Sustainable Development and Biodiversity 27

Ajar Nath Yadav *Editor*

Soil Microbiomes for Sustainable Agriculture

Functional Annotation

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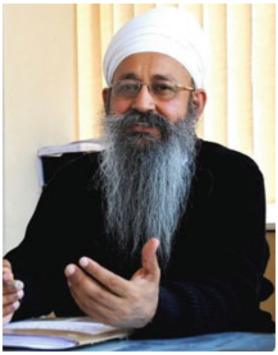
Foreword by Davinder Singh



Microbes are ubiquitous in the environment and can survive in most habitats. They play a major role in the ecosystem and are even excellent for plant growth promotion for agro-environmental sustainability. It is expected that the fast-growing world population will make food security a big issue in the future. Agricultural sustainability is facing to be a formidable task by using chemical-based fertilizers and pesticides in order to increase the yield of the crop plants. To fulfill the increasing demand of food supply with the problems like shrinking farmlands, and global warming is one of the major challenges. The soil microbiome has found diverse and complex habitats, which consist of billions of bacteria, fungi, and other living organisms.

Beneficial microbes play an essential role in nutrient cycling and plant shielding from destructive effects of biotic and abiotic stresses. Intensive farming practices lead to an increase in crop production, but they also have detrimental effects on the biological and physiological properties of soils. The macronutrients for plant growth are generally provided via chemical fertilizers. In comparison to chemical and synthetic fertilizers, biofertilizers and biopesticides improve plant growth and crop productivity in an eco-friendly way. Along with plant growth promotion, beneficial microbes could be used for mitigation of diverse abiotic stresses using diverse plant growth-promoting mechanisms such as fixation of atmospheric nitrogen, solubilization of macronutrients (phosphorus, potassium, and zinc) and micronutrients (magnesium, selenium), production of ACC deaminase, antagonistic substances, plant growth hormones (auxin, cytokinin, and gibberellins), and siderophores (iron chelators). Thus, using beneficial soil microbiomes for sustainable agriculture is gaining vast attention worldwide.

I recommend this book to researchers and students working on the emerging and fascinating field of microbiology, biotechnology, and related subjects. The book will advance the knowledge to a greater extent in these areas with significant broader research on soil microbial communities and their biotechnological role for agricultural sustainability. The editor of this book deserves credit for such a splendid and innovative contribution to microbiology research.

Dr. Davinder Singh
Vice Chancellor
Eternal University, Baru Sahib, Himachal
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Foreword by Amrik Singh Ahluwalia

Microbes are the hidden wonders of the planet Earth that stuns humans with their diversity, habitats, and functional capabilities. Archaea, bacteria, and fungi are the three major microbial domains that comprise millions of microbes that are present in various habitats like soil, water, air, plant, and animal externals and irrefutably play various roles. Among all habitats, the soil is the one habitat that is known to comprise a large portion of microbial diversity and these microbes are believed to play a large number of ecosystem processes. Nitrogen fixation, carbon cycling, phosphorus cycling, weathering of rocks, decomposition of dead, and decay matter are some of the roles that soil microbes play in the ecosystem. The functional annotation of microbes could be advantageous to many sectors including the agriculture environment and industry. Nowadays, plant growth-promoting microbes as biofertilizers and biopesticides are known as the sustainable input that enhances crop productivity and soil fertility. Soil microbes undergo different mechanisms to improve crop productivity like solubilization of micro- and macronutrients, fixation of nitrogen, chelation, and mitigation of biotic and abiotic stress.

The present book *Soil Microbiomes for Sustainable Agriculture: Functional Annotation* is to provide the recent advances in mechanisms of plant growth promotion and applications of soil microbiomes for mitigation of different abiotic stresses in plants. The proposed book encompasses current knowledge of soil microbiomes and their potential biotechnological applications for plant growth, crop yield, and soil health under the natural as well as harsh environmental conditions for sustainable agriculture. The book volume comprises 19 chapters. The Chap. 1 by Bose et al. describes the soil microbiomes, their beneficial attributes of the plant growth promotion, and potential applications in agriculture, whereas Mokrani and Nabti highlight diverse soil microbial communities from different crops and their roles for crop productivity in Chap. 2. Chapter 3 by Boroujeni et al. describes soil microbes with multifarious plant growth-promoting attributes for enhanced production of food crops. Chapter 4 by Emami-Karvani and Chitsaz-Esfahani highlights the mechanisms, recent advancement, and future challenge of phosphorus solubilizing microbiomes. Berde et al. describe potassium solubilization, its mechanism, and functional impact on plant growth in Chap. 5. In Chap. 6, Kumar et al. have given the details about soil microbiomes with siderophores production and zinc solubilizing attributes for cereals biofortification. Jatav et al. highlights the diverse soil microbes for plant growth promotion and mitigation of abiotic stress of drought in Chap. 7. In Chap. 8, Maitra et al. describe the current status and future outlook of mitigation of heat stress by thermotolerant soil microbes. Mukhtar et al. highlight the potential applications of halophilic soil microbes for the mitigation of salt stress in Chap. 9. Jha et al. explain the role of psychrotrophic soil microbes in the alleviation of cold stress in plants in Chap. 10. Mitigation strategies for abiotic stress tolerance in plants through stress-tolerant PGP microbes have been described by Dhevagi et al. in Chap. 11. Chapter 12 by Maitra et al. describes the omics strategies for abiotic stress responses and microbe-mediated mitigation in plants. Zia et al. highlight the technical challenges and emerging solutions for enhancing food crops using plant probiotics in Chap. 13. Salimi and Hamedi highlight the soil microbes as biofertilizers for agricultural productivity in Chap. 14 and soil microbes as biopesticides for agricultural sustainability in Chap. 15. Mycorrhiza as a plant growth-promoting and biocontrol agent for crops growing under the stress condition is discussed in Chap. 16 by Hussain et al. Thakur et al. highlights entomopathogenic soil microbes for sustainable crop protection in Chap. 17. Subrahmanyam et al. explain global scenario of soil microbiome research in Chap. 18. Finally, the conclusion and future prospects of functional annotation and biotechnological applications of soil microbiomes have been described by the editor and co-authors in the last chapter.

Overall, great efforts have been carried out by Dr. Ajar Nath Yadav, his reviewer team, and scientists from different countries to compile this book as a highly unique and up-to-date source on soil microbiome for sustainable agriculture for the students, researchers, scientists, and academicians. I hope that the readers will find this book highly useful and interesting during their pursuit of microbiology and related subjects.

Prof. Amrik Singh Ahluwalia
Pro-Vice Chancellor
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Preface

The microbes are ubiquitous in nature. The soil is a natural hotspot of the soil microbiome. The soil microbiome plays a critical role in the maintenance of global nutrient balance and ecosystem functioning. The soil microbiomes are associated with plant ecosystems through the intense network of plant–microbe interactions. The microbes present in bulk soil move toward the rhizospheric region due to the release of different nutrients by plant systems. The rhizospheric microbes may survive or proliferate in the rhizospheric zone depending on the extent of influences of the chemicals secreted into the soil by roots. The root exudates contain the principal nutrients factors (amino acids, glucose, fructose, and sucrose). The microbes present in the rhizospheric region have the capabilities to fix atmospheric nitrogen, produce different phytohormones, and solubilize phosphorus, potassium, and zinc. The plant systems take these nutrients for their growth and development. These soil- and plant-associated microbes also play an important role in the protection of plants from different plant pathogenic organisms by producing a wide range of secondary metabolites such as ammonia, hydrogen cyanide, siderophores, and hydrolytic enzymes. The soil microbiomes with plant growth-promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. The soil microbiomes promote plant growth, enhance crop yield and soil fertility via different direct or indirect plant growth-promoting mechanisms. The soil microbes help the plant for adaptation in extreme habitats by mitigating the abiotic stress of high/low temperatures, hypersalinity, drought, and acidic/alkaline soil. These PGP microbes could be used as biofertilizers/bioinoculants to replace the harmful chemical fertilizers for sustainable agriculture and environments.

The aim of volume *Soil Microbiomes for Sustainable Agriculture: Functional Annotation* is to provide the recent advances in mechanisms of plant growth promotion and applications of soil microbiomes for mitigation of different abiotic stresses in plants. The proposed book encompasses current knowledge of soil microbiomes and their potential biotechnological applications for plant growth, crop yield, and soil health under the natural as well as harsh environmental conditions for sustainable agriculture. The book will be useful to scientists, researchers, and students related to microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects.

Baru Sahib, Himachal Pradesh, India Ajar Nath Yadav

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Editor and Contributors

About the Editor

Ajar Nath Yadav is an Assistant Professor (Senior Scale) and Assistant Controller of Examinations at Eternal University, Baru Sahib, Himachal Pradesh, India. He has 8 years of teaching and 12 years of research experience in the field of Microbial Biotechnology, Microbial Diversity, and Plant-Microbe-Interactions. He obtained a doctorate in Microbial Biotechnology, jointly from IARI, New Delhi, and BIT, Mesra, Ranchi, India; M.Sc. (Biotechnology) from Bundelkhand University and B.Sc. (CBZ) from the University of Allahabad, India. He has 250 publications, with an h-index of 58, i10-index of 160, and 9050 citations (Google Scholar- on 06/06/2021), and 112 research communications in different national and international conferences. He is the editor of 18 Springer-Nature, 7 Taylor & Francis, 2 Elsevier, and 1 Wiley book.

