated with various diseases of banana and potato (Vrancken et al. 2013). There are certain factors which determines the severity as well as outcome of disease like biotic factors (like plant microflora), favorable environmental factor, host susceptibility, and population size of pathogens (Lareen et al. 2016). Both aboveground plant microflora and belowground microflora have been found to increase the resistance in host via commensal interactions of pathogen or due to modification in plant defense system (Igiehon and Babalola 2018b).

The plant microbiota uses diverse biocontrol mechanism like antibiotic production, siderophore production, lytic enzyme production, and pathogen-inhibiting volatile compound production to prevent the disease and pathogenic invasion (Compant et al. 2005). Few plants modulate the hormone level and induce resistance in plant to protect them from plant pathogens. Therefore, agricultural lands containing disease-suppressing microbes build pressure on pathogens and make it the disease-suppressive soil (Gómez Expósito et al. 2017). Particularly, *Bacillus, Burkholderia, Enterobacter, Paenibacillus, Pantoea, Paraburkholderia, Pseudomonas,* and *Streptomyces* have been found to play the main role in pathogen suppression (Yadav et al. 2017b). Carrión and his colleagues revealed that *Paraburkholderia graminis* PHS1 produces cysteine desulfurase and dimethyl sulfoxide reductase (sulfurous volatile compounds), which provide suppressive ability against fungal root pathogens (Carrión et al. 2018). On the other hand, Durán and his colleagues highlighted the role of endospheric bacteria belonging to *Enterobacter* and *Serratia* family, which have the biocontrol activity against *Gaeumannomyces graminis* (Durán et al. 2017).

14.8 Advancements in Plant–Microbiome Research (PMR)

Prediction about the advances in plant–microbiome research is quite difficult (Thijs et al. 2016). But following are the three points which help us in shaping the future of both applied and basic studies of soil microbiome.

14.8.1 Upgradation of Culturing Techniques

The advent of molecular techniques has rapidly increased the genomic data of uncultured microbial taxa persisting in the soil, for which closely related strains are currently unknown (Warinner et al. 2017). There is an exponential increase in data because of culture-independent approach like single-cell genomics or by the assembling of individual genome obtained via metagenome analysis (Blainey 2013). Although we have the genomic information of all the microbes present in the soil, still we lack to understanding about their functionality. Therefore, categorizing them in ecological taxa considering their genomic data is risky (Peršoh 2015). Additionally, the slow-growing microbe is another challenge. Therefore, approaches which use genomic data to intercept the information about ideal cultivation and isolation of uncultured microbes will unquestionably be helpful for the field to me in forward direction (Streit and Schmitz 2004).

14.8.2 Role of Viruses in Soil Microbiome

Approximately, 10^7–10^9 virus particles are found in one gram of soil, and this number is less than the number of viruses found in the aquatic ecosystem (Jacquet et al. 2010). Apparently, these viruses found in soil are highly diverse and remained unexplored (Williamson et al. 2017). Marine studies have revealed that phages play chief role in nutrient dynamics, as they maintain the nutrient dynamics by killing the 20–40% microbial population present in the water column (Sime-Ngando 2014). Various researches have demonstrated soil to be the reservoir for phages which specifically targets bacteria like *Rhizobium* spp. and *Xanthomonas* spp., still the effect of these viruses on activity and composition of soil remains comprehended (Buttimer et al. 2017). According to statistics, $> 90\%$ of viruses found in soil mainly get absorbed by clay as well as other soil surfaces, which leaves very low number of viruses in soil. Additionally, it is also uncertain that these viruses are capable enough to infect the plant–microbiome (Andika et al. 2016). Due to advancement in viral metagenomic field and development of new techniques, there is an enumeration in viral population, and it has prompted us to explore new viral community as well as study the effect of these viruses on microbial processes and populations (Jacquet et al. 2010). Basically, it clear to develop a holistic understanding of how these microbes (directly or indirectly) interact with each other instead of studying the individual microbial group (Tshikantwa et al. 2018).

14.8.3 Importance of Horizontal Gene Transfer

There are three main mechanisms of horizontal gene transfer, i.e., conjugation, transduction, and transformation, by which microbes their gene from one generation to another (Von Wintersdorff et al. 2016). Genes contains the sequence of various different traits like arsenic detoxification, antibiotic resistance, and xenobiotic degradation. Therefore, mobile genes may cause evolution of new phenotypic characteristic and may generate close relation with dissimilar genomes (Janssen et al. 2005). However, horizontal gene transfer can impose dilemma during the attempt of linking particular gene to targeted phylogenetic lineages. This definite control of horizontal gene transfer, its frequency in soil microbial communities, and their effect on the soil population are the topics which nurtures this expedition and motivate us to work in this direction (Andrews et al. 2018).

14.9 Use of Plant–Microbiome as a Biocontrol Agent

Worldwide, plant diseases have been held responsible for farmers' losses. FAO stated that 25% of crop loss occurs due to plant diseases and pests. Therefore, there is need for control plant disease (Savary et al. 2012). To achieve this, specific plants which are resistant to various diseases are bred along with different cultivation techniques like use of pathogen-free seeds, crop rotation, or by using biological and chemical agents (Cheng and Cheng 2015). All these plant protection methods influence the microbiome of plant; hence, information gathered from plant protection strategies should be taken into consideration during cultivation (Berg et al. 2014). In various cases, the onset of disease takes place due to imbalance of plant–microbiome and obstructs the desired objective of whole microbiome. Hence, analyzing metabolic pathway and plant–microbiome of the host plant unlock new opportunities to advance biocontrol approaches (Thijs et al. 2016).

Overall, better understanding unfolds the information about the diverse microbes which aid in plant growth and produce antagonistic chemicals against phytopathogens (Bargaz et al. 2018). Mosses are known to have unique microbial diversity and harbor microbes with exceptional antagonist potential because of their ecology (Bragina et al. 2012). Moreover, medicinal plants are also to be known to nurture diverse microbes as their secondary metabolites determine the composition of microbiome (Berg et al. 2015). Because of large diversity among microbes, it is believed that endophytes, especially seed endophytes, can emerge as the unique biocontrol agent (Ryan et al. 2008). Till now, largely bacteria as well as fungi have been used for biocontrol purposes (Whipps 2001). Recently, Archaea have been exploited to become the member of plant–microbiome but its biocontrol potential is still under evaluation (Müller et al. 2015).

As stated above, microbes linked with plant develops a network which gets influence during pathogen invasion. Therefore, these networks will enable us to develop new model and enhance disease management of the plant–soil microbes (Hassani et al. 2018). Even researchers have developed a framework to decipher these microbiome networks and showed the benefit of these frameworks to test their hypothesis for targeted microbes responsible for particular plant disease. They proposed four types of network analysis: (a) first type involves the general analysis of network to discover the aspiring taxa to maintain the existing microbial community; (b) second type involves the analysis majorly focusing on host as well as plant response; (c) third type involves the identification of pathogenic taxa which are directly or indirectly associated with prior known taxa of pathogens; and (d) last type involves the identification of those taxa which are associated with disease (Poudel et al. 2016).

Now, most of the biocontrol agents are screened through in vitro antagonisms effective against particular pathogen. As this screening allows the identification of potent biocontrol agent, still intense debate is going on about this screening approach (Larran et al. 2016). The chief reason is that biocontrol and plant growth-promoting (PGPR) microbes during in vivo evaluation show no antagonisms, whereas in the case of in vitro studies it shows modest result (Beneduzi et al. 2012). Different high-throughput techniques have been developed for plant assays but were found to be ineffective as includes artificial characters (Rasheed et al. 2017). For instance, rapeseed treated with *Paenibacillus* showed plant growth in natural soil, whereas no negative effect was observed in sterile soil under gnotobiotic conditions. Therefore, there is need for testing the potential of biocontrol and plant growth-promoting strains in soil as well as evaluation of their effect on soil type and plant species also be done (Bashan et al. 2014). Another research study showed the presence of similar genera of *Pseudomonas* in lettuce rhizosphere in three different soil samples from the field. This confirms that soil types do not play any role in biocontrol activity and rhizo-competence (Schreiter et al. 2018).

Additionally, targeted enhanced diversity is also being exploited as biomarker for screening purpose by researchers. These applicability and development in biological control is attaining attention globally (Atanasov et al. 2015), whereas previously only one microbe was used in biocontrol strategies, which explains about inconsistency.

But recent advancements have enabled us to develop microbiome-dependent biocontrol strategy (Ab Rahman et al. 2018). In 1999, Emmert and Handelsman stated Gram-positive bacteria to be potential candidate in biocontrol practices. On assessing the registered products for biocontrol and along with those that are in pipeline, almost all the products are bacillus based (Emmert and Handelsman 1999). There is technical reason for using *Bacillus* sps. as the base product in contrast to other Gram-negative bacteria, as form spores under unfavorable condition for survival. This spore formation increases their shelf-life (Berg et al. 2017). On examining the plant-associated microbes which harbor large number of bacterial species, it make us realize that we are seeing the very small portion of taxonomic diversity for biocontrol purpose (Chowdhury et al. 2017).

Moreover, the researchers have reported that 2% mean population is occupied by Bacillus species from the total bacterial community in the soil (Li et al. 2017). As an exception, another researcher published a paper in which they stated that 37% of *Bacillus* and *Paenibacillus* species are found in arid soil (Köberl et al. 2013). Still, the debate is going on comprehending the role of *Bacillus* on the plant and against its pathogen, or does it trigger the plant growth hormones or induce resistance as they are involved in plant–microbe interaction. It is already known that *Bacillus* and *Paenibacillus* strains synthesize various antibiotics and secondary metabolites (Mhlongo et al. 2018). As per studies, strains and spores of both *Bacillus* and *Paenibacillus* are predominantly found in the environment and this might be reason for reducing number of plant-associated microbial community. Hence, more emphasis is given on increasing the microbial diversity within products during biocontrol activity. This prompts to develop new strategies to explore the antagonistic potential of microbes associated with plants (Yadav et al. 2017c).

Nowadays, antibiotic resistance is becoming the global concern and making our treatment ineffective as a result people is suffering from disability, prolonged illness, and at last death (Laxminarayan et al. 2013). Regrettably, strategies used in agriculture like use of antibiotics in livestock are increasing the resistance level. These livestock aid in transferring the resistance in plant production system, which causes the enrichment of resistant bacteria in the rhizosphere (Founou et al. 2016), even though many microbes have developed resistance and are highly prevalent in the environment. Therefore, risk management studies to suppress the emergence of resistant microbes have become our first priority (Larsson et al. 2018). Though the different biocontrol products have shown lower persistence on soil and plant, usage of spore-forming bacteria will change the whole scenario (Paul et al. 2019). Additionally, soil microbes are found to be bacterial antagonists in nature. In particular, *Paenibacillus* have been found to contain not only the antibiotic synthesis gene but also contain antibiotic gene, justifying about their antagonistic ability within the microbiome (Cycoń et al. 2019). Therefore, further investigation is required to understand the mobilization of resistant gene through different ways of horizontal gene transfer (Bengtsson-Palme et al. 2017b).

