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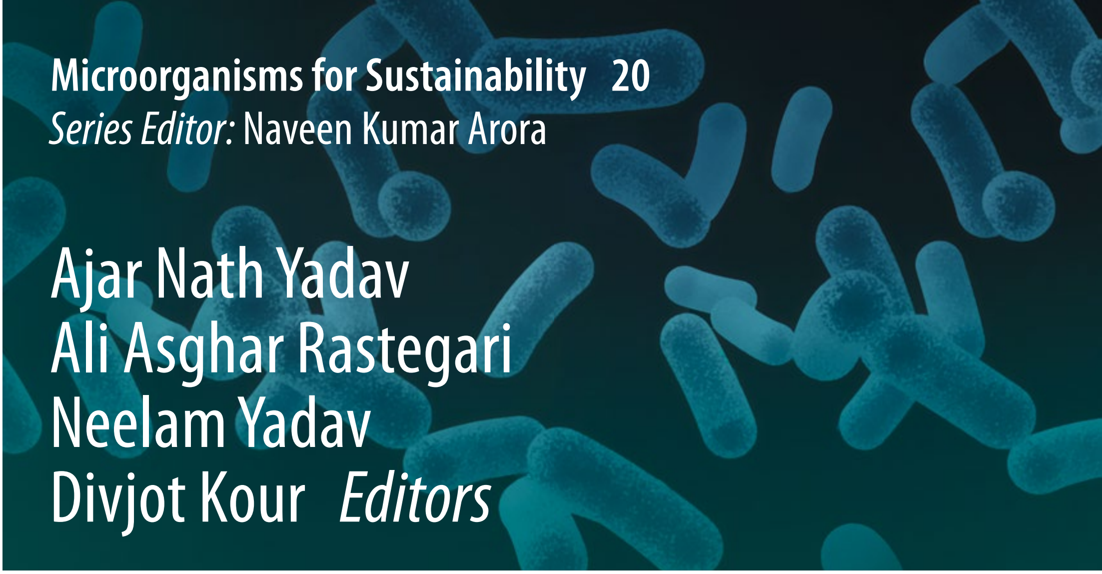

Ajar Nath Yadav
Ali Asghar Rastegari
Neelam Yadav
Divjot Kour *Editors*

Advances in Plant Microbiome and Sustainable Agriculture

Functional Annotation and Future Challenges

Springer

Microorganisms for Sustainability

Volume 20

Series editor
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Foreword

Microbes are ubiquitous in nature. The vast microbial diversity has been found to associate with the plant systems. The plant-microbe interactions are the key strategy to colonize and establish in a variety of diverse habitats. Microbes are associated in three ways with any plant systems in the form of epiphyte, endophyte, and rhizosphere, which are collectively termed as plant microbiomes. Plant microbiomes play an important role in the growth and development of plants and in the health of soil. Plant microbiomes 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 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. This book encompasses current knowledge of plant microbiomes and their potential biotechnological applications for plant growth, crop yield, and soil health for sustainable agriculture. It will be highly useful to the faculty, researchers, and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects.

This book, ***Advances in Plant Microbiome and Sustainable Agriculture****: Functional Annotation and Future Challenges*, is a very timely publication providing state-of-the-art information in the area of agricultural and microbial biotechnology focusing on plant microbiomes and their plant growth-promoting attributes for plant growth and soil fertility for sustainable agriculture. It comprises 11 chapters. In Chap. 1, Patel and Goswami describe the biodiversity of phosphorus-solubilizing and phosphorus-mobilizing microbes, mechanisms, and their applications in agriculture. In Chap. 2, Khati et al. highlight the biodiversity of potassium-solubilizing microbes and their functional impact on plant growth for sustainable agriculture. In Chap. 3, Jatav et al. describe the biodiversity of zinc-solubilizing microbes and their applications in agriculture as tool for cereal biofortification for micronutrients. Chapter 4 by Verma et al. Highlights the microbial ACC deaminase-producing microbes and their role in the mitigation of different abiotic stress. In Chap. 5, Yachana Jha describes the biodiversity of phytohormone-producing microbes and their role in plant growth promotion and adaptation under stress conditions, while Enespa et al., in Chap. 6, deal with the mechanisms of plant growth promotion by microbes and their functional annotation in mitigation of abiotic stress. In Chap. 7, Challa et al. highlight the recent advancements in microbes from hypersaline environments and their role in mitigation of salt stress in plants. In Chap. 8, Meena and his colleagues describe in detail the alleviation of cold stresses in plants by psychrotrophic microbes. Jain et al. highlight the recent trends and future challenges of microbe-mediated mitigation of drought stress in plants in Chap. 9. Mondal et al. explain the future perspective in agriculture by microbial consortium with multifunctional plant growth-promoting attributes in Chap. 10. Finally, in Chap. 11, Gunaswetha et al. describe the roles of cyanobacteria as biofertilizers, their current research, commercial aspects, and future challenges.

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

Dr. H. S. Dhaliwal is presently the Vice Chancellor of Eternal University, Baru Sahib, Himachal Pradesh, India. He completed his PhD 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 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); Visiting Professor, Department of Plant Pathology, Kansas State University, Kansas, USA, (1989); Senior Research Fellow, CIMMYT, Mexico, (1987); Senior Scientist and Wheat Breeder-cum-Director, PAU Regional Research Station, Gurdaspur (1979–1990); Research Fellow FMI, Basel, Switzerland (1976–1979); and D.F. Jones Postdoctoral Fellow, University of California, Riverside, USA (1975–1976). He was elected as Fellow of the National Academy of Agricultural Sciences, India (1992). 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 in 1988. He has to his credit more than 300 publications including 250 research papers, 12 reviews, 15 chapters contributed to books, 105 abstracts and papers presented in meetings and conferences, 18 popular articles, and a number of project report/books/bulletins/manuals. His important research contributions are the identification of a new species of wild diploid wheat *Triticumu urartu*; gathering of evidences to implicate *it* as one of the parents of polyploid wheat; being the Team Leader in the development of seven wheat varieties, namely, 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 semidwarfing 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. Dr.Dhaliwal 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 in the Department of Biotechnology, Ministry of Science and Technology, Government of India, New Delhi, and ICAR, New Delhi. Currently, 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 (DBT), and RAC of IIAB, Ranchi, ICAR.

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Preface

Microbes are ubiquitous in nature. The vast microbial diversity has been found to associate with the plant systems. The plant-microbe interactions are the key strategy to colonize and establish in a variety of diverse habitats. Plant microbiomes play an important role in the growth and development of plants and in the health of soil. These microbiomes 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 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 present book, ***Advances in Plant Microbiome and Sustainable Agriculture**: Functional Annotation and Future Challenges*, covers biodiversity of plant microbiomes and their functional attributes for plant growth promotion under the natural as well as the abiotic stress environmental conditions. It will be immensely useful to biological sciences, especially to microbiologists, microbial biotechnologists, biochemists, researchers, and scientists of microbial and plant biotechnology, as well as to the faculty, researchers, and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects. We are honored that the leading scientists who have extensive, in-depth experience and expertise in plant-microbe interaction and microbial biotechnology took the time and effort to develop these outstanding chapters. Each chapter is written by internationally recognized researchers/scientists, providing readers an up-to-date and detailed account of the microbial biotechnology and innumerable agricultural applications of plant microbiomes.

Sirmour, Himachal Pradesh, India	Ajar Nath Yadav
Isfahan, Iran	Ali Asghar Rastegari
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All authors are sincerely acknowledged for contributing up-to-date information on the plant microbiomes, their biodiversity, and biotechnological applications for sustainable agriculture and environment. We are thankful to all authors for their valuable contributions.

We 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 Prof. Naveen Kumar Arora, Ms. Aakanksha Tyagi, and Mr. Beracah John Martyn for the assistance and supports.

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

Contents

About the Series Editor

Naveen Kumar Arora is a Professor and Head of the Department of Environmental Science at Babasaheb Bhimrao Ambedkar University (A Central University), Lucknow, Uttar Pradesh, India. He received his PhD in Microbiology. He is a renowned researcher in the field of environmental microbiology and biotechnology. His specific area of research is plant-microbe interactions, particularly plant growth-promoting rhizobacteria. He has more than 75 research articles published in premium international journals and several articles published in magazines and dailies. He is an editor of 25 books, published by Springer. He is a Member of several national and international societies, Fellow of International Society of Environmental Botanists (FISEB), Secretary General of Society for Environmental Sustainability, in editorial board of 4 journals, and reviewer of several international journals. He is also the editor in chief of the journal *Environmental Sustainability* published by Springer Nature. He has delivered lectures in conferences and seminars around the globe. He has a long-standing interest in teaching at the PG level and is involved in taking courses in bacteriology, microbial physiology, environmental microbiology, agriculture microbiology, and industrial microbiology. He has been advisor to 134 postgraduate and 11 doctoral students. He has been awarded for excellence in research by several societies and national and international bodies/organizations. Although an academician and researcher by profession, he has a huge obsession for the wildlife and its conservation and has authored a book, *Splendid Wilds*. He is the President of the Society for Conservation of Wildlife and has a dedicated website www.naveenarora.co.in for the cause of wildlife and environment conservation.

Editors and Contributors

About the Editors


2019/11/23 14:

Ajar Nath Yadav is an Assistant Professor (SS) in the Department of Biotechnology, Dr. Khem Singh Gill Akal College of Agriculture, Eternal University, Baru Sahib, Himachal Pradesh, India. He has 11 years of teaching/research experiences in the fields of Microbial Biotechnology, Microbial Diversity, and Plant-Microbe Interactions. He obtained his doctorate degree in Microbial Biotechnology jointly from IARI, New Delhi, and BIT, Mesra, Ranchi, India, his MSc in Biotechnology from Bundelkhand University, and his BSc in CBZ from the University of Allahabad, India. He has 174 publications with h-index of 37, i10-index of 75, and 3253 citations (Google Scholar). He has published 115 research communications in different international and national conferences and has received 12 Best Paper Presentation Awards and 1 Young Scientist Award (NASI-Swarna Jayanti Puraskar). He received "Outstanding Teacher Award" in the 6th Annual Convocation 2018 from Eternal University, Baru Sahib, Himachal Pradesh. He has a long-standing interest in teaching at the UG, PG, and PhD level and is involved in taking courses in microbiology and microbial biotechnology. He is currently handling two projects and is guiding three scholars for PhD degree and one for MSc dissertations. He has been serving as an Editor/Editorial Board Member and Reviewer of the different national and international peer-reviewed journals. He has a lifetime membership in the

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Ali Asghar Rastegari currently works as an Assistant Professor in the Faculty of Biological Science, Department of Molecular and Cellular Biochemistry, Falavarjan Branch, Islamic Azad University, Isfahan, Islamic Republic of Iran. He has 13 years of experiences in the fields of Enzyme Biotechnology, Nanobiotechnology, Biophysical Chemistry, Computational Biology, and Biomedicine. He received his PhD in Molecular Biophysics in 2009 from the University of Science and Research, Tehran Branch, Iran; MSc in Biophysics in 1994 from the Institute of Biochemistry and Biophysics, University of Tehran; and BSc in Microbiology in 1990 from the University of Isfahan, Iran. To his credit, he has 39 publications [21 research papers, 2 books, 16 book chapters] in various supposed international and national journals and publishers. He is editor of 7 books. He has issued 12 abstracts in different conferences/symposiums/workshops and has presented 2 papers at national and international conferences/symposiums. He is a Reviewer of different national and international journals. He is a Lifetime Member of Iranian Society for Trace Elements Research (ISTER) and Biochemical Society of Islamic Republic of Iran, and is a Member of the Society for Bioinformatics in Northern Europe (SocBiN), Boston Area Molecular Biology Computer Types (BAMBCT), Bioinformatics/Computational Biology Student Society (BIMATICS), Ensembl Genome Database, and Neuroimaging Informatics Tools and Resources Clearinghouse (NITRC).

Neelam Yadav currently works on microbial diversity from diverse sources and their biotechnological applications in agriculture and allied sectors. She obtained her postgraduate degree from Veer Bahadur Singh *Purvanchal* University, Uttar Pradesh, India. She has research interest in the area of beneficial microbiomes and their biotechnological applications in agriculture, medicine, environment, and allied sectors. To her credit, she has 51 research/review/book chapter publications in different reputed international and national journals and publishers. She is editor of 8 books. She is Editor/

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Divjot Kour currently works as Project Assistant in DEST-funded project "Development of Microbial Consortium as Bio-inoculants for Drought and Low Temperature Growing Crops for Organic Farming in Himachal Pradesh." She obtained her doctorate degree in Microbial Biotechnology from the Department of Biotechnology, Dr. Khem Singh Gill Akal College of Agriculture, Eternal University, Baru Sahib, Himachal Pradesh, India; her MPhil in Microbiology in 2017 from Shoolini University of Biotechnology and Management Sciences, Solan, Himachal Pradesh; and her MSc in Microbiology (2015) and her BSc (2014) both from the University of Jammu, Jammu and Kashmir. She has research experience of 5 years. To her credit, she has 45 publications in different reputed international and national journals and publishers. She is Editor of two books in Springer. She has published 18 abstracts in different conferences/symposiums/workshops, has presented 9 papers in national and international conferences/symposiums, and has received 5 Best Paper Presentation Awards. To her credit, she has isolated more than 700 microbes (bacteria and fungi) from diverse sources. She is a Member of the National Academy of Sciences and Agro Environmental Development Society, India.

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Chapter 1
Phosphorus Solubilization and Mobilization: Mechanisms, Current Developments, and Future Challenge

Dhavalkumar Patel and Dweipayan Goswami

Abstract Plants require nutrients for their proper growth and development. After nitrogen phosphate is the second significant element required for plants. Phosphorus is commonly found in form of polyprotic phosphoric acid (H_3PO_4); however, phosphorus intake is naturally in the form of H_2PO^{-4}. The complete phosphorus conversion movements are mineralization and immobilization, weathering, and precipitation besides adsorption and desorption. Organic phosphate is liberated in soil environment by three groups of enzymes, while inorganic phosphate mineralization is achieved by microbial species. The solubilization of phosphate can be elaborated by acid production theory and proton and enzyme theory. The bioformulations of potent phosphorus-solubilizing microbes are used to stimulate the accessibility of phosphate to plant roots. Once potent strain is screened, the metabolic flux of that strain can be improvised, and more bioformulations can be prepared. Several phosphate-solubilizing microbial strains have already been commercialized as formulated products and sold as biofertilizer. However, the use of the biofertilizer is still insufficient. Despite of extensive research in past few decades, a cooperation of basic and applied approaches is still required to reveal hidden potentials of phosphate solubilizers which may not have documented until now.

Keywords Phosphate solubilization · Phosphate mobilization · Microbial strains · Bioformulations · Biofertilizer

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1.1 Introduction

Microbes are involved in vital functions of the soil and interact with plant roots and aerial parts of plants making several endophytic and non-endophytic associations. Nutrients acquisition by roots from soil is accomplished by the exchange of cations, in which root hairs propel hydrogen ions (H^+) keen on the surrounding environment passing through the proton pumps (Puga et al. 2015). Hydrogen ions which are formed causes shift in cations that are bonded to soil particles which are anionic in nature and makes the accessibility of the cations that can be easily taken up by the roots. Stomata in the leaves open and absorb carbon dioxide and in return exorcize oxygen. Here carbon dioxide serves as the source of carbon that is required in photosynthesis (Sakimoto et al. 2017). Nitrogen is a chief component of several vital plant constituents. After nitrogen, phosphate is the second significant element required for plants (Razaq et al. 2017).

Identical to nitrogen, phosphorus is tangled with many dynamic plant processes. In the interior of plant, phosphate is bonded chiefly as an essential factor of the nucleic acids, i.e., deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), in addition to an integral of fatty phospholipids, which are significant in development of membrane and for its functioning (Van-Berkum and Bohlool 1980). Both inorganic and organic forms of phosphate are freely translocated inside the plant. The transfer of energy, i.e., adenosine triphosphate (ATP), in the plant cell is critically reliant on phosphorus. Overall with living individual, phosphorus is an element of the ATP, which is of an immediate routine in all metabolisms that impose energy by the cells (Meyrat and Von-Ballmoos 2019). Activity of various enzymes can be modified by phosphorus, i.e., by phosphorylation, and it can also be secondhand for cell signaling. Phosphorus is intense at the most vigorously emergent points of a plant and stockpiled within seeds in expectancy of their germination (Roy and Saha 2018; Yadav et al. 2018).

Phosphorus is utmost present in the form of polyprotic phosphoric acid (H_3PO_4) from the soil; nevertheless, phosphorus is utilized most readily in H_2PO^{-4} form. Phosphorus is not accessible to crops in adequate amount from the soils since it's discharging is very slow from insoluble phosphates; besides, it is rapidly fixed yet again (Khan et al. 2019; Kaur et al. 2020; Singh et al. 2020). Under utmost environmental circumstances, phosphate is the element which confines the growth as of this compression and owing to its supplementary requirement by plants and microorganisms. Plants' phosphur requirement can be intensified by mutualism with mycorrhiza (Yang et al. 2018). Penetrating reddening in leaves (owing to lack of chlorophyll) or green coloration in plant are the characterized symptoms of phosphorus deficiency. In extreme conditions the leaves become denatured and illustrated as dead leaves. Sporadically, the leaves possibly will seem purple due to an accretion of anthocyanin. Mature leaves will demonstrate the primary signs of deficiency as phosphorus are mobile nutrient (Criado et al. 2017).

Phosphorus deficit can yield symptoms analogous to those of nitrogen deficit; however, as renowned by Russel, "Phosphate deficiency diverges from nitrogen deficiency in being tremendously problematic to identify, in addition crops can be misery from life-threatening starvation deprived of there being any apparent signs that lack of phosphate is the source" (Carstensen et al. 2018, 2019).

1.2 Sources of Phosphate in Soil

Phosphorus occurs in various diverse forms in soil. Aimed at applied purposes, it can be grouped into four overall forms: (1) inorganic phosphorus, the only form which is available to plant; besides three other forms that are not available to plant are (2) organic phosphorus, (3) adsorbed phosphorus, and (4) mineral phosphorus (Zemunik et al. 2015: Nottingham et al. 2015). Figure 1.1 displays all phosphorus forms as they flow in soil. The overall phosphorus conversion progressions are mineralization along with immobilization, weathering, and precipitation besides adsorption as well as desorption. Weathering, desorption, and mineralization augments plant accessible phosphorus. Immobilization, adsorption, and precipitation decline plant accessible phosphorus (Menezes-Blackburn et al. 2017; Yadav 2017; Yadav et al. 2020).

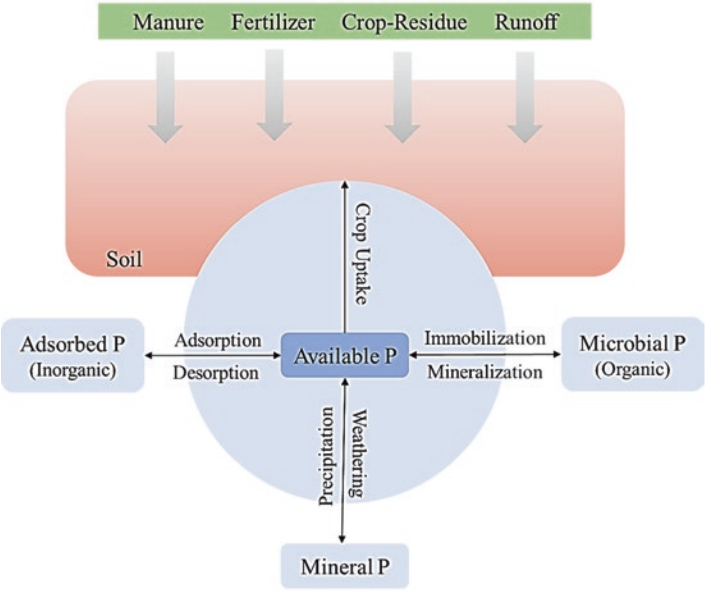

Fig. 1.1 Display the elementary phosphorus cycle in soil

1.2.1 Mineralization and Immobilization

Microbial alteration of organic phosphorus to the ionic forms, $H_2PO_4^-$ or HPO_4^{-2}, is known as mineralization (Kour et al. 2019a). Phosphorus forms which are plant accessible are identified as orthophosphates. Immobilization ensues when these phyto-accessible phosphorus forms are expended by microbes, whirling the phosphorus to the organic phosphorus forms that are not accessible to plants. The bacteriological phosphorus will turn out to be accessible over spell as the microbes perish (Yadav et al. 2015). Upholding soil organic stuff intensities is an imperative in phosphorus managing. This progression diminishes the necessity for fertilizer practice plus the peril of runoff in addition leaching may be the outcome from supplementary phosphorus (Bhatti et al. 2017; Kour et al. 2020b; Rana et al. 2020b).

1.2.2 Weathering and Precipitation

Farm soils indeed comprise phosphorus minerals that are weathered in excess of extensive eras of interval and deliberately make accessible to the plants. Phosphorus can turn out to be inaccessible over precipitation, that take place if plant accessible inorganic phosphorus retorts with dissolved iron, aluminum, manganese (in lower pH soils), or calcium (in higher pH soils) to formulate phosphate minerals (Stockdale et al. 2016).

1.2.3 Adsorption and Desorption

The biochemical binding of plant accessible phosphorus to soil particles is called adsorption, which later become inaccessible to plants while desorption is the proclamation of adsorbed phosphorus as of its bounded form into the soil environment (Fink et al. 2016). Adsorption (or “fixing”) happens rapidly although desorption is generally a sluggish progression. Adsorption fluctuates commencing precipitation as adsorption is a reversible chemical requisite of phosphorus to the particles of soil whereas precipitation take in an additional perpetual alteration in the chemical assets of the phosphorus as it is detached from the soil environment. Soils that contains high amount of aluminum and/or iron are likely to adsorb extra phosphorus than normal soils (Moran-Salazar et al. 2016). Phosphorus is available in most plant accessible form as soon as the pH of soil gets little acidic. When the pH gets high, phosphorus is precipitated with calcium. As the pH gets low, phosphorus inclines to be sobbed to iron and aluminum amalgams in to the surrounding. All soil contains a supreme quantity of phosphorus which can be adsorbed. Phosphorus can also be lost to the surroundings over leaching and/or runoff upsurge with phosphorus inundation level. Precise fertilizer settlement can decline phosphorus desorption or adsorption effects by abating phosphorus interaction with soil plus segregating phosphorus into a minor zone (Lynch et al. 2017).

1.2.4 Leaching

The elimination of dissolved phosphorus from soil by perpendicular water crusade is known as leaching. Leaching is an apprehension in comparatively great phosphorus soils (neighboring or at phosphorus permeation), exclusively wherever privileged flow or uninterrupted influences by tile plumbing be existent (Madiba et al. 2016).

1.2.5 Runoff

Runoff, the foremost reason of phosphorus forfeiture from farms soil. Water transmits away soil-bound particulate phosphorus in battered dregs, over and above dissolved phosphorus from fertilizers and pragmatic manure. Wearing away of soil control practices decline the phosphorus losses by means of decelerating water flow over the surface of soil besides cumulative infiltration (Lippmann and Schlesinger 2017).

1.3 Process of Solubilization

1.3.1 Organic Phosphate Solubilization

Organic phosphate solubilization is often known as organic phosphorus mineralization; also it ensues in soil surrounding at the outflow of animals and plant leftovers that hold huge sum of compounds which contain organic phosphorus. The putrefaction of organic substance in soil environment is processed by the exploit of abundant saprophytes that yield the proclamation of radical orthophosphate from the structural carbon molecule (Liste 2003). The organophosphates be able to correspondingly grieve a course of mineralization once fatalities by biodegradation. The mineralization of phosphorus (organic) by microbes is strappingly inclined by surrounding strictures; in actual fact, sensible alkalinity string pulls organic phosphorus mineralization. Degradability of the organic phosphorous amalgams be contingent principally on the physicochemical and biochemical assets of their molecular structure, e.g., phospholipids, sugar phosphates, and nucleic acids are straight forwardly fragmented; nevertheless polyphosphates, phosphonates, and phytic acid are disintegrated extra sluggishly (Turner et al. 2006: Kruse et al. 2015; Yadav 2019).

Phosphorus possibly could be unconfined from organic amalgams in soil environment by mainly three groups of enzymes: first is nonspecific phosphatases that accomplish dephosphorylation of phospho-ester phosphor anhydride bonds in organic stuff, second is phytases that precisely cause phosphorus discharge from phytic acid, and finally phosphonatases and C–P lyases, enzymes that achieve carbon–phosphorus cleavage in organophosphonates (Gong et al. 2018; Lusk et al. 2017; Kour et al. 2020c; Rastegari et al. 2020a). The chief commotion apparently resembles to the reactions of phytases and acid phosphatases for instance their substrates predominant presence in the soil (Zhang et al. 2018).

1.3.2 Inorganic Phosphate Mineralization

Quite a few data reports have recommended the capability of diverse microbial species to solubilize insoluble inorganic phosphate amalgams, for example, dicalcium phosphate, tricalcium phosphate, rock phosphate, and hydroxyapatite. About 65% of entirely arable farm soils have alkaline pH, so that maximum mineral phosphorus is in the formula of low-slung soluble calcium phosphates (CaPs) (Purushotham et al. 2017). Microbes indispensably assimilate phosphorus by means of membrane transport; consequently suspension of CaPs to Pi (H_2PO_4) is well-thought-out crucial to the overall phosphorus cycle. Assessment of trials from these soils throughout the ecosphere has revealed that, usually, the direct oxidation pathway delivers the biochemical root for extremely effective solubilization of phosphate in Gram-negative bacteria through dissemination of the robust organic acids formed in the periplasm into the head-to-head soil environment (Kahlon 2016).

Consequently, the quinoprotein glucose dehydrogenase (PQQGDH) possibly will reveal a crucial part in nutritional ecophysiology of soil microflora mainly bacteria. MPS bacteria possibly will be rummage-sale for industrial down processing of rock phosphate minerals (a replaced fluorapatite) otherwise even intended for straight inoculation as a “biofertilizer” in the soils equivalent to bacteria used for nitrogen fixation. Mutually the ecological and agronomic characteristics of the direct oxidation interceded MPS trait (Ganeshamurthy et al. 2015). The bacterial genera reported to solubilize inorganic phosphate are *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Bacillus*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Erwinia*, and *Flavobacterium* (Kudoyarova et al. 2017; Verma et al. 2019; Yadav et al. 2017a).

1.3.3 Acid Production Theory

Bestowing to current theory, the progression by PSM of phosphate solubilization is owing to the release of organic acids that is convoyed by the lowering the pH (i.e., acidification) of the environment. The study of culture filtrates obtained of PSMs has revealed the occurrence of a few of organic acids such as glyoxalic, malic, succinic, tartaric, fumaric, oxalic, alpha-keto butyric, citric, and 2-ketogluconic in addition to gluconic acid (Kumar et al. 2016: Hamim et al. 2019)

The volume and nature of the organic acid forms speckles with the microbes. The organic acids unconfined in the culture scum retort by means of the insoluble phosphate. The quantity of soluble phosphate unconfined hinge on the asset and form of acid. Moreover, aliphatic acids are tending to be extra operative in phosphorus solubilization compared to citric acids and phenolic acids (Menezes-Blackburn et al. 2016). Fumaric acid has the chief phosphorus-solubilizing aptitude. Dibasic and tribasic acids are also supplementary active than monobasic acids in phosphorus solubilization. Existence of dibasic acids and tribasic acids exhibit an ancillary effect that give an impression owing to capability of these acids to form unionized connotation amalgams with calcium in so doing removes calcium from the environment and cumulative soluble phosphate meditation (Edelson et al. 2016).

Organic acids subsidize to the dropping of environment pH as these acids detach in a pH hooked one equipoise, keen on their corresponding anions and protons. Organic acids shield environment pH besides will linger to separate as protons expended by the suspension reaction (Meers et al. 2008; Verma et al. 2017). Correspondingly, microbes frequently disseminate organic acids by means of anions. Above and beyond organic acids, the inorganic acids for instance sulfuric acid and nitric acid are also formed by *Thiobacillus* through the oxidation of inorganic compounds of sulfur and nitrogenous by the nitrifying bacteria that retort with calcium phosphate in addition alter them into resolvable forms (Kumar et al. 2019; Rajawat et al. 2020; Sahu et al. 2018). In Gram-negative bacteria, the most competent mineral phosphate solubilization (MPS) phenotype grades from extracellular oxidation of glucose to gluconic acid through the enzyme quinoprotein glucose dehydrogenase. The subsequent pH alteration and decline potential are believed to be accountable for the suspension of phosphate in the microbial medium (Bharti et al. 2017).

Glucose dehydrogenase (GDH) enzyme carries the gluconic acid biosynthesis with the help of cofactor, i.e., pyrroloquinoline quinone (PQQ). *Erwinia herbicola* is well known for mineral phosphate solubilization, and a gene was cloned by Goldstein and Liu (1987). The manifestation of this gene permitted the yield of gluconic acid; besides mineral phosphate solubilization commotion in *E.coli* HB101 was also studied (Yu et al. 2019). Gluconic acid is one of the prime organic acids which are produced through *Pseudomonas* sp., *Pseudomonas cepacia*, *Erwinia herbicola* and *Rhizobium leguminosarum*, *Rhizobium meliloti*, and *Bacillus firmus* yield perceptible sum of 2-ketogluconic acid (El-Badry et al. 2016; Kour et al. 2020d; Rana et al. 2020c; Unden et al. 2017). Khanghahi et al. (2018) testified microbial solubilization for insoluble zinc oxide in addition to zinc phosphate, arbitrated by 2-ketogluconic and gluconic acid produced. Additional organic acids, such as isovaleric, lactic, isobutyric, glycolic, acetic, oxalic, succinic, and malonic acids, are also produced by various phosphate-solubilizing bacteria (Kaur et al. 2016; Rawat et al. 2018).

Goebel and Krieg reported that *A. lipoferum* or else *A. brasilense* when cultivated on fructose (a mutual source of carbon) gluconic acid was not bent all through the growth of and was only formed during development of glucose. Valdehuesa et al.

(2018) testified that gluconic acid can be produced by *A. brasilense* when it is full-grown on fructose (in vitro) and modified with glucose which serves as an inducer to produce gluconic acid and possesses phosphate-solubilizing aptitude (in vitro).

For the formation of gluconic acid, glucose serves as the precursor which has been recommended for phosphate solubilization by these strains is arbitrated by gluconic acid or else glucose metabolism. Phosphate solubilization is achieved by heralded exposure of gluconic acid to the environment, possibly even low-slung amount of the acid (even underneath the for HPLC detection) in progress to dissolve parsimoniously soluble phosphate. On contrary, ingesting of the gluconic acid by increasing cells could similarly take place. In *A. brasilense*, after incubation for 48 h there is a drop in the amount of soluble phosphate and that can be enlightened as auto ingesting of soluble phosphate by rising of bacterial inhabitants (Sabalpara and Mahatma 2019).

The concluding may consequence from gluconic acid production with NH^{4+} uptake that possibly will release protons to the environment. In the quicker cultivation of *A. brasilense* strains, possibly the cells cast off supplementary NO^{-3} after the incubation period is over, thereby liberating OH^-, that gives justification for the rise in pHv (48 h later). The metabolic machinery of gluconic acid formation remains unrevealed (Madhaiyan et al. 2013)

The phosphate-solubilizing aptitude was considerably higher of gluconic acid as related to 2-ketogluconic acid in the dregs of CC-Al74 strain culture. The course of chelation and acidification by 2-ketogluconic acid and gluconic acid thaws tricalcium phosphate (TCP) in medium containing culture. The chelation characteristics of gluconic acid empower it towards formulating insoluble composite. Insoluble metal possibly will be solubilized via protons, through Ca^{++} delivering phosphates (Lin et al. 2006: Joshi et al. 2014). Protons are driven to the exterior environment by several membrane associated pumps that arrange ionic gradients intended for the procurement of nutrients. Furthermore, organic acids give rise to protons which are released and also possess an organic acid anion that are generally accomplished of forming an intricate with metal cation (Fasim et al. 2002).

The yielding of gluconic acid or citric acid also the extrusion of H^+ up shot as of membrane transport mechanisms is described as probable progression for disbanding rock phosphate from aluminum phosphate, hydroxyapatite, and iron phosphate by *Penicillium rugulosum* (Walia et al. 2017). These progressions are inclined by the springs of the phosphate, carbon, and nitrogen. If nitrate is the solitary nitrogen source for production of citric acid, then the consequential volume of phosphate dissolution is augmented. Since citric acid is not solitary one to be involved in the phosphate dissolutions but then again in iron dissolution along with other metals as of minerals, the method of nitrate accretion in soils possibly will show an imperative part for the rock weathering all together (Güler et al. 2017). The type of acid and its nature production is mostly reliant on the source of carbon available. Overall, oxalic acid, citric acid, and gluconic acid are biotite, phyllosilicates, and feldspar stout-solubilizing agents (Kour et al. 2020a; Rana et al. 2020a; Sindhu et al. 2016). Some PSMs (phosphate-solubilizing microorganisms) that produce different acids are précised in Table 1.1.

Table 1.1 Organic acid productions by different phosphate-solubilizing microorganisms

Phosphate-solubilizing microorganisms	Organic acid production
Acetobacter sp.	Gluconic acid
Aspergillus flavus	Gluconic, fumaric, succinic, acetic, oxalic, citric
Penicillium sp. *and Aspergillus niger*	Gluconic acid
Burkholderia cepacia *Burkholderia* sp.,	Gluconic acid
Serratia sp., *Ralstonia* sp., *Pantoea* sp.	Gluconic acid
Citrobacter sp.	Gluconic acid
Enterobacter sp.	Gluconic, succinic, acetic, glutamic, oxaloacetic, pyruvic, malic, fumaric, alpha-ketoglutaric
Escherichia freundii	Lactic acid
Penicillium bilaii	Citric and oxalic acid
Penicillium regulosum	Citric and gluconic acid
Pseudomonas aeruginosa	Gluconic acid and 2-ketogluconic acid
Pseudomonas putida	Gluconic acid and 2-ketogluconic acid
Pseudomonas fluorescens	Citric acid and gluconic acid
Pseudomonas striata	Tartaric and citric acid
Rhizobium leguminosarum	2-ketogluconic acid
Serratia marcescens	Gluconic acid
Sinorhizobium meliloti	Malic, succinic and fumaric
Stenotrophomonas maltophilia	Gluconic acid

1.3.4 Proton and Enzyme Theory

Enzymes of esterase type are identified to be tangled in delivering phosphorus commencing organic phosphatic amalgams. PSMs are similarly identified to yield phosphatase enzyme accompanied by acids that roots the solubilization of phosphate in marine environs (Eida et al. 2017). Din et al. (2019) conveyed that four proficient phosphates-solubilizing microbes, *Penicillium simplicissimum*, *Aspergillus niger*, *Penicillium aurantiogriseum*, and *Pseudomonas* sp., and out of these four strains only *A. niger* possibly yield organic acids. Two utmost plausible elucidations for this are as below.

Solubilization deprived of production of acid is owing to the discharge of protons supplementing respiration otherwise ammonium assimilation (Kishore et al. 2015: Hajiboland 2018). Superfluous solubilization take place with ammonium salts than by nitrate salts as per the accessibility of nitrogen source in the medium (Lowrey et al. 2016: Kashyap et al. 2017). Above and beyond these two mechanisms, the assembly of chelating elements CO_2, H_2S, siderophores, mineral acids, and biologically active phytohormone like gibberellins, indole acetic acids, and cytokinins is as well associated with solubilization of phosphate. Chelation implicates the development of at least two coordinate bonds among an anionic and/or polar molecule with cations, occasioning in a ring structure moiety. Organic acids (mainly anions), using oxygen that contain carboxyl and hydroxyl groups, devour the capability to form firm complexes thru cations such as Fe^{3+}, Fe^{2+}, Ca^{2+}, and Al^{3+} which are frequently bound to phosphate in feebly forms (Adusei-Gyamfi et al. 2019).

Phosphate dissolution in soil environment is an actually a vital process for plant's overall growth and development. More than a few researches have revealed that the phosphate intake by plants can be evidently amplified by mycorrhizal fungi (Zhang et al. 2019) or inoculation of soil with species are proficient in free phosphate solubilizing, for instance, *P. bilaii* (Mukherjee 2017).

1.4 Phosphate Solubilization Bioformulation

Soil microbes are associated in a series of practices that distress phosphate transformation besides addition thus stimulates the successive accessibility of phosphate to roots of plant as free-living PSM permanently exist in soils. The inhabitants of inorganic PSM are every so often little, less than even 10^2 CFU (colony forming unit) per gram of soil as detected in Northern Spain's soil (Meena et al. 2016). In soils of four Quebec, the number of PSM are aorund 26-46% of total micro flour (Mpanga et al. 2019). As observed with soil microbes other than PSM, the amount of them are more significant in the rhizosphere soil compared to non-rhizosphere soil (Field et al. 2019). However, inoculation data intended to refining phosphate in plants nutrition comprises bacteria as well as fungi and is obtainable commercially in Western Canada as per the phosphate inoculant JumpStart (Philom Bios, Saskatoon, Sask.). They are traded for canola, mustard, wheat, and other legumes that comprise *Penicillium bilaii* bacterial strain (http://www.philombios.ca/).

Biofertilizers improve the nutrient superiority in the soil. The foremost bases of biofertilizers are bacteria, fungi, as well as blue-green algae (cyanobacteria). Plants have several associations with those microbes (Rastegari et al. 2020b; Singh and Yadav 2020). Afterward contribution by chemical fertilizers through the preceding ten decades, farmers were pleased with the amplified harvest from the agriculture. Nevertheless, gradually chemical fertilizers underway demonstrate their unfriendly paraphernalia such as contaminating water basins, leaching out, terminating normal flora and fauna which include approachable organisms, creating vulnerability for crops to the occurrence of diseases, tumbling the fertility of soil, and thus triggering irretrievable impairment to the ecosystem (Kour et al. 2019b; Sohail et al. 2019).

The principle behind phosphate-solubilizing bioformulation is that microbes owe countless capabilities that could be oppressed for healthier agriculture performs. Some benefit in brawl diseases, while others have the aptitude to reduce soil multifaceted compounds into meeker forms that are employed by crops for their overall growth and development. They are tremendously advantageous in elevating the soil by fabricating organic nutrients into the soil. To transform insoluble phosphates to available form to the plants, resembling orthophosphate, is an imperative attribute for a PGPB for accumulative yields of plant (Rodriguez et al. 2006). Microbes devising the capacity to dissolve substantial sum of phosphates is frequent. They are even now used as marketable biofertilizers for enhancements of agricultural soil. The practice of microbial harvests has positive recompenses over conservative chemicals as they are measured harmless than various chemicals that are in routine now; they don't get accrue in the food-chain; the marked organisms rarely progress resistance as it stands when chemical proxies are used; and biofertilizing proxies are carelessly injurious to ecological progressions or the environs (Nayak et al. 2017: Kumar and Yaashikaa 2018).

1.5 Metabolic Flux of Phosphate Solubilizers

Utmost phosphate-solubilizing bacteria (PSB), discharge phosphate from frugally soluble mineral phosphates (counting the *Pseudomonas* spp.) through creating in elevation of gluconic acid as of glucose that is available extracellularly, in reaction which is metabolized thru periplasmic glucose dehydrogenase, a crucial constituent of glucose catabolism of pseudomonads. Buch et al. (2008) explored the alterations in the glucose breakdown of gluconic acid yielding PSB pseudomonads and low gluconic acid yielding/non-PSB strains; more than a few parameters affecting to growth and glucose use under phosphate adequate and phosphate scarce environments were scrutinized for the PSB isolate *Pseudomonas aeruginosa* P4 (yielding 46 mM gluconic acid and liberating 437 mM phosphate) besides non-PSB *P. fluorescens* 13525. Their consequences showed fascinating variances in glucose channeling to gluconate and promote catabolic end products like acetate and pyruvate regarding phosphate grade for both the strains. Nevertheless, *P. aeruginosa* P4 (PSB strain), to one side from demonstrating healthier growth under equally little and more attentiveness of inorganic phosphorous, fluctuated from *P. fluorescens* 13525 in its capability to hoard gluconate under phosphate-solubilizing conditions.

These amendments in cultivation, glucose consumption along with acid excretion, were revealed to be interrelated with enzyme activities of glucose-6-phosphate dehydrogenase, glucose dehydrogenase, and pyruvate carboxylase. The aptitude to move glucose to a direct oxidative pathway beneath phosphate deficit is ventured to trigger the discrepancy gluconic acid-mediated phosphate-solubilizing capability detected among pseudomonads. Both their *Pseudomonas* strains premeditated diverged in the phosphorylative towards the direct oxidative pathway the minute phosphate were restrictive. On the other hand, the direct oxidative pathway preponderated in both of the strains under phosphate constraint surroundings. Such research elucidates the metabolic tractability associated to gluconic acid excretion in phosphate-solubilizing pseudomonads that may perhaps enable metabolic engineering tactics for improving the phosphate-solubilizing flux of *Pseudomonas* strains (Stark et al. 2015).

1.6 Commercialization, Future Scope, and Limitation

Several phosphate-solubilizing microbial strains are commercially offered in formulated products that are cast off as biofertilizers (Goswami et al. 2016). Fungal phosphate solubilizers are generally set as fine particles formulation, coarse powder in addition fluid-bed pellets by means of using binder, i.e., dextrin. Alginate gel are used in formulating fungal and bacterial bioformulations (Miller et al. 2016; Yadav et al. 2017b, c). Formulation of the Gram-positive bacteria (sporulating) is by desiccation as they are impervious to high temperature castoff in the process. Gram-positive microbes hold heat-resistant spores which are browbeaten to frame steady and parched powder products (Elisashvili et al. 2018). Substitute to solid bioformulation (powdered) is the microbial suspension in oil, where the aim is to eliminate oxygen that averts respiration (Goswami et al. 2016). Accumulation of silica gel to oil bioformulation improves the shelf life such as it is testified to mutate conidia (Arora et al. 2017).

Despite several Gram-negative bacterial strains such as *Pseudomonas* that are known to own competent phosphate-solubilizing aptitude, they are problematic to formulate for the reason that they don’t bear spores, their bioformulations have brief shelf life, and besides the bacteria are straight forwardly slain as soon as the formulations are dehydrated (Molina-Santiago et al. 2018). Commercialization of phosphate-solubilizing bioformulation is at a flourishing state, and quite a few industries are commercializing fungal and bacterial stains as biofertilizers; some examples are represented here like bioformulation of *Fusarium oxysporum* is commercialized by Biofox that is functioning in contrast to *Fusarium moniliforme* (www.biofox.com). Bacterial bioformulation of *Pseudomonas aureofaciens* commercialized by Ecosoil that is functioning in contradiction of anthracnose, dollar spot, *Pythium aphanidermatum* and Microdochium patch (pink snow mold) (www.ecosoil.com). *Streptomyces griseoviridis* strain K61 has been commercially formulated by AgBio which is branded to constrain *Fusarium* spp., *Alternaria brassicicola*, *Botrytis* spp., *Phomopsis* spp., *Pythium* spp., and *Phytophthora* spp. that is the source of seed rot, root rot, stem rot, and wane ailment of vegetable and ornamental crops (http://www.agbio-inc.com). Biofertilizer encompassing spores of *Bacillus licheniformis* SB3086 produced by novozymes act as phosphate solubilizer; besides it is also effective against dollar spot sickness in plants.

Commercial *Coniothyrium minitans* bioformulation by BIOVED, Ltd., Hungary, is operational in conquering *Sclerotinia minor* and *Sclerotinia sclerotiorum* that are phytopathogen-stainting cucumber, capsicum, tomato, lettuce, and ornamental flowers. Commercial biocontrol “EcoGuard,” promoted as a concerted suspension of *Bacillus licheniformis* SB3086 spores has been establish active as a natural inhibitor of a variability of agronomically significant fungal ailments predominantly anthracnose and dollar spot (https://www.harrells.com/uploads/products/labels/ecogua.pdf). Other phosphate-solubilizing bioformulation products are concise in Table 1.2.

Table 1.2 List of commercially available phosphate-solubilizing bioformulation inoculants of India

Trade name	Microbes	Suitable for
Gmax Phosphomax, KisanPSB, Astha PSB	*Bacillus megaterium*, *Pseudomonas striata*	All crops
Gmax Tricon, SKS TV	*Trichoderma viride*	All season all crops
Gmax FYTON, Astha PF, SKSPF	*Pseudomonas fluorescens*	Tomatoes, chili, cut flowers, orchards, vineyards ornamentals, potato, cucumbers, and eggplant
GmaxSugarmax	*Gluconacetobacter diazotrophicus*	Sugar-containing plants like sugarcane and sweet sorghum and not suitable for other crops
UPAJ-K, Eco-Potash	*Bacillus mucilaginosus*	All crops
UPAJ- Z, BioZinc, zinc-cure	*Bacillus* spp., *Pseudomonas* spp., *Xanthomonas* spp.	All crops
AgriVAM, bio e rich	*Glomus* sp.	All crops
Novozymes	*Bacillus licheniformis*	All crops
Ecosoil	*Pseudomonas aureofaciens*	Cucumber, tomato, wheat, and barley
Anubhav liquid bioformulation	*Bacillus coagulans*	All crops
SKS VL	*Verticillium lecanii*	All crops

1.7 Conclusion and Future Prospective

Notwithstanding the midpoint of curiosity for many research centers, agricultural departments, and industrial producer, the practice of biofertilizer is inadequate. Their production faces the encounter of airing and formulation development for the optimal outcome. On the customer's side, farmers are not even gratified with the erratic eminence of biofertilizers leading to a dearth of acceptance. Inclusive the unfortunate performance of biofertilizers can be attributed to unproductive production by assortment of strains which are prone to contrary environmental situations, methods used for sterilization, carriers, fermentation, and contamination of the closing product owing to poor packing and transportation amenities and last but not the least to the nonexistence of information handover to the farm producers about the precise way of biofertilizer applications. The worldwide acceptance of biofertilizers necessitates lessening of these gaps among their production and application, and only then the extension of their market can be accomplished.

Regardless of such extensive research concluded the over the decades a lot of additional exertion, mutually basic and applied, leftover to be completed to reveal some unseen capabilities of phosphate solubilizers which possibly would have not been recognized yet. Concentrating commercial souk of phosphate solubilizers as biofertilizers, a lot of rigid work is still to be carried out as numerous potential phosphate solubilizers have been exposed by researchers and they haven't up till now commercialized resourcefully. For the most part, it can be alleged that researchers have implicit the elementary mechanics of phosphate solubilization and their action;

still more comprehensive research is to be supported to better realize how plant and microbes intermingle, and on commercial scale, a lot of determination is still obligatory to brand phosphate solubilizers an effectual auxiliary to chemical phosphate fertilizers.

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Chapter 2
Potassium Solubilization and Mobilization: Functional Impact on Plant Growth for Sustainable Agriculture

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Abstract To attain the sustained agriculture production, soil fertility, and its nutrient status should be optimal. Potassium is a crucial component of plant nutrition package that also limits crop quality and yield. Despite the sufficient level of K in soil, its deficiency is mainly because of inefficient utilization of different available forms by plants. The occurrence of potassium in complex mineral forms hinders its utility for plant growth. The plants have to face numerous deficiency symptoms due to unavailability of sufficient potassium required for their metabolism, which checks the productivity of crop. The potassium-solubilizing bacteria act as biofertilizers and can provide a sustainable solution to mineral deficiency in plants. Plant growth promoting (PGP) bacteria can help in K solubilization in soil due to their versatile requirement for environmental and nutritional condition. The present study focused on overview on current trends, K-solubilizing mechanism and ability for growth promotion along with their present constraint and future scope to achieve sustainable agriculture production.

Keywords Potassium solubilization · Potassium-solubilizing bacteria · PGPR · Plant growth promotmion · Weathering

2.1 Introduction

In order to achieve the food demand of burgeoning population, future agriculture production must be sufficient and sustainable. Unfortunately, our current agriculture production is mostly dependent over the use of chemical fertilizers that are

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synthesized through energy-intensive process putting an immense burden on natural resources (Willer and Lernoud 2017). On the other hand, most of the soils in agriculture are deficient for nutrient mostly nitrogen (N), potassium (K), and phosphorus (P) that are essentially required for the plant's growth and development. Among these primary nutrients, potassium plays important role in metabolic activity, activation of ~80 enzymes, starch synthesis, sugar degradation, photosynthesis, disease resistance, etc. (Gallegos-Cedillo et al. 2016). Plant uptake K only from soil which contain ~98% in non-exchangeable or mineral form and ~2% in exchangeable and soil solution form (Mengel and Kirkby 2001). Exchangeable and soluble K remain in equilibrium to each other and availability of potassium depends on rate of release of K from non-exchangeable to soil solution.

The soil solution K pool in agriculture soils may vary from 2 to 5 mg l^{-1} (Sparks and Huang 1985) and readily available for plants and microorganism and equally subjected to leaching losses in light texture soils. However, K losses from soil system by crop removal, runoff, erosion, or leaching result in K release to exchangeable from non-exchangeable and soil solution but only to a limited extent (Meena et al. 2014a, b; Xiao et al. 2017). In addition to this, intensification of agriculture, introduction of high yielding variety and imbalanced fertilization aggravate K depletion and lead to K deficiency in the soil which ultimately reduces the agriculture production (Meena et al. 2015a, b; Singh et al. 2015). Most of the agricultural soils are abundant in K that ranges between 0.04% and 3% attributed by the presence of minerals such as mica and feldspar (Etesami et al. 2017) and unused portion of applied potassium fertilizer due to lower nutrient use efficiency (NUE). Despite lager content of K in soil, just 2% of it is available to plants (Sparks and Huang 1985) and remaining portion exists in tightly bound non-exchangeable or mineral form.

To maintain the optimum K status in soil for sustainable production, exploitation of already available mineral reserve using K-solubilizing microbes could be a viable alternative. Soil microbes actively participate in nutrient cycling and influence their availability via mineralization, immobilization, storage, and nutrient release (Parmar and Sindhu 2013). From different study, it was reported that various saprophytic bacteria, actinomycetes, and some fungal strains could effectively solubilize the less soluble forms of K from soils (Etesami et al. 2017). In this regard, different groups of bacteria such as *Acidithiobacillus ferrooxidans*, *Bacillus mucilaginosus Pseudomonas*, *Burkholderia*, *B. circulans*, *B. edaphicus*, and *Paenibacillus* spp., are successfully reported to release the K from different minerals (Zeng et al. 2012; Zhang et al. 2013; Saha et al. 2016). Theses K-solubilizing bacteria (KSB) improve the solubility of K minerals either by producing organic or inorganic acids, chelation of silicon complex to bring the potassium ion in solution, acidolysis, complexolysis, and exchange reactions (Zarjani et al. 2013a, b; Parmar and Sindhu 2013). Other than bacteria, fungi such as *Aspergillus*, *Aspergillus niger* and arbuscular mycorrhiza (AM) also found potential candidate to enhance the

K-solubilization from mineral compounds (Wu et al. 2005; Prajapati et al. 2012; Verma et al. 2017).

The inoculation of KSM and their positive results on plant's growth and yield have been observed successfully in crops like rape and cotton (Sheng 2005), Maize (Archana et al. 2012) cucumber and pepper (Han et al. 2006), wheat (Savaliya et al. 2017), sorghum (Badr 2006), and tobacco (Zhang and Kong 2014). The application of KSB adds some extra advantages to environment by limiting the use of hazardous chemical fertilizers along with its eco-friendly nature (Sindhu et al. 2010).

2.2 Potassium Status of Indian Soil

After nitrogen and phosphorus, potassium is third most essential element for the plant's growth and development (Rana et al. 2019). Strong affinity with exchange sites of minerals makes its less mobile in soil. Available K map of Indian soil was first prepared by Ramamurthy and Bajaj (1969), which revealed 20% districts in low, 52% medium, and 28% high category. While after 7 years Ghosh and Hasan (1976) prepared soil tests report after summarizing 4.5 million samples and compared them to earlier report they observed a positive shift in K status of 40 districts spread out in 10 states. Recently Srinivasrao et al. (2011) summarized the 11 million of soil samples and found 21, 51, and 28% districts are in the low, medium, and high range, respectively. Earlier in 1980s, it was believed that the Indian soils are potassium rich and had shown poor response to fertilizers applied that promoted blanket application of K fertilizer. With the progress of time, N and P fertilizer application increased, while K consumption shows declining trend that led to mining of nutrient and causes imbalanced nutrition to the plants.

In the country, nutrient uptake and their removal by crops were 7.7 Mt of nitrogen, 1.3 Mt of phosphorus, and 7.5 Mt of potassium and shows positive balance of 1.0 and 1.4 Mt for P and N, respectively, while negative balance of 3.3 Mt for K (Pathak et al. 2010) (Fig. 2.1). The negative balance indicates crop removal of K is greater than fertilizer addition and it accounted 10.2 Mt/year K depletion with mining index of 8.0 at nation level (Ramamurthy et al. 2017). Large proportion of K removal by plants ~75% is retained by straw and remaining portion in grains, fruits, or nuts. Therefore, biomass of crop that contains large K content must come back to soil to maintain a favorable soil K balance or otherwise fertilizer application is needed to fulfill the crop nutrient demands. Moreover, most of the K recommendation given during 1970 must be revalidated to fill the gap of K removal and application (Ramamurthy et al. 2017).

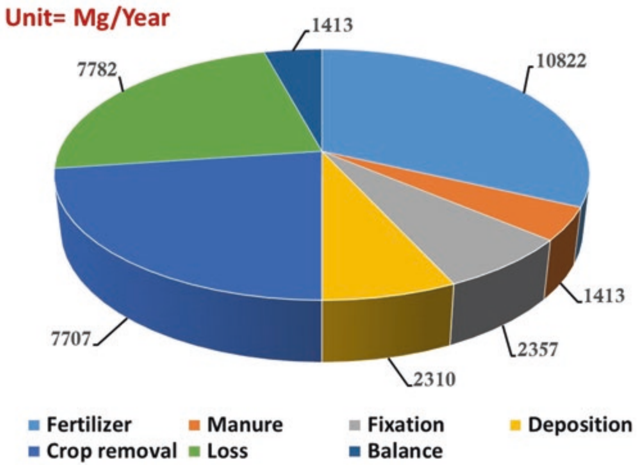

Fig. 2.1 Input, output, and balance of K in India (the values are in ‘000 Mg year^{-1}). (Modified from Pathak et al. 2010)

2.3 Potassium Form, Availability, and Fixation in Soil

Potassium constitutes 2.4% (weight basis) of the Earth’s crust as a seventh most abundant element. Despite its greater abundance in Earth’s crust, the plant’s availability is very low accounting a mere 1–2% (Sparks and Huang 1985). Potassium persists in soil in three pools namely soil solution pool, exchangeable pool, and mineral or non-exchangeable pool. First two pool, that is, solution and exchangeable pool supply the K immediately, while non-exchangeable pool releases the K in very limited or almost negligible amount to satisfy the needs of crops in field. The most common minerals of K in soil are mica and feldspar (Manning 2010) that release K by weathering process and which is dependent on soil and climatic factors. In addition to K release, fixation of solution K in soil minerals can also influence their availability in soil significantly. Minerals such as vermiculite, montmorillonite, and weathered micas mainly tend to fix the K ion and adsorb them on their planer surface (p), edges (e), or interlayer surface (i).

The potassium held on p surface maintains equilibrium with soil solution K. The K ion fixation is due to size of divalent K ion that is almost equal to hexagonal cavity formed due to juxtaposition of the two tetrahedral sheets that are made up of three-layer silicate minerals. More specifically, electrostatic force develops because of negatively charged layer and positive interlayer cation allows the layer to come together and helps in fixation of K ion against rehydration. K release and fixation remains in equilibrium to each other and can occur simultaneously in a system. However, K fixation is not a completely irreversible step, but the K release process is very slowly (Oborn et al. 2005). The K fixation mechanism or release depends on various factors such as nature and amount of clay, pH, concentration of other cation, wetting and drying alternatively, lime content, moisture, cation-exchange capacity, organic matter, etc. Other than above described factors fixation of K largely depends upon K and H+ concentration in soil (Schiavon et al. 2010).

Greater H^+ ion concentration in soil solution reduces its pH and either increases the completion between hydronium (H_3O^+) ions and K for interlayer space or deformed the lattice surface. Release or fixation of K is very crucial step for K management and needs to be understood fully before recommendation of K fertilizer application. Recently, the importance of K fertilization gained much attention on regulating water-holding capacity by improving the physical structure of soil and to boost up the agriculture production under water-scarce areas (Holthusen et al. 2010).

2.4 Factors Affecting Potassium Uptake by Plants

Despite of the fact that K availability in soil is good, there are different other factors responsible for regulating its plant uptake. These factors are categorized into two (soil and plant):

2.4.1 Soil Factors

- Soil structure that includes the material, vegetation, type, and amounts of clay minerals, and the climate responsible for its formation. There is one form of K+, but soil have three basic clay types (muscovite, illitic, and montmorillonite) that trap or hold potassium and make it available (Manning 2010).
- Cation-exchange capacity indicating the potential of soil for holding K and various other cations along with their accumulation for crop uptake. The higher CEC of soil allows greater storage and supply of K (Oborn et al. 2005).
- Potassium availability in soil comprising water-soluble K and exchangeable K (Schiavon et al. 2010).
- Non-exchangeable K in soil. The crop yield was mostly observed to be reduced when it depends on non-exchangeable K (Oborn et al. 2005).
- Soil ability to fix potassium. Different types of clay in soil can fix major part of potassium from fertilizers, further reducing its availability for plant.
- Density of subsoil layers and amount of K in the subsoil. Some subsoils are rich in K that is made available to roots. If subsoil develops dense layers, the penetration of roots decreases that in result reduces the K availability (Oborn et al. 2005).
- Temperature of soil. Lowering of temperature causes reduced potassium availability and uptake by the plants. Various studies reported 85 °F as optimum temperature of soil needed for K uptake.
- Soil moisture required for K movement and uptake by plant roots. Moisture also develops turgor pressure that is required for good root growth through the soil for efficient supply and diffusion of K to plants.
- Soil tilth is mandatory for respiration of roots that further helps in efficient K uptake (Armstron 1998).

2.4.2 *Plant Factors*

- Varieties of crops do differ in their K uptake potential that mainly relies on type of root system and their surface area. For example, grasses due to their fibrous and branched root structure exhibit much greater capacity for potassium uptake.
- Type of root system and metabolic potential also affects availability and K uptake by plants.
- Increase in plant populations and yields of some crops lead to increased demands of potassium in soil.
- High crop yield results in increased total K uptake (Armstrong 1998).

2.5 Physical and Chemical Weathering of Potassium Minerals

Different processes include physical, chemical, and biological process, where the most commonly followed by microbes is biological one.

2.5.1 *Physical Weathering*

- Thermal weathering: This occurs by continuous contraction and expansion of rocks due to variation in temperature (Kevin 1999).
- Frost weathering: Exfoliation by freeze thawing, where ice is there (Stephen 1930).
- Pressure release: Removal of underlying rock material release pressure, which cause rocks to expand and fracture.
- Salt crystal growth: When salt enters the grooves and evaporate leaving crystals in rocks, these crystals tends to enlarge on heating and form cracks in rocks.

2.5.2 *Chemical Weathering*

- Solution: Carbon dioxide (CO_2) produced from organic matter decomposition results in formation of weak carbonic acid. It further reacts with limestone that dissolves carbonates and yields the aqueous solution of bicarbonate and calcium ions.
- Oxidation and hydration: Iron found in combined form reacts with water and oxygen to generate hydrated iron oxides that result in dissolution reaction in mineral rocks (Gordon 2005).
- Hydrolysis: It helps in clay formation, which is one of the essential soil components. A typical hydrolytic reaction takes place when feldspar reacts with acidic water to generate potassium ions, clay minerals, and silica (Arnold 1960).

2.6 Interaction Among Plants–Soil–Microbes

The interaction among plant, soil, and microbe is very crucial. Plants mostly rely on soil and microbes around their roots for fulfilling the nutrient requirement, whereas microbes can obtain nutrients through root exudates released by plants and nutrient cycling. Soil is composed of minerals, water, organic matter, air, and billions of organisms. Plants and microbes in cooperation play crucial role in maintaining the health and fertility of soil. Soil with good fertility is capable to deliver the crucial plant nutrients such as N, P, K, and other micronutrients, in required amount as they are present in soil in limited quantities. Rhizosphere region involves important association of important microbes with roots (de Zelicourt et al. 2013). Several mechanisms are available through which microorganisms fulfill plant nutrients requirement (Zhao et al. 2016).