In his credit, one granted patent "Insecticidal formulation of novel strain of *Bacillus thuringiensis* AK 47". He has got 12 Best Paper Presentation Awards and 1 Young Scientist Award (NASI-Swarna Jayanti Puraskar). He received the "Outstanding Teacher Award" in the 6th Annual Convocation 2018 by Eternal University, Baru Sahib, Himachal Pradesh. He has a long-standing interest in teaching at the UG, PG, and Ph.D. levels and is involved in taking courses in microbiology and microbial biotechnology. He is currently handling two projects, one funded by the Department of Environments, Science & Technology (DEST), Shimla, and one by the HP Council for Science, Technology &

Environment (HIMCOSTE). He has guided two Ph.D. candidates and one M.Sc. scholar, and presently, he is guiding four scholars for Ph.D. degree and one M.Sc. In his credit, ~6700 microbes (Archaea, bacteria, and fungi) are isolated from diverse sources, and ~550 potential and efficient microbes are deposited at the culture collection ICAR-National Bureau of Agriculturally Important Microorganisms (NBAIM), Mau, India. He has deposited **2423** nucleotide sequences and **3** whole-genome sequences (*Bacillus thuringiensis* AKS47, *Arthrobacter agilis* L77, and *Halolamina pelagica* CDK2) and **2** transcriptomes to NCBI GenBank databases: in the public domain. The niche-specific microbes from extreme environments were reported as specific bioinoculants (Biofertilizers) for crops growing in normal and diverse abiotic stress conditions. He and his group have developed technology for screening archaea for phosphorus solubilization for the first time. He is the editor-in-chief for “Journal of Applied Biology and Biotechnology”. He has been serving as an editor/editorial board member and a reviewer for 49 different national and international peer-reviewed journals. He has lifetime membership in the Association of Microbiologist in India and the Indian Science Congress Council, India. Please visit https://sites.google.com/view/ajarnathyadav/ for more details.

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Chapter 1
Plant Growth-Promoting Soil Microbiomes: Beneficial Attributes and Potential Applications

Pragya Tiwari, Subir Kumar Bose, and Hanhong Bae

Abstract Soil microbiome constitutes an integral component of plant–soil–microbe associations and has a key impact on the ecosystem. The soil microbiome influences key biological processes namely bio-geochemical cycling, plant nutritional uptake and carbon sequestration. The present era has witnessed the emerging significance of soil microbiome as a dynamic system influencing plant productivity and conferring stress tolerance to the plants, having a major impact on the ecosystem. Comprehensive knowledge about plant–soil microbiome is essential for increasing agricultural output, maintenance of soil health towards more sustainable agriculture. Discussing the emerging significance of soil microbiomes in the recent perspective, this chapter extensively focuses on the soil microbiome diversity and distribution in nature, providing an overview of its integral association and dynamics in association with the plants. Moreover, the beneficial attributes of the soil microbiome and its socio-economic applications in a biotechnological perspective are herein discussed. Recent approaches in bioengineering soil microbiomes provide a key platform to enhance food security and sustainable agriculture for millions across the globe.

Keywords Metabolic engineering · Metagenomics · Plant colonization · Plant growth promotion · Secondary metabolites · Soil microbiomes · Sustainable agriculture

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1.1 Introduction

Soil microbiome constitutes a plethora of diverse microbes in close proximity with plants and influences plant growth. Plant-associated microbial communities enhance plant tolerance to environmental stress, nutrition uptake and contributing to plant growth (Bakker et al. 2018; Kour et al. 2020). Recent statistics by the Food and Agriculture Organization (FAO, United Nations) suggests that to sustain an estimated 10 billion world population, the global food production has to be increased up to 70% by 2050. This can be achieved by the increase in crop production through agriculture to compensate for the depleting natural resources, indiscriminate use of natural products, threatened plant species, among others (Sergaki et al. 2018; Sharma et al. 2021). The vital functions in the ecosystem are governed by soil microbes, ranging from carbon sequestration, nutrient re-cycling to agricultural output. The soil microbiome comprises of microbial communities exhibiting enormous diversity and abundance (Thakur and Geisen 2019). Moreover, the microbial communities inhabiting the rhizosphere include mainly soil bacteria and fungi, performing multiple functions in the ecosystem (Bardgett and Van Der Putten 2014; Kour et al. 2019). Any fluctuations in climatic condition directly or indirectly affect the plant–soil microbiome and its dynamics (Tripathi et al. 2015). The existence of microbial diversity in the ecosystem and its association with plants highlight the beneficial prospects in biotechnological applications, restoration of ecological balance, agriculture and pharmaceutical sectors (Dubey et al. 2019; Hesham et al. 2021).

Therefore, understanding the dynamics of plant–soil microbiome and their maintenance is the key to sustainable agriculture and crop productivity. In the present context, researchers across the globe are working on increasing the beneficial prospects of soil microbiome, aiming for increased agricultural production. Plant–soil microbiome is indispensable to plant productivity with significant role in cycling of nutrients, carbon sequestration and increase in plant growth (Verma et al. 2017a, b; Yadav et al. 2021). Modern scientific techniques for plant–soil microbiome profiling hold potential for the identification of plant-associated microbes and their functional dynamics, providing insights into the influence of climate changes on their distribution and diversity in the soil. With an overview of microbial communities in soil microbiomes and their distribution, the chapter discusses the importance of understanding plant–soil microbiome dynamics in the context of sustainable agriculture. Moreover, recent trends in genetic engineering approach towards synthetic symbiosis and bioengineering plant–soil microbiomes hold enormous potential towards maximum utilization of these beneficial microbes towards increased crop productivity in agriculture.

1.2 Plant and Soil Microbiomes

The naturally occurring microbes in the rhizosphere include a group of microorganisms classified as bacteria, fungi, protozoans, nematodes and micro-arthropods. The plant rhizosphere consists of the upper surface of the soil, with widespread root networks (Kumar et al. 2015b; Singh et al. 2019). The plant root secretes several primary and secondary metabolites comprising of amino acids, lipids and carbohydrates, which promotes microbial population towards the plant (Yadav 2021). The above soluble metabolites bind to receptors on bacterial membrane and attract microbial communities, which colonize and adhere to the roots of the plant (rhizosphere). This is correlated and promotes plant tolerance to environmental stress, plant growth promotion and plant productivity (Singh et al. 2019; Santoro et al. 2015; Kumar et al. 2015a; Subrahmanyam et al. 2020). Moreover, plant growth-promoting bacteria (PGPB) are defined as the microorganisms, which promote plant growth, yield and production (Glick et al. 1999; Babalola 2010) (Table 1.1).

Studies have discussed the association of complex microbial communities with a diverse group of plants including herb, shrub and trees (Yasmin et al. 2016; Sandhya et al. 2017). The microbial components of the plant holobiont comprise of microbiota and microbiome (Lucaciu et al. 2019). The presence of plant microbiota and microbiome (microorganisms and microbial genomes) in endosphere, phyllosphere and rhizosphere demonstrates significant functions in plant growth and disease management (Sczyrba et al. 2017; Sanchez-Canizares et al. 2017; Lucaciu et al. 2019; Yadav 2020).

Nowadays, crop production is challenged by exposure to toxic chemicals and heavy metals, climate changes, and an ever-increasing need to enhance global agricultural output. Plant growth-promoting rhizobacteria (PGPR) improves plant health and aids in higher crop yield and production, these microorganisms are designated as biofertilizers (Prasad et al. 2021). In the present context, there has been a growing scientific interest in employing biofertilizers in agricultural practices (Di-Benedetto et al. 2017). Presently, biofertilizers are commercially marketed in many brand names, such as Galltrol, Diegall, Gmax PGPR, Nitromax, Azo-Green, Custom N_2, Custom GP, BaciGold, Subtilex, YieldShield, RootShield, Plus WP and others (Table 1.2). Microorganisms that are closely associated with a particular plant species are specific for exudate secretion of plants roots (Fig. 1.1) and not dependent on soil conditions, respectively.

1.2.1 Diversity and Composition

Microbial communities are present in close proximity with plant species and constitute the “soil microbiome”. Plants display interaction with the microbial communities, namely the phyllosphere and soil/rhizosphere, among others (Hardoim et al. 2015). The microbiota associated with roots is horizontally transferred, although

Table 1.1 Plant growth-promoting bacteria as bio-fertilizer and their functional role in plant growth promotion

Host/Microorganism	Region	PGP attributes	Host plant	References
Alcaligenes faecalis str. S8	Endophyte	P-solubilization IAA production	*Withania somnifera*	Abdallah et al. (2016)
Pseudomonas putida	Rhizosphere	P-solubilization Siderophore production IAA production	*M. piperita*	Santoro et al. (2015)
Enterobacter sp. TAP02	Rhizosphere	IAA production N_2 fixation P-solubilization	*T. amplexicaulis*	El-Sayed et al. (2014)
Pseudomonas fluorescens WCS417r *Bacillus amyloliquefaciens* GB03	Root inoculation	Increase the drought tolerance	*M. piperita*	Chiappero et al. (2019)
Bacillus subtilis P-20 *B. subtilis* Daz-26	Rhizosphere	PGPRs Essential oil yield	*M. arvensis*	Maji et al. (2013)
Achromobacter xylosoxidans Fd2 *Herbaspirillum seropedicae* Oci9 *Ochrobactrum rhizosphaerae* Oci13	Rhizosphere	IAA production Siderophore production	*Ocimum sanctum*	Barnawal et al. (2012)
Serratia ureilytica Bac5	Rhizosphere	Siderophore production ACCdeaminase P-solubilization	*O. sanctum*	Barnawal et al. (2012)
Pseudomonas stutzeri CSP03, *Bacillus subtilis* TTP02 *Pseudomonas putida* PHP03	Rhizosphere	IAA production N_2 fixation P-solubilization Siderophore production	*Capparis spinosa*	El-Sayed et al. (2014)
Arthrobacter sp. SMR3, *B.subtilis* SMR15	Endophyte	IAA production ACC deaminase	*Papaver somniferum*	Pandey et al. (2016)
Bacillus sp. *Pseudomonas putida* (ECL5)	Endophyte, IAA	P-solubilization Siderophore production	*Curcuma longa*	Kumar et al. (2016a, b)
Clavibacter michiganensis	Endophyte	IAA production	*C. longa*	Kumar et al. (2016a, b)
Azotobacter chroococcum CL13	Rhizosphere	IAA, HCN, ammonia P-solubilization	*C. longa*	Kumar et al. (2014)

(continued)

Table 1.1 (continued)