14.10 Studies Related to Plant Microbiomes

Even though plant–microbiome is a broad topic, microbial group associated with plant is an active research area. The major reason is the exponential increase in publications in recent year on this topic as well as research targeting the niche of specific plant and how interaction takes place among particular microbial community (Naylor and Coleman-Derr 2018). Additionally, it has been observed that microbial assembly varies according to environmental conditions and plant species. This creates curiosity to learn more about how microbes are acquired by plant, either the microbes are subsequently passed to next generation or recruited from the environment (Yu and Hochholdinger 2018).

In spite of the role of the microbes in promoting the plant growth and nutrient cycle, we still require to gain more insight about microbial interaction which makes up the plant microbiome. This will allow us to comprehend the functioning of plant microbiome to changing agricultural practices and environmental conditions (Garcia and Kao-Kniffin 2018).

Various studies are being conducted to extend the link the shift in environmental condition with microbiome response (Purahong et al. 2018). For instance, the researcher conducted on the grape vineyard using culture-independent method revealed the presence of dynamic microbial community on different stages of plant lifecycle, enlightening the effect of agrochemicals on the plant (Morgan et al. 2017). Numerous studies have associated microbiome with physiology of plant, as microbes found in plant–microbiome in desert aid in providing the resistance to plant to survive in unfavorable conditions (Vurukonda et al. 2016). In 2012, Marasco and his colleague proposed that plant microbiomes are essential to develop resistance against drought stresses (Marasco et al. 2012). Another effective interaction was reported by another research group, where the described role of microbiome determines the composition of plant root exudates. These examples highlight the role of soil microbiome not only in plants but also in their evolutionary mechanism, regulated by host–microbe interaction (Lareen et al. 2016).

14.11 Conclusion and Future Prospects

The microbial communities possessing beneficial traits act as a powerful tool to elevate the sustainable agriculture by reducing the usage of fertilizes and combatting plant diseases to enhance the crop yield. The potential of microbiome is to elicit the plant growth, generate stress resistance, and improve plant health. Various microbial inoculants have been developed to achieve field success by either designing smart microbial consortia or engineering the microbiota with beneficial characteristics. In order to upsurge the crop yield and support the enhanced technologies, new plant breeding practices and suitable formulations are required. To achieve these goals, there is need to gather insight about the plant–microbiome interaction, microbial community of soil, and their stability during environmental changes. As single microbes are the key regulators within microbial community, therefore comprehensive investigation on these microbes along with microbial community of soil can assist us in expanding the horizon of this field. Moreover, the knowledge gained will enable us to completely comprehend the impact of these microbes on disease resistance, nutrient cycles, and yield of the crop. Furthermore, it will prompt us to explore novel strategies for microbiome engineering to move toward the sustainable agriculture.

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Chapter 15
Current Aspects and Applications of Biofertilizers for Sustainable Agriculture

Modhurima Misra, Ashish Sachan and Shashwati Ghosh Sachan

Abstract There has been a sharp increase in the world's population over the past few decades which can be threatening in terms of the food security of the people. Thus, to cater to the huge demand of food, agricultural production should be increased within a short span of time and with limited worldwide agricultural land resources. This situation has driven the farmers all over the world to rely heavily on the commercially available chemical fertilizers for enhanced agricultural productivity. Though there has been a significant rise in the production of crops, these fertilizers have proved to be detrimental for our ecosystem as well as animal and human health. The deteriorative effects of the large chemical inputs in the agricultural systems have not only challenged the sustainability of crop production but also the maintenance of the environment quality. Using biofertilizers is a natural, low-cost, environment-friendly way out to this problem. Biofertilizers comprise living microorganisms capable of supplying sufficient nutrients to the plants, while maintaining high yield. The present chapter aims at describing in brief the requirement of biofertilizers in the first place, as well as their choice over the conventional synthetic ones, the different types, their roles in agriculture, their production and mode of action and most importantly advantages and demerits. The inputs from various literature mentioned herein will help in understanding the immense importance of their usage in modern-day farming with a cleaner ecosystem.

Keywords Biofertilizers · Consortium · Microbiome · Plant growth promotion · Sustainable agriculture

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15.1 Introduction

In the recent years, environmental pollution has become a matter of concern worldwide, with various industries and agricultural systems being the two most significant contributors. The components of agriculture which affect the environment are the different chemicals used for better production of crops that includes fertilizers, pesticides, insecticides, etc. Even though these can cause rapid production of crops (Santos et al. 2012) and put an end to the scarcity of food, their retention in the ecosystem, once introduced, can have deleterious effects on civilization in the long run. These are industrially manipulated compounds, having known quantities of different elements like nitrogen, phosphorus, sulphur, potassium, etc. Groundwater, contaminated from leaching of nitrates can cause a severe disease called Blue Baby Syndrome (Knobeloch et al. 2000). In this regard, safer, eco-friendly approaches are being sought after as potential alternatives to synthetic fertilizers. Thus, keeping these problems in mind, biofertilizers have been developed, which are often regarded as one of the best gifts to modern agricultural science. These have been proved to be quite successful in increasing the crop yield without disturbing the ecological balance. Europe and Latin America have started using biofertilizers significantly, due to the strict regulations on their consumption of chemical fertilizers (Raja 2013).

Numerous definitions of biofertilizers are available which can be attributed to the improved understanding of these compounds from time to time. Biofertilizers contain various microbes which mobilize nutritional elements through their regular metabolic activities (Vessey 2003), thereby enhancing their accessibility and uptake by the host plants. Mazid et al. (2011) defined them as "substances which contain living microorganisms that colonize the rhizosphere or the interior of the plants and promote growth by increasing the supply or availability of primary nutrients to the target crops, when applied to soils, seeds or plant surfaces". They are renewable, "eco-friendly" agro input of organic origin and consist of microorganisms which can be nitrogen fixers, phosphate solubilizers, sulphur oxidizers or organic matter decomposers (Vessey 2003). The application of microbial inoculum dates long back and started with small scale compost production that showed potential as a biofertilizer (Khosro and Yousef 2012).

The commercialization of biofertilizer dates back to 1895 when Nobbe and Hilther launched the product "Nitragin" (Yimer and Abena 2019). As of today, other microorganisms like *Azotobacter*, Blue-green algae are being used as potential biofertilizers. With the passage of time, these biofertilizers have become an indispensable part of modern-day organic farming, an environmentally sustainable form of agriculture that emphasizes protection and preservation of natural resources along with preventing the use of chemical fertilizers and pesticides (Barman et al. 2017).

15.2 Biofertilizers—A Natural Gift for Sustainable Agriculture

Indiscriminate use of chemical fertilizers for crop production can have hazardous effects on our environment which is of great concern in the context of sustainable agriculture as well as environmental remediation. These synthetic molecules, apart from being costly, contaminate the air, water and soil as well as cause eutrophication of surface water bodies (Youssef and Eissa 2014). These agrochemicals are capable of increasing the crop yield to a certain level and their excessive use can have long-lasting effects and negatively affect human health. Their overuse can lead to the decrease in soil fertility by increasing the salt content (Aggani 2013) and may have a role to play in greenhouse effect, depletion of ozone layer and acidification of soil and water (Kumar et al. 2018) (Fig. 15.1). They make the plants more susceptible to infections by weakening their roots.

In this regard, the exploitation of various microorganisms in augmenting nutrients to the host plants has gained significant importance as they have shown great potential as a substitute for the chemical fertilizers. The important benefits of these biofertilizers can be listed as follows:

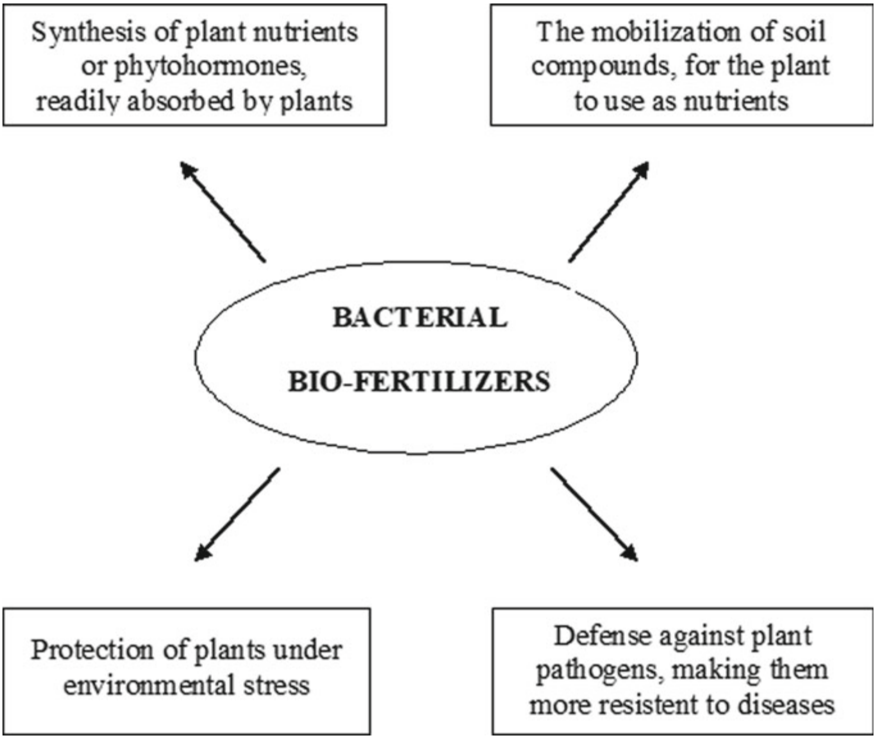

Fig. 15.1 Major functions of bacterial biofertilizers

- Being cost effective and ecosystem friendly (Khosro and Yousef 2012).
- They enrich the soil environment by accumulating various micro- and macronutrients through nitrogen fixation, phosphate solubilization and decomposition of organic matter (Sinha et al. 2010).
- They increase crop productivity by releasing different growth-regulating substances and synthesis of phytohormones.
- They help to increase the biodiversity of the soil where they are applied by inviting the localization of different beneficial bacteria and fungi.
- Biofertilizers form a part of nutrient cycling when applied as seed or soil inoculants (Singh et al. 2011).
- These beneficial microorganisms make the host plants more resistant towards environmental stress, like drought, salinity, etc., (Bhardwaj et al. 2014).
- The microbes are vital constituents of the Integrated Nutrient Management (INM) system by continuously and slowly releasing metabolic intermediates (Adesemoye and Kloepper 2009).