Soil is colonized by variety of microbes such as fungi, bacteria, protozoa, actinomycetes, algae, and protozoa. Among these the most common group is that of bacteria). About 60,000 different types of bacterial species have been estimated in the soil and each bacterium exhibits specific role and potential. Factors affecting population and the diversity of microbes in soil include organic carbon, temperature, moisture electrical conductivity, different chemicals and variety of flora found in particular environment. One can say soil-grown plants are present in ocean of microorganisms (Glick 2012). Recently many studies concluded microbial interactions important for survival of plants (Ma et al. 2016). Additionally, selection of microflora depends on the plants and their root exudates. Plants can interact with microbes through variety of chemicals or signals they release in the rhizosphere (Ma et al. 2016). The beneficial bacteria in agriculture are defined by their colonization ability around plant roots after seeds inoculating and their plant growth promoting effects. The interaction among plant soil and microbe for their mutual benefit is shown in Fig. 2.2.

2.7 Potassium Solubilization and Mobilization by PGPR

Plant growth promoting rhizobacteria (PGPR) are the microorganisms associated with roots of plants and make the nutrients available for proper growth and development of plants. This association is made possible through secretion of specific root exudates by plant roots that attract the microbes. These PGPRs regulate various biogeochemical cycling among which nitrogen, carbon, phosphorous, and potassium are the most important ones. Despite of sufficient levels of K in soil, its complex nature (biotite, orthoclase, muscovite, feldspar, illite, and mica) hinders its availability at sufficient level to plants. These complexes of potassium are mostly silicates that can be solubilized by most of the PGPR microorganisms. Microbes produce variety of organic and/or inorganic acids to degrade complex silicate minerals (Barker et al. 1997). In potassium-deficient soil, the increased exudation of roots is accompanied by accelerated microbial proliferation (Van Veen et al. 1989).

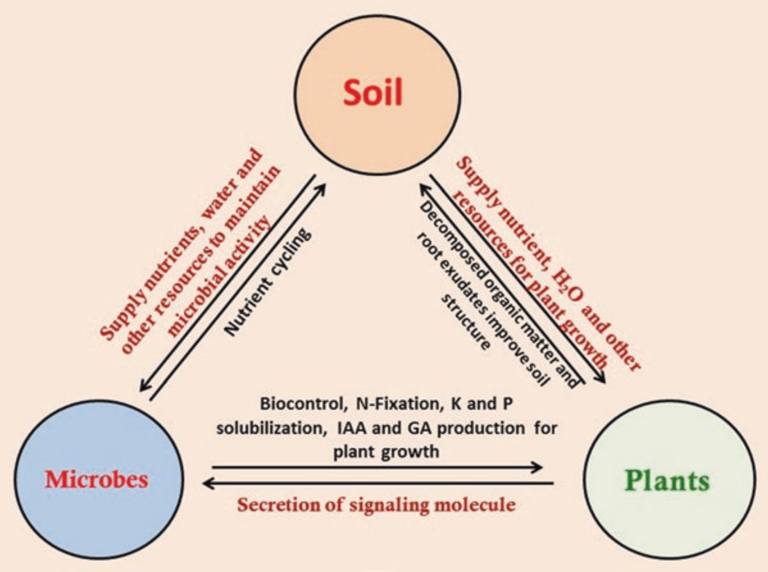

Fig. 2.2 Beneficial soil–plant–microbe interactions for mutual benefits

Few microbes produce enzymes that specifically help in mineral solubilization analogous to chitinase and celluloses (Barker et al. 1997).

Some of the organisms live freely (*i.e.,* planktonic) in solution, most of which bacteria attack the surfaces of minerals (Hazen et al. 1991; Holm et al. 1992), where they can affect surface chemistry, water-to-rock interaction, dissolution and precipitation of rock minerals, and hence the soil formation (Barker and Banfield 1998). Complete degradation of organic carbon by microbes elevates carbonic acid level at soil surface, minerals, and groundwater (Barker and Banfield 1998), which further affects rate of weathering. In addition, microbes excreted a variety of different organic acids during various processes like degradation or fermentation of organic macro-molecules, or as a response to nutrient stress (Paris et al. 1996). Different microorganisms involved in K solubilization are listed in Table 2.1.

2.8 Impact of KSB on Growth of Plants

All the crops mandatorily require nitrogen, phosphorus, potassium (NPK) macronutrients for rapid growth and development, and thus require addition of fertilizers. These chemical fertilizers not only provide enhanced crop production but also cause serious environmental hazards. Plant rhizosphere-associated microbes are found with great potential of promoting plant growth through solubilization of different minerals and improvement in nutrient uptake by plants. These PGPR include

Table 2.1 Microorganisms involved in potassium solubilization in soil

Microorganisms	References
B. mucilaginosus, B. circulanscan, B. edaphicus, *Burkholderia, A. ferrooxidans, Arthrobacter* sp., *Enterobacter hormaechei, Paenibacillus mucilaginosus, P. frequentans, Cladosporium, Aminobacter, Sphingomonas, Burkholderia*, and *Paenibacillus glucanolyticus*	Sheng and He (2005) and Meena et al. (2016)
Bacillus spp., *Enterobacter* spp., and *Pseudomonas* spp.	Gundala et al. (2013) and Dong et al. (2019)
Pseudomonas spp., *Burkholderia* spp., *Bacillus edaphicus*, *B. circulans, Paenibacillus* spp.	Liu et al. (2012) and Bagyalakshmi et al. (2017)
Aspergillus spp., *A. terries*	Prajapati et al. (2013)
A. niger	Lian et al. (2002) and Prajapati et al. (2012)
Penicillium sp.	Sangeeth et al. (2012)
Ectomycorrhizal fungi (UFSC-Pt22 and UFSC-Pt186)	Alves et al. (2010)
Arbuscular mycorrhizal (*G.mosseae* and *G. intraradices*)	Wu et al. (2005)
B. mucilaginosus	Zhao et al. (2008), Basak and Biswas (2009), and Zarjani et al. (2013a, b)
B. edaphicus	Sheng (2005)
B. circulanscan	Lian et al. (2002)
Burkholderia, *A. ferrooxidans*	Sheng and Huang (2002) and Sheng and He (2006)
Arthrobacter sp.	Zarjani et al. (2013a, b)
Enterobacter hormaechei (KSB-8)	Prajapati et al. (2013)
Paenibacillus mucilaginosus	Liu et al. (2012)
P. frequentans, *Cladosporium*	Argelis et al. 1993
Paenibacillus glucanolyticus	Sangeeth et al. (2012)
Aminobacter, *Sphingomonas*, *Burkholderia*	Uroz et al. (2007)
B. mucilaginosus sub spp. Siliceus	Aleksandrov et al. (1967)
Bacillus subtilis	Leaungvutiviroj et al. (2010)
Bacillus pseudomycoides strain O-5	Pramanik et al. (2018)
Janthinobacterium sp. (IARI-R-81), *Janthinobacterium lividum* (IARI-R-71), *Janthinobacterium* sp. (IARI-R-700	Muthukumarasamy et al. (2017)
Aspergillus. niger	Lopes-Assad et al. (2010)

phosphate-/potassium-solubilizing bacteria, N_2-fixing bacteria etc. that can be used as biofertilizers instead of chemical fertilizers. Major portion (90–98%) of total K in soil is mainly present in its insoluble form which is unavailable for plant uptake. Silicate minerals such as biotite and K-feldspars are the most common types available in the Earth's crust and supply inorganic form of nutrients in soils to maintain optimal nutrition for crops. The KSB could be used as potential alternatives along with rock K materials. Potassium is an essential nutrient regulating different crucial process in plants required for maintaining and supporting the plant growth.

Some of the effect of K nutrition on plant physiology can be presented as follows:

- The K nutrition plays key role in primary metabolism of plants. Activity of near 60 enzymes is regulated by K availability which is essential for sugar and nitrogen metabolism (Wyn Jones and Pollard 1983).
- The level of K helps to maintain the rate of photosynthesis (Peoples and Koch 1979; Bednarz and Oosterhuis 1999).
- K controls CO_2 fixation in chloroplast (Pfluger and Cassier 1977).
- It regulates activity of Ribulose Bisphosphate Carboxylase (RuBisCo) enzyme (Peoples and Koch 1979).
- Potassium controls the opening and closing of guard cell and hence regulates the transpiration rate (Blatt 1988).
- Potassium maintains osmotic gradient, pH, and voltage between phloem and parenchyma cells, essential for phloem transport.
- Potassium imparts rigidity and turgidity to cell walls (Marschner 1995).
- Potassium decreases the incidence of bacterial and fungal attack (Fuchs and Grossmann 1972; Perrenoud 1990).
- Potassium interacts with early defense response and enhances the jasmonic acid level (Shin and Schachtman 2004).
- Potassium assists in maintaining root nitrate transportase activity (Armengaud et al. 2004).
- Allocation of root born metabolite (e.g., amino acids and nitrate) in root: shoot (Graham and Ulrich 1972).
- Potassium helps in regulating the water potential in xylem vessels (Baker and Weatherley 1969).
- Potassium maintains the allocation and translocation of sugar through phloem (Ashley and Goodson 1972; Hartt 1969).
- Potassium deficiency causes increase in glutamine, aspartate, and glutamate levels (Yamashita and Fujiwara 1967).
- Synthesis of high molecular weight compounds (sugar, starch, and amino acids) is hindered during potassium deficiency (Marschner 1995).
- K deficiency leads to increased sugar and amino acids level (Marschner 1995).

2.9 Action Mechanisms of K Solubilization by KSB

Microorganisms help in release of K+ from complex K minerals through different mechanisms. Very few studies are available on action mechanisms of K solubilization by KSB (Table 2.2). The major mechanisms involved are production of inorganic and/or organic acids and H+ release (acidolysis mechanism) (Maurya et al. 2014). This helps in conversion of insoluble potassium (mica, muscovite, and biotite feldspar) to its soluble forms, easily uptake by the plants (Wang et al. 2000; Meena et al. 2014a, b). Several organic acids have also been reported for K solubilization such as 2-ketogluconic acid, tartaric acids, gluconic acid, succinic acid, oxalic acid, propionic acid, malic acid, lactic acid, citric acid, fumaric acid,

Table 2.2 Different mechanisms of potassium solubilization by microorganisms in soil

Mechanisms of K solubilization	References
Released of H^+ also known as acidolysis mechanism can directly dissolve the mineral K as a result of slow releases of exchangeable K	Maurya et al. (2014)
Production the organic and inorganic acids (oxalic acid, tartaric acids, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, lactic acid, propionic acid, glycolic acid, malonic acid, fumaric acid) also decrease pH and release K.	Meena et al. (2015a, b), Sheng et al. (2008), and Uroz et al. (2009)
Microbial decomposition of organic materials also produces ammonia and hydrogen sulfide that can be oxidized in the soil to form the strong acids such as nitric acid (HNO_3) and sulfuric acid (H_2SO_4).	Huang et al. (2013)
Chelation of Si^{4+}, Al^{3+}, Fe^{2+}, and Ca^{2+} ions with K minerals	Römheld and Kirkby (2010) and Štyriaková et al. (2003)
Production of various extracellular polymers (primarily proteins and polysaccharides) can also release of K from K bearing minerals. These substances serve as attachment structures to mineral or rock surface.	Shelobolina et al. (2012)
Naturally occurring polymers (exopolysaccharides) can affect the mineral dissolution probably by forming complexes with framework ions in solution.	Welch and Vandevivere (1994)
Biofilm formation on aluminosilicate increases the residence time of water as compared to the residence time at the bare rock or mineral surface and enhances the mineral weathering.	Meena et al. (2014a, b)
Production of indole acetic acid	Etesami et al. (2015)
Forming biofilm on rhizospheric mineral surface	Etesami et al. (2017)

malonic acid, and glycolic acid (Krishnamurthy 1989; Saiyad et al. 2015). Among these 2-ketogluconic acid, succinic acid, citric acid, tartaric acid, and oxalic acid are the major acids released by KSB (Meena et al. 2014a, b). Decomposition of organic matter by microbes may lead to the ammonia and hydrogen sulfide production that further gets oxidized in the soil to produce strong acids. Acidolysis helps to displace K+, from the insoluble part in the soil through cation-exchange method (Jones et al. 2003; Huang et al. 2013). In addition to decrease in soil pH, the organic acids secreted by KSB can also dissolve K ions from the complex minerals by chelation Si^{4+}, Al^{3+}, Fe^{2+}, and Ca^{2+} ions complexed with K minerals (Römheld and Kirkby 2010). Abou-el-Seoud and Abdel-Megeed (2012) reported the weathering of phlogopite mineral through aluminum chelation and acidification of the mineral's crystal structure by KSB.

Huang and coworkers (2013) reported the potential of *B. altitudinis* strain in dissolving potash feldspar by producing organic acids, with significant release of more Al, Si, and Fe elements. These bacteria also synthesized biofilms so as to create a microenvironment around microbial cells to carry out weathering (Meena et al. 2014a, b). Biofilm formation on aluminosilicate minerals increases the retention time for water in comparison to that in bare rock that enhances the weathering of minerals. It is now an accepted fact that the microbial biofilms in addition to accelerating the rock weathering also regulated the denudation losses, as it acts as a protective layer that covers the root–hair interface in any rhizosphere. Besides, biofilm formation on surface of mineral increases the corrosion of potassium shale and the release of Al, K, and Si (Man et al. 2014). KSBs when inoculated in soil, serve for different functions such as enhanced nutrient uptake, organic matter decomposition, K solubilization, and many other plant growth-promoting activities (Kloepper et al. 1991). Growth promotion of plants by KSBs can be through direct or indirect mechanisms.

Direct mechanisms involve P-solubilization, N_2-fixation, production of various plant growth hormones (Sheng and Huang 2001), organic acid production, and K solubilization (Park et al. 2003). However, indirect mechanisms enhance plant growth by siderophores production, antibiotics, starch hydrolysis, antifungal compounds, and cellulose degradation (Meena et al. 2014b). Through the combined effects these potential microbes support plant's growth and help them to combat the diseases. For example, some microbes release potassium, silicon, and aluminum through weathering of minerals and secrete phytohormones, which improves the defense by providing disease resistance and tolerance to external stresses to enhance plant growth, plant nutrition, and competitiveness (Lian et al. 2002). Thus, KSBs play important role in improving the fertility of soil and eventually promote plant growth (Rajawat et al. 2012). Numerous studies evaluated the impact of KSBs on plant's growth and K solubilization. Patten and Glick (1996) found positive impact on growth and yield of Brinjal after inoculated with *Bacillus mucilaginous* in the nutrient limited soil. Inoculation of seeds with KSBs showed significant improvement in yield, plant growth, seedling vigor, germination percentage, and uptake of K by plants under pot and field conditions (Anjanadevi et al. 2016; Zhang and Kong 2014). Lin et al. (2002) reported increase (150%) in K uptake after inoculating tomato plant with *B. mucilaginosus* strain RCBC13 as compared to control.

Furthermore, inoculation of KSB-HWP47 in wheat (*Triticum aestivum* L.) var. WH711 also showed 55.5% increase in dry weight of root after 60 days of sowing (Parmar 2010). Similarly, 44.3% increase in dry weight of shoot was observed in HWP47 inoculated plants. KSB application on sorghum also enhanced dry matter yield by 65.0%, 48.0%, and 58.0%; and potassium uptake by 93.0%, 41.0%, and 79.0% in sandy, clay, and calcareous soils, respectively (Badr et al. 2006). Previous reports showed various positive effects on eggplant (Han and Lee 2005), rape and cotton (Sheng 2005), wheat (Sheng and He 2006), peanut (Youssef et al. 2010), cucumber and pepper (Sangeeth et al. 2012), maize (Abou-el-Seoud and Abdel-Megeed 2012), tea (Bagyalakshmi et al. 2012), potato (Abdel-Salam and Shams 2012), Sudan grass (Basak and Biswas 2009; 2010), tomato (Lynn et al. 2013), and okra (Prajapati et al. 2013) on inoculating with KSBs. Hence, above reports indicate that the application of KSB for agriculture benefits can reduce the chemical fertilizer's use and support environmentally friendly crop production (Archana et al. 2013). Less awareness among the farmers and higher prices of K fertilizers worsens the situation. Rhizospheric microbes have shown significant contribution toward K solubilization through their specialized mechanisms. Several studies proved that K content in plant and soil increased when inoculated with KSBs that further result in better plant growth and resistance to different biotic and abiotic stresses. In addition, with K solubilization KSBs are also known to possess various other plant growth-promoting attributes.

2.10 Challenges and Potentialities of KSB in Industry

Potassium solubilizers increase its availability by increasing the weathering processes using different action mechanisms, especially during a direct contact with the surface of mineral (Meena et al. 2016). Although KSB could serve as good alternatives to solubilize potassium from its insoluble to soluble form, their use in agricultural practice is still prevented due to several factors. For example, (1) slow effect on yield improvement of crop, (2) less interest in KSB amongst the scientific community, (3) insufficient awareness amongst the farmers, (4) loss of efficient stains restrict the development of culture collection, and (5) and poor technology for product formulations. These are some of the major limitations of the industry, which need to be improved in the near future.

2.11 Conclusion and Future Perspectives

Generally, K solubilization via microorganisms is strongly affected by different factors such as oxygen, pH, kinds of K minerals, and the bacterial strains. Thus, the optimal conditions required for K solubilization through KSB need to be assessed in the future. Study regarding KSB is very scarce under the field conditions, which may be due to difficulties while soil inoculation in field conditions. The results in greenhouse or under in vitro conditions may differ from field results. Therefore, further field studies need to be done for (1) the assessment of potential in such techniques and their evaluation for better agricultural production and soil health; (2) to study the impact of KSB on the availability of other nutrients such as N, P, Zn, Fe, etc., as affected by pH; (3) the effect of other PGPRs on KSB must be studied such as ACC deaminase producers, IAA producers, phosphate solubilizers, and N_2 fixers on the availability of K; (4) to study the interactions between KSB and other PGPRs for increased availability of K; (5) assessment of optimal growth conditions for better KSB activity; (6) assessment of different plant species for their effectiveness in K uptake and KSB populations. The interaction of KSB with different plants in different location should be studies to understand the suitability of bacteria for different plant type in a given situation; (7) the inoculant survivability in the soil and extensive evaluation of soil properties before being finally inoculated; and (8) basic research of KSB at molecular level also requires more attention. Taken all together, large-scale, well-designed, and long-term field trials are necessary to study the feasibility of KSB application to increase the K availability.

KSMs are crucial component of soil and these KSMs have huge potential for not only increasing the availability of K but also causing its slow release. The K solubilization mechanism by microorganisms is a complex phenomenon that is influenced by different factors, such as nutritional status of soil, KSMs used, mineral type, soil, amount, and size of mineral and other environmental factors. However, the stability of the KSMs after inoculation in soil is another also crucial factor responsible for crop growth and development. Another big problem is the multiplication of potassium-solubilizing consortium at commercial scale, their storage, preservation, and also transportation at farmer's fields for crop production. Therefore, a crucial need for further study is required to understand the exact issue for development of indigenous and potent potassium-solubilizing microbial consortium for improvement in growth and yield of crops.

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Chapter 3
Zinc Solubilization and Mobilization: A Promising Approach for Cereals Biofortification

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Abstract Plants are an important component of the ecosystem and vital for survival of human beings. As human beings need nutrition for their proper growth and development, plants also require different nutrients to complete their life cycle. Among the all essential nutrients, zinc is one of the important nutrients required not only by plants but also by human beings. Several researchers have reported the decline in zinc level of Indian soils. An approx. 47–49% of Indian soils are facing zinc deficiency, which is continuously rising up. The deficient soils are not able to supply the crop the required amount of nutrients, since soils with zinc deficiency are unable to provide an adequate amount of nutrients. The cereal crop like rice is prone to face zinc deficiency worldwide. Keeping in view such global crop issues, a greater attention is required to fulfil the zinc requirement of crop by different agronomic and plant breeding approaches. Zinc biofortification becomes one of the promising strategies to supply zinc in the crop at an optimum level. Zinc solubiliza-

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tion and mobilization are one of the suitable strategies to overcome zinc-deficiency issues. The chapter has emphasized on mechanism of biofortification and its challenges and limitations for adoption at ground level.

Keywords Biofortification · Cereals · Crop nutrition · Zinc solubilization · Zinc

3.1 Introduction

Human beings, animals, and other living organisms require an appropriate quantity of nutrients for their survival and proper growth and development. The essential nutrients are also required by the plants for their proper growth and metabolic activities. The deficiency of any nutrient leads to inappropriate growth of plants as well as humans (Newell-McGloughlin 2008). Micronutrient deficiency or hidden hunger hinders the development and improvement of crops and inhabitants. Soil micronutrients can improve the profitability of plants and feed people (Sanchez and Swaminathan 2005). Most soils in sub-Saharan Africa are plagued by various nutrient deficiencies along with N; P; K; secondary nutrients S, Ca, and Mg; and Zn, Fe, Cu, Mn, Mo, and B micronutrients (Vanlauwe et al. 2015). Zinc (Zn) is a necessary micronutrient for all living livelihood including microorganisms, plants, and humans for their metabolic activities. The Zn deficiency in plants decreases photosynthesis and nitrogen metabolism and causes decreased flowering, fruit production, phytohormone production, reduced carbohydrate synthesis, and delayed crop maturity, resulting in decreased crop yield and dietary performance of grains (Yadav et al. 2017; Mumtaz et al. 2017). Biofortification is the measure by which agricultural practices, traditional plant breeding or existing biotechnology boost the nutritional quality of food crops. Biofortification differs from normal fortification in that biofortification aims to increase additional harvest levels during crop production rather than by manual methods during yield handling.

Biofortification is the production of higher micronutrient rates of sustenance crops. Impressive progress has been made over the last two decades for

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biofortification (Bouis et al. 2017). Biofortification normally includes utilizing conventional breeding to choose for sustenance-related qualities that will enhance the yield's micronutrient content (Nestel et al. 2006). However, in addition, biofortification also includes transgenic methods, in which genes are shifted from one species to a different species to boost micronutrient content (Blancquaert et al. 2017). Eventually, a significant foliar and soil application of micronutrients containing fertilizers can also achieve agronomic biofortification, resulting in increased nutrient uptake by the crop (Cakmak and Kutman 2018). The commonly used Zn fertilizers in agriculture with their nutrient content are depicted in Table 3.1.

Table 3.1 Commonly used Zn fertilizers with their nutrient content

Compound	Zn content (%)	
Inorganic compounds		
Zinc sulphate monohydrate	33	
Zinc sulphate heptahydrate	21	
Zinc oxysulphate	20–50	
Zinc oxide	50–80	
Zinc carbonate	50–56	
Zinc chloride	50	
Zinc nitrate	23	
Zinc phosphate	50	
Zinc frits	10–30	
Organic compounds		
Disodium zinc EDTA	8–14	
Sodium zinc HEDTA	6–10	
Sodium zinc EDTA	9–13	
Zinc polyflavonoid	5–10	
Zinc lingosulphonate	5–8	
Fortified fertilizers		
Zincated urea	2	
Zincated phosphate (suspension)	17.6	
DAP with 0.5% zinc	18: 46: 0: 0.5	
NPK with 0.5% zinc	10: 26: 26: 0.5	
Water-soluble complex fertilizer		
NPK with 3.5% zinc-EDTA	7.6: 23.5: 7.6: 3.5	
Customized fertilizers		
Nutrients	Nutrient content	Specifications
N:P:K:S:Zn	11: 24: 6: 3: 0.5	Manufactured by Nagarjuna fertilizers and chemicals for rice crop in Telangana district of Andhra Pradesh

Source: Alloway (2008), Das and Green (2013), Brouwer (2010) and Das et al. (2018)

3.2 Zinc Solubilization and Mobilization

In India, if we talk about agricultural soils, there are approximately more than 50% of soils which are Zn deficient. Any method to improve zinc uptake and its transportation to grain has a significant practical consequence (Kabata-Pendias 2000). Zinc is one of the nutrients which are compulsory for the plants even in small quantity. Generally, plants absorb Zn from soil solution (Reed and Martens 1996). At global concern, the Zn deficiency in the crop might be due to low or less solubility of Zn, rather than Zn availability in soil (Iqbal et al. 2010). It is estimated that approximately 50% of the Indian soils are zinc deficient which is a matter of worry. Zn deficiency is correlated with several factors depending on the soil circumstance such as at high pH (>7.0) solubility of Zn reduces. The application of zinc to agriculture fields by zinc sulphate (soluble) gets transformed to altered insoluble forms like $Zn(OH)_2$ at high pH soil, $ZnCO_3$ in calcium-rich alkali soils, zinc phosphate in near neutral to alkali soils with huge application of P fertilizers and ZnS under reducing conditions particularly during flooding (Sarathambal et al. 2010). These details advocate that the solvent type of Zn fertilizer connected to the fields turns out to be promptly insoluble structures that can't be acclimatized by plants, prompting the Zn inadequacy in harvests (Yadav et al. 2020). The Zn deficiency could be surmounted by utilization of Zn manures in the fields, yet for the most part concoction composts are in all respects expensive and have an unfavourable impact on the condition. In this form, to defeat this circumstance eco-friendly and cost-effective methodologies are required.

Zn solubilization by the different soil microorganisms has better perspectives as compared to chemical fertilizers. The use of advantageous microorganisms in sustainable agriculture and soil reestablishment is getting enormous interest. In the modern era, solubilization of insoluble Zn compounds [ZnO, $ZnCO_3$, Zn_3 $(PO_4)_2$] by plant growth-promoting rhizobacteria (PGPR) has been identified by Krithika and Balachandar (2016). The application of ZSB (Zn-solubilizing bacteria) enhances the availability of native zinc for plant adaptation and eventually plant growth and development (Rana et al. 2019; Verma et al. 2013, 2014, 2015).

3.3 What Is Biofortification?

Present agriculture practices are able to fulfil the food requirements of the low-income population in developing countries. The cereal production has been the main focus in agriculture research from the last 40 years. Nowadays, there is a transformation in agriculture research; focus is not only on production to feed the hungry population but also on the production of nutritive food to reduce the hidden hunger of the population. Due to lack of proper nutritive food, i.e. lack of vitamins, minerals, proteins, etc. in their food, one-third of the population of the world is suffering from hidden hunger, which causes health problems to them (Kennedy 2016). The main target of biofortification is to increase nutrient content in an edible portion of the food plants. The large population of the world uses cereals as a staple food, but cereals are having a low content of zinc and other essential nutrients required by the body.

The big problem in plant biofortification is the root-shoot barrier and grain filling process in cereals. As per new findings, the zinc distribution in root-shoot is mainly governed by heavy metal transporting P1B-ATPases and the metal tolerance protein (MTP) family. Good knowledge about the zinc transport system will help scientists to improve the nutrient level in crops and reduce the accumulation of toxic metals. Biofortification is the approach of breeding to increase nutrients into food crops, providing a comparatively cost-effective, sustainable, and long-term means of delivering more micronutrients. It will not only increase the nutrition in the food of severely malnourished population of the world but also reduce the number of malnourished people in the world who are treated by food supplements for their malnutrition. Further, for the poor and rural people who have very little access to the fortified foods and supplements available in the urban markets, biofortification also provide economical ways to reach them.

“Biofortification” or “biological fortification” means the use of breeding methods, agronomic practices, biotechnological approach and other latest techniques to produce nutrient-rich food crops in a way that they can be available to a large population of the world. The effect of different agronomic management practices in increasing Zn concentrations is given in Table 3.2.

3.3.1 Implementing Biofortification

To show that biofortification can be fruitful, specialists completed a progression of exercises along the effect pathway, characterized into three periods of revelation, advancement, and conveyance, which have been portrayed in detail (Bouis et al. 2017; Saltzman et al. 2013). Throughout the most recent 15 years, biofortification research exhibited that a significant piece of the general arrangement is to improve the profitability of an extensive rundown of nonstaple sustenance crops. A modified flow impact path of breeding approach for biofortification is presented in Fig. 3.1.

The achievement of this objective requires an exceptionally enormous venture, the components of which are not tended here.

For biofortification to be fruitful, three expansive inquiries must be taken into consideration:

- Can breeding enhance the micronutrient uptake in sustenance staples to achieve target levels that will have a quantifiable and noteworthy effect on nourishing status?
- When consumed under controlled conditions, will the extra nutrients bred into the food staples be bioavailable and absorbed at sufficient levels to improve micronutrient status?
- Will ranchers become the biofortified assortments and will customers purchase and eat them in adequate amounts?

Table 3.2 Effect of different agronomic management approaches in increasing Zn concentrations

Treatments	Percent increase over control		Source
0.5% $ZnSO_4.7H_2O$ foliar spray at stem + booting stage of wheat	80 kg N ha^{-1}	59.37%[a] 82.6%[b]	Cakmak et al. (2010)
	240 kg N ha^{-1}	56.75%[a] 44.82%[b]	
0.5% $ZnSO_4.7H_2O$ foliar spray at booting + milk stage of wheat	80 kg N ha^{-1}	75%[a] 113.04%[b]	
	240 kg N ha^{-1}	51.35%[a] 89.65%[b]	
0.5% $ZnSO_4.7H_2O$ foliar spray at milk + dough stage of wheat	80 kg N ha^{-1}	78.12%[a] 91.30%[b]	
	240 kg N ha^{-1}	72.97%[a] 75.86%[b]	
0.5% $ZnSO_4.7H_2O$ foliar spray at booting + anthesis + milk stage of wheat	80 kg N ha^{-1}	81.25%[a] 130.43%[b]	
	240 kg N ha^{-1}	75.67%[a] 106.89%[b]	
0.5% $ZnSO_4.7H_2O$ foliar spray at stem + booting + milk + dough stage of wheat	80 kg N ha^{-1}	103.12%[a] 143.47%[b]	
	240 kg N ha^{-1}	89.18%[a] 117.24%[b]	
Soil Zn at 50 kg $ZnSO_4.7H_2O$ ha^{-1}	5.7% in unhusked rice		Phattarakul et al. (2012)
	2.4% in brown rice		
	0.9% in white rice		
Foliar Zn at 0.5% $ZnSO_4.7H_2O$ solution	65.5% in unhusked rice		
	24.7% in brown rice		
	10.4% in white rice		
Soil + foliar Zn application	73.6% in unhusked rice		
	31.9% in brown rice		
	15.1% in white rice		
Soil application at 20 kg $ZnSO_4.7H_2O$ ha^{-1}	17% in brown rice		Saha et al. (2013)
Soil + foliar application (2 sprays at pre flowering and grain formation stage) at 0.5% $ZnSO_4.7H_2O$ solution	95% in brown rice		
Alternate wet and dry cycle (here increase is in respect of continuous flooding treatment)	2.0 to 3.9% in brown rice		Wang et al. (2014)
	13.8 to 15.5% in polished rice		
$ZnSO_4.7H_2O$ (5 mg kg^{-1})	10.6% in brown rice		
	6.3% in polished rice		
Zn-EDTA (5 mg kg^{-1})	7.5% in brown rice		
	6.6% in brown rice		
Water regime × zinc treatment interaction effect	Not significant in brown rice		
	Significant in polished rice		

[a] Cukurova University Research Farm in Adana

[b] Black Sea Agricultural Research Institute in Samsun (Das et al. 2018)

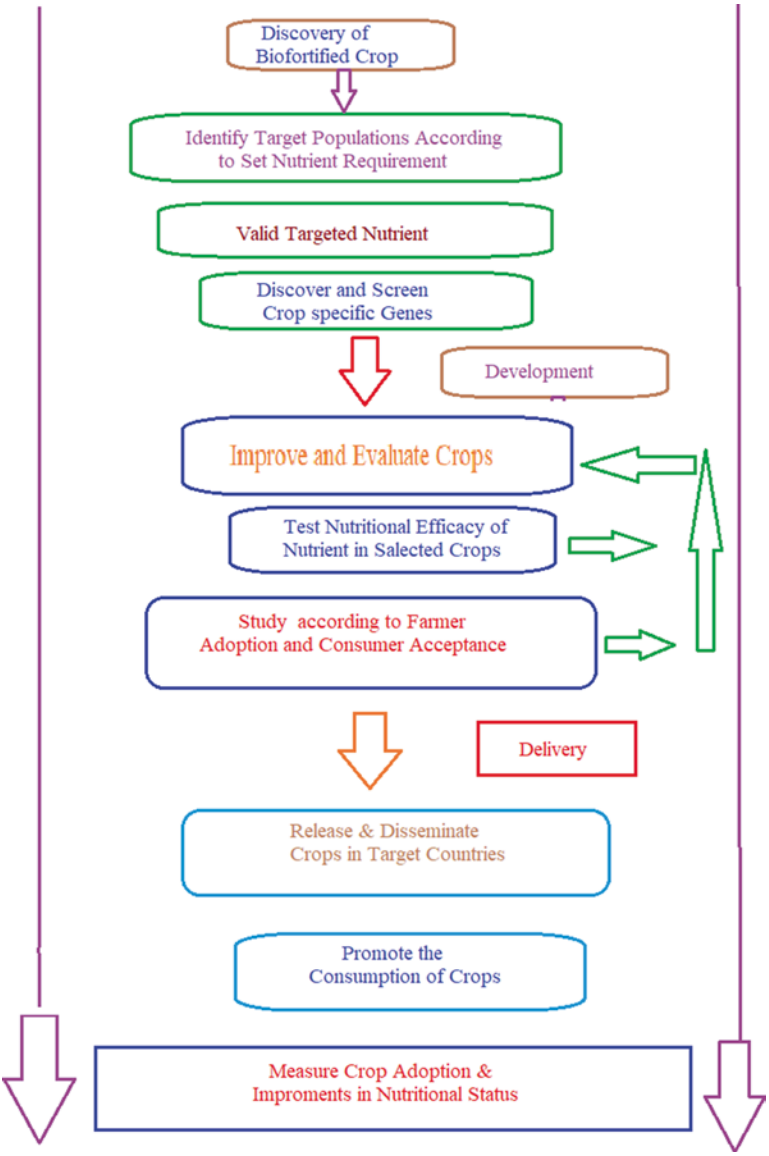

Fig. 3.1 Flow impact path of breeding approach for biofortification. (Modified figure of Saltzman et al. 2013)

A significant part of the proof accessible to address the above three inquiries has been produced under the HarvestPlus program. Reap Plus leads a worldwide interdisciplinary coalition of research organizations and executing offices in creating biofortified assortments of rice, wheat, maize, cassava, pearl millet, beans, and sweet potato. Under HarvestPlus, rearing targets are set with the end goal that, for preschool youngsters 4–6 years of age and for non-pregnant, non-lactating ladies of regenerative age, the gradual measure of iron will give roughly 30% of the Estimated Average Requirement (EAR); steady zinc will give 25% of the EAR; and steady ace nutrient A will give 50% of the EAR. Bioavailability of iron was initially thought to be 5% for wheat, pearl millet, beans, and maize (10% for rice, cassava, and sweet potato), that of zinc 25% for every staple yield, and for master nutrient A 8.5% for every single staple harvest (12 μg of beta-carotene produce 1 μg of retinol, the type of nutrient An utilized by the body) (Hotz and McClafferty 2007). To address these inquiries, scientists must do a progression of exercises characterized in three periods of disclosure, advancement, and scattering. This impact pathway is illustrated in Fig. 3.1 (Bouis et al. (2017)).

3.3.1.1 Discovery

The extent beyond cropping patterns, expenditure trends, and prevalence of micronutrient undernourishment, as well as cost-benefit analyses, determine target populations and focus crops. Nutritionists then work with breeders to establish nutritional breeding targets. These objective levels consider the normal sustenance admission and constant nourishment utilization examples of target populace gatherings, supplement misfortunes during capacity and preparing, and supplement bioavailability (Hotz and McClafferty 2007). Under HarvestPlus, rearing targets are set with the end goal that, for preschool youngsters 4–6-year-old and for non-pregnant, non-lactating ladies of regenerative age, the gradual measure of iron will give around 30% of the Estimated Average Requirement (EAR), that steady zinc will give 40% of the EAR, and that gradual expert nutrient A will give half of the EAR. Bioavailability of iron was initially thought to be 5% for wheat, pearl millet, beans, and maize (10% for rice, cassava, and sweet potato), that of zinc 25% for every single staple harvest, and for expert nutrient A, 8.5% for every staple yield (12 atoms of beta-carotene produce 1 molecule of retinol, the type of nutrient An utilized by the body).

3.3.1.2 Dissemination

Biofortified crops must be largely unconfined in the target countries prior to their delivery to the target populations. Economists lead consumer acceptance, varietal adoption, and seed and grain value chain studies is required to have an effective, efficient, and targeted delivery and marketing strategies in order to maximize adoption and consumption of these crops (Table 3.3).

3.3.1.3 Development

The development of new improved varieties requires all breeding methods. International Research Institutes of the specific crops initiate the development of nutrient-rich high-yielding varieties as well as some additional favoured buyer

Table 3.3 Product release of biofortified crops

Crop	Nutrients	Countries of first release	Agronomic trait	Release year
Wheat	Zinc, iron	India, Pakistan	Disease and lodging resistance	2013
Rice	Zinc, iron	Bangladesh, India	Disease and pest resistance, cold and submergence tolerance	2013
Maize	Provitamin A	Zambia, Nigeria	Disease resistance, drought tolerance	2012
Pearl millet	Iron, zinc	India	Mildew resistance, drought tolerance	2013

characteristics. After the development of varieties with the desired characteristic, they are tested at the national or regional level, and after these tests, the best promising varieties are selected and provided to the government of these nations for release in their country or area. When promising high-yielding, high supplement lines rise, they are tried by national research accomplices and the best performing lines they chose to submit to national governments for discharge. The formal discharge procedure differ from nation, however, a variety is developed and assessed in a few unique areas (called multi-location trials) for at least two crop seasons, and its performance is compared with established varieties. After that, the national government releases the variety. The whole process can take 6–10 years from development to release of a variety. Other than crop development, parallel research is also conducted to assess the variety about their nutrient retention under storage, post-harvest, and cooking processes and bioavailability to humans. Firstly, their nutrient's absorption is tested under in vitro and in vivo using animals. The best variety derived from these tests is directly tested on a human under controlled conditions. Randomized, efficacy trials show the effect of biofortified crops on hidden hunger on micronutrients, and it is proving as an alternative to provide micronutrient to undernourished people of the third world.

3.4 Type of Biofortification

3.4.1 Transgenic Biofortification

When there is very low or no genetic variation is available in the crop, the transgenic approach of biofortification can provide a way to develop biofortified varieties (Brotanek et al. 2005). This method can harness vast genetic content available in nature through the transfer and expression of desired genes from species to another species, which could be not related to the desired crop. In addition to this, we can also add a micronutrient in the crop which is not naturally present in that crop by transgenic methods (Pérez-Massot et al. 2013). The key to the success of transgenic crops is to identify and characterize the function of a gene and utilize it to make a desirable change in plant metabolism. Moreover, many bacterial and viral genes are also transferred in crops to get required pathways for metabolic engineering.

These methods can also be utilized for the parallel addition of genes that are required for the development of micronutrient concentration, their bioavailability, and reduction in the antinutrients which reduce the bioavailability of nutrients in plants. Further, transgenic methods can also be used to develop varieties in which more micronutrients will be available in the edible portion of the commercial crops, by increasing the biochemical activities in edible tissues or development of new pathways (Agrawal et al. 2005). At first, these methods require a lot of time, hard work, and money during research and development stage, but in the end, it is a most feasible and sustainable approach, unlike nutrition and agronomic biofortification programs.

There are various crops in which micronutrients are enhanced by a transgenic approach. Various transgenic crops have been developed using inter- and intraspecies genes to enhance micronutrients especially essential amino acids, vitamins, minerals, and essential fatty acids. Examples of some of genes that are specific under biofortification are lycopene, carotene desaturase, β-cyclase and *PSY* for vitamins; Nicotinamide synthases and ferritin for minerals and for essential amino acids, albumin.

3.4.1.1 Transgenic Rice

Rice is the main targeted crop to cure malnutrition on the world level. The main challenge for the undernourished population is vitamin due to its high cost. Golden rice was an effective tool to reduce vitamin A deficiency disease as it provides provitamin A (beta-carotene) by expressing genes encoding *PSY* and carotene desaturase (Datta et al. 2003; Iqbal et al. 2010). By encoding 23-fold enrichment in beta-carotene precursor, i.e. phytoene is reported similarly for anaemia and pregnancy vitamin B9 (folic acid) (Naqvi et al. 2009). About 150-fold foliate content is enhanced by *Arabidopsis* GTP-cyclohydrolase (Blancquaert et al. 2015). Increasing Fe content by encoding, nicotianamine amino transferase (NAAT) (Takahashi et al. 2001), Iron transporter *OsIRT1* (Lee and An 2009), 1 (*OsNAS1*) and 2 (*OsNAS2*) (Drakakaki et al. 2005) has been reported. Similarly in barley, mugineic acid gene synthesis from [*HvNAS1*] has been done (Masuda et al. 2008).

3.4.1.2 Transgenic Wheat

Wheat is one of the most broadly grown staple sustenance crops on the planet. Analysts have attempted to address the difficulties of most inadequate supplements like nutrient iron and quality proteins through wheat. Provitamin has been improved by [*CrtB, CrtI* (Cong et al. 2009)]. Resistant amylose starch has been enhanced SBE [*SBEIIa* (Sestili et al. 2010)].

3.4.1.3 Transgenic Maize

Maize is one of the significant staple foods in creating healthy nations, and it has been tended for nutrients, minerals, and quality protein and against supplement parts by methods for hereditary building. Endosperm of maize has been advanced with provitamin A (Decourcelle et al. 2015). Tocopherol and tocotrienol content in maize improved by the HGGT (homogentisic acid geranylgeranyl transferase) (Cahoon et al. 2003). Vitamin C (L-ascorbic acid) which is soluble in water component has antioxidant properties that have a significant role in cardiovascular function (heart-related) as well as utilization of iron and immune cell development (Levine et al. 1995). By the expression of dehydroascorbate reductase, the level could be improved as shown in study of Naqvi et al. (2009). Micronutrient bioavailability is slowed down by antinutrient components. Iron bioavailability can be increased by expressing soybean ferritin and *Aspergillus* phytase, soybean ferritin, and *Aspergillus niger phyA2* (Chen et al. 2008) and reducing the appearance of ATP binding cassette transporter and multidrug resistance-associated protein (Shi et al. 2007).

3.4.1.4 Transgenic Barley

Emphasis is given to developing high micronutrient varieties of barley because it is a model cereal crop. The zinc content of barley is increased through the overexpression of zinc transporters (Ramesh et al. 2004). Phytase activity has been increased in barley seeds to improve the bioavailability of iron and zinc, by expression of the phytase gene (*HvPAPhy*_a). Lysine which is an essential amino acid is also increased in barley by expressing the DHPS gene [*dapA* (Ohnoutkova et al. 2012)]. The β-glucan level has been enhanced in barley by overexpression of cellulose synthase-like gene [*HvCslF*] which helps the human body to reduce the risks of serious human diseases such as cardiovascular disease and type II diabetes (Burton et al. 2011). Amylose which is a resistant starch has been produced in barley through RNAi approach in which all genes coding for SBE [*SBE I*, *SBEIIa*, *SBEIIb*] has been suppressed. Polyunsaturated fatty acids, γ-linolenic acid, and stearidonic acid (STA) have been improved in barley by expressing Δ^6-desaturase [*D6D*] which are very good for human health. Other than above-mentioned qualities, many medicinally and industrially important biochemicals including enzymes and antibiotics have been expressed in barley.

3.4.1.5 Transgenic Sorghum

Sorghum belongs to millions of poor rural people as their important staple foods. It is a hardy crop that can grow well in adverse environments. Emphasis has been given to increase provitamin (beta-carotene) by expressing *Homo188-A* (Lipkie et al. 2013) in sorghum. Lysine content which is an essential amino acid has been enhanced in sorghum by the introduction of a high lysine protein [HT12 (Zhao et al. 2003)]. One of the issues with sorghum consumption is that its grains are less digestible than the other major staple crops. The seed storage proteins and γ-kafirin of sorghum are resistant to protease digestion due to which it is less digestible than the other major staple crops. Its digestibility index has been improved in transgenic sorghum by RNAi silencing of the *γ-kafirin* and combined suppression involving three genes [*γ-kafirin-1, γ-kafirin-2*, and α-*kafirinA1*] (Grootboom et al. 2014)].

3.4.2 Agronomic Biofortification

Biofortification of crops with agronomic methods is done by the application of nutrients in crops which temporarily improve the nutritional and health status of crops and thus by consumption of these crops improves the nutritional status of humans (Cakmak and Kutman 2018). The organic forms of minerals are easily absorbed in the human body as compared to inorganic forms, as the organic forms are more available to humans; and their toxicity symptoms are less intensive and are less excreted. Agronomic biofortification mostly depends on the application of fertilizers and increment in the solubilization and mobilization of fertilizers from soil to edible parts of plants. The agronomic biofortification concept is presented in Fig. 3.2.

Agronomic biofortification has been so far most effective with Zn and Se (Cakmak 2014). This improved the Se intake of the nation to well above nutrition recommendations. Nowadays, the main target of research is Zn, as it is the most prevalent deficiencies in humans and an important limiting factor in crop yield.

It has been found that Zn fertilization in crops increases both yields and nutritional quality of crops. In Turkey, it has been reported that several portions of cereal (maize, sorghum, barley, wheat) and dicotyledonous (soybean, safflower, pea, common bean, canola, common vetch) crops showed increased yields and grain Zn concentrations by Zn fertilization (Cakmak et al. 2010). It was found that by soil and foliar Zn application, there has been a threefold increase in yields and Zn concentrations in wheat. The same results also showed that in India, yields and Zn concentrations in grain increased three times in rice by field application of Zn (Cakmak 2009). Apart from the above-mentioned benefits, another agronomic benefit is that plants with high Zn concentration have better growth performance and are more resistant to adverse climatic conditions; it increases the productivity also for next cropping generation. Moreover, P uptake and the accumulation of phytate in grains are reduced by Zn fertilization, which may increase the Zn bioavailability for humans (Yadav et al. 2018).

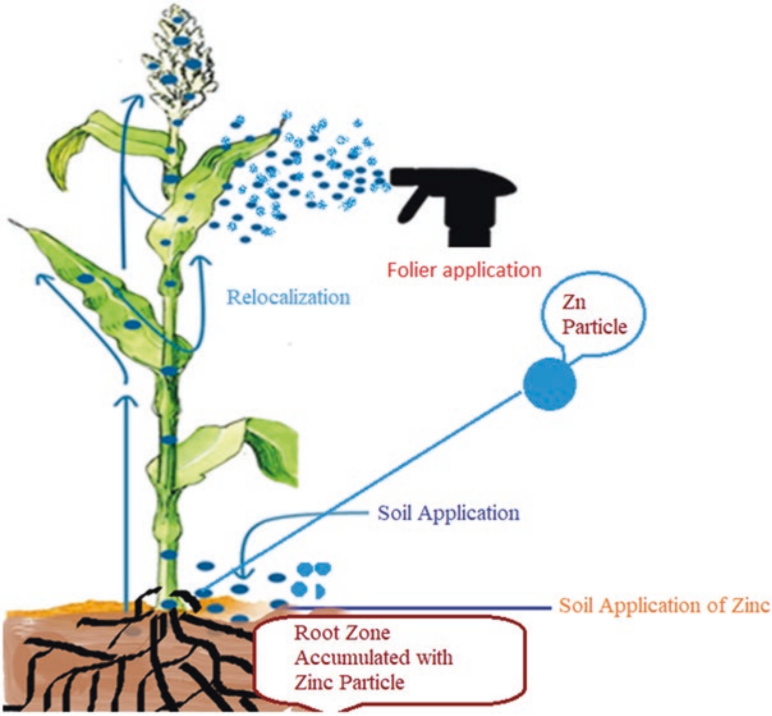

Fig. 3.2 Agronomic biofortification is the application of micronutrient containing zinc mineral fertilizer in blue circles. (Modified figure of de Valença et al. 2017)

3.4.2.1 Rice Agronomic Biofortification

Rice is a most significant agronomy crop; micronutrient biofortification by the agronomical practices is an elective methodology to decrease the iron and zinc deficiency in rice grain Cakmak (2010). The biofortification of rice plants by foliar spray of iron was a viable method to promote iron fixation in rice grains (Yuan et al. 2013). The application of zinc as foliar has been reported as an efficient agronomic practice to encourage zinc concentration in rice grain and also zinc bioavailability (Wei et al. 2012). The zinc concentration in the unhusked grain of different varieties of rice grown with different Zn fertilizer is presented in Fig. 3.3. The application of zinc fertilizer as foliar spray proves to be a significant approach to boost the grain zinc content with low background levels of zinc (Guo et al. 2016).

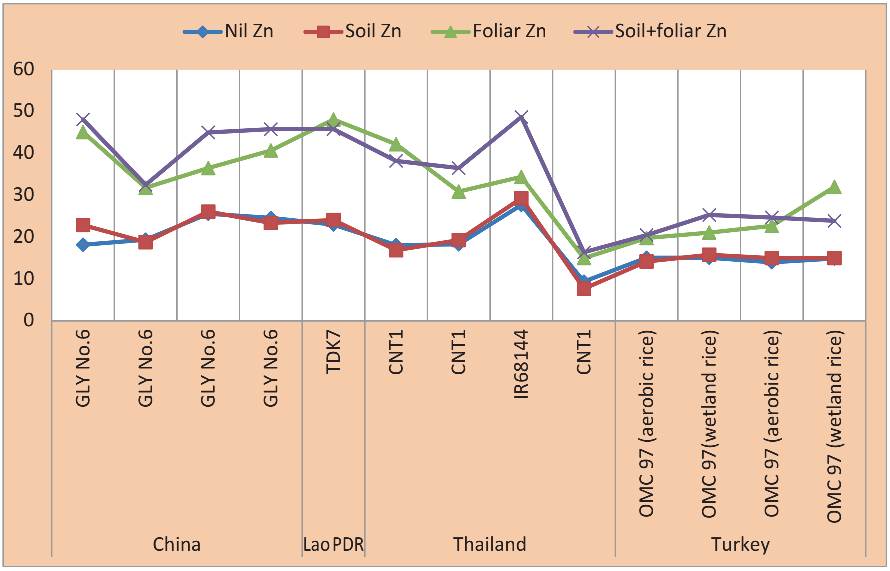

Fig. 3.3 Zinc concentration (mg kg^{-1}) in a un-husked grain of different varieties of rice grown with different Zn fertilizer treatments in four countries (Das et al. 2018)

3.4.2.2 Wheat Agronomic Biofortification

Biofortification, by the agronomic approach is one of the best ways to economically increase quality of the wheat. Application of iron as foliar is one of the suitable practice to enhance positively correlated high iron accumulation in the plant. The foliar application of zinc also reduces the human zinc deficiency in the region where zinc deficiency is potentially occurring. Simultaneously, it also reduces the antinutrient factor, viz. phytic acid. A global estimate of phytic acid content of cereal grains and legume seeds is presented in Fig. 3.4.

Considering the present era, the use of zinc-containing fertilizers is improved. The zinc concentration in the grain is obviously contributed to human nutrition and health, especially in rural areas, where malnutrition problem is occurring or we can say where wheat provided more than 50% of the daily calorie intake (Cakmak 2008). Besides chemical and organic fertilizers, the scientist has also investigated that significant application of biofertilizers also improved the yield of grains. Mycorrhizal fungi along with organic and inorganic fertilizers are comprehensively being used for biofortification.

3.4.2.3 Maize Agronomic Biofortification

Considering all micronutrients, zinc is one of the elements which is crucially required for maize to enrich the grain as well as yield. For attaining proper growth and development, the plant requires an optimum zinc concentration. For achieving

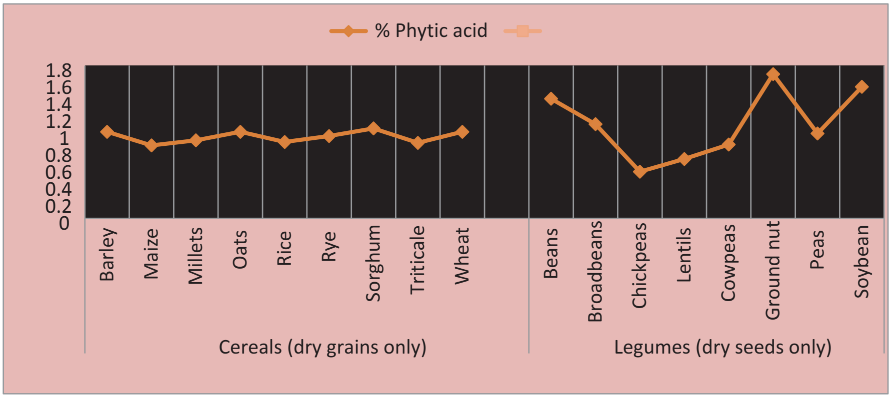

Fig. 3.4 A global estimate of phytic acid content (%) of cereal grains and legume seeds (Lott et al. 2000; Das et al. 2018)

the properly required concentration by the plant, the foliar application is one of the steps to overcome zinc deficiency situation in maize crop (Wang et al. 2012). The PGPR (plant growth-promoting rhizobacteria) is also considered to play key role for proper fortification in the plant. This comes under the agronomic approaches. This could be considered as effective biofortification strategies for staple crops. For example, maize is one of the effective examples with increased zinc content (Prasanna et al. 2015).

3.4.2.4 Barley Agronomic Biofortification

The profile of micronutrient in case of barley has been (improved) superior by the appliance of a variety of organic and inorganic biofertilizers. The zinc and iron concentration in grains can be improved by the appliance of biofertilizers along with the intervention of inorganic fertilizers and the vermicompost.

3.4.2.5 Sorghum Agronomic Biofortification

Sorghum crop is civilized or cultivated worldwide for grain and fodder (mainly animal feeding). Sorghum is generally affected by the challenge of growing in nutrient-deficient soil or contaminated soil. The nutrient profile for sorghum crop has been enhanced by the application of fertilizers (both organic and inorganic) that will have a preservative effect on the yield or crop outcome. The innovative scientist has planned to get better nutrient uptake and change the metabolic profile of sorghum by the intervention of PGPR (plant growth-promoting rhizobacteria) and AMF (arbuscular mycorrhizal fungi). The sole *Azospirillum* inoculation along with PSB (phosphate solubilizing bacteria) improved sorghum grain yield simultaneously and protein content as well by improving the addition of phosphorus and nitrogen in the soil (Patidar and Mali 2004).

3.4.3 *Breeding Approach in Biofortification*

The breeding approach is very efficient in bringing biofortification of cereals that can be accomplished by the underprivileged (poor) in rural areas; it has low persistent costs, is sustainable in the long term, but is time taking and, needs an upfront investment. Micronutrient impenetrable cereal varieties have been used with advantage for breeding improved resistance to disease as well for environmental stresses (Bouis 2003). There is a need for breeding for specific dietary qualities that require nutrient density traits in high-yield cultivars.

Utilizing this technique, plant reproducers quest seed or germplasm banks for existing assortments of harvests normally high in nutrients. They at that point crossbreed these high supplement assortments with high-yielding assortments of harvests, to furnish the seed with exceptional returns and expanded dietary benefit. The crop must be reared with adequate measures of supplements to have a quantifiable positive effect on human wellbeing. Thusly, they should be created with the contribution of nutritionists who study whether the shoppers of the improved harvest can assimilate the additional supplements and the degree to which stockpiling, handling, and cooking of the yields influence their accessible supplement levels. This technique is predominant at present, as it is faster, less expensive, and less disputable than hereditarily building harvests. For instance, HarvestPlus, a noteworthy NGO in the advancement of biofortified crops, fundamentally utilizes ordinary reproducing systems and has not yet spent over 15% of their examination spending plan on hereditarily altered yields when customary strategies neglect to meet healthful prerequisites.

3.4.3.1 Rice Breeding

Rice is significantly popularized for micronutrient enhancement. It is considered as one of the most consumed staple food crops. Biofortification in rice can have a considerable effect on malnutrition challenge (lace of nutrition in human). Old varieties of rice with more iron and zinc content in grain have been identified as the mineral trait. The concentration of Zn is also affected by milling time. There is a significant concentration of Zn variation presented due to milling in Fig. 3.5. In India and the Philippines, an improved line (IR68144-3B-2-2-3) was identified (Gregorio et al. 2000)].

3.4.3.2 Wheat Breeding

Wheat is a staple crop thus attatracts the focus of biofortification. A wide variety of iron and zinc dense cultivars are available in wheat and its related wild species have been seen that are used for the development of present-day first-class cultivars (Monasterio and Graham 2000). Using this variety HarvestPlus has discharged a

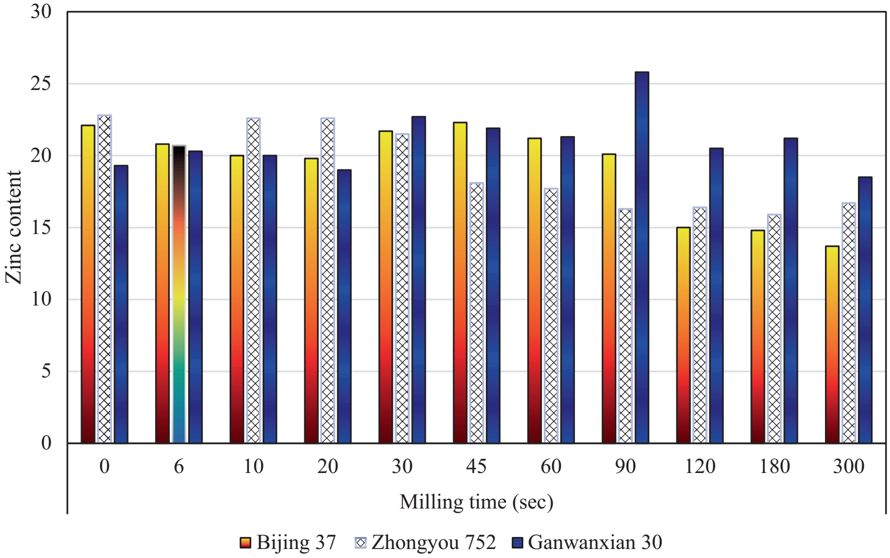

Fig. 3.5 Effect of milling time on seed Zn contents (mg kg^{-1}) of three rice cultivars (Das et al. 2018)

few assortments of wheat with 4–10 ppm higher zinc content. Six assortments of high zinc wheat (BHU 1, BHU 3, BHU 5, BHU 6, BHU 7, and BHU 18) were discharged in India in 2014 pursued by the arrival of four assortments in Pakistan in 2015 (NR 419, 42, 421, and Zincol). Two assortments BHU 1 and BHU 6 have a high return, malady opposition notwithstanding high zinc. As of late, assortment with high zinc (PBW1Zn) has been discharged by Punjab Agricultural University, India. Another assortment with high zinc and iron substance (WB2) has been created and discharged by the Indian Institute of Wheat and Barley Research, India. Aside from discharging cultivars, a few scientists have revealed an expansion in the zinc and iron substance of wheat by plant rearing (Cakmak et al. 1999). Countless ongoing durum wheat assortments discharged in various nations in the previous decade show fundamentally higher YPC than the old assortments discharged before the 1970s (Digesù et al. 2009). Improvement of cancer prevention agent properties contributed by anthocyanins had likewise been a region of huge research in wheat.

3.4.3.3 Maize Breeding

Maize is a cash crop commonly grown for feeding of animals, production of sugar, oil, starch, and ethanol and also used for human utilization. The immense hereditary assorted variety of maize has been the reason for the reproducing programs that have created a great part of the higher-yielding maize utilized around the world. Researchers have found assortments that have normally higher amounts of provitamin A. HarvestPlus are utilizing these lines to breed high-yielding assortments of biofortified maize with larger amounts of provitamin A to battle nutrient An insufficiency. The provitamin A maize is one of the critical accomplishments in the field of biofortification. Biofortified orange maize assortments have been developed industrially in Zambia (GV662A, GV664A, and GV665A), Nigeria {Ife maizehyb-3, Ife maizehyb-4, Sammaz 38 (OPV), Sammaz 39 (OPV)}, and Ghana {CSIR-CRI Honampa (OPV)} since 2013.