Host/Microorganism	Region	PGP attributes	Host plant	References
Bacillus subtilis LK14	Endophyte	P-solubilization IAA production	*Moringa peregrine*	Khan et al. (2016)
B. subtilis CT-1 *A. tumefaciens* CT-2 *P. putida* CT-4 *Pseudomonas* sp. CT-5	Endophyte	IAA production, Ammonia production P-solubilization	*Cassia tora* L.	Kumar et al. (2015a)
*Achromobacter xylosoxidans*AUM54	Endophyte	IAA production, Phosphate solubilization Siderophore production	*Catharanthus roseus*	Karthikeyan et al. (2012)
Rhizobium sp.	Rhizosphere	Cytokinin production	*Mimosa pudica*	Sabat et al. (2014)
Pseudomonas stutzeri P3	Endophyte	IAA production	*Echinacea*	Lata et al. (2006)
Paenibacillus borealis BR 32	Rhizosphere	IAA production N_2 fixation Phosphate solubilization	*Juniperus* sp.	Navarro-Noyaa et al. (2012)
Acinetobacter sp. ALEB16	Endophyte	Abscisic acid production Salicylic acid production	*Atractylodes lancea*	Wang et al. (2015)
Paenibacillus durus BR 30	Rhizosphere	IAA production N_2 fixation Phosphate solubilization	*Asphodelus* sp.	Navarro-Noyaa et al. (2012)
Brevundimonas diminuta EGEB-1 *Agrobacterium tumefaciens* EGE-B-5 *Stenotrophomonas rhizophilia* EGE-B-6	Endophyte	IAA production Phosphate solubilization	*Prunus persica*	Liaqat and Eltem (2016)
Bacillus strains OSU-142 and M3	Rhizosphere	Auxin and cytokinin production (N_2 fixing) and phosphate solubilizing) M3 produce Zeatin	Raspberry	Orhan et al. (2006)

(continued)

Table 1.1 (continued)

Host/Microorganism	Region	PGP attributes	Host plant	References
Pseudomonas BA-8 *Bacillus* OSU-142 *Bacillus* M-3	Rhizosphere	Auxin and Cytokinins	*Fragaria* × *ananassa*	Pırlak and Kose (2009)
Stenotrophomonas maltophilia R551-3	Endophyte	IAA synthesis ACC deaminase	*Populus* sp.	Taghavi et al. (2009)
Paenibacillus graminis BR 35	Rhizosphere	N_2 fixation Phosphate solubilization	*Aster gymnocephalus*	Navarro-Noyaa et al. (2012)
Azospirillum lipoferum KYR F6	Rhizosphere	IAA synthesis N_2 fixation Phosphate solubilization	*Haplopappus* sp.	Navarro-Noyaa et al. (2012)
Rhizobium sp. *Azospirillum* sp.	Endophyte	IAA synthesis N_2 fixation	*Oryza sativa*	Sev et al. (2016)
Pseudomonas aeruginosa FTR, *Enterobacteras buriae* MRC12 *Acitenobacter brumalii* MZ30V92	Endophyte	Ammonia production Phosphate solubilization Siderophore production	*Zea mays*	Sandhya et al. (2017)
Pseudomonas monteilii FMZR2 *Sinorhizobium meliloti* MRC31	Endophyte	Ammonia production Phosphate solubilization,	*Z. mays*	Sandhya et al. (2017)
Serratia sp. Rh269	Rhizosphere	IAA synthesis Siderophore production Phosphate solubilization	*Oryza sativa*	Yasmin et al. (2016)
Bacillus sp. Rh219	Rhizosphere	Siderophore production	*O. sativa*	Yasmin et al. (2016)
Pseudomonas sp. E227	Rhizosphere	IAA synthesis Siderophore production HCN Phosphate solubilization	*O. sativa*	Yasmin et al. (2016)
Azospirillum brasilense *Pseudomonas fluorescens*	Rhizosphere	–	*Triticum aestivum*	Naiman et al. (2009)
Azospirillum sp. *Azotobacter* sp.	–	–	*T. aestivum*	Namvar and Khandan (2013)
Azospirillum brasilense	Inoculation of seeds with bacteria culture	–	*T. aestivum* cultivar CD 150	Piccinin et al. (2011)

(continued)

Table 1.1 (continued)

Host/Microorganism	Region	PGP attributes	Host plant	References
Glomus intraradices BEG72, *Glomus mossae* *Trichoderma atroviride* MUCL 45632	Coated seeds of wheat with a microbial consortium	Enhance growth, nutrient uptake, yield and grain quality	*Triticum durum*	Colla et al. (2015)

vertical transmission for bacteria through seeds has also been observed in nature (Rana et al. 2020; Rana et al. 2019b). The microbial communities present in rhizosphere colonize the plant through roots, which offers a unique ecological niche (Hartmann et al. 2009). However, some studies also suggested that the microbial communities present in rhizosphere show variation with time. Plant roots are colonized by diverse bacterial endophytes, in a symbiotic network with the plant species. Diverse bacterial species present as endophytes in grapevine roots comprise of Acidobacteria, Actinobacteria, Chloroflexi, Planctomycetes, Proteobacteria, Verrucomicrobia, beside others (Fierer 2017). The aboveground zone, the phyllosphere provides a unique environment for the epiphytes microbial communities. The endophytes may enter the plant tissues through aerial parts or from xylem to the stem, and leaves, respectively (Compant et al. 2011). The plant microbiota, which is above ground, mainly thrives from soil, air and seed and several environmental factors affect their presence and distribution. The epiphytes and endophytes enhance plant growth and improve stress (biotic and abiotic) tolerance, respectively (Hardoim et al. 2015; Rana et al. 2019a).

1.2.2 Factors Affecting the Soil Microbiomes

Soil and rhizosphere microbial communities (soil microbiomes) are affected by the environmental stresses: biotic factors–host genotypes, cultivars, developmental stages, proximity to root and root architecture. In the case of abiotic factors, these influence soil composition of microbial communities including soil type and soil quality (Buyer et al. 1999; Li et al. 2018), the physical factor includes light, pH, seasonal variation, moisture content, temperature and soil mineral composition. The soil porosity is a critical determinant of plant growth and development because it provides oxygen (O_2) to the roots of the plants (Berendsen et al. 2012; Chaparro et al. 2012; Turner et al. 2013; Kumar et al. 2019).

1.2.2.1 Soil Type and Composition

Soil environment plays a key role in rhizosphere microbial communities' growth, in direct and indirect manner. The root secretions (exudates) have a key effect on the

Table 1.2 The commercial products (based on plant growth-promoting rhizobacteria) marketed for plant growth promotion and disease management

Bioagents/microbial source	Trade name/formulation	Use/Recommended crops	Weblink
Agrobacterium radiobacter strain K1026	Nogall	Block infections by crown gall-causing pathogenic agrobacteria	http://bio-caretechnology.com
A. radiobacter strain K84	Galltrol Diegall	Prevention and eradication of crown gall	https://agbiochem.com/wpcontent/uploads/2014/08/Revised-Galltrol-Gallex-Pamphle
Azospirillum brasilense *Azotobacter chroococcum*	Gmax PGPR Nitromax	Nitrogen nutrition, phosphate nutrition, plant protection from diseases	https://www.greenmaxagrotech.com
A. brasilense	Azo-Green (*Azospirillum*)	N-supplementation contains an efficient strain of *Azospirillum*	https://pdf.indiamart.com/impdf/4177237333/MY-863282/azogreen-azospirillum
Nitrogen-fixing bacteria	Custom N_2	Nitrogen-fixing bacteria	http://living-soils.com/custom-n2-nitrogen-fixing-bacteria
Trichoderma sp.	Custom GP	Increase soil performance	http://living-soils.com/trichoderma-benefits-plants
B. subtilis MB1600	BaciGold (Fungicide)	Fungicide	https://www.indiamart.com/proddetail/bacigold-4576463473.html

(continued)

Table 1.2 (continued)

Bioagents/microbial source	Trade name/formulation	Use/Recommended crops	Weblink
Bacillus subtilis strain MBI 600	Subtilex (Bio-Fungicide)	Bio-fungicide and protection against diseases caused by *Rhizoctonia solani*, *Fusarium* sp. and *Pythium* sp.	https://www.seedranch.com/Subtilex-NG-Fungicide-6-X-2-Oz-p/subtilex-ng-case.htm
Bacillus pumilus GB 34	YieldShield (biological seed treatment)	Yield Shield 200 FS applied as a water-based slurry either alone or with other registered seed treatment insecticides and fungicides	https://www3.epa.gov/pesticides/chem_search/ppls/000264-01117-20101020
Trichoderma harzianum—1.15% *Trichoderma virens*—0.61%	RootShield Plus WP (Biological Fungicide)	It mainly grows on roots and shielding them against root-damaging fungi	https://www.seedranch.com/RootShield-Plus-WP-Biological-Fungicide-1-Lb-p/rootshield-plus-wp-1
B. pumilus QST2808	Sonata ASO	Control or suppression of many plant diseases	https://agrobaseapp.com/unitedstates/pesticide/sonata-aso
Beneficial bacteria, fungi/mycorrhiza	Microbeact (growth accelerator)	For garden plants, vegetables, fruits, shrubs, trees, lawn, sod and turf (contains photosynthetic cultures)	https://www.microbeact.com/growth-acel
Bacillus licheniformis SB3086	EcoGuard, Green Releaf (Biofungicide)	It is used on ornamental plants and ornamental turf to prevent and treat many fungal diseases	https://patents.google.com/patent/CA2451555C/en
Burkholderia cepacia	Blue Circle, Deny, Intercept	Increase plant P nutrition in high P-fixing soils	
Pseudomonas fluorescens A506 (71%)	BlightBan A506	Suppression or control of fire blight on pome fruits and the suppression of frost damage on cherry, apple, pear, almond, peach, tomato, potato and strawberry	https://nufarm.com/uscrop/product/blightbana506

(continued)

Table 1.2 (continued)

Bioagents/microbial source	Trade name/formulation	Use/Recommended crops	Weblink
Pseudomonas syringae ESC-100	Bio-Save 10, 11, 100, 110,1000, and 10 LP	Biological decay control agent. Bio-Save is labelled for post-harvest applications for the control and prevention of disease on a variety of fruits and vegetables that include, among others: seed and storage white potatoes and sweet potatoes	https://iviair.com
Pseudomonas chlororaphis	Cedomon (Biological seed dressing solution)	Biological seed dressing solution Cedomon® is commonly used, especially in Sweden	http://orgprints.org/11271/1/fnytt105
Streptomyces griseovirdis K61	Mycostop (Biological fungicide)	Mycostop is used by farmers for diseases caused by *Pythium*, *fusarium*, *botrytis*, *alternaria*, *phomopsis*, rhizoctonia and *phytophthora*. It also increases plant vigour and yields even in the absence of root pathogen activity	https://www.planetnatural.com/product/mycostop
4 species of beneficial soil fungi and 5 species of beneficial soil bacteria	Biota Green™	It is a probiotics for golf courses	http://living-soils.com/biota-green-probiotic-for-golf-greens
Beneficial bacteria and fungi spore	BiotaMax	Soil probiotics, seed germination, root developments and plant growth	http://living-soils.com/product/biotamax