15.3 Types of Biofertilizers

Both rhizospheric and endophytic microbial communities can significantly determine crop vigor in agricultural systems through interactions with the host plants. The microorganisms which are important for agriculture can be distinguished as plant growth-promoting rhizobacteria (PGPRs), nitrogen-fixing cyanobacteria, phosphate-solubilizing microorganisms (PSMs), potassium-solubilizing microorganisms (KSMs), siderophore and phytohormone producing organisms, mycorrhiza, plant disease-suppressive bacteria, stress-tolerant endophytes and biodegrading microbes (Singh et al. 2011). The rhizosphere can have up to 10^{11} microbial cells per gram of root (Egamberdieva et al. 2008) and above 30,000 prokaryotic species (Mendes et al. 2013) that may automatically increase the crop productivity by enhancing the soil physicochemical properties, biodiversity of soil microbiome, plant growth and development (Sahoo et al. 2014). Figure 15.2 gives a brief idea about the major groups of biofertilizers (Table 15.1).

15.3.1 Nitrogen-Fixing Microorganisms

Nitrogen is considered to be one of the fundamental elements for plant development. The crops are dependent on bioavailable form of nitrogen for their growth, which is quite limited in nature. The process by which atmospheric nitrogen gets converted to organic forms like ammonia and nitrate, for ready utilization by the plants, is known as biological nitrogen fixation (BNF) (Gothwal et al. 2007). The different microorganisms capable of fixing atmospheric nitrogen can be grouped under three

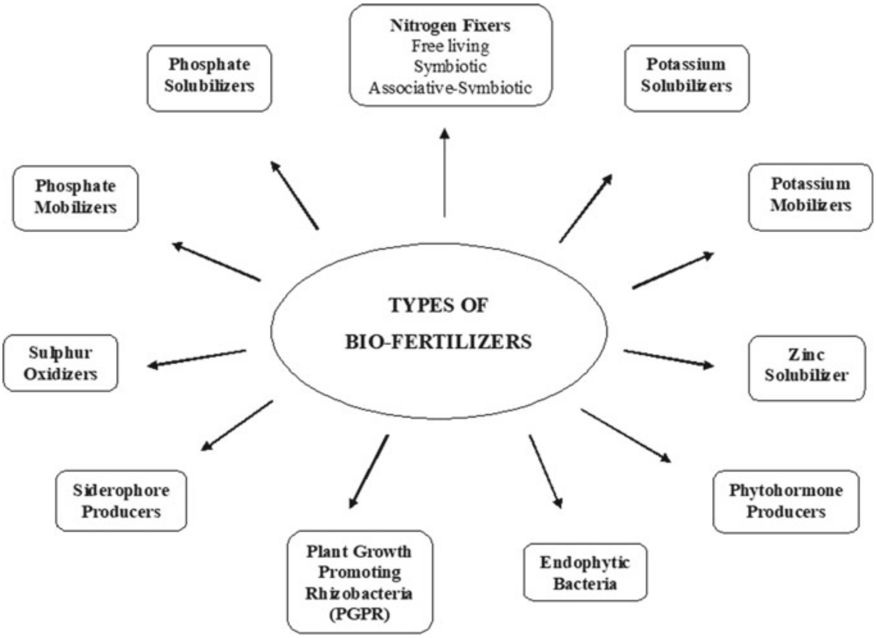

Fig. 15.2 Major groups of biofertilizers

categories—symbiotic, free living and associative (Gupta 2004). Symbiotic associations account for majority of BNF in nature. Nitrogen-fixing biofertilizers are crop specific in nature (Choudhury and Kennedy 2004; Yadav 2017a, b). Some of the important bacteria and algae which play a crucial part in this process are discussed below (Table 15.2).

15.3.1.1 *Rhizobium*

It is a symbiotic bacterium that colonizes the roots of the leguminous plants forming tumourous out growths known as root nodules, which helps in ammonia production. It fixes atmospheric nitrogen even in symbiotic association with a non-legume called *Parasponia* sp (Mahdi et al. 2010). They utilize the photosynthetic products of the plants as their carbon source and in return fix atmospheric nitrogen for their benefactor. The morphological and physiological characteristics of *Rhizobium* at free-living condition are different from those of the bacteroid form in nodules (Kumar et al. 2018). These are considered to be the most proficient biofertilizer for legumes as far as the amount of nitrogen fixed is concerned (Jehangir et al. 2017; Yadav et al. 2019a, b, c). The nodulation and nitrogen fixation by the bacterium is attributed to the nod, nif and fix genes.

Table 15.1 Major groups of biofertilizers with their types and examples

Major groups	Microorganisms	Examples
N_2—Fixers	Free living	*Azotobacter sp., Beijerinkia sp., Clostridium sp., Klebsiella sp., Anabaena sp., Nostoc sp.*
	Symbiotic	*Rhizobium sp., Frankia sp., Anabaena azollae*
	Associative Symbiotic	*Azospirillum sp., Anabaena sp.*
P—Solubilizers	Bacteria	*Bacillus sp., Pseudomonas sp., Rhizobium sp., Burkholderia sp., Micrococcus sp., Achromobacter sp., Agrobacterium sp., Aereobacter sp., Flavobacterium sp., Erwinia sp.*
	Fungi	*Penicillium sp., Aspergillus awamori, Aspergillus niger.*
P—Mobilizers	Arbuscular mycorrhiza	*Glomus sp., Gigaspora sp., Acaulospora sp., Scutellospora sp., Sclerocystis sp.*
	Ectomycorrhiza	*Laccaria sp., Pisolithus sp., Boletus sp., Amanita sp.*
	Ericoid mycorrhizae	*Pezizella ericae*
	Orchid mycorrhiza	*Rhizoctonia solani*
K—Solubilizers	Bacteria	*Bacillus mucilaginosus, Bacillus edaphicus, Bacillus circulans, Acidithiobacillus ferrooxidans, Paenibacillus* spp
	Fungi	*Aspergillus sp*
K—Mobilizers	Bacteria	*Bacillus* Spp
S—Oxidising	Bacteria	*Thiobacillus sp*
Zn—Solubilizers	Bacteria	*Bacillus subtilis, Thiobacillus thioxidans*
	Yeast	*Saccharomyces sp*
Phytohormone producers	Bacteria	*Galactomyces sp., Pseudomonas sp., Azospirillum sp., Bacillus sp., Arthrobacter sp., Acinetobacter sp.*
	Fungi	*Gibberella fujikuroi*
Endophytic microorganisms	Bacteria	*Azoarcus* sp., *Gluconoacetobacter diazotrophicus, Herbaspirillum seropedicae, Serratia marcesens*
	Fungi	*Trichoderma stromaticum*, *T. evansi*, *T. amazonicum*, *T. taxi*, *T. martiale*, *T. theobromicola*
Plant Growth-Promoting Rhizobacteria (PGPR)	Bacteria	*Bacillus spp., Pseudomonas fluorescence, Azospirillum sp.*, *Azotobacter sp.*, *Burkholderia sp.*, *Enterobacter sp.*, *Klebsiella sp.*

Source Modified from Barman et al. (2017)

Table 15.2 A comparative study of the different N_2 fixers

N_2 fixers	Type	Family	Important species	N_2 fixed (Kg N/Ha)	Recommended crops
Rhizobium	Symbiotic	Rhizobiaceae	*R. meliloti* *R. leguminosarium* *R. ciceri* *R. etli* *R. tropici* *R fredii*	50–100	Pulse legumes like chickpea, red-gram, pea, lentil, black gram, etc., oil-seed legumes like soybean, groundnut and forage legumes like berseem and lucerne
Azotobacter	Free living	Azotobacteriaceae	*A. chroococcum,* *A. vinelandii,* *A. beijerinckii,* *A. insignis* *A. macrocytogenes*	20	Rice, wheat, barley, oat, sunflowers, maize, line, beetroot, tobacco, tea, coffee and coconuts
Cyanobacteria (BGA)	Symbiotic, Free living and Symbiotic-Associative	–	*Nostoc sp.,* *Anabaena sp.,* *Gloetrichia sp.,* *Tolypothrix sp.,* *Aulosira sp.,* *Aphanotheca sp.*	20–30	Submerged rice, barley, oats, tomato, radish, cotton, chilli, sugarcane, maize, lettuce
Azolla	Symbiotic-Associative	Salviniaceae	*A.caroliniana,* *A. microphylla,* *A. filiculoides* *A. Mexicana*	30–50	Submerged rice with maximum temperature
Azospirillum	Symbiotic-Associative	Spirilaceae	*A.lipoferum,* *A.brasilensehave* *A.amazonense,* *A.halopraeferens,* *A.brasilense,* *A. trakense*	20–40	Maize, sugarcane, sorghum, pearl millet

Source Compiled from Kumar et al. (2017) and Kumar et al. (2018)

15.3.1.2 *Azotobacter*

It is saccharophilic, aerobic, heterotrophic in nature and commonly an inhabitant of the neutral to alkaline soils. The most common species found in arable soils is *A.chroococcum* (Wani et al. 2013). It produces abundant slime helping in soil aggregation. *Azotobacter* sp is a potential nitrogen fixer in rice crops (Sahoo et al. 2014). Besides fixing atmospheric nitrogen, this bacterium is known to produce some antifungal substance which lessens the seedling mortality (Subba Rao 2001), as well as some growth-promoting substances (Mahdi et al. 2010), phytohormones like indole acetic acid, gibberellin, cytokinin (El-Fattah et al. 2013) and group B vitamins like thiamine and riboflavin (Revillas et al. 2000), antibiotics, exo-polysaccharides and pigments (Jimenez et al. 2011).

15.3.1.3 Cyanobacteria

Cyanobacteria or Blue-Green Algae (BGA) are photosynthetic prokaryotes found in snow and hot springs. Besides fixing atmospheric nitrogen, they induce growth of plants by producing auxins and gibberellins. It has been reported that the production of rice increased from 15% to 38% with the supplementation of BGA inoculants (Kumar et al. 2018). In India, free-living and symbiotic cyanobacteria have been applied in the cultivation of rice (Thajuddin and Subramanian 2005).