Malawi, Zimbabwe (ZS242), and Tanzania have likewise discharged biofortified orange maize as of late. As a beneficial outcome, an expansion in the pupillary reaction was seen among Zambian youngsters devouring nutrient A biofortified maize. Raisers have assessed cell reinforcements like tocochromanols, oryzanol, and phenolic mixes in star VA biofortified maize. Another noteworthy accomplishment in the field of maize biofortification is quality protein maize (QPM). Maize beers have created QPM with high fundamental amino acids lysine and tryptophan by consolidating murky 2 (o2) freak quality from normally happening maize into the maize cultivars (Pixley et al. 2013).

3.4.3.4 Sorghum Breeding

The micronutrients and beta-carotene-rich sorghum breeding have been examined. Sorghum assortments have been screened for high in minerals, zeaxanthin, lutein, protein, and beta-carotene substance. The Fe and Zn rich sorghum lines are ICSR 14001 and ICSH 14002 which have been developed by ICRISAT and released in India for cultivation.

3.4.3.5 Millets Breeding

Pearl millet is the least expensive iron and zinc wellspring, and a huge variety for these micronutrients have been found in its germplasm. In India, ICRISAT and HarvestPlus launched in 2014 the biofortified (iron and zinc) pearl millet variety “Dhanashakti” and a hybrid ICMH 1201 (Shakti-1201). In addition, two varieties are currently under development, ICMH 1202 (Nirmal-7) and ICMH 1301. There have been records of numerous well-adapted commercial crops with high grain content of iron and zinc.

3.5 Challenges

In spite of the fact that few items in different harvests were created as a proof of idea for biofortification, efficient investigations of their nourishing effect are required with the goal that the interest for biofortified sustenance drives research and item improvement (concerning diabetic rice):

- There is a need for strong policy interventions to establish a connection between biofortified products and various national programs such as Rashtriya Krishi Vikas Yojana (RKVY). Higher profits would make those improved cultivars interested in producing. The main problem with the production of fortified crops for GM technology is the expense of analysis and regulatory compliance.
- Adequate information programs are needed to raise the public's awareness of the adoption of varieties by farmers and the public's acceptance by consumers, particularly if there are obvious changes in the quality of the crop, such as the colour of golden rice and white maize.
- Research cooperation between agriculture and sustenance professionals needs further strengthening in order to establish the objective level of proteins and micronutrients, their maintenance after ability, handling and cooking, and the possible rates of utilization by the objective population.
- The integration of biofortified grain into the midday meal scheme and several government-sponsored programs such as the National Food Security Mission and the Integrated Child Development Program would provide an impetus for its popularization.

3.6 Limitations of Biofortification

3.6.1 Low Acceptability

There may incidentally be troubles in persuading biofortified nourishments to be acknowledged whether they have various qualities to their unfortified partners. For instance, nutrient upgraded nourishments are frequently dull yellow or orange in shading; this, for instance, is risky for some in Africa, where white maize is eaten by people and yellow maize is contrarily connected with creature feed or sustenance help or where white-fleshed sweet potato is liked to its moister, orange-fleshed counterpart.

3.6.2 Varying Impact Throughout the Life Cycle

Biofortified staple nourishments can add to body stores of micronutrients, for example, iron, zinc, and nutrient A (the three objective supplements) all through the lifecycle, including those of kids, young people, grown-up ladies, men, and the older. The potential advantages of biofortification are not comparable over the measure that are used by all others means available for providing micronutrients in human nutrition.

3.6.3 Risk

There is a hypothetical risk that a quality embedded by a genetic engineering (GE) process (e.g., the quality that codes for beta-carotene, the forerunner of vitamin A) could go to related harvest or wild plants with obscure impacts. There is no proof to help this risk; however for this and different reasons, GE yields require obligatory field testing to survey ecological dangers. These are probably going to be exorbitant and guidelines in numerous nations may imply that a GE way to deal with biofortification is just legitimized in utilizing an ordinary rearing innovation that is incomprehensible. When all said is done, GE methodologies face obstruction in numerous nations. Showcasing in creating nations isn't simple, and customer acknowledgment is basic for a biofortification system to decrease lack of healthy sustenance.

3.7 Conclusion and Future Prospects

Biofortification is a new promising technology that could be a feasible solution to various children malnutrition issues in the place where citizen does not have sufficient quality food. But due to some scientific intervention, there is still need for some improvement in the biofortification process, so a suitable agronomic and breeding approach could become a great emphasis to overcome the malnutrition challenge. Hence biofortification came out as the most prime suitable way to overcome different malnutrition problems that we are presently facing. There is still need for more detailed study as well as more crops to be identified which are promptly suitable for biofortification approach.

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Chapter 4
Microbial ACC-Deaminase Attributes: Perspectives and Applications in Stress Agriculture

Pankaj Prakash Verma, Shiwani Guleria Sharma, and Mohinder Kaur

Abstract Agricultural production is exaggerated by the adverse environmental conditions. The changing temperature, precipitation patterns, and carbon dioxide concentration result in reduced crop productivity. Plant microbe interactions are also influenced by change in environmental conditions. Under biotic and abiotic stress conditions, ethylene is synthesized from 1-aminocyclopropane-1-carboxylate (ACC) in plants. The production of ethylene retards growth and causes plant senescence. However, rhizospheric microorganisms can produce ACC-deaminase which has the ability to breakdown ACC into ammonia (NH_3) and α-ketobutyrate ($C_4H_6O_3$). Thus, ACC-deaminase-producing, plant growth-promoting rhizobacteria (PGPR) promotes stress resistance in plants. Expression of ACC-deaminase gene (AcdS) in plants can be an alternative approach to mitigate stress. The transgenic plants with AcdS gene have been developed and tested against diverse environmental stresses. This chapter provides an overview on microbial ACC-deaminases, their biochemistry and genetics, and their prospective under diverse environmental stress conditions. The role of ACC-deaminase in overcoming stress tolerance to flooding, drought, heavy metals, salinity, etc. has been discussed.

Keywords ACC-deaminase · Biotic and abiotic stress · Ethylene · PGPR · Plant microbiome · Sustainable agriculture

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4.1 Introduction

Microbial communities associated with roots are diverse and play many crucial roles in natural and agroecosystem functioning (de Vries and Griffiths 2018). They play a vital role in the management of crop production, plant health, and biogeochemical cycling. The abundance and functioning of microbial communities are affected by climate change. The alteration in microbial communities is mainly due to their varied physiology, temperature sensitivities, and growth rates (Ladau et al. 2018; Briones et al. 2014; Delgado-Baquerizo et al. 2014).

The interaction among soil community members are considered as beneficial, pathogenic, or neutral and can change with environmental or ecological stress (Vandenkoornhuyse et al. 2015; Yadav 2017). Plant growth-promoting rhizobacteria (PGPR) bind to the roots (the rhizosphere), leaves (the phyllosphere), and to the inner surfaces of the plant (the endophytes) in order to promote growth of plant (Glick 2014). Several researchers have documented the use of PGPR in stimulating plant development and protecting crop plants from phytopathogens and abiotic stressors (Nascimento et al. 2014; Kang et al. 2014; Glick 2014).

The PGPR promote plant growth and development through a number of direct mechanisms such as phytohormones synthesis, phosphate solubilization, iron sequestration, and nitrogen fixation and indirect mechanisms such as induced systemic resistance (ISR) (Verma et al. 2017b). The use of ACC-deaminase-producing PGPR in agriculture provides an attractive and environmentally sustainable technology to mitigate environmental stress. The ACC-deaminase cleaves ACC (the immediate ethylene precursor in plants) to NH_3 and α-ketobutyrate, thereby lowering the stress ethylene levels (Kour et al. 2019d). The stress ethylene is synthesized endogenously in plants and can induce diverse physiological changes in plants. PGPR with ACC-deaminase activity are beneficial to reduce biotic and abiotic constraints in plants. This chapter provides the new insights into the use of ACC-deaminase-producing microbes for stress mitigation in agriculture.

4.2 Plant Growth-Promoting Rhizobacteria in Sustainable Agriculture

Agricultural production has increased noticeably, ever since the beginning of the twentieth century to cope with undergoing demographic transformations. The agricultural practices largely depend on high inputs of pesticides and mineral fertilizers to increase the production/yield. The change in conventional cultivation practices and use of excessive agrochemicals has resulted in soil deterioration (Yadav et al. 2017b). The agrochemical residues did spread in aquatic and terrestrial ecosystems, causing significant contamination and environmental hazards. The worldwide usages of these agricultural practices contribute potential threat to the environment, humans, and sustainable agriculture (Carvalho 2017). Environmental and human health concerns related to indiscriminate usage of agrochemicals have led to a strong interest in alternate strategies to ensure competitive crop yields and protection against phytopathogens.

The microbial diversity in soil can serve the same purpose and is important for maintaining sustainable agricultural production systems. The microbiomes associated with different crop plants have tremendous potential to increase the growth and yields sustainably in farming systems (Verma et al. 2016a, 2019; Yadav 2019; Yadav and Yadav 2019). The microbes and their products have the potential to complement agrochemicals and mineral fertilizers (Trivedi et al. 2017). These beneficial microbes belong to PGPR and PGPF (plant growth-promoting fungi). The use of these microbes is progressively increasing in agriculture as biofertilizers, biopesticides, phytostimulators, and rhizoremediators (Somers et al. 2004; Sharma et al. 2017; Verma et al. 2016b).

The PGPR belong to the group of rhizobacteria inhabiting the rhizosphere and rhizoplane (Glick 2012). They stimulate plant growth through acquiring nutrient, modulating phytohormone levels, maintaining soil structure, bioremediating contaminated soils, and suppressing disease. Numerous studies are being conducted to understand the microbial diversity of rhizosphere and their importance in soil and crop productivity (Saxena et al. 2016; Yadav et al. 2020; Prasad et al. 2019). In this particular perspective, research is being carried out to explore the diverse rhizobacteria having novel traits like pesticide degradation (Ahemad and Khan 2010), heavy metals detoxification (Ma et al. 2011; Wani and Khan 2010), salinity tolerance (Tank and Saraf 2010), and biocontrol of insects and phytopathogens (Russo et al. 2008) along with other PGP traits. All these characteristics increase agricultural productivity and sustainability (Nath et al. 2017; Sarkar et al. 2017; Verma et al. 2017c).

The PGPR are generally classified into extracellular PGPR (present in the rhizosphere, rhizoplane and inside spaces present in between root cortex cells) and intracellular PGPR (within root cells). The extracellular PGPR belong to diverse bacterial genera, for example, *Agrobacterium, Azospirillum, Bacillus, Caulobacter, Erwinia, Flavobacterium, Hyphomicrobium, Pseudomonas, Micrococcus*, and *Serratia.* The intracellular PGPR include *Allorhizobium*, *Rhizobium*, *Azorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Frankia* (Mhlongo et al. 2018; Bhattacharyya and Jha 2012; Yadav et al. 2017a; b). The PGPR are found in generally much higher abundance and activity around the plant roots than in the bulk soil. This indicates that plant roots exude a rich diversity of molecules like sugars, amino acids and organic acids, etc. into the rhizosphere which can be used by soil microbial communities as food source (Olanrewaju et al. 2017). The plant rhizodeposits provide congenial environment for microbes to colonize in the rhizosphere which is of great importance to agriculture sustainability. The rhizomicrobiome plays a vital role in neutralizing the plant stress response. They have been shown to fight against the various biotic (plant pathogen, insects, and pests) and abiotic stress (drought, salinity, alkalinity, and temperature), via their biological activities (Backer et al. 2018; Verma et al. 2017b; Yadav et al. 2018a; c).

4.3 Environmental Stress and Ethylene Biosynthesis in Plants

Plants largely depend on their associated microbial communities or microbiome which is found in and around their roots. The plant microbiome has significantly increased the metabolic efficiency of plants and nutrient uptake, promote stress tolerance, and can improve crop productivity (Yadav et al. 2017c). Plants play a pivotal role in shaping their microbiome as evidenced by the fact that diverse plant species harbor distinct microbial communities (Vionnet et al. 2018). Microbial communities successfully colonize and support plant growth, development, and health (Armanhi et al. 2018). These diverse microbial communities have a positive or negative impact on the host plant. The pathogenic microbes secrete toxins and enzymes, degrading plant tissues, whereas other enhance mineral/nutrient uptake, nitrogen fixation, degradation of xenobiotic compounds, and protection against phytopathogens (Nascimento et al. 2018).

Plants are often exposed to a wide range of unfavorable environmental stresses (biotic and abiotic stresses) which limit crop production. The biotic stress occurs mainly from the damage caused by bacteria, fungi, nematodes, viruses, and insects, whereas abiotic stress arises from water deficit (drought), temperature (heat, cold and frost), salinity, and mineral toxicity. The various environmental stresses increases the production of intracellular Ca^{2+} levels and reactive oxygen species (ROS) molecules such as hydroxyl radical (OH^-), superoxide anion (O_2^-), and hydrogen peroxide (H_2O_2) in plants (Kour et al. 2019c). The plants have developed intricate mechanisms to enable optimal growth and developmental response to combat such adverse environmental conditions (Verma et al. 2016c). Plant hormones play vital roles in adapting plants to unfavorable environmental conditions because of their ability to crosstalk between each other (Podlešáková et al. 2018). Their intricate signaling pathways are interconnected to facilitate efficient stress response. Plant hormones control growth and development from embryogenesis to reproductive development (Denancé et al. 2013). The major plant hormones include auxin, cytokinins, gibberellins, ethylene, abscisic acid, jasmonates, brassinosteroids, strigolactones, systemin, and salicylic acid. Plant response against pathogens and other stress conditions is mainly regulated by four hormones viz. abscisic acid, ethylene, salicylic acid, and jasmonates (Wang et al. 2018a, b; Nakashima and Yamaguchi-Shinozaki 2013; Kour et al. 2019d; Yadav et al. 2018b). The small amount of these endogenous hormones is capable of playing an essential role in the plant's life.

The abiotic stress conditions trigger ethylene biosynthesis. Ethylene, a natural regulator of plant physiological and molecular processes, has also been regarded as a stress responsive hormone (Khan et al. 2017). In plants, the two key enzymes ACC synthase and ACC oxidase are transcriptionally and posttranscriptionally regulated to modulate ethylene biosynthesis. The ethylene biosynthesis occurs in a series of chemical reactions. In the first step, the amino acid L-methionine is converted to S-AdoMet (S-adenosyl-methionine) by SAM synthetase (S-AdoMet synthetase).

Approximately 80% of this methionine is converted to S-AdoMet and the rest being utilized for protein synthesis. S-AdoMet serves as the precursor for ethylene and a number of biosynthetic pathways. S-AdoMet is changed to ACC by ACC synthase (S-adenosyl-methionine methylthioadenosine lyase). In ethylene biosynthesis, ACC is the immediate precursor of ethylene. ACC is oxidized by ACC oxidase in the last step and is finally converted into ethylene. Thus, this process, ACC synthase or ACS, is the rate-limiting step (Xu and Zhang 2015).

The change in ethylene levels to below or above the optimum can lead to senescence and inhibition of plant growth. The optimum ethylene level depends upon the type of plant species and the response (Chang 2016). As ethylene production gets enhanced under both biotic and abiotic environmental stress, it becomes imperative to control its formation in the plant rhizosphere (Raghuwanshi and Prasad 2018). The microbial strains with ACC-deaminase activity provide plants to overcome the stress and survive in adverse environmental conditions.

4.4 Microbial ACC-Deaminase: Biochemistry, Genetics, and Ecological Significance

The increased ethylene production in response to extreme temperature, salinity, drought, chemicals (organic and inorganic), heavy metals, ultraviolet light, pathogens, insects, and nematode leads to significant damage (Raghuwanshi and Prasad 2018). ACC-deaminase hydrolyses ACC into ammonia and α-ketobutyrate and thus is able to lower plant ethylene levels. Diverse microbes are reported to produce ACC-deaminase and support plant to overcome stress. Under stress, the ACC concentration increases inside the plant root. The significant portion of which is then exuded from the roots through diffusion and subjected to hydrolysis by ACC-deaminase-producing microbial communities. Rhizospheric microbes with ACC-deaminase have the ability to enhance ACC efflux from roots. The plant secretes a large amount of ACC in order to keep equilibrium in ACC inside as well as outside. As a result, the growth is accelerated of microbes containing ACC-deaminase is accelerated in the rhizosphere, thus decreasing the ACC concentration within the plant roots and leading to the lowering of ethylene biosynthesis and increasing plant growth (Glick et al. 2007; Nadeem et al. 2010; Gamalero and Glick 2015). There are several rhizospheric microbes possessing ACC-deaminase activity that can promote plant growth under stressed conditions (Table 4.1).

4.4.1 Biochemistry

ACC-deaminase (EC 3.5.99.7) belongs to a pyridoxal phosphate (the cofactor)-dependent enzyme which is related to the tryptophan synthase superfamily. The ACC-deaminase is commonly found in diverse bacterial and fungal genera,

Table 4.1 Several studies reporting ACC-deaminase activity of different microbial species against biotic and abiotic stress are summarized

Stress type	Microbial species with ACC-deaminase activity	ACC-deaminase (nmol/mg/h)	Crop type	Experiment type	Effect	References
Water stress	*Variovorax paradoxus* and *Pseudomonas* sp.	–	Wheat (*Triticum aestivum* L.)	Glasshouse	Improved plant growth and foliar nutrient concentrations; significant positive changes in antioxidant properties	Chandra et al. (2019)
Salinity stress	*Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp.	1677 and 1589	French bean (*Phaseolus vulgaris* L.)	Pot	Increased root and shoot length, fresh weight, root and shoot biomass, and total chlorophyll content	Gupta and Pandey (2019)
Drought stress	*Ochrobactrum pseudogrignonense* RJ12, *Pseudomonas* sp.RJ15 and *Bacillus subtilis* RJ46	RJ12(125 ± 2.14); RJ15(57 ± 1.06); RJ46 (116 ± 1.21)	*Vigna mungo* L. and *Pisum sativum* L.	Pot	Increased seed germination percentage, root and shoot length, dry weight of plants	Saikia et al. (2018)
Salinity stress	*Bacillus* sp.	47.32 μmol α-KB/mg/h.	*Capsicum annuum* L.	Pot	Shoot and root length, fresh and dry weight of plants	Wang et al. (2018a, b)
Drought stress	*Pseudomonas fluorescens, Enterobacter hormaechei* and *Pseudomonas migulae*	39.40 ± 0.68 to 3.24 ± 0.58	Foxtail millet (*Setaria italica* L.)	–	Increased seed germination and seedling growth	Niu et al. (2018)
Salinity and desiccation	*Viridibacillus arenosi* IHB B 7171	190–16	Tea (*Camellia sinensis*)	–	Enhanced plant height, leaf number, and weight and increase in yield	Thakur et al. (2017)
Biotic stress (against *Peronospora* sp.)	*Pseudomonas putida* (WPTe)	–	Poppy (*Papaver somniferum* L.)	Pot	Increased plant growth and tolerance against downy mildew	Barnawal et al. (2017)

Salinity stress	*Bacillus licheniformis* HSW-16	267.50 ± 19	Wheat (*Triticum aestivum*)	–	Increased plant growth in terms of root and shoot length, fresh and dry weight	Singh and Jha (2016)
Salinity stress	*Pseudomonas fluorescens* YsS6, *Pseudomonas migulae* 8R6	YsS6 (12.5 μmol/mg/h), 8R6(10.9 μmol/mg/h)	Tomato (*Solanum lycopersicum*)	Pot	Higher fresh and dry biomass, chlorophyll contents, greater number of flowers and buds	Ali et al. (2014)
Drought stress	*Pseudomonas aeruginosa* GGRJ21	17.14 ± 0.88 μmol α-KB/mg/h	Mung bean (*Vigna radiata* (L.)	Field	Increased biomass and better plant growth	Sarma and Saikia (2014)
Salinity stress	*Pseudomonas putida* UW4	–	Tomato (*Solanum lycopersicum*)	–	Increased shoot length, shoot fresh and dry mass, chlorophyll concentration of tomato seedlings	Yan et al. (2014)
Waterlogged stress	*Achromobacter xylosoxidans* (Fd2), *Serratia ureilytica* (Bac5), *Herbaspirillum seropedicae*(Oci9), *Ochrobactrum rhizosphaerae* (Oci13)	Fd2(525.53 ± 15.13); Bac5(193.72 ± 5.86); Oci9 (868.96 ± 11.18); Oci13(403.27 ± 5.27	*Ocimum sanctum*	Pot	Maximum plant growth and yield of herb	Barnawal et al. (2012)
Water stress	*Bacillus safensis* and *Ochrobactrum pseudogregnonense*	–	Wheat (*Triticum aestivum*)	–	Increased plant height, root and shoot biomass, yield, and chlorophyll content	Chakraborty et al. (2013)
Drought stress	*Pseudomonas fluorescens* (ACC-5), *P. fluorescens* (ACC-14), and *P. putida* (Q-7)	ACC-5 (174.2 ± 8.20); ACC-14 (25.7 ± 3.4); Q-7 (140.0 ± 5.3)	Peas (*Pisum sativum*)	Pot	Increased fresh and dry weight, root and shoot length, number of leaves, and water use efficiency	Zahir et al. (2008)

catalyzing the ring opening of ACC to ammonia and α-ketobutyrate. This multimeric enzyme occurs within the cytoplasm and was first discovered by Honma and Shimomura in 1978. ACC-deaminase was purified from different species of *Pseudomonas*, i.e., *Pseudomonas* sp. ACP, *P. chlororaphis* 6G5, *P. putida* GR12–2, and *P. putida* UW4 (Klee et al. 1991; Jacobson et al. 1994; Hontzeas et al. 2004). The ACC-deaminase has a native size of 100–112 kDa (Singh et al. 2015). The Km value (1.5–15 mM) of the enzyme indicates its low affinity for ACC. The lowest amount of substrate required by *Pseudomonas* sp. ACP and *P. putida* GR12-2 for induction of enzyme reaction was 100 nM. The amino acids like L-alanine, DL-alanine, D-serine, and γ-aminoisobutyric acid can also induce enzyme activity to a low and almost the same level as that of ACC. The majority of organisms contain a basal level of ACC-deaminase activity and is directly associated with the substrate. The maximum absorption (416 and 326 nm) was observed at a pH value of 6 and 9 and the temperature optimum for ACC-deaminase was 25–30 °C (Glick 2014).

4.4.2 Genetics and Expression

ACC-deaminase genes (both the structural and regulatory) have been reported in several bacterial and fungal genera. ACC-deaminase activity has been found in a broad range of Gram-positive and Gram-negative bacteria (Timmusk et al. 2011; Tak et al. 2013), symbiotic rhizobia (Ma et al. 2003a, b; Uchiumi et al. 2004), bacterial endophytes (Rashid et al. 2012), and fungi such as *Phytophthora sojae, Penicillium citrinum*, and *Trichoderma asperellum* (Nascimento et al. 2014; Checcucci et al. 2017). However, the expression level of the AcdS gene encoding ACC-deaminase varies among organism. The AcdS gene was found in different strains of genera *Acidovorax*, *Brenneria*, *Burkholderia*, *Bordetella*, *Collimonas*, *Curvibacter*, *Cupriavidus*, *Dickeya*, *Halomonas*, *Herbaspirillum*, *Methylibium*, *Phytophthora*, *Pantoea*, *Pseudomonas*, *Polaromonas*, *Ralstonia*, *Serratia*, and *Xenophilus* (Verma et al. 2017a; b). The small number of archaeal strains viz. *Archaeoglobus fulgidus*, *Pyrococcus furiosus*, *Pyrococcus abyssi*, and *Thermococcus nautili* also showed the presence of an ACC-deaminase gene.

Many researchers have designed a different set of primers for detection of the AcdS gene in bacteria (Duan et al. 2009; Jha et al. 2012). Duan et al. (2013) reported the genetic makeup of microbial ACC-deaminase gene. Nucleotide sequences of dcyD and yedO genes that encode for pyridoxal phosphate-dependent enzyme (D-cysteine sulfhydralase) are closely related to AcdS nucleotide sequence (Riemenschneider et al. 2005; Singh et al. 2015). Nascimento et al. (2014) differentiated sequences of ACC-deaminase from D-cysteine sulfhydralase by analyzing AcdS nucleotide sequences for Lys51, Ser78, Tyr295, Glu296, and Leu322, the key protein residues using *Pseudomonas* sp. strain UW4. These residues play a key role in ACC-deaminase activity and any change in its given locations will represent D-cysteine sulfhydralase (Singh et al. 2015).

The transcriptional regulation and AcdS gene expression depend upon the substrate (ACC) concentration, the presence and absence of oxygen, and the product accumulation. The mechanism of regulation of an ACC-deaminase gene (AcdS) in *Pseudomonas putida* UW4 has been well documented (Li et al. 2000). The two main regulatory elements are the promoter regions for regulatory protein binding (Lrp box, AcdB box, FNR box, and CRP box) and AcdR located 5′ upstream of AcdS gene. The Lrp (leucine-responsive protein), AcdB, FNR, and the CRP box binds Lrp protein, AcdB protein, fumarate nitrate reductase protein, and cyclic AMP receptor protein, respectively (Cheng et al. 2008; Singh et al. 2015; Soni et al. 2018). The interaction among all these regulatory elements and products are involved in the transcription of the AcdS gene. Glycerophosphoryl diester phosphodiesterase, i.e., AcdB, forms a complex with ACC. The active octamer unit of Lrp binds to ACC and AcdB protein complex (Cheng et al. 2008). This tri-parental complex initiates AcdS gene transcription by binding to its promoter region (Li and Glick 2001). The amino acid leucine negatively regulates the AcdS gene. As the leucine concentration increases, it binds to Lrp octamer forming the inactive Lrp dimer, eventually leading to shutting down the AcdS gene transcription. The regulatory mechanism for AcdS gene expression varies among different species such as:

- Regulated by LRP-like protein (*Bradyrhizobium japonicum* strain USDA 110).
- Regulated by σ^{70} promoter (*Rhizobium leguminosarum* bv. *viciae* strain 128C53 K) (Kaneko et al. 2002; Ma et al. 2003a, b).
- ACC-deaminase expression requires the nitrogen-fixing regulatory gene nifA2 in *Mesorhizobium loti* (Nukui et al. 2006).

PGPR with ACC-deaminase activity promote development and growth of plants under adverse environmental conditions. Certain pathogens has the ability to induce ethylene level like *Agrobacterium tumefaciens* (Hao et al. 2011), *Pyricularia oryzae* (Amutharaj et al. 2012), *Pythium aphanidermatum* (El-Tarabily 2013), etc. PGPR with ACC-deaminase activity protect the plants from different phytopathogens and external environmental stimuli, delay senescence, and favor legume nodulation (Glick 2014; Raghuwanshi and Prasad 2018; Gupta and Pandey 2019). The inoculation of ACC-deaminase-producing *Pseudomonas putida* strain UW4 leads to the reduction of nematode *Bursaphelenchus xylophilus* causing pine wilt disease (Nascimento et al. 2012). The use of ACC-deaminase-producing rhizobacteria presents a valuable tool to boost plant growth and resistance against phytopathogens and environmental stresses.

4.5 Perspectives and Applications of ACC-Deaminase in Stress Agriculture

4.5.1 Drought Stress

Drought stress is one of the prevalent abiotic stresses limiting agricultural productivity and having a significant impact on the ecosystem (Kour et al. 2019a; b; Yadav and Yadav 2018). It affects plant-water relations, causing specific and nonspecific reactions and plant damage. It is distinguished by the decrease in water content, leaf water potential, turgor loss, and growth reduction (Toscano et al. 2019). At present, one alternative to fight against drought stress is the use of PGPR. These microbes are found in association with the plant roots and facilitate growth in optimal, biotic and abiotic stress conditions (Cassan et al. 2009). Microorganisms produce extracellular polymeric substances or exopolysaccharides (EPS) to survive against drought stress by retaining the water and diffusion of carbon sources. Microbial EPS enhances soil aggregation, maintaining soil moisture, carbon storage, and nutrient entrapment (Costa et al. 2018). It also helps in the attachment and colonization of the microbial cells to plant roots. The microbial ACC-deaminase plays an important role in protecting plants from stress conditions. Several PGPR have been shown to alter the effects of drought stress by reducing stress ethylene in plants (Mayak et al. 2004; Arshad et al. 2008) and have been summarized in Table 4.1 Gagné-Bourque et al. (2016) showed that Timothy grass (*Phleum pratense*) inoculated with *Bacillus subtilis* B26 led to increased photosynthesis rate, shoot and root biomass, and stomatal conductance under drought stress. The consortium of *Bacillus cereus* strain AR156, *B. subtilis* SM21, and *Serratia* sp. induced drought tolerance and maintained chlorophyll content in cucumber plants (Wang et al. 2012). The inoculation with *Azospirillum lipoferum* containing ACC-deaminase increased yield (by 109%), nitrogen content, and auxin concentration in wheat (Arzanesh et al. 2011). The inoculation of ACC-deaminase-producing *Pseudomonas* sp. restored pea (*Pisum sativum*) nodulation, eliminating the adverse effects of drought stress (Arshad et al. 2008).

4.5.2 Flooding Stress

Flooding or waterlogging causes a substantial loss in agricultural productivity. Soil flooding stimulates several physiological changes in plants like reduced photosynthesis, poor plant growth, stomatal closure, and yield reduction. It creates an anaerobic condition in the soil due to which the plants undergo an oxygen-deficient stress, affecting plant's vital processes (e.g., ion uptake, etc.). The flooding stress triggers the synthesis of enzyme ACC synthase (ACS), elevating the ACC level in plant roots (Li et al. 2012). In anoxic condition, the ACC is transported to shoots and finally converted to ethylene by ACC-oxidase (Vanderstraeten and Van Der Straeten 2017). Ethylene accumulation in plants causes epinasty, necrosis, leaf chlorosis, and stunted growth (Li et al. 2013). Many researchers have reported ACC-deaminase-containing PGPR to alleviate stress stimulated by flooding (Barnawal et al. 2012; Li et al. 2013).

Pseudomonas putida UW4, expressing ACC-deaminase, facilitate the growth of canola (*Brassica napus*) plants exposed to flooding stress under field conditions (Farwell et al. 2007). Jaemsaeng et al. (2018) demonstrated that ACC-deaminase-containing *Streptomyces* sp. GMKU increases root and shoot elongation, leaf chlorophyll content, leaf area, plant biomass, and adventitious roots in mung bean under flooding conditions. The PGPR strains expressing ACC-deaminase viz. *Achromobacter xylosoxidans*, *Serratia ureilytica*, *Herbaspirillum seropedicae*, and *Ochrobactrum rhizosphaerae* protected *Ocimum sanctum* plants from detrimental changes of waterlogging stress like reduced chlorophyll content, nutrient uptake, and higher ethylene production (Barnawal et al. 2012).

4.5.3 Heavy Metals Stress

The harmful contaminants from industrial wastes like heavy metals, metalloid, etc. affects the biological and chemical properties of soil (Chen et al. 2016). The augmentation of such toxic compounds into the soil has exhibited many undesirable effects on growth, yield, and reproduction of plant (Tran and Popova 2013; Pramanik et al. 2018). The higher concentration of metal ions like cadmium (Cd), copper (Cu), cobalt (Co), nickel (Ni), lead (Pb), and zinc (Zn) are sturdily toxic to metalloenzymes, thereby hindering the growth and development of plants.

The ACC-deaminase-producing PGPR facilitate growth promotion by lowering ethylene levels under metal stress (Zhang et al. 2011). Grobelak et al. (2018) Showed that the inoculation of plant with ACC-deaminase-containing bacteria resulted in higher root and shoot biomass and resulted in increased phytoremediation of heavy metals. The genus *Bacillus* and *Pseudomonas* have the highest ACC-deaminase activity in heavy metal contaminated sites. *Agrobacterium fabrum* and *Stenotrophomonas maltophilia* isolated from wheat rhizosphere have the ability to reduce the Cd uptake and enhance the growth of wheat under Cd toxicity (Zafar-Ul-Hye et al. 2018).

4.5.4 Salinity Stress

Salinity induces physiological and metabolic alteration in plants, affecting growth, development, and yield (Jouyban 2012). The reduction in plant growth is induced by plasmolysis, osmotic stress, nutrient imbalance, interfering photosynthesis, Na^+ and Cl^- toxicity, ROS production, and ethylene production (Sairam and Tyagi 2004). During salt stress, ROS act as a signaling molecule simultaneously damaging the root and shoot tissues of plant. This damage is caused by distressing enzymes and cell wall and membrane functions (Bharti and Barnawal 2019).

Plant growth-promoting strains *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. possessing ACC-deaminase increased growth, root and shoot biomass, and total chlorophyll content in the French bean (*Phaseolus vulgaris*) under saline conditions (Gupta and Pandey 2019). Plant growth-promoting *Streptomyces* sp. strain GMKU 336 facilitates growth of rice plants under salinity stress by reducing ethylene level via the action of enzyme ACC-deaminase (Jaemsaeng et al. 2018). *Pseudomonas fluorescens* TDK1 possessing ACC-deaminase activity resulted in increased growth and yield in groundnut (*Arachis hypogaea*) plants under saline-affected soils (Saravanakumar and Samiyappan 2007). Brígido et al. (2013) demonstrated that *Mesorhizobium ciceri* strain G-55 having ACC-deaminase promoted chickpea nodulation and growth under salinity stress. The nodule formation and functioning is inhibited by ethylene production under salt stress (Middleton et al. 2007; Ding and Oldroyd 2009). Ahmad et al. (2013) demonstrated that the consortium of *Rhizobium* and *Pseudomonas* containing ACC-deaminase lowers the adverse effects of salinity on *Vigna radiata* under field conditions. Barnawal et al. (2014) showed that ACC-deaminase-producing *Arthrobacter protophormiae* SA3, promoted nutrient uptake and growth of *Pisum sativum* under salt stress.

4.5.5 Temperature Stress

The ethylene produced under stress conditions has been more damaging to plants as compared to its direct effects (Ali et al. 2014). Several studies showed that chilling temperature stress stimulated production of ethylene by increasing ACC levels (Concellón et al. 2005). The ethylene biosynthesis and CO_2 production occurs in avocado (*Persea americana* cv. Arad) fruits under orchard chilling conditions (Hershkovitz et al. 2009). Subramanian et al. (2015) demonstrated that *Flavobacterium* sp. OR306 and *Pseudomonas frederiksbergensis* OS211 expressing ACC-deaminase gene resulted in growth promotion in tomato plants under chilling conditions. They found that the ethylene production and ACC oxidase activity were considerably reduced in inoculated tomato plants. The ACC-deaminase gene expression in psychrotolerant bacterial strain *Sphingomonas faeni* resulted in alleviating cold stress and increasing root and shoot length and the dry weight of millet (Srinivasan et al. 2017).

4.6 Conclusion and Future Prospects

Numerous studies have shown that regulating ACC and ethylene levels can lessen the extent of growth inhibition accruing from different stress. The plants have been genetically modified to express the ACC-deaminase gene, resulting in less ethylene accumulation. The application of PGPR having ACC-deaminase activity is one of the promising and eco-friendly technologies to diminish the harmful effects of environmental stress on the growth of plants. Rhizobacteria with ACC-deaminase inoculation into plant roots or the expression of bacterial ACC-deaminase gene into plants could be very effective in assisting the growth and development under stress conditions. The development of ACC-deaminase-containing PGPR formulations is economical, environmentally sustainable, and efficient in combating plant stress levels. The major challenge is to exploit the potent PGPR which can survive under adverse environmental and varied geographical conditions.

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Chapter 5
Plant Microbiomes with Phytohormones: Attribute for Plant Growth and Adaptation Under the Stress Conditions

Yachana Jha

Abstract Plant microbiomes are the group of microbes residing in/on the plant under symbiotic relation. In such symbiotic relation, microbes get nutrient and residence from host plant; at the same time, plants are able to get insoluble and unavailable nutrients by the help of such microbes. Such plant-associated microbes are also able to produce plant hormones important for the growth and development of plants. Plant hormones are an important biomolecules responsible for the potential of the plant to survive in changing environment by regulating all the metabolic as well as physiological activity. Microbiomes associated with plants also have the ability to modulate the phytohormone level in the host plant to help the host plant survive under biotic and abiotic stress. Different stresses are the major cause of crop loss worldwide. To meet the food needs of the world's growing population, preventing crop losses due to stress and producing more foods are demands of hour. Plant microbiomes are therefore one of the best environmentally friendly options for increasing food production and developing tolerance/resistance against various stresses.

Keywords Diversity · Phytohormones · Plant microbiomes · Stress conditions · Sustainable agriculture

5.1 Introduction

The diverse groups of microorganism are residing in soil including fungi and bacteria and also remain associated with the plant root. Plant roots profoundly remain associated with such microorganisms, because root exudates are a rich source of nutrient for its growth. The root exudates released by the plant root contain various types of organic compounds like sugars, amino acids, and fatty acids, which are

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utilized by the microorganism for their growth and development. Such symbiotic association among the microbes and plants has positive impact on the plant growth and development under normal conditions as well as under advert environmental conditions. To protect the host from environmental stress, these microbiomes induce and modulate several metabolically active compounds such as antibiotics, lytic enzymes, compatible solutes, antioxidants, and phytohormones (Kour et al. 2019a; Rana et al. 2019a). These metabolically active compounds play an important role in plant growth and its protection under stress. Furthermore, the plant-associated microbiomes protect plants against different phytopathogens, help in the nutrient acquisition, and provide resistance against abiotic and biotic stress conditions, thereby inducing plant growth and development under stress conditions (Egamberdieva et al. 2017; Kour et al. 2019c; Kumar et al. 2019a, b; Yadav and Saxena 2018).

Plant microbiomes mostly have beneficial effect on the host plant, which develop the ability of the plant host to acquire tolerance against extreme environmental conditions by different mechanisms as nitrogen fixation, solubilization of mineral nutrients, accumulation of osmoprotectants, and production of antibiotics, pathogenesis-related proteins, antioxidant enzymes, and phytohormones (Mishra et al. 2017; Yadav et al. 2017b, 2019c). The microbial phytohormone is one of the mechanisms for plant growth and development as well as to develop tolerance against stress (Rastegari et al. 2020b; Singh and Yadav 2020). The phytohormones produced by the microbes are directly involved in endogenous metabolic pathway and proportionally modify the growth physiology to protect host plant under environmental stress (Kour et al. 2020b). The microbial phytohormones alter the root morphology, regulate conduction of water and nutrient, and modulate enzyme activity of the host plant under stress.

The plant microbiomes that belong to different genera and species of microbes may be rhizospheric, endophytic, symbiotic, and free living as *Rhizobium*, *Bacillus*, *Acinetobacter*, *Pantoea*, *Enterobacter*, and *Pseudomonas* (Sgroy et al. 2009; Yadav et al. 2018), which can produce diverse group of phytohormones. A special class of organic compound synthesized by the plant and required in very low concentration for the growth and metabolism of plant is known as plant hormone (Kumar et al. 2019a, b; Rajawat et al. 2020). There are five classes of plant hormones: abscisic acid, ethylene, cytokinins, auxins, and gibberellins. There are several reports on the group of microbes like *Pseudomonas*, *Enterobacter*, and *Stenotrophomonas* which remain associated with plants that produce a group of plant hormone like ethylene, abscisic acid, a*uxins*, cytokinins, and gibberellins (Khan and Doty 2009; Rana et al. 2019c).

de Santi Ferrara et al. (2012) reported that plant microbiomes like *Klebsiella* and *Enterobacter* from sugarcane have the ability to synthesize IAA. Similarly microbiomes, like *Bacillus*, *Arthrobacter*, *Pseudomonas*, and *Azospirillum*, produce cytokinin, as reported by Naz et al. (2009). Production and modulation of such plant hormones by the plant microbiomes can be a better choice, to transform crop production and induce desired qualities in it. There is tremendous pressure of the growing world population to increase the agricultural yield, which results in a large-scale use of chemicals in the form of fertilizers and pesticides (Kour et al. 2019c). Such application of chemical in the agricultural field affects the soil fertility and quality. Hence attention has been shifted toward the ecologically safer and productive means of agricultural practices (Kour et al. 2020a). So plant microbiome having an ability for growth promotion, stimulating root/shoot growth, enhancing stress tolerance and disease resistance, etc. is the choice of the hour. Plant hormones producing microbiomes increase resistance to environmental factors and regulate the expression of genes and the induced production of enzymes, pigments, and metabolites in the plant (Yadav et al. 2020).

5.2 Isolation, Identification, and Inoculation of Plant Microbiomes

The plant microbiomes are most commonly symbiotic bacteria or fungus residing in plant tissue without doing substantive harm. It belongs to many genera such as *Pseudomonas*, *Herbaspirillum*, *Azoarcus*, *Pantoea*, *Klebsiella*, *Gluconobacter*, and *Burkholderia* (Kandel et al. 2015; Yadav et al. 2017a). Common characters of the plant microbiomes include the ability to synthesize plant hormones, solubilize phosphate, and secrete siderophores to encourage plant growth as well as develop resistance to biotic and abiotic stresses (Gaiero et al. 2013; Kour et al. 2019d). Some plant microbiomes have an ability of biological nitrogen fixation due to gene for the conversion of dinitrogen gas (N_2) into nitrate and ammonium useful for the host plant. In a study, such beneficial plant microbiomes have been isolated from the roots of *Suaeda nudiflora* wild mosque plant (Jha et al. 2011). Appearance of veil-like pellicle just below the surface of semisolid NFb medium indicated the potential of the microbiome for biological nitrogen fixation, which has been further transferred to NFb agar plate with bromothymol blue. The bromothymol blue is a pH indicator dye, and growth of nitrogen fixer bacteria on NFb agar plate with bromothymol blue changes plate color from green to blue, thus indicating a change in pH of the medium toward alkalinity, due to nitrogen fixation.

For further confirmation these microbiomes are scanned for presence of nitrogenase reductase *nif*H gene, necessary for nitrogen fixation. PCR amplification of *nif*H gene with the gene-specific primer is used for confirmation of presence of structural gene in the microbiomes. The PCR product of 420 bp is obtained on agarose gel and eluted for sequencing. The obtained sequence is BLAST with NCBI database, and the DNA sequence data is matched with the *nif*H sequence.

The identification is carried by PCR amplification followed by sequencing by Sanger method. The obtained sequences are used for the construction of phylogenetic tree using BLAST software by comparing the sequence of microbiomes with the related genera from a database using the neighbor-joining (NJ) algorithm and maximum likelihood (ML) method.

The ability of these plant microbiomes for production of phytohormones and its modulation to protect plant under stress has been analyzed on maize plant. As per our published method, the seeds of maize have been inoculated with isolated microbiomes with some modification (Jha and Subramanian 2013a, b). The surface-sterilized seed are tested for possible contamination by incubating it on tryptophan glucose yeast extract agar medium and incubating overnight in the dark at 30 °C. The contamination-free seed are used for inoculation with isolated microbiomes. The ability of the isolated microbiomes on the maize physiology and phytohormone production has been analyzed by inoculating the isolates in maize root. For inoculation 20 ml Hoagland's nutrient medium has been co-inoculated with the isolated microbiome inoculums in the concentration of 6×10^8 cfu ml^{-1} and sterilized maize seeds. The inoculated tubes are incubated for 12 h light-dark cycle in a growth chamber at 27 °C. The association of the microbiomes with the maize root has been confirmed by incubating the inoculated plant root overnight with 2, 3, 5-triphenyltetrazolium chloride stain (Jha and Subramanian 2011). The cross sections of the stained root are examined for the presence of microbiome as red-colored cells, in the root cortex region under an image analyzer microscope (CarlZeiss).

5.3 Modification of Phytohormonal Activity by Plant Microbiomes for Plant Growth

The plants produce different types of hormones including gibberellins, abscisic acid, cytokinins, indole acetic acid (Rana et al. 2019b), and ethylene, which are important for the growth and development of the plant (Egamberdieva 2010). The action of numerous hormones, which takes place either at the site it produced or remote to it, is responsible for the regulating and coordinating plant development as per the genetically programmed developmental potential or in responses to environmental stimuli. A critical requirement for the survival of the plant as sessile organisms, the plant hormone modifies the biochemical as well as physiological activities in response to change in the plant environment (Yadav 2017b; Yadav et al. 2020).

One most significant plant hormone which regulates numerous aspect of plant life is auxin. The auxin regulates cell division, cell differentiation and elongation, tropistic response, apical dominance, root initiation, fruit ripening, flowering, and senescence (Yadav et al. 2019a). The studies show that plants inoculated with auxin-producing plant microbiomes enhance root growth and formation of lateral roots and root hairs, thus increasing water and nutrient uptake ability of plant, helping plants to grow at its full potential as well as to deal with water deficit under stress. The ability to synthesis IAA has been detected in many plant microbiome genera including *Pseudomonas*, *Rhizobium*, *Xanthomonas*, *Azospirillum*, and *Bacillus* (et al. 2010; Verma et al. 2019; Yadav and Yadav 2019).

Table 5.1 Effect of plant microbiomes on the photosynthetic pigment in maize plant by phytohormone regulation

Treatments	Chl a (mg g^{-1}FW)	Chl b (mg g^{-1}FW)	Carotenoid (mg g^{-1}FW)	ACC deaminase (μg/ml)	Auxin (μg/ml)	Gibberellin (μg/ml)
Normal						
Control	0.786^{d}	0.511^{d}	0.521^{cd}	0.654^{ef}	0.691^{cd}	0.762^{cd}
Control + *P. aeruginosa*	0.975^{c}	0.721^{c}	0.643^{bc}	0.768^{cd}	0.704^{c}	0.835^{ab}
Control + *P. pseudoalcaligenes*	1.123^{b}	0.789^{ab}	0.722^{ab}	0.834^{bc}	0.764^{ab}	0.944^{bc}
Control + *P. aeruginosa* + *P. pseudoalcaligenes*	1.467^{a}	0.913^{a}	0.798^{a}	0.968^{b}	0.798^{a}	1.211^{a}
Stressed						
Control	0.562^{h}	0.356^{h}	0.296^{gh}	0.853^{a}	0. 562^{d}	0.628^{de}
Control + *P. aeruginosa*	0.683^{g}	0.437^{f}	0.412^{ef}	0.815^{de}	0.632^{c}	0.759^{f}
Control + *P. pseudoalcaligenes*	0.678^{ef}	0.376^{fg}	0.366^{fg}	0.762^{gf}	0.682^{b}	0.781^{fg}
Control + *P. aeruginosa* + *P. pseudoalcaligenes*	0.861^{e}	0.541^{e}	0.484^{e}	0.744^{h}	0.771^{a}	0.822^{h}

Values are the means of replicates. Values with different letters are significantly different at $P < 0.05$ (Duncan's test). Values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

Another most common phytohormone is gibberellins playing a vital role in regulating plant growth naturally and involved in several physiological and developmental activities, like seedling emergence, seed germination, growth of leaves and stem, induction of flower and fruit, delay senescence, and regulation of reproductive and vegetative dormancy. Gibberellins in combination of other hormone directly regulate shoot elongation (Yadav et al. 2019b) (Table 5.1).

The plant hormone cytokinin is responsible for response to light by the shoot and uptake of nutrient by the root. So this hormone helps in fine-tuning of growth-related activity in plant. Another polyhydroxy steroidal plant hormone, brassinosteroids (BRs), also regulates many activities like initiation and development of flower, plant growth, and development (Wani et al. 2016). So these phytohormone works in coordinated manner for the proper plant growth as per the endogenous and environmental stimuli. The phytohormone production by the plant microbiomes stimulates the modulation of concentration of endogenous hormone to enable plants to survive under stress by increasing tolerance in the host. The common bean (*Phaseolus vulgaris* L.) inoculated with *A. brasilense* show enhanced specific root length, root area at root projection region compared to noninoculated control. The plant microbiomes like *Pseudomonas* and *Bacillus* are reported to produce cytokinins, in addition to auxins (Fig. 5.1).

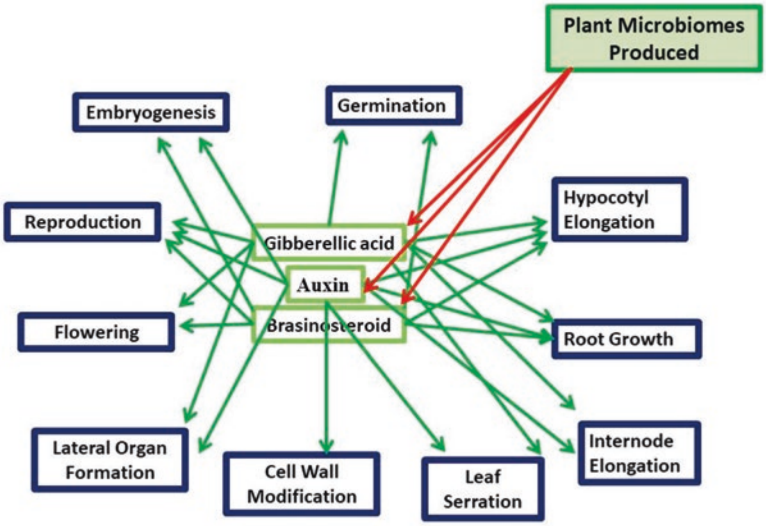

Fig. 5.1 The role of plant microbiome phytohormones in different plant growth activities

The plant hormone ethylene is known as ripening and stress hormone. ACC act as a direct precursor in the synthesis of ethylene, where synthesis of S-adenosylmethionine takes place first, which has been converted into 1-aminocyclopropane-1-carboxylic acid (ACC). The microbiomes which have the ability for the production of ACC deaminase can sequester and degrade ACC produced in the host plant to supply energy and nitrogen to the plant, thereby promoting plant growth (Jha et al. 2014). Mayak et al. (2004) reported that ACC deaminase-producing bacteria *Achromobacter piechaudii* ARV8 considerably reduced the ethylene production in stressed plant under drought stress and enhanced the dry and fresh weight of tomato and pepper seedlings. Another stress tolerance phytohormone is abscisic acid, which confers abiotic stress tolerance in crop plants. A remarkable increase in the level of this hormone has been observed under stress like high salinity, extreme temperature, and drought (Ng et al. 2014). Plant hormone ABA has manifold roles in plants and also is required for normal plant growth and development. A study showed that ABA production and ACC deaminase activity significantly enhanced in the isolated microbiomes with an increase in time duration (Rastegari et al. 2020a). A broad range of bacterial genera such as *Achromobacter*, *Alcaligenes*, *Azospirillum*, *Agrobacterium*, *Acinetobacter*, *Rhizobium*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Burkholderia*, *Ralstonia*, and *Serratia* are the bacterial strains showing ACC deaminase activity and ability for the ABA production (Kang et al. 2010; Kour et al. 2020c; Yadav 2017a).

5.4 Modification of Phytohormonal Activity by Plant Microbiomes for Better Pigmentation

Plant acts differently upon interaction with stress and implemented complex mechanisms. However every plant diversely responds to salinity, as having different potential for stress tolerance. The capacity of plants to adapt to changing environments is mediated by plant hormones, which regulate in allocation of nutrient for the growth and development of plant. Plant hormone is produced in less concentration and reaches to the site where regulation of metabolic process is required. All plant physiological activities are directly or indirectly regulated by the phytohormones (Shah et al. 2015). Plant pigment like chlorophyll is considered as one of the important measures for photosynthetic activities and is remarkably affected by abiotic stress. The plant hormones like indole-3-acetic acid and gibberellic acid are responsible for enhanced pigment content in stressed plant. This phytohormone under stress increased the number of chloroplasts per mesophyll cell in salted wheat leaves (Jha 2019c).

The main physiological/metabolic processes are regulated by phytohormone kinetin, under abiotic stresses in diverse crops. The phytohormones like ethylene, abscisic acid, and salicylic acid are involved in plant adaptation response under adverse environmental condition. The production, accumulation, and distribution of abscisic acid are the rapidest response of plant toward the abiotic stress for stomatal closure to prevent water loss during transpiration and ultimately restricting cellular growth (Peleg et al. 2011). The study showed that IAA or GA_3 or ABA remarkably augmented chlorophylls a and b and carotenoid concentration of plant leaves under salinity like abiotic stress. To analyze the effect of plant microbiomes on the chlorophyll pigment concentration, total chlorophyll has been extracted from 0.5 g of fresh leaves, by using 80% acetone. The supernatant of the extract obtained after complete bleaching of leaves is used to measure chlorophylls a and b and carotenoid at 663, 645, and 470 nm, respectively, using a spectrophotometer. In the study, chlorophyll content augmented in the plant inoculated with plant microbiomes, having ability for the production of IAA and GA_3. Chlorophylls *a* and *b* and carotenoid considerably are reduced under salinity stress, but inoculation with bacterial strain considerably increased the concentration of photosynthetic comparison to control plants. The plant microbiomes having ability to regulate the concentration of abscisic acid in the stressed plants resulted in larger chloroplast having greater amounts of grana and stroma for the efficient photosynthesis.

5.5 Plant Microbiomes Maintain the Photosynthetic Efficiency by Regulating Ethylene Phytohormone

The fundamental activities in plant life are maintained by the photosynthesis like important process for the production of carbohydrates/energy. The production, transportation, utilization, and storage of carbohydrates/energy are dynamic processes, which are directly reliant on the growth stage of the plant, plant organ, environmental state, and plant cell physiology. The synchronized environmental stimulus as availability of light, water, soil nutrients, or stress factors, as well as internal metabolic or physiological response, is straightly regulated by plant hormones, and the capacity of plants to react and adjust in the level of photosynthate is completely under the coordinated control of all above factors (Agulló-Antón et al. 2011). The plants and plant-associated microbiomes regularly produce plant hormone in normal as well under various stresses, to regulate all the metabolic and physiological activities of the plant.

The stress hormone ethylene is a common growth/stress regulator, and the level of ethylene under stress conditions like heavy metal toxicity, water logging, salinity, drought, or pathogenicity has deleterious effects and affects the overall plant growth response, but the presence of the plant microbiomes remarkably regulates it (Fig. 5.2) (Jha and Subramanian 2018). The report showed that ACC deaminase-containing plant microbiomes having ability to hydrolyze ACC, the precursor of ethylene, reduced the level of ethylene to rescue plants from stress-generated inhibitory effects, generated due to enhanced production of ethylene under stress, and regulate the process of photosynthesis, to protect its host (Jha 2019a, b).

Several metabolic processes may get affected by the overproduction of ethylene under stress, which induces defoliation and reduces photosynthesis and crop performance (Bhattacharyya and Jha 2012). The ACC deaminase enzyme-containing plant microbiomes can decrease ethylene concentration in plant and induce tolerance against the salinity stress, to enhance plant production (Zahir et al. 2010). Our results showed that the ACC deaminase activity increased with time after

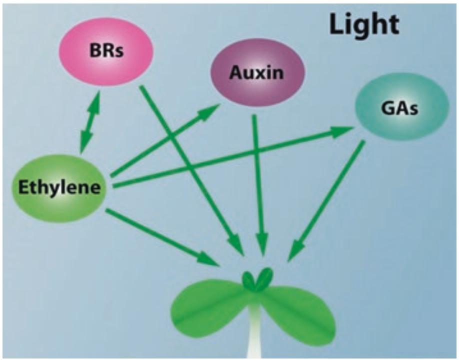

Fig. 5.2 The roles of plant microbiome phytohormones in cross talk between phytohormone signaling in plant

inoculating the plant microbiomes in suitable medium, indicating ACC deaminase activity of both the plant microbiomes.

5.6 Plant Microbiome Phytohormones Enhance Cell Wall Modification

Every cell of the plant is surrounded by cell wall and forms an active physical barrier to protect the cell from environmental factor and plant microbiome interaction. The cellulose, pectins, hemicelluloses, and glycoproteins are the main components of the plant cell wall, but the exact proportion of the cell wall polysaccharides varies between tissues to tissues/in the same tissue depends on its developmental stage. The cell wall endures vigorous chemical and structural changes, like change in callose deposition pattern, accumulation of antimicrobial compounds/reactive oxygen species, and formation of cross-linking in cell wall protein and cell wall lignifications (Eggert et al. 2014) upon pathogen infection, which cumulatively restrict the pathogen invasion/pathogen progression. The cell wall integrity of the plant can be activated by phytohormone-signaling cascades during intracellular events, to activate defense responses. The controlled and coordinated cell division, differentiation, and growth of plant cell are main functions of plant hormones.

The phytohormone auxin is involved in various developmental processes and is responsible for cell expansion during the normal growth as well as during infection (Zhao 2010). During infection/acid growth, phytohormone auxin lowers down the pH of the infected cell by stimulating plasma membrane proton pumps, responsible for the activation of expansions which relax the cell wall, but the production of expansions is stimulated by ABA, ethylene, and cytokinin phytohormone. The phytohormone auxin produced by plant microbiomes modulates the activity and expression of the cell wall modifying enzymes under unfavorable environmental condition. Auxin produced by plant microbiomes also inducts the most important defense proteins like class III peroxidase, main players for remodeling of secondary cell, and helps in the polymerization of phenolic monomers into suberins and lignins. In the study lignin monomers and total lignin were analyzed by homogenizing the leaf sample in 50 mM sodium phosphate buffer at pH 7.0, purified in 1% Triton X-100, 1 M NaCl, and acetone and centrifuged for 15 min.

The pellet obtained was protein freed from cell wall which was properly dried and used for quantification of lignin monomers and total lignin. Lignin monomers are quantified by using alkaline nitrobenzene peroxidation, and lignin is quantified by thioglycolic acid. Plant cell wall is necessary for protection, strength, shape, and rigidity and to glue cells together with the entire plant. Under abiotic stress lignin has two main interfaces: (i) lignin biosynthesis gets affected by many abiotic stresses and results in variation in lignin content of the plant, and (ii) lignification is one of the important ways to confer tolerance to abiotic stresses by altering the plant fitness. In a study, maize plant inoculated with isolated microbiomes shows enhanced

Table 5.2 Effect of plant microbiome phytohormone on the cell membrane stability, phenols, flavonoid, lignin, and lignin monomer in maize plant

Treatment	Cell membrane stability	Phenols (mgg^{-1} of the gallic acid equivalent)	Flavonoids (ODg^{-1})	Lignin	Lignin monomers
Normal					
Control	143.4^{cd}	0.72^{cd}	7.83^{cd}	1.24^{cd}	0.71^{d}
Control + *P. aeruginosa*	157.1^{bc}	0.86^{bc}	8.65^{c}	1.46^{c}	1.13^{c}
Control + *P. aeruginosa*	169.7^{b}	0.94^{ab}	9.53^{ab}	1.63^{b}	1.34^{b}
Control + *P. aeruginosa* + *P. pseudoalcaligenes*	182.3^{a}	1.21^{a}	9.86^{a}	1.72^{a}	1.46^{a}
Stressed					
Control	69.1^{cd}	0.86^{cd}	8.72^{cd}	0.91^{d}	0.91^{cd}
Control + *P. aeruginosa*	76.4^{bc}	0.93^{c}	9.84^{bc}	1.36^{bc}	1.21^{c}
Control + *P. aeruginosa*	84.7^{ab}	1.22^{b}	10.8^{ab}	1.48^{b}	1.37^{ab}
Control + *P. aeruginosa* + *P. pseudoalcaligenes*	91.6^{a}	1.42^{a}	11.7^{a}	1.59^{a}	1.52^{a}

Values are the means of replicates. Values with different letters are significantly different at $P < 0.05$ (Duncan's test). Values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

deposition of lignin monomers and total lignins under normal as well as salinity stress (Table 5.2). Similarly higher gathering of lignin monomers took place in the plants treated with *P. aeruginosa* as reported by Martinez et al. (2004). Wang et al. (2012) also reported enhanced deposition of lignin in transgenic rice line under salinity which is more tolerant than its wild type.

Similarly the total phenols and flavonoids are also analyzed by using 20 mL methanol (80:20, v/v) extract of (1 g) leaf for 15 min. The total phenolic content has been estimated by using this leaf extract by taking absorption at 735 nm, and gallic acid is used for standard curve. Similarly the colorimetric assay (735 nm) is used for estimation of flavonoid by using leaf extract in aluminum chloride. Phenolics are most abundant secondary metabolites of plant and are frequently distributed in the plant kingdom, having one or more aromatic rings with one or more hydroxyl groups. It includes tannins, flavonoids, phenolic acids, lignans, and stilbenes. Other common secondary metabolite in plant like phenolic acids is flavonoids, synthesized by the polypropanoid pathway, and phenylalanine molecule acts as precursor. The study showed that inoculation of plant microbiomes having ability for phytohormone production is efficiently sufficient for the enhanced production of phenolic and flavonoid content in maize plant, while further increase has been observed under salinity. Ghasemzadeh et al. (2010) reported that synthesis of phenolics and flavonoids in ginger can be increased and affected by under abiotic stress.