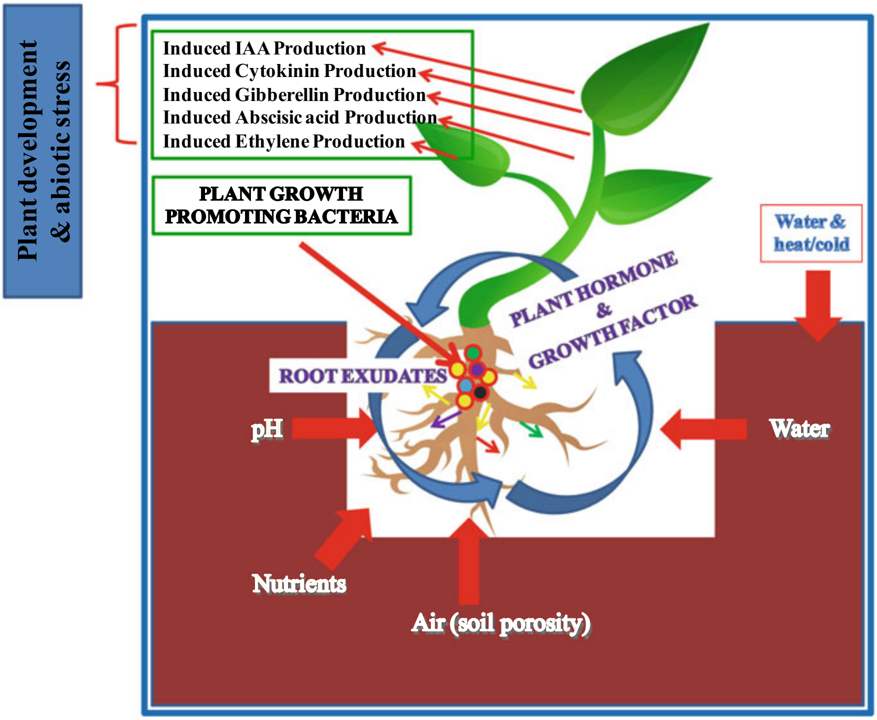

Fig. 1.1 Diagrammatic representation of the influence of the soil factors and PGPR on plant roots and soil microbes, which modify the soil environment and induce chemical signalling and growth hormone production, promoting plant health and yield

soil microbes as signalling molecules for microbes, creating a complex and intricate interaction between plants and the microbiome (Chaparro et al. 2012).

A key study by Broeckling et al. (2008) suggested a close dynamics between the composition of soil microbial population and their interaction with the plant species. Some fungal communities (soil-borne fungus) altered the composition and nature of soil and decreased the total biomass of a non-native model plant (Broeckling et al. 2008). The experiments were conducted in two plant species, *Arabidopsis thaliana* and *Medicago truncatula.* Both plants were cultivated in their natural environments (presence of their natural microbiomes) and in the non-native soil. *Arabidopsis* plants (root secretions) supported the native fungal community in natural soil conditions (as compared to non-native soil), when cultivated alone. The beneficial microbial population was disproportionate (in non-native soil) and while other microbial species were increased due to this uneven population of microbes (fungal biomass), microbial population and plant growth were also affected, when compared with or without treatment with root exudates in *Arabidopsis* plants. The similar observation was recorded in case of *M. truncatula* plants. These results strongly suggested that the secretion of chemicals from plant roots (roots exudates) and, therefore, individual plants influenced the total population and composition of soil microbiomes.

1.2.2.2 Soil pH Effect

Soil pH is a measure of soil acidity/alkalinity and governs the composition of microbial communities (Fierer and Jackson 2006; Yang et al. 2017). The soil pH showed a negative correlation with soil biomass and a positive correlation with average well colour development (AWCD) (Zhong et al. 2010; Chen et al. 2015), distinct fungal and bacterial interactions with soils of diversified texture, nitrogen and phosphorous content (Frey et al. 2004; Chaparro et al. 2012; Girvan et al. 2003; Yadav et al. 2020b), and pH of the soil (Fierer and Jackson 2006; Rousk et al. 2010). The optimum soil pH range for plant growth is 5.5–7.5. Soil pH influences the plant nutrients availability, micro or macronutrient and directly affects the growth of plants and their productivity. Therefore, soil pH governs the growth of the plant and adaptation to the environment. Moreover, a plant may be sensitive to a pH range in some soil conditions but not for others, for example, a low concentration of molybdenum (Mo) in soil may not be optimum for *Glycine max* (pH 5.5), but soils with optimum Mo leads to better growth at that pH (Sumner and Yamada 2002). Bacterial decomposition of organic contents and some fertilizers release nitrogen (chemically synthesized fertilizers), which influence soil properties and pH, the optimum pH for bacterial growth being 5.5–7.0 range. In soil with pH < 5.0, most of the plant nutrients demonstrate soil leaching (mainly acidic condition) (Loncaric et al. 2008).

Recent research evidence proves that the pH of the soil may critically affect the soil bacterial communities (Fierer and Jackson 2006). Soil sample analysis by Rousk et al. (2010) was performed in pH range that varies from 4.0 to 8.3, while all other factors and variables in soil were regulated. In the above study, the diversity and composition of the bacterial population showed correlation with soil pH (Rousk et al. 2010). It was assumed that the correlation between soil bacterial communities and soil pH structure was attributed to the pH sensitivity of bacterial cells, the bacterial taxa being tolerant to a relatively narrow pH range (Rousk et al. 2010). Other evidence suggested that soil pH was a key factor for soil microbial diversity, highlighting that altitude, phosphorous concentration and the ratios of Ca^{2+}, Mg^{2+}, and Al^{3+} ions in the soil, are key determinants (Faoro et al. 2010).

1.2.2.3 Nutrient Composition

The nutrient composition of soil is a key determinant of soil health and has a critical effect on plant growth (Ryan and Sommer 2012). Soil basically comprises of three nutrients: nitrogen (N), phosphorus (P) and carbon (C) (Ryan and Sommer 2012), while other factors, namely iron, also influence the presence of rhizosphere microbiome (Yang and Crowley 2000). Optimum nutrient content in soil is crucial to plant growth and deficiency of any factor is overcome by the application of chemical fertilizers (Geiger et al. 2010). Moreover, the fertility of the soil is determined by a complex interaction between the biotic and the abiotic components, the soil microbes aiding the organic content decomposition and nutrient generation for plant growth. The growth of the plant facilitates the acquisition of nutrients and root colonization by the microbes (Berendsen et al. 2012). In addition, disproportionate soil nutrient content also has a critical impact on biodiversity in ecosystem and cultural practices for land use, thereby having a profound effect on the soil microbiome (Joergensen and Emmerling 2006).

Another key nutrient, phosphorous modulates the microbiome in rhizosphere (Kour et al. 2021). A study by Coolon et al. (2013) showed that grassland burning would increase phosphorous and nitrogen availability and studied the effect of phosphorous and nitrogen increase on grasslands in North America. The study showed the effect of soil phosphorous and nitrogen on natural ecosystems. Moreover, the presence of nitrogen in the soil has a profound effect on plant productivity and bacterial communities (Clark et al. 2007). Studies have shown that an increase in nitrogen enhanced plant productivity but adversely affected lower plants and bacterial communities (Suding et al. 2005). This study demonstrates the significance of soil nutrients in diversity and distribution of soil microbes and plant growth, respectively.

1.2.2.4 Climate Changes

The global rising temperature results in fluctuating climatic conditions, thereby adversely affecting the soil microbiome. Studies have shown that the microbial communities, which were selective for *Arabidopsis* root exudates, responded to changes in the environment (Badri et al. 2013). In another study, the structure and function of rhizosphere microbes were modified by increased CO_2 concentration in root exudates. The changes in climatic conditions altered the gene expression in microbial communities (Bardgett et al. 2013). Moreover, the depletion in ozone layer had increased the penetration of UV-B radiations (Müller et al. 1997), and ecosystems in the polar region been prone to climatic changes (Caldwell et al. 1982). UV-B radiation directly affects soil microbes leading to altered growth, carbon assimilation, changes in pigments, synthesis of amino acids, among others (Formanek et al. 2014). Compared to the rhizosphere, the phyllosphere microbes are more sensitive to ultraviolet (UV) radiations, thereby only a few taxa are present in the phyllosphere as compared to rhizosphere regions (Dohrmann and Tebbe 2005).

The soil microbiomes are directly affected by increased UV-B radiation levels (Johnson et al. 2002); but the microbial communities in rhizosphere display different levels of sensitivity to damage by UV-B radiation (Arrage et al. 1993). The bacterial population adopts multiple mechanisms to tolerate UV radiations. The bacterium, *Pseudomonas syringae*, includes a plasmid having *rulAB* operon functions in DNA repair process (Cazorla et al. 2008), as a protective mechanism. In *Xanthomonas campestris*, the bacteria show UV tolerance by producing an extracellular polysaccharide, which absorbs UV radiations (Hugenholtz et al. 1998). Moreover, the bacterial communities in phyllosphere produce pigments as a UV protection mechanism

(Whipps et al. 2008). The UV-B radiation affects the nutrient cycle in soil, thereby having a key effect on soil microbes (Caldwell et al. 2007). The root biomass is reduced on exposure to UV radiation, leading to less colonization and little nutrients in the soil, disturbing the soil microbiome. Moreover, the increase in atmospheric CO_2 (Hu et al. 2001) and elevated temperature (global warming) directly affects the soil microbial communities (Carson et al. 2010).

1.2.2.5 Geographical Factors

Few studies have shown the effect of latitude, longitude and altitude on the diversity and distribution of the soil microbiome. Van Horn et al. (2013), suggested that abiotic factors, namely organic content, pH, etc., govern the biodiversity of Antarctic soil. The study further discussed the importance of geographical sampling for the determination of geographical factors affecting soil microbial communities. Moreover, studies have shown that the combinations of different abiotic factors are responsible for biogeographical changes, rather than altitude, latitude and longitude, respectively (Chu et al. 2010).