15.3.1.4 *Azolla-Anabaena* Symbiosis

BGA fixes nitrogen by forming symbiotic association with different organisms like fungi, ferns, flowering plants, etc. The most common association forms between *Azolla* and *Anabaena azollae*—a blue-green alga. *Azolla*, a free-floating aquatic fern, finds extensive use in the cultivation of rice as a substitute for synthetic nitrogen fertilizers (Yao et al. 2018). Moreover, they have a role in maintaining the soil quality by enhancing the fertility of the soil. It quickly decomposes in the soil (Kannaiyan 1990) and can also be supplied as a green manure before planting of rice saplings (Mahdi et al. 2010). Other advantages include supplementation of significant amount of elements like phosphorus, potassium, sulphur, zinc, iron, molybdenum and other micronutrients. The most common species found in India is *A. pinnata* (Mahdi et al. 2010).

15.3.1.5 *Azospirillum*

It is Gram-negative and heterotrophic in nature. It mainly forms associative symbiosis with plants which use the C4-dicarboxylic acid pathway or Hatch and Slack pathway for photosynthesis as it grows and fixes nitrogen on salts of malic acid and aspartic acid (Mishra and Dash 2014; Arun 2007). These are non-nodule forming and not only colonize around the roots of the host plants but also reside inside the root tissues (Mahdi et al. 2010; Verma et al. 2016a, b, 2015; Yadav et al. 2016). Currently, it is used as a pre-sowing seed treatment (Kumar et al. 2018). Mostly, *A. lipoferum* and *A. brasilense* have proved to be the successful inoculants worldwide. These are also noted for phytohormones and/or siderophores production and phosphate solubilization (Puente et al. 2004). Other advantages with *Azospirillium* sp inoculation include disease resistance, biocontrol activity (Bashan and De-bashan 2010) and unwanted stress (drought, salinity, toxic compounds) tolerance (Creus et al. 1997).

15.3.2 Phosphate Solubilizing Microorganisms

The plants are unable to utilize the inorganic form of phosphorus present in the soil as they are only capable of absorbing its two soluble forms—monobasic and dibasic. Regular usage of phosphate fertilizers is disadvantageous to the environment, and often it is too expensive for the farmers of the developing nations. The phosphate solubilizing microorganisms (PSMs) consist of different bacteria and fungi which are capable of fulfilling about 20–25% phosphorus necessity of the plants which also helps to lessen the manufacturing costs of phosphate fertilizers (Chang and Yang 2009; Verma et al. 2017b, 2015, 2018c). Phosphate solubilizing bacteria (PSBs) make up to about 1–50%, while phosphate solubilizing fungi (PSFs) are only 0.1–0.5% among the P-solubilizers (Chen et al. 2006). Recently, actinomycetes are also being experimented upon as potential phosphate solubilizing organisms as they can tolerate extreme environments like drought, antibiotics and phytohormones. Hamdali et al. 2008 had stated that approximately 20% of actinomycetes can solubilize phosphorus. These PSMs employ different mechanisms for phosphate solubilization like chelation, lowering of soil pH, mineralization, etc.

15.3.2.1 Phosphate Solubilizing Bacteria

Phosphate solubilizing bacteria consist of both aerobic and anaerobic strains. *Bacillus megaterium* is a Gram positive, rod, also known as “Phosphobacterium”, has been reported to increase inorganic phosphorus (P) solubilization (Lach et al. 1990) as well as zinc, potassium, iron and manganese solubilizing potential (Amalraj et al. 2012). It helps the plants to avail the phosphorus up to the extent of 10–15 kg/ha and also causes proliferation of roots by releasing growth-promoting hormones. A novel strain, Micrococcus sp NII-0909 has been found to exhibit phosphate solubilizing capability as well as siderophores production (Dastager et al. 2010).

15.3.2.2 Phosphate Solubilizing Fungi

The important phosphate solubilizing fungi include *Aspergillus* sp and *Pencillium* sp. It has been reported that *Aspergillus niger* improved the quantity of dry biomass of chickpea plants by 22–33% with respect to the non-inoculated control (Kapri and Tewari 2010). Apart from these species, symbiotic nitrogenous rhizobia (Khan et al. 2009) and nematofungus *Arthrobotrys oligospora* (Khan et al. 2009; Thakur et al. 2014) have also shown phosphate solubilizing activity.

15.3.3 Phosphate Mobilizing Biofertilizers

These are microorganisms which scavenge phosphorus from a phosphorus enriched environment and channelize it to the plants. They can even solubilize organic phosphorus with the help of hyphal enzymes like phosphatase (Ezawa et al. 1995). Arbuscular mycorrhizal fungi (AMF) are significant contributors of phosphate mobilization. The potential of these fungi can be fully realized when the soil is deficient in phosphorus (Ghorbanian et al. 2012). This group of fungi remains symbiotically associated with the root of the plants in the rhizosphere and enhance phosphorus uptake by the extensive external fine absorbing hyphae that can exploit a larger soil volume (Jakobsen et al. 1992). These in turn receives the carbon requirements from the host plants. Studies by Yao et al. (2001), reveal that the AMF not only mobilize soil phosphates when its availability is low but also provide a greater surface area which permits increased contact with the phosphates with respect to the non-mycorrhizal root systems. The supply of phosphorus to the host plants depends upon the amounts of external mycelium produced by the fungi. Transfer of nutrients from the fungus to the plant mostly occurs at the arbuscular interface (Karandashov et al. 2004). The kinetics of nutrient uptake by the mycorrhizal roots are quite different from that of the non-mycorrhizal ones (Cress et al. 1979). Colonization of the roots by AMF thus helps in enhanced growth of the plants in low fertility soils or in soils with uneven distribution of nutrients. The PMBs are generally considered as broad-spectrum fertilizers (Itelima et al. 2018).

15.3.4 Potassium-Solubilizing Microorganisms

Only 1–2% potassium is available for uptake by the plants, though soil contains sufficient quantity of it. It is one of the fundamental elements for the plants and occurs primarily as silicate minerals in the soil which are inaccessible to plants. The microorganisms solubilize the silicates with the help of organic acids thus making them readily available to plants (Itelima et al. 2018). Different bacteria, fungi and actinomycetes have been reported for solubilizing soil potassium. Bacteria solubilize potassium by producing various organic and inorganic acids, acidolysis, chelation and exchange reactions (Archana et al. 2013; Meena et al. 2015; Verma et al. 2017a, b).

15.3.5 Potassium Mobilizing Biofertilizers

An example of potassium mobilizing biofertilizers (KMB) is *Bacillus* sp which mobilizes inaccessible forms of potassium in the soil and makes them accessible to the plants. Some established phosphate solubilizers like *Bacillus* sp and *Aspergillus* sp are known to mobilize potassium as well, along with solubilizing phosphate (Itelima et al. 2018). These microbes thus perform dual function.

15.3.6 Plant Growth-Promoting Rhizobacteria

These microorganisms reside in the rhizospheric soil and exhibit beneficial effects on crop productivity. They help to maintain the plant health and development in a holistic way. Directly they aid in the uptake of macro- and micronutrients as well as by modulating the levels of different phytohormones. Indirectly, they improve plant health by eliminating the harmful effects of plant pathogens (Kumar et al. 2018; Yadav et al. 2018a, b) (Fig. 15.3). Plant growth-promoting rhizobacteria (PGPR) not only promotes plant growth but also enhances the yield through different mechanisms. Several research works in the past as well as in the present have been devoted to the better understanding of the diverse nature, dynamics, significance and role of these PGPR in agriculture. Using PGPR species as biofertilizers has some definite economic and ecological advantages; still their administration should be carefully monitored as they behave as opportunistic pathogens in nosocomial infections (Tomar et al. 2016) (Table 15.3).

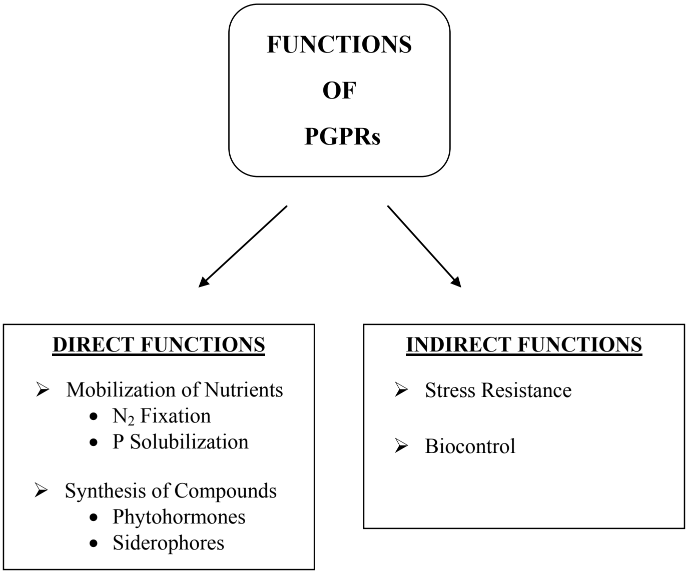

Fig. 15.3 Schematic representation of different functions of PGPRs

Table 15.3 Commercial biofertilizer products of plant growth-promoting rhizobacteria

Product	Company	Bacterial strains
Cell-Tech®	Novozymes	rhizobia
Nitragin Gold®	Novozymes	rhizobia
TagTeam®	Novozymes	rhizobia + *Penicillium bilaii*
Accomplish®	Loveland Products, Inc.	PGPR + enzymes + organic acids + chelators
Nodulator®	BASF Canada Inc.	*Bradyrhizobium japonicum*
Nodulator® N/T	BASF Canada Inc.	*Bacillus subtilis MBI 600* + *Bradyrhizobium japonicum*
Nodulator® PRO	BASF Canada Inc.	*Bacillus subtilis* + *Bradyrhizobium japonicum*
Nodulator® XL	BASF Canada Inc.	*Rhizobium leguminosarum biovar viceae 1435*
Bioboots®	Brett-Young Seeds	*Delftia acidovorans*
Bioboots® (soybean)	Brett-Young Seeds	*Delftia acidovorans* + *Bradyrhizobium* sp.
EVL coating®	EVL Inc.	PGPR consortia
Nitrofix®	Labiofam S. A.	*Azospirillum* sp.
Bioativo®	Instituto de Fosfato Biológico (IFB) Ltda.	PGPR consortia
VitaSoil®	Symborg	PGPR consortia
Azotobacterin®	JSC “Industrial Innovations”	*Azospirillum brasilense* B-4485
Mamezo®)	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (in peat)
R-Processing Seeds®	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (coated legume seeds)
Hyper Coating Seeds ®	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (coated grass legume seeds)
Life®	Biomax	PGPR consortia
Biomix®	Biomax	PGPR consortia
Biodine®	Biomax	PGPR consortia
Biozink®	Biomax	PGPR consortia

Source García-Fraile et al. (2015)

15.3.7 Vesicular-Arbuscular Mycorrhizae

In agricultural soils, the fungi which are most commonly encountered are vesicular-arbuscular mycorrhizae (VAM) which play a significant role in sustainable agriculture. These are usually intracellular, endosymbiotic fungi belonging to the genera *Glomus, Gigaspora, and Sclerocysts* (Kumar et al. 2017; Rana et al. 2019a, b). This inoculant is generally recommended to different fruit plants, like banana, papaya, pineapple, etc., and ornamental plants. Besides, VAM has also been reported to decrease metal toxicity like aluminium. Their major roles are as follows:

- Helps in improved uptake of elements like potassium, zinc, iron, copper, etc.
- They secrete different organic acids which support enhanced availability of both macro- and micronutrients by the plants.
- These fungi increase the conduction of water by the roots of the plants even when the level of water is low in the soil (Bhattacharjee and Dey 2014).
- The mesh of hyphae helps in arresting the soil particles to form bigger aggregates as well as better carbon uptake by the plants. They also maintain the soil quality by synthesizing specific protein known as 'Glomulin' (Mahdi et al. 2010).
- Plants supplied with VAM exhibit elevated phytohormone (IAA, cytokinin) synthesis, thus indirectly helping if plant growth and development.
- VAM-inoculation causes a significant rise in phenolic and phytoalexin activity which renders the plant more resistance towards stress (Bhattacharjee and Dey 2014) (Fig. 15.4).