The phytohormone cytokinin also regulates expansin and directly influences the cytokinin-induced change of wall extensibility, whereas auxin secreted by the plant microbiomes suppresses the cytokinin-induced stress genes to suppress the cell wall invasion (Choi et al. 2011). ABA phytohormone also promptly boosts accumulation of pectic arabinan in plant cell, and arabinan is tangled in the cell-to-cell connection and influences the mechanical property of the cell wall (Verhertbruggen et al. 2013). The microbial phytohormone has direct relation with cell growth and is irreversible. All cell has ability for rapidly initiating and stopping the process of cell enlargement in fraction of minute, indicating the well-managed molecular mechanism for the irreversible wall expansion is modulated by plant microbiomes for its dynamical control. Burton et al. (2010) reported that the primary wall of growing cell is a dynamic, delicate, versatile structure having exceptional properties and functions in the life of the plant. Several auxin-responsive genes have been shown to be upregulated in elongating plant part, and cell wall-related genes encoding wall-loosening and pectin modification are also under the influence of plant microbiomes.

5.7 Plant Microbiomes Develop Resistance Under Biotic Stress by Regulating Phytohormone

Plants have continuous interaction with several different microbes. Rarely plants get effected by pathogen during such interaction as plant is able to discriminate efficiently among the potential pathogen/other microbes. Upon interaction with pathogen in their vicinity, plant induces defense mechanism that blocks colonization of environmental microbes responsible for plant disease (Spoel and Dong 2012). At the same time, plant pathogens also develop a diverse mechanism for invading plant tissue or to minimize the host defense effects, for its colonization in plant tissue. Such colonization is necessary to avail the nutrient from the host for its growth and disease development (Kaur et al. 2020; Singh et al. 2020). Plant develops the ability to identify the common pathogen-origin compounds like peptidoglycan, lipopolysaccharide, and flagellin proteins, for the instant induction of its defense response.

The series of defense response simultaneously activated in the plants are stomatal closure, production of antimicrobial compounds, induction of lytic enzymes, and accumulation of higher levels of defense-signaling hormones and rapid oxidative burst, which act mutually to protect the microbial growth in the plant cell. The most common plant defense hormones are ethylene, salicylic acid, and jasmonates, which play a main role in modulating defenses against pathogen. The level of ethylene in the infected plant cell is well modulated by plant-associated microbiomes, to protect their host from biotic stress (Fig. 5.3). The biotrophic and hemi-biotrophic pathogens generally colonizing living tissue are regulated by salicylic acid, and the necrotrophic pathogens generally vigorously killing plant cells to get nutrients are regulated by jasmonate. By adapting lipoxygenase (LOX) pathway, jasmonate plant hormone is directly related with wound infection and stimulates the production of antibacterial proteins. Afterward methylation of jasmonate takes place to act as a signal transduction molecule for the activation of plant defense mechanism in entire plant. The jasmonate production in plant is also induced by plant microbiomes,

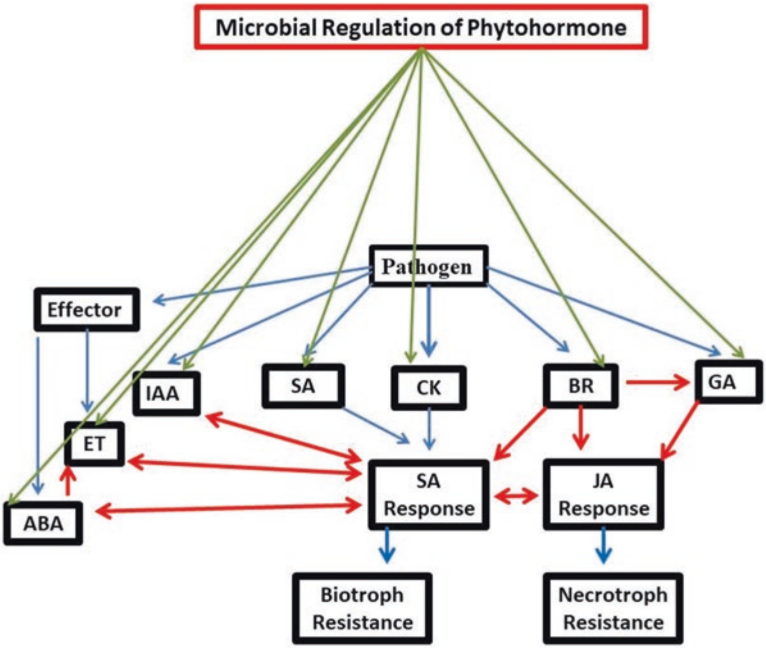

Fig. 5.3 The possible roles of plant microbiomes phytohormones in biotic stress and cross talk between phytohormone signaling

which, further enhanced by ethylene signaling, results in reduced SA signals (Jia et al. 2013). At the same time, SA production in plant induced by plant microbiomes nullifies the effect of ABA.

Ethylene a well-known stress hormone has many roles in plant as in seed germination and growth response toward environmental stimuli (Kour et al. 2019b). Hence for the proper growth of plant under normal as well stress condition requires perfect regulation of phytohormone as a survival response. Although regulation of plant defenses is relatively complex, several studies show existence of remarkably coordinated interaction among the SA, JA, and ethylene defense signaling for the establishment of perfect signaling network (Jha 2019d). Not only that, this perfect signaling network is further regulated by many other phytohormones like gibberellins, auxin, and abscisic acid, and finally the plant-associated microbiomes by producing and regulating phytohormone try to manage plant in any condition. But sometimes, this mechanism has been mimicked by the plant pathogen to establish infection by producing virulence factors or phytohormones, to modify hormone signaling (Kazan and Lyons 2014). The auxins produced by the plant microbiomes in the infected host plant cell initiate several pathogenesis-related mechanisms like stimulation of gall formation, epiphytic colonization, restriction of pathogen growth, and activation of host defenses (McClerklin et al. 2018). Many times auxin produced by pathogens themselves, which may act as a virulent factor for stimulating the plant defense mechanism.

These hormone pathways lead to the expression of defense-related genes also that suppress pathways for pathogen progression, and each hormone modulation is necessary for specific cross talk between growth response variables and environmental stimuli. And such fine-tuning of hormonal level in plant is mostly achieved by plant-associated microbiomes. In the context of necrotrophic interactions and biotrophic interactions, the roles of ABA are better understood in plant resistance toward phytopathogens. ABA can stimulate stomatal closure to interfere with the pathogen entry in plant cell, making it a specific mechanism for developing resistance toward a variety of necrotrophic pathogens (López-Baena et al. 2008). Upon induction of ABA by plant microbiomes, there is increased resistance against *A. brassicicola* and *P. cucumerina* (a necrotrophic pathogens) in host plant (Ton and Mauch-Mani 2004), achieved through improved production of callose and arabinan, which alter the permeability of the cell wall. The rapid initiation and enhanced level of ROS burst during infection as well as altered gene expression involved in cell wall modification takes place due to regulated expression of phytohormone by the plant microbiomes.

5.8 Plant Microbiomes Develop Resistance Under Abiotic Stress by Regulating Phytohormone

Abiotic stress like extreme temperature, heavy metals, drought, and salinity has detrimental effect on plant morphology and physiology. Plants being static are continuously exposed to different stress factors, which affect the process of genetic regulation for important biochemical pathways. So plant also developed multiple mechanisms to overcome the effect of environmental stress, which may be responsible for the alteration of metabolic pathway. Plant growth is naturally regulated by plant hormones, having a protruding influence on plant metabolism and also having a positive role in activation of plant defense response against the potential stress factors (Kour et al. 2020d). Even exogenous supplement with phytohormone implies positive response on plant growth and develops tolerance against the abiotic stress. Previous studies showed that phytohormones are also produced by plant microbiomes in the plant host and improved plant growth response and tolerance against stresses (Fig. 5.4).

Under abiotic stress, the plant activities are controlled by ethylene hormone, and the level of ethylene in the plant has direct relation with abiotic and biotic stresses. In the biosynthetic pathway of ethylene, S-adenosylmethionine is converted by 1-aminocyclopropane-1-carboxylate synthase to 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor for ethylene production. The plant hormone ethylene endogenously controls plant homoeostasis, resulting in reduced root and shoot growth under stress. The ACC of the plant is degraded and confiscated by

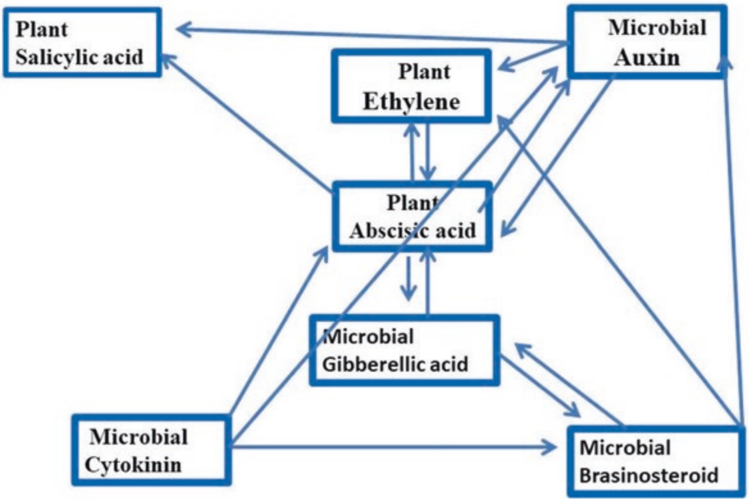

Fig. 5.4 The possible roles of plant microbiome phytohormones in abiotic stress tolerance and cross talk between phytohormone signaling

ACC deaminase enzyme produced by plant microbiomes to fulfill its energy and nitrogen requirement. So such plant microbiomes reduce the level of ACC to reduce the deleterious effect of stress and enhance plant growth (Jha et al. 2014). Mayak et al. (2004) reported that *Achromobacter piechaudii* ARV8 remarkably improved the dry and fresh weight of two crops pepper and tomato and reduced ethylene production under drought condition by ACC deaminase activity. ABA having multiple functions is normally necessary for the growth and development of plant.

ABA also encourage complete or partial opening of stomata, which is generally stimulated by the light for gas exchange. ABA-induced complete or partial closure of stomata caused reduced gas exchange and finally caused reduced transpiration and photosynthate production (Mittler and Blumwald 2015). By decreasing transpiration and increasing water influx into roots, ABA is able to regulate the cell turgor. In this study, both the isolated microbiomes have the ability for the production of phytohormones like ABA, gibberellic acid, auxin, and ACC deaminase. The expression of stress-responsive genes is mainly synchronized by ABA-mediated and ABA-induced signaling under abiotic stress, leading to an efficient stimulation of stress tolerance responses in plant (Sah et al. 2016). During stress a sudden increase in ABA level in stress cell can result in retarded plant growth, to also modulate tolerance responses against stresses (Asgher et al. 2015). However, positive regulation of ABA resulted in reversing the unfavorable effects of stress. In addition, ABA also regulates root growth and water content under saline/drought stress conditions.

The phytohormone like abscisic acid is an important hormone responsible for improving stress responses and adaptation under stress. So such plant microbiomes can be significant for metabolic engineering objectives for stimulating host tolerance to abiotic stress. Due to upcoming techniques in genetic engineering, the identification of phytohormone biosynthetic pathways and phytohormones normally involved in the normal growth of plant as well as in helping plants to develop tolerance against biotic or abiotic stress is nowadays possible.

5.9 Conclusion and Future Visions

The regulation of phytohormone plays an important role in developing ability of plant to develop resistant/tolerance against the stress. Plant microbiomes having ability for the production and regulation of plant hormone is one of the new ways for sustainable crop production in an eco-friendly manner for growing population under changing environmental condition. The improved photosynthetic pigment, regulated photosynthesis, which helps in the growth and development of crop plant under stress. Plant microbiomes having ability for the production and regulation of plant hormone will be obliging to agricultural microbiologists and plant physiologists in developing the strategies and mechanisms for the designing of broad-spectrum microbial inoculants for sustainable crop production under unreceptive environments.

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Chapter 6

Mechanisms of Plant Growth Promotion and Functional Annotation in Mitigation of Abiotic Stress

Enespa, Prem Chandra, and Ranjan Singh

Abstract Rhizomicrobiome improves abiotic stress tolerance in plants and promote their improvement. These plant growth-promoting microbiomes stimulate the growth of the plants by diverse mechanisms. These microorganisms help the plants in acquisition of unavailable nutrients such as phosphorus, zinc, and potassium and produce siderophores and different phytohormones such as auxins, gibberellins, and cytokinins. They secrete subordinate metabolites and antibiotics that further stimulate the growth of the plants during stress condition. Therefore, use of PGPB is a novel approach, and use of such approaches in research is needed to appreciate the ecological, genetic, and biological associations in the territory.

Keywords Abiotic stress · Antibiosis · HCN · PGPR · Resistance · Siderophore · Tolerance · Volatile

6.1 Introduction

Rhizospheric microbiomes play an important role in regulating the growth of the plants ultimately improving the productivity (Lemanceau and Blouin 2018; Raiesi and Salek-Gilani 2018). They promote plant growth through biogeological rotations of complex nutrients in the soil (du Jardin 2015; Chen et al. 2019; Zhang et al.

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2019a, b). They protect the plants from phytopathogens (Hanafi 2013; Chandra and Singh 2016). They also play a vital role in decontaminating the environment by biodegrading the complex xenobiotic compounds such as chemicals and also decreasing the biological or physical stress of plants (Bajguz and Hayat 2009; Maksymiec 2007). In fact, the microflora has established itself sufficiently next to the roots of plants (rhizobacteria), which is responsible for great flexibility in collecting, fluctuating, and dissolving the ingredients associated with those from soils (Souza et al. 2015; Beattie 2007).

The executive system of plant ingredients integrated is much prosperous for promoting the construction of crop among biologists and agronomists by using biotic methodologies (Robertson and Swinton 2005; Altieri and Toledo 2011). In this perception, these rhizobacteria which have innovative traits such as heavy metal-reclaiming aptitudes, saline forbearance, elimination of pest chemicals, and biocontrol of phytopathogens and beetles (Oliver and Martinez 2014; Janson et al. 2008), such as phytohormones, nitrogenase activity, ammonia formation, and solubilization of phosphate along with the naturally phytogrowth enhancing possessions (Uphoff et al. 2006), and also vital for productiveness of soil, should be exposed frequently and globally for greater sustenance (Kuzyakov 2010; Power 2010). Consequently, the symbiotic and non-symbiotic microbial inoculants are consumed worldwide to stimulate the development of plant and under several pressures such as organic and inorganic complexes (Ahemad and Kibret 2014; Hayat et al. 2010).

Several stresses such as flooding and salinization of crop in cultivated area and the existence of environments for the development and improvement of harvests are the consequences of change in climate (Miraglia et al. 2009). The unfavorable conditions, comprising a diversity of contrary ecological disorders (i.e., drought, flooding, saline soil, toxicity of pesticide and heavy metal, scarcity of nutrient, and high temperatures), lead to a series of physiological, morphological, molecular, and biological alterations affecting the growth and productivity of crops and worldwide subsistence (Spinelli et al. 2011; Hajiboland 2012; Ramírez and Maiti 2016). Plants adopted these stresses and developed various mechanisms to respond (Sunkar et al. 2012). A multiple signaling pathways of common network which facilitated various stresses such as salinity, flooding, scarcity, and extreme temperatures pressure responses in plants recommended on molecular and physiological basis (Cramer et al. 2011; Huang et al. 2012; Yadav 2017). For example, the drought and salinity exposed largely as osmotic stress, following the interference of homeostasis and ionic delivery in cell (Qiu et al. 2012; Ilangumaran and Smith 2017; Gantait and Mondal 2018). The abiotic stress such as salt, drought, and high temperature stress causes oxidative stress and leads to denaturation of executive and physiological proteins (Farooq et al. 2009; Yadav and Yadav 2018).

Stress cell signaling pathways activate metabolic activities in plants for subsisting and molecular responses, like antioxidants induction, production, and accumulation of compatible solutes and stress proteins (Chinni 2016; Thangaraj et al. 2019). This chapter elaborates the theory of rhizospheric bacteria and their plant growth promotion mechanisms and remediation of abiotic stress with latest updates (Fahad et al. 2015; Ojuederie and Babalola 2017; Chandra and Enespa 2019c). Rhizobacteria which mitigate the abiotic stress in various agro-biotas have been offered to harvest the wide range of perspectives about their applicability is the modernized examples (Chandra and Enespa 2016; Enespa and Chandra 2019).

6.2 Biodiversity of Plant Growth-Promoting Bacteria

Inter- and intraspecies variations at species level in living organisms in ecology are known as biodiversity (Rosselló-Móra and Amann 2015; Stat et al. 2017). Additional revenue can be generated using exploit to beneficial soil microbes isolated and characterized for the sustainable agriculture and human health (Bouis and Welch 2010; Altieri 2018). In soil rhizospheric ecosystem, the microbial diversity overdoes more than eukaryotic entities (Podolich et al. 2015; Kuppusamy et al. 2018). The association of microbial biodiversity with crops belong to various genera as follows *Arthrobacter*, *Brevibacterium*, *Cellulomonas*, *Corynebacterium*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Mycobacterium*, *Rhodococcus*, and *Streptomyces*), *Bacteroidetes* (*Flavobacterium psychrophilum*, *Flavobacterium* sp., *Sphingobacterium* sp., *Chryseobacterium humi*), *Balneolaeota*, *Basidiomycota*, *Cyanobacteria*, *Firmicutes* (*Bacillus aerophilus*, *B. alcalophilus*, *B. altitudinis*, *B. amyloliquefaciens*, *B. aquimaris*, *B. cereus*, *B. circulans*, *B. endophyticus*, *B. flexus*, *B. fusiformis*, *B. licheniformis*, *B. megaterium*, *B. methylotrophicus*), *Proteobacteria (Pseudomonas fluorescens*, *P. protegens,* and *Azotobactor agilis*, *A. chrococcum*, *A. beijerinckii*, *A. vinelandii*, *A. ingrinis*), and *Spirochaetes* (Verma et al. 2015a, b, 2016; Yadav et al. 2017e, 2020; Enespa et al. 2020). *Firmicutes* has been found to be the most dominant among all reported phylum followed by *Proteobacteria*. The α-, β-, and γ-proteobacteria group have been reported from paddy fields such as rice, maize, sugarcane, and chick pea (Reddy and Lalithakumari 2009; Marasco et al. 2012). These microbes advantageous to ecosystem have been reported commonly as well as niche or host-unambiguous. These microflora perform a significant part in specific crop plants in diverse abiotic stress provinces (Yuan et al. 2010; Gaiero et al. 2013; Pieterse et al. 2014).

6.3 Interactions of Plant-Microbes

The plant-microbe interactions may be useful and detrimental depends on characteristic of the bacterial community and its interaction pathway (Turner et al. 2013; Hardoim et al. 2015). These rhizospheric microflora promote plant growth and provide high yields in crops and also work as a biocontrol against phytopathogens (Beneduzi et al. 2012; Ahemad and Kibret 2014; Chandra and Enespa 2019c).

Furthermore, the observations indicate that the PGPR have capability to boost abiotic stresses (Grover et al. 2011; Kang et al. 2014). The attribution of rhizobacteria functions can be used to remove the pesticidal, heavy metal, and chemical fertilizer pollutions (Lenart-Boroń and Boroń 2014; Ayangbenro and Babalola 2017; Kour et al. 2019c). A wide range of metabolites and hormones like indole acetic acids (IAA), ethylene, and gibberellins secreted by PGPR enhance the germination of seed, shoot, and root growth of plant and regulate the cell content according to ambient biotic and abiotic stresses (Iqbal 2014; Yadav et al. 2017a, c, f). These rhizospheric bacteria have capability to provide nitrogen, Zn, K, and mineral phosphates (Mohammadi and Sohrabi 2012; Ahmad et al. 2016).

These PGP bacteria have close relationship between the host plants and rhizobacteria (Francis et al. 2010; Rolli et al. 2015; Abbamondi et al. 2016). Bacteria first occupy the rhizosphere during the colonization process (Hardoim et al. 2008; Kim et al. 2011; Etesami et al. 2015a, b). The endophytes enter through the root zone and have capabilities to enter in plant tissues and infiltrate the plant cells often conversing valuable properties on hosts (Lattanzio et al. 2008; Bright and Bulgheresi 2010; Chandra and Enespa 2019a, b). The machineries like parasitism, competition, and antibiosis achieved through the biological control unfavorably affect the suitability, existence, and imitation of nematodes (Raaijmakers et al. 2009; Oliver et al. 2010; Verma et al. 2017b).

6.4 Mechanisms of Plant Growth-Promoting Rhizobacteria

The ingredients secreted from root exudates of plants perform a significant character to take up and stimulating rhizobacteria (Dennis et al. 2010; Doornbos et al. 2012). These microbes' doorknobs utilize the organic constituents of exudates as sources of energy which depends on the nature and concentrations (Moe 2013; Rana et al. 2020a; Verbon and Liberman 2016). Agriculturally important microbes associated with plants can improve the plant biomass and also nutritional quality through the biological N_2 fixation and other mechanisms (Adesemoye and Kloepper 2009; Kour et al. 2020a; Pineda et al. 2010). The secretion of phytohormones like IAA and cytokines; plant growth-promoting rhizobacteria biocontrol of phytopathogens through the production of antifungal or antibacterial agents, siderophore, nutrient competitions and induction of assimilated host resistance or augmenting the bioavailability of minerals through the PGPB (Lacava and Azevedo 2013; Rastegari et al. 2020b; Singh and Yadav 2020). The microflora of rhizospheric niche promotes the growth of plants after secretion of various biochemical compounds through the PGPR mechanisms (Kaur et al. 2020; Kumar et al. 2019; Rajawat et al. 2020; Singh et al. 2020) (Table 6.1). The growth of plants promoted directly through rhizospheric bacteria using soluble mineral phosphate, emancipating siderophore which liquefy the sequester irons and atmospheric nitrogen fixation and regulate the levels of phytohormones at several growth stages of plant (Gamalero and Glick 2011; Souza et al. 2015). Plant growth promotion mechanism arises indirectly after the

Table 6.1 List of plant growth-promoting rhizobacteria and its mechanism

PGPR	Crops	Mechanisms of PGPR	Remarks	Application	References
Herbaspirillum	*Oryza sativa*	Nitrogen fixation	GFP-tagged cells of *Herbaspirillum* sp. strain B501gfp1 were apparently localized in intercellular spaces of shoot tissues of 7-day-old seedlings of *O. officinalis* W0012	Seed was inoculated	Verma (2019)
Azorhizobium	*Triticum aestivum*	Nitrogen fixation	Five weeks after inoculation with *A. caulinodans* IRBG314, there were approximately five times more short lateral roots, each up to 3 mm in length, present on inoculated wheat	2 mL of rhizobial culture were added four times to each wheat plant, once during the planting of the seeds, and subsequently three times at 1-week intervals	Palaniappan and Annadurai (2018)
Pseudomonas putida, *Azotobacter chroococcum*	*Ocimum basilicum*	Antibiotic production	Increased vitamin, flavonoid, and antioxidant activity	Seedling was inoculated	Jiménez-Gómez et al. (2017)
Rhizobium	*Lactuca sativa L.*	Siderophore production	The colonies of strain TPV08 were surrounded by a yellow-orange halo (3.5 mm radium around colonies) indicative of siderophore production	Seed Inoculation Seedlings were inoculated with 250 lL plant’1 of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5^109 CFU/mL´1)	Zaidi et al. (2017)
Azoarcus	*Oryza sativa*	Nitrogen fixation	The presence of *Azoarcus* in the steel, especially in the stelar tissue of culms, suggests that these bacteria might spread systemically in situ and underline their endophytic life style	Plants were grown gnotobiotically with a mutant of strain BH72 expressing the β-glucuronidase gene constitutively	Vejan et al. (2016)

(continued)

Table 6.1 (continued)

PGPR	Crops	Mechanisms of PGPR	Remarks	Application	References
Bacillus	*Medicago sativa*	Antibiotic production	Filtrates of cultures suppressed alfalfa disease caused by *P. medicaginis* and inhibited the growth of the pathogen in an agar plate assay	Seedling was inoculated	Vejan et al. (2016)
Phyllobacterium	*Fragaria x ananassa*	Phosphate solubilization	Strain PEPV15 was able to solubilize moderate amounts of phosphate (5 mm radius around the colonies)	The strawberry seedlings were inoculated with 1 mL of 108 CFU/mL suspensions	Flores-Felix et al. (2015)
Phyllobacterium	*Fragaria x ananassa*	Siderophore production	The strain grew on the CAS indicator medium where the colonies were surrounded by a yellow-orange halo (3.5 mm radius around colonies) indicative of the siderophore production	The strawberry seedlings were inoculated with 1 mL of 108 CFU/mL suspensions	Flores-Felix et al. (2015)
Gluconacetobacter	*Saccharum officinarum*	Nitrogen fixation	The endophytic establishment of *G. diazotrophicus* within stems of sugarcane was confirmed by the scanning electron microscopy	Root-dipping of seedlings for 1 h	Baldani et al. (2014)
Bacillus	*Arachis hypogaea*, *Zea mays*	Induction of plant stress resistance	Increasing salt concentrations, biological N fixation may be competitive, becoming a more economic and sustainable alternative to chemical fertilization. The bacterial inoculants increased the total N, P, and K contents of the shoot and root of maize in calcisol soil from 16% to 85% significantly as compared to the control counterpart	Plants were inoculated with 1 mL of a 108 cfu suspension Seed-dipping for 30 min	El-Akhal et al. (2013)
Chryseobacterium	*Lycopersicon esculentum*	Siderophore production	Siderophore production increased as bacterial biomass increased after 16 h of culture	Soil drenched	Radzki et al. (2013)

Rhizobium	*Piper nigrum*, *Lycopersicon esculentum*, *Lactuca sativa*, *Daucus carota* subsp. *sativus*	Indole acetic acid synthesis	The dry weight of the inoculated seedlings (shoots and roots) was more than twice with respect to the uninoculated seedlings. Concentrations of N, P, and Ca were significantly higher in inoculated plants, indicating that they had higher potential for nutrient uptake than control plants	Seed Inoculation Seedlings were inoculated with 250 μL plant^{-1} of a bacterial suspension with a turbidity of 5 inMcFarland standards (1.5 × 109 CFUmL^{-1})	Flores-Felix et al. (2013)
Rhizobium	*Piper nigrum*, *Lycopersicon esculentum*, *Lactuca sativa*	Indole acetic acid synthesis	The dry weight of the inoculated seedlings (shoots and roots) was more than twice with respect to the uninoculated seedlings. Concentrations of N, P, and Ca were significantly higher in inoculated plants, indicating that they had higher potential for nutrient uptake than control plants	Seed Inoculation Seedlings were inoculated with 250 μL plant^{-1} of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5 × 109 CFUmL^{-1})	Garcia-Fraile et al. (2012)
Bacillus	*Piper nigrum*, *Cucumis sativus*	Potassium solubilization	The results showed that there was a relatively higher availability of P and K in soils planted with pepper than with cucumber	Seedling was inoculated with 1 mL of inoculum containing around 108 cells	Poorter et al. (2012)
Bacillus	*Cucumis sativus*	Cytokinin synthesis	Cucumber seedlings subjected to bacterization had well-developed lateral roots	Seed-dipping 106 cells/mL (106 CFU/mL)	Sokolova et al. (2011)
Bacillus	*Solanum tuberosum*	Auxin synthesis	Both the strains enhanced the auxin content of inoculated plants up to 71.4% and 433%, respectively, as compared to non-inoculated plants	Seed-dipping (108 mL^{-1} cfu)	Ahmed and Hasnain (2010)

(continued)

Table 6.1 (continued)

PGPR	Crops	Mechanisms of PGPR	Remarks	Application	References
Bacillus	*Piper nigrum*, *Cucumis sativus*	Potassium solubilization	The results showed that there was a relatively higher availability of P and K in soils planted with pepper than with cucumber	Seedling was inoculated with 1 mL of inoculum containing around 108 cells	Schwarz et al. (2010)
Pseudomonas	*Cajanus cajan*	Chitinase and β-glucanases production	*P. fluorescens* LPK2 and *S. fredii* KCC5 showed chitinase activity on chitinase minimal medium. β-1,3-glucanase activity was more pronounced in the fluorescent pseudomonads strains	The method of Weller and Cook (1983) was adopted for seed bacterization	Kumar et al. (2010)

decreasing of detrimental effect of microbial phytopathogens through rhizospheric bacteria (Huang et al. 2013; Glick 2014; Verma et al. 2018).

6.4.1 Direct Mechanisms

6.4.1.1 Plant Hormone Production

The growth of plant regulated by phytohormones, in response to environmental factors work as molecular signals that limit the growth of plants or in uncontrolled condition becomes lethal (Harb et al. 2010). The hormone balance in plants is manipulated by several rhizospheric bacteria to secrete hormones for root absorption and improvement of growth and stress response (Nadeem et al. 2014; Venturi and Keel 2016; Kour et al. 2019c; Rana et al. 2019; Suman et al. 2016).

Auxins The auxins secretion to extent strongly effects development of root and shoot predominantly (Francis et al. 2010; Mitter et al. 2013; Pereira et al. 2016). The auxin is known as indole-3-acetic acid (IAA) secreted by PGPR, which involved in collaborations of plant-microbes. The exogenous utility of IAA is dependent in plants on the endogenous IAA levels, and the solicitation of bacterial IAA may have neutral, positive, or negative effects on the growth of plants (Martínez-Viveros et al. 2010). In auxins the transcriptional changes in hormone, defense, and cell wall-related genes which have been observed (Stearns et al. 2012) induce longer roots, decrease stomata size and density, increase root biomass, and stimulate auxin response genes that augment the growth of plants (Niu et al. 2012). Auxin (indole-3-acetic acid/indole acetic acid/IAA) documented for a cell division and differentiation as well as cell elongation responses in plant produced by microbial plant hormones (Chaiharn and Lumyong 2011). From the rhizospheric regions, 80% microbes have capability to yield auxins as secondary metabolites from various crops. Plant hormones ABA, IAA, and cytokinins linked to nitrogen signaling industriously and provide perception that nitrogen and phytohormones signals are integrated in order to alter the morphological and physiological characters of plants.

Cytokinins Cytokinins are widely distributed in both prokaryotes and eukaryotes, but a little information is accessible on the roles of bacteria-produced cytokinins. Cytokinins are produced and translocated from root tips to shoot tips through the xylem and also control the cell differentiation in plant meristematic tissues (Bashan and De-Bashan 2010; Olanrewaju et al. 2017). The first cytokinin discovered from yeast not from plants was kinetin so it is considered as a “synthetic” cytokinin (Higuchi et al. 2004; Arteca 2013). Zeatin was isolated and identified from *Zea mays* plants firstly. On basis of structure, two groups of cytokinins, the adenine and phenyl urea type, are found (Sakakibara 2010; Cassán et al. 2014). Kinetin and zeatin are adenine type, and diphenyl urea and thidiazuron are phenyl urea (Ricci and Bertoletti 2009). The cytokinins regulate apical dominance, cell division, root elongation, seed sprouting, xylem and chloroplast differentiation, flowers and fruit development, nutritional signaling, leaf senescence, and interactions of plant-pathogen (Ruan 2014; Arnao and Hernández-Ruiz 2015). The gene expression in cytokinin is the evident, and their flourishes to growing plants alter the plant's phytohormone composition in several PGPB.

The content of cytokinin and plant growth has been increased in lettuce with the inoculation of *Bacillus subtilis* (Halpern et al. 2015; Etesami and Beattie 2018). It is observed that the cytokinins delay the senescence in plants by the accumulation of chlorophyll, tissue, root hair formation, initiation of stem, and elongation of leaves based on experimentations (Evert 2006; Bowman 2012). Cytokinin overproduced from a genetically engineered strain *Sinorhizobium meliloti* was tested for its capability to protect the alfalfa plants against senescence resulting from drought conditions (Carmen and Roberto 2011; Forni et al. 2017). The fivefold production of cytokinin was observed in transformed bacterium than wild type (Cortina and Culiáñez-Macià 2004). The alfalfa plant size increases marvelously after inoculation of transformed strains compared to the non-transformed strain in extreme drought conditions (Pillay 2012; Almerei 2016). The rhizobial strains synthesize higher cytokinins and have capability to increase the tolerance of scarcity in alfalfa plant which has been indicated in experiments (Holguin Zehfuss 2001; Xu et al. 2012; Van Oosten et al. 2017).

Ethylene Ethylene is an active gaseous hormone at enormously less concentrations (0.05 mL L^{-1}) and is a "stress hormone," as established by its kindness determined during several abiotic and biotic pressures. The ethylene increases leniency of plants or worsen stress response signals and senescence in response to stress (Dubois and Inzé 2015; Swift 2016; Nguyen 2018). In both unfavorable and favorable conditions, PGPR functions have been revealed more growth stimulation in stress conditions such as scarcity (Dodd and Ruiz-Lozano 2012; Naveed et al. 2014a; Backer et al. 2018). For the plant stress, tolerance expands some PGPR ethylene and plays an important role (Berg 2009). Synthesis of ethylene in higher plants involves the following enzymes: (i) the S-adenosyl-l-methionine (SAM) synthetase enzymes catalyze the alteration of methionine to SAM (Eustáquio et al. 2009; Chu et al. 2013), (ii) 1-aminocyclopropane-1-carboxylic acid (ACC) synthase accelerates the hydrolysis of SAM to ACC and 5'-methylthioadenosine (MTA) (Sauter et al. 2013; Van de Poel and Van Der Straeten 2014), and (iii) ACC oxidase catalyzes the renovation of ACC to ethylene, carbon dioxide, and cyanide (Abeles et al. 2012). The ethylene production reduces in plants which are secreted by 1-aminocyclopropane-1-carboxylase (ACC) deaminase (Jha and Saraf 2015; Santoyo et al. 2016). Several observations have been revealed that the production of ACC deaminase enhanced the stress leniency in plants through the booster with PGPR. It seems that the PGPR have the capability to maintain the ethylene levels from reaching levels adequate to decrease plant growth monitored in *Camelina sativa* (Ahmad et al. 2018).

Gibberellins Large amounts of gibberellins can promote some PGPR strains to enhance the shoot and plant biomass (Kurepin et al. 2014). The root architecture is altered with the interactions of this hormone with auxins (Spaepen et al. 2014). A group of tetracyclic diterpenoid carboxylic acids having C20 or C19 carbon skeletons includes in gibberellins (Thomas and Hedden 2018). There are a total of 136 gibberellin structures represented as GA1–GA136 (Studt and Tudzynski 2014). There are four structures, GA1, GA3, GA4, and GA20, identified in bacteria (Khan et al. 2014), in which the GA1 and GA4 are the most active (Eriksson et al. 2006). These hormones are applicable for growth stimulation and activation of vital growth practices such as stem elongation, seed germination, flowering, and fruit setting (Rademacher 2015) and increase the rate of photosynthesis and the chlorophyll content of plant (Elias et al. 2012; Voesenek and Bailey-Serres 2015). The PGPR-produced cytokinins also lead to boost of root exudate production by the plant (Liu et al. 2013). *Achromobacter xylosoxidans*, *Gluconacetobacter diazotrophicus*, *Acinetobacter calcoaceticus*, *Rhizobia*, *Azotobacter* spp., *Bacillus* spp., *Herbaspirillum seropedicae*, and *Azospirillum* spp. are the PGPB genera which has been observed for the production of these hormones (Huang 2014; Garoutte 2016; Mustafa et al. 2019; Kour et al. 2020d; Rana et al. 2020c).

6.4.1.2 Biological Nitrogen Fixation

Nitrogen is the most important essential nutrient for the development of all living organisms like plants and bacteria. The large amounts of nitrogenous fertilizers are used in order to decrease the deficiency of nitrogen in soil for the development, growth, and the maximum yields of plants (Mata et al. 2010). Most of the organisms are not accessible for the gaseous nitrogen because of its unsuitability for plant assimilation until conversion to ammonia (Erisman et al. 2007). A significant amount of energy is required for conversions to ammonia due to the presence of stable triple bond in N_2 (g) (Dos Santos 2011; Van der Ham et al. 2014). The initiation of iron-protein, Fe-Mo cofactor biosynthesis, transfer of electron, and controlling genes mandatory for the synthesis of enzymes nitrogenase (*nif*) genes convoluted, both symbiotic and non-symbiotic classifications process (Poza-Carrión et al. 2014). The BNF accounts for two thirds of nitrogen fixed globally, and the remaining percent of the nitrogen manufactured by the Haber-Bosch process are the industrially based (Benckiser et al. 2016; Ussiri and Lal 2018). Metalloenzyme consists of two modules: dinitrogenase reductase is the iron-protein and dinitrogenase has a metallic cofactor. The dinitrogenase reductase activity electron transferred with high reducing influence, and the dinitrogenase enzyme converted N_2 into the NH_3 due to the production of these electrons (Reinbothe et al. 2010; Yang et al. 2017).

The iron-nitrogenase, vanadium nitrogenase, and Mo-nitrogenase are the three different types of N-fixing systems and recognized on the basis of the metallic cofactor, molecular-genetic, and structural analyses of the NifHDKX proteins of nitrogenase system (Lahiri 2006). Between different bacterial genera, the existence of N_2-fixing system varies and found in all diazotrophs which is accepted by the society of the Mo-nitrogenase (Bhat et al. 2015). Two metalloproteins consisted of two nitrogenase enzyme and are refined from various resources. MoFe protein is the first component, and iron-protein is the second (Rees et al. 2005; Spatzal et al. 2014 and 2016). The condensed connotation of *nif* genes is determined mostly. The *nifD*, *nifK*, and *nifH* are the three structural genes codes for the Mo-nitrogenase polypeptides, for the Mo-protein subunits, and for the Fe protein, correspondingly (Franche et al. 2009). The core nif genes nifH, nifD, nifK, nifY, nifB, nifQ, nifE, nifN, nifX, nifU, nifS, nifV, nifW, and nifZ are compulsory for the production of nitrogenase activity, and catalysis that is well-sustained in all the diazotrophs is also documented (Dos Santos et al. 2012; Wang et al. 2013). Nitrogenase action based on the system innumerable genes are accountable and codes for the instruments of biological electron transport chains rnfABCDGEF cluster codes the ferredoxin, flavodoxin, and the NADH-ubiquinone oxidoreductase (NQR) to nitrogenase, molybdenum endorsement, and homeostasis, including respiratory chains reformed to oxygen circumstances at which the biological nitrogen fixation procedure can activate (Rogers et al. 2009; Canfield et al. 2010).

The biosynthesis of superfluous nif genes which are convoluted in the production of FeMoCo (nifB, nifQ, nifE, nifN, nifX, nifU, nifS, nifV, nifY, also nifH) the accumulation of nitrogenase involves and also in association of iron-sulfur clusters (nifS and nifU) and developed the nitrogenase mechanisms (nifW and nifZ) (Duffus et al. 2012; Jiménez Vicente 2014; Garcha and Maan 2017). Broad ranges of nitrogen-fixing bacteria have been identified including a number of organisms that fix nitrogen symbiotically with detailed plants (mostly legumes). *Rhizobium*, *Sinorhizobium*, *Azorhizobium*, *Allorhizobium*, *Mesorhizobium*, *Bradyrhizobium, Frankia*, *Azoarcus*, *Achromobacter*, *Burkholderia*, and *Herbaspirillum* are the examples of symbiotic nitrogen fixers (Burns and Hardy 2012; Reddy 2014; Mus et al. 2016; Kumar et al. 2019b; Rana et al. 2019).

6.4.1.3 Phosphate and Potassium Solubilization

The phosphate solubilization is a collective trait between microorganisms with altered crops; for example, *Burkholderia*, *Enterobacter*, *Halolamina*, *Pantoea*, *Pseudomonas*, *Citrobacter*, and *Azotobacter* are found in wheat, rice, maize, and legume crops and have phosphate-solubilizing property (Kour et al. 2019a; Yadav et al. 2016, 2017b). The enzymes, namely, C-P lyases, nonspecific phosphatases, and phytases, involve in organic bound phosphate are possible mechanisms for solubilization (Khan et al. 2010; Othman and Panhwar 2014). The gluconate, ketogluconate, acetate, lactate, oxalate, tartrate, succinate, citrate, and glycolate are the organic acids produced by bacterial genera for solubilizing phosphate (Baig et al. 2010; El-Hamshary et al. 2019). The highest amount of phosphorus is solubilized by the *Paenibacillus polymyxa* BNW6 in comparison to *Sporosarcina* sp. BNW4. The highest amount of potassium and zinc is solubilized by *Planococcus salinarum* BSH13 and *Bacillus pumilus* BCZ15, respectively. Potassium (K) is the third major essential macronutrient for plant growth (Maathuis 2009).

In the soil more than 90% of potassium exists in the form of unsolvable rocks and silicate minerals, and the concentrations of solvable potassium in the soil are usually very less (Meena et al. 2016). Furthermore, potassium deficiency is becoming one of the major constraints in crop production due to the excessive fertilizer application (Gupta et al. 2015). Due to the deficiency of potassium, the plants will have poorly developed roots and slow growth, consist of small seeds, and reduce the production of crop yields. Plant growth-promoting rhizobacteria (PGPB) have capability to solubilize potassium rock through production and secretion of organic acids. The plant growth-promoting rhizobacteria reported to release potassium from potassium-bearing minerals in soils in access are *Acidithiobacillus ferrooxidans*, *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Burkholderia*, *Paenibacillus* sp., and *Pseudomonas* sp. (Podile and Kishore 2007; Forchetti et al. 2010; Sessitsch et al. 2013; Verma et al. 2017a; Yadav et al. 2017d, 2019c, e).

Potassium-solubilizing plant growth-promoting rhizobacteria as biofertilizer for agriculture improvement can reduce the use of agrochemicals and support eco-friendly crop production (Gouda et al. 2018; Kour et al. 2020b; Rana et al. 2020b). The deficiency of potassium in agriculture could be ameliorated by the use of K-solubilizing bacteria (Dotaniya et al. 2016; Etesami and Maheshwari 2018).

6.4.1.4 Siderophores

The side chains of functional groups have small peptide molecules which bind ferric ions known as siderophores (Hider and Kong 2010; Lemire et al. 2013). They serve as iron carriers and have a highest affinity for some ligands and are also known as iron chelators. Slightly an enormous number of them have been detached and applied from microbial flora and can also be species-specific (Wandersman and Delepelaire 2004; Winkelmann 2017). Decreasing the quantity of iron by pathogen proliferation that is obtainable to a pathogen prevents or lessens by siderophore-producing microbes (Fgaier and Eberl 2011; Wang et al. 2014). Siderophore production takes place by PGPB which prevent the propagation of phytopathogens by concealing siderophores with a tremendously affinity for iron (Tortora et al. 2011; Saha et al. 2013; Yadav et al. 2019a; Kour et al. 2019b). The siderophores bind tightly in the rhizospheric region to most of the Fe^{3+} of the host plant taking up the bound iron either into the PGPB or the host plant. The siderophore prevents any fungal and bacterial pathogens in the rhizospheric host plant, where the biocontrol PGPB is bound, from obtaining adequate iron for their growth (Penrose and Glick 2003; Glick 2012) (Kour et al. 2019d). So, the pathogens are incapable to multiply because of deficiency of iron, causing them to drop the capability to performance as pathogens (Heydari and Pessarakli 2010). This biocontrol method is grounded on the fact of efficacy that the PGPB siderophores have a more innovative attraction for iron than the fungal siderophores (Gamalero et al. 2009; Costa et al. 2018). As the iron chelators, the siderophore activities have been seen in several interpretations like siderophores from *Chryseobacterium* spp. C138 which were active in the stream of iron in tomato plants when supplied to the roots and in the supplementation of *Pseudomonas* strains in another case which displayed substantial proliferation in sprouting and plant growth (Babalola 2010; Schmid 2014; Zecchin 2016). Microflora secreted carboxylate, citrate or ethylenediamine and hydroxamates siderophores (Stevanovic et al. 2013; Lukkani and Reddy 2019).

Hydroxamate-type siderophores is common in fungal species, while catecholates are common in bacterial siderophores, which bind iron more tightly than hydroxamates (Crowley 2006; Saha et al. 2016). Mugineic and avenic acids are the plant siderophores examples and are linear hydroxy- and amino-substituted iminocarboxylic acids, respectively. They have capability to bind iron more competently than bacterial siderophores (Ratering et al. 2006; Muleta 2007; De Carvalho and Fernandes 2010). Bacterial siderophores have more affinity than negatively charged molecules for iron. Moreover, several other trivalent and divalent metal ions bind bacterial siderophores, however with a much lesser affinity.

6.4.2 Indirect Mechanisms

The microbes are an eco-friendly approach to control the plant pathogens and hence used as a biocontrol agent (Arora et al. 2010; Kannan and Sureendar 2009). Rhizospheric bacteria used as biocontrol agents are indirect mechanisms of plant growth promotion (Bashan and De-Bashan 2005; Santoyo et al. 2012). Generally, the main kinds of biocontrol activity in PGPR are the antagonism for nutrients, niche elimination, induced systemic resistance, and antifungal metabolites production (Compant et al. 2005; Saxena et al. 2016). The HCN, 2,4-diacetylphloroglucinol, pyrrolnitrin, pyoluteorin, phenazines, viscosinamide, and tensin are the antifungal metabolites produced by various rhizospheric bacteria (Loper and Gross 2007; Bhattacharyya and Jha 2012). The plant confrontation against some pathogenic microflora such as bacteria, fungi, and viruses is the result of plant-root interaction of some rhizospheric bacteria known as induced systemic resistance (ISR) (Van Loon 2007; Berendsen et al. 2012). Furthermore, the ethylene hormones inspire the host plant's defense replies against several phytopathogens, and the ISR mechanisms involve for ethylene signaling within the plant (Pieterse et al. 2009). Lipopolysaccharides (LPS), siderophores, flagella, homoserine lactones, 2, 4-diacetylphloroglucinol, cyclic lipopeptides, and volatiles like acetoin and 2, 3-butanediol encourage the specific microbial mechanisms (Lugtenberg and Kamilova 2009; De Vleesschauwer and Höfte 2009).

6.4.2.1 Antibiosis

The biocontrol abilities of *Pseudomonas* strains depend on incompatible root settlement start of cooperative engagement in plants and manufacturing of antimicrobial antibiotics principally (Chandra and Singh 2016). The antibiotic assembly mechanism linked usually with the rhizospheric bacteria to enact as intimidating representatives against plant pathogens (Cook 1993; Gottwald et al. 2002). Cyclic lipopeptides, pyrrolnitrin, phenazines, phloroglucinols, and pyoluteorin are found in the diffusible form and hydrogen cyanide (HCN) in volatile form (Haas and Défago 2005) and are the antibiotic complexes and better associated with the biocontrol of root diseases (Arzoo and Prakash 2017; Saha et al. 2017). *Pseudomonas fluorescens* BL915 strain produced pyrrolnitrin antibiotic which has the ability to control the injury of *Rhizoctonia solani* throughout damping-off of cotton plants (Beneduzi et al. 2012). Various *Pseudomonas* and *Bacillus* species form lipopeptide biosurfactants which are used as biocontrol agent due to their possible progressive impact on functional associations with microorganisms like fungi, oomycetes, protozoa, nematodes, bacteria, and some plant species (Raaijmakers et al. 2010; Kobayashi and Crouch 2009). A 2,4-diacetylphloroglucinol (DAPG) antibiotic formed by *Pseudomonads* which injures membrane to *Pythium* sp. yields the interference for zoospore development in the oomycete (de Souza et al. 2003; Islam and Von Tiedemann 2011) and performs as a biocontrol of bacterial canker of tomato. *Pseudomonas* sp. retains the redox activity and eliminates the pathogenicity of plants, such as *F. oxysporum* and *Gaeumannomyces graminis* (Dixon and Tilston, 2010).

P. chlororaphis PCL1391 bacterium sequestered from roots of tomato plants which manufactured phenazine-1-carboxamide compounds has capability to discharge the soluble form of iron from ferric oxides at neutral pH and gives to iron deployment in soils (Chin-A-Woeng et al. 2000; Haas and Defago 2005; Hernandez et al. 2004). A popular *Bacillus* sp. secreted circulin, colistin, and polymyxin antibiotics which are vibrant against phytopathogens (Evans et al. 1999). Various plant pathogens manufactured the induced systemic resistance (ISR) mechanism for particular antibiotics due to the upgraded convention of these isolates after too much use of antibiotic-producing rhizobacteria as biocontrol agents for plant growth promotion (Beneduzi et al. 2012). For the anticipation of this type of admiration, numerous investigators misused those biocontrol strains that produce more than one antibiotic (Lugtenberg and Kamilova 2009).

6.4.2.2 Hydrogen Cyanide

Various rhizobacteria synthesize hydrogen cyanide (HCN) and work as biocontrol. These bacteria can synthesize and produce HCN, antibiotics, and cell wall-breaking enzymes (Olanrewaju et al. 2017; Filya et al. 2000; Singh et al. 2016). The HCN toxicity affected its capability to impede cytochrome c oxidase in addition to other important metalloenzymes (Ryall et al. 2008). Thus, HCN created by PGPB performs synergistically with other approaches of biocontrol engaged by the same bacterium (Bashan and De-Bashan 2005). Moreover, it has been observed that the low level of HCN produced by the bacterium progresses the effectiveness of antifungal engaged against fungal pathogens, thereby confirming that the fungi do not develop battle to the specific antifungal in question (Khalid et al. 2009). Thus, HCN produced by PGPB seems to perform synergistically with other approaches of biocontrol involved by the same bacterium (Glick 2015). The HCN toxicity is pretentious in its capability to obstruct cytochrome c oxidase as well as other significant metalloenzymes (Way 1984). *Rhizobium*, *Pseudomonas*, *Alcaligenes*, *Bacillus*, and *Aeromonas* species of bacteria have been observed for the HCN production (Martínez-Viveros et al. 2010; Pereg and McMillan 2015), which suppresses the root knot infection of tomato caused by *Meloidogyne javanica* nematode (Nico et al. 2004) and also control the *Odontotermes obesus*, a pest of crop in India (Marull et al. 1997).

6.4.2.3 Induced Systemic Resistance (ISR)

Activating a confrontation instrument in plants, nonpathogenic microorganisms improve the damaging effects of phytopathogens; this procedure is known as induced systemic resistance (ISR) (Choudhary et al. 2007; Romera et al. 2019; Glick 2012). In several rhizobacterial-inoculated plants, ISR mechanism has been observed (Pineda et al. 2012), and protected plants counter to development restriction, using *Pseudomonas fluorescens* WCS417r strain against the fungal pathogen *Fusarium oxysporum* f. sp. *dianthi* (Alsanius and Wohanka 2019). ISR does not board rigorous pathogens but rather summits the plant counter to a range of dissimilar pathogens, and it is not only articulated at position of initiation (Schulze-Lefert and Panstruga 2003; Silva-Rocha and de Lorenzo 2010). Various PGPB have been observed to harvest salicylic acid (SA) that can perform as a signal molecule to turn on a machinery similar to ISR in plants that is called “systemic acquired resistance” or SAR (Pretali et al. 2016; Brock et al. 2018). However, SAR is customarily stimulated by plant pathogens, and salicylic acid (SA) is generally not scrupulous to perform a role in PGPB-induced plant resistance to plant pathogens (Twardowski and Małyska 2015; Petersen et al. 2017). Consequently, the SA may activate the plant phytopathogen-protective mechanisms fashioned by PGPB; compared to ISR, this trait is measured to be particularly rare in PGPB (Olanrewaju et al. 2017).

Moreover, SAR is coordinated by the initiation of pathogenesis related (PR) genes which encode PR proteins. Pathogenesis-related protein 1 (PR1) which is mostly used as a biomarker for SAR one of the best categorized PR gene is PR-1 (Mohammadipanah and Zamanzadeh 2019). In the directive of ISR and SAR is the redox-regulated protein non-expressor of PR genes 1 (NPR-1), which is a majorly involved protein (Stahl et al. 2016; Hartmann and Zeier 2019). Though the intermolecular disulfide bonds are manufactured in cytoplasm as an oligomer, its function in transcriptional regulation has been well recognized (Skelly et al. 2016; Caarls et al. 2015). The NPR-1 protein which is programmed by the npr-1 gene stimulates SAR founding by motivating PRs genes after getting signal from the gathering of SA (Jain et al. 2016; Withers and Dong 2016). The NPR-1 protein which is encoded by the npr-1 gene activates SAR establishment by activating PRs genes after receiving signal from the accumulation of SA (Olanrewaju et al. 2017). PGPB-mediated ISR and SA-dependent SAR are arranged by various signaling ways which were sustained by the annotations that both PGPB-mediated ISR and pathogen-induced SAR are operative control mechanisms, but their degree of efficiency is to some extent dissimilar (Gkizi et al. 2016; Haney et al. 2018).

6.4.2.4 Cell Wall-Degrading Enzymes

Various plants reply to contamination by fungal phytopathogens through motivating plant-determined production of more cell wall-degrading enzymes by fungi (de Wit 2016). The chitin degrading enzyme chitinase (Husson et al. 2017), β-(1, 4)-N-acetyl glucosamine polymer is the residue of it and a vital part of the cell wall of several phytopathogenic fungi; β-1, 3-glucanase is an alternative of cell wall carbohydrate (Ruiz-Herrera 2016), protease, which can condense cell wall proteins; and lipase, which can degrade some of the cell wall-associated lipid, all of which can to several amount exclusively lyse fungal cells (Flannagan et al. 2015; Yadav et al. 2020). In addition to plant-encoded cell wall-breaking enzymes, various biocontrol PGPB produce a comparable section of cell wall-breaking enzymes (Santoyo et al. 2016). Chitinase genes can be overexpressed, and strains cotransformed with the inclusion of acetamidase gene were observed where the pyruvate constitutive promoter fruitfully upgraded the chitinase action in amended strains (Salehi Jouzani and Taherzadeh 2015). Chitinases, peroxidases, and β-1, 3-glucanases are part of PR proteins, and their triggering can essentially induce ISR in plants (Oliveira et al. 2016). Exposure of *Bacillus* sp. JS caused an upregulation of the PR-2 and PR-3 genes which encode β-1, 3-glucanase and chitinase correspondingly (Kim et al. 2015).

6.4.2.5 Bacteriophages

Some specific bacteriophages or bacterial viruses may be lysed by some bacterial phytopathogen (Buttimer et al. 2017). The target bacterial phytopathogen must be clearly recognized down to the strain equal for this methodology to work. Successively, several bacteriophages have been isolated and characterized systematically that can lyse only to target pathogen without upsetting any other bacterial isolates (Nassal et al. 2018; Day et al. 2017). The bacteriophages are scattered onto an infected plant as a combination of various bacteriophage isolates, all directed in contradiction of the targeted bacterial pathogen to kill the target bacterial phytopathogen (Rodríguez-Rubio et al. 2016). A mixture of bacteriophage strains may be used to decline the possibility that bacteriophage-resistant mutants of the target pathogen will develop (Kering et al. 2019). This is because of the several binding positions of the bacteriophages on the shallow of the bacterial pathogen. The mostly bacteriophages are temperately subtle to UV light (Gonzalez et al. 2018); they are characteristically squirted onto plants at sunset when the intensity of UV light is low. *Xanthomonas campestris* pv. *vesicatoria* bacterium pathogen forms lesions on tomatoes and peppers few bacteriophage-based biocontrol managers which accepted for use (Akimoto-Tomiyama et al. 2018). Additional negotiations on bacteriophages as biocontrol representatives have been intricately go through in the work of Buttimer et al. (2017), and others (Lin et al. 2017).

6.4.2.6 Volatile Compounds

The volatile organic compounds (VOCs) formed by rhizospheric bacteria stimulating the plant growth and inducing systemic resistance provide a new perception in PGPB-plant interactions (Ma et al. 2016; Choudhary et al. 2016). Various types of VOCs produced by rhizobacteria have been observed and lay a vital role in plant defense. Dodecane, 2-undecanone, 2-tride-canone, 2-tridecanol, tetramethyl pyrazine, 2, 3-butanediol, and 3-hydroxy-2-butanone (acetoin) are the some common VOCs (Shameer and Prasad 2018; Li et al. 2015). The two VOCs 2, 3-butanediol and 3-hydroxy-2-butanone are the most significant and latest investigation on the bacterial-produced VOCs which established their role in elicitation of ISR (Zhalnina et al. 2018; Venturi et al. 2016; Draper et al. 2018). *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a bacteria consistently release 2, 3-butanediol and 3-hydroxy-2-butanone and treated *A. thaliana* plants; these strains have shown significant resistance against the challenge inoculation of *Erwinia carotovora* subsp. *Carotovora* SCC1 (Zamioudis et al. 2015; Song et al. 2019).

The VOCs to encourage resistance against diseases was described with a hereditarily amended *Bacillus* strain which is incapable to produce VOCs (Zhou et al. 2019; Enespa and Chandra 2017). Several strains of *Pseudomonas fluorescens* were also reported for the production of VOCs and were shown to be more effective in controlling root and seedling diseases (Raza et al. 2016; Sharifi and Ryu 2018; Khan et al. 2016; Choudhary et al. 2016). Plant growth-promoting rhizobacteria serve as biocontrol agents by the biopriming method which is a popular approach of seed treatment method and includes inoculation of seed with beneficial microorganisms to protect the seed from various seed- and soilborne diseases (O'Callaghan 2016; Panuccio et al. 2018). Seed priming and osmo-priming are commonly being used in many horticultural crops to amplify the growth and uniformity of seed germination. Consequently, PGPR are becoming a sustainable substitute for inorganic chemicals (Bisen et al. 2015; Mahakham et al. 2017).

6.5 Plant Growth Promotion Under Abiotic Stress Using PGPR

The stress tolerance-regulated mechanisms are complicated and multifarious, in part because plants are sessile things (Islam et al. 2015; Hasanuzzaman et al. 2016; Bellard et al. 2012) to stand where they are and “take it” (Funk et al. 2019). Cultivating the stress tolerance in cultivated plants by the expected upbringing is a long and capital-intensive run-through, while the inherited manufacturing is allied with the virtuous and societal recognition issues (Arzani and Ashraf 2016; Hu and Xiong 2014). Microorganisms play an important role is achievement importance in supervision of stress and the improvement of climate change spirited cultivation (Jacoby et al. 2017; Schillaci et al. 2019). Current observations have browbeaten molecular procedures to recognize the mode of action of the plant-microbe dealings ensuing in encouraged stress lenience (Schmid et al. 2017; Bloemberg and Lugtenberg 2001).

Plant growth can be affected directly using PGPR due to atmospheric N_2 fixation into naturally obtainable N compounds or by manufacturing phytohormone and hindering the growth of phytopathogens (Weyens et al. 2009; Hayat et al. 2010). Microorganisms are found in abundance in rhizosphere than bulk soil (Shu et al.

2012). The colonization of plants root is not homogenous; in several parts of the root system, the specific bacterial density varies and is likely to be related to different root exudates released by different parts of the roots (Benizri et al. 2001; Haas and Keel 2003). The colonization of the rhizosphere is regulated by another mechanism known as quorum sensing which regulates the expression of gene and compelled by bacterial density and finds both within the bacteria of same species and between dissimilar species (Rutherford and Bassler 2012). The competitiveness of bacteria can influence by the quorum sensing, so affecting the root colonization patterns (Berendsen et al. 2012; Compant et al. 2010). Plant growth-promoting rhizobacteria which are useful for abiotic stress in plants are given in Table 6.2.

6.5.1 Abiotic Stress Tolerance Associated with PGPR

The secretion and addition of osmolytes like glycine betaine, proline having capability of ROS scavenging in *Pseudomonas putida* MTCC5279 upgraded scarcity stress in *Cicer arietinum* (chickpea) plants (Kaushal 2019; Backer et al. 2018). The bacteria in gap manifestation of genes elaborated in the manufacturing of salicylic acid (PR1), ethylene (ACO and ACS), LEA and DHN (dehydrins), DREB1A (dehydration-responsive element-binding protein 1A), NAC1 (transcription factors expressed under abiotic stress), jasmonate (MYC2) transcription activation, the antioxidant machinery which includes superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and guaiacol peroxidase (GPX) positively modulated in stress responses (Herrera-Vásquez et al. 2015; Betsuyaku et al. 2017; Blanco et al. 2005; Caarls et al. 2015). *Bacillus thuringiensis* NEB17 produced thuricin 17 to (*Glycine max*) soybean under the deficiency of water conditions and caused alteration of root constructions with extension of biomass, nodulation, length, ABA, and nitrogen content (Subramanian et al. 2016; Bacon et al. 2015).