1.3 Scientific Techniques for Plant–Soil Microbiome Profiling

For gaining insights into the beneficial plant and microbe interaction and dynamics (Fierer 2017; Singh et al. 2019), the plant–soil microbiome needs to be explored using scientific approaches (Lucaciu et al. 2019). Nowadays, sophisticated scientific techniques are employed to decipher information and correlate them (Fierer 2017; Singh et al. 2019; Lucaciu et al. 2019). The newer scientific techniques comprise of microbiome 16S r-RNA gene-sequencing technique, sequence analysis, microarrays analysis, shotgun metagenomics approaches, among others (Table 1.3). Table 1.3 discusses modern techniques and scientific tools used for plant–soil microbiome profiling.

The techniques specifically employed for the *insilico* studies of shotgun metagenomes include target-gene assembly, taxonomic profiling, and genome binning and taxonomic binning. From whole-genome sequence data, scientists collect and use genomic data, which improves phylogenetic resolution and functional annotation. The strategy employed to estimate the extent of sequencing essential to delineate information for a particular genome requires preliminary metagenomics data and existing 16S rDNA amplicon data, respectively (Tamames et al. 2012; Ni et al. 2013; Rodriguez et al. 2018). Other techniques are meta-transcriptomics, and meta-proteomics employed in plant–microbe association studies. Additionally, sequencing of amplicon of functional genes acting in key biogeochemical reaction in soil and the rhizosphere zone is done. The important ones include *pmoA*

Table 1.3 Modern techniques and scientific tools used for plant–soil microbiome profiling

Name of techniques/approaches	Main function	References
16S r-RNA gene-sequencing technique (Using sequencing technique and databases platform e.g. Greengenes, Silva and RDP)	Sequencing analysis strategies to estimate how much sequencing is necessary to recover information for a target genome require existing 16S r-DNA amplicon data and/or a preliminary metagenomics data set	Tamames et al. (2012)
Shotgun metagenomic approaches (computational analysis of genomic DNA sequence)	There are four techniques typical for the computational analysis of shotgun metagenomes: including, taxonomic binning, taxonomic profiling, target-gene reassembly and genome binning	Ni et al. (2013)
Metagenomics (Microarray-based Metagenomics analysis)	It is the study of genetic material recovered directly from environmental samples. The broad field may also be referred to as environmental genomics, ecogenomics or community genomics	Riesenfeld et al. (2004)
Meta-transcriptomics (RNA-sequencing analysis)	Transcript sequences from the organisms in a microbiome	Chaparro et al. (2014)
Meta-proteomics (meta-proteomics mostly utilizes methods originating from mass spectrometry (MS)-based proteomics)	Meta-proteomics is the study of the proteins in a microbial community from an environmental sample	Hettich et al. (2013)
Metabolomics (Nuclear magnetic resonance (NMR), and liquid chromatography–mass spectrometry (LC-MS) and gas chromatography–mass spectrometry (GC-MS))	It is the large-scale study of metabolites molecules, within cells, biofluids, tissues or organisms. Collectively, these small molecules and their interactions within a biological system are known as the metabolome	Cajka and Fiehn (2016)

and *amoA* (methanotrophs) and ammonia oxidizers (Suddaby and Sourbeer 1990; Pester et al. 2012), *mcrA* gene (methanogens) (Zeleke et al. 2013) and *dsrB* for sulphite and sulphate reducers (Jochum et al. 2017; Vigneron et al. 2018; Zeleke et al. 2013), *nifH* for diazotrophs (Collavino et al. 2014; Angel et al. 2018) *nxrB* for nitrite oxidizers (Pester et al. 2014), a comprehensive overview and omics database platform of functional genes may be retrieved from Fungene (Fish et al. 2013).

The analytical methods and technologies employed for the study of metabolomics include nuclear magnetic resonance (NMR), liquid chromatography–mass spectrometry (LC-MS) and gas chromatography–mass spectrometry (GC-MS). The estimation of metabolites employing MS-based techniques provides better resolution than

NMR (Emwas 2015). However, an extensive MS sample preparation method and the detection of metabolites (that ionize into the detectable mass range) project few limitations. The NMR-based metabolic profiling works well with compounds that are difficult to ionize or derivatization is required (Markley et al. 2017).

1.4 Beneficial Attributes of Soil Microbiomes

The constant applications of synthetic chemical fertilizers and pesticides have a harmful consequence on the natural microbiomes, which include bacteria, archaea, protozoan, cyanobacteria, fungi, nematodes and micro-arthropods inhabiting the rhizosphere (microbiomes) and the frequent use leads to disturbance in soil natural ecosystem and chemical properties of the soil (pH, bacterial population) and correlation between them (Mazid and Khan 2014; Devi et al. 2020). Moreover, the extended use of synthetic chemical fertilizers and pesticides leads to damage of soil property, texture quality and soil microbial communities influencing the yield and productivity of plants. To address this concern, scientists are focusing on sustainable agriculture for restoration of soil health and promote crop yield and production, by employing natural methods without affecting natural soil microflora. For sustainable agriculture, the concerns associated with chemical fertilizers and pesticides for mitigation of climate influence need to be addressed (Kumar et al. 2017a, b). Sustainable agriculture is the possible way to compensate for the rising demand for organic fertilizers of biological origin, then employing agro-chemicals. Organic farming maintains the diversity of natural microbes in the soil and natural microflora contribute to plant growth. The microflora comprise of bacteria, actinomycetes, fungi including arbuscular mycorrhiza fungi (AMF), cyanobacteria, to manage disease (disease management), salt tolerance, drought tolerance and heavy metal toxicity (Gupta 2012; Mishra et al. 2014; Kumar et al. 2021).

The rhizosphere zone constitutes the upper soil layer; in close proximity to the root surface (Kumar et al. 2015b). In the rhizosphere zone, root secretion comprises of lipids, amino acids and carbohydrates, respectively. These chemicals attract microbial population, which colonize the plant roots, and participate in promoting plant growth and tolerance to diseases (Oku et al. 2012; Kumar et al. 2015a, b). Plant-associated beneficial microbes influence the biomass, yields and productivity of the host plant and are known as plant growth-promoting bacteria (PGPB) (Babalola 2010; Kumar et al. 2016a, b). The PGPB also induce phytohormone production, ammonia production, phosphate solubilization, siderophores and hydrogen cyanide (HCN) production, among other functions (Yadav et al. 2020c).

Nitragin is a potent biofertilizer (legume inoculants and growth promotants) marketed by Merck KGaA, Darmstadt, Germany. The statistics suggested that the global market of Nitragin is $85 million dollar in agriculture because the farmers prefer organic and sustainable agriculture. Presently, the global market for bio-inoculants is projected at an annual cost of $85 million (with $50 million in the USA alone).

Azotobacter is a free-living Gram-negative bacteria (diazotrophic), primarily found in neutral to alkaline soils (pH range 7.0), on some plants and in aquatic environments. One of the distinct abilities of *Azotobacter* is that it can survive in dry soils, in the form of cysts for up to 24 years. Moreover, it fixes atmospheric nitrogen by conversion to ammonia (biological nitrogen fixation). Blue-green algae (BGA) (cyanobacteria) are prokaryotes, consisting of free-living bacteria and the endo-symbiotic plastids, found in some eukaryotes. They perform photosynthesis for energy generation and shows freshwater or terrestrial origin. Few cyanobacteria perform biological nitrogen fixation in anaerobic conditions by specialized cells called heterocysts. The heterocysts of BGA are able to fix atmospheric nitrogen (N_2) into ammonia (NH_3), nitrites (NO_2^-) or nitrates (NO_3^-), readily assimilated by the plants (Golden and Yoon 1998; Fay 1992). Free-living cyanobacteria inhabit the water content of rice paddies and play important role in increasing the yield and production of rice crop through a biological process.

Considering the current demand for organic farming, PGPB is a potential biofertilizer, safe and effective for increasing crop yields and productivity in agriculture. Recently in organic farming, several bacterial species were used, such as *Arthrobacter*, *Azospirillum, Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Pseudomonas* and *Serratia* (Saharan and Nehra 2011; Kumar et al. 2015a, b). In plants, phytohormones play a major role in the growth and secondary metabolites production (Bose et al. 2013). *Azospirillum* fixes atmospheric nitrogen, produces phytohormones and confers abiotic and biotic stresses tolerance to the plants (Fukami et al. 2018; Bashan and de-Bashan 2010; Naiman et al. 2009).

The study of beneficial plant–microbe interactions and the increase in plant growth by *Hordelymus europaeus* (also known as wood-barley) were undertaken. In this study, the effect of microorganisms (Protozoa, Nematoda and Lumbricidae) increased shoot/root ratio up to 3.4–5.6 in *H. europaeus* (Alphei et al. 1996). The N_2-fixing bacteria, *Azospirillum lipoferum* and *Azotobacter chroococcum*, were used as biofertilizers and its effect on the growth and productivity of three *Mentha* species was studied (El-Hadi et al. 2009). The study showed that microbiological parameters (total fungi, total microbial counts, *Azotobacter* and *Azospirilla*) were enhanced with the treatments of above biofertilizers, and *Mentha* essential oil yield was also increased.

1.5 Biotechnological Applications in Agriculture

To improve crop productivity and sustainable agriculture, researchers are exploring innovative methods in agriculture. Approaches for enhancing sustainable agriculture are required to boost crop productivity and maintain ecological balance. The plants showing higher adaptation to changing environmental conditions and biotic and abiotic stress tolerance would lead to a higher agricultural output (Pretty et al. 2011; Singh et al. 2020) (Tiwari et al. 2021). The soil microbiomes comprise of the rhizosphere and phyllosphere microbes in close association with the plant. The beneficial microbe in soil serves as an important bioresource for nutrition uptake (mineral solubilization) and siderophores production. The plant growth-promoting microbes or biofertilizers define an eco-friendly method for sustainable agriculture. Besides agriculture, microbes producing phytases show good prospects in nutritional applications as human food (Kumar et al. 2016a, b, 2017a, b). Moreover, the mineral bioavailability was increased by exogenous phytase addition (Penella et al. 2008), while improved iron bioavailability was seen in oat, rice and maize porridges by phytase supplementation (Hurrell et al. 2003). The bio-fortification method has been used to increase micronutrients in the major food crops. PGP bacteria were used in place of synthetic pesticides and fertilizers, which mobilize nutrients by chelation, organic acids release and acidification (Verma et al. 2017a, b; Kaur et al. 2020).