15.3.8 Endophytic Microorganisms

These microorganisms stimulate the development of non-leguminous crops and cause their nutritional enrichment through nitrogen fixation, phosphate solubilization and production of siderophore (Szilagyi-Zecchin et al. 2014) (Fig. 15.5). Besides they are also involved in the production of phytostimulators (phytohormones), cofactor pyrroloquinoline quinone (PQQ) and volatile acetoin (Tomar et al. 2016). They also help in combating stress by secreting stress modulators. Some species of *Trichoderma* make the plants resistant towards diseases and other abiotic stresses (Bae et al. 2009). These endophytic organisms are known to avoid any sort of competition with their rhizospheric counterparts (Yadav 2019; Yadav et al. 2017a, b, c; Yadav and Yadav 2019).

15.3.9 Sulphur Oxidizing Biofertilizers (SOBs)

These microorganisms oxidize sulphur to sulphates so that the plants can utilize it. *Thiobacillus* sp is one of the sulphur oxidizing biofertilizers (Itelima et al. 2018).

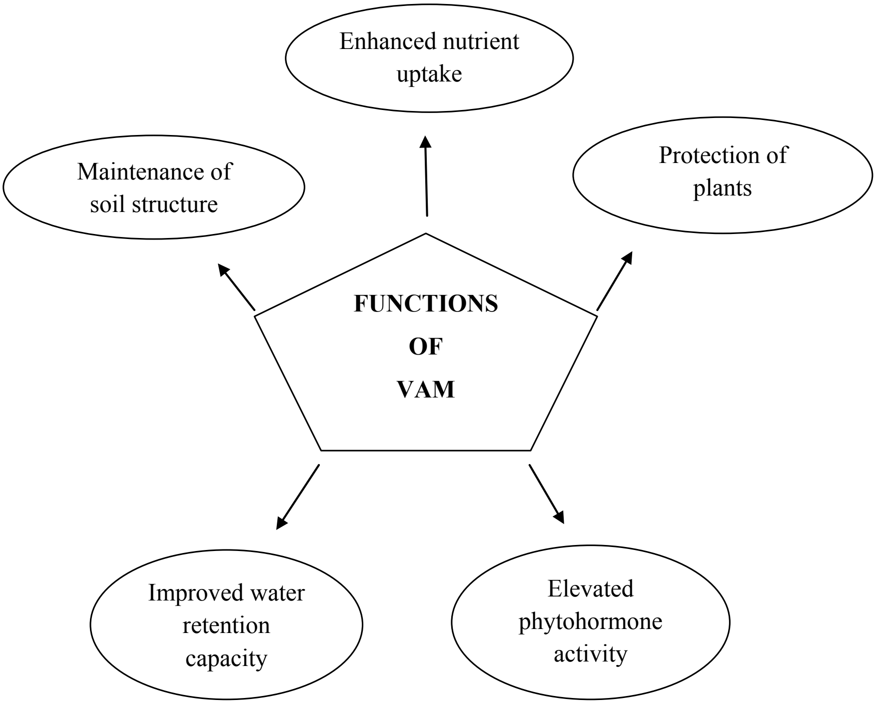

Fig. 15.4 Schematic representation of various functions of VAM

15.3.10 Zinc Solubilizing Microorganism

A wide array of microorganisms is there which help the host plants in the uptake of various micronutrients like zinc, iron, copper, etc. More than half (50%) of the Indian soils are deficient in zinc (Katyal and Rattan 1993). This is compensated by adding soluble zinc sulphate ($ZnSO_4$) from external sources of which only 1–4% is utilized by the crop and the rest 75% gets converted to different mineral fractions, not absorbed by the plants. Two mechanisms have been proposed for zinc fixation—one is applicable in acidic soils and is related with cation exchange and other occurs by chemisorptions of zinc on calcium carbonate with simultaneous complexation by organic ligands under alkaline conditions (Kumar et al. 2018). *Bacillus* sp has been conjugated with cheap, insoluble zinc compounds like zinc oxide, zinc carbonate and zinc sulphide in place of costly zinc sulphate and successfully applied for zinc solubilization (Mahdi et al. 2010; Yadav and Saxena 2018) (Kumar et al. 2019; Yadav et al. 2019d).

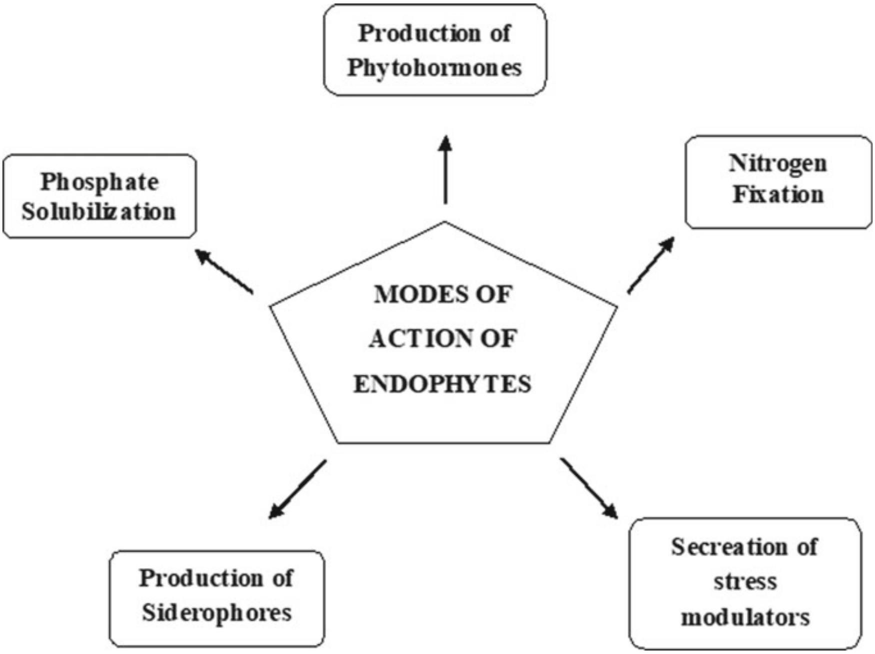

Fig. 15.5 Important functions of endophytic microorganisms

15.3.11 Siderophores Producers

Iron is quite abundantly available in nature; still its accessibility is limited. Iron is accumulated in the form of oxides and oxyhydroxides which make it more difficult for organisms to avail it. Microorganisms acquire Fe^{3+} by active transport through siderophores. These siderophores are low molecular weight compounds secreted by the microbes which act as iron scavengers. These compounds lessen plant stress due to high concentrations of heavy metals in soil. Plants can assimilate iron from bacterial siderophores by special mechanisms like ligand exchange, chelation or direct acquirement of iron siderophore complexes (Colo et al. 2014).

15.3.12 Phytohormone Producing Microorganisms

Phytohormones are organic compounds which are in charge of the overall development of the plant. They are synthesized in two ways—either endogenously by plant tissues or exogenously by PGPRs. The microorganisms inhabiting the soil and responsible for the production of phytohormones are *Galactomyces* sp., *Pseudomonas* sp., *Azospirillum* sp. and *Bacillus* sp. (Waqas et al. 2014; Lei and Ya-qing 2015; Rana et al. 2019c; Yadav et al. 2018a, b, c).

Microbial auxins help in the elongation of root as well as increase in its surface area, thus helping in better utilization of the soil resources. PGPR secreted auxins play a crucial role in plant–microbe interactions and phytostimulation (Spaepen and Vanderleyden 2011). The most common fungus which synthesizes almost 20 types of gibberellins is *Gibberella fujikuroi*. Recent studies by Ullah and his coworkers confirmed that *Photorhabdus temperate*—an entomopathogenic bacterium can produce unlike forms of gibberellic acid (Ullah et al. 2014). Another important plant hormone which helps in cellular differentiation, auxillary bud development, etc., is cytokinin and its most common microbial sources are *Azotobacter chroococcum, Azotobacter beijerinckii, Paenibacillus polymyxa, Pseudomonas putida* and *Pseudomonas fluorescens* (Kudoyarova et al. 2014; Arkhipova et al. 2007).

ACC-deaminase, the enzyme responsible for maintaining the ethylene levels in plants can also be synthesized by the PGPRs. It has been found to make the plants more tolerant towards high concentration of salts (Zahir et al. 2008, 2009) and provide resistance against radiation, poly-aromatic hydrocarbons, insect predation, wounding, etc. (Glick 2012). Rhizobacterial inoculants, synthesizing the hormone, induce plant shoot growth, root elongation, increase in nodulations in *Rhizobium* and promote mycorrhizal colonization (Glick 2012). Several rhizobacteria, like *Acinetobacter* sp., *Azospirillum* sp., *Agrobacterium* sp., *Achromobacte* sp., *Ralstonia* sp., *Enterobacter* sp., *Bacillus* sp., *Rhizobium* sp., *Serratia* sp., *Pseudomonas* sp., etc., have been reported for ACC-deaminase activity (Kang et al. 2010). Recently, *Pseudomonas stutzeri* A1501 capable of synthesizing ACC-deaminase has been reported to assist the cultivation of rice in the presence of salts and heavy metals (Han et al. 2015).