The advantageous microorganisms also provide assistance to plants and manage with the overflowing water (Chen et al. 2016). *Pseudomonas fluorescens* REN1 augmented the root length under continuously overflowing water circumstances in the seedlings of paddy crops (*Oryza sativa*) due to the assembly of ACC deaminase (Etesami et al. 2015a, b; Yoolong et al. 2019). ACC deaminase also diminished the salt stress (Wang et al. 2016b). Pea plants (*Pisum sativum*) inoculated with *Variovorax paradoxus* had better electron transport, composed the homeostasis of ion by improved flow of KCl in shoots and statement of NaCl on roots, improved photosynthetic amount and also biomass salt scarcity at 70 and 130 mM NaCl, and diminished the stomata resistance and stability of pressure in xylem due to the assembly of ACC deaminase (Koprivova et al. 2019; Etesami and Alikhani 2019). In *Abelmoschus esculentus* (okra) plant, GPR generating ACC boosted salt tolerance, improved antioxidant enzyme accomplishments, and upregulated ROS pathway genes (CAT, APX, GR, and DHAR) (Habib et al. 2016; Patwardhan and Bhatt (2016). *Bacillus*

Table 6.2 Plant growth-promoting rhizobacteria mitigating abiotic stress in plants

Microbe (PGPR)	Target plant species	Mitigating stress	Tolerance strategy	References
Serratia, *Enterobacter* sp. *MN17*	*Abelmoschus esculentus*, *Chenopodium quinoa*	Acidic condition, salinity	Increase germination rates, loss of membrane integrity	Ali and Xie (2019)
Pseudomonas simiae	*Glycine max*	Salt	Quinoline and *Glycine max* 4-nitroguaiacol promote seed germination	Narsing Rao et al. (2019)
Enterobacter sp. *MN17*	*Cicer arietinum*	Drought tolerance	Increase physiology and root growth	Khan et al. (2018)
Pseudomonas koreensis S2CB35	*Zea mays*	Salinity	Decreased the Na + and enhanced the K concentration	Selvakumar et al. (2018)
Bacillus licheniformis strain K11	*Capsicum annum*	Drought	Stress-related gene and protein	Ilangumaran and Smith (2017)
Stenotrophomonas	*Triticum aestivum*	Sandy soils	Influenced water conservation and fertility status	Khan et al. (2017)
Rhizobium leguminosarum	*Brassica juncea*	Zn toxicity	Metal-chelating molecules	Adediran et al. (2016)
Pseudomonas simiae	*Glycine max*	Salt	Quinoline and *Glycine max* 4-nitroguaiacol promote seed germination	Vaishnav et al. (2016)
Photobacterium spp.	*Phragmites australis*	Hg toxicity	Mercury reductase, IAA	Mathew et al. (2015)
Pseudomonas koreensis strain AK-1	*Glycine max L. Merrill*	Salt	Reduction in Na + level and increase in K+ level	Kasotia et al. (2015)
Pseudomonas koreensis AGB-1	*Miscanthus sinensis*	Cd, AS, Cu, Pb, and Zn toxicity	ACC deaminase, IAA production	Babu et al. (2015)
Bacillus thuringiensis AZP2	*Triticum aestivum*	Drought	Enhanced volatile organic compounds	Timmusk et al. (2014)
Burkholderia phytofirmans, *Enterobacter* sp. FD17	*Zea mays*	Drought	Enhanced photosynthesis	Naveed et al. (2014b)
Pseudomonas aeruginosa	*Triticum aestivum*	Zn toxicity	Improve plant growth, soluble protein uptake of nutrients	Islam et al. (2014)
Bacillus amyloliquefaciens, *Azospirillum brasilense*	*Triticum aestivum*	Heat	Reduced regeneration of reactive oxygen species, preactivation of heat shock transcription factors, changes in metabolome	El-Daim et al. (2014)

(continued)

Table 6.2 (continued)

Microbe (PGPR)	Target plant species	Mitigating stress	Tolerance strategy	References
Root-associated plant growth-promoting rhizobacteria (PGPR)	*Oryza sativa*	Sal	Expression of salt stress-related RAB18 plant gene	Jha et al. (2014)
Enterobacter intermedius MH8b	*Sinapis alba*	Zn toxicity	ACC deaminase, p solubilization	Plociniczak et al. (2013)
Bacillus licheniformis strain K11	*Capsicum annum*	Drought	Stress-related gene and protein	Lim and Kim (2013)
Curvularia proturberata isolate Cp4666D	*Dichanthelium lanuginosum*, *Solanum lycopersicum*	Heat and drought	Colonization of roots	de Zelicourt et al. (2013)
Phyllobacterium myrsinacearum	*Sedum plumbizincicola*	Pb/Zn toxicity	Resistance to 350 mg/L Cd, 1000 mg/L Zn, 1200 mg/L Pb	Ma et al. (2013)
Bacillus cereus AR156, B. subtilis SM21 and *Serratia* sp. *XY21*	*Cucumis sativa*	Drought	Production of monodehydroascorbate, proline, and antioxidant enzyme, expression of genes	Wang et al. (2012)
Azospirillum brasilense and *Pantoea dispersa* (Co-inoculation)	*Capsicum annuum*	Salinity	High stomatal conductance and photosynthesis	del Amor and Cuadra-Crespo (2012)
miR393 (*Sinorhizobium meliloti*)	*Arabidopsis*	Salinity, drought	Tolerant to salt excess	Gao et al. (2011)
Bacillus thuringiensis AZP2	*Mentha piperita*, *Triticum aestivum*	Drought, salinity	Enhanced volatile organic compounds	Vilchez and Manzanera (2011)
Pseudomonas putida Rs-198	*Gossypium hirsutum*	Salinity	Prevented salinity-induced ABA accumulation in seedlings	Yao et al. (2010)
Bacillus megaterium	*Zea mays*	Osmotic stress	High hydraulic conductance, increased root expression of two ZmPIP isoforms	Marulanda et al. (2010)

amyloliquefaciens SQR9 inoculated with seedlings of *Zea mays* (Maize) had enhanced salinity tolerance and content of chlorophyll, linked with the control. These physiological appearances were further confirmed by the up regulation of RBCS, RBCL, H(+) -PPase, HKT1, NHX1, NHX2 and NHX3, as well as downregulation of NCED expression, as determined by quantitative reverse transcription-polymerase chain reaction (El-Esawi et al. 2018; Ilangumaran and Smith 2017).

Dietzia natronolimnaea halotolerant bacterium inoculated in *Triticum aestivum* (wheat) plants displayed upregulation of genes elaborate in the ABA-signaling pour, salt exceedingly sensitive (SOS) pathway, ion transporters, and antioxidant enzymes; stress lenience is induced by intonation of multifarious linkage of gene families (Talaat 2018; Bensidhoum and Nabti 2019; Orhan 2016; Schlaeppi and Bulgarelli 2015; Singh et al. 2018). *Serratia nematodiphila* inoculated in *Capsicum annum* (pepper) plant upturned the development in below temperature stress circumstances after gibberellin production. Inoculated plants enclosed additional GA4 and ABA and reduced salicylate and jasmonate (Kang et al. 2015; Turan et al. 2017).

Burkholderia phytofirmans PsJN controlled carbohydrate metabolism to diminish the terrifying damage plantlets exposed to low temperature stress after inoculation with *Vitis vinifera* (grape vine) (Wang et al. 2016a; Su et al. 2015). *Pseudomonas vancouverensis* OB155 and *P. frederiksbergensis* OS261 augmented manifestation of cold acclimation genes and antioxidant movement in leaf tissues after inoculation of *Solanum lycopersicum* (tomato) plants when visible to low temperatures (Bulgari et al. 2019; Subramanian et al. 2015). A freshly purified rhizobacteria, *Ochrobactrum intermedium*, maintained the subsistence capability of altering its membrane phospholipid conformation when undecided to stress disorder and also generating indole acetic acid and siderophores (Fu et al. 2016; Husen 2016). The tolerance of water scarcity stress boosted the quality of nitrate (NO_3^-) and proline (amino acid) in vaccinated plant cowpea when *Bradyrhizobium* sp. symbiont assisted (Enebe and Babalola 2018; Yasmeen et al. 2019; Chandra et al. 2020). An enormous amount of amino acids which was derivative from the nitrogenase-catalyzed transformation of atmospheric N_2 to NH_4^+ ions necessary for amino acid and protein formation in the plant when the *Bradyrhizobium* sp. inoculated in groundnut under drought conditions (El-Batal et al. 2015; McMahon and McCarthy 2016) (Fig. 6.1), displaying that the results of abiotic stresses (like drought, flood, chilling, salinity, and heat) are dissimilar but adoptive approaches of plants against varieties of abiotic stresses are analogous in nature.

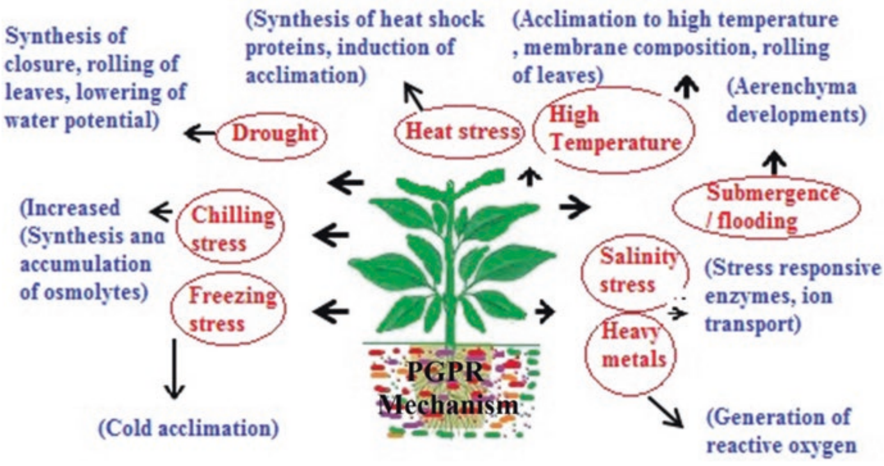

Fig. 6.1 Diverse abiotic stresses and the strategic defense mechanism adopted by the plant

6.6 Effects of Abiotic Stress on Agriculture

In the world, mostly the cultivated soils are categorized as existence suboptimal (Kour et al. 2020c; Rastegari et al. 2020a; Remigi et al. 2016). From prime development circumstances, any abnormality origins numerous interrelated responses in plants that can be chosen as an endeavor to acclimatize to new ecological circumstances in an effort to sustain the homeostasis (Zhang et al. 2019a, b; Reiter et al. 2015). If the stress is lengthy and harmful, it can forever harm the plant and consequently lead to death. Several plants have capability to acclimatize stress, the procedure which requires energy that is averted from active growth, resulting in smaller accustomed plants (Atwell 2016; Jorge et al. 2016). Stresses caused by nonliving factors or environmental factors which are known as abiotic stresses are supposed to be the main reason of globally crop loss with deteriorated yields of more than 50% yearly (Gilliham et al. 2017). Salinity and drought are two of the most serious abiotic stresses which are more effective ecological exposures for agriculture crops, principally in semiarid and arid areas which are already potential the harvesting limits and due to increasing the temperature and soils degradation agriculturally point of view these areas may not nourishment for the long time for agriculture after this (Altieri and Nicholls 2017; Pittelkow et al. 2015; Kour et al. 2019b; Yadav and Saxena 2018).

6.6.1 Climate Change

Social and economic stability is positively correlated with food security; expected climatic modification is intimidating the productivity of food, there are protracted and multifaceted consequences (de Moraes Sá et al. 2017; Cheeseman 2016; Kumar et al. 2019a). The regular heating has been amplified by 0.8 °C, since the mid-nineteenth century, and the heating is anticipated to upsurge between 1.8 and 4 °C by the end of the century (Oliva-Urcia et al. 2018). In modern agriculture N_2 fertilizers are commonly used and produced nitrate (NO_3^-) to molecular nitrogen gas (N_2) is a step-down reduction reaction forming nitrite (NO_2^-), nitric oxide (NO) and nitrous oxide (N_2O) as intermediate compounds (Coskun et al. 2017). The total nitrogen fertilizer used to cereal crops was more than half in 2014–2015 alone. In N-depleted soil, reestablishment of N is a critical cultivated preparation that has led to improve the crops over the last limited periods (Wang et al. 2019; Liu et al. 2019). However, it is estimated that the use of N enricher is ineffective and only one third of the useful N is engaged by plants, with the additional being lost in external overflow, percolating in water-table aquifer, or into the distinctive volatilization (Tong 2019; Maqsood et al. 2016). N_2O is less abundant in atmosphere than the CO_2 but have 300 times supplementary potential as a greenhouse gas (DelSontro et al. 2018). Greenhouse gas emissions caused climate change and directly affected the productivity of crops systems in just about every part of the sphere (Nunes et al. 2016). Globally the average heating rises of 4 °C by 2100 will rigorously decrease the productivity of food in almost all the republics in worldwide (Rogelj et al. 2016). And almost 23 thousand billion US$ economic losses take places under the Southeast Asian and under developed republics of Africa forecasted to suffer the major damages (21 and 26% of GDP, respectively) (Kompas et al. 2015; Schillaci et al. 2019).

6.6.2 Agricultural Soil Degradation

Soil humiliation is chief apprehensions for affecting the productivity of agriculture, particularly in tropical and subtropical regions (Gomiero 2016). Worldwide, various forms of deterioration have affected one third of lands (Purvis et al. 2018; Pacheco et al. 2018; Yadav et al. 2019b, c, d). Inappropriate cultivation practices, with extremely crop filtrate elimination and more usage of inorganic nourishments, can cause diminution of the superiority of soil, depletion of organic matter stocks, and increasing of the soil erosion (Maltas et al. 2018). Removal of crop residue from the site causes the elemental losses which are essential for the growth of plants, and these essential elements vanish from the main soil, and the productivity decreases (Schillaci et al. 2019). These soils when used for cultivation purposes also cause the deprivation of water springs, due to the discharge of ruined nourishments into groundwater (Tuğrul 2019; Blaesing and Amelung 2018). In developing countries, various rivers have severe water contaminations and eutrophication problems (Bei et al. 2019). To obtain the adequate output to meet the food difficulties in various and arid and semiarid regions, an essential management strategy is needed in irrigation, but it can lead to detrimental properties (Chen et al. 2018). Saline-sodic soils increase due to the improper irrigation techniques which are occurred in more than 20% of irrigated acreages (Ganjegunte et al. 2018; Günal et al. 2015).

6.7 Conclusion and Future Prospect

The consumption of policies is required for sustainable agriculture to upturn or sustain the current scenario of food manufacturing while dropping loss to the atmosphere and social well-being. The microflora used as growth promoters of crop is an unconventional to unadventurous cultivated machineries. PGP microbes can affect the growth and development of plant ultimately. The PGP microbes promote the plant growth directly, encompasses as long as the plant with a compound that is manufactured by the bacterium cell or smoothing the endorsement of various nutrients from the rhizospheric atmosphere. The microorganism associated with plants performs a very imperative character to increase plant stress tolerance through a different mechanism such as accumulation of osmolytes, phytohormones, and exopolysaccharide, produce volatile compounds, modulate the expression of stress-related genes, and also inhibit and/or kill the phytopathogens in the soil. The microorganism not only increases the plant stress response but also enhances the crop yield which is the basic demand of the growing population. Life-threatening proceedings such as continued droughts, deep rains, waterlogging conditions, heat waves, and frost injury are likely to further proliferate in the imminent due to climate change. A widespread variety of versions and alleviation approaches are requisite to cope with such impacts. The improvement of pressure-accepting crop diversities over genetic manipulations and plant propagation can help to incredulous stresses to some extent.

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Chapter 7
Microbiomes Associated with Plant Growing Under the Hypersaline Habitats and Mitigation of Salt Stress

Surekha Challa, Titash Dutta, and Nageswara Rao Reddy Neelapu

Abstract Food security means when all people access safe and nutritious food for a healthy life. Appropriate production and supply of food is the only way to meet the challenge of food security. The major challenge for food production is availability of arable land for agriculture. Among the challenges for availability of arable land, salinity is one of the reasons for decreased land availability. Plant is colonized by millions of microorganisms influencing or promoting plant growth. Literature reports microbiome associated with plants growing under the hypersaline habitats. These microbes mitigate salt stress and provide salt tolerance to the plants growing in salt stress. These microbes have a tremendous application in the field of agriculture. This chapter reviews the salt tolerance, plant microbiome and their interaction with plants, and plant growth-promoting (PGP) attributes of microbiome for salt tolerance. This chapter provides information on how microbiome is promoting stress resistance and plant growth.

Keywords Halotolerant microbes · Hypersaline habitats · Microbiome · PGP attributes · Plant microbiome · Salt stress

7.1 Introduction

Food security means when "all people, at all times, have physical, social and economic access to sufficient, safe and nutritious food which meets the dietary needs and food preferences for an active and healthy life. Food insecurity exists when people do not have adequate physical, social or economic access to food as defined above" (FAO 2003; Challa et al. 2019a, b). The major risk for food security is

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exponential increase of population worldwide (Challa et al. 2019a, b). This exponential growth of population requires appropriate agricultural production and supply of food. One of the major challenges with agriculture and food security is availability of arable land for agriculture. The arable land for agriculture is decreasing at a pace than it is expected. The probable reasons for decrease in land for agriculture are (a) agricultural lands are occupied for construction of houses, mining activities, and construction of road; (b) usage of chemical fertilizers and pesticides changed the fertility of soil; (c) modern agricultural techniques, shift in cultivation, floods, and droughts lead to barren agricultural lands; (d) improper irrigation leads to saline soils (Pitman and Läuchli 2002); and (e) intensive cultivation and monoculture of crop harms the soil and decreases the productivity of food.

Globally, agricultural lands are decreasing by 1–2% every year due to soil salinity (Kafi and Khan 2008). Worldwide, around one billion hectares are affected due to salinity (Szabolcs 1989; Rengasamy 2006) (Fig. 7.1). Around 30% of the Australian continent is saline (Rengasamy 2006). Similarly, the coastline of Mediterranean in Europe is also affected by salinity (Daliakopoulos et al. 2016). The global annual loss estimated in agriculture due to soil salinity is US$ 27 billion (Qadir et al. 2014). At the same time 50% yield losses are estimated in India due to salinity of the soil (Qadir et al. 2014). There are two types of soil salinization's – primary salinization of soils and secondary salinization of soils. If salinization of soils is a naturally occurring process, then it is known as primary salinization of soils, whereas if salinization of soils is due to several anthropogenic processes, then it is known as secondary salinization of soils. The examples of primary saline soils are salt lakes, salt pans, and salt marshes. The examples of secondary saline soils are irrigation-induced saline soils (Fig. 7.2) and dryland saline soils. This chapter discusses in detail the effect of salt stress on plants, plant microbiome mitigating salt stress growth under hypersaline conditions, and plant microbiome role in growing plants under hypersaline conditions.

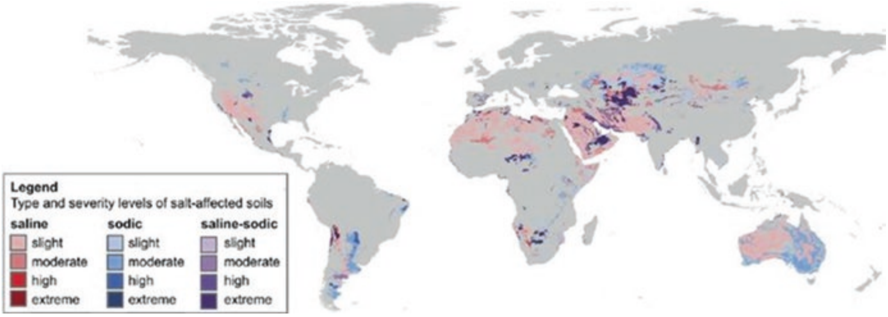

Fig. 7.1 Global map of land affected due to soil salinity. (Source: Wicke et al. 2011)

Fig. 7.2 Salinized agricultural land in the Colorado River Basin, Utah, United States, an example for irrigation-induced saline soils or secondary salinization of soils. (Source: Ron Nichols, USDA Natural Resources Conservation Service)

7.2 Salt Stress and Plant Microbiome

Salinization of soils affects all the organisms living in the hypersaline habitats, and the effect is known as salt stress. Understanding the effect of salt stress on plants and plant microbiomes is of utmost importance. This provides information, to increase the agriculture production and to tackle salt stress.

7.2.1 Salt Stress on Plants: Effects and Response

Exposure to salinity severely affects plant growth and development. Mild to prolonged exposure is capable of inducing a cascade of morphological, physiological, metabolic, and molecular alterations (Challa et al. 2015; Neelapu et al. 2015). For instance, salinity induces osmotic stress which subsequently leads to disruption of cellular and ionic homeostasis (Wani et al. 2017). Munns and Termaat (1986) proposed a biphasic response and associated it with plant growth inhibition under salinity. When plants were exposed to saline environment, a two-phase response mechanism was induced: disruption of cellular homeostasis (osmotic, first phase) and disruption of ion distribution (ionic, second phase). As plants are subjected to salinity, the osmotic phase of the growth response is initiated. The osmotic phase is characterized or observed with high rate of salt accumulation, which increases the extracellular Na^+ and Cl^- ion levels, whereas intracellular Na^+ and Cl^- ion levels remain static. The alteration in the Na^+ and Cl^- ion levels initiates a state of water deficit as the water-intake capacity of the plants is diminished leading to prominent changes like morphological changes in leaf, reduced root growth, as well as stomatal closure.

The ionic phase earmarks the second of the biphasic growth response and is due to the toxicity of the salt ions accumulated during the osmotic phase. The increase in extracellular Na^+ and Cl^- ion beyond a threshold level witnesses a sudden influx of Na^+ and Cl^- ions in plant cells and accumulates in old leaves. High cytosolic levels of Na^+ and Cl^- ions are detrimental for plants as they initiate various changes such as disruption of membrane structure and organelles, alteration of photosynthetic activity, inhibition of enzyme activity, and reduction in transpiration rate (Gilroy et al. 2014). The biphasic model has been thoroughly investigated and documented in maize (*Zea mays* L.) (Fortmeier and Schubert 1995), wheat (Wakabayashi et al. 1997), tomato (Maggio et al. 2007), rice (Negrão et al. 2011), and barley (Adem et al. 2014). Moreover, the biphasic model has been instrumental in unravelling the cross talks among the various types of abiotic stresses and elucidating the genes involved in plant response during exposure to abiotic stress.

7.2.2 Halophytes and Glycophytes

All plant species can be divided into two categories halophytes and glycophytes, based on their ability to thrive under saline conditions. Halophytes (salt-tolerant plants) are able to withstand high levels of salt concentrations, whereas glycophytes (salt-sensitive plants) are unable to thrive, even under low concentrations of salts (Etesami and Beattie 2018). Halophytes comprise 1% of all dicots and monocots and can withstand 1M NaCl concentration. They are widespread in arid, semiarid, and saline wetlands surrounding the tropical and sub-tropical coastal regions (Kumari et al. 2015). Halophytes are generally categorized as euhalophytes (true halophytes), pseudohalophytes (salt avoiders) and crinohalophytes (salt excreters). Halophytes can further be classified into obligate halophytes (requires saline conditions) and facultative halophytes (requires freshwater conditions) depending on the requirement of saline environments.

7.2.3 Effects of Salt Stress on Plant Microbiome

Microbiome colonizes plants leaf, stem, and roots; and understanding the association between plant and microbiome is important. Understanding these aspects requires knowledge on plant microbiome, role of plant microbiome, types of plant microbiome, halophilic microbiome, halotolerant plant growth-promoting rhizobacteria (PGPRs), etc., This section of the chapter elaborates on the above aspects to improve our understanding on plant microbiome and their role in relieving plants from saline stress, especially those living in hypersaline habitats.

7.2.3.1 Plant Microbiome

Plant root systems are colonized by millions of microorganisms forming a complex ecological niche which potentially influences mutualistic association between plants and microbes (Schmidt et al. 2014). These microbes are predominantly found in the rhizosphere, endosphere, and phyllosphere of plants and are involved in regulation of water-plant-soil interactions, plant growth, and stress alleviation. Plant microbiomes comprise plant growth-promoting bacteria (PGPBs), arbuscular mycorrhizae fungi (AMF), other endophytes, and rhizobacteria (Yadav et al. 2020). PGPBs are special bacteria that colonize the plant especially the root area. PGPBs are well-known as plant growth promoters and increase the crop yield (Yadav et al. 2017). They are also known for activating plant defences in plant to thrive in unfavourable conditions (stress) (Glick 2012). AMF is symbiont fungus belonging to phylum *Glomeromycota* and colonizes roots of plants in the form of arbuscules or vesicles, thereby increasing the root surface area. These fungi connect plants with soil and help in uptake of nutrients like nitrogen and phosphorus indirectly promoting plant growth (Berruti et al. 2016). The bacterium or fungus living in the plants as endosymbionts is known as endophyte (Rana et al. 2019c). The key roles performed by endophytes are stimulating plant defence responses, promoting plant growth, remediating abiotic stresses, etc. (Khare et al. 2018). Rhizobacteria or plant growth-promoting rhizobacteria (PGPRs) are in association with root of the plant and mostly present near plant root-soil interphase (Kour et al. 2019b). The primary role of PGPRs is promoting plant growth and also acting as biocontrol agents to control phytopathogens (Vacheron et al. 2013).

The diversity of the plant microbiomes depends on the plant species, on environmental conditions, as well as on the soil properties (Li et al. 2018; Yadav et al. 2018a, 2019a). It has been observed that different species of plants assembled specific microbiome community. For example, the rhizosphere of *Halimione portulacoides* is dominated by *Acidimicrobiales*, *Myxococcales*, and *Sphingomonadales*, whereas the rhizosphere of *Puccinellia limosa* is associated with *Halomonas* and *Nesterenkonia* species (Oliveira et al. 2014; Borsodi et al. 2015). Studies focussing on unravelling various plant-microbe interactions and their potential role in alleviating abiotic stress are of prime importance as we struggle to maintain sustainable food production for the growing population (Singh et al. 2016; Yadav et al. 2019b).

7.2.3.2 Plant Microbiome and Their Role

Plant microbiome have garnered significant attention in the present decade for their role in promoting plant growth and alleviating abiotic stresses, predominantly salinity and drought. They promote plant growth by enhancing certain plant growth-promoting (PGP) attributes either directly or indirectly (Fig. 7.3). The direct mechanisms involve elevating nutrient uptake via nutrient fixation and solubilization (phosphorous, zinc, and potassium) (Kumar et al. 2019; Rajawat et al. 2020); enhancing phytohormone production (indole acetic acid, cytokinin, auxin, abscisic acid, and gibberellic acid); quorum sensing; and 1-aminocyclopropane-1-carboxylase (ACC)-deaminase activity (Ansari 2018; Kour et al. 2019c; Rana et al. 2019b; Verma et al. 2017a, 2019). The indirect methods include enhanced synthesis of ammonia, hydrogen cyanide, Fe-sequestering siderophores, exopolysaccharides (EPS), various cell wall-degrading enzymes, and secondary metabolites (Verma et al. 2016). These are capable of boosting the plant defence mechanisms against the

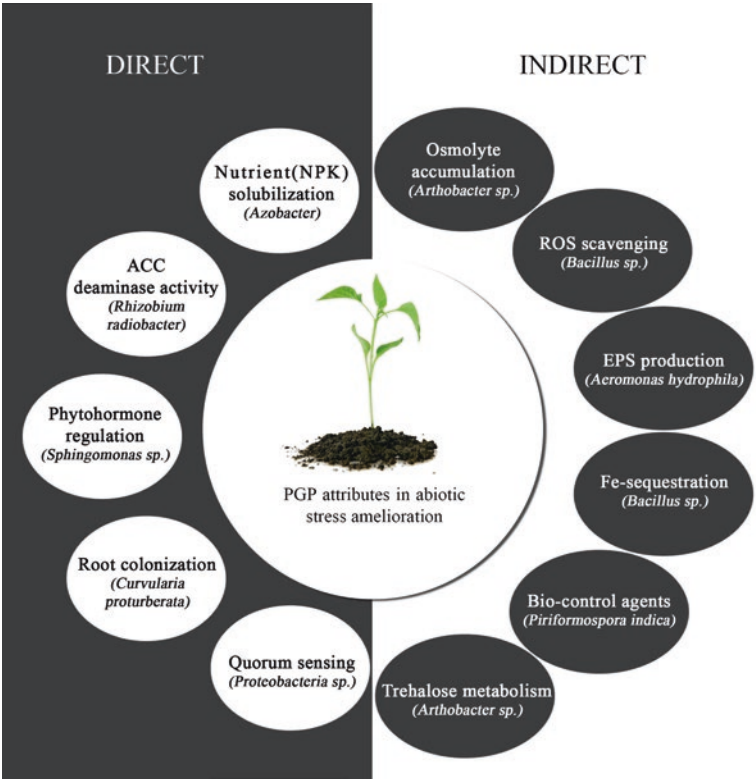

Fig. 7.3 Plant growth-promoting (PGP) attributes enhancing plant growth by promoting plant growth and alleviating salt stresses either directly or indirectly when plants are exposed to hypersaline soils

pathogens and drastic environmental conditions (Yadav and Saxena 2018; Upadhyay et al. 2011). Moreover, they can also serve as biocontrol agents and regulate the release of essential antibiotics and toxins to counter harsh and extreme conditions (Verma et al. 2018; Kour et al. 2020d; Rana et al. 2020c).

7.2.3.3 Types of Plant Microbiome

In nature rhizopheric microbes (10^6–10^9 bacterial cells/gram of soil) are more abundant than endophytic microbes (10^4–10^6 bacterial cells/gram of root tissue) (Liu et al. 2017). Endophytes colonize the rhizosphere as well as different parts of the plants (roots, stem, flowers, leaves, seeds, and fruits). Endophytes are being considered potential sources to counter the detrimental effects of abiotic stresses due to their ability to retain the PGP attributes (Rana et al. 2019a). Endophytes retain the PGP attributes even under extreme and prolonged stressful conditions unlike rhizopheric bacterial species which tends to lose these attributes (Suman et al. 2016;

Yadav 2019). Among the endophytic bacterial community, species of *Proteobacteria* phylum are most abundant followed by *Firmicutes*, *Actinobacteria*, and *Bacteroidetes* (Sharpton 2014; Kaul et al. 2016). Some isolated and common endophytic bacterial species include *Bacillus*, *Burkholderia*, *Pseudomonas*, *Stenotrophomonas*, *Micrococcus*, *Pantoea*, and *Microbacterium* (Marquez-Santacruz et al. 2010; Romero et al. 2014).

Plant microbes can also be classified based on the type of nutrient they fix and solubilize; nutrients such as phosphorous, nitrogen, and potassium are essential for plant growth and development (Verma et al. 2017b; Yadav et al. 2018a). The major phosphorous-solubilizing microbes include *Aspergillus*, *Azotobacter*, *Burkholderia*, *Citrobacter*, *Enterobacter*, *Haloarcula argentinensis*, *Haloferax alexandrinus*, *Haloferax larsenii*, *Haloferax volcanii*, *Pantoea*, *Penicillium*, *Piriformospora*, *Pseudomonas*, and *Trichoderma* (Vazquez et al. 2000; Kour et al. 2019a; Yadav et al. 2015, 2019a). The nitrogen-solubilizing microbes associated with biological nitrogen fixation include *Anabaena*, *Azospirillum*, *Azotobacter*, *Beijerinckia*, *Clostridium*, *Drexia*, *Enterobacter*, *Gluconacetobacter*, *Klebsiella*, *Nostoc*, *Pseudomonas*, and *Rhizobium* (Lacava and Azevedo 2013; Rana et al. 2019b; Yadav et al. 2018b). Microbes isolated and characterized for potassium solubilization are *Achromobacter*, *Arthrobacter*, *Bacillus*, *Duganella*, *Ensifer*, *Enterobacter*, *Exiguobacterium*, *Klebsiella*, *Lysinibacillus*, *Methylobacterium*, *Microbacterium*, *Ochrobactrum*, *Paenibacillus*, *Penicillium*, *Planococcus*, and *Pseudomonas* (Verma et al. 2017a; Yadav and Saxena 2018).

7.2.3.4 Halophilic Bacteria

The rhizosphere of halophytes serve as a rich source of halophilic (salt loving) bacterial species which can be harnessed to promote plant growth and development under salinity (Goswami et al. 2014; Jha et al. 2015). Various bacteria isolated from the rhizosphere community of halophytes include *Brachybacterium* sp. (Jha et al. 2012; Shukla et al. 2012), *B. licheniformis* (Goswami et al. 2014), *Exiguobacterium oxidotolerans* (Bharti et al. 2013), *Pseudomonas* sp. (Egamberdieva and Lugtenberg 2014), and *Halobacillus* sp. (Ramadoss et al. 2013).

7.2.3.5 Halotolerant PGPRs

The rhizosphere of several halophytes is potential source of halotolerant microbes. Scientists have isolated several genera of halotolerant bacterial species from halophytes. They are *Rosa rugosa* (Bibi et al. 2011), *Salicornia bigelovii* (Rueda-Puente et al. 2010), *Salicornia brachiate* (Jha et al. 2012), *Halocnemum strobilaceum* (Al-Mailem et al. 2010), *Sesuvium portulacastrum* (Bian et al. 2011; Anburaj et al. 2012), and *Avicennia marina* (El-Tarabily and Youssef 2010). High salt concentrations are a prerequisite for optimal growth and development of halotolerant microbes under both normal and saline environments. This key observation prompted researchers to explore hypersaline environments such as solar salterns, hypersaline lakes, the Dead Sea, hypersaline microbial mats, and underground salt deposits in search of potential halotolerant microbes. Several halotolerant microbes have been isolated from hypersaline environments. These include *Actinobacteria*, *Bacteroidetes*, *Euryarchaeota*, *Firmicutes*, *Proteobacteria*, and *Spirochaetes*. The other halophilic microbes include *Ammoniphilus*, *Arthrobacter*, *Azospirillum*, *Bacillus*, *Brevibacillus*, *Brevibacterium*, *Haloarcula*, *Halobacillus*, *Halococcus*, *Haloferax*, *Halolamina*, *Halomonas*, *Halorubrum*, *Haloterrigena*, *Lysinibacillus*, *Marinobacter*, *Marinospirillum*, *Oceanobacillus*, *Paenibacillus*, *Penicillium*, *Pontibacillus*, *Pseudomonas*, *Sediminibacillus*, *Sporosarcina*, *Streptomyces*, *Thalassobacillus*, and *Thermonema* (Ruppel et al. 2013; Gaba et al. 2017; Saxena et al. 2016; Yadav and Saxena 2018).

Halotolerant PGPRs have garnered a lot of attention in the present decade due to their ability to retain their PGP traits even under prolonged saline exposure (Rastegari et al. 2020b; Singh and Yadav 2020). This attribute prompted scientists to consider them for developing salt-tolerant transgenic plants in order to enhance tolerance thereby promoting growth and productivity. The intricate mechanisms employed by halotolerant PGPRs to promote plant growth are:

- Upregulating antioxidant enzyme activity (catalase, superoxide dismutase, peroxidase) to facilitate scavenging of ROS (Jha and Subramanian 2014; Qin et al. 2016)
- Promoting nutrient solubilization (Etesami and Beattie 2017; Etesami 2018)
- Increasing uptake of K^+ ions to maintain high K^+/Na^+ ratio and displace toxic Na^+ and Cl^- ions by regulating the activity of ion transporters (Shukla et al. 2012)
- Increasing EPS production to facilitate binding of cations (NA^+) to the hydroxyl, sulfhydryl, carboxyl, and phosphoryl binding sites of EPS thereby preventing Na^+ translocation to leaves and tissues (Dodd and Pérez-Alfocea 2012; Qin et al. 2016)
- Increasing ACC deaminase activity which subsequently reduces the ethylene accumulation and shields the plants from ethylene-mediated plant growth inhibition attributes (Glick 2014; Singh et al. 2015)
- Altering root morphology and architecture (Arora et al. 2012)
- Accumulating compatible solutes (proline, gycinebetaine, trehalose, mannitol, etc.) (Dutta et al. 2018; 2019; Etesami and Beattie 2017)
- Restoring photosynthetic activities and stomatal conductance (del Amor and Cuadra-Crespo 2012)
- Expression of stress-responsive genes such as RAB18 (late embryogenesis-abundant protein), RD29A and RD29B units of ABA-responsive elements (ABRE), and dehydration-responsive elements (DRE) and high-affinity K+ transporter (HKT1) (Qin et al. 2016)
- Inducing the expression levels of aquaporin synthesis genes such as PIP2, ZmPIP1–1, and HvPIP2–1 (Qin et al. 2016)

The plethora of beneficial actions of halotolerant PGPRs strongly recommends their use to alleviate salt stress responses in plants and induce tolerance. Some halotolerant PGPRs have been isolated and characterized for plant growth and development. Ullah and Bano (2015) reported that halotolerant PGPRs isolated from the rhizosphere of several halophytes, namely, *Haloxylon salicornicum*, *Lespedeza bicolor*, *Suaeda fruticosa*, and *Salicornia virginica*, were capable of increasing morphophysiological attributes in salt-stressed maize plants. Ullah and Bano (2015) observed accumulation of osmolyte (proline) and increased antioxidant enzyme activity (catalase, superoxide dismutase, and peroxidase). Similarly, Siddikee et al. (2010) observed increased root length, biomass, and dry weight, when seeds of canola were inoculated with halotolerant PGPRs in comparison with un-inoculated seeds.

7.3 Interaction of Microbiome with Plants

Understanding interaction of microorganisms with plants requires the knowledge of colonization of plant by microbiome, quorum sensing among plant microbiome, interaction between plants and microbiome, and cross talk between plants and microbiome (Kour et al. 2020c; Rastegari et al. 2020a). This section of the chapter elaborates on the above aspects to improve our understanding on interaction of microorganisms with plants.

7.3.1 Colonization of Plant by Microbiome

Microbes colonize roots, leaves, and stem of plants at various developmental phases via root, stem, and leave. Microbes enter (a) roots of plants via primary root, horizontal roots, root hair, root crack, wounds, and nodules (Baldotto et al. 2011; Huang et al. 2011; Prieto et al. 2011) and (b) leaves via stomata in leaves. Microbes live in symbiosis (mutual association) or as epiphytes (surface of plant parts) or as endophytes (“in ethereal parts of the plant and vascular tissue cortex”). Figure 7.4 shows colonization of different parts of plant by microbiome. Once the plants are colonized by microbiomes, two possible parallel events occur in the nature. The first event allows microbes to interact among themselves via quorum sensing mechanism, and the second event is cross talk between plants and microbiomes (Kour et al. 2020b; Rana et al. 2020b).

7.3.2 Quorum Sensing Among Plant Microbiome and Interkingdom Species

Microbes in the microbiome establish a communication process or system known as quorum sensing. N-Acyl-homoserine lactones (AHLs), 2-heptyl-3-hydroxy-4--quinoline, and autoinducer-2 are the well-known signalling molecules, which are used by microbes for communication (Challa et al. 2018, 2019a, b; Challa and

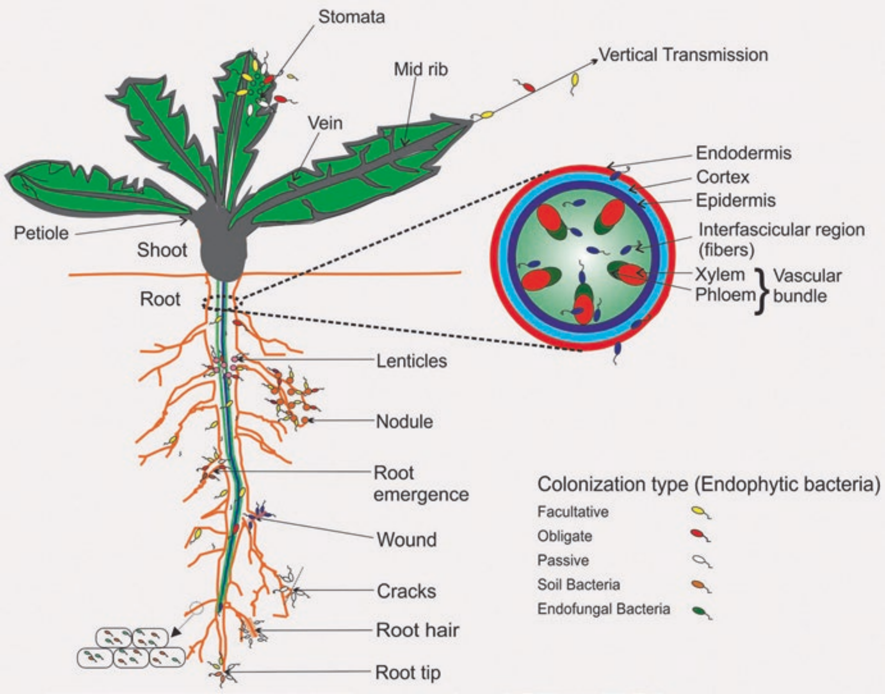

Fig. 7.4 Colonization of different parts of the plant by microbiomes. (Source: Vaishnav et al. 2019)

Neelapu 2018; Mohana Sheela et al. 2018; Neelapu et al. 2018). AHLs in *Proteobacteria*, gammabutyrolactones in *Streptomyces*, cis-11-methyl-2-dodecanoic acid in *Xanthomonas*, and oligopeptides in Gram-positive microorganisms act as signalling molecules (Danhorn and Fuqua 2007). The three types of communication systems used by the plant microbiome are intraspecies communication system, interspecies communication systems, and interkingdom communication system, as the microbiome is made up of multiple microbial species in the plant habitat (Mohana Sheela et al. 2018). Intraspecies communication system enables effective communication among the same species of microbes in the microbiome. This allows detecting cell densities of the same species of microbes in the microbiome, to synchronize and control several cellular and physiological processes (Mohana Sheela et al. 2018). Interspecies communication system enables effective communication between different species of microbes in the microbiome. This allows detecting cell densities of different species of microbes in the microbiome to control global gene expression in the microbiome (Mohana Sheela et al. 2018). Interkingdom communication system enables effective communication between different species (bacteria and fungi) of microbes in the microbiome and also between microbiome and the plant (Mohana Sheela et al. 2018). The best known example for interkingdom communication is between *Agrobacterium* and plant (Neelapu et al. 2018). Both interspecies and intraspecies communication help in horizontal gene transfer of genetic material from the donor to the host leading to evolution in nature. The ultimate use of quorum sensing in plant-microbiome interactions is to sense the surrounding environment and adjust to changing ecological conditions by enhancing supplement uptake or other means which are described above and below. Though we can understand that these three different mechanisms of quorum sensing exists in the nature when microbes colonize plant, still there is need to establish the evidence in favour of these communication systems.

7.3.3 Interaction Between Plants and Microbiome

Pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs) are the molecular patterns on microbes detected by plants. These patterns can either be located on cell surface or located within the cell. The well-known PAMPs or MAMPs are bacterial flagellin, Ef-TU proteins, intracellular effector proteins, lipopolysaccharides, peptidoglycans, or tissue damage (Boller and Felix 2009; Allen et al. 2004; Rivas and Thomas 2005). These PAMPs or MAMPs are recognized by pattern recognition receptor (PRR) of plants (Boller and Felix 2009; Allen et al. 2004; Rivas and Thomas 2005) and thereby activate plant immune system.

7.3.4 Plant Immune System

"The plant immune system comprises of four levels. In level 1, PAMPs of microbes are recognized and bind to specific PRRs located on the cell surface that triggers the plant immune system and leads to enhanced immunity (PTI), which prevents colonization and proliferation (Boller and Felix 2009; Tör et al. 2009; Bakker et al. 2012; Newman et al. 2013). In level 2, several pathogens induced effectors enhance virulence. The effectors hinder with PTI and lead to effector triggered susceptibility. In level 3, nucleotide-binding leucine rich repeat receptor proteins recognize the effector, which activate the effector-triggered immunity (ETI) that leads to disease resistance. In level 4, natural selection has motivated pathogens to conquer ETI by emerging effectors promoting virulence until plants have developed new receptors".

7.3.5 Cross Talk Between Plants and Microbiomes

Apart from interaction between microbiome and plants, there are several cross talks between plants and microbes during their interaction using different signalling molecules. Various microbes are harmful to plants that limit growth and development. In general, plant root exudates comprising of sugars, amino acids, and organic acids attract the microbes. Plants have mechanism to recognize certain compounds released by microbes and enhance defence responses. During plant-microbe interaction, once the plant recognizes microbe, plant signalling hormones, such as salicylic acid, jasmonic acid, and ET, activate the defence machinery in response to salt stresses (Koornneef and Pieterse 2008; Yi et al. 2014; Jalil and Ansari 2018).

In the case of fungi-plant interactions, sugar levels are increased during fungi-plant interactions where sugar molecules act as priming molecules and are sensed by plant cells and act as a signalling molecule. This subsequently interacts with plant hormone signalling network thereby reprogramming the plant cells (Morkunas and Ratajczak 2014). When fungi are in the proximity of a plant cell, then sugar levels are increased which are important for providing energy and structural material for plant defence processes. Sugar priming increases oxidative burst, cell walls (lignification), and flavonoid synthesis and also induces pathogenesis-related proteins. This induces plant immune system and also provides resistance to plants against fungi (if it is a pathogen) (Morkunas and Ratajczak 2014).

7.4 Salt Tolerance Mechanisms of Microbiome

Microbes in the microbiome have developed intricate mechanisms to thrive under salt stress exposure. The major challenge is to prevent alteration of ionic homeostasis and osmolarity. They employ various strategies such as construction of specific membranes in cell wall, “salting-out” or pumping ions extracellularly, and intracellular adaptations via osmolyte accumulation. These adaptive mechanisms have been elucidated in a wide range of microbes of different genera such as *Bacillus*, *Nesterenkonia*, *Zhihengliuella*, *Halomonas*, *Stenotrophomonas*, *Alkalimonas*, and *Litoribacter* (Shi et al. 2012; Yadav 2017; Yadav and Yadav 2019).

7.4.1 Cell Wall Construction

Microbes prevent intracellular salt accumulation and water loss by construction of specific cytoplasmic membranes as observed in archaea and cyanobacteria. These membranes are chemically composed of either ether lipids (halophilic archaea) or tetraether lipids (thermophilic archaea). These lipid membranes are temperature-resistant and prevent entry of ions/protons. However tetraether lipids are most suitable under high salt stress due to their nondegradable and impermeable nature (van de Vossenberg et al. 1998). In the case of *Halobacteriales*, the cell wall is dominated by a high-molecular-weight glycoprotein having four- or sixfold symmetry which requires high NaCl concentrations for stability. Cyanobacteria have more complex three-membrane systems that encompass its cell wall. The outer membrane protects the periplasmic space, whereas cytoplasmic inner membrane envelopes the cytoplasm, and the inner thylakoid membrane surrounds the photosynthetic machinery.

This intricate triple membrane protection is instrumental for Na^+ion extrusion as well as maintaining osmolarity. Several other modifications and cell wall constructions have been elucidated such as sulphate-rich heteropolysaccharide (*Halococcus* species), presence of poly (L-glutamine) glycoconjugate units (*Natronococcus occultus*), and exopolysaccharide-rich cell walls (rhizobacterial species) (Upadhyay et al. 2011; Ruppel et al. 2013).

7.4.2 Pumping Ions Out of the Cell

In general salt-sensitive species are unable to regulate Na^+ion transport, high K^+(100–200 mM), and low Na^+(less than10–20 mM) (Carden et al. 2003). Under such scenario reestablishment of ionic homeostasis is critical for survival and can be achieved by enhancing the levels of certain cellular proteins, like vacuolar antiporter proteins. Na^+ion compartmentation involves vacuolar Na^+/H^+antiporter channels, vacuolar membrane H^+-ATPase, and H^+-pyrophosphatase proteins that direct the toxic Na^+ions into vacuoles from the cytosol and also regulate cellular water uptake (Suneetha et al. 2016; Neelapu et al. 2019). Majority of the microbiomes, like plants, are capable for Na^+ion extrusion via vascular antiporter proteins (Oren 2006). Under high salt stress, halophilic archaea, cyanobacterium *Synechococcus* sp. PCC7942, cyanobacterium *Aphanothece halophytica*, and bacterium *Alkalimonas amylolytica* expressed increased activity of Na^+/H^+antiporter (Waditee et al. 2002; Wutipraditkul et al. 2005; Zhong et al. 2012). Zhong et al. (2012) reported that transgenic tobacco BY-2 lines harbouring *A. amylolytica* AaNhaD gene were able to enhance its salt tolerance than its wild-type counterparts. Similar observations were made when the microbiomes of the Dead Sea were evaluated (Jacob et al. 2017).

7.4.3 Intracellular Adaptations

Prolonged exposure to salinity results in loss of intracellular water, a phenomenon known as cellular dehydration. To overcome the loss of water from the cells and prevent denaturation of cellular functional proteins, microbes tend to accumulate specific organic compounds called osmolytes. These specific compatible solutes or osmolytes are involved in osmoprotection, and they include proline, betaine, polyols, sugar alcohols, and soluble sugars. Denaturation of functional proteins is due to increased cellular hydrophobic and electrostatic interactions which subsequently reduces the water uptake capacity below critical level (Oren 2006). To thrive under such conditions and carry out essential metabolic pathways, microbes undergo several intracellular adaptations, such as uptake and biosynthesis of osmolytes, enhanced energetic capacity, and structural adaptations of proteins. Different microbes differ in their salt-tolerant capacity and accumulate osmolytes accordingly. For example, low halotolerant *Cyanobacteria* spp. accumulate sucrose/trehalose, and moderately halotolerant (marine) species accumulate glycosyl glycerol (GG), whereas halophilic species accumulate glycine betaine (GB) as their major osmolyte (Hagemann 2011). Microbes belonging to *Halobacteriaceae* class have been observed to accumulate high levels of acidic amino acids (glutamate and aspartate) in comparison to basic (lysine and arginine) and hydrophobic (aserine and threonine) amino acid residues. Such intracellular adaptations of amino acid composition has been associated with increased salt tolerance due to regulation of water loss as acidic amino acids possess highest degree of water binding capacity among all amino acid residues. Similar results were observed in various halophilic strains and thermophilic *Halothermothrixorenii* among others (Ruppel et al. 2013).

7.5 PGP Attributes of Microbiome for Salt Tolerance

PGP microbes help the plants in accumulation of osmolytes and antioxidants, reduction of ethylene levels, regulation of phytohormone levels, increase of nutrient uptake, and increase in expression of aquaporins to provide tolerance towards salt stress.

7.5.1 Accumulation of Antioxidants and Osmolytes

Microbes accumulate antioxidants and osmolytes, which adjust osmotic potential and stabilize cell components and free radical scavengers. Pepper plants (*Capsicum annuum* L.), when treated with *Arthrobacter* sp. and *Bacillus* sp., stimulated proline accumulation in leaves when compared with non-treated plants (Sziderics et al. 2007). Similarly, rice plants when treated with *Pseudomonas pseudoalcaligenes* induced glycine betaine accumulation and contributed to salt tolerance (Jha et al. 2011). Likewise, *Brassica napus* (canola) when treated with *Pseudomonas putida* expressed antioxidant proteins and showed tolerance to salt (Cheng et al. 2012). Similarly, cucumber when treated with *Pseudomonas aeruginosa* PW09 showed tolerance to salt and pathogens (Pandey et al. 2012). *P. aeruginosa* PW09 treatment stimulated accumulation of antioxidants (proline and total phenolic contents) and increased the activity of defence enzymes (polyphenol oxidase, phenylalanine ammonia lyase) and scavenging enzymes (SOD) under salt stress (Pandey et al. 2012). *P. aeruginosa* PW09 treatment also showed tolerance towards pathogen *Sclerotium rolfsii* (Pandey et al. 2012). In the same way, when wheat plants were treated with *B. phytofirmans*, PsJN antioxidant activity increased and showed tolerance to drought (Naveed et al. 2015).

Likewise, grass *Brachypodium distachyon* when treated with *Bacillus subtilis* B26 exhibited increased fructose, glucose, starch contents, and total soluble sugars and showed tolerance to drought stress (Gagne-Bourque et al. 2015). In the same way, chickpea plants when treated with *Bacillus subtilis BERA 71* showed tolerance to salt stress (Abd Allah et al. 2018). Increased antioxidant enzymes activities (SOD, POD, CAT, and GR), non-enzymatic antioxidants activities (ascorbic acid, glutathione, and total phenol content), plant biomass, chlorophyll content, and nutrients (N, P, K, Ca, and Mg) were observed when chickpea was treated with *BERA 71*. At the same time, reduced ROS, lipid peroxidation levels, and sodium accumulation were observed when chickpea was treated with *BERA 71*. Similarly, soybean plants when treated with *P. simiae* AU induced proline and total soluble sugar content showing tolerance towards drought (Vaishnav and Choudhary 2018).

7.5.2 Reduction of Ethylene Levels

Plants in general tend to accumulate ethylene in response to saline stress (Flowers and Colmer 2015). Ethylene accumulation in plants usually inhibits plant growth (shunted root and shoot growth) (Gupta et al. 2016). 1-AminoCyclopropane-1-Carboxylate (ACC) is the precursor for production of ethylene, and ACC is converted to ethylene in the presence of enzyme ACC oxidase (Bleecker and Kende 2000). The ACC deaminase enzyme (E.C. 4.1.99.4) cleaves ACC into α-ketobutyrate and ammonia. This regulates ethylene production and reduces the levels of ACC in plant (Glick et al. 2007; Choudhary et al. 2015; Hardoim et al. 2015). Plants when treated with microbes showed ACC deaminase activities blocking the production of ethylene, and thus microbes can be considered as good plant growth promoters (Santoyo et al. 2016). Majority of the halotolerant bacterial species have been associated with ACC deaminase activity. The following bacterial species are associated with ACC deaminase activity: *Brachybacterium saurashtrense*, *Brevibacterium casei*, *Cronobacter sakazakii*, *Haererehalobacter*, *Halomonas*, *Mesorhizobium*, *Pseudomonas*, *Rhizobium radiobacter*, *Vibrio*, and *Zhihengliuella* (Jha et al. 2012; Qin et al. 2014).

Iniguez et al. (2005) treated *Medicago truncatula* with *Klebsiella pneumoniae* strain 342 which controlled ethylene levels via enzyme ACC deaminase activity. In a study, canola plant when treated with bacteria *Burkholderia phytofirmans* PsJN promoted plant growth via ACC deaminase activity (Sessitsch et al. 2005; Sun et al. 2009). In another study, *Catharanthus roseus* when treated with bacteria *Achromobacter xylosoxidans* AUM54 showed higher ACC deaminase activity and contributed towards tolerance to salt stress (Karthikeyan et al. 2012). In a similar study, tomato when treated with bacteria *Pseudomonas fluorescens* YsS6 and *Pseudomonas migulae* 8R6 showed higher ACC deaminase activity and contributed towards tolerance to salt stress (Ali et al. 2014). Bacteria like *Arthrobacter*, *Bacillus*, *Isoptericola*, *Klebsiella*, *Microbacterium*, *Pseudomonas*, *Serratia*, and *Streptomyces* inhabiting *Limonium sinense* (halophyte) contributed to ACC deaminase activity and showed salt tolerance (Qin et al. 2014). In another study, rice, when treated with *Pseudomonas stutzeri* A1501, exhibited salt tolerance and promoted plant growth (Han et al. 2015). Similarly, bacteria *Brachybacterium paraconglomeratum* inhabiting plant *Chlorophytum borivilianum* showed higher ACC deaminase activity, chlorophyll levels and IAA contents; at the same time reduced oxidative damage, osmotic damage, lower level of lipid peroxidation, ABA, and ethylene contributing towards salt tolerance (Barnawal et al. 2016).

7.5.3 Regulation of Phytohormone Levels

Plants when treated with bacteria regulated levels of phytohormones (ABA, auxins gibberellins, and cytokinins) in the host via signalling pathways and promoted plant growth when subjected to stress conditions (Glick 2012). In a study, rice when treated with bacterial *Bacillus amyloliquefaciens* RWL-1 induced salicylic acid production (signalling pathways) and ABA production (phytohormones) in plants and showed tolerance to salt stress in rice plants (Shahzad et al. 2017). In another study, tomato when treated with *Sphingomonas* sp. LK11, isolated from *Tephrosia apollinea*, produced gibberellins, increased chlorophyll contents, and promoted growth in plants (Khan et al. 2014). Similarly, when rice was treated with bacteria *Burkholderia kururiensis*, IAA activities increased in rice plants and promoted plant growth (Mattos et al. 2008).

In another study, 51 bacteria (α-*Proteobacteria*, γ-*Proteobacteria*, *Actinobacteria*, and *Firmicutes*) were isolated from ginseng stems. These bacteria promoted plant growth via IAA activities (Vendan et al. 2010). Similarly, 18 bacteria were isolated from apple tree buds. These bacteria showed increase in IAA activity (1.2–2.4 μg/mL) (Miliūtė and Buzaitė 2011). Likely, halotolerant bacteria like *Acinetobacter*, *Bacillus*, *Enterobacter*, *Marinobacterium*, *Pantoea*, *Pseudomonas*, *Rhizobium*, and *Sinorhizobium* were isolated from *Psoralea corylifolia* L. These bacteria showed IAA activity and promoted plant growth under salt stress conditions when plants were treated (Sorty et al. 2016). Ali et al. (2017) also reported the role of bacteria in producing IAA hormones and promoting plant growth. Bhore et al. (2010) treated cucumber with bacteria *Pseudomonas resinovorans* and *Paenibacillus polymyxa* isolated from sambung nyawa. This treatment enhanced cytokinins and thus promoted plant growth. In another study, alfalfa plants when treated with bacterium *Sinorhizobium meliloti* (engineered for overproduction of cytokinin) enhanced tolerance in the plants (Xu et al. 2012). In another different study, rice was treated with *Pseudomonas putida* REN5 (rhizospheric) and *Pseudomonas fluorescens* REN1 (endophytic) bacteria. Co-inoculation increased colonization of both bacteria with plant roots, modulating phytohormone signalling and promoting plant growth and tolerance under stress conditions (Etesami and Alikhani 2016).

7.5.4 Increase of Nutrient Uptake

Green revolution has increased the use of chemical fertilizers creating a lot of environmental issues. Sustainable agriculture is possible when chemical fertilizers are replaced with biofertilizers. Literature lists out the microbes that can improve the nutrient uptake and enhance plant growth. Nitrogen-fixing bacteria, phosphate solubilizing bacteria, and bacteria which can increase iron uptake help the host in uptake of nutrients.

7.5.4.1 Increase of Nitrogen Uptake

Nitrogen (N) is a very important component for plant growth and is additionally provided to plant as a chemical fertilizer. It is well established that nitrogen-fixing bacteria in plants promote plant growth efficiently. In legumes symbiosis between plants and nitrogen-fixing bacteria leads to formation of root nodules, where atmospheric nitrogen is reduced to ammonia by the enzyme nitrogenase. The root-nodulating bacteria are *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, *Sinorhizobium*, etc. But, endophytic bacteria should be more efficient in fixing nitrogen than rhizospheric bacteria (root nodulating bacteria) due to low availability of oxygen which is essential for N fixation (Kour et al. 2020a; Rana et al. 2020a). The endophytic bacteria include *Acetobacter*, *Azospirillum*, *Herbaspirillum*, *Klebsiella*, etc. (Lacava and Azevedo 2013). Nearly 75 endophytic bacterial isolates with N-fixing ability belonging to *Enterobacteriaceae* and *Pseudomonadaceae* groups were isolated from soybean (Kuklinsky-Sobral et al. 2004). Sessitsch et al. (2012) performed a metagenomic study on endophytic root microbiome of rice and identified N fixation-related genes. This suggests that endophytes might have involved in N cycle processes (Sessitsch et al. 2012). In another study, *Paenibacillus polymyxa* P2b-2R was isolated from rhizosphere and endosphere of maize. This was identified as a nitrogen-fixing bacterium which was able to promote plant growth.

7.5.4.2 Increase of Phosphate Uptake

After nitrogen, phosphorus is one of the limiting macronutrient for plants which are important for production of plant biomass. “Phosphorus is in immobilized form and not available for plants”. Reports exist on microbes colonizing root surface and inner part of the tissue. These microbes solubilize phosphate and make phosphate available to plants as a fertilizer (Kaur et al. 2020; Singh et al. 2020). Several reports exist on different endophytic species which were able to solubilize mineral phosphates (Lacava and Azevedo 2013). Two species *Bacillus subtilis* and *B. megaterium* that can solubilize phosphate are isolated from strawberry and were able to enhance plant growth (Dias et al. 2009).