Probiotics are defined as food supplements made to improve human health and consist of live microbes, which positively influence the host by the maintenance of microbial balance. Probiotics were prepared for pharmaceutical application and showed improvement in the immune system in a host (Rekha et al. 2020). A better immune response to *Salmonella typhi* oral vaccine in a person taking *Lactobacillus johnsonii* and *Bifidobacterium lactis* as probiotic was observed (Olivares et al. 2007) and *Lactobacillus fermentum* showed promising effects in influenza (Arunachalam et al. 2000). Moreover, probiotics also affects the behaviour of a person and initial human trials suggested that probiotic consumption may induce gastro-intestinal symptoms and behaviour (Yadav et al. 2017; Benton et al. 2010).

1.6 Presence of Soil Microbiomes and Management Practices

The agricultural management practices affect the diversity of soil microbiomes. These management practices are classified as conventional and organic: the organic farming was defined as “an ecological production management system that promotes and enhances biodiversity, biological cycles and soil biological activity”. The organic farming targets replenishing and maintains ecological balance (Gold 1995) and does not use synthetic fertilizers. However, the conventional farming practice employs pesticides and synthetic chemicals for crop protection and crop production. These management practices greatly affect the soil microbiome, the use of synthetic pesticides in conventional agriculture may change the diversity of soil microbial communities (Liu et al. 2007; Sugiyama et al. 2010; Yadav et al. 2020a). However, the organic farming may combat plant pathogens by methods that promote the diversity of microbial communities (Sugiyama et al. 2010). Moreover, studies have suggested that soil microbiome is affected by stress and environmental changes (Degens et al. 2001), agri-management practices, etc. (Lumini et al. 2011).

1.7 Towards Synthetic Symbiosis: Bioengineering Plant–Soil Microbiomes

Soil microbiomes influence the distribution and productivity of plants (Lau and Lennon 2011; van der Heijden et al. 2008), therefore, studies in the present time are investigating the functional dynamics of microbial communities and plants. Moreover, studies in the past have highlighted that plant health and yield may be predicted by an increase in soil microbial communities (Lau and Lennon 2011; Schnitzer et al. 2011). Advances in scientific technologies have provided significant information on the diversity and functions of soil microbiome (Nannipieri et al. 2003), for instance, plant growth and productivity increased with a diversity of fungal species (Maherali and Klironomos 2007). Moreover, the plant–microbe association displays a feedback mechanism, the soil microbiome and the plant community changes in response to each other.

The presence of soil microbiome is critical for plant productivity and intensive agriculture practices hamper the diversity and functions of associated microbes, which in turn leads to less crop yield and production. To address this concern, collaborative UK research projects (funded by the Soil Security Programme) are co-integrating genomics and field studies to gain insight into the functional dynamics of the soil microbiomes and to manipulate them for benefit of farmers. In a related "Roots of Decline" project, the researchers studied the outcome of continuous cropping on causing diseased microbiomes in oilseed rape and how to use different OSR varieties for disease improvement (www.soilsecurity.org/roots-of-decline). Additionally, the "MycoRhiza soil" project aims to study the different combination of wheat varieties and their cultivation may promote beneficial crop–microbe associations, leading to better soil health and disease resistance (www.soilsecurity.org/mycarhizasoil).

Advances in synthetic biology approaches have put forth possibilities of bioengineering "soil microbiome" for more sustainable agriculture. For example, the leguminous crops have an inherent property to fix atmospheric nitrogen but not present in cereal crops (maize, wheat, etc.). Researchers are exploring the possibilities to transfer genes from nitrogen-fixing bacteria to bacteria associating with cereal crops (www.synthsym.org). The advantages include the increased crop yield in low-income areas and would improve the damages caused by intensive agricultural practices. However, the science of "synthetic symbiosis" by bioengineering soil microbiomes needs to find scientific approval since genetic manipulations remain a controversial area in scientific research.

1.8 Perspectives in Sustainable Agriculture and Food Security

With the rising global population and a requirement to provide food to the billions, agriculture calls for a more sustainable approach by increasing food production and security (Gupta 2012). The agricultural methods should focus on enhancing the plant–microbe associations to promote diversity of soil microbiome. This will increase the crop yield and production while utilizing the minimum use of resources (Chaparro et al. 2012). Research studies have demonstrated the beneficial effects of plant microbial communities in improving plant growth and productivity (Lambers et al. 2009; van der Putten et al. 2009). According to guidelines of U.S. National Research Council, the objectives of sustainable agriculture should focus on the development of productive farming systems that conserve energy and are environmentally sound (Lakshmanan et al. 2014). In this direction, the ideal approach would be to use beneficial microbes for nutritional enhancement and tolerance to biotic and abiotic and stress conditions. Different formulations of beneficial microbes were used in soil applications, bio-priming, seed treatment, etc. in the respective plant. Several key areas in sustainable agriculture include microbial isolate optimization, identification of healthy microbiomes and their agricultural applications (Lakshmanan et al. 2014). Moreover, comprehensive knowledge about plant–soil microbiome interaction will serve as a platform to increase crop productivity, stress tolerance and plant growth.

1.9 Recent Trends and Outcome in Plant–Soil Microbiome Research

The “soil microbiome” represents a diverse ecosystem with interacting microbial communities. With the changing environmental conditions, the microbial communities have evolved mechanism for adaptation and survival (Jansson and Hofmockel 2020), however, the impact of changing climatic conditions has a major impact on the presence and stability of the soil microbial communities. With the progress in high-throughput methods, it is possible to determine the effect of climatic change on the diversity of soil microbial communities and their composition. Moreover, the determination of functional mechanisms of soil microbial communities, for example, soil respiration process, is a very critical aspect in understanding soil microbiome science and may be studied by multi-omics strategies. The presence and functions of the soil microbiome in maintaining healthy soil and providing nutrition to the plants are vital for optimum functioning of ecosystem. The recent trends in the maintenance of soil microbiome and sustainable agriculture call for a more integrated approach to use soil management practices, biodiversity maintenance, carbon sequestration and increased tolerance to climate changes (Jansson and Hofmockel 2020). Moreover, different omics-technologies, namely proteomics, metabolomics, transcriptomics, etc., provided clear insights into the plant–microbe dynamics, contributing to better genetic and functional prospects of soil microbiome (Dubey et al. 2018; Malla et al. 2018a, b). Additionally, advanced methods, namely stable isotope probing, helped in the estimation of diversity and function of soil microbial communities (Mau et al. 2015; Zhang et al. 2018). In the present era, emerging, sophisticated technologies, namely amplicon sequencing, had been employed for taxonomic classification of bacterial communities within ecosystems (Sanschagrin and Yergeau 2014). Moreover, the large dataset obtained by 16SrRNA gene sequencing provided details about the presence of microbial species but no insight into the function (Fierer et al. 2012). To address this concern, metagenomics approaches were employed to decipher the diversity and functional mechanisms of microbial communities (Zhou et al. 2015). The bioinformatics resources namely Functionalize R (Kristiansson et al. 2009), MG-RAST (Glass and Meyer 2011), Galaxy portal (Goecks et al. 2010) and others are available to analyze and interpret the biological data. A key area in this direction defines exploring the molecular basis of plant–microbe interactions, in order to promote the functioning of plant and thereby respective ecosystem.

1.10 Conclusion and Future Prospects

Soil microbes constituting the “soil microbiome” are the key soil components of soil, which provide nutrients to the plants and protection against pests. Soil microbiome constitutes a determining factor of ecosystem health, and there has been increasing momentum in deciphering the functional dynamics of soil microbiome as a component of ecosystem and climate change. Studies have shown the emerging importance of soil microbial communities in plant associations and as plant pathogens, having a major impact on the ecosystems. However, high-throughput technologies and omics approaches are required for gaining insights into the microbial pathways and their functional mechanism. Moreover, next-generation sequencing and metagenomics are promising areas employed to monitor climate changes. In the present era, with the global population increase and climate changes, it is necessary to adopt scientific methods to boost sustainable agriculture. These scientific methods to study soil microbial communities would aim at delineating information about microbial communities sensitive to climate changes and its influence on microbial community and its function. Such studies exhibit significant prospects in the maintenance of soil health and a productive ecosystem. Attempts towards understanding the dynamics of soil microbiomes and adopting scientific approaches towards maintaining and improving soil microbiomes and their beneficial functions would be the prospective approaches towards sustainable agriculture.

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Chapter 2
Microbes Associated with Crops: Functional Attributes for Crop Productivity

Slimane Mokrani and El-hafid Nabti

Abstract Microorganisms associated with plants can affect their health positively or negatively, thus influencing hugely crop yield and productivity. Several investigations have reported that the microbes associated with different plants are much diversified. Especially, those microorganisms of agricultural interest belong mainly to bacteria and fungi. Additionally, they are various mechanisms of plant/microorganisms interaction, which are already elucidated and well documented, bringing together two principal categories; by one side, the implication of germs in biotic and abiotic stress reactions; by the other side, the all aspects related to plant responses. This work aimed to expose some aspects of the microbe's associates to plants and the functional attributes for ameliorating crop productivity and yields.

Keywords Crop productivity · Mechanisms · PGP traits · Plant microbiome

2.1 Introduction

The industrial revolution of farming in the twentieth century has drastically transformed and accelerated the market and agricultural activities; in order to raise crops and feed the planet's increasing population (Zorner et al. 2018). In addition, modern agriculture faces several problems, including environmental issues, and an increase in supply for durable manufacturing (Compant et al. 2019; Sharma et al. 2021). In particular, eco-friendly and durable farming techniques are vital for ensuring food safety, like the use of effective farm-benefit microorganisms (bioinoculants) that play potential roles in sustainable crop manufacturing due to their vast characteristics for plant increase, improving adaptability and viability under stressful conditions; and

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other important utilizations that can efficiently reduce the use of pesticides and fertilizers in modern farming (Singh et al. 2016; Kumar et al. 2021). These microbes ensure a crucial function in various farm ecosystems (Deveau et al. 2018; Prasad et al. 2021). Since ancestor plant lines colonized the land 450 million years ago, plants and their microorganisms interacting there formed an association of organisms often designed as a “holobiont.” (Hassani et al. 2018). Particularly in the last years, intensive efforts have been dedicated to elucidate the interaction between plants and bacteria, both beneficial and pathogenic (Degrassi et al. 2012).