15.4 Production, Storage and Quality Control of Biofertilizers

Several parameters should be kept in mind during the production of biofertilizers, such as growth summary of the microbe(s) used, their types, optimum conditions of the microorganism(s), formulation of inoculums, etc. The formulation of inoculum method of administration and maintenance of the products plays an important role in the overall success of biofertilizer production. Biofertilizers can be amended with a carrier molecule (solid biofertilizer) or it can be produced in the form of liquid inoculants (liquid biofertilizers), both having their advantages and demerits. According to Somasegaran and Springer (1994), few things should be kept in mind while choosing the carrier molecule like

- It must be cheap and readily available when required
- The material should be such that bacterial nutrients can be added easily
- It should support easy sterilization by autoclaving or gamma irradiation
- Can be processed easily and there should not be any lump forming substances
- It should be non-toxic to the microorganisms and the plants,
- Moisture absorption capacity should be high for the material to be a good carrier.

- Water retention capacity of 50% or above should be preferable.
- It must stick to the seeds properly.
- The pH buffering capacity must be high.
- High organic matter content in the material is usually preferred.

The solid biofertilizers are associated with carriers to enhance the effectiveness and water ration capacity. Integration of microorganisms into carrier materials helps in easy handling as well as long term storage (Khosro and Yousef 2012). These are cost effective and easy to produce. Common carrier molecules used are saw dust, talcum dust, clay, peat, vermiculite, bentonite, diatomaceous earth, manure, rice or wheat bran, zeolite, rock phosphate pellets, charcoal, compost, etc. Though it is difficult to find a substance having all the characteristics of a suitable carrier, researches are still going on to develop one satisfying most of the criteria. Polymer-based carriers are close to the suitable ones. Usually, these are alginate beads, which immobilize the bacteria in their matrix, gradually releasing them in the soil environment after application. *Azospirillum brasilense* (> 10^{11} cfu/g inoculant) has been successfully encapsulated using alginate beads with a diameter in the micro range (100–200 μm) and this biofertilizer enhanced the production of wheat and tomato (Bashan et al. 2002).

In India, mostly carrier-based biofertilizers are manufactured and the microorganisms used usually have a shelf life of only 6 months (Rana et al. 2013). They are susceptible to UV and not thermostable beyond 30°C. At the time of production, the microbial density is only 10^8 cfu/ml, which reduces with time and the count is practically negligible at the end. This is one of the main reasons these biofertilizers could not be of much use and failed to draw the farmers, while another problem is that these are prone to contamination.

To overcome these problems, liquid biofertilizers were developed and marketed, which is quite a breakthrough in the history of biofertilizer production and truly a novel, innovative approach. These are specific microbial formulation supplied with certain additional chemicals or special cell protectants that stimulate the formation of resting spores or cysts for better shelf life and tolerance towards different abiotic stress. Some of the commonly used cell protectants are glycerol, molasses and sugars like glucose, maltose, sucrose, trehalose, etc. (Brar et al. 2012).

The microbes used in the preparation of liquid biofertilizers usually have a shelf life of 2 years. They are thermostable (can tolerate temperature as high as 55 °C), tolerant to UV radiations and contamination free. The count is around 10^9 cfu/ml, which remain constant up to 24 months. So, application of 1 ml of liquid biofertilizer is equivalent to that of 1 kg of 5 months old carrier-based counterparts (1000 times) (Mahdi et al. 2010). These are easy to handle and apply in the fields by the farmers. They are applied in various ways. Using hand sprayers, power sprayers or fertigation tanks are quite common. It can also be used basal manure and mixed along with farm yard manure. However, these biofertilizers are costly which hinders its widespread usage (Mahdi et al. 2010).

These bacterial products can be stored in water-in-oil emulsions. They are generally administered to the crops through irrigation systems (VanderGheynst et al. 2006).

The packets of formulated biofertilizers should provide certain pertinent information for the marketing of the products. They are (i) product name, (ii) the particular microorganism or consortia used in its formulation, (iii) specific crops to which it is applicable and is appropriate, (iv) the manufacture and expiry dates and (v) relevant instructions and directions for its administration.

Quality control of the entire production process is extremely important. Quality of the bioproduct determines the success and its acceptance by the farmers. The key steps in the production process that require quality control are (i) the fermentation, (ii) preparation of carrier, (iii) preparing a mixture of bacterial broth and the carrier, (iv) packaging and (v) storage. The carrier must be sterilized and aseptic conditions should be maintained at each step to avoid any contamination. Finally, the product should be stored specific temperature and humidity to ensure the viability of the microorganism during the expected lifespan of the biofertilizer. The final product should be checked for several parameters at different environments to explore its efficiency and limitations in order to guarantee its quality (Fig. 15.6).

15.5 Application of Biofertilizers

The application of solid and liquid biofertilizers in the field is different and is based on their formulations. In ideal situations, the farmer should be able to apply it with his own setup, such that no additional infrastructure is required. Liquid formulations can be applied to the soil using irrigation systems or with the help of different sprayers. For peach orchards and plants, like citrus, mango, vines, guava, apple, etc., spraying is usually recommended. Spreader centrifuges can be used to spread powdered or encapsulated products over the fields. In other cases, the seeds may be coated with the inoculants. The solid ones may be applied and mentioned below.

15.5.1 Seed Treatment

It is the most extensively used method. For every 5 kg of seeds, 100 gm fertilizer is applied. The amount of seed to be sown in a field is the determining factor behind the quantity of fertilizer required to apply per acre of agricultural land. A mixture of the biofertilizer and water in the ratio of 1:2 is prepared to form slurry which is poured in the container along with the seeds before its application. The combination is subjected to a gentle mixing using an adhesive like gum acacia, jaggery solution, etc. such that the seeds are uniformly coated with the biofertilizer (Kumar et al. 2017). The seeds are then spread on a clean sheet or cloth, dried under the shade for about 30 min to avoid direct sunlight and then sown immediately. For crops like pulses, oilseeds and fodder this method is usually suggested (García-Fraile et al. 2015).

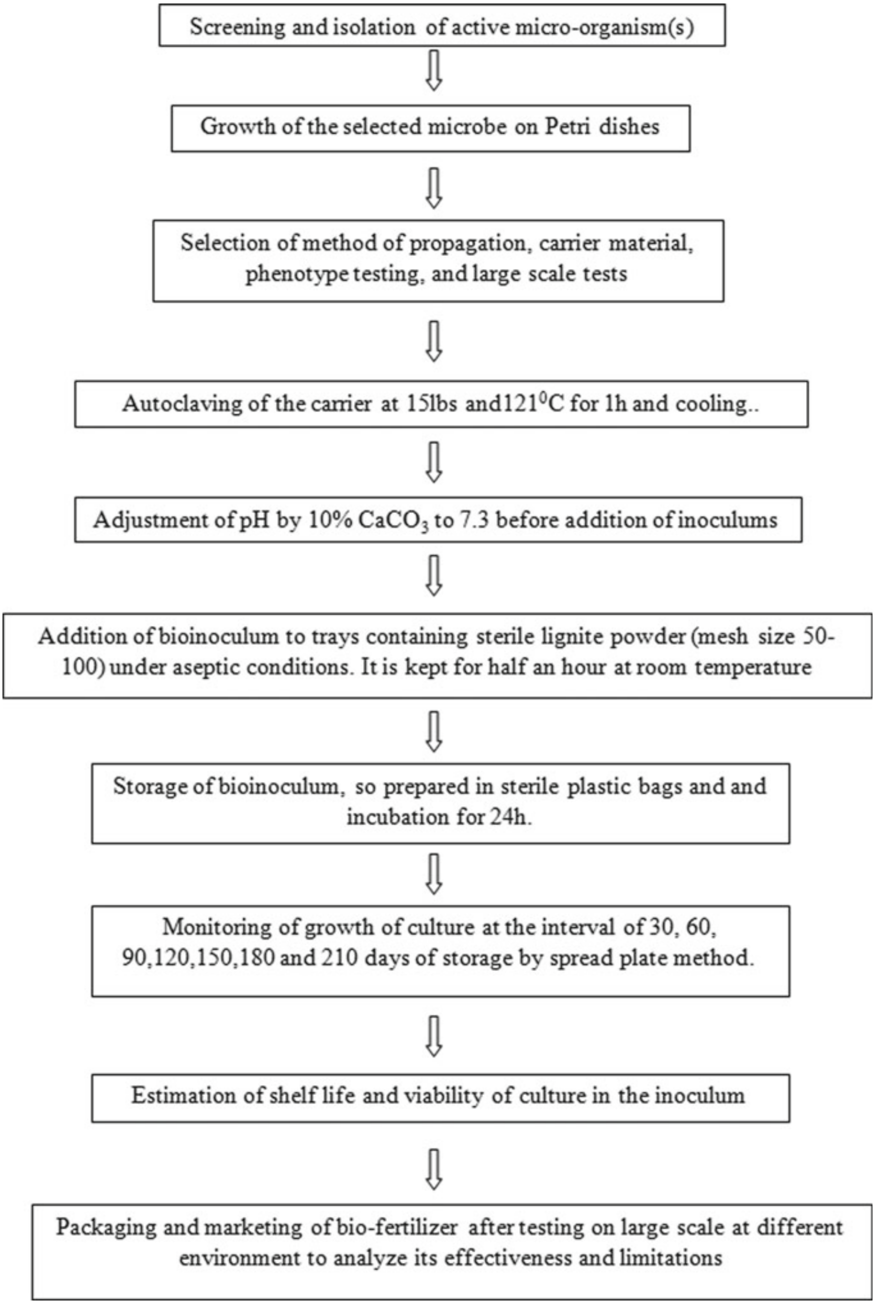

Fig. 15.6 Production of solid biofertilizers

15.5.2 Seedling Root Dip

A diluted formulation of about 1 part of biofertilizer in 10 parts of water is required for this type of treatment. This method is generally recommended for transplanted crops. For rice, a bed is made in the field and filled with water mixed with the specific biofertilizers. The roots of seedlings are dipped into this solution for 8–10 h and then transplanted. This method is suggested for crops which are replanted at seedling stage like paddy, tomato, potato, cabbage, onion, brinjal, chilly, etc. It can also be applied for treating ornamental plants like rose, jasmine, dahlia, marigold, chrysanthemum and many more (García-Fraile et al. 2015).

15.5.3 Soil or Main Field Treatment

The recommended biofertilizers (4 packets) are mixed with specific quantity of compost or dried, powdered manure from the farmyard (20 kg) and kept overnight. This mixture is then applied in the soil at the time of sowing of seeds or just before transplanting (Rana et al. 2013).

15.5.4 Set Treatment

For this type of treatment, biofertilizer and water are mixed in the ratio of 1:50. The explants are dipped into the solution containing the biofertilizer for 30 min with subsequent drying under the shade and planting in the field. This technique is generally applicable for crops like sugarcane, banana, grapes and strawberries (Rana et al. 2013). In a more direct approach, the biofertilizer is usually mixed with different carriers, like soil, compost, manure, rice husks, etc., in the ratio of 1:25 (1 kg per 25 kg of carrier) and applied in the soil.