7.5.4.3 Increase of Iron Uptake

Iron is another essential nutrient for plants which is important for plant growth. Iron also exists as insoluble form which is not available to plants. Literature reports microbes which chelate iron, convert iron to soluble form, make it available to plants, and help the plant to grow in low-iron soil (Choudhary et al. 2015). Bacteria inhabiting ginseng plants showed the ability to produce siderophores demonstrating that production of siderophores is common among endophytes (Vendan et al. 2010). Sessitsch et al. (2012) showed that genome of endophytic root microbiome of rice was abundant with siderophore biosynthesis genes which code for proteins used in reception and storage of iron. These microbiomes help the plants in uptake of iron. Rungin et al. (2012) used wild and siderophore-deficient mutants of *Streptomyces* sp. GMKU 3100 to confirm the role of siderophores in iron uptake. When rice plants were treated with *Streptomyces* sp. GMKU 3100, higher accumulation of iron was observed when compared with the plants treated with siderophore-deficient mutant (Rungin et al. 2012). In addition, siderophores are a means through which endophytes involved in biocontrol mechanisms reduce the availability of iron for phytopathogens (Choudhary et al. 2015).

7.5.5 Increase in Expression of Aquaporins

Managing salt stress involves the use of aquaporins or water channels to transport water in plants. Halotolerant PGPRs have been associated with inducing the expression levels of aquaporin synthesis genes such as PIP2, ZmPIP1-1, and HvPIP2-1. Halotolerant PGPRs thereby regulate the cellular water potential levels under salinity (Qin et al. 2016). The halotolerant PGPRs *Azospirillum brasilense*, *Pantoea agglomerans*, and *Bacillus megaterium* were known to regulate cellular water potential levels via aquaporins under salinity (Qin et al. 2016).

7.6 Concluding Remarks and Future Prospects

Food security is the greatest challenge to mankind, and food security to the growing population is possible when sustainable agriculture is implemented for food production. Sustainable agriculture needs solutions to the problems like salinity faced in agriculture. Salinity leads to salt stress on both plants and microbiome-colonizing plants. Plants encounter osmotic and ionic phases when exposed to salinity stress, and plants when treated with microbiome showed tolerance to salinity. The salinity tolerance mechanisms adapted by plant microbiome are cell wall construction, pumping ions out of the cell, and intracellular adaptations. Salt tolerance is only possible when microbiome and plant interact with each other. Microbiomes interact with plant, initially by colonizing the plant and its part, and later communicate among themselves and with the plant via quorum sensing. Quorum sensing is the plausible mechanism of communication among the microbes of microbiome and plants. The exact line of the quorum sensing followed by microbes of microbiome is yet to be established. Cross talk between plants and microbiome is known, but the exact molecules in the plant and microbes which act as signalling molecules in the cross talk are yet to be identified and established. The exact pathway or multiple pathways converging or responsible for cross talk between plants and microbiome is also yet to be established. This provides better information and understanding on cross talk between plant and microbiome. Then the cross talk between the plant and the microbiome modulates the phytohormone signalling leading to different PGP attributes. The different PGP attributes of microbes in the microbiome providing salt tolerance to plants are accumulation of osmolytes and antioxidants, reduction of toxic levels of ethylene via ACC deaminase activity, regulation of phytohormones, increase in nutrients (N, Fe P) uptake, increase in aquaporins, etc. In conclusion, PGP attributes of microbes in the microbiome mitigate salt stress and provide salt tolerance to the plants growing in salt stress.

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Chapter 8
Alleviation of Cold Stress by Psychrotrophic Microbes

Meena Sindhu, Kamla Malik, Seema Sangwan, Anuj Rana, Nayan Tara, and Sushil Ahlawat

Abstract Psychrotrophs have the ability to survive in extreme conditions of lower temperature ranges from 0 °C to 20 °C. Psychrotrophic microorganisms mainly include bacteria, archaea and yeast, but among them, bacteria predominate in polar environment and archaea are more widespread in cold and deep ocean waters. They have evolved a variety of adaptation mechanisms such as gene expression modification and production of cold stress protein to cope up with stress induced at such a lower temperature. Cold active enzymes produced by psychrotrophs have wide applications in the food and pharmaceutical industry. Moreover these have wide applications in agriculture as they have the ability to promote plant growth at low temperature.

Keywords Adaptation · Agriculture cold stress · Microbes · Psychrotrophs

8.1 Introduction

Psychrotrophs are those microbes which can survive and thrive at extremely cold conditions and grow at a wide range of temperature from 0 °C to 20 °C. Psychrotrophs have the ability to sustain in soil, surface, deep sea water, food and Antarctic ecosystem. These are distributed widely in soil and water in temperate regions. In the

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permafrost soil and ice, microbial activity is mainly restricted to unfrozen water. They have high salt concentrations along with particulate matter, so fluid flow is regulated by gradients of concentration and temperature (D'Amico et al. 2006). They have adapted themselves to survive at low temperature by involving modification in expression of genes (Seki et al. 2003) and producing cold acclimation proteins, anti-freezing proteins, unsaturated fatty acids, increase in proline content, cold-active enzymes, high sugar concentration and total phenolics, carotenoids and cryoprotectants (Ait Barka et al. 2006). Alteration in physiological and metabolic activities permit osmotic adjustment for continuation of water uptake include production of osmotic regulator, i.e. proline, sucrose, sugar and alcohols (Kasuga et al. 2004; Zhu 2002; Hasegawa et al. 2000; Yadav 2015). Psychrotrophs have attracted interest of scientific community to study these adaptations. This adaptation can be used to encourage agricultural plant growth. Psychrotroph's ability to generate cold-adaptive enzymes can be used in a wide variety of agricultural, industrial and medical fields/processes.

Low temperature is one of the main abiotic stresses that lead to adverse effect on plant development and production. Psychrotroph's ability to survive at low temperature could be utilized for considerate adjustment at low temperatures. Cold-sensitive enzymes could be utilized in leather processing industry as cleaning agents. The other applications include xenobiotic compounds biodegradation at low temperature, heterologous gene expression at molecular level and food processing (bakery, cheese manufacture and fermentation). Psychrotrophic microbes can ameliorate cold stress in plants which could be valuable to use in agriculture (Yadav et al. 2019a, b, 2020). Climate changes due to greenhouse gases lead to increase in tempeature that are favourable for survival of microorganisms in extreme conditions. Moreover cropping cycle that is subjected to low temperature periods has a negative impact on plant growth and psychrotrophs are the solution, with ability to fix nitrogen and solubilize phosphorus under such extreme climate. In cold climatic conditions, the use of psychrophiles as biofertilizers, biocontrol agent and bioremediators opens a new window in agriculture field under low temperature climatic conditions.

8.2 Alleviation to Cold Stress by Microbes

Psychrotrophs has adapted them to grow at low temperature. Microbes survive in unfavourable conditions by triggering physiological response in them. Several mechanisms that have been adapted by psychrotrophs to cope with cold stress are mentioned in Fig. 8.1.

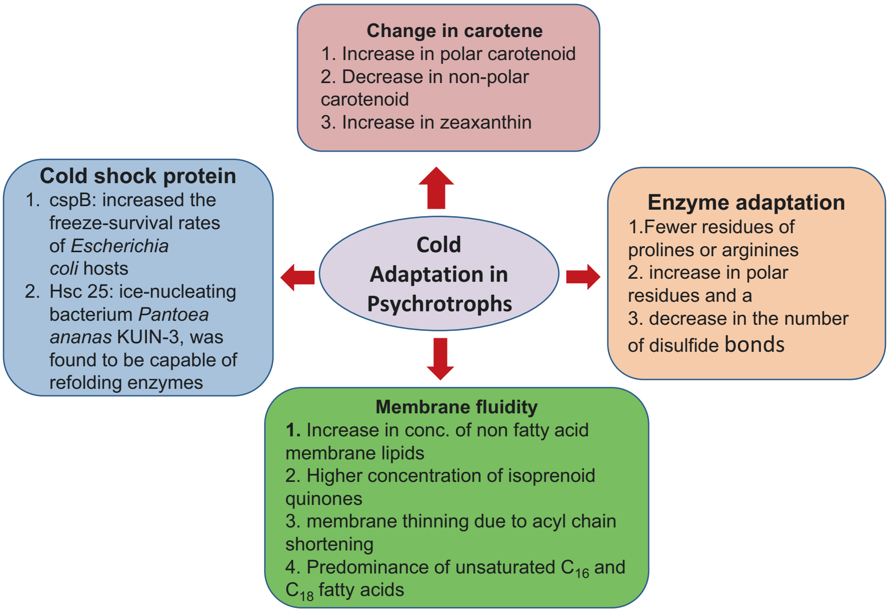


Fig. 8.1 Alleviation of cold stress by microbes

8.2.1 Membrane Fluidity

Maintenance of membrane fluidity plays an important role for adaptation to low temperature (Ray 2006). Lipid composition varies with change in habitat of organism. It was found that increases in nonfatty acid membrane lipid amount and higher concentration of isoprenoid quinones have been significantly improving adaptation to low temperature in *L. monocytogenes* strains as studied by Seel et al. (2018). In marine bacterium, *Synechococcus* responded to cold temperature, and membrane thinning due to acyl chain shortening with specific desaturation activities was observed. Along with it, membranes that were found almost devoid of C-18 rather contain C-14 and C-16 chains with no more than two unsaturated activities (Pittera et al. 2018). Singh et al. (2017) isolated *Leeuwenhoekiella aequorea, Pseudomonas pelagia, Halomonas boliviensis, Rhodococcus yunnanensis* and *Algoriphagus ratkwoskyi* from Kongsfjorden (an Arctic fjord) and found that the unsaturated fatty acids, primarily cis-10-penta-decenoic, palmitoleic and oleic acid, were mainly responsible constituents for adaptation capability to cold stress.

The Antarctic psychrotriphic bacterium *Pseudomonas syringae* was more sensitive to polymyxin B at 4 °C temperature than at 22 °C for growth. Due to this leads to increase the fluidity of lipopolysaccharides and improving outer membrane fluidity activities (Kumar et al. 2002). Mykytczuk et al. (2010) studied that psychrotrophic strains of *Acidithiobacillus ferrooxidans* had a comparatively higher rigid membrane with *P*- range (0.41–0.45), lower T_m (transition midpoint temperature), i.e. 2.0 °C, and broader transition range as compared to mesophilic strains (P range = 0.38–0.39; T_m = 2.0–18 °C) at low temperatures. Decrease in 12:0 fatty acids in psychrotrophic strains as compared to those of the mesophilic strains showing decreases in range of 16:0, 17:0 and cyclo-19:0 fatty acids clearly distinguished 5 °C fatty acid profiles of psychrotrophic strains. High amounts of unsaturated FAs that lead to the constitutive expression of FA desaturases in the bacterial cells is a major characteristic or feature of psychrotolerant bacteria.

8.2.2 Change in Carotene/Carotenoids

Carotenoids are polyisoprenoid hydrocarbon produced in response to extreme environmental stress. Pigments present in Antarctic bacteria have the ability to localize in the membrane and provide rigidity to the membrane. The amount of polar carotenoids increased with decreased temperature and the amount of nonpolar carotenoid also decreased (Chattopadhyay and Jagannadham 2001). The increase in decreased membrane fluidity due to polar carotenoid has been observed by Subczynski et al. (1992). Chattopadhyay and Jagannadham (2001) observed in the Antarctic bacteria that synthesized membrane-rigidifying polar carotenoids increase with synthesis of membrane-fluidizing fatty acids and compensate the effects of FA. Jousse et al. (2018) also reported key cold shock biomarkers that included cryoprotectants and their precursors, alkaloids and secondary metabolites involved in energy metabolism from *Pseudomonas syringae* isolated from cloud water. A psychrotrophic bacterium *Arthrobacter agilis* was isolated from the Antarctic sea ice. At low temperature the C-50 carotenoid production was observed that could contribute to cold stress membrane stabilization (Fong et al. 2001).

8.2.3 Enzyme Adaptation

In psychrotrophic organisms, different enzymes use multiple strategies to get adapted at lower temperature. These include reduction in number of ionic pairs and their hydrophobic interactions, decreased inter-subunit interactions, improved interaction with the solvent, core having reduced nonpolar fraction, active site with higher convenience, nonpolar residues improved in the solvent, decline in cofactor binding and glycine residues clustering with lower arginine and proline content (D'Amico et al. 2006). Cold-tailored microorganisms synthesize lipases which increase their tolerance to cope with the extremely frosty environment with elevated biocatalytic activity (Kour et al. 2019a). Cold tolerance of enzymes includes decrease in ratio of arginine to arginine + lysine, decrease in hydrophobic residues that attached with polar residue, smaller residues of prolines or arginines and also decrease in the number of disulfide bonds (D'Amico et al. 2006). In *Moritella marina*, malic dehydrogenase (MDH) was found to be stable between temperature 0° and 15 °C, and enzyme lost its properties with increase in temperature at 30 °C.

8.2.4 Cold Shock Protein

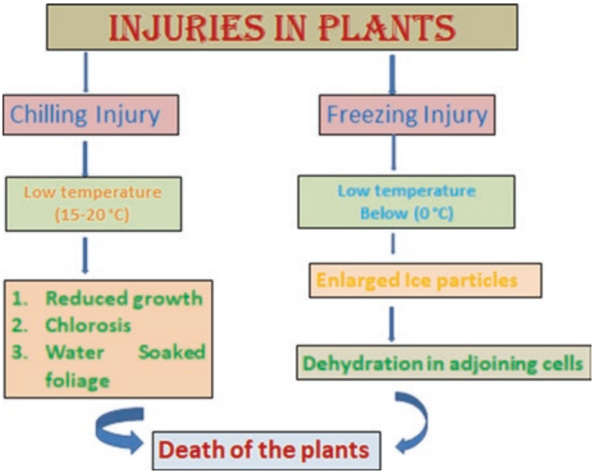
Proteins play a significant role in alleviating cold stress among organisms. Two types of proteins are formed in reaction to low temperature, viz. cold shock and cold acclimation proteins. The cold acclimation proteins are exclusively by psychrotrophs while cold shock proteins are produced in both mesophiles and psychrophiles. Cold shock proteins (Csps) inhibit mRNA secondary structure development by acting as nucleic acid chaperons at low temperature and thus make possible the commencement of translation. Cold shock proteins also contribute to osmotic, oxidative, starvation, pH and ethanol stress tolerance as well as to host cell invasion (Keto-Timonen et al. 2016). Gene coding for a Csp family protein, *cspB*, was cloned from an Arctic bacterium, *Polaribacter irgensii* KOPRI 22228, and overexpression of *cspB* increased the freeze-survival rates of *Escherichia coli* hosts (Jung et al. 2018). Thirteen proteins were induced in *Escherichia coli* when exposed to a temperature shock from 37 °C to 10 °C (Jones et al. 1987).

In the mesophilic bacteria, CSPs facilitated transcription and translation processes at low temperature, but their exact role is yet to be confirmed. Kawahara et al. (2000) found that *Pantoea ananas* KUIN-3 ice-nucleating bacterium produces cold acclimation protein (Hsc 25) which has an enzyme-refolding capability and further denature via high and low temperature and guanidine hydrochloride. Affinities of these proteins are higher for cold as compared to heat-denatured enzymes, as compared to Gro EL. Panicker et al. (2002) observed the superior expression of 8 kDa protein at 4 °C in *Pseudomonas* spp. 30–3 and suggested the role of Cap B protein in tolerance and survival at subzero temperatures. Drouin et al. (2000) studied that at 0 °C, the number of Csps synthesized was higher in the cold-adapted strains such as *R. leguminosarum* bv. *viciae* from the legumes *Lathyrus japonicus* and *Lathyrus pratensis* in northern Quebec than in the cold-sensitive strains. Mazzon et al. (2012) observed that cspA and csp B, cold shock genes from *Caulobacter crescentus*, have an important role in mRNA stabilization and cold adaptation. CspD, a cold shock domain protein, was produced in psychrotolerant Antarctic *Janthinobacterium* sp. Ant5–2 (ATCC BAA-2154) at low temperature (Mojib et al. 2011). H-NS and Huβ are plasmid-encoded cold shock proteins which participate in supercoiling of DNA when bacteria are exposed to cold stress. Metabolic state of the cell gets modified due to DNA structure reorganization and gene expression modification (Giangrossi et al. 2002).

8.3 Effect of Cold Stress on Agriculture

Cold stress held back the development and yield of plants (Janda et al. 2003). Response of plants towards lower temperature is given in Fig. 8.2. Cold stress leads to production of reactive oxygen species (ROS) in plants which are highly reactive and detrimental metabolic products. Plants had evolved a number of mechanisms to

Fig. 8.2 Effect of cold stress on plants



reduce oxidative injuries in plants by evolving various enzymatic mechanisms that reduce reactive oxygen species. O_2 is converted to hydrogen peroxide (H_2O_2) by superoxide dismutase (SOD) which is then scavenged by catalase (CAT) by reducing the two electrons from oxygen. Peroxidase (POD) participates in lignin biosynthesis and indole acetic acid (IAA) degradation and converts H_2O_2 to H_2O (Agarwal et al. 2005). A MAPKK (maize mitogen-activated protein kinase kinase), gene *ZmMKK1*, was reported to induce chilling tolerance efficiency in tobacco by improving antioxidant enzyme activity and osmolyte accumulation and increased expression of reactive oxygen species (ROS)-related genes significantly (Cai et al. 2014). Accumulation of melatonin and sugars raffinose also confers chilling tolerance through the reactive oxygen species (ROS)-scavenging mechanism in plants (Zhang et al. 2015; ElSayed et al. 2014). Therefore, improvement of ROS-scavenging activity is the mechanism to perk up low temperature adaptation in the plants (Yadav et al. 2019a).

When warm-habitat plants such as maize (*Zea mays*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), tomato (*Lycopersicon esculentum*) and banana (*Musa* sp.) are exposed to low temperature, they exhibit symptoms of injuries (Lynch 1990; Guy 1990; Hopkins 1999). However, this symptom varies from plants to plants and depends upon the plant sensitivity to cold stress. Cold stress generally results in reduced germination, undersized reduced seedlings, yellowing of leaves, wilting, reduced tillering and necrosis in plants (Jiang et al. 2002). It also results in production of sterile pollen which leads to reduction in capitulate (Suzuki and Mittler 2008). The lower temperature leads to leaf tissue damage confirmed via observing electrolyte seepage and malondialdehyde concentration in tomato plant. Significantly improved root-and-shoot ratio and enhanced antioxidant enzyme were observed in tomato when its seeds were inoculated with plant growth-promoting psychrotolerant bacteria (Subramanian et al. 2016) (Fig. 8.3).

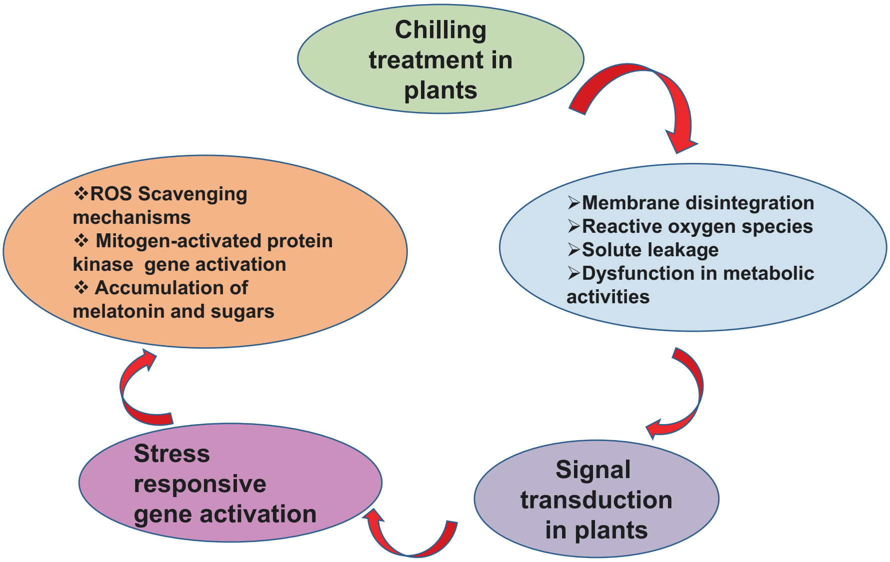


Fig. 8.3 Response of plants to cold temperature

8.4 Plant Growth-Promoting Rhizobacteria Ameliorates Cold Stress in Plants

Growth-promoting rhizobacteria are the bacteria living in the area around plant roots which are necessary for plant development. Novel group of microbes can be isolated from extreme environments representing unique ecosystems such as acidophiles, alkalophiles, halophiles, psychrophiles, thermophiles and xerophiles (Saxena et al. 2016; Yadav et al. 2017). Cold stress in the plants can be ameliorated with the help of cold-tolerant plant growth-promoting rhizobacterial strains (Ait Barka et al. 2006; Cheng et al. 2007). For sustainable agriculture, there is need to consider microbial diversity associated with crops. Under different abiotic stress conditions, PGPR associated with crops are able to promote the plant growth. Plant growth-promoting microorganisms have been reported and belong to the different genera including *Arthrobacter*, *Bacillus*, *Paenibacillus*, *Brevundimonas*, *Pseudomonas*, *Burkholderia*, *Flavobacterium*, *Citricoccus*, *Exiguobacterium*, *Janthinobacterium*, *Methylobacterium*, *Kocuria*, *Lysinibacillus*, *Microbacterium*, *Providencia* and *Serratia* (Saxena et al. 2015; Verma et al. 2015b; Singh et al. 2016; Yadav et al. 2016a, b, 2018).

At lower temperature *Bacillus*, *Exiguobacterium* and *Pseudomonas* have been found the good characteristics for plant growth promotion (Mishra et al. 2011; Selvakumar et al. 2011; Yadav et al. 2015c, 2016a, b). Under cold conditions and hilly areas, psychrophilic/psychrotrophic microbes could be used as a biofertilizers, biocontrols and bioremediators agent in agriculture. Cold-adapted enzymes produced by psychrophilic/psychrotolerant microbes have potential because they provide opportunities to study the adaptation of microbial life at lower temperature (Saxena et al. 2016; Yadav et al. 2019a, b). Subramanian et al. (2015) isolated psychrotolerant bacteria from soil of agricultural field in winter. Around 32 isolates were able to produce plant growth-promoting attributes such as ACC deaminase, salicylic acid, IAA, siderophores and tricalcium phosphate solubilization under lower temperature up to 5 °C. These psychrotrophs have ability to alleviate chilling stress in tomato plants (*Solanum lycopersicum* cv Mill).

Electrolyte seepage and lipid peroxidation in leaf tissues under cold stress was significantly reduced by strain *P. vancouverensis* OB155. Turan et al. (2013) studied that when Plant growth-promoting bacteria along with Boron were applied to wheat and barley, they induced the cold tolerance in plants by alteration in mineral uptake, enhancement of chlorophyll content, photosynthetic activity and relative water content and decreasing membrane damage.

Verma et al. (2015a) investigated that at lower temperature conditions, appreciable level of K solubilization was exhibited by *Bacillus amyloliquefaciens* IARI-HHS2-30. After 30 days of inoculation in wheat, *Bacillus amyloliquefaciens* IARI-HHS2-30 increases root/shoot length, fresh weight and chlorophyll content. PGP attributes having psychrophilic ability suggest that in low-temperature and high-altitude condition, these endophytic bacteria might be exploited as bio-inoculants for various crops. Yadav et al. (2016a, b) studied that PGP attributes in psychrotrophic bacterial species, viz. *Bacillus licheniformis*, *Bacillus muralis*, *Paenibacillus tylopili, Desemzia incerta* and *Sporosarcina globispora*. They observed that biofertilizers could be developed from these bacterial species for growing crops at low-temperature conditions.

8.4.1 ACC (1-Aminocyclopropane-1-Carboxylate) Deaminase Activity

At low temperature, there is an enormous increase in production of ethylene which triggers senescence and abscission in plants. ACC deaminase found in many bacteria can cleave ACC, intermediate of ethylene in plants. In this way, endophytic bacteria associated with plants help them to cope up with cold stress (Kour et al. 2019b; Verma et al. 2017). Tiryaki et al. (2019) isolated 6 psychrotolerants from the leaf apoplast of cold-adapted wild plants exhibiting ACC deaminase activity (57.60–166.11 nmol α-ketobutyrate/mg protein/h). These bacteria also secrete specific extracellular proteins at cold conditions. Bacterial inoculants decreased freezing injury and ROS levels while stimulating antioxidant system parameters in the bean seedlings. When canola plants were treated with ACC deaminase-producing bacterium *Pseudomonas putida* UW4, the plant growth was enhanced by lowering salt-induced ethylene synthesis (Cheng et al. 2007).

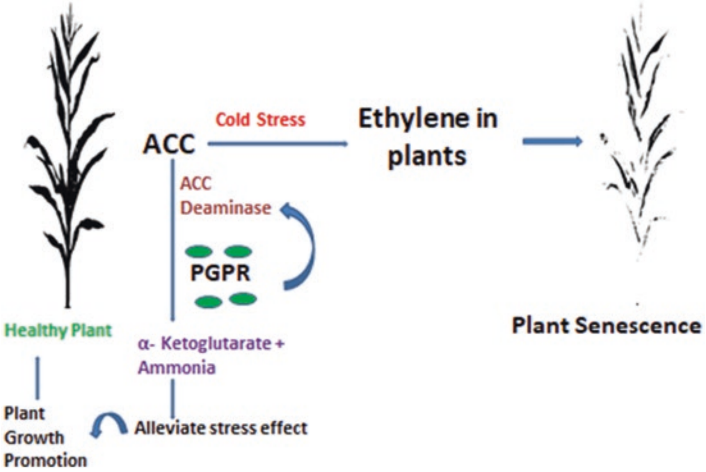


Fig. 8.4 ACC deaminase activity by PGPR in cold stress

Kadioglu et al. (2018) isolated 32 1-aminocyclopropane-1-carboxylic acid deaminase-producing cold-tolerant bacteria that were isolated from the 20 rhizospheric soils of wild plants collected from high altitudes (1760–2724 m) in different mountains in Erzurum, Eastern Anatolia, Turkey. The most effective four species in α-ketobutyrate producing potential from ACC were *Stenotrophomonas maltophilia* GBK 4 (1.207 mg^{-1} h^{-1}), *Leucobacter iarius* GBK 2 (0.993 mg^{-1} h^{-1}), *Pseudomonas fluorescens* GBK 3 (0.962 mg^{-1} h^{-1}) and *Pseudomonas migulae* GBK 1 (0.951 mg^{-1} h^{-1}), respectively. The plant growth-promoting bacteria has been reduced negative effect under cold stress condition in plants growth by antioxidant enzyme activities accumulation, decrease in reactive oxygen species (ROS) such as H_2O_2, O_2 and OH, hormonal, photosynthetic and other stress related pathways. ACC deaminase activity of psychrotrophs to degrade ACC is mentioned in Fig. 8.4.

8.4.2 Phytohormones

Psychrotolerant *Pseudomonas lurida* strain M2RH3 have produced various plant growth properties like indole-3-acetic acid production, siderophores, P-solubilization ability at low temperature and seed bacterization in *Triticum aestivum* with the positive results at cold growing temperature about the growth and nutrient uptake efficiency of wheat seedlings cv. VL 804 (Selvakumar et al. 2011). Cold-tolerant plant growth-promoting bacteria, e.g. *Pantoea dispersa* (strain 1A) and *Serratia marcescens* (strain SRM), have the ability for IAA production at 4 °C and 15 °C temperature, which have been isolated from the North-Western Indian Himalayas (Selvakumar et al. 2008a, b). At cold temperatures, seed bacterization of wheat seedlings inoculated with these bacterial strains had significantly enhanced plant growth, biomass and nutrient uptake efficiency in wheat plants.

IAA production at low temperature was reported by Mishra et al. (2008, 2009) in bacteria *Pseudomonas* sp. (strain PGERs17) and NARs9, respectively. At lower-temperature conditions, these bacterial strains have enhanced the seed germination as well as root and shoot lengths of wheat seedlings. Barka et al. (2006) reported that PGPR have the ability to produce or modify plant growth hormones, e.g. gibberellins, which play an important role in germination and thus help in cold stress alleviation. Kolesnichenko et al. (2003) and Chang et al. (2010) reported that in warm climate crops such as rice (*O. sativa* L.), cucumber, cassava and sunflower, PGPB ameliorated the harmful effects of stress condition on plant growth. Ortiz-Ojeda et al. (2017) observed that psychrotrophic bacteria associated with maca (*Lepidium meyenii* Walp.) show positive results for IAA production, 12 produced IAA at 22 °C, 8 at 12 °C and 16 at 6 °C. At 22 °C, LMTK39 produced maximum amount of the phytohormone (60.6 μg/ml) which decreased to 31.1 μg/ml at 12 °C. Strain LMTK11 showed the highest ability to produce IAA at 6 °C (14.1 μg/ml). Subramanian et al. (2016) reported that bacterial strains isolated from soils collected in regions with an average temperature of about 2 °C have the ability to produce IAA at 5 °C. IAA production by these strains was found to be in the range of 0.3 to 17 μg/ml.

Yadav et al. (2015a) isolated 12 bacteria from the cold desert of the Himalayan region that showed the ability to produce gibberellic acid. About two dozens of wheat combined with psychrotolerant bacterial strains also produced gibberellic acid which were isolated from the northern hills of India. Only 11 psychrotrophic bacterial strains that produced gibberellic acid were reported by Yadav et al. (2015b).

8.4.3 N_2 Fixation

Nitrogen is one of most important minerals which are essential for plant growth and development. Under extreme cold conditions, N_2 become deficient. Bacteria fix nitrogen by symbiotic and asymbiotic means. Competitiveness and functioning of nodule are affected by cold temperature. Various plant growth-promoting psychrotrophs can help plant to grow by providing nitrogen through symbiotic and asymbiotic means and help them to cope up with stress (Rana et al. 2019a, b). Zhang et al. (2003) studied that nitrogen fixation of soybean and its nodulation was positively influenced by *Rhizobia* originating from cooler climate of North America than that of warmer climate of South America. Psychrotolerant *Pseudomonas* sp. strain L10.10 (CP012676) bacteria isolated from Lagoon Island, Antarctica, having the ability of N_2 fixation along with other plant growth properties has been observed by See-Too et al. (2016).

Mishra et al. (2009) studied that co-inoculation of cold-tolerant *Pseudomonas* sp. Strain PGERs17 along with *Rhizobium leguminosarum*-PR1 significantly ($P > 0.05$) increased nodulation (156.2%) and 57.1% higher plant biomass. About

66.3% N uptake, 23.3% P uptake, 47.1% K uptake and 2.75-fold Zn uptake of shoots were enhanced on co-inoculation compared with uninoculated control. Zhang et al. (2006) studied that *Rhizobia* isolated from North America in colder region were able to influence the nodulation and nitrogen fixation of soybean positively. Prevost et al. (2003) studied that psychrotroph *Sinorhizobium meliloti* improves growth of alfalfa under cold and anaerobic (ice encasement) stresses after over-wintering, enhancing adaptation for abiotic stress. Kaushik et al. (2001) observed growth-promoting ability of two strains of *A. brasilense* in wheat crop. Devanand et al. (2002) observed that in pigeon pea yield, dry weight and plant height nodule number increased when *Azospirillum* spp. and *Pseudomonas striata* are coinoculated with *Rhizobium* spp. Ek-Jandér and Fåhraeus (1971) studied that clover rhizobia isolated from subarctic environment in Scandinavia showed earlier nodulation of their host plant and more vigorous acetylene reduction than that from southern Scandinavia.

8.4.4 Phosphorus Solubilization

In the rhizosphere ecosystem, plant growth-promoting rhizobacteria (PGPR) could be promoted growth by solubilization of insoluble phosphorous compounds (Gull et al. 2004). Katiyar and Goel (2003) observed that *P. fluorescens* having higher P-solubilization ability under cold stress increased plant growth at 10 °C in *Glycine max* and *Pisum sativum*. Organic acids produced by *Pseudomonas* which was isolated from glacial ice samples with various temperatures ranges from 4 °C to 30 °C and optimum conditions for P solubilization at 15 °C dissolve sparingly soluble P in the rhizosphere region and thus increased P availability to plant roots (Balcazar et al. 2015). Nineteen efficient fluorescent *Pseudomonas* having phosphate-solubilizing ability isolated from the cold deserts of the trans-Himalayas have been reported by Vyas et al. (2009).

Trivedi et al. (2007) suggested that at lower temperatures, bacteria isolated from the Himalayan soils have the ability to solubilize phosphate. The selected bacterial isolates showing low-temperature adaptation and possessing various plant growth promotion abilities are suitable for the development of carrier-based, easy-to-use inoculants for improved plant performance in colder regions. Auxin and phosphate-solubilizing *Pseudomonas* and Bacillus strains were isolated by Cakmakcl et al. (2007), and it was observed to be significantly increased in biomass, N, K and P uptake efficiency and enzyme activities as compared to control on wheat and spinach plants. Better results were found in growth parameters and nutrient uptake efficiency of wheat seedlings cv. VL 804 in pot-culture conditions under cold conditions when seed bacterization inoculated with *Pseudomonas lurida* M2RH3. Gulati et al. (2009) isolated *Acinetobacter rhizosphaerae*, a phosphate-solubilizing and rhizosphere-competent strain from cold desert of Indian Himalayas. Cold temperature causes significant reduction in plant growth. Psychrotrophs have abilities to tolerate chilling temperature. Moreover these have the ability to retain various plant growth-promoting characteristics, e.g. production of phytohormones, nitrogen fixation and phosphate solubilization under adverse conditions. These properties of psychrotrophs could be utilized to promote plant growth under different stress conditions. Thus, psychrotrophs could help to alleviate cold stress in plants.

8.4.5 Biocontrol Activity

The increased use of pesticides and insecticides has become the major cause for environmental pollution. Microorganisms having the ability to control pathogenic organisms can be used as biocontrol agents to reduce the use of chemical pesticides and insecticides. Yarzábal et al. (2018) isolated 25 *Pseudomonas* spp. bacterial strains from Antarctic soils at Greenwich Island of South Shetland Islands, Antarctic Peninsula. These isolates were found to possess antifungal activity against plant pathogenic fungi such as *Fusarium oxysporum*, *Pythium ultimum* and *Phytophthora infestans* which suggested that these could be used as biocontrol agent and biofertilizer. Balcazar et al. (2015) isolated nine psychrotrophic bacteria having phosphate solubilization ability from glacial ice collected from two small tropical glaciers which was located above 4.900 m in the Venezuelan Andes. Four *Pseudomonas* spp., PGV024, PGV284, PGV094 and PGV085, showed biocontrol activity against *P. infestans*, *P. ultimum* and *F. oxysporum.*

Raaijmakers et al. (2002) observed that several psychrophilic *Pseudomonas* spp. inhibited the growth of plant pathogenic fungi by cell wall degradation using hydrolytic enzymes, production of antibiotics such as 2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin, pyrrolnitrin siderophore production and production of several cyclic lipodepsipeptides (LDP). Vero et al. (2013) studied that psychrotrophic yeasts isolated from Antarctic soils could be used as potential biocontrol agents for the management of postharvest and control the diseases of apple during cold storage. Isolate *Leucosporidium scottii* designated At17 showed biocontrol activity for blue and grey mould of two apple cultivars.

8.4.6 Siderophores Production

At low iron concentration, iron-chelating compounds called siderophores are produced by microorganisms. These are small in size molecules (500–1200 Da) that increasing the bioavailability of iron specifically by binding ferric iron with high affinity. Kube et al. (2013) studied iron acquisition by psychrophilic bacterium *Oleispira antarctica*. Bioprospecting studies suggested siderophore production by psychrotrophic bacterial species such as *Actinobacteria*, *Firmicutes*, b-Proteobacteria and c-Proteobacteria such as pyochelins, pyoverdines, aerobactins, bacillibactins and yersiniabactins (Yadav et al. 2015a).

Mishra et al. (2008) isolated *Pseudomonas* sp. PGERs17 (MTCC 9000) from the northern Indian Himalayas and produced pyoverdines and pyochelins siderophore at 4 °C. Three hundred and twenty-five bacterial isolates were isolated from cold desert soil by Yadav et al. (2015b). On CAS agar plates, 29 strains out of 325 isolates produced siderophore at low temperature. Siderophores were bacillibactin, sanguibactin, pyoverdine and pyochelin produced by *Bacillus*, *Sanguibacter*, *Arthrobacter* and other species. Psychrotrophilic *Bacillus* sp. PZ-1 was found to be siderophore producer (Ren et al. 2015). Seventeen-fold increases in root colonization with increased siderophore production in cold-tolerant mutant of *Pseudomonas fluorescens* was observed. Plant growth promotion in *Vigna radiata* was observed at 25 °C and 10 °C by this mutant strain. Selvakumar et al. (2009) isolated a novel siderophore producing bacterium *Exiguobacterium acetylicum* strain from north-western Indian Himalayas. This bacterium has the ability to be used as biocontrol agents that inhibit the fungal growth of *Fusarium oxysporum, Pythium, Rhizoctonia solani* and *Sclerotium rolfsii*.

8.4.7 Resistance Induction by Cold-Tolerant PGPR

Metabolic activities of the plants are affected by cold temperature which leads to yield reduction in plants. *Burkholderia phytofirmans* strain PsJN, a plant growth-promoting bacterium, increased physiological movement and grapevine growth at a temperature (low) in *Vitis vinifera* cv. Chardonnay explants. It was observed that the plantlet biomass increased sixfold at 26 °C and 2.2-fold at 4 °C, whereas root growth increased 11.8-fold at 26 °C and 10.7-fold at 4 °C, respectively (Barka et al. 2006). The psychrotolerant bacteria were isolated from the apoplast leaf of wild plants (cold-adapted) and inoculated on leaves of bean seedling that enhanced the cold resistance of bean seedlings. At cold conditions, these bacteria secreted specific extracellular proteins and showed ACC deaminase activity (Tiryaki et al. 2019).

Mishra et al. (2009) isolated a cold-tolerant bacterium *Pseudomonas* sp. NARs9 (MTCC9002) from the Indian Himalayas and also studied growth encouragement activities. Seed bacterization with isolate increased the germination, shooting and root lengths of 30-day wheat seedlings, respectively, by 19.2, 30.0 and 22.9 percent compared to uninoculated controls. Selvakumar et al. (2008a) studied *Pantoea dispersa* 1A (MTCC 8706), a cold-tolerant plant growth-promoting bacterium isolated from sub-alpine soil in the northwestern Indian Himalayas, to be used as an inoculant in cold wheat-growing environments to achieve the desired results of bacterization. Wu et al. (2019) studied that at 10 °C, *Bacillus pumilus*, *Bacillus safensis* and *Bacillus atrophaeus* promote the growth of winter wheat seedlings in pot house under cold condition. So these can act as promising candidates for sustainable agriculture under extreme climate of cold conditions. Various psychrotrophs having plant growth-promoting properties with isolation source are mentioned in Table 8.1.

Table 8.1 Plant growth-promoting psychrotolerant bacteria associated with crops

Microorganisms	Isolation source	PGP properties	References
P*seudomonas fragi, P. chlororaphis, P. fluorescens, P. proteolytica and Brevibacterium frigoritolerans*	Leaf apoplastic fluid of *Draba nemorosa*, Galanthus *gracilis*, Colchicum *speciosum*, Scilla *siberica, Erodium cicutarium*	ACC deaminase activity	Tiryaki et al. (2019)
Flavobacterium sp. OR306 and *Pseudomonas frederiksbergensis* OS211	Agricultural soil in winter	1-Aminocyclopropane-1-carboxylate deaminase (ACCD) gene	Subramanian et al. (2015)
Bacillus species	Qinghai-Tibetan plateau	Biocontrol activity	Wu et al. (2019)
Pseudomonas frederiksbergensis OS261	Chungbuk agricultural research and extension services, Ochang-eup, South Korea	ACC deaminase activity	Subramanian et al. (2016)
Pseudomonas sp. strain NARs1	Rhizospheric soil of *Amaranth* plant	Nutrient uptake, N_2 fixation	Mishra et al. (2011)
Pseudomonas lurida M2RH3 (MTCC 9245)	Uttarakhand Himalayas	Phosphorus solubilization	Selvakumar et al. (2011)
Pseudomonad strains	NW Himalayas	Biofertilizer	Mishra et al. (2011)
Serratia marcescens strain SRM *(MTCC 8708)*	Flowers of summer squash *(Cucurbita pepo)*	Phosphorus solubilization, IAA production, HCN, siderophore production	Selvakumar et al. (2011)
Pseudomonas spp.	Antarctic soils at Greenwich Island (South Shetland Islands, Antarctic peninsula)	Phosphorus solubilization, IAA production, HCN, biocontrol activity	Yarzábal et al. (2017)

8.5 Future Prospects and Challenges

Microorganisms have ubiquitous distribution all over the world. Microbes have the ability to grow under extreme conditions whether it is the colder regions of Himalayas and Alpine and polar region or thermal hot springs and deserts. The importance of microbes growing under such extreme conditions is increasing worldwide to study the adaptation they undergo for survival and growth under adverse conditions. Climate change has further enhanced the importance of their study among scientific communities. A temperate agro-ecosystem has a short growing season and low temperature which leads to cold temperature stress among plants and microbes. Cold stress has a negative impact on agriculture because it causes chilling and freezing injury among the plants. Moreover, in different parts of the world, cropping systems have to face transient colds which leads to negative impact on nitrogen fixation and plant growth promotion. Disease infestation also gets enhanced among plants at such a lower temperature. Psychrotrophs could be used as biofertilizer and biocontrol agents in such extreme conditions of lower temperature. There is a need to isolate microbes from extreme climates such as alpine and polar regions because these are adapted to grow under such adverse conditions, so it could be used to enhance plant growth, crop yield and agriculture productivity.

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Chapter 9
Microbes-Mediated Mitigation of Drought Stress in Plants: Recent Trends and Future Challenges

Deepti Jain, Laccy Phurailatpam, and Sushma Mishra

Abstract Drought is accepted as one of the major constraints for crop growth, development and productivity worldwide. Drought-tolerant plants either employ *drought avoidance mechanisms* like elongation of root, reduction of leaf area and decreased stomatal number and conductance or *drought tolerance mechanisms* like accumulation of osmoprotectants (glycine betaine, proline, sugar alcohols, etc.) and other cellular and biochemical modifications. Another mechanism of drought tolerance in plants is their association with some beneficial rhizospheric or endophytic microbes. Plant growth-promoting (PGP) microbes help the crops to tolerate drought conditions by different mechanisms like secretion of phytohormones, exopolysaccharide and antioxidants, solubilization of essential micro and macro nutrients, accumulation of osmolytes and induction of stress-responsive genes. In this chapter, we review the role of PGP microbes in general stress mitigation strategies, with specific emphasis in imparting drought stress tolerance to plants.

Keywords Drought stress · Endophytes · Microbes · Plant-microbe interaction · Plant stress tolerance

9.1 Introduction

In the past few decades, a number of factors such as increasing population, urbanization, deteriorating soil quality and climate change have led to reduced agricultural productivity all over the world. Hence, in order to avert the resulting food

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crises, there is a critical need to tackle the various biotic and abiotic stresses that limit the crop yield (Yadav and Yadav 2018). Drought, salinity, low or high temperature, high acidity or alkalinity, heavy metals and nutrient-limiting conditions are the major abiotic stresses that limit crop productivity (Lata et al. 2018). These stresses primarily affect photosynthesis, cause protein denaturation and generation of reactive oxygen species (ROS) and alter membrane fluidity (Mishra et al. 2019). Among all the abiotic stresses, drought stress is the most destructive one that alters physiological, morphological, biochemical and molecular traits of plants (Jaleel et al. 2009; Bhargava and Sawant 2013; Kour et al. 2019a). It has been speculated to affect more than 50% of arable lands by 2050 (Vurukonda et al. 2016). Apart from drought, other abiotic stresses like high salinity, extreme temperatures and high light intensity also cause water-deficit conditions in plants (Kumar et al. 2019; Yadav et al. 2015; Yadav and Yadav 2018). In some cases, however, there may be enough soil water content, but plants are still unable to absorb it. This type of drought stress is known as pseudo-drought or physiological drought (Athar and Ashraf 2009; Arbona et al. 2013; Salehi-Lisar and Bakhshayeshan-Agdam 2016). Recent advancements in molecular biology and functional genomics have increased our understanding about the complex signalling networks of plants that contribute towards tolerance to drought stresses.

One of the important ways by which plants improve growth, productivity and stress tolerance response is through their association with beneficial microbes. Microorganisms are the natural inhabitants of the most extreme environmental conditions that pose threat to other life forms including plants. The beneficial microbes present either inside the plant tissues (*endophytes*) or in the rhizosphere (*rhizospheric microbes*), confer enormous metabolic and biochemical capabilities to plants under adverse environmental conditions. Our main intention is to highlight the microbe-mediated drought stress tolerance in plants, an aspect that has not been well-explored. We first begin with an overview of the effect of drought stress and general plant defence mechanisms, followed by some of the success stories involving microbes in imparting drought stress tolerance to higher plants.

9.2 Effects of Drought Stress on Plants

Drought is a multidimensional stress, which affects the plants at various levels: subcellular, organ and whole plant level (Jaleel et al. 2009; Rahdari and Hoseini 2012). The most obvious effect of drought stress is altered plant growth and development, which primarily results from the reduced photosynthetic potential of the plant. Prolonged drought stress causes inhibition of photosynthesis by affecting the photosystems (Xu and Zhou 2006) and decreasing the chlorophyll content (Anjum et al. 2011; Rahdari et al. 2012). At the whole plant level, drought stress leads to reduced leaf size, seed number and germination rate and decreased root growth (Osakabe et al. 2014; Xu et al. 2016; Lata et al. 2018). At the cellular level, drought stress causes decline in water potential and loss of membrane integrity. This further leads to reduced availability of soil nutrients and decreased transport of essential nutrients such as calcium, magnesium, nitrate and sulfate (Selvakumar et al. 2012). Due to lower nitrate uptake, drought also affects the activity of nitrate reductase, the enzyme that catalyses the reduction of nitrate to nitrite during nitrate assimilation (Caravaca et al. 2005). In addition, drought is one of the main causal factors to induce formation of free radicals leading to oxidative stress. High ROS concentrations can cause membrane deterioration, lipid peroxidation and degradation of proteins, lipids and nucleic acids (Vurukonda et al. 2016; Yadav et al. 2020).

9.3 General Plant Response Mechanism Against Drought Stress

Plants have evolved several mechanisms to perceive and respond to stress signals; these could be broadly categorized into stress avoidance responses and stress tolerance responses (Mishra et al. 2019). The drought stress avoidance mechanisms include altered leaf angle, leaf rolling, stomatal closure and inhibition of shoot growth. This is accompanied by a deeper root system through increased allocation of photosynthates to root tips for increased ability of water uptake. All these morphological and physiological changes minimize the water loss due to transpiration. In contrast, the stress tolerance mechanisms involve biosynthesis of certain proteins and metabolites called osmoprotectants that enable plants to counteract stress. Osmoprotectants exist as chemically diverse biomolecules such as amino acids (proline), amines (glycine betaine and polyamines), sugars (trehalose) and sugar alcohols (mannitol, sorbitol). These compounds primarily function to regulate water uptake and retention (in order to maintain turgor pressure) and to stabilize cellular macromolecules like proteins, nucleic acids and lipids (Chen and Murata 2002). Under different abiotic stresses, plants often respond through various interwoven metabolic and regulatory pathways. This complex phenomenon involves various changes at transcriptomic, proteomic, metabolic and physiological levels (Atkinson and Urwin 2012). The complexity of plant responses to individual stresses lies in regulating specific gene expression followed by metabolic programming in cells. Different signaling molecules such as calcium (Ca^{2+}), nitrate (NO_3^-), abscisic acid (ABA), inositol phosphates, etc., play a central role in activating the stress tolerance mechanisms.

Root architecture is most sensitive in sensing and responding to water-deficit conditions in the soils (Khan et al. 2016). ROS generation is a common process that occurs in response to various stress responses (Bian and Jiang 2009). Drought-tolerant responses of different plant species vary in the activity of superoxide dismutase (SOD), an antioxidant enzyme involved in ROS metabolism (Xu et al. 2014). In bluegrass (*Poa* sps.), expression of genes encoding FeSOD and Cu/

ZnSOD is downregulated by drought stress; but in alfalfa, their expression is upregulated, suggesting that defence responses varies across different species (Foyer and Noctor 2005; Naya et al. 2007).

Although drought and salt stress reduce the levels of some amino acids, it increases the level of proline, a crucial osmoprotectant (Matysik et al. 2002). Similarly, production of nitric oxide, modulation of hormones and synthesis of glycine betaine are some other drought-induced changes in plants (Gupta and Huang 2014). Apart from the osmoprotectants, phytohormones like abscisic acid (ABA), salicylic acid (SA), Jasmonic acid (JA) and ethylene are also involved in regulating stress responses. JA-mediated signaling is effective in induced systemic resistance (microbe-mediated induction of abiotic stress responses) and defence responses against parasitic pathogens (Matilla et al. 2010).

9.4 Plant Microbiome

Plant-microbe interactions are crucial to the adjustment and survival of both the accomplices under any environmental condition. These interactions may be unfavourable if the host-pathogen interactions in plants result in disease development or favourable if the plant-microbe interactions stimulate the plant growth (Biswas et al. 2018; Verma et al. 2015, 2016; Yadav et al. 2019a). In the latter case, i.e. for beneficial microbes, also called as plant growth-promoting microbes (PGPMs), such interactions confer stress tolerance to plants and enable revitalization of contaminated and degraded soils (Yang et al. 2009; Abhilash et al. 2012). In recent years, the role of microbes in regulating abiotic stress tolerance in plants has been the area of major interest by the researchers (de Zelicourt et al. 2013; Nadeem et al. 2014; Souza et al. 2015). PGPMs colonize plant root system, forming a complex ecological community that influences plant growth and productivity through metabolic activities and interactions with the plant (Lugtenberg and Kamilova 2009; Schmidt et al. 2014; Yadav et al. 2017b, 2018). Microbes with their inherent genetic and metabolic capabilities assist in abiotic stress tolerance of plants (Gopalakrishnan et al. 2015; Mintoo et al. 2019).

Rhizosphere constitutes the soil portion in the immediate proximity of plant roots. Interestingly, the mean count of microorganisms in this microenvironment is very high than the rest of the soil. Rhizosphere, with its diverse nutrient, mineral and metabolite composition, is the major factor responsible for attracting microorganisms and facilitating its association with plant roots (Kour et al. 2019c; Verma et al. 2019; Yadav et al. 2019a). As roots grow through soil, they generally release water-soluble compounds such as amino acids, sugars and organic acids that serve as food for the microorganisms and play a vital role in microbial colonization (Yadav et al. 2017a). The favourable root microbiome mitigates plant stress by various mechanisms, and among them, PGPR (plant growth-promoting rhizobacteria) can effectively improve micronutrient uptake, enhance phytohormones homeostasis and/or stimulate the immune system against phytopathogens (Rolli et al. 2015). The selection of traits across plant populations is often influenced by soil microbiome mitigating the effects of abiotic stress (Lau and Lennon 2011). In one of the studies, *Brassica rapa* grown in soils with simplified microbial communities were smaller with reduced chlorophyll content and fewer flowers, in comparison to plants grown in association with more complex soil microbial populations (Lau and Lennon 2011).

Besides bacteria, fungi, particularly the mycorrhiza, are also an important part of the rhizosphere (Yadav et al. 2020). Principally, these are divided into ectomycorrhizal fungi that remain associated with the host plant externally, and vesicular-arbuscular mycorrhizal (VAM) fungi, that may form endosymbiotic associations. The extensive networking of very fine hyphae improves water, carbon, phosphorus and nutrient uptake by the roots. In this chapter, we have made an attempt to discuss the intricate crosstalk between PGPMs, plant and soil during drought stress that together establish the dynamics in the root microbiome (Fig. 9.1).

9.5 Stress Mitigation by Microbes

9.5.1 Drought Tolerance by Bacteria

Generally, as a consequence of resource limitation, total bacterial biomass goes down under drought (Hueso et al. 2012). In some instances, the soil bacterial biomass may either remain stable (Hartmann et al. 2017) or might go up (Fuchslueger et al. 2014). This might be due to bacterial attenuation to repeated drought exposure (Hueso et al. 2011) and/or altered functional capabilities to support in resilience (Bouskill et al. 2016). Rhizobacteria-induced drought endurance and resilience (RIDER) includes altered levels of defence-related proteins and enzymes, antioxidants, polysaccharides and phytohormones. This phenomenon has been observed for microbe-mediated plant responses. Such approaches enable plants to combat adverse stress conditions (Kaushal and Wani 2016). In due course, the translocated signal is sensed by the distant plant cells and the defence mechanisms get triggered. For various rhizobacteria belonging to the genera *Pseudomonas*, *Azotobacter*, *Azospirillum, Pantoea, Bacillus, Enterobacter, Bradyrhizobium* and *Cyanobacterium,* the role in plant growth promotion and abiotic stress tolerance has been well documented (Meena et al. 2017; Verma et al. 2017; Yadav 2019; Yadav et al. 2017b) (Table 9.1). *Burkholderia phytofirmans* strain PsJN has been reported to combat drought stress in wheat (Naveed et al. 2014a) and maize (Naveed et al. 2014b). Likewise, sorghum and wheat seedlings inoculated with *Pseudomonas* sp. strain AKM-P6 and *P. putida* strain AKM-P7 showed improved tolerance to high temperature stress (Anjum et al. 2011).

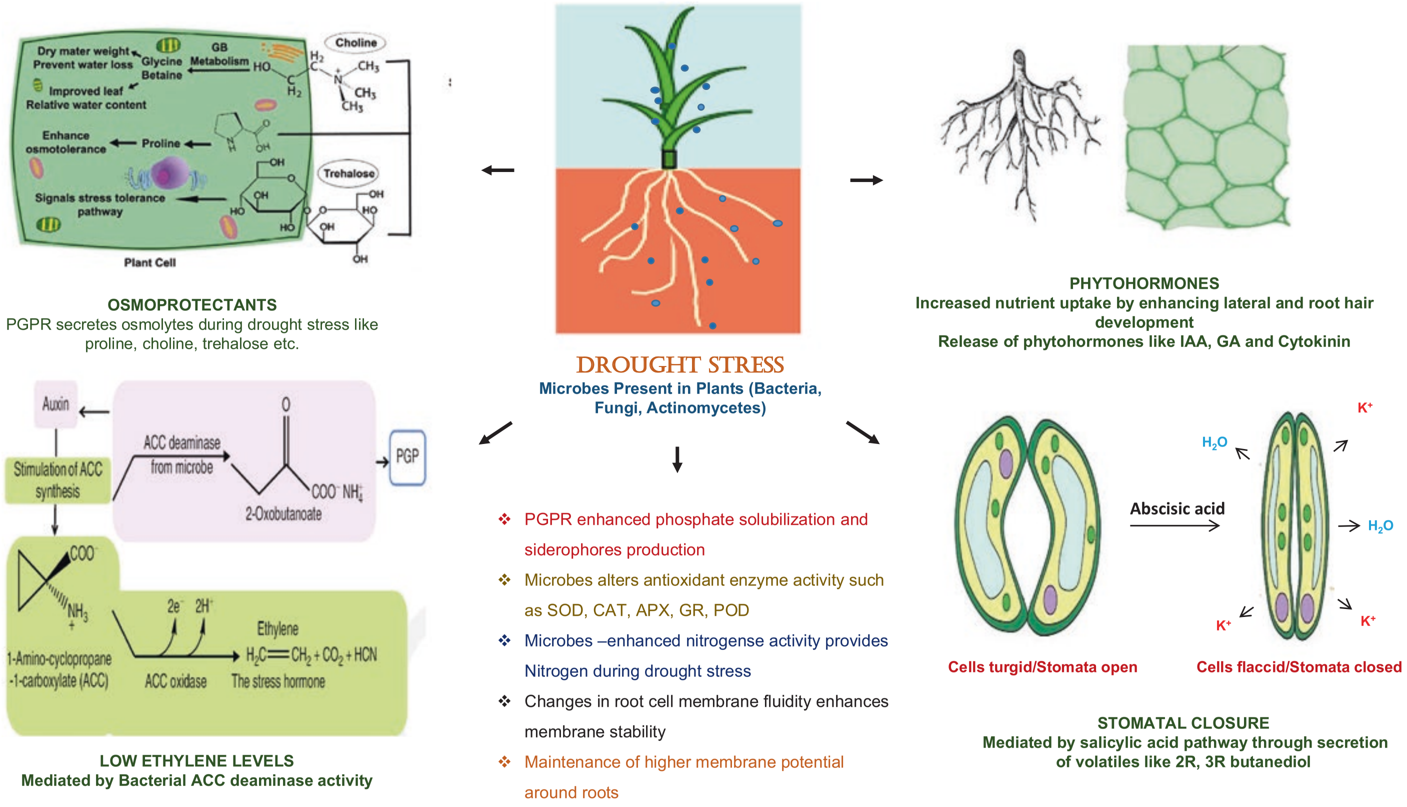

Fig. 9.1 Microbe-mediated drought stress response in plants. Some of the common mechanisms/pathways triggered by microbes for imparting drought stress tolerance in plants have been presented

Table 9.1 Microbe-mediated drought tolerance in plants

Host plant	PGP microbe	Tolerance strategy	References
Rhizobium tropici and *Paenibacillus polymyxa* (co-inoculation)	*Phaseolus vulgaris*	Upregulation of stress regulated genes	Figueiredo et al. (2008)
Burkholderia phytofirmans, Enterobacter sp. FD17	*Zea mays*	Increased photosynthesis, root and shoot biomass	Naveed et al. (2014b)
Bacillus thuringiensis AZP2	*Triticum aestivum*	Production of VOCs	Timmusk et al. (2014)
Pseudomonas chlororaphis O6	*Arabidopsis thaliana*	Production of 2R,3R butanediol	Cho et al. (2008)
Pseudomonas putida strain GAP-P45	*Helianthus annuus*	EPS secretion	Sandhya et al. (2009)
Bacillus licheniformis strain K11	*Capsicum annum*	Upregulated stress-related genes and proteins	Lim and Kim (2013)
Bacillus cereus AR156, *B. subtilis* SM21 and *Serratia* sp. XY21	*Cucumis sativa*	Induced expression of monodehydroascorbate, proline and antioxidant enzyme genes	Wang et al. (2012)
Sinorhizobium meliloti	*Medicago sativa*	Induced *SOD* activity	Naya et al. (2007)
Piriformospora indica	*Brassica campestris* ssp. chinensis	Increased level of peroxidases, catalases and SODs	Sun et al. (2010)
Gluconacetobacter diazotrophicus	*Saccharum officinarum* cv. SP70–1143	Induced IAA and proline production	Vargas et al. (2014)
Trichoderma harzianum TH-56	*Oryza sativa*	Upregulation of aquaporin, dehydrin and malondialdehyde (MDA) genes	Pandey et al. (2016)
Azospirillum lipoferum	*Zea mays*	GB increased ABA levels	Cohen et al. (2009)
Phyllobacterium brassicacearum strain STM196	*Arabidopsis*	Enhanced ABA content resulted in decreased leaf transpiration	Bresson et al. (2013)
Bacillus subtilis	*Platycladus orientalis*	Cytokinin elevated ABA levels in shoots and resulted in stomatal closure	Liu et al. (2013)
Achromobacter piechaudii ARV8	*Lycopersicum esculentum* and *Piper*	Reduced ethylene production and increased fresh and dry weight	Mayak et al. (2004)
V. paradoxus 5C-2	*Pisum sativum*	Increase in xylem ABA, growth, yield and water potential	Belimov et al. (2009)
Consortia of *Bacillus isolate* 23-B and *Pseudomonas* 6-P with *Mesorhizobium ciceri*	*Cicer arietinum*	Higher proline concentration, improved germination, root and shoot length	Sharma et al. (2013)
Bacillus thuringiensis AZP2	*Triticum aestivum*	Reduction of volatile emissions and higher photosynthesis	Timmusk et al. (2014)

(continued)

Table 9.1 (continued)

Host plant	PGP microbe	Tolerance strategy	References
Pseudomonas putida GAP-P45	*Zea mays*	Proline accumulation improved plant biomass, RWC and leaf water potential	Sandhya et al. (2010)
Azospirillum lipoferum	*Zea mays*	Accumulated free amino acids and soluble sugars improved plant growth	Bano et al. (2013)
Rhizobium etli	*Phaseolus vulgaris*	Overexpressed trehalose upregulated genes related to tolerance and carbon and nitrogen metabolism	Suárez et al. (2008)
Klebsiella variicola F2, *Pseudomonas fluorescens* YX2 and *Raoultella planticola* YL2	*Zea mays*	Choline and GB accumulation improved leaf RWC	Gou et al. (2015)
Bacillus amyloliquefaciens 5113 and *Azospirillumbrasilense* NO40	*Triticum aestivum*	Upregulation of stress associated genes APX1, SAMS1, and HSP17.8	Kasim et al. (2013)

9.5.2 Drought Tolerance by Fungi

Fungi forming a relationship with the roots of most vascular plants are known as mycorrhizae. Ectomycorrhizae colonize plant roots extracellularly and arbuscular mycorrhizae colonize intracellularly. In vascular plants, arbuscular mycorrhizae penetrate deep into the cortical cells of the roots forming an obligate symbiosis with highly branched arbuscules that are the prime sites for water and nutrient exchange. Arbuscular mycorrhizae help their host plants to overcome the effects of drought by improving water uptake and absorption of mineral nutrients (especially phosphorus), altering root architecture, modifying antioxidative responses and inducing plant hormone abscisic acid (ABA), which play an important role in regulating plant's response to different stresses especially drought (Yadav et al. 2019b, c).