Colonization is arduous for microbial populations in their niches, particularly because of their huge diversity, dynamic interactions, constant genetic interchange and deficiency of adequate analytical techniques (Singh et al. 2010). Equally, the microbes associated with plants include algae, bacteria, fungi and viruses. Depending upon their localization on the host plant, they can be endophytic and/or epiphytic. Endophytic microbial interrelationships affect the inner part (Rana et al. 2020a; Singh et al. 2020), whereas epiphytic microbial interrelationships affect the outer surface of plants (Kumar et al. 2017). Notably, in the last decade, diverse studies have indicated the complicated microbial accumulations related to various plants, and particular plant compartments (Reinhold-Hurek 2015). Moreover, several researches reported the benefits of rhizobacteria and endophytic bacteria belonging to the specific phylogenetic group on the biological characteristics of different vegetable crops (Vansuyt et al. 2007). Generally, epiphytic, endophyte or rhizophyte interrelations can be harmful or beneficial to both the microbe or the plant and may be considered competition, amensal, synergism, commensal, mutual, parasitism or neutral (Montesinos 2003; Yadav 2021).

2.2 Microbes Linked with Crops

2.2.1 Rhizospheric Microbiomes

Rhizosphere is the region in which the roots and related microbes engage in diverse interactions and is characterized by wide microbial diversity (Patra et al. 2016). The exudation of roots comprises of a mixture of compounds such as sugars, organic acids, amino acids and vitamins, which attracts a diverse microbial population (Bertin et al. 2003; Kour et al. 2019b). Proteobacteria, especially those of tα and β groups, tend to dominate. Acidbacteria, Verrucomicrobia, Actinobacteria, Bacteroidetes, Firmicutes and Planctomycetes are among the other principal groups (Turner et al. 2013). Particularly, root and rhizosphere microbial communities are named plant growth-promoting rhizobacteria (PGPR) play key functions in determining plant health and productivity (Verbon and Liberman 2016; Hesham et al. 2021).

2.2.2 Epiphytic Microbiomes

Plant aerial parts are the habitat of several epiphytic microorganisms, which could be noxious or useful to the plant (Sharma et al. 2019). Epiphytic microbes live on fruit, flowers, leaves, buds and stems (Whipps et al. 2008; Mukhtar et al. 2010). Apparently, microbial interrelations in the phyllosphere may influence soil health in native populations, crop yield production and the security of human-consuming horticultural products (Whipps et al. 2008). This analysis points toward the soil and air as important sources of leaf and root microbial inoculums (Kumar et al. 2019a, 2019b).

The action of insects, wind and rain could allow microorganisms to reach the surface or to leave the plant surface. This analyzes the air and soil as key root and leaf microbial inoculum provenances (Lilley et al. 1997). The complexity, role and relation to the microbiota of the rhizosphere are also emerging research areas (Bai et al. 2015). The content and richness of bacterial communities are specific to host, memberships of the alphaproteobacteria predominate and are widely spread in phyllosphere microbiotas, and the genera *Methylobacterium* and *Sphingomonas* are frequently observed among various hosts (Delmotte et al. 2009).

2.2.3 Endophytic Microbiomes

Endophytes comprise all species occupying plant organs that could populate interior plant tissues at any stage of their life without doing any obvious damage to the host (Petrini 1991; Rana et al. 2020b). Endophytes are ecologically ubiquitous and diversified in the majority of plant species and perform various fundamental functions in nature for plant productiveness, mainly by metabolism and enhancement of nutrient assimilation, synthesizing plant development hormones, controlling the host's defensive gene expression and other elementary metabolic processes (Zhou et al. 2017).

In particular, plant-associated endophytes, including endophytic fungi, are widely distributed in nature (Jia et al. 2016). Also, endophytic bacteria–plant relationships have been widely studied for their various roles, mainly in the improvement of plant increase, biocontrol, phytopathogenicity, resistance toward stressful factors and bioremediation (Fester et al. 2014; Yadav et al. 2021b). Figure 2.1 shows the microbes associated with crop ecology.

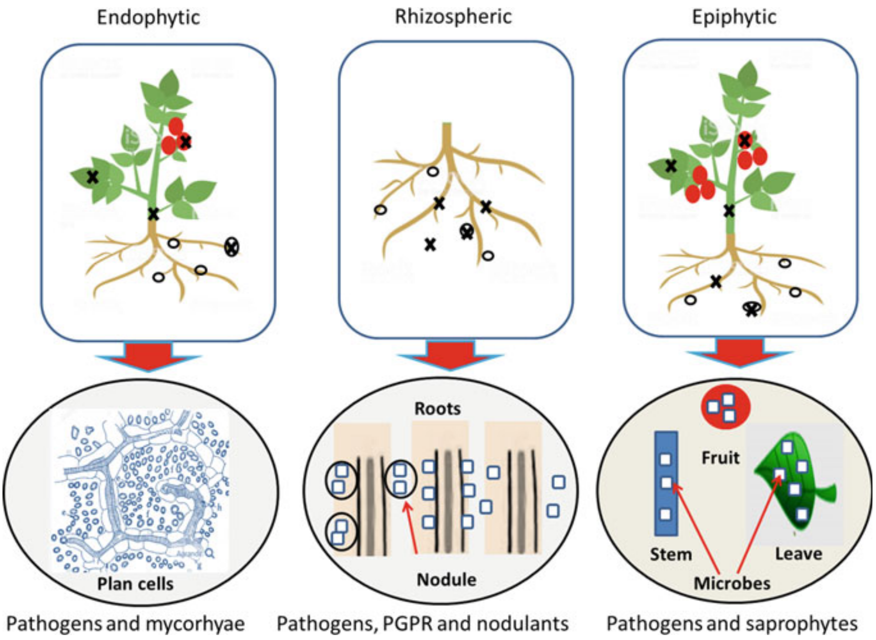

Fig. 2.1 Microbes associated with crops ecology. Free-living microbes are holobionts in plants: in rhizosphere as well as in phyllosphere like epiphytic and endophytic in the whole plant. In addition, they have important ecological roles evolved by living in pathogens, PGPR or saprophytes. Most such microbes–host interactions are beneficial, adversely to others which are harmful, inducing an increase or loss of crops yield and productivity

2.3 Mechanisms of Increasing Crop Productivity and Yield

Among the benefits of plant-useful microorganisms, different mechanisms can be listed like plant increase improvement, synthesizing various antibiotic/antifungal molecules inhibiting several phytopathogens, resistance to numerous environmental stress factors and microorganism-assisted elimination of organopollutants (Wu et al. 2009). Furthermore, soil microbial populations are essential for several of the earth's biogeochemical cycles like mineralization of nutritional compounds, organic carbon decomposition and nitrogen cycle (Patra et al. 2016). Notably, a number of soil microbial mechanisms convert unavailable nutritional elements to be easily assimilated by plants (Lalitha 2017). Endophytes and epiphytes have no negative impacts on the plant; instead, they cause the production of certain essential chemicals like hormones (Kumar et al. 2017). Additionally, some other microbes can synthesize auxin, which improves growth and ensures a crucial function in plant life cycle (Fernandes et al. 2011). Globally, inside rhizosphere PGPR assist the indirect and direct increase of plants through various mechanisms. They participate in nutrient uptake, nitrogen fixation, phosphate solubility, siderophores formation, IAA and other diverse phytohormones (Pahari et al. 2016; Rai et al. 2020; Subrahmanyam

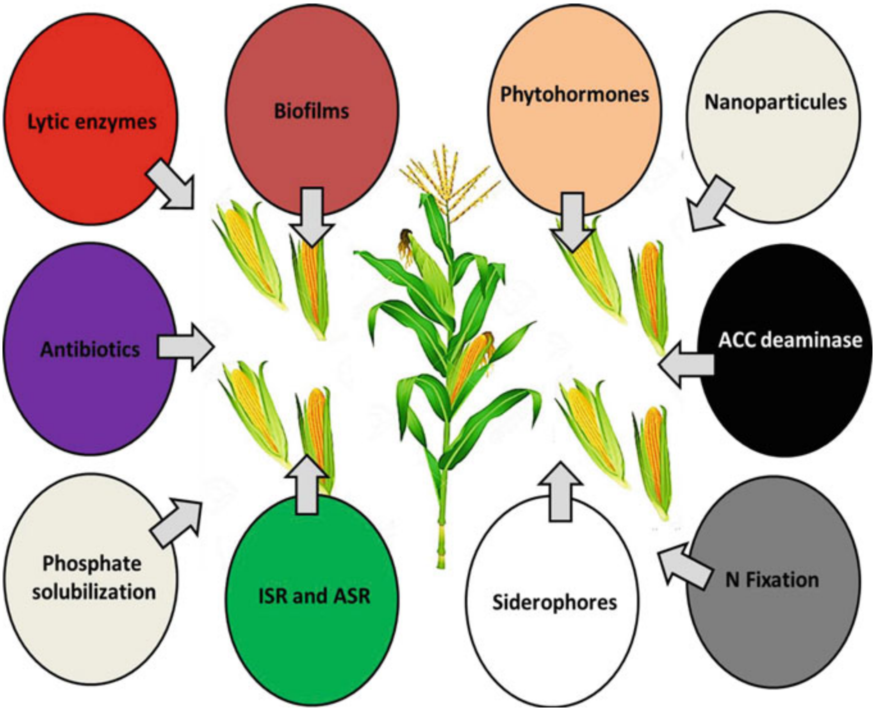

Fig. 2.2 Mechanisms developed by plant-associated microbes for protecting and increasing crop productivity and yields. (ISR: Induced Systemic Resistance; ASR: Acquired Systemic Resistance)

et al. 2020; Abdel-Azeem et al. 2021). Figure 2.2 illustrates the mechanisms developed by plant-associated microbes for protecting and increasing crop productivity and yields.

2.3.1 Phosphate Solubilization

It is well established that plants need at least 14 mineral elements for sufficient nutrition, in addition to water, carbon dioxide and oxygen (Mengel et al. 2001). Insufficiency of any of these mineral elements decreases plant growth and crop yields (El-Ramady et al. 2014). In particular, microbes of various genera are capable of transforming insoluble phosphate into soluble compounds, which are then available to plants, and are generally known as phosphorus solubilizing microbes or PSMs (Shrivastava et al. 2018; Kour et al. 2020, 2021). Phosphorus-solubilizing bacteria ensure a function in phosphate nutrition via increasing its accessibility to plants, releasing phosphate pools from organic and inorganic soil and solubilizing and mineralizing mechanisms (Khan et al. 2009). Enhanced crop productivities arise from PSM solubilization of fixed soil P and applied phosphates (Zaidi 1999). They also improve soil fertility and crop productivity in organic farming (Kaur and Reddy 2014).