15.6 Precautions in Using Biofertilizers

One should be cautious of the following factors while applying biofertilizers (Itelima et al. 2018).

- It should be never mixed with nitrogen fertilizers.
- Biofertilizers should not be administered along with any fungicides.
- The seeds soaked in liquid formulations, if required may be dried under the shade. Exposure of the biofertilizer to direct sunlight must be avoided.
- The optimum temperature for storing the biofertilizers is generally room temperature.

15.7 Constraints Regarding Utilization of Different Biofertilizers

Though the biofertilizer technology is a low cost, eco-friendly one, there are several restraints that have limited the widespread application or implementation of this technology. The restrictions may be:

15.7.1 Production Constraints

Though there is demand of biofertilizers over the conventional synthetic ones, the progress in the field of biofertilizer production is quite limited because of the following reasons:

Unavailability of appropriate and efficient strains—The biofertilizers are crop as well as soil specific in nature but the availability of region-specific strains is often a problem (Itelima et al. 2018).

Unavailability of suitable carrier—The search for a proper carrier molecule for the solid biofertilizers is still on which will maintain the microbe throughout its shelf life. Peat is a good option but in India poor quality peat is available which is low in carbon content (Kumar et al. 2017).

Unavailability of infrastructure—the lack of proper set-up, equipments, etc. limits its production.

Mutation during fermentation—Biofertilizers comprises microbes which are very much prone to mutation during the process of fermentation, which ultimately increases the production cost as well as makes it difficult for quality control.

15.7.2 Market Level Constraints

One of the important problems that hinder the use of these biofertilizers is lack of proper marketing strategies, retail outlets or commercial network for the producers (Mahdi et al. 2010).

Lack of awareness of farmers—Inspite of the considerable efforts in recent years to raise awareness regarding the use of biofertilizers, most of the farmers are not well versed in their application. They are not properly instructed about the benefits and often they are skeptical to accept any new development. The farmers are often seen using the chemical ones knowing very well about their hazardous effects.

Lack of quality assurance—corruption in marketing sector leads to the sale of inferior quality biofertilizers which results in loss of faith among farmers.

Seasonal and unassured demand—less demand of these fertilizers with simultaneous cropping operations has led to their occasional production which is not a continuous one.

15.7.3 Resource Constraint

Limited resource generation for biofertilizer production—it is a low investment industry and the private sectors dealing with this rely on demand based productions as the shelf life of these bioproducts is short. Sufficient funds are not available for a steady production.

15.7.4 Field Level Constraints

Soil and climatic factors—extreme environmental conditions like unfavorable pH, high temperature, drought, high nitrate level, and deficiency of important elements like phosphorus, copper, cobalt, molybdenum or presence of toxic compounds in the soil affect the growth of the microbes and crop response (Bhattacharjee and Dey 2014).

Native microbial population—Antagonistic microorganism already residing in soil may be dominating in nature and they may restrict the effective establishment of the microbial inoculants by outcompeting them (Mahdi et al. 2010).

15.8 Rejuvenation Strategies for Biofertilizers

The following strategies can be used for invigorating the sustainable agricultural practices:

- Identification and selection of suitable locations, crops, soil and specific strains for nitrogen and phosphorus fixation and zinc solubilization for different climatic conditions.
- Application of biotechnological methods for strain improvement
- Observing the activity of the different microbial cultures during storage to circumvent natural mutants.
- Development of suitable substitute formulations like liquid inoculants or granular formulations for all bio-inoculants, standardization of the media preparation, inoculation technique etc., for the new formulations.
- Employing experts like microbiologists in production units to supervise the production of the biofertilizers.
- Development of cold storage facilities in production units.

- Providing technical guidance on the production of biofertilizers as well as quality control of the products and rendering advice and projects to manufacturers.
- Providing organizational training to the extension workers and farmers for the widespread acceptance of the technology.
- Circulating information through mass media, publications and bulletins to make the users and consumers aware of these bioproducts (Gupta 2004).

15.9 Tripartite Relationship Among Different Biofertilizers

Knowledge regarding the synchronized administration of phosphate solubilizers and diazotrophs to the plants in presence of AMF is inadequate and there lies the scope of further research. However, it is seen that when there is dearth of both the essential elements—phosphorous and nitrogen, AMF aid in assimilating phosphates, thus helping in the growth of the plants. Elevated phosphorous content supports the diazotrophs in plants which further boosts up the nitrogenase activity. This helps in improving the rate of nitrogen fixation, which ultimately assists in the growth of roots and development of mycorrhiza. This is the exquisiteness of intergeneric interaction which makes further research all the more interesting.

15.10 Conclusion and Future Prospects

With the ever-growing population, there seems no end to the demand for food but with the availability of the chemical fertilizers, it was thought that the problem could be tackled. But the abundance in crop productivity came with a huge price, as in due course of time, these compounds started to affect our ecosystem in a negative way. On one hand, when one could be rest assured that the availability of food is ensured but at the same time, alleviation of the hazardous effects of the chemical fertilizers from the environment surfaced as a huge concern. These problems necessitated the search for safer alternatives. Amidst all these confusion, biofertilizers were developed and these seemed to be a viable option to put an end to the problem. They are able to enhance the productivity of crops without harming the environment thus playing a significant role in sustainable agriculture. Moreover, these compounds have the potential to minimize the ecological damages, to some extent, that have already been caused by the excessive use of the chemical fertilizers. Even if they cannot fully compensate for the chemical fertilizers, they can still be used as a supplement with the synthetic ones. This will help to reduce the total amount of chemical fertilizers to be used. Thus, the biofertilizer industry, in spite of having some limitations, does not fail to garner interest among recent researchers. Human population is getting more aware of the benefits of these biofertilizers with the passage of time and people all over the world are interested in consuming food grown with organic fertilizers rather than crops grown with chemical fertilizers.

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Chapter 16
Plant Microbiomes for Sustainable Agriculture: Current Research and Future Challenges

Ajar Nath Yadav

Abstract The plant microbiomes play important role in plant growth promotion and soil fertility for sustainable agriculture. Plant and soil are valuable natural resource harbouring hotspots of microbes. The soil microbiomes play critical roles in the maintenance of global nutrient balance and ecosystem function. The microbes associated with plant as rhizospheric, endophytic and epiphytic with plant growth-promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. PGP microbes promote plant growth directly or indirectly, either by releasing plant growth regulators; solubilization of phosphorus, potassium and zinc; biological nitrogen fixation or by producing siderophore, ammonia, HCN and other secondary metabolites which are antagonistic against pathogenic microbes. The PGP microbes belonged to genera such as *Achromobacter, Arthrobacter, Aspergillus, Azospirillum, Azotobacter, Bacillus, Burkholderia, Gluconoacetobacter, Methylobacterium, Paenibacillus, Pantoea, Penicillium, Piriformospora, Planomonospora, Pseudomonas, Rhizobium, Serratia* and *Streptomyces*. These PGP microbes could be used as biofertilizers/bio-inoculants at place of chemical fertilizers for sustainable agriculture. This chapter exclusively concluded the horizon covered book content of plant microbiomes for sustainable agriculture. The concluding remark envisioned the future beneficial role of plant microbiomes in plant growth promotion and soil fertility.

Keywords Endophytic · Epiphytic · Microbial diversity · Plant microbiomes · Rhizospheric · Sustainable agriculture

This book contains current knowledge about plant microbiomes. The diverse groups of microbes are the key components of soil–plant systems, where they are engaged in an intense network of rhizosphere/endophytic/phyllosphere interactions. The rhizospheric, endophytic and epiphytic microbes with plant growth-promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. PGP microbes promote plant growth directly or indirectly, by releasing

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plant growth regulators; solubilization of phosphorus, potassium and zinc; biological nitrogen fixation or by producing siderophores, ammonia, HCN and other secondary metabolites which are antagonistic against pathogenic microbes. These PGP microbes could be used as biofertilizers/bio-inoculants in place of chemical fertilizers for sustainable agriculture. The aim of the present book is to collect and compile the current developments in the understanding of the rhizospheric, endophytic and epiphytic microbial diversity associated with plants. The book encompasses current knowledge of plant microbiomes and their potential biotechnological applications for plant growth, crop yield and soil health for sustainable agriculture. The book will be highly useful to the faculty, researchers and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology and related subjects.

Rhizosphere harbours potential microbiomes which play a pivotal role in nutrient cycling, enhancing soil fertility, maintaining plant health and productivity. Specific microbiomes that are assembled near roots are considered to be some of the most complex ecosystems on the Earth. Heterogeneous microbial communities of rhizospheric microbiomes considerably vary by soil type, land use pattern, plant species and host genotype. It is demonstrated that root exudates act as substrates and signalling molecules which are required for establishing plant–rhizobacterial interactions (Kour et al. 2019b; Mendes et al. 2013). These research priorities may enable us to manipulate agricultural microbiomes and thereby to develop management strategies for increased production and productivity of global agriculture in a sustainable manner. One of the challenges for future research work includes protection and conservation of rhizosphere biodiversity and their potential application in agricultural soils. Figure 16.1 represents the isolation, characterization and application of plant microbiomes for sustainable agriculture.

Endophytes are the microorganisms that live in the internal tissues of plants. Endophytic microbes hold great importance for the roles that they play in association with the host plants. Endophytes are known to promote the growth of the host plants by various activities such as detoxification of toxic compounds, protection against pathogens and production of plant growth-promoting hormones (Rana et al. 2019b; Suman et al. 2016). Many biotechnologically important metabolites are also produced by the endophytes such as anticancer and antimicrobial compounds. There is a rich diversity of endophytes that needs to be explored for biotechnological purposes. Such endophytes play an important role in plant growth promotion as these provide resistance to plant against different environmental stresses and toxic compounds, protect host plants against several pathogens, and produce many plant growth-promoting hormones. Endophytic microbes are also significantly important as biotransformers of different chemicals and help in recycling of nutrients. The endophytes also find many industrial usages as they are known for the production of many important enzymes and metabolites (Yadav et al. 2019a, b, c).