Various physiological changes in plants that are induced by their association with arbuscular mycorrhizae under drought stress have been well documented (Marulanda et al. 2003; Khalvati et al. 2005; Aroca et al. 2007). The root fungal endophyte *Piriformospora indica* imparts salt tolerance in barley (Baltruschat et al. 2008) and drought tolerance in Chinese cabbage (Sun et al. 2010). In rice, *Trichoderma harzianum* upregulated the stress-related genes like dehydrin, malondialdehyde and aquaporin under stress (Pandey et al. 2016). In spite of these findings, a detailed understanding of the biochemical and molecular nature of the tripartite interaction between plants, arbuscular mycorrhizae and PGPB remains to be elucidated (Kour et al. 2019c, d). Detailed studies of this complex relationship need to be done to facilitate the development of microbial strategies to develop more drought-resistant plants.

9.5.3 Drought Tolerance by Viruses

Viruses are obligate intracellular systems that cannot survive without their host tissue. The pathological effects of viruses are well established, but their beneficial effects have been often overlooked. A breakthrough research demonstrating the improved drought tolerance of ten different plant species, following infection with four different RNA viruses, Brome mosaic virus (BMV), cucumber mosaic virus (CMV), tobacco mosaic virus (TMV) and tobacco rattle virus (TRV), was reported by Xu et al. (2008). It was predicted that the viral infection induced a signaling mechanism that might be a part of an elaborate cascade utilized by plants to combat adverse stress conditions. Another breakthrough study showed the increased levels of several osmoprotectants and antioxidants in BMV-infected rice and CMV-infected beet plants under stress.

9.6 Molecular Mechanisms Involved in Drought Tolerance

9.6.1 General Mechanisms Followed by PGPMs under Drought Stress

PGPMs employ several direct and indirect mechanisms to combat drought stress (Hayat et al. 2010). Direct mechanisms involve synthesis of bacterial compounds that facilitate uptake of essential nutrients (iron and zinc sequestration, phosphorus and potassium solubilisation, siderophore production and atmospheric nitrogen fixation) from the soil and production of plant growth regulators. On the other hand, antagonistic activity towards plant pathogenic organisms, production of antifungal compounds and tolerance against abiotic stresses are some of the indirect mechanisms induced by the PGPRs.

Phosphorus, an essential macronutrient, is also one of the major limiting nutrients due to its least availability and mobility. Many beneficial microbes are efficient in solubilizing nutrients like phosphorous from soil (Yadav et al. 2017a, b, c). Iron (Fe) is another vital nutrient important for plant growth, as it acts as the cofactor for different enzymes and is involved in photosynthesis, respiration and nitrogen fixation (Solano et al. 2008).Though Fe is abundantly present in the soil, it is not available for plants as the oxidized form of iron (Fe^{3+}) reacts forming oxides and hydroxides. Under such limiting conditions, PGPRs has the capacity to produce siderophores, which are the low-molecular-weight iron-chelating compounds responsible for Fe^{3+} acquisition (Whipps 2001).

9.6.2 Phytohormone-Based PGPMs Responses under Drought Stress

Another important role of PGPRs is the synthesis of various plant growth regulators/phytohormones like auxins, indole acetic acid (IAA), cytokinins and gibberellins. There are diverse bacterial genera such as *Acinetobacter, Arthrobacter, Bacillus, Corynebacterium, Methylobacterium, Micrococcus, Pantoea* and *Pseudomonas* that reportedly produce various phytohormones (Kour et al. 2019b; Verma et al. 2014, 2019). The plant hormone ethylene regulates a wide range of physiological and metabolic responses like tissue differentiation, fruit ripening, leaf abscission, flower wilting and the plant response to various stresses. However, high concentration of ethylene is inhibitory for the plant growth. PGPB possess an enzyme called 1-amin ocyclopropane-1-carboxylate deaminase (ACCd), which converts ACC, the immediate precursor of ethylene, to α-ketobutyrate and ammonium. This reaction lowers the inhibitory concentration of ethylene and promotes plant growth and delayed senescence during stress conditions (Glick et al. 1998; Glick 2004). Further, in tomato and peppers, a Gram-negative bacterium that produce ACC deaminase induced tolerance to drought stress (Mayak et al. 2004). Similarly, reports have shown that *Pseudomonas* spp., *Burkholderia caryophylli* and *Achromobacter piechaudii* reduce endogenous ethylene levels in plants by producing ACCd, thus resulting in increased root growth and improved tolerance to drought stress (Wu et al. 2009). *Trichoderma atroviride* or *Pseudomonas putida* enhanced ACCd activity in the tomato rhizosphere and improved growth and stress tolerance (Gravel et al. 2007). *Burkholderia phytofirmans* strain PsJN improves leaf area, chlorophyll content and photosynthetic rate in a wide spectrum of host plants, including potato, tomato and grapevine, under various abiotic stresses (Mitter et al. 2013). Likewise, *Achromobacter piechaudii* ARV8, a root-colonizing bacterium, deaminates ACC and thus lowers the production of ethylene in the root (Mayak et al. 2004). The lowering of ethylene levels causes increase in ABA levels (because of cellular antagonism) that in turn leads to stomatal closure and hence prevention of subsequent water loss. Further, ABA is one of the most important phytohormones involved in the recognition of drought stress in plants. It is well known that ABA synthesis is triggered after the perception of drought stress, which further regulates downstream signal transduction pathways culminating in drought tolerance in plants (Shinozaki and Yamaguchi-Shinozaki 2007).

PGPB are also known for synthesizing other phytohormones like IAA, a natural auxin analogue. IAA and other auxins have growth-stimulating effect, resulting in root growth initiation and development of lateral roots (Glick 1995). Maize plants inoculated with *Azospirillum lipoferum* alleviated drought stress through the production of ABA and gibberellins (Cohen et al. 2009). *Arabidopsis* plant inoculated with *A. brasilense* Sp245 had elevated levels of ABA compared to non-inoculated plants (Cohen et al. 2015). Cytokinin treatment of *Platycladus orientalis* seedlings producing *Bacillus subtilis* boosted the ABA levels in shoots and increased the stomatal conductance, imparting drought stress resistance (Liu et al. 2013).

9.6.3 Role of Volatiles in Inducing Drought Tolerance

During the last decade, a number of researchers have found that specific strains of PGPR secrete volatile organic compounds (VOCs) without physical contact with plant roots. Volatiles like 2R, 3R butanediol are induced when plants are subjected to various stresses (Loreto and Schnitzler 2010), resulting in promotion of growth in *Arabidopsis* seedlings (Ryu et al. 2003). These stress-induced volatiles play a key role for inducing systemic responses within the same and in neighbouring plants (Choudhary et al. 2008). Volatiles are potential candidates for fast and non-invasive technique to improve crop drought stress. VOCs regulate different biological processes, including whole-plant auxin redistribution, leaf cell expansion, root branching, augmented photosynthesis and increased iron uptake capacity (Zhang et al. 2007). Application of butanediol causes IST to drought by root-colonized *B. subtilis* GB03 (Zhang et al. 2010) and *P. chlororaphis* O6 (Cho et al. 2008); both have been demonstrated to promote plant growth (Ryu et al. 2003). *Arabidopsis* roots colonized with *Pseudomonas chlororaphis* O6 secreted 2R, 3R-butanediol, which prevented water loss by stomatal closure. Cho et al. (2008) reported that volatiles like 2R, 3R-butanediol are key players in inducing resistance to drought in *Arabidopsis* through the SA-dependent mechanism. In wheat, root colonization of *Bacillus thuringiensis* AZP2 resulted in enhanced plant biomass and higher survival under severe drought. This report strongly suggests that bacterial colonization improved plant stress tolerance (Timmusk et al. 2014).

9.6.4 Role of Osmolytes in Inducing Drought Tolerance

Plants often adapt to drought stress through many metabolic adjustments such as accumulation of several compatible solutes called osmolytes or osmoprotectants, which include proline, glycine betaine, sugars and sugar alcohols. Under drought stress, PGPR secrete osmolytes that act synergistically with plant-produced osmolytes and promote plant growth (Paul et al. 2008). Proline content was increased by a sizeable quantity when *P. Fluorescens* was inoculated in maize plants during drought stress (Ansary et al. 2012). Likewise, *Bacillus thuringiensis* inoculation in *Lavandula dentata* roots enhanced shoot proline accumulation when compared to control plants under drought stress (Armada et al. 2014). Increased levels of proline help in maintaining cell water status and protect membranes and proteins from stress (Sandhya et al. 2010).

Another osmoprotectant, trehalose, a non-reducing disaccharide, help in stabilizing the dehydrated enzymes and membranes during water deficit conditions (Yang et al. 2010). *P. vulgaris* plants inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase gene showed enhanced drought tolerance in comparison with plants inoculated with the wild strain (Suárez et al. 2008). Similar responses were observed in maize plants inoculated with *A. brasilense* overexpressing trehalose biosynthesis gene (Rodríguez-Salazar et al. 2009). Thus, trehalose play a vital role as a signaling molecule and its metabolism in PGPR is key for signaling plant adaptation to abiotic stress.

Choline, another important osmoprotectant, works as a precursor in glycine betaine (GB) metabolism. It enhances GB synthesis, whose accumulation improves leaf relative water content (RWC) and thus plays a critical role in plant stress tolerance. *B. subtilis* GB03 in *Arabidopsis* induces choline accumulation (Zhang et al. 2010). Likewise, inoculation of *Klebsiella variicola* F2, *P. fluorescens* YX2 and *Raoultella planticola* YL2 in maize showed enhanced choline accumulation, thereby inducing GB levels and making the plant more stress-tolerant than wild-type plants (Gou et al. 2015). Under stress conditions, PGPR strains enhance accumulation of solutes like GB that prevents water loss caused by osmotic stress, thus regulating plant stress responses (Bashan et al. 2014).

Similarly, polyamines also work as plant growth-regulating compounds. Among the various polyamines, cadaverine was correlated with promoting root growth or osmotic stress mitigation in plants. In rice seedlings, cadaverine-producing *A. brasilense* Az39 promoted root growth and helped to mitigate osmotic stress (Cassan et al. 2009).

9.6.5 Role of Exopolysaccharide in Mitigating Stress Conditions

Under drought stress, the physicochemical and biological properties of soil become unsuitable for soil microbial activity and crop yield. The soil water content indirectly influences soil microbial community. Under unsuitable conditions, microbes produce exopolysaccharides (EPS) that enable their survival. The EPS released into soil forms a protective capsule around soil aggregates containing bacteria and plant roots, thus providing a microenvironment that protects against water loss (Sandhya et al. 2009; Kaushal and Wani 2016). Plants associated with EPS-producing bacteria show increase in relative water content, sugar and proline. On the other hand, the activities of antioxidant enzymes were found to be decreased, thus showing enhanced tolerance to drought stress (Bensalim et al. 1998; Naseem and Bano 2014).

9.6.6 PGPB Alter Antioxidative Defence Signaling for Eliciting Stress Tolerance

Under drought stress, plants stimulate the production of various reactive oxygen species (ROS) including singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), hydroxyl radical (HO^-) and the superoxide radical (O^{2-}) (Cruz de Carvalho 2008). ROS impairs the normal metabolic processes of the plants by causing oxidative damage to the proteins, lipids and deoxyribonucleic acid, ultimately leading to cell death (Hasanuzzaman et al. 2013). The plant antioxidant defence system possesses certain enzymatic and non-enzymatic oxidants that prevent ROS accumulation and help in minimizing negative effects of the drought stress (Miller et al. 2010). The most important enzymatic components include catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR). Cysteine, glutathione and ascorbic acid form the non-enzymatic components (Kaushal and Wani 2016). Maize plants inoculated with *Bacillus* species showed reducing activity of the antioxidant enzymes, APX and glutathione peroxidase (GPX), thus providing protection against drought stress (Vardharajula et al. 2011).

Under drought stress, basil plants (*Ocimum basilicum* L.) treated with *Pseudomonas* sp. showed increased CAT enzyme activity (Heidari and Golpayegani 2012). Inoculation of *B. thuringiensis* in *Lavandula dentata* and *Salvia officinalis* promoted growth and drought avoidance by decreasing the activities of GR and APX under drought conditions (Armada et al. 2014). Above reports proved that PGPR application enhances drought tolerance of plants by altering the antioxidant activity under stress conditions.

9.7 Future Research and Challenges

Drought stress is the most detrimental abiotic stress to limit plant growth and productivity. The improvement of stress tolerance and productivity of the crops is thus the major goal of agriculture in solving future food security issues. PGP microbes is an emerging field of science that has great potential in developing plant resistance and adaptation to various abiotic stresses. This can be acquired by different mechanisms like production of phytohormones, ACC deaminase, siderophores, nutrient solubilization, etc. PGPMs can affect plant growth directly by facilitating the uptake of certain nutrients from the environment or indirectly by preventing the deleterious effects of one or more biotic/abiotic stresses. Thus, PGPR inoculation in plants opens a new arena for improving crop growth and productivity under drought stress. Though many reports have been documented regarding the PGP microbe-mediated stress mitigation, unfortunately the detailed drought-induced signaling involving soil-plant-microbe tripartite relation is still challenging. This is primarily due to the complex and interwoven mechanisms that govern the establishment of root microbiome. At the same time, it also becomes essential to have an in-depth knowledge of microbe-mediated stress-mitigating mechanisms in plants for crop improvement. Recently, multi-omics approaches have enabled integrated studies on the interaction of plants with microbes under stress, which have significant chance for implementation in the fields. Genetic engineering and plant breeding techniques are often used for the development of drought-tolerant crop varieties, but it is a long-drawn process. PGPR inoculation in soil, on the other hand, can achieve the desired goals in much less time. Taking into consideration the current reports, future research is needed for (i) developing molecular and biotechnological approaches to identify potential microbes; (ii) preparation of proper microbial consortium, so that the endophytes/microbes are not antagonistic to each other; (iii) addressing the issue of delivery systems; and finally (iv) field evaluation of the effect of beneficial organisms on plants.

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Chapter 10
Microbial Consortium with Multifunctional Plant Growth-Promoting Attributes: Future Perspective in Agriculture

Subhadeep Mondal, Suman Kumar Halder, Ajar Nath Yadav, and Keshab Chandra Mondal

Abstract The relationships between plant and plant growth-promoting microorganisms (PGPMs) are an integrated part of earthborn ecosystem. We are in the era of global warming when excessive use of chemical fertilizers engulfs the entire environment and society. In this scenario, it is our paramount liability to exploit PGPMs in agricultural sector for their invaluable role in sustainable crop production. Though PGPMs are colonized at/near the root of the plant, their wave of efficacy hits the doorstep of major functional aspects of the entire plant. PGPMs provide a wide array of remunerative roles to their host plant, viz., betterment of seedling and seedling vigor, root and shoot growth, photosynthetic efficiency, flowering, crop yield, disease resistance, and so forth. In this review the major beneficial aspects of consortia of PGPM on the plant growth are comprehensively addressed.

Keywords Agricultural sustainability · Induced systemic resistance · Microbial consortium · PGP attributes · Plant growth promotion

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10.1 Introduction

We are living in an age when global climate change devoured all living entities on this earth. In this scenario, one of the leading challenges will be an eco-friendly and sustainable way for crop production to meet gradual increasing demand of food. As per the report of the World Population Clock (2019), the world's population will rise from 7.7 billion in 2019 to 10 billion in 2050, and in accordance with that, 70% surplus food will be required for our future generations by 2050 (FAO United Nations 2009). To attain such unprecedented food demand, additional agricultural land of 2.7–4.9 MHa/year is required (Abhilash et al. 2016a, b). As land is a limited resource and 33% of cultivated land is no longer available (due to pollution or anthropogenic activities), tremendous pressure on the crop production is currently a challenging and addressing issue (Adesemoye et al. 2009; Berg 2009). Furthermore, deleterious plant pathogens repeatedly pricked different plant population which creates more worry in this concern (Miller et al. 2009). Therefore, decisive agro-biotechnological interventions are required for substantive and sustainable agricultural propagation to meet the global challenge (Abhilash et al. 2016a, b).

The plant-associated microorganisms provide beneficial consequences on plant health and growth, enhance stress tolerance, ameliorate disease resistance, increase nutrient availability, and also improve biodiversity (Lugtenberg et al. 2002; Morrissey et al. 2004; Yadav 2017; Yadav et al. 2017b). The plant-associated microbial communities show a certain level of plant specificities based on the specific secondary metabolic products and morphological diversity (Berg 2009; Yadav et al. 2019a). This insight is still to be investigated in agricultural biotechnology. Although utilization of soil microbiomes to enhance crop yield is an ancient culture, evidence can be alluded to ~ 300 BC (Vessey 2003). From the end decades of the nineteenth century, research repeatedly proves the positive roles of fungi and bacteria on host plant by facilitating plant growth in various manners. PGPMs are defined as the microbes able to colonize root/rhizosphere, competing with other microbiota, and promote plant growth (Yadav et al. 2017a). Plant growth encouragement can be acquired either by direct relationship between salutary microorganisms and the host plant or indirectly through their antagonistic relationship with the harmful pathogens of the host plant (Berg 2009; Kumar et al. 2019; Rajawat et al. 2020). The roots promote the uptake of water and minerals and secrete a variety of chemicals as root exudates which alter the physicochemical properties of soil and also control the microbial population surrounding the rhizosphere (Yadav et al. 2012, 2019b, 2020; Verma et al. 2018). Bacteria are the most plentiful microbial community in soil followed by fungi (Kour et al. 2020d; Rana et al. 2020c). Fungi cause putrefaction of various complex plants and animal bodies to their basic components such as celluloses, hemicelluloses, lignins, pectins, starches, oils, and waxes which ultimately enrich soil. Bacteria finish the putrefaction by eating the digestible materials. Other important communities of microbial world that are found in smaller quantities are actinomycetes, algae, cyanobacteria, protozoa, and nematodes (Yadav et al. 2012; Bhaduri et al. 2015; Kaur et al. 2020; Singh et al. 2020).

The major PGPMs are fungi and bacteria that are living in soil in a close intimate relationship with plant root (Rastegari et al. 2020b; Singh and Yadav 2020). Plant growth-promoting bacteria (PGPB) are either free living or in symbiotic association with the plant roots, enhancing plant growth by nitrogen fixation, potash mobilization, phosphate solubilization, zinc solubilization, siderophore production, other micronutrient mobilization, and also plant hormone secretion (auxin, cytokinin, abscisic acid, gibberellins, ethylene, strigolactones) (Akhtar and Siddiqui 2010; Kumar 2016; Verma et al. 2017a, b; Yadav et al. 2017c). Similarly, arbuscular mycorrhizal fungi (AMF) increase phosphate availability and micronutrient mobilization, extend surface area of root, provide biotic and abiotic stress tolerance, and develop soil quality and porosity (Akhtar and Panwar 2011; Kumar 2016; Kour et al. 2019b).

To attain the highest-level efficiency in terms of reducing the utilization of chemical fertilizers and pesticides, improving plant health and production better, and maintaining sustainable environment, the application of PGPMs-based technology should be practiced with appropriate levels of fertilization. The success and efficiency of PGPMs as inoculants for plant growth are regulated by numerous factors such as the capability of the inoculant microbes to colonize the plant root, the chemical nature of exudates secreted by plant root, and the soil health by means of soil type, soil moisture content, nutrient pool, toxic metal concentrations, existent microbial diversity, and soil disturbances by climatic or anthropogenic sources (Souza et al. 2015; Verma et al. 2017b; Yadav et al. 2018). Application of PGPMs as inoculants has several advantages over chemical/biochemical pesticides and fertilizers: (1) they are more secure to the ecosystem and to the human health, (2) they show much more specificity and effectiveness in small quantities, (3) they promote growth of the host plant along with its associated microbiota, (4) they degraded more quickly than conventional fertilizers and pesticides, (5) development of resistance is negligible, and (6) they can be also applied in conventional or integrated management systems (Berg 2009; Kour et al. 2020b; Rana et al. 2020b).

10.2 Microbial Consortium for Plant Growth and Development

The beneficial microbe having the multifarious plant growth-promoting attributes could be used as biofertilizers as singly or as consortium for agricultural sustainability (Kour et al. 2020b, c; Rana et al. 2020b; Rastegari et al. 2020a). Van Veen et al. (1997) determined the reasons behind the imperfect execution of microbial inoculants when applied in the rhizosphere of host plants and point out the efficacy of using microbial consortia for multifaceted benefits in lieu of using a single strain for a trait. Plant growth-promoting microorganisms are generally presumed to be advantageous for all plant genera they associate with, because of their ancient, conserved beneficial abilities. Three types of interactions gain major importance in sustainable agroecosystem. These are (i) the cooperation between PGPMs for improving N_2-fixation, phosphate solubilization, IAA production, siderophore production, and other plant growth-promoting characters; (ii) biocontrol of the plant pathogens provided by antagonistic activities of helpful host microbes; and (iii) interactions among various rhizosphere microbes to set up a beneficial mycorrhizosphere (Rana et al. 2019). Amalraj et al. (2015) conducted a study to determine the ability of microbial consortia including *Bacillus megaterium* var. *phosphaticum*, *Azospirillum brasilense*, *Trichoderma viride*, and *Azotobacter chrococcum* for nutrient availability and their role in sunflower growth promotion (*Helianthus annuus* L.). Jha and Saraf (2012) showed the co-inoculation potential of *Micrococcus* sp., *Acinetobacter calcoaceticus*, *Brevibacillus brevis*, and *Bacillus licheniformis* for ameliorating the yield of *Jatropha curcas* L. The bioinoculants consortia have the capability to produce IAA, ACC deaminase, and siderophore and solubilize inorganic phosphorus.

Kalaiyararsi and Victoria (2016) found that effective microbial (EM) inoculation (*Lactobacillus casei* + *Trichoderma harzianum* + *Saccharomyces cerevisiae*) imparted maximum influence on plant growth parameters to improve the nodulation ability of the leguminous plants (*Vigna unguiculata* L.) and to fix high atmospheric nitrogen. The microbes in EM produce hormones, amino acids, and alcohol substances. Rajasekhar et al. (2016) performed an experiment to understand the effectiveness of mixed inoculants *Rhizobium* (R), *Bacillus subtilis* (BS), *Trichoderma harzianum* (TH), and *Pseudomonas fluorescens* (PF) on pigeon pea (*Cajanus cajan* L.) in different combinations to make consortia under greenhouse environment and in diminution activities of the majority of soil-based plant pathogens: T1 (TH+PF), T2 (TH+BS), T3 (TH + Rh), T4 (PF+BS), T5 (PF+ Rh), T6 (Rh+BS), and T7 (TH+PF+ BS + R). The consortia including PGPR (T5, T4, and T3) show better improvement in the seedling vigor of pigeon pea. At 15 and 30 days, treatments with T5 (PF+ Rh) (1.480 gram) and T4 (PF+BS) (1.323 gram) result in plants with highest fresh weight, whereas treatments with T7 (TH+PF+BS+Rh) (86 %), T2 (TH+BS) (82 %), and T5 (PF+Rh) (77 %) lead to the remarkable reduction in disease incidence.

Trichoderma strains impose antagonistic activity against many phytopathogens of fungal origin, either directly by the mechanism of mycoparasitism or indirectly by modifying the habitat environment by introducing plant-induced defense mechanisms, antibiosis, promoting plant growth, and competing for available nutrients and space. *Bacillus subtilis* acts as potent antagonist against phytopathogens as well as performs as efficient PGPR. The presence of *Pseudomonas fluorescence* as bioinoculants with other microbes resulting in improved yield of pulse crops. Trimurtulu et al. (2011) conducted a study to understand the response of chili (*Capsicum annum* L.) to the microbial consortia of *Azospirillum*, plant growth-promoting rhizobacteria, phosphate-solubilizing bacteria, arbuscular mycorrhizal (AM) fungi, and chemical fertilizers by measuring the AM fungal root colonization by AM fungi, soil microbial population load, various plant growth parameters, and production. Jayashree and Jagadeesh (2017) reported the beneficial influence of the microbial consortia including *Azospirillum*, *Pseudomonas striata*, *Pseudomonas* sp. B15, *Leuconostoc mesenteroides*, and potassium-solubilizing bacterium on growth improvement of the vegetable seedlings (tomato, brinjal, and chili) in a farmer's nursery.

Schoebitz et al. (2016) demonstrated that combined infliction of microbial consortium (*Bacillus licheniformis*, *B. subtilis*, *B. megaterium*, *B. macerans*, *B. polymyxa*, *Pseudomonas putida*, *P. fluorescens*, *Nocardia corallina*, *Trichoderma viride*, and *Saccharomyces cerevisiae*) and humic substances to expand the growth of blueberry seedlings along with the improvement in biological and physicochemical characteristic of a volcanic ash-evolved soil, and a 50% and 43 % dry weight increment in shoot and root respectively compared to the control was reported. Raja et al. (2006) investigated the impact of bioinoculant consortia (*Pseudomonas fluorescence* Pf-1, *Azospirillum lipoferum*-Az 204, and *Bacillus megaterium* var. *phosphaticum*) on rice root exudates under hydroponic growth culture conditions by measuring amino nitrogen content, total and reducing sugars, nitrogen fixation efficiency, and plant growth-stimulating substances in root exudates. It was demonstrated that *Arabidopsis thaliana* specifically introduce three bacterial species (*Microbacterium* sp. WCS2014-259, *Stenotrophomonas* sp. WCS2014-113, and *Xanthomonas* sp. WCS2014-23) in the root of rhizosphere as the signal evolves during foliar defense activation when the host plant is infected by the *Hyaloperonospora arabidopsidis* (Hpa), a downy mildew pathogen (Berendsen et al. 2018).

The introduced microbial genera synergistically interact to form biofilm and thereby induce resistance against Hpa but also induce plant growth. Romero et al. (2017) observed that the application of consortium of desiccation-tolerant microorganisms (*Pseudomonas putida* KT2440, *Acinetobacter* sp. EMM02, *Sphingomonas* sp. OF178, *Azospirillum brasilense* Sp7) improves the maize plant growth. Inoculation with the bacterial consortia increased the plant height, diameter, and shoot-root dry weight, compared to the control, and also promoted improved seed germination during the desiccation period as the inoculants adhere to the seed and effectively colonize the host root rhizosphere. Now in this chapter, we also elaborately mention the role of fungi, bacteria, and algae as PGPMs, which directly or indirectly influence the growth and productivity of large types of host plants through numerous mechanisms.

10.2.1 Seed Germination and Seeding Vigor

The beneficial effects of PGPMs are observed from the very early stage of plant development influencing germination and seedling growth. Various species of PGPM differ greatly in their effect on seed germination and seedling growth (Kour et al. 2019b).

Various species of PGP fungi differ greatly in their effect on seed germination and seedling growth. Cucumber seeds sown in soil ameliorated with *Trichoderma harzianum* propagules showed a ~30% enhancement in seedling rise, after 8 days of implanting (Yedidia et al. 2001). A significant improvement in early seedling rise and vigor was executed by tomato after tomato seeds were bioprimed with *Trichoderma harzianum* TriH_JSB27, *Phoma multirostrata* PhoM_JSB17, *Trichoderma harzianum* TriH_JSB36, *Penicillium chrysogenum* PenC_JSB41, and

Trichoderma harzianum Bi application (Jogaiah et al. 2013). Carrot and onion seeds inoculated with the *Clonostachys rosea* cause improved rate and time of seedling rise (Bennett et al. 2009). Maize seeds bioprimed with *Trichoderma harzianum* showed reduced infection by *Fusarium verticillioides* and fumonisin occurrence and improved the seedling rise (Nayaka et al. 2010). Arredondo et al. (2007) found that *Rhizopus* sp. was moderately effective in staving dormancy of *Thelocactus hexaedrophorus* seeds.

Delgado-Sánchez et al. (2011) observed that inoculation of *Opuntia streptacantha* seeds with *Penicillium chrysogenum*, *Trichoderma koningii*, and *Phoma* sp. helped to stave seed dormancy. Scanning electron microscopy revealed that these fungi have been able to erode the funiculus, thus reducing its resistance to germination. It may be possible that enzyme production by the fungal hyphae assists in seed stratification or replacement of scarification process. By growing on the testa, fungi may also erode the hard-stony endocarp. Therefore, fungi were able to alleviate mechanical barrier to germination (Morpeth and Hall 2000). The other possibilities were production of germination-inducing volatiles and degradation of water-soluble germination inhibitors associated with the outer surface of the seed (de Boer et al. 2005). Orchid seeds also need a fungus for germination in nature. Orchid seeds lack endosperm and no significant food reserves. Exogenous purvey of sugars is required for orchid seed germination. After the formation of the protocorm, additional development does not occur until sugar molecules are supplied. Symbiotic fungi are the principal source of sugars. When hyphae are broken, sugars are freed into the orchid cells. The fungal genus *Rhizoctonia* is mainly responsible for stimulating germination of orchids and ameliorates the growth of protocorms and seedlings (Chou and Chang 2004). Production of hormones such as gibberellic acid (GAs) and cytokinin (CK) by the fungi was responsible for stimulating seed germination (Gupta and Chakrabarty 2013).

Germination vigor of *Codonopsis pilosula* seed was overcome by soaking the seed with the suspension culture of the soil bacterium *Bacillus subtilis* GB03 and also exposure of its volatile compounds released (Wu et al. 2016). The enhancement of germination efficiency and seedling vigor of wheat was found following co-inoculation of seeds with *Azospirillum lipoferum* and *Azotobacter chroococcum* (Mohammad 2014). Such result and outcome may be possible because (i) phosphate-solubilizing bacteria could change the components of root exudate, impressing the colonization of PGPM community at root and related plant growth, and (ii) co-inoculation supplied more adequate nutrition by means of nitrogen, phosphorus, and other growth-promoting substances to the plant, and the synergistic effect associated with the interactions among PGPB and other colonizing microbes could cause proper exploitation of poorly available soil phosphorus sources. Rice (*Oryza sativa L.*) seeds treated with *Bradyrhizobium* sp. UPMR48 and UPMR29 leads to an improved seedling rise, seedling vigor, seedling root growth, and also vegetative growth (Mia and Shamsuddin 2009). The reasons behind the enhancement of seedling vigor index by PGPB include increased synthesis of the plant growth-related hormones such as cytokines and auxin as well as hormones stimulating cell division and cell elongation (Bharathi 2004; Anzala 2006).

Biari et al. (2008) documented the increment in seed production of maize treated with PGPB is associated with better absorption of nutrients such as nitrogen, potassium, phosphorus, iron, manganese, copper, and zinc. Nitrogen is the main limiting nutrient for the plant growth. It is an essential constituent of nucleotides, membrane lipids, and amino acids (enzymatic and structural proteins). Phosphorus performed a principal role in plant photosynthesis, storage and energy transfer, respiration, cell division, and elongation. It is inevitable for seed formation, and seed is the largest reservoir of phosphorus in the plant. Flowering, fruit setting, and fruit swelling followed by seed maturation – these physiological processes of plant are largely maintained by such kinds of indispensable nutritive elements. The major physiological activities regulated by potassium are root growth, absorption of cations (NH^{4+}, Ca^{2+}, Mg^{2+}, Cu^{2+}, and Fe^{2+}), activation of photosynthetic enzymes, gathering protein hydrates, maintaining cell turgid pressure, stomata's regulation, frost resistance, and countering drought and diseases, and also it is necessary for the transportation of assimilates to storage organs (bulbs and tubers) (Agbodjato et al. 2016).

Tomato inoculated with *Enterobacter* P-19 strain promotes seed germination and seedling growth under osmotic stressed environments (Bhatt et al. 2015). Inoculating with selected bacterial strains significantly raising the growth indices including increased root and shoot length may be imposed to the better establishment and adherence of bacteria to the seed coat of osmotically stressed seeds, before being shifted to water, and their subsequent revival and plant growth progress under normal hydrated conditions. Combining efficiency of *Azospirillum brasilense*-bioprimed aged grass seeds with chemical fertilizer improves germination character and seedling growth (Liu et al. 2019). Here, *Azospirillum brasilense* conduct hydration process, which leads to the promotion of germination in aged seeds, and also contribute to phytohormone signaling between PGPB and aged seeds through GA and IAA production.

Demir et al. (2006) showed the effect of seaweed suspension (green algae (*Codium tomentosum*), red algae (*Gracilaria gracilis*), and brown algae (*Cystoseira barbata*)) on germination of tomato (*Lycopersicon esculentum* L.), pepper (*Capsicum annuum* L.), and aubergine (*Solanum melongena* L.) seeds. Jennings (1968) reported that gibberellic acid contained by the brown and green algae play an essential role in seed germination. The extracts prepared from the brown seaweed (*Sargassum myricocystum*), red seaweed (*Gracilaria edulis*), and green seaweed (*Caulerpa racemosa*) which contain phytohormones mainly cytokinins act as biostimulant to overcome the seedling vigor of sunflower (*Helianthus annuus L.*) var. TN (SUF) 7 seeds (Rayorath et al. 2008a, b; Sujatha et al. 2015). The extract obtained from *Ascophyllum nodosum* influenced GA3-independent amylase activity, but it facilitates the GA-dependent amylase synthesis resulting in an elevated seed germination and seedling vigor of barley (Rayorath et al. 2008a, b). Algal extracts from the thalli of *Jania rubens* and *Padina pavonica* alleviate salinity stress on the seeds of *Capsicum annuum* var. *Baklouti* (Rinez et al. 2016). The improving behavior of germination may be explained by a metabolism change of the seed during germination. Indeed, it was reported that certain proteins are synthesized only during the priming, such as the globulins (Job et al. 2000). The activation and expression of the aquaporin genes ensure transport of water, resulting in the acceleration and the betterment of the imbibition following the biopriming (Gao et al. 1999). The activation and expression of the aquaporin genes in turn activates the degradative enzymes of the reserve such as lipase, results in better mobilization of the reserve and consequently a better germination (Sung and Chang 1993).

10.2.2 Root and Shoot Growth

The soil microbial communities intimately associated with plant root system; therefore, the root system functions directly influenced by the microbial interaction. Many reports attested the role of PGPMs in significant growth of the plant root. There is wide array transformation in the phenotypic exposure of shoots, determining the systematic impacts of the PGPMs (Kour et al. 2019a; Verma et al. 2015). Plants bioprimed with PGPF had greater root biomass and faster and prolonged periods of root growth leading to well-organized root systems (Björkman et al. 1998; Zhang et al. 2012; Hossain et al. 2014). Cucumber plant inoculated with *Penicillium simplicissimum* GP17-2 in potting medium containing barley grain showed significantly longer and larger root system after 3 weeks of planting. Many PGPF strains have the ability to modify root system architecture (RSA) of a plant. RSA is a complex notation involving root structure and root shape (Pages 1992; Yadav et al. 2020), which ultimately regulates nutrient and water absorption ability of a plant and also determines the interaction between the plant and the rhizosphere (Orman-Ligeza et al. 2013). The RSA is associated with two major physiological consequences, viz., intermediate growth of the main root and development of lateral root (LR) and root hair (RH) (Scheres et al. 2002). However, LR and RH develop the principal characteristic root architecture that facilitates water and mineral absorption. *Trichoderma* spp. were highly efficient in inducing LR production in *Arabidopsis thaliana* (Contreras-Cornejo et al. 2009). RH development was highly improved in *Arabidopsis thaliana* and Chinese cabbage (*Brassica rapa* L.) (Lee et al. 2011).

Colonization of *Piriformospora indica* on root resulted in an approximately 2-fold rise in the diameter of elongation zone, 1.4-fold higher biomass, and 1.5-fold thicker epidermal and cortex layer of the LR than the untreated group (Dong et al. 2013). Stimulation of LR development seems to be an early phase of interaction in nonphytopathogenic, root-colonizing fungi (Felten et al. 2009). Meristematic elongation zone in root is the main target of signals originated from various PGPF strains, leading to the growth-stimulating events (Dong et al. 2013). A reduction in cytokinin content by the *Trichoderma* spp. promotes the root growth of melon plants (Martínez-Medina et al. 2014). Similar results were observed by Sofo et al. (2011) in *Trichoderma harzianum* T-22-inoculated plants in which there is a significant reduction in two highly active cytokinins dihydrozeatin and trans-zeatin present in plant roots and shoots. Although the root tips are considered to be the principal site of cytokinin synthesis, the aforementioned results indicate that cytokinins play a negative role in root growth (Aloni et al. 2005). Cytokinins deficiency in transgenic plants [by overexpression the cytokinin oxidase/dehydrogenase (CKX) genes] resulted in an extended root meristem, origin of LR nearer to the root apical meristem, improved root branching, and facilitated adventitious root formation (Lohar et al. 2004). Similarly, in *Trichoderma harzianum* (T-4, T-7, and T-22)-inoculated plants, the titer of abscisic acid and ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) were decreased (Martínez-Medina et al. 2014).

Application of root endophytic *Trichoderma* spp. isolates significantly enhanced plant height of a second-generation energy crop *Miscanthus giganteus* (elephant grass) (Chirino-Valle et al. 2016). Shoresh and Harman (2008) revealed that proteins related to sugar metabolism are strongly affected in the shoots because of maize root colonization by *Trichoderma* spp. In this respect, the major identified proteins are fructokinase (FRK), fructose-bisphosphate aldolase (FBA), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), 3-phosphoglycerate kinase, malate dehydrogenase (MDH), oxalate oxidases, and β-glucosidases. FRK2 gene isolated from tomato was shown to be highly expressed in leaves leads to vascular development and stem growth (Odanaka et al. 2002; Damari-Weissler et al. 2009). Improper expression of this gene leading to reduced cell size in the xylem and phloem tissue resulting in extremely shorter plant (Odanaka et al. 2002; Damari-Weissler et al. 2009). Fructokinase gene of tomato (LeFRK1) implanted in cotton plant had larger leaf areas and stem diameters (Mukherjee et al. 2015). Increased FBA level in plastids improves the growth of tobacco plants (Uematsu et al. 2012). MDH, one of the enzymes of TCA cycle, is responsible for supplying reduced power and also involved in photosynthetic CO_2 fixation (Nunes-Nesi et al. 2005). Gene knockout study of mitochondrial MDH gene transformed in *Arabidopsis* showed no detectable MDH activity, and the resulted plants showed stunted growth.

The *Centella asiatica* inoculated with culture filtrate of *Trichoderma harzianum* results in significantly improved shoot dry weight (Prasad et al. 2012). Fungal culture filtrate containing gibberellic acids (GA4, GA9, and GA34), indole-3-acetic acid (IAA), and high doses of phosphate is responsible for promoting host shoot growth (Khan et al. 2008; Kang et al. 2015). Co-cultivating plants with volatile organic compounds (VOCs)-producing fungi induces shoot growth. VOCs emitted by different *Trichoderma* spp. augmented plant biomass and size of *Arabidopsis* (Lee et al. 2016). Similar outcome was found when tobacco plant was grown in the presence of VOCs synthesized by *Phoma* sp. (Naznin et al. 2014). The VOCs of the PGPF show diverse chemical structures, which are synthesized as mingle of hydrocarbons, alcohols, aldehydes, amines, ketones, terpenes, thiols, ethers, esters, acids, and their derivatives (Lemfack et al. 2013; Lee et al. 2016). And the effectiveness of those VOCs depends on fungal origin, culture conditions, inoculating stage of plant development, and duration of the treatment (Hung et al. 2013; Lee et al. 2015).

According to Delshadi et al. (2017a, b), co-inoculation of *Azotobacter vinelandii* and *Pantoea agglomerans* promotes increased sainfoin (*Onobrychis sativa* L.) shoot dry weight. The causes for this increased result are extra absorption of the micro- and macronutrients and increased hormone production. Maize (*Zea mays L.*) growth throughout the world is highly impeded by salinity. Co-biopriming with

Pseudomonas syringae and *Pseudomonas fluorescens* along with the use of NPK fertilizers improved maize growth rate related to root and shoot in saline-sodic soil (Hye et al. 2015). Salinity raising the level of endogenous ethylene in plants hampers proper root and shoot growth. However, bacteria having the enzyme 1-aminocyclopropane-1-carboxylate deaminase metabolize 1-aminocyclopropane-1-carboxylic acid into α-ketobutyrate and ammonia in lieu of ethylene (Glick et al. 1998). The plant probiotic bacteria *Bacillus amyloliquefaciens* BChi1 and *Paraburkholderia fungorum* BRRh-4 facilitate better growth, yield, and antioxidant content in strawberry fruit (Rahman et al. 2018). The longest shoot and root length (20.50 cm and 23.5 cm, respectively) were observed in BRRh-4-treated plants in contrast with the control plants where the shortest were found (18.58 cm and 19.25 cm, respectively).

PGPB controls plant growth principally either directly by facilitating nutrient availability (nitrogen, phosphorus, and essential minerals) or intensification of plant hormone status or indirectly by deterring the growth of various plant pathogens. Egamberdieva (2008) isolated following PGPB viz. *Bacillus lentus*, *Bacillus subtilis*, *Cellulomonas* sp., and *Bacillus* sp., and phyllosphere, *Bacillus lentus*, *Bacillus cohnii*, *Pseudomonas fluorescens*, *Kocuria varians*, *Bacillus halodurans*, *Cellulomonas* sp., *Microbacterium* sp., and *Bacillus* sp. from wheat and pea growing on loamy sand soil, were known to be effective in root and shoot growth of wheat and peas, and also nodulation of peas. These PGPB improve plant growth by producing plant growth elicitors, inducing resistance against plant pathogens, their nitrogen-fixing ability, and their nutrient uptake capability (Hofte et al. 1991; Zablotowicz et al. 1991). The root-colonizing nitrogen-fixing bacteria *Azotobacter* and *Azospirillum* separately ($T_1$and T_2, respectively) or in combination (T_3) increased growth and production of one of the chief oilseeds *Brassica juncea* L. (Khan et al. 2010). The plants under T_3 inoculation resulted in significant increase of root and shoot length, fresh weight, dry weight, and seed yield over T_0 (control), T_1, and T_2. Biostimulating compounds like gibberellins and vitamins produced by the *Azotobacter* may be directly responsible for different parameters of plant growth (Pandey et al. 1989). *Azospirillum* also produces plant growth factors (auxins) that cause the plant to produce more roots. The better root system and stronger plants produce more food (Okon 1985). These properties make *Azospirillum* as an efficient biofertilizer in nourishing crop plants.

In Fabaceae, root nodules are formed at the root tip where rhizobial colonization process initiated (Desbrosses and Stougaard 2011). Lateral roots and root hairs produced in the monocotyledonous plant family Poaceae are mainly by PGPB colonization and their synthesis of beneficial biostimulating agents (Pothier et al. 2007; Combes-Meynet et al. 2011). The well-known plant probiotic *Pseudomonas* spp. (*Pseudomonas fluorescens* WCS417, *P. fluorescens* WCS374, and *Pseudomonas putida* WCS358) improved plant growth and facilitated developmental plasticity in the roots of *Arabidopsis* by promoting the emergence of lateral root and root hair with simultaneous prohibition of primary root extension (Zamioudis et al. 2013). Normally, root growth and development encourages by both ethylene and jasmonic acid signaling pathway, which interferes with the processes related to auxin transport and signaling (Růzicka et al. 2007; Chen et al. 2011), but in this case isolated

Pseudomonas spp. through their synthesized bioactive agents, increasing the auxin responses in the root of *Arabidopsis* and stimulates the physiological activities related to primary root, LR, and RH development with simultaneously intervening the postembryonic system of root developmental along with the cellular and signal transduction responses.

Similar result was observed by Lifshitz et al. (1987) where seeds of canola (*Brassica campestris*) treated with *Pseudomonas putida* (GR 12-2) having the nitrogen fixing ability show drastic increment in seedling root length growing in sterile medium pouches. This effect was not caused by bacterial nitrogen fixation for the following reasons: (i) the incorporation of chemical nitrogen salts (NH_4NO_3, KNO_3) declined, rather than enhanced; (ii) mutants, incapable of nitrogen fixation (nif), retain the ability to improve root elongation (not significantly different from wild type); and (iii) other pseudomonads (wild types), incapable to fix nitrogen, were also active in improving root elongation. Enhancement in root and shoot length occurred when both K_2HPO_4 and *Pseudomonas putida* GR12-2 are applied in comparison to the individual treatments of either K_2HPO_4 or bacteria alone. The bacteria affect root elongation consistently by promoting the uptake of phosphorus by the roots and its translocation to the shoots. The bacteria mediated increase in phosphorus uptake by the plant, determined by two possible mechanisms: (i) the bacteria first stimulated root elongation via a "hormone-like factor," which then increased the nutrient and water absorptive capacity of the plant, and (ii) the bacteria first increased the phosphorus absorption ability of the plant that causes root elongation, which in turn further increased the water and nutrient uptake capacity of the plant.

The positive role of two algae *Nostoc muscorum* and *Ulva lactuca* on AMF colonization and their overall influence on the growth of faba bean (*Vicia faba*) in the presence of *Rhizobium leguminosarum* with reduced level of nitrogen and phosphorus fertilizers (50 and 33.3%, respectively) were investigated (Gamal et al. 2009). Such kind of treatment combination compared to the uninoculated plants allows significant variation in root and shoot length and dry weight, the number and dry weight of nodule, branches and pods number, pigment content, seed weight, and nutritional status of the plants with the biological activity in rhizosphere zone. Caire et al. (2000) reported that the application of exopolysaccharides of the two algal species (*Ulva lactuca* and *Nostoc muscorum*) along with their biomass into soil facilitates improved plant growth rate through the availability of essential nutrients by increased activities of soil enzymes. The benefits of seaweed liquid fertilizer (SLF) of *Nizimuddinia zunardini*, *Ulva fasciata*, and *Gracilaria corticata* on wheat seed germination, growth parameter (root and shoot length, fresh weight, and dry weight), pigments (chlorophyll a, chlorophyll b, carotenoids), and carbohydrate content were observed (Shahbazi et al. 2015). According to Ordog (1999), the suspension of algal extract consists of bioactive compounds, which are applied for delaying senescence, root and shoot development, decreasing transpiration, and increasing leaf pigment as well as protein content.

Similarly, Anisimov et al. (2013) studied the efficiency of water extracts of brown alga *Stephanocystis crassipes* and red algae *Neorhodomela larix* and *Ahnfeltiopsis flabelliformis* on the growth of buckwheat seedling roots. Such algal extracts showed improved growth of the seedling roots by up to 16, 20, and 15%

over control plants, respectively. Besides their advantages as farmyard manure (FYM), liquid suspension seaweed extract (LSF/SLF) has recently attained appreciation in agricultural field as foliar sprays for several crops because such suspension is composed of growth-promoting hormones cytokinins and auxins, minerals (Fe, Mn, Zn, Cu, Co, Mo, Ni), amino acids, and vitamins (Sivasankari et al. 2006). Sivasankari et al. (2006) found that application of the aqueous extracts of *Caulerpa chemnitzia* and *Sargassum wightii* in low concentration (20%) on cowpea (*Vigna sinensis* L.) improved significant seedling growth including the parameters of root and shoot length, fresh and dry weight, chlorophylls, carotenoids, proteins, vitamins, amino acids, reducing and total sugar content of shoot and root, and α-amylase and β-amylase activities in comparison to the control plants. Kumari et al. (2011) observed similar kind of result by applying aqueous extract of brown alga *Sargassum johnstonii* in foliar spray form as well as soil drabble on tomato (*Lycopersicon esculentum*) resulted in significant effect on vegetative growth, reproductive growth, and biochemical composition. According to Rathore (2009), in addition to stimulating the plant growth and yield, suspension of seaweed extracts also develops resistance to environment stress, improves mineral absorption from soil, and ameliorates antioxidative properties.

10.2.3 Photosynthetic Efficiency

The principal carbon source of green plants is photosynthesis, leading to improved carbon assimilation which in turn is the basis for rapid development and higher biomass accumulation. Many reports attested that PGPM clearly influences photosynthesis-related mechanisms in plants (Kour et al. 2020a; Rana et al. 2020a).

The changes in leaf architecture, leaf numbers, leaf chlorophyll levels, and photosynthetic rate are often the effects associated with plant's response to PGPF colonization. The abundance of light-harvesting chlorophyll a/b-binding proteins LHCI and LHCII was markedly supreme in *Epichloe typhina*-inoculated orchard grass (*Dactylis glomerata* L.) (Rozpądek et al. 2015). PGPF is utilized to enhance photosynthesis under suboptimal conditions. Bae et al. (2009) observed increased chlorophyll contents in the drought-tolerant *Trichoderma hamatum* DIS 219b-colonized seedlings. *Metarhizium anisopliae* LHL07-treated soybean showed significantly higher chlorophyll contents, photosynthetic and transpiration rate, and also leaf area, under salt stress conditions (Khan et al. 2012). PGPF may have pertinence to switch the cellular mechanisms in the shoot, in consequence increasing photosynthetic efficiency. In order to understand the key changes in photosynthesis-related protein levels in plant shoots, Shoresh and Harman (2008) have investigated the expression profile of proteins in maize shoot after colonization by *Trichoderma asperellum* T-22. Transcriptional upregulation was investigated in four key photosynthetic genes: two forms of large subunit of Rubisco and Rubisco along with PSII oxygen-evolving complex protein 2, in the shoots of *Trichoderma harzianum* T-22-inoculated plants. Similarly, Vargas et al. (2009) detected the transcriptional upregulation of two photosynthetic genes: small subunit of Rubisco (rbcS) and the oxygen-evolving enhancer 3–1 (oee3–1), in leaves of *Trichoderma virens*-treated maize plants. Transcriptional upregulation of rbcS was also identified in the leaves of *Trichoderma*-deficient common bean plants (Pereira et al. 2014).

Increased sugar level causes photosynthetic feedback inhibition in plants (Rolland et al. 2006). Degradation of sucrose inside fungal cells might have a positive effect on the photosynthesis, as it reduces sugar levels. Vargas et al. (2009) demonstrated that plants having mutualistic association with *Trichoderma virens* exhibited upregulation of photosynthetic gene and photosynthetic efficiency in leaves were reliant on sucrose breakdown in cells of its mutual partner. Subsequently, when *Trichoderma* colonizes roots of host plant, it increases demand of the photoassimilates in the leaves resulting in encouragement of the photosynthetic process (Vargas et al. 2013). On the contrary, *Alternaria alternata* VOC-endorsed augmentation of photosynthesis was attended by storage of higher amount of sugars in plant leaves (Sánchez-López et al. 2016). The lack of photosynthetic inhibition by high sugar concentration in leaves of VOC-exposed plants might be due to enhanced cytokinin synthesis, as cytokinins and sugars act oppositely at translational level (Kushwah and Laxmi 2014).

Bacillus subtilis GB03 was reported to ameliorate photosynthetic efficiency of *Arabidopsis thaliana* by reducing glucose and abscisic acid levels, improving light energy conversion effectiveness along with increasing chlorophyll content (Zhang et al. 2008). In addition to increment in photosynthetic efficiency, GB03 exposure induces transcriptional upregulation of the chloroplast ferredoxin-NADP reductase (downfall of this protein resulting in stunted plant growth and restricted photosynthetic efficiency) (Hajirezaei et al. 2002), chloroplast FtsH proteases (controlled the repair cycle of PSII in thylakoid membranes) (Sakamoto et al. 2003), and GTP binding protein (At1g02280) (utilized for the transportation of NADPH-protochlorophyllide oxidoreductases B across the chloroplast membrane (Kim et al. 2005) which in turn are beneficial for chlorophyll synthesis (Frick et al. 2003). The photosynthetic apparatus sensitiveness and its biogenesis are determined by iron availability (Spiller and Terry 1980). At transcriptional level GB03 exposure facilitates plant iron uptake. GB03 suppresses the glucose-mediated inhibition of hypocotyl germination or elongation by struggling for plant sugar absorption. Furthermore, the increased hexose level in GB03-exposed plants sets up the concept that GB03 minimizes glucose inhibitory effects by interfering sugar signaling, rather than by reducing sugar storage. On the other side, ABA signaling entangled with the glucose signal transduction, therefore, in GB03 exposed plants; the lower level of ABA explains the attenuated glucose signaling. At the transcriptional level, GB03 decreases plant ABA production. Several researchers approved the aforementioned concept. Zhang et al. (2008) found that certain PGPB magnify photosynthetic efficiency in *Arabidopsis* by regulating endogenously overlapping sugar/abscisic acid (ABA) signal transduction pathways and satisfy the regulatory role of PGPB in plant energy acquirement. According to Kumar et al. (2015), by influencing the physiological behavior of the whole plant, PGPB perform a prime role in plant growth and crop yield. Plants utilize their photosynthetic output by means of root exudates that drug and control bacterial root colonization inside the soil, introducing huge mutual benefits, including the improved plant abiotic stress tolerance (Liu and Zhang 2015).

Potato tubers treated with the PGPB originated from the roots of sweet potato (*Ipomoea batatas* L.) showed significant improvement in vegetative growth status and concentration of photosynthetic pigments (chlorophyll a/b, carotenoids) and nitrogen, phosphorus, and potassium content compared with control (Dawwam et al. 2013). Among the bacterial isolates, P35 and P18 displayed indicative increment in chlorophyll a/b content of approximately 32.8% and 46.01%, respectively, over untreated plants, whereas P39 displayed indicative increment in carotenoid content of approximately 73.49% over control plants. Such results are analogous to the observation of Abou El-Yazeid and Abou-Aly (2011), where rock phosphate bioprimed with *Paenibacillus polymyxa* and *Bacillus megaterium* ameliorates total sugar and chlorophyll content. Eleiwa et al. (2012) observed that when *Bacillus polymyxa* or *Azospirillum brasilense* were used as biofertilizers to inoculate wheat seeds, auxin produced by those inoculants causes significant rise in the chlorophyll a/b and carotenoid content as compared to the control. Another photosynthetic improvement-based study was conducted by Samaniego-Gamez et al. (2016) where pepper (*Capsicum chinense*) was treated with *Bacillus subtilis*, *Bacillus amyloliquefaciens*, and *Bacillus cereus* which elevate photosystem II (PSII) efficiency and electron transfer rate of PSII, thereby enhancing photosynthesis. Comparing with control, plants treated with the bacterial strains facilitate an improvement in both CO_2 assimilation rate in photosynthesis and photochemical quenching efficiency. The PGPB *Arthrobacter agilis* UMCV2 regulate the FRO transcription and the morphogenesis of *Sorghum bicolor* iron uptake system through VOC emission (Castulo-Rubio et al. 2015). Iron (Fe) is an indispensible and limited micronutrient for plant growth. In general, plants use two routes for iron uptake: one route depends on the plant root ferric reductase (FRO) activity to increase iron uptake. Another route depends on the phytosiderophore production to raise iron uptake. Usually various plant growth-promoting rhizobacteria trigger plant first route for iron uptake systems through the emission of VOCs. But in the study conducted by Castulo-Rubio (2015), VOCs produced by *Arthrobacter agilis* UMCV2 follow second route for FRO transcription of *Sorghum bicolor* and improve its chlorophyll content and modulates the root architecture system. Dimethylhexadecylamine, a VOC made by the UMCV2 strain, has a tremendous impact on plant growth by means of 1.8-fold increment in shoot fresh weight and also improved shoot length, chlorophyll concentration, as well as lateral root number.

D-Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) present in both plants and algae is the principal enzyme responsible for assimilating atmospheric CO_2 (Andersson and Backlund 2008). Lin et al. (2014) demonstrated that incorporation of efficient Rubisco from the blue-green algae (BGA) *Synechococcus elongatus* PCC7942 resulted in elevated photosynthesis in tobacco. Because of unthrifty oxygenase activity and slow enzymatic activity of Rubisco, it gains special targets for increasing the photosynthetic skill of vascular plants (Parry et al. 2012). Incorporating the CO_2-concentrating mechanism (CCM) from blue-green algae into plants could be expected to enhance crop yield (Price et al. 2012). The genetically modified tobacco plants are photosynthetically more efficient for their enhanced Rubisco to fix more CO_2. According to Grzesik et al.(2017), the usefulness of BGA and green algae (*Anabaena* sp. PCC 7120, *Microcystis aeruginosa* MKR 0105, and *Chlorella* sp., respectively) was found in increasing the photosynthetic efficiency and growth of willow plants (*Salix viminalis* L.) by applying minimized chemical fertilizers. Such type of biofertilization improved the stability of cell membranes, chlorophyll content, photosynthetic rate, stomatal conductance, and transpiration, and decreased intercellular CO_2 concentration. The improved length of shoots, branching, and biomass of willow, upon exposure to foliar spray of the applied microalgae strains, could be results in several intensifying physiological activities and also plant affluence with auxins, cytokinins, gibberellins, amino acids, macronutrients (N, P, Ca, Mg K), microelements (S, Mn, Cu, Mo, Zn, Fe, Co), polyamines, and other secondary metabolites synthesized by blue-green algae and green algae (Perez-Garcia et al. 2011, Sahu et al. 2012, Markou and Nerantzis 2013). Application of *Ascophyllum nodosum* (a brown alga) extract in a low concentration on the leaves of tomatoes leading to the leaves with high chlorophyll content compared to the unprimed plants (Whapham et al. 1993). Betaines in the seaweed extract lower chlorophyll degradation, thereby improving the chlorophyll content. Since iron is a vital molecule for chlorophyll biosynthesis, higher chlorophyll content needs improved iron uptake, which may be directly facilitated by the betaines that exist in the seaweed extract (Whapham et al. 1993; Spinelli et al. 2009). Glycine betaine has the potential to delay the damage of photosynthetic activity of stored isolated chloroplasts by suppressing chlorophyll degradation (Genard 1991). Betaines improved crop yield by increasing the chlorophyll quantity in leaves of different crop plants (Genard 1991; Whapham et al. 1993).

10.2.4 Flowering

PGPM strains facilitate the phenotypic plasticity of flowering, which is an essential ecological character for plant communities. Studies conducted with PGPF showed that root colonization by them may facilitate flower numbers, flowering time, and flower size in the host plant. Earlier studies regarding the effects of the *Trichoderma* spp. on floricultural crops revealed that when the fungus was applied to soil as a peat-bran formulation, the number of flower buds was enhanced in chrysanthemum and petunia, and in periwinkle, alyssum, and marigold, flowering time is reduced (Chang 1986). The root-colonizing nematophagous fungus *Pochonia chlamydosporia* hastened flowering in tomato and *Arabidopsis* (Zavala-Gonzalez et al. 2017). Exposure to VOCs emitted by PGPM such as *Trichoderma viride*, *Penicillium chrysogenum*, *Saccharomyces cerevisiae*, and *Penicillium aurantiogriseum* resulted in elevated number of flowers in *Arabidopsis* (Sánchez-López et al. 2016). Plants are getting benefitted from various overlapping physiological mechanisms, including photoperiod, vernalization, nutrient uptake, hormone biosynthesis, and senescence pathways to hasten flowering by reducing the vegetative growth (Song et al. 2013). Following one or more aforementioned mechanisms with plant nutrient uptake especially potassium resulted in increased flowering rate in *Arabidopsis* (Perner et al. 2007). Bud production and early flowering in plants are maintained by gibberellins (Zhang et al. 2014), and its faster transportation is dependent on the higher concentration of cellular potassium (Das et al. 2012). Furthermore, cytokinins also perform vital roles in flowering by influencing floret primordial differentiation and ovule development (D'Aloia et al. 2011; Zhang et al. 2014). In contrast to the abovementioned positive factors for flowering, nitric oxide (NO) also plays a negative role in plant flowering (Shi et al. 2012). Cytokinins present in VOCs produced by PGPF promoted early flowering by overcoming the negative impact of NO (Sánchez-López et al. 2016).

Implantation of *Paraburkholderia phytofirmans* PsJN gene in wheat (*Triticum aestivum* L.) seeds resulted in earlier spike onset of offspring plant compared to control plants (Mitter et al. 2017). Variation in anthesis of PsJN-implanted *Arabidopsis* plants was due to the earlier introduction of the flowering regulative genes compared to the noninoculated plants (Poupin et al. 2016). *Paraburkholderia phytofirmans* PsJN applied on flowers colonized the seed embryo through two principal routes: (1) penetration through nectarthodes and, alternatively, (2) installation on the stigma that enabled further colonization through the style, finally reaching into the ovary (Mitter et al. 2017; Pusey 2000; Pusey and Curry 2004). Wagner (2014) observed that the PGPB change flowering phenology and flowering period in *Boechera stricta*, a wild relative of *Arabidopsis*. In this study, the author found that PGPB facilitate phenotypic plasticity of flowering time as well as changed the intensity and choice of flowering period. According to Lau and Lennon (2011), in dry atmosphere, *Brassica rapa* flowered faster because the soil microbiota has the history to speed up the flowering compared to the wet-adapted similar microbiota. Rhizosphere microbiota could modify the timing of *Arabidopsis* flowering by improved and long-lived nitrogen bioavailability through nitrification, which in turn delayed flowering time by producing the phytohormone IAA from tryptophan, thus downregulating the expression of genes that regulate flowering leading to the further plant growth (Lu et al. 2018). The cultivable portion of a plant microbiota keeps the early flowering effect in *Arabidopsis thaliana*, but cryopreservation of the cultivable microbiota upsets the microbial benefits on flowering time (Panke-Buisse et al. 2017) that might be due to poor survival of taxa related with these plant traits (Mazzilli et al. 2006). The microbiota present on flower tops act as symbolic place for pollinator visitation (Ushio et al. 2015). Following contact, the portion of the microbiota transferred to the insect body outward, and this microbiota determined potential pollinator insect community of that plant. An insect individually on its body outward sheltered approximately 12.2×10^5 microbial cells. The composition of microbiota on flower tops is altered after interaction with an insect, revealing that microbes are relocated from the insect body to the flower surface. Two plant growth-promoting endophytic bacterial strains, *Pseudomonas migulae* 8R6 and *Pseudomonas fluorescens* YsS6 colonized on the stems of the cut flowers, reducing the flower ethylene levels by the action of 1-aminocyclopropane-1-carboxylate deaminase and delaying flower senescence by 2–3 days (Ali et al. 2012).

In many crop plants, their productions are intimately linked with the flower number at maturity. Since the plant growth and development is deeply related to the onset and development of flowering and the number of flowers flourished, seaweed extracts might boost flowering by strongly impelling plant growth (Khan et al. 2009). The reason behind higher yield of seaweed-inoculated crop plants might be the presence of hormonal substances in the extracts, mainly cytokinins (Featonby-Smith and van Staden 1983, 1984, 1987). Cytokinins are responsible for the mobilization of nutrients in plant vegetative organs along with reproductive organs (Gersani and Kende 1982; Davey and van Staden 1978). Ramya et al. in 2015 observed the effectiveness of liquid extract as foliar spray of seaweed *Stoechospermum marginatum* on flowering of brinjal (*Solanum melongena* L.). Significant increment in number of flowers (34 %) and fruit weight (33 %) was found after treatment with *S. melongena*. Inoculation of tomato seedlings with SWC (seaweed concentrate) from *Ecklonia maxima* causes earlier numerous flowerings earlier than the noninoculated plants (Crouch and van Staden 1992). Amplification of flower numbers and seeds in marigold (up to 50% over the untreated plants) resulting from the treatment of its seedling with *Ecklonia maxima* (van Staden et al. 1994). Abetz and Young (1983) documented that application of *Ascophyllum nodosum* in cauliflower resulted in enhancement of the curd diameter and heart size of the florets.

10.2.5 Crop Yield

Many studies have proposed to use PGPM as an eco-friendly and sustainable tool to enhance the yield of different crop plants. Application of *Trichoderma harzianum* and *T. viride* was pointedly effective in enhancing millable canes (~5–30%), yield (~6–38%), and CCS (commercial cane sugar) t/ha (~30–34%) over the unprimed plants (Srivastava et al. 2006). Several researchers observed such kind of improvement in various crop yields by the application of *Trichoderma*. An amalgam treatment of 50% *Trichoderma* with 50% nitrogen fertilizer on mustard and tomato leads to an improvement in production up to ~108% and ~203%, respectively, over the uninoculated plants (Haque et al. 2012). Utilizing *Trichoderma* spp. for the production of strawberry, chickpea, pea, and lettuce shows significant outcome (Hossain et al. 2013; Akhtar et al. 2015). Barley root colonization by the well-known PGPF *Piriformospora indica* resulted in an overall increment in grain production (Waller et al. 2005) and oil production in fennel (*Foeniculum vulgare*) and thyme (*Thymus vulgaris*) in comparison to the nontreated plants (Dolatabadi et al. 2011). The reason behind the increased yields is probably due to greater supply of nutrients by PGPF to plants. Yedidia et al. (2001) suggested that the presence of PGPF in the rhizosphere increases the diameter of root surface area allowing the roots to reach a larger part of soil, resulting in more nutrient availability for the plants of nutrient-deprived soil environment. From the *in vitro* studies, it was concluded that root-colonizing PGPF make phosphorus, nitrogen, as well as other micronutrients available to the plants from the unpalatable soil sources (Wakelin et al. 2007; Alberton et al. 2013).

According to Kaur and Reddy (2014), well-known phosphate-solubilizing bacteria (PSB) *Pantoea cypripedii* and *Pseudomonas plecoglossicida* were responsible for promoting significant enhancement in soil fertility and crop yield of wheat and maize. The effectiveness of PSB on increasing crop yield and phosphorus uptake in wheat and maize crop becomes more efficient when rock phosphate was applied along with seed bioinoculation that might be because of betterment in absorbing phosphorus from the soil nutrient pool with the help of PSB (Rahi et al. 2010). *Pantoea agglomerans* was also efficient in promoting rice growth and its production (Khalimi et al. 2012).

Lettuce (*Lactuca sativa* L.) bioprimed with a mixture of several *Bacillus* species imparted multifunctional biofertilizering potential and showed 25% increment in production (Young et al. 2003). *Pseudomonas* sp. DSMZ 13134-inoculated plants had enhanced growth and production under nutrient deprivation in comparison to the unprimed plants (Frohlich et al. 2012). In field trials, the quality of grains, as discerned by starch and protein level, was not affected and the overall production enhanced by up to 20%. In in vitro conditions, *Pseudomonas* sp. DSMZ 13134 is also responsible for solubilization of insoluble phosphates, decreases soil pH, and synthesizes siderophores. Such kind of properties causes an improvement in plant mineral absorption from soil under nutrient-depleted soil environment. Co-inoculation of chickpea (*Cicer arietinum* L.) with *Mesorhizobium ciceri* and *Pseudomonas jessenii* improved seed production (52% more than the control plants) and fresh weight of nodules (Valverde et al. 2006). Earlier reports have attested positive impact of the treatment with *Pseudomonas* spp. on nodulation, plant growth, and seed production of legumes (Dashti et al. 1998; Sindhu et al. 1999).

Ascophyllum nodosum extracts cause improved yield of "Thompson seedless" grape (*Vitis vinifera* L.) continuously through a 3-year period (Norrie and Keathley 2005). They found that the *A. nodosum*-inoculated plants always outdo (by means of berries per bunch, berry weight and size, rachis length, and the number of chief bunches in each plant) the uninoculated plants under the standard crop management system, leading to an improved fruit size (13% increase), weight (39% increase), and yields (60.4% increase over the control). BGA cause a significant improvement in the synthesis of paddy crop by improving plant height and grain quality which is driven by their nitrogen fixation ability (Alam et al. 2014). They grow on the plants surface of rice fields to enrich the field water as a good source of soluble nitrogen (Baral et al. 1988; Paudel et al. 2012). Gurung (2004) reported that BGA inoculation causes an improvement in rice production up to 5 to 24.1%. Mishra and Pabbi (2004) also observed that the production elevated up to 12.3 to 19.5% on BGA inoculation in rice field.

10.2.6 Induced Systemic Resistance

Induced systemic resistance (ISR) is a physiological situation of improved defensive ability of the plant induced by biological or chemical agents, which defends plant tissues not from the initial exposure to the attack but against subsequent oncoming attack by plant pathogens and herbivorous insects (Van Loon et al. 1998). ISR is thought to act as a barrier to lower the occurrence and/or severity of different plant pathogens, fungus, bacteria, virus, nematode, oomycete, and insect, which cause diseases on a diverse array of plant communities (Walters et al. 2013). The earliest reports on ISR were documented around middle periods of the twentieth century, when Bernard disclosed that the orchid embryos inoculated with a strain of nonpathogenic mycorrhizal *Rhizoctonia* leading to an enhanced capability of the embryo to protect infection caused by a pathogenic strain of *Rhizoctonia* (Gäumann 1950; Allen 1959). Microbial elicitors, upon detection, would induce the ISR response by the action of numerous plant hormones (Pieterse et al. 2014; Sharifi and Ryu 2018; Tyagi et al. 2018). Within these elicitors, several are microbe-associated molecular patterns (flagellin, lipopolysaccharides, and chitin), while other elicitors are VOCs (including alcohols, alkanes, sulfides, terpenoids, sesquiterpenes, esters, and ketones) or siderophores (Zhang et al. 2008, 2009; Jankiewicz and Koltonowicz 2012; Orozco-Mosqueda et al. 2013; Pieterse et al. 2014; Zamioudis et al. 2015; Garnica-Vergara et al. 2016; Martínez-Medina et al. 2017; Sharifi and Ryu 2018; Tyagi et al. 2018; Villena et al. 2018). Although ISR provides effective and endurable resistance to the plants, most triggering inducers in ISR response curtailed disease incidence by up to 85% (Walters et al. 2013).

Among the different fungal species *Trichoderma* spp., *Piriformospora indica*, non-pathogenic strains of *Fusarium oxysporum*, *Penicillium* spp., *Phoma* sp., and AMF are the mostly investigated PGPF agents to elicit ISR response (Koike et al. 2001; Shoresh et al. 2010; Fravel et al. 2003; Elsharkawy et al. 2012; Sultana et al. 2009; Pozo et al. 2009). The proficiency of *Trichoderma* spp. to trigger ISR has been well-documented in agriculturally necessary crops such as rice, wheat, bean, tomato, lettuce, maize, cotton, bean, tobacco, and cucumber against most plant pathogens from fungi to oomycetes to bacteria and even virus also (Yedidia et al. 2001; Harman et al. 2004; Shoresh et al. 2005; Saksirirat et al. 2009; Elsharkawy et al. 2014; Vitti et al. 2016). Several *Penicillium* species have been extensively studied for exploring their potentiality to induce ISR response in plants and found promising against fungi (Hossain et al. 2014), bacteria (Hossain and Sultana 2015), and viruses (Elsharkawy et al. 2012). *Phoma* sp. has analogous-type ISR-triggering capabilities (Sultana et al. 2008, 2009). Few nonpathogenic strains of *Fusarium oxysporum* were also able to show ISR response against root-knot nematodes (Dababat and Sikora 2007) and also against the burrowing nematode *Radopholus similis* in banana (Athman et al. 2006); *Verticillium* wilt in eggplant (Ishimoto et al. 2004); *Fusarium* wilt in watermelon (Larkin and Fravel 1999), sweet potato (Ogawa and Komada 1986), and tomato (Patil et al. 2014); *Phytophthora infestans* in potato (Quintanilla 2002); and *Pythium ultimum* in cucumber (Benhamou et al. 2002) and pea root rot pathogen (Peters and Grau 2002).

The hypovirulent strains of *Rhizoctonia* introduced ISR response to shield bean and tomato (Cardinale et al. 2006) and *Arabidopsis* (Sharon et al. 2011), against plant pathogens. Earlier reports proved that *Piriformospora indica* triggers ISR response in rice to protect them from leaf blast caused by *Magnaporthe oryzae* (Mousavi et al. 2014); powdery mildew disease in barley caused by *Blumeria graminis* (Harrach et al. 2013); bakanae disease caused by *Fusarium proliferatum*

(Hajipoor et al. 2015); and sheath blight caused by *Rhizoctonia solani* (Nassimi and Taheri 2017). Evidence revealed that filtered extract from culture of certain *Penicillium*, *Fusarium*, *Phoma*, and sterile fungi provides improved resistance than living inoculation, suggesting that root colonization is not the only strategy of host defense mechanisms but certain chemical compounds synthesized by fungi are responsible for ISR response in plants against diverse plant pathogens (Hossain et al. 2007; Sultana et al. 2008; Kojima et al. 2013). Different types of microbial metabolic molecules were studied for their ability to elicit ISR response in plant communities, such as chitin oligomers, cell wall lipid, protein with enzymatic activity, and glycopeptides (Hyakumachi 1997). For instance, *Trichoderma virens* synthesized a peptide antibiotic peptaibols along with a small protein Sm1 which were responsible for inducing ISR response to protect the maize leaves against *Cochliobolus heterostrophus* and *Colletotrichum graminicola* (Djonović et al. 2007; Gaderer et al. 2015). Terpenoid-type volatile β-caryophyllene ejaculated by *Talaromyces wortmannii* FS2 successfully increased the defense response in *Brassica campestris* against *Colletotrichum higginsianum* (Yamagiwa et al. 2011). Cocktail volatile organic compounds mainly m-cresol and methyl benzoate (MeBA) discharged from *Ampelomyces* sp. and *Cladosporium* sp., respectively, were able to induce ISR response in *Arabidopsis* against *Pseudomonas syringae* pv. tomato DC3000 (Naznin et al. 2014).

Some PGPB have been involved to induce ISR response (De Vleesschauwer and Höfte 2009), such as *Pseudomonas* spp. (Van Peer and Schippers 1992), *Bacillus* spp. (Kloepper et al. 2004), and *Serratia* spp. (Press et al. 1997). The ancient report regarding bacterial determinants in ISR response related to *Pseudomonas fluorescens* lipopolysaccharides (Van Peer and Schippers 1992) and siderophores (Maurhofer et al. 1994). *Pseudomonas* sp. has been well-known to trigger ISR response against broad spectrum of phytopathogens, viz., fungus, bacteria, and virus (Bhattacharyya and Jha 2012). As an example, *P. fluorescens* WCS417r was reported to induce ISR response in plants by a different type of signal transduction pathways like salicylic acid-independent jasmonic acid-ethylene-dependent signaling, NPR 1-dependent signaling, and ISR-related gene expression (Choudhary and Johri 2009). Introduction of ISR response in plants by *Bacillus* spp. to protect against a variety of infectious diseases has been clearly described by Choudhary and Johri (2009). Several species of *Bacillus* (*B. amyloliquefaciens*, *B. cereus*, *B. mycoides*, *B. pasteurii*, *B. pumilus*, *B. sphaericus*, and *B. subtilis*) have been known to promote ISR response to reduce the disease incidence in a wide range of host plants (Ryu et al. 2004). Different strains of PGPM activate a wide variety of defense-related enzymes like chitinases, peroxidase, β-1,3-glucanase, polyphenol oxidase, and phenylalanine ammonia lyase to introduce ISR response in plants (Bharathi 2004).

In the LPS of bacteria, the O-antigenic side chain acts as triggering agents together with other bacterial properties which were involved in ISR response (Van Peer and Schippers 1992). Introduction of ISR response in *Arabidopsis* and tobacco has been done by pseudobactin siderophores together with other siderophore, psedomonine. In radish, induction of ISR response by siderophores was thought to be related with salicylic acid (SA). Nonpathogenic strain of *Pseudomonas fluorescens*

WCS 417r acts as an inducer of ISR response to protect host plants against various types of pathogens, including the bacterial foliage pathogen *Xanthomonas campestris* pv. *armoraciae* and *Pseudomonas syringae* pv. tomato, the fungal foliage pathogen *Alternaria brassicicola*, the fungal root pathogen *Fusarium oxysporum*, and the oomycete foliage pathogen *Peronospora parasitica*. The leaf pathogen *Pseudomonas syringae* pv. tomato, when infecting their host plants, becomes primed and induces faster ISR response by the identical pathogen in subsequent attack. Investigation with the mutant strains of *Arabidopsis thaliana* found that JA/ethylene-triggering defensive pathway was responsible to induce ISR response in plants, while the SA-triggering pathway was responsible to induce systemic acquired resistance (SAR). In bean, ISR response triggered by *Pseudomonas putida* leads to an increased synthesis of hexenal (volatile antifungal compound) along with increased expression of enzymes, involved in hexenal production (Choudhary et al. 2007). PGPB are only able to introduce ISR response in their host plants when their density achieves a minimal level of 10^5–10^7CFU gram^{-1} of root for several days (Jankiewicz and Koltonowicz 2012; Pieterse et al. 2014). In general, the microbial density of rhizosphere could be ranging from 10^8 to 10^9 bacteria gram^{-1}, and such a density could not be present in the bulk soil. Root exudates specifically attract members of the microbial community to enrich the root microbiota of the host plant (Pii et al. 2016; Stringlis et al. 2018).

Marine algae are a reservoir of numerous inducers, including β-1,3-glucans (laminarin), β-1,3-sulfated fucans, carrageenans, and ulvans which are responsible for triggering ISR response to promote protection in plants against pathogens (Cluzet et al. 2004; Jaulneau et al. 2010). Ulvans, complex sulfated heteropolysaccharides extracted from the green alga *Ulva*, act as elicitors, were revealed to defend *Medicago truncatula* against *Colletotrichum trifolii*, and also provide protection to *Phaseolus vulgaris* against *Colletotrichum lindemuthianum* (Cluzet et al. 2004; Paulert et al. 2009). The extract of *Ulva lactuca* provides ISR response in potato (*Solanum tuberosum* L.) against late blight disease involving *Phytophthora infestans* (Ahmed et al. 2016). A crude extract of *Ulva armoricana* was used to defend bean, cucumber, and grapevine against powdery mildew disease (Jaulneau et al. 2011). When the algal extract at a concentration of 6 gram liter^{-1} of dry matter was applied, disease severity decline of up to 90% was achieved. The extract of *Laminaria digitata* was found to trigger some resistance reactions in tobacco cell suspension cultures (Klarzynski et al. 2000). It also triggered ISR response in grapevine against *Plasmopara viticola* and *Botrytis cinerea* (Aziz et al. 2003). Cell wall materials of marine brown algae trigger the synthesis of antifungal agents in alfalfa cotyledons (Kobayashi et al. 1993). Such agents provide protection in tobacco suspended cells and consistently trigger both ISR and SAR response to tobacco mosaic virus (Klarzynski et al. 2003). Inducers obtained from the cell walls of red algae were found to trigger laminarinase (1,3 (beta)-D-glucanase) and phenylalanine ammonia lyase enzymes implicated in plant defense (Patier et al. 1995) and also performed as potent inducers of defense response in tobacco plants (Mercier et al. 2001). Other important attributes of fungi, bacteria, and algae are mentioned in Table 10.1.

Table 10.1 A glimpse of reports of plant growth-promoting potential of few microorganisms

PGPMs	Attributes	References
Fungi		
Penicillium, *Chaetomium*, *Choanephora* spp.	Stimulating germination of orchid seeds	Baskin and Baskin (2014)
Piriformospora indica	Staving the seed dormancy of wheat (*Triticum aestivum* L.), chickpea (*Cicer arietinum* L.), and green bean (*Phaseolus vulgaris* L.)	Varma et al. (2012)
Clonostachys rosea	Regulates pre- and postemergence mortality caused by *Alternaria dauci* and *Alternaria radicina*, leading to a better seedling growth in carrot	Jensen et al. (2004) and Szopińska et al. (2010)
Trichoderma spp. SL2	Enhanced rice seed germination and vigor	Doni et al. (2014)
Trichoderma sp.	Roots have greater surface area and are more robust and reach far deeper inside the soil	Harman et al. (2004)
Aspergillus ustus	Increment in root growth and lateral roots and root hairs number of *Arabidopsis thaliana* and potato (*Solanum tuberosum* L.)	Salas-Marina et al. (2011)
Penicillium menonorum	Significantly improved the cucumber shoots dry biomass (~52%)	Babu et al. (2015)
Penicillium simplicissimum GP17-2	Cucumber plants grew larger and produce ~1.5–2.0-time larger leaf than normal plants	Hossain et al. (2014)
Fusarium oxysporum and *Trichoderma viride*	Improved shoot dry weight of *Arabidopsis* and tomato	Bitas et al. (2015) and Lee et al. (2016)
Aspergillus fumigatus LH02	Significantly increased leaf area, chlorophyll level, and rate of photosynthesis of soybean (*Glycine max* L.)	Khan et al. (2011)
Penicillium funiculosum LHL06	Increased chlorophyll contents in soybean plant under copper stress	Khan and Lee (2013)
Penicillium simplicissimum GP17-2 *and Penicillium janthinellum* GP16-2	Increased number of rosette leaves of *Arabidopsis*	Hossain et al. (2007), (2008)
Trichoderma atroviride TaID20G	Improved the chlorophyll and carotenoid synthesis in maize seedlings, contributing to the alleviation of the drought stress	Guler et al. (2016)
Trichoderma sp.	Enhanced the numbers and weight of flowers in verbena and the numbers of flowers and buds in petunia	Ousley et al. (1994)

(continued)

Table 10.1 (continued)

PGPMs	Attributes	References
Piriformospora indica	Early onset of vigorous flowering was also seen in *Coleus forskohlii*	Das et al. (2012)
Penicillium chrysogenum PenC_JSB41 and *Trichoderma harzianum* TriH_JSB27	Early onset of flowering in tomato	Jogaiah et al. (2013)
Penicillium menonorum	Enhanced yield of cucumber plants	Babu et al. (2015)
Fusarium oxysporum	Increased yield ranging from ~20 to ~36% of banana plants	Waweru et al. (2014)
Fusarium oxysporum	Trigger ISR response against *Pseudomonas syringae* in *Arabidopsis*	Kojima et al. (2013)
Rhizoctonia sp.	Trigger ISR response against various plant pathogens in kidney bean	Tohid and Taheri (2015)
Piriformospora indica	Trigger ISR response against *Fusarium* head blight severity in wheat	Rabiey and Shaw (2016)
Bacteria		
Pseudomonas fluorescens and Pseudomonas putida	Ameliorate seed germination and vegetative growth of maize (*Zea mays* L.)	Agbodjato et al. (2016)
Pseudomonas alcaligenes PsA15, *P. denitrificans* PsD6, *Bacillus polymyxa* BcP26, and *Mycobacterium phlei* MbP18	Increased the growth of root and shoot of cotton and pea in nutrient-poor condition	Egamberdiyeva and Hoflich (2004)
Azospirillum brasilense and Bradyrhizobium japonicum	Increased root and shoot growth, nodule numbers, and biological nitrogen fixation of soybean (*Glycine max L.*)	Groppa et al. (1998)
Rhizophagus irregularis and *Bacillus amyloliquefaciens*	Improved photosynthetic efficiency and plant biomass of *Campanula rotundifolia*, *Fragaria vesca*, *Antennaria dioica*, *Geranium sanguineum*, *Thymus serpyllum*, *Trifolium repens*, *Viola tricolor, and Lotus corniculatus*	Xie et al. (2018)
Klebsiella oxytoca 10MKR7, *Pseudomonas* sp. 4MKS8, and *Enterobacter sakazakii* 8MR5	Improvement in plant growth and agronomic features of maize	Babalola and Odhiambo (2007)
Burkholderia ambifaria (V9), *Bacillus megaterium* (V16), *Enterobacter cloacae* (L1), *Pantoea ananatis* (LB5), and *Pseudomonas* sp. (StB5, A3, A6, and A61)	Enhanced plant growth and yield while lowering the dependence on nitrogen fertilization	Kifle and Liang (2016)

(continued)

Table 10.1 (continued)

PGPMs	Attributes	References
Algae		
Ulva lactuca, *Ulva reticulata*, *Kappaphycus alvarezii*, *Gracilaria corticata*, *Padina pavonica*, and *Sargassum johnstonii*	Germination of aged seed of *Allium cepa* L. and *Brassica oleracea* var. *capitata*	Patel et al. (2018)
Sargassum fusiforme	Promotes ISR through the reactive oxygen species generation and hypersensitive reaction in tomato (*Solanum lycopersicum* L.)	Sbaihat et al. (2015)

10.3 Conclusion and Future Perspective

Knowledge about the associations between plant and PGPM is inevitable for flourishing new strategies for controlling plant growth and diseases. By exploration of diverse range of effects exhibited by PGPM on plant make them as effective biofertilizers to substitute chemical fertilizers as well as to overcome increasing food demand and environmental stresses. Recent technological advances at molecular level provide more insight into the cellular signaling mechanisms in plant growth and stress tolerance, resulting from plant-PGPM interactions. Continuous efforts are needed to achieve high-performing, genetically modified PGPM of improved characteristics by introducing innovative biotechnology. With development consciousness is required regarding the influence of genetically modified plant or microbes to their surrounding ecosystem, which needs to be precisely assessed in non-field studies.

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Chapter 11
Cyanobacteria as Biofertilizers: Current Research, Commercial Aspects, and Future Challenges

Gunaswetha Kuraganti, Sujatha Edla, and Veera Bramhachari Pallaval

Abstract Increase in global human population and depletion of natural resources of energy, the viable supply of food, and energy without posing any threat to the environment is the current demand of our society. With limiting land and growing population, the option of better eco-friendly management tools for increasing soil fertility and agricultural population promises a successful long-term food security. The use of synthetic fertilizers and pesticides in agricultural practices deteriorates environmental qualities. Since microbes have been known to contribute in determining the soil fertility, the structure of soil and sustainable green energy production, microalgae including cyanobacteria emerged as potential candidates for their application in the development of environment-friendly and sustainable agricultural practices. As natural biofertilizer algalization, cyanobacteria play an important role in the maintenance of soil structure by soil aggregation through polysaccharides, enhanced soil fertility, fixing atmospheric nitrogen (N) by reclamation, increase in soil pores by producing adhesive substances, increasing growth by excreting growth promoting hormones (auxin, GA, vitamins, amino acids), increasing water-holding capacity, decreasing soil salinity, increase in soil phosphate by excretion of organic acids, and recycling of solid wastes. Much attention has been paid to study cyanobacteria with beneficial effects in fields like rice, paddy, wheat, soybean, tomato, radish, cotton, maize, sugarcane, and many more. There are research on inoculants of heterocystous cyanobacteria genera, which are used as biofertilizers in crops by enhancing the plant shoot/root length, dry weight, and yield.

Keywords Cyanobacteria · Biofertilizer · Environmental protection · Soil fertility · Green energy production · Plant growth

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11.1 Introduction

For decades, agriculture has been associated with the production of essential food crops, which plays a crucial role in the entire economy. Agriculture is considered as a backbone of the economic system of ample opportunities to a very large percentage of population. As the green revolution evolved into the world economy, it revolutionized the agriculture sector by adopting new technologies like ontogeny of high-yielding seed varieties, augmentation of irrigation, distribution of hybridized seeds, and commencement of the use of synthetic fertilizers and pesticides to elevate crop yield (Ayesha and Shahid 2017). Although the green revolution initially brought a positive impact on agriculture, the excessive use of chemical fertilizers in larger amounts not only increased crop productivity but also caused adverse effects on the soil structure distribution and physicochemical properties. (Patra et al. 2016; Kour et al. 2019a; Yadav et al. 2018).

Prolonged use not only perturbs the soil structure but also causes devastation to beneficial microbes; insects and nematodes in the soil are largely responsible for the maintenance of soil fertility and indispensable micro- and macronutrients to plants. The agriculture sector worldwide could not afford of losing soil fertility, as soil is a nonrenewable source; remediation of polluted soil to avoid soil deterioration is an extreme priority. As a solution, the microbial-based fertilizers emerged as a sustainable agricultural practice. In order to reduce the harmful effects of polluted soil, biofertilizer-based remediation of polluted sites was considered as a significant approach toward the sustainable development of the environment.

The term biofertilizers generally refers from manures to plant extracts. Biofertilizers commonly are substances that hold microbial inoculants, artificially multiplied cultures of certain soil microbes that colonize the rhizosphere. Nonetheless, these microbial inoculants improve the soil fertility and crop production by increasing the supplement or availability of primary micro- and macronutrients, growth-stimulating substances on the target crop (Mazid and Khan 2015). The plant roots surrounded by a narrow zone of soil called rhizosphere comprises of up to 10^{11} microbial cells per gram (Egamberdieva et al. 2008) and above 30,000 prokaryotic species (Mendes et al. 2013) that generally help in plant productivity.

The microbes–plant rhizosphere interaction determines the crop health in a natural agro-ecosystem by providing numerous services to crop plants, viz., organic matter decomposition, nutrient acquisition, water absorption, nutrient recycling, weed control, and biocontrol (Berg et al. 2013; Yadav et al. 2017a; Yadav and Yadav 2019). Nevertheless, the use of chemical fertilizers in high quantity alters the rhizosphere microbial communities, also a matter of interest in sustainable agriculture and bio-safety program. In the present scenario, the prime focus anticipates safe and eco-friendly methods by employing beneficial microorganisms in sustainable crop production. These diversified microorganisms are inoculated to soil ecosystem as biofertilizers play an imperative role by rejuvenating the soil physiochemical properties, viz., improving soil fertility by fixing atmospheric N, enhancing both the soil microbial biodiversity and maintenance of soil health by mobilizing the plant nutrients, solubilizing insoluble soil phosphates, producing plant growth–promoting hormones (PGPH), and developing crop productivity (Mazid and Khan 2015; Yadav et al. 2017b, c).

The bioinoculants such as plant growth–promoting rhizobacteria (PGPR), dinitrogen (N_2)-fixing cyanobacteria, P-solubilizers, S-oxidizers, mycorrhiza, disease-suppressive bacteria, stress-tolerant endophytes, and organic matter decomposers act as a biofertilizer (Kour et al. 2019c). These bioinoculants act as a complimentary component to soil and improve the crop management by crop rotation, decreasing the soil salinity, tillage management, recycling of soil residue, soil fertility restoration, and biocontrol of soil pathogens and pests that considerably increase in the growth as well as crop production (Sahoo et al. 2013). Cyanobacteria are the free-living photosynthetic prokaryotes that exist in single and filamentous morphological forms. These prokaryotes are extended from fresh, marine, and terrestrial habitats (Chikkaswamy 2015). These possess vegetative and specialized heterocyst cells for photosynthesis and N_2 fixation, respectively (Nozue et al. 2017). Cyanobacteria fix atmospheric N_2; secrete secondary metabolites; are available to higher plants; and improve soil structure, fertility, and increase crop productivity, hence making them exceptional biofertilizer (Himani et al. 2015). Biofertilizers act as additional nutrients to the soil through fixing atmospheric nitrogen naturally, solubilizing phosphates, and synthesizing growth-promoting substances that stimulates the plant growth. They can be categorized in different ways based on their nature and function**.** One simple widely spread classification is as follows.

11.2 Phosphorus Biofertilizers

Phosphate is the second most essential macronutrient to the plant that plays a vital role in plant metabolism and also acts as a key enzyme that controls the metabolic pathways that affects the crop productivity (Aslam et al. 2019). Regarding the phosphate that is made available to the crop chemically, about only 25–35% of phosphate is only utilized by the plant, and the remaining remains in insoluble form, which leads to the increase in salinity of soil (Yadav and Saxena 2018). Some microorganisms have the capacity of solubilizing this insoluble form of phosphate and are generally called phosphate-solubilizing microorganisms (PSM) (Kumar et al. 2016; Kour et al. 2019b; Verma et al. 2016; Yadav et al. 2015). Some of the active P solubilizers include *Bacillus*, *Pseudomonas*, *Micrococcus*, *Halococcus*, *Haloferax*, *Fusarium*, *Flavobacterium*, *Aspergillus*, *Sclerotium* and *Penicillium* (Pindi and Satyanarayana 2012; Yadav et al. 2019), *Arthrobacter*, *Rhodococcus*, *Delftia* sp. (Wani et al. 2005), and *Phyllobacterium* and *Azotobacter* (Kumar et al. 2001).

11.3 Nitrogen Biofertilizers

Since nitrogen is the limiting factor for the plant growth, plants need a certain amount of nitrogen in the soil to thrive. For this nitrogen, biofertilizers help to maintain the nitrogen levels in the soil (Rana et al. 2019). Different biofertilizers show an optimum effect for different soils; hence, the utilization of nitrogen biofertilizer relies upon the type of crop that has been cultivated (Raja 2013). The nitrogen biofertilizers that use the bioinoculants may associate with the plant either in a symbiotic or nonsymbiotic way (Stancheva et al. 2013). For legume crops, rhizobia are utilized, whereas *Azospirillum/Azotobacter* for nonlegume crops, *Acetobacter* for sugarcane, blue-green algae, and *Azolla* for grassland rice paddies (Ghumare et al. 2014).

11.4 Nitrogen Fixation by Cyanobacteria

The high-yield nitrogen acts as an important factor. The transformation of inert dinitrogen (N_2) to a combined form by nitrogenase enzyme through a catalytic process is called biological nitrogen fixation (BNF) (Kulasooriya and Magana-Arachchi 2016). The nitrogen-fixing prokaryotes can be aerobic or anaerobic and autotrophic or heterotrophic. The photosynthetic free-living cyanobacteria fix atmospheric nitrogen to organic nitrogen that is utilized by higher plants or simply by crop plants since cyanobacteria do not compete with crop plants and heterotrophic soil microflora for carbon and energy (Lau et al. 2015). Cyanobacteria use ammonia or ammonium (NH_4^+) from the soil through passive diffusion by precise uptake system. The nitrogen fixation is carried out by a specific high-molecular metalloprotein enzyme nitrogenase, which reduces molecular nitrogen to ammonia in the presence of hydrogen (Himani et al. 2015).

Cyanobacteria fix atmospheric nitrogen with ammoniacal-N under 40 ppm concentration; more than 70 ppm is toxic to the cell metabolic system (Kaushik 2014). The utilization of cyanobacterial species as biofertilizers is differentiated by specialized structures called heterocyst. They are heterocystous like *Aulosira*, *Anabaena*, and *Nostoc*; non-heterocystous like *Aphanothece*, *Gloeocapsa*, and *Gloeothece*; and filamentous like *Oscillatoria* and *Plectonema*. The heterocystous and filamentous cyanobacteria that belong to the order Nostocales and Stigonematales are considered as potential biofertilizers in which the nitrogenase enzyme activity is usually light dependent. The nitrogen fixation in cyanobacteria can be differentiated between heterocystous and non-heterocystous, and the function of nitrogen-fixing bacteria can be categorized into symbiotically and free-living (nonsymbiotic), respectively (Adams et al. 2013).

11.4.1 Filamentous and Heterocystous Cyanobacteria

Majority of cyanobacteria contain heterocysts that show aerobic nitrogen fixation and are generally filamentous. Among the filamentous cyanobacteria, the capital adaptation for N_2 fixation under aerobic conditions is due to structural changes of their vegetative cells (Kulasooriya and Magana-Arachchi 2016). Compared to vegetative cells, heterocysts have thicker cell walls, are larger in size and lighter in color, and have thickenings called polar nodules at the points of attachment to adjacent cells (Flores et al. 2016). The outer fibrous polysaccharide layer of heterocyst is shown to be specifically important site for N_2 fixation and limits the access of O_2 into heterocysts (Flores et al. 2015). Heterocysts are photosynthetically inactive; they do not fix CO_2 nor produce O_2. Since heterocysts are covered with thick cell wall that do not access the entry of O_2 or any other atmospheric gases, internally, the heterocysts are anoxic, which is ideal for nitrogenase enzyme that is notoriously O_2 sensitive (Brocke et al. 2018).

In an experimental study on *Anabaena cylindrica*, the isolated heterocysts contained very little chlorophyll-a and were devoid of phycocyanin and phycoerythrin pigments, which are associated with the O_2 evolving photosystem-II of photosynthesis (Bentzon-Tilia et al. 2015). Kulasooriya and Magana-Arachchi (2016) quoted evidently the existence of nitrogenase in isolated heterocysts using ^{13}N radioactive isotope in experimental study. Heterocysts are spaced at regular intervals along the filaments and exhibit structural and metabolic orientation to impart a conventional microaerobic environment. NtcA a nitrogen regulator and specific regulator HetR control transcriptional development of heterocysts (Olmedo-Verd et al. 2019), and cell undergoing differentiation under nitrogen deficiency induce or repress a large number of genes. The mature heterocyst cumulates cyanophycin and fixes nitrogen, which is later disseminated to vegetative cells from which heterocysts receive the reduced carbon (Flores et al. 2015).

11.4.2 Non-Heterocystous Cyanobacteria: Unicellular Cyanobacteria

In contrast with heterocyst cyanobacteria, non-heterocyst cyanobacteria do not show cellular differentiation and are thought that they are inadequate in N_2 fixation until 1960s (Bentzon-Tilia et al. 2015). There were also reports on spotting of nitrogenase activity in certain unicellular non-heterocystous and filamentous species of cyanobacteria. Wyatt and Silvey (1969) have given the first report that indicated nitrogenase activity in *Gloeocapsa* (syn. *Gloeothece*, *Cyanothece*), a unicellular species having potential of fixing atmospheric nitrogen under micro-oxic or anoxic conditions, followed by reports on other unicellular species such as *Synechococcus* and *Aphanothece* and Oscillatoriales, namely, *Phormidium*, *Limnothrix*, *Porphyrosiphon*, *Lyngbya*, *Pseudanabaena*, *Microcoleus*, *Oscillatoria*, and *Plectonema*, which were isolate from rice crop (Singh et al. 2014). Nitrogenase activity was found in 46 strains of non-heterocystous strains during a survey of 133 species, which initiated the inclusion of all nitrogen-fixing unicellular species into a single genus *Cyanothece* (Kulasooriya and Magana-Arachchi 2016). N_2 fixation in *Cyanothece* takes place in the dark, supported by ATP and carbon substrates produced during the preceding light period. The N_2 fixation levels by heterocystous cyanobacteria were found to be 300 μmoles where unicellular species that fix N_2 have been found to be within a range of 27 to 80 μmoles (Prasanna et al. 2009). Genetically modified non-heterocystous cyanobacteria can be cultivated and applied as a potential biofertilizer in rice production.

11.5 Free-Living Nitrogen-Fixing Cyanobacteria

Anabaena, *Nostoc*, *Aulosira*, *Tolypothrix*, *Cylindrospermum*, and *Stigonema* are some of the photosynthetic free-living cyanobacteria that are renowned as blue-green algae, which possess the capability to fix free atmospheric nitrogen. As a consequence, the soil is nourished by the addition of organic matter and extra nitrogen to the soil. These chlorophyll-containing prokaryotic cyanobacteria fix atmospheric free nitrogen. *Aulosira fertilissima* is known as one of the active nitrogen fixers in paddy fields contrastingly, and *Cylindrospermum licheniforme* grows in maize fields and sugarcane (Saiz et al. 2019).

11.6 Symbiotic Nitrogen-Fixing Cyanobacteria

Cyanobacteria form symbiotic associations with non-photosynthetic and photosynthetic organisms like diatoms, fungi, algae, liverworts, hornworts, mosses, bryophytes, pteridophytes, angiosperms, and gymnosperms (Sarma et al. 2016). Nitrogen-fixing cyanobacteria form symbiotic associations with several plants, for example, liverworts, cycad roots, lichenized fungi, and *Azolla* (fern). *Azolla pinnata* is a small free-floating freshwater fern found in paddy cultivation, which proliferates rapidly, doubling every 5–7 days, and is found in temperate climate. It fixes nitrogen in association with nitrogen-fixing Cyanobacterium, *Anabaena azollae* (Mahanty et al. 2017). Cyanobacterium releases ammonium into the water when paddy fields are inoculated with foam-immobilized *A. azollae* strains. Azolla provides favorable environment, and in exchange, *Anabaena azollae* fix nitrogen and also produce certain growth hormones (Singh et al. 2016).

11.7 Cyanobacteria as Biofertilizers for Sustainable Agriculture

Recent studies signify that photosynthetic cyanobacteria and microalgae are successfully used as biofertilizers and soil conditioners (Priyadarshani and Rath 2012; Sharma et al. 2012). Cyanobacteria are only photosynthetic prokaryote that is able to produce oxygen (Singh et al. 2014). Cyanobacteria nitrogen fixation is considered as an important biological process for harnessing soil health as well as for assuring economic, environmental, and agronomic benefit (Ahmad et al. 2016). Among 30,000 species of cyanobacteria comprising both unicellular microalgae and complex multicellular organisms, about 2000 species of 150 are listed in applications of vivid sectors like wastewater treatment, biofuel production, biogas production, biomass for aqua feed, as biofertilizers, and bioremediate agriculture soil (Kumar 2016).

In agriculture, cyanobacterial biomass is directly employed as bioinoculants to increase the crop productivity. In maintaining and building up soil fertility by consequently increasing the yield, cyanobacteria play a vital role as natural biofertilizer (Song et al. 2005). Cyanobacteria exhibit various unique features as an effective biofertilizer source to improve soil physicochemical properties (Fig. 11.1) such as the following:

- Fixing atmospheric nitrogen (N_2), and by its filamentous structure, it increases soil porosity.
- Water-holding capacity because of its jellylike structure.
- Excretion of plant growth hormones and secondary metabolites like auxin, gibberellin, amino acids, and vitamins.

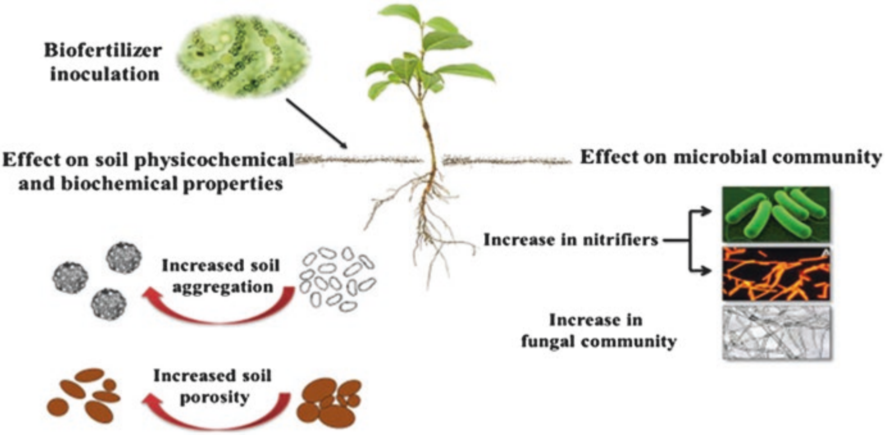

Fig. 11.1 Effect of cyanobacteria biofertilizers on microbial community and soil

- Promote the transportation of soil nutrients from soil to plant, which leads to agglomeration of soil.
- Decreasing the soil salinity.
- Preventing weed growth.

Their wide distribution and tolerance to ecological stress is due to their diverse morphological and physiological properties.

11.8 Cyanobacterial Biofertilizers in Improvement of Soil Physical Properties

In addition to nitrogen contribution, cyanobacterial biofertilizers benefit the soil fertility by improving the physicochemical properties of the soil by enriching them with carbon, nitrogen, and available phosphorous, decreasing the pH and conductivity of the soil, and defending the plant against biotic and abiotic stress (Kaushik 2014). The polysaccharides, peptides, and lipids that are excreted extracellularly thereby diffuse around the soil particles and form like glue and firmly hold the soil particles together forming microaggregates (Kumar et al. 2016). The growing algal filaments also help in forming soil aggregates. The result of algal inoculation leads to the improvement of water-holding capacity of the soil by its mucilaginous thali.

11.9 Production of Growth-Promoting Substances

The cyanobacterial biofertilizers benefit the crop production by providing different growth-promoting substances. These metabolites revive plant growth directly and also indirectly, increasing nutrient availability by communing with soil microorganisms by plant–microbe symbiosis (Singh et al. 2016; Verma et al. 2019; Yadav et al. 2017a). These growth hormones like gibberellins, cytokines B/B12 vitamins, and abscisic acids generally lead to increase in seed germination, grain weight, root and shoot growth and protein content of wheat, seed development of wheat, fruit weight of tomato, and seed germination of radish (Win et al. 2018). Tantawy and Atef (2010) conducted an experiment on *Lupinus termis*, in which the soil was treated with plant growth–enhancing substances of bacteria and cyanobacteria compared with treated and untreated by hormones (cytokines, IAA, and GA3). The affluent utilization of cyanobacterial species and other microalgae for the establishment of sustainable agriculture practices requires their large-scale cultivation.

11.10 Mass Cultivation of Cyanobacteria Biomass

In early 1950s, the mass cultivation of cyanobacteria at high rate for large-scale production (>50 L) for commercial production was cultivated. The fruitfulness of any growth system designed for autotrophic growth of cyanobacteria are decided by the five critical abiotic parameters such as temperature, light, pH, nutrient supplements, and carbon dioxide (Flynn et al. 2010). Generally, the cultivation of cyanobacteria requires light; nutrients like C, N, P, S, K, and Fe, which are given in low quantities; and water. As economically and commercially viable crops, few strains of cyanobacteria and microalgae like *Chlorella*, *Arthrospira*, *Dunaliella*, and *Haematococcus* have been cultivated on a large scale (Rosenberg et al. 2008). Generally, the mass cultivation systems of cyanobacteria have both positives and negatives; however, control over the parameters determines the production of the biomass. Notably, continuous light supply to the cultures determines the biomass along with the surface area of the system to maximum light absorption (Fig. 11.2). The commercial production of cyanobacteria biomass can be achieved by the three systems given below.

11.10.1 Cultivation Using Sunlight in Open System

Circular model shallow open ponds are utilized for mass cultivation of cyanobacteria and also microalgae. These systems usually have large raceways or sometimes open ponds where natural light is the source of energy; since solar radiation is free of cost, these systems are advantageous. By maintaining the specific unique growth conditions and parameters, prevention of the growth of other organisms can be avoided (Ugwu et al. 2008).

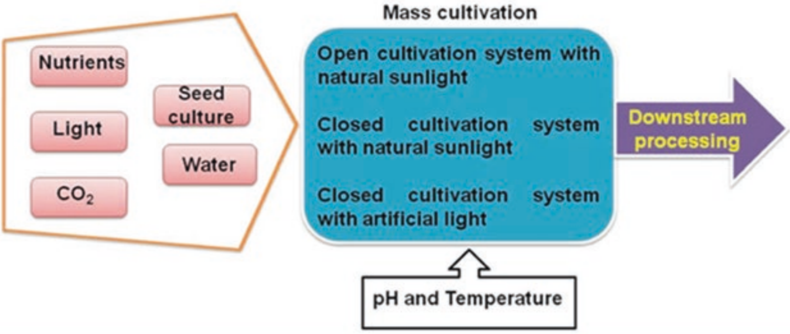

Fig. 11.2 Mass cultivation of cyanobacteria

11.10.2 Cultivation Using Sunlight in Closed System

In these systems, the vessels are designed with transparent material made up of plastic or glasses, which are placed outdoors, where solar radiation is utilized as natural light source and energy (Khatoon and Pal 2015). These transparent materials reduce the contamination by grazers and competitors. These designed systems are feasible for higher surface volume ratio, and therefore, the cell densities obtained were often higher compared to open systems (Carvalho et al. 2006).

11.10.3 Cultivation Using Artificial Light in Closed System

Cultivation of the cyanobacteria in the closed system utilizes the artificial light as source of energy (Pathak et al. 2018). These designs are found to be more similar to conventional fermenters, which are driven by an organic carbon source with the working principle to as photobioreactors, and these photobioreactors are driven by light unlike the fermenters. The continuous use of plastic or glass material for the manufacture of the vessels and power utilization makes this system more costly for biomass production compared to outdoor systems. However, most high-quantity and high-quality biomass are the final output of these systems.

11.11 Cyanobacteria Biofertilizer Production Technology

As blue-green algae (BGA) are free-living photosynthetic nitrogen fixers, with significant role in conserving along with build-up of soil fertility, which leads to the increase in rice growth and yield as a natural biofertilizer, they secrete or produce growth-enhancing substances that include B_{12}, improve water-holding capacity by soil aeration, and add to biomass after completion of life cycle. High percentage of macronutrients and considerable amount of micronutrients and amino acids exist in dry green algae (Mohapatra et al. 2013). Several algologists developed a potential techno economic practicability for algal production technology, which is easy to adapt, operate, and produce extra income from the spectrum of algal biofertilizer. Generally, four methods of algal production have been reported so far, which are listed as follows:(a) trough or tank method, (b) pit method, (c) field method, and (d) nursery-cum-algal production method. From these methods, trough and pit methods are obligatory for individual farmers, and the consequent two are for bulk production on a commercial scale (Moheimani et al. 2015).

11.11.1 Trough (Tank) Method

In this method, galvanized iron sheet, shallow tray, or permanent tanks were prepared with the size of 2 m × 1 m × 23 cm. The size can be increased if high production of biomass is required. Approximately 4–5 kg of river soil is spread by mixing well with

100 g of superphosphate along with 2 g sodium molybdate. To this, about 5 to 15 cm of water is poured in the trays, which depends upon local parameters, that is, rate of evaporation; mix the ingredients properly. To avoid insects and mosquitoes, 10–15 g of Furadan/Malathion granules are mixed. The soil and water mixture are permitted to settle for 8–10 h. At this point, about 200 to 250 g mother culture of blue-green algae will be added to the surface of water without interrupting the water level.

The reaction of the soil should be maintained neutral; in case the soil pH is acidic, $CaCO_3$ should be added in order to bring the pH of the soil to neutral. Within 10–15 days on the surface of the water/soil, the growth of the blue-green algae are visible like hard flakes if the sunlight and temperature are normal distribution, and water level will also be reduced due to evaporation. This way, water in the tray/pit is allowed to evaporate, and the growth of the algae flakes is allowed to dry. The dried algal growth is separated from the soil after the soil becomes dry after complete evaporation, which are later collected and stored in plastic bags. In this way, about half a ton in kg blue-green algal growth may be perhaps obtained from tray/pit till 1 m^2. Water was added again to trays in order to store the soil well. Then, the algae will be allowed to grow in this way, by not adding the mother culture or superphosphate. In this manner, one can harvest growth of algae two to three times.

11.11.2 Pit Method

Pit method for cultivation of blue-green algae does not conflict with the trough method. Unlike tough, tank pits are dug in the ground and are later layered with thick sheets of polythene to hold the water, or it can also be plastered with one-half cement. This method can be executed in an easy way by small farmers, which are also less expensive (Baweja et al. 2019).

11.11.3 Field Method

The field scale cultivation of blue-green algae is a scaled-up operation of trough method in producing the biomass on economical scale. In field method, first the demarcation of area of 40 m^2 in the field for algal production is done. Right after crop harvest, algal production is anticipated immediately, the stubbles are removed, and in case the soil is loamy, it is well puddle to facilitate water-logging conditions. The demarcated area is covered with water to a depth of 2.5 cm. Flooding is repeated to restore the water standing in field scale method. Then, superphosphate of about 12 kg/40 m^2 is added. In order to control the insect and pest attack, carbofuran (3% granules)/Furadan 250 g for 40 m^2 is applied. However, no fresh algal application is essential in case the field has already received previous algal application for at least two consecutive cropping seasons, and if not the composite algal culture of 5 kg/40 m^2 will be applied.

In clayey soils, algae good growth takes place within 2 weeks in clear, sunny weather, while in loamy soils it takes about 3 to 4 weeks. After the algae have grown highly and form floating mats and are thereby dried in the sun, dried algal flakes are collected in sunny bags for further use. By reflooding the plot with application of superphosphate along with pesticides, algal growth from the same area could be incessantly collected. During summer months like April and June, 16–30 kg/40 m^2 of average yield of algae per harvest is obtained.

11.11.4 Nursery-Cum-Algal Production Method

Farmers usually can cultivate algal biomass along with seedlings in their nurseries. Precisely, if 320 m^2 of land are allotted to prepare a nursery, then an additionally 40 m^2 alongside can be prepared for algal production as field method. The purchase of algal inoculants could be reduced if farmers produce the algal material required to inoculate their own land, which eventually leads to the reduction in expenditure. One can also lessen the cost of chemical fertilizers to be applied as recommended.

A defined mixture of cyanobacterial species to inoculate soil is termed as "algalization." Farmers after getting the soil-based starter culture can produce the biofertilizer on their own with minimum additional inputs as a major advantage of this technology (Mishra and Pabbi 2004). It has been suggested that the cyanobacteria introduced as a result of algalization can establish themselves permanently if inoculation is done consecutively for three to four cropping seasons (Saadatnia and Riahi 2009). About 500 g of BGA biofertilizer is mixed with 4 kg dried and sieved farm soil, which is later visible on standing water 3–6 days after transplantation. Excess utilization BGA does not affect the production of crop but only enhance the multiplication and establishment of biomass in field. After inoculation, the field should be water-logged for about 10–12 days to allow good growth of BGA. Normal pest control measures and other management practices do not interfere with the establishment and activity of BGA in the field. After BGA inoculation, application of a small dose of phosphate fertilizer accelerates multiplication of BGA (Sahu et al. 2012).

11.12 Formulations of Algal Biomass

For commercialization, algal biofertilizer formulations have been developed and tested. Many scientists proposed some of the techniques used for the formulation of cyanobacterial fertilizers. For example, for longer duration, clay-based strain inoculation in soil was proposed by Dubey and Verma (2009) even after 4 months, and the algae biomass in soil was 10–70 times higher when compared to non-inoculated plots. The approach called fly-ash (FA) approach proposed by Mishra and Pabbi (2004), wherein the cyanobacteria along with nitrogen fertilizers were mixed to enhance growth rate and production of rice plants, leads to reduced utilization of nitrogen fertilizers. In comparison with traditional soil-based cyanobacterial biofertilizer, cyanobacterial biofertilizers were formulated to produce maximum crop productivity when these cyanobacterial-based fertilizers were employed with two carriers; one is wheat straw and the other multani mitti-clay carrier (Tripathi et al. 2008). It is pertinent that both the straw-based and soil-based biofertilizer treatments were shown to possess high yields when supplemented with 90 and 120 kg, respectively. In another formulation, paddy straw compost/vermiculite (1:1) as carrier-based formulation, cyanobacterial adaptation rates were higher in rice field where vermin-compost acted as a carrier (Prasanna et al. 2013, 2014; Renuka et al. 2016). It is notable that cyanobacterial biofertilizers not only showed high yield in paddy crops but also in vegetative crops.

11.13 Production and Demand of Cyanobacterial Biofertilizers in Economic Aspect

The growth of market would be increased with the increasing pressure on global food production and development in technologies of fertilizer production, which resulted in expectation of increase on the demand for fertilizers. The biofertilizer market has been segmented on the basis of crop type, microorganism, region, form, and mode of application. Other than rice crop, algalization enhanced nearly 34% of yield. In India, agrochemical conditions materialize to be commendatory where blue-green algae technology has been put forward, in which field scale production of algae biofertilizer is also possible. About 20–25 kg dry algae can be obtained on 40 m field. By adopting this method, 15 t ha^{-1} of wet BGA can be obtained by the farmers, and in turn, farmers can also produce algae for count yard of the house (Saurabh et al. 2014).

11.14 Trade for Biofertilizers

In 24 countries, about 170 organizations are occupied in commercial production of biofertilizers. To develop farm-based technology for the use of *Azolla* fertilizer for rice, in 1982, the Philippines implemented the National Azolla Programme (NAAP). About US$30 billion is valued for organically raised agricultural products in current global market with the growth rate of around 8% (Sheng et al. 2009). Biofertilizer production units that are lodged in different states rely on their source of funding, which can be categorized into the following two groups:

1. Units financed by the Government of India (GOI)
2. Units financed by other sources

So far, 64 biofertilizer production units have been established with the support of the Government of India (GOI). Production and distribution of different biofertilizers were also undertaken but subsequently discontinued as the centers redefined their role toward R&D and HRD-related activities (Mazid and Khan 2015). Polythene bags made of 50–70 mm thick and low-density sheets were used to pack the biofertilizers. Information regarding name of the product, crop for which intended, date of manufacture with expiry date, storage instructions and directions for the use of biofertilizers, and net quality meant for 0.4 hectare should be labeled carefully on each pack along with the ISI certified mark.

11.15 Development of Cyanobacterial Biofertilizer Strains for Stress Tolerance

Algae possess incredible ability toward environmental stress tolerance. Regarding pesticide resistance, Ningthoujam et al. (2013) found that *Anabaena variabilis* were able to tolerate 100 μg/ml Malathion. Sinha and Häder (2006) deliberated about the photoprotective technique of cyanobacteria against UV-B, which played a crucial role in the growth of agricultural crops as biofertilizers. In order to explore the potential of cyanobacteria and to control the effects of biotic and abiotic factors on algae and their production, proper use of novel approaches to produce cyanobacterial mutants for possible solutions should be practiced (Gupta et al. 2013; Singh and Datta 2006). Another crucial piece of evidence from the findings of Singh and Datta (2007) clearly demonstrated that *A. variabilis* mutant strains under exterior conditions in flooded soils when exposed to herbicides resist the herbicide and increase rice growth. Genetic analysis of the different isolates revealed the presence of new uncharacterized strains, which are potential biofertilizers. Genetic study on the regulation of *nif* gene and *cnfR* gene of heterocyst and non-heterocyst cyanobacteria in adopting the low-oxygen level in triggering the transcription of *nif* genes in operating nitrogenase enzyme of different soil cyanobacteria samples is limited, which has to be adopted in different field samples (Tsujimoto et al. 2014).

11.16 Future Technology Development

As biofertilizer cyanobacteria possess potential application in agriculture sector, recent development in advanced techniques like culturing and screening of cyanobacteria and genetic engineering has enabled us to utilize the potentiality of these microbes. To exploit these organisms as green factories, a synthetic biology is one of the approaches for the production of new lines of commodities, with progress of genetic manipulation techniques. The significant development in adopting new strategies like modern technologies for biomass production, identifying efficient strains, implication of new inoculation techniques for effective inception of inoculums into the soil are implimented in demonstrating their beneficial effects on crop yield. The olive milling process generates about 1.2–1.8 m^3 of wastewater for each ton of olive. Olive oil–milling wastewater can be utilized for the cyanobacteria cultivation for biofertilizer (Rashad et al. 2019), with the advantage of minimizing the ecological disturbance and cost-effectiveness (Mohapatra et al. 2013). Cyanobacteria when cultivated in larger scale should be optimized to improve the productivity and decrease in cost. The utilization of cyanobacteria in salt-influenced soil remediation will reproduce green agriculture and advance the reasonable improvement of human society with optimizing the other technical issues like harvesting and contamination.

11.17 Conclusions and Future Perspectives

Algae-based biofertilizers have demonstrated huge advantages in the advancement of green agriculture. Traditional conservation-based method with modern technology can reduce farmers' dependence on chemical fertilizers and pesticides, as well as to reduce the farming costs and environmental hazards. Biofertilizers, for example, cyanobacteria, can present a reasonable enhancement to the compound composts, and 'organic farming' can turn into a reality later on. Algae and cyanobacteria secrete exopolysaccharides and bioactive substances that have proven their role in recovering soil nutrients along with mobilization of insoluble forms of inorganic phosphates. Development of genetically modified stress-tolerant cyanobacteria has better prospects as biofertilizers, and transfer of stress-coping transgenes into crop plants has a great future worth investing by the researchers (Bravo-Fritz et al. 2016).

Cyanobacteria and other microalgae either in symbiotic or nonsymbiotic association can be used for the development of sustainable agriculture practices by implementing raceway ponds and photobioreactors for large-scale biomass production. However, cyanobacterial cultivation using these systems requires high amount of investment in the form of capital. Combining both raceway and photobioreactor method of cultivation of cyanobacteria reduces capital and operational cost (Singh et al. 2017). The production cost and net profitability can be achieved by using wastewater from seed-milling refineries as a water source for the cyanobacteria cultivation. Abiotic and biotic stress factors should be regulated at optimal level for high production with less contamination during large-scale production.

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