Endophytes constitute an important component of microbial diversity since 20 years, remarkable progress in the field revealed the significance of endophytic microorganisms. Endophytic microbes are unexplored group of organisms that has

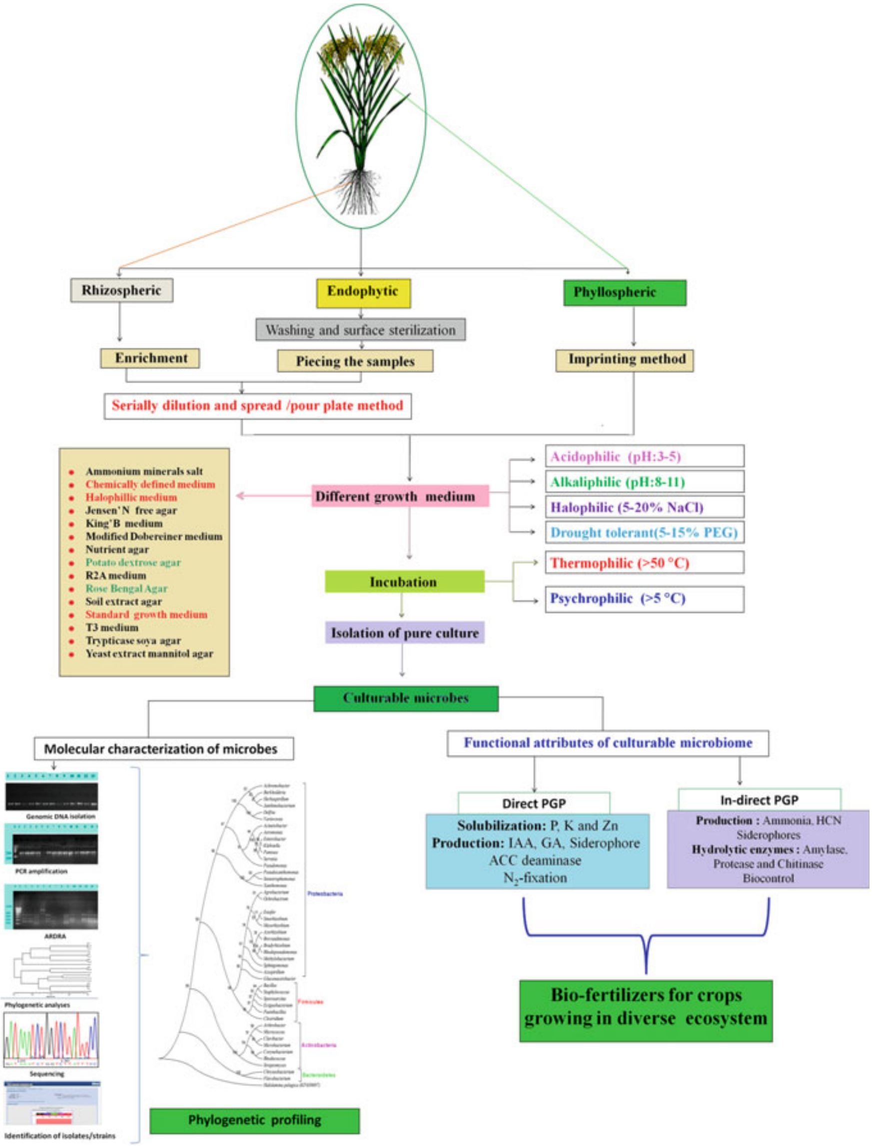

Fig. 16.1 A schematic representation of the isolation, characterization, identification and potential application of culturable and un-culturable microbiomes of crops. Adapted with permission from Verma et al. (2017)

huge potential for innovative pharmaceutical substances; they are established as anticancer, antioxidants, antifungal and antiinflammatory. Likewise in recent years, an incredible progress was made in developing them as therapeutic molecules against diverse ailments. In recent years more studies are warranted in bioprospecting new endophytic microorganisms and their applications. Bacterial and fungal endophytes are ubiquitous reside in the internal tissue of living plants. Endophytic fungi distributed out from tropical region to arctic region possess vast potential in terms of secondary metabolite production. It is pertinent to know that the various bioactive indispensable compounds evaluated by these endophytic fungi are host-specific. They are very significant to augmenting the adaptability of the endophyte and its host plants, for instance, biotic and abiotic stress tolerance (Rana et al. 2019a; Yadav 2018).

The phyllosphere referred to the total aerial plant surfaces (above-ground portions), as habitat for microorganisms. Microorganisms establish compositionally complex communities on the leaf surface. The microbiome of phyllosphere is rich in diversity of bacteria, fungi, actinomycetes, cyanobacteria and viruses (Kumar et al. 2019; Müller et al. 2016). Microbes commonly established either epiphytic or endophytic mode of life cycle on phyllosphere environment, which helps the host plant and functional communication with the surrounding environment. The phyllosphere is a unique environment colonized by a wide variety of microorganisms including epiphytes, beneficial and pathogenic, bacteria, fungi and viruses (Bargabus et al. 2002). Understanding the phyllosphere community structure, networking and physiology is a great challenge. However, extensive research on phyllosphere microbiota gives great potential for the applications in economic plant productivity specifically, agriculture and forestry, ecosystem cleaning and health.

Climate variability has been and continues to be, the principal source of fluctuations in global food production in developing countries Oseni and Masarirambi (2011). The important risks of increasing warming of globe are variable and untimely rainfall events, unstable winter seasons, more disease occurrences and crop failures (Adger et al. 2005). Extreme environments represent unique ecosystems which harbour novel biodiversity. Microbial communities associated with plant growing in most diverse conditions, including extremes of temperature, salinity, water deficiency and pH. In order to survive under such extreme conditions, these organisms referred to as extremophiles, have developed adaptive features, which permits them to grow optimally under one or more environmental extremes, while polyextremophiles grow optimally under multiple conditions. These extremophiles can grow optimally in some of the earth's most hostile environments of temperature (−2°–20 °C—psychrophiles; 60°–115 °C—thermophiles), salinity (2–5M NaCl—halophiles) and pH (<4 acidophiles and >9—alkaliphiles) (Yadav et al. 2015c). Microbes associated with crops are able to promote the plant growth. Several microbes have been reported that they can promote plant growth either directly or indirectly. Microbes have been shown to promote plant growth directly, e.g. by fixation of atmospheric nitrogen, solubilization of minerals such as phosphorus, potassium and zinc; production of siderophores and plant growth hormones such cytokinin, auxin and gibberellins.

Several bacteria support plant growth indirectly, via production of antagonistic substances by inducing resistance against plant pathogens (Glick et al. 1999; Tilak et al. 2005).

Salinity of the agriculture soil is the serious issue all over the world and it is also an important environmental factor for reduction of growth and yield of agricultural crops. The density of more salt available in soil may alter the physiological and metabolic activities in the agricultural crops and reduces the growth and production of crops both qualitative and quantitative ways. For combating against soil salinity, many transgenic salt-tolerant crops have been developed but far too little is a success. For solution, In the soils, the use of plant growth-promoting rhizobacteria (PGPR) can be reduced soil salinity, load of chemical fertilizers and pesticide in the agricultural field and improve soil health, seed germination, crop growth and productivity under saline condition PGPR accepted as potential microbes that can tolerant various atmospheric circumstances like more temperature, pH, and saline soils (Yadav and Saxena 2018). Halophilic microbes are isolated from saline soils or rhizosphere of halophytic plants and show plant growth-promoting characters directly like the production of IAA, solubilization of phosphate, production of siderophore, fixation of N_2, deaminase ACC activity or indirectly ways by controlling of phytopathogens under saline condition (Verma et al. 2017). Knowledge of plant–microbe interactions facilitates policies for the protection of crops and saline soil remediation and this type of interaction also observed in the area for ecological appreciative of microbes and which promotes halophyte to adaptability in salinity rich environment.

Drought is a conspicuous stress causing deleterious effect on plant growth and productivity. In order to compensate the yield loss due to drought, efficient and sustainable strategies are required for its management. Drought stress tolerance is a complex trait involving clusters of genes; hence, genetic engineering to generate drought-resistant varieties is a challenging task. In this context, the application of plant growth-promoting microbes (PGPM) to mitigate drought stress is gaining attention as an attractive and cost-effective alternative strategy (Kour et al. 2019a, b, c).

Microorganisms capable of coping with low temperatures are widespread in these natural environments where they often represent the dominant flora and they should, therefore, be regarded as the most successful colonizers of our planet. Psychrophilic microorganisms are adapted to thrive well at low temperatures close to the freezing point of water (Yadav et al. 2015a, b, 2016). Microbial activity of psychrophiles has even been reported at subzero temperatures. In general, psychrophilic microorganisms exhibit higher growth yield and microbial activity at low temperatures compared to temperatures close to the maximum temperature of growth and have more often been put forth as an explanation to successful microbial adaptation to the natural cold environment. Prospecting the cold habitats has led to the isolation of a great diversity of psychrotrophic microorganisms. The cold-adapted microbes have potential biotechnological applications in agriculture, medicine and industry. The bacterial diversity from the cold environment could serve as a database for selection of bioinoculants with PGP ability and could be used for improving the growth and yield of crops grown at high altitudes with prevailing low temperatures (Yadav et al. 2018; 2019d).

Biofertilizers are typically microbial formulations in organic carrier materials that improve soil health and crop growth and development. Of late the use of biofertilizers has gained much acceptance and research interest especially in the developed countries due to ecological impacts associated with the use of synthetic inorganic fertilizers in farming. Microbial formulations could be organism-specific or a consortium of organisms. Many soil microorganisms are endowed with an array of capabilities ranging from production of growth-enhancing substances to the release of substances which ameliorate the effects of various abiotic stress conditions such as drought, salinity, pH stress, heat stress, pollutants and nutrient deficiency.

There has been a sharp increase in the world's population over the past few decades which can be threatening in terms of the food security of the people. Thus, to cater to the huge demand of food, agricultural production should be increased within a short span of time and with limited worldwide agricultural land resources. This situation has driven the farmers all over the world to rely heavily on the commercially available chemical fertilizers for enhanced agricultural productivity. Though there has been a significant rise in the production of crops, these fertilizers have proved to be detrimental for our ecosystem as well as animal and human health. The deteriorative effects of the large chemical inputs in the agricultural systems have not only challenged the sustainability of crop production but also the maintenance of the environment quality. Using biofertilizers is a natural, low-cost, environment-friendly way out to this problem. Biofertilizers comprise living microorganisms capable of supplying sufficient nutrients to the plants, while maintaining high yield. With the ever-growing population, there seems no end to the demand of food but with the availability of the chemical fertilizers, it was thought that the problem could be tackled.

This book will be useful not only to the researchers, but also to each and every stakeholder that contributes toward evergreen agriculture. The enriched efforts of contributors and editorial team have resulted in a volume, which systematically describes to different issues, and applications of plant microbiomes in sustainable agriculture and environments. Needless to mention, that maybe, such volumes will be needed to place the biofertilizers and biopesticides technology in the field to its potential, but this particular book stands on its merit for the information and contents, which will be useful to all.

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