2.3.2 Siderophores

Iron is a crucial plant nutritional element that operates as a cofactor in various enzymes of the respiratory system, photosynthetic activity and nitrogen fixation. Although iron is quite prevalent in soil, it is often inaccessible to microbes and plants because it arises under aerobic environment primarily as a trivalent state iron Fe(III) (Bano and Ilyas 2012). Iron deficiency can adversely impact plant, beneficial and phytopathogenic microorganisms. For instance, the microbial surface hydrophobicity significantly reduces under iron-deficient growth conditions that also distort the surface protein constitution (Simões et al. 2007). On the other hand, siderophores are secondary metabolites with low molecular weight and an iron-chelating capability (Kour et al. 2019c; Sharaff et al. 2020). These are substances characterized by small peptide molecules with laterally chains and operational groups that have a ligand with great affinity that binds ferrous ions into the cellular membrane (Niehus et al. 2017). Nearly, all microbes develop them in reaction to an iron insufficiency (Crowley 2006). Siderophore production is controlled by well-established bacterial and fungal transcriptional factors (Troxell and Hassan 2013); in particular, the bacteria generating siderophores are frequently isolated from the rhizospheric plant area (Calvente et al. 2001). Plants may also produce Fe(III)-chelating molecules designed phytosiderophores forming unique and solid Fe(III) structures (Ma 2005; Kraemer et al. 2006).

A number of investigations explain the function of siderophores as an important component in ISR protection effects (Vleesschauwer and Hofte 2009). Mahmoud and Abd-Alla (2001) mentioned that hydroxymate, a kind of siderophore produced by *Pseudomonas* sp., which stimulated the formation of nodules and fixation of nitrogen by mung bean seedlings as compared to sowing infested with *Bradyrhizobium* sp. strain solely. Furthermore, bacteria-forming siderophores play a major function in the suppression of some phytopathogenic microorganisms (Beneduzi et al. 2012).

2.3.3 Phytohormones

Ethylene, cytokinins, abscisic acid, gibberellins and auxins are widespread among various regulating factors of growing plants and are well known for their acting processes (Kashyap et al. 2017; Suyal et al. 2021). In this case, microorganisms interacting with plants generate main plant growth hormones such as auxins and gibberellins. Generation of gibberellins is the most usual for the development of root-associated microorganisms and auxin is widespread into whole plant-related microbes (Yadav et al. 2017; Tiwari et al. 2020). Especially, the great effective and typical auxin in plants is indole 3-acetic acid (IAA) (Kashyap et al. 2017). Patten and Glick (1996) mentioned the synthesis and secretion of auxin as elementary molecule of around 80% of rhizosphere microorganisms. Notably, auxins are important in phototropism and geotropism, differentiation of the vascular tissue, apical dominance, lateral and adventitious root initiation, cellular division, extension of root and stem (Grobelak et al. 2015; Rastegari et al. 2020a, 2020b).

2.3.4 N_2 Fixation

Nitrogen is an important element responded in different ecosystems. For instance, inorganic nitrogen in the marine ecosystem ranges from nitrate to ammonia in various oxidation forms (Ravikumar and Kathiresan 2007). Moreover, nitrogen is among the most essential nutrients affecting the production of crops. Especially, leguminous in combination with rhizobia provide an invaluable function, in the natural and agricultural environments, to the global nitrogen balance (Vance 2001; Rana et al. 2019). It has been estimated that the price of utilizing N-fixing microorganisms is 1% more than the price of utilizing chemical products (Stokstad 2016).

2.3.5 ISR and ASR

Most plants respond to a local attack by herbivores or pathogenic microorganisms through the formation of compounds aiming to mitigate or prevent further attacks, or the effectiveness of their enemies. The reactions occur in either the initially attacked plant organ (local reaction) or remote but not damaged sections (systemic reactions). One of these reactions is the induced systemic resistance (ISR), and the other is systemic acquired resistance (SAR) forming together the plant defensive system against plant pathogens (Heil and Bostock 2002). Furthermore, a number of PGPR induce transformations related to chemical or physical protection system in the plant (Van Loon et al. 1998). Nevertheless, combined ISR and SAR present greater protection than any of them alone, suggesting that they might act synergistically to promote pathogen tolerance (Van Wees et al. 2000).

2.3.6 ACC Deaminase

This enzyme metabolizes ACC (1-aminocycle-1-carboxylate) in plant tissues, which is the initial precursor to ethylene (Yang and Hoffman 1984; (Kour et al. 2019a). Moreover, ethylene, usually, is involved in crucial plant processes like differentiation of tissues, shoot and root formation primordia, root ramification and extension, the implementation of the lateral bud, floration, flora senescence, fruit maturation and abscission, formation of anthocyanin, the elaboration of volatile organic substances responsible for the fruits aroma production (Glick 2014). Moreover, for the germination of seed, ethylene is necessary, as it is established by its rate of production rising considerably during germination and planting growing (Abeles et al. 1992). Additionally, ACC deaminase is a plant hormone that is largely stimulated by stress factors and can limit considerably the activity of increasing plants (Dikilitas et al. 2021). On the other hand, a number of microorganisms could reduce the plant's rate of ethylene by assimilating the ACC, the main plant's produced ethylene precursor (Ajar et al. 2017). ACC deaminase-producing microbes convert ACC into ammonia and α-ketobutyrate (Glick 2005). In particular, plant growth-promoting rhizobacteria endowed with ACC deaminase properties stimulate plant development and productivity and can be effectively enclosed in bioengineering of biofertilizers (Shaharoona et al. 2006). The root-interacting bacteria decrease the rate of ethylene by ACC cleavage ultimately plant stress tolerance (Van de Poel and Van Der Straeten 2014). Importantly, it has been reported that the use of bacteria-producing ACC deaminase against a variety of biotic and abiotic factors improved plant resistance against different stressful factors (Glick 2014; Yadav et al. 2020a, 2020b, 2021a).

2.3.7 Lytic Enzymes

Several plant growth-promoting bacteria secrete various lytic enzymes like lipase, protease, chitinase or β 1,3 glucanase, all of which contribute to cellular fungal degradation (Chet and Inbar 1994). Thus, these enzymes affect the growth and development of phytopathogenic fungi (El-Tarabily 2006). PGPB have been reported to have biocontrol effect toward a number of phyopathogenic fungi like *Pythium ultimum*, *Rhizoctonia solani*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Botrytis cinerea* and *Phytophta* spp. by synthesis of one or more lytic enzymes (Frankowski et al. 2001; Singh et al. 1999). Whereas, other particular enzymes of plant-associated microbes like cutinases were identified as necessary for spore fixation on the surface of many phytopathogens such as *Blumeria graminis, Colletotrichum graminicola* and *Uromyces viciae-fabae* (Deising et al. 1992; Pascholati et al. 1993). Generally, such activities of the diverse hydrolase enzymes are very important in rhizosphere soil, as they reflect soil capability to ensure complex biochemical processes, the fertility of the soil and plant productiveness conservation (Burns 1982; Shukla and Varma 2011; Schloter et al. 2018). Microbial enzymes are important for soil operation and quality because of their implication in organic matter dynamics and nutrient cycles, organic compound degradation, mineralization and the release of nutritional elements including nitrogen, carbon and other important metals (Khare and Yadav 2017; Yadav et al. 2020c).

2.3.8 Nanoparticles

Nanomaterials and nanoparticles are generally described as molecules of approximately 1–100 nm measurements that demonstrate characteristics not observed in the bulk state (Bulgari et al. 2019; Patil et al. 2021). They are incorporated into the ground through a range of human practices, which include deliberate land releases via water and soil treatment, the extensive utilization of farming (e.g. chemical fertilization) and unconscious water, air and wastewater disposal onto the soil (Mishra and Kumar 2009); or are produced biologically in situ in the soil by microorganisms (bacteria and fungi) in contact with contaminants such as silver. This is of particular concern for soil benefit microbes since AgNPs act as antimicrobials by inhibiting enzymatic activity, damaging DNAand generating reactive oxygen species that lead to cell death (Li et al. 2010). Several microbial suppressive impacts of nanoparticles have been observed impacting directly microbe's survival (Lovern and Klaper 2006). Generally, antiphytopathogenic activity, seed germination enhancement and improving crop development were reported using zinc oxide and silver nanoparticles (Gogos et al. 2012).

2.3.9 Biofilms

Historically, microbes had been explored as planktonic cells (or free swimmings). The majority of these cells has been established in multi-cell joint to surfaces, called biofilms (Rudrappa et al. 2008). According to Costerton et al (1999), a biofilm is described as "a structural community of bacterial cells enclosed in a self-produced polymeric matrix and adherent to an inert or living surface. On plant surfaces, they are formed mostly by bacteria in pathogenic, mutualistic, or symbiotic association on leaves, roots, and in the soil (Cavalcante et al. 2017). It is a property in plant growth-promoting bacteria that enable them to resist various abiotic stresses (Bouskill et al., 2016). Especially, biofilm formation on plant roots appears to be associated with symbiotic interactions. For instance, these structures help to create protective niches for Rhizobia (Barriuso, 2017). Recently, it has been shown that biofilm-mediated microcolonies formed on root hairs of finger millet by endophytic *Enterobacter* sp. conferred protection against colonization by the pathogenic organisms (Mousa et al. 2016). Apart from the root surface, microbial biofilms are also reported on the phyllospheric region and vasculature (Torres et al. 2006). Epiphytic microbes are often formed in biofilms, likely because these microenvironments protect bacteria from harsh environmental conditions (Monier and Lindow 2004). Furthermore, certain bacteria in biofilm matrices have been found to stimulate plant growth and protect plants from phytopathogens while others are involved in pathogenesis (Bogino et al. 2013).

2.3.10 Antibiotics

Antibiotics produced by microorganisms play a major role in plant pathogens and the diseases they cause (Pal and McSpaddenGardener 2006). The production of antibiotics is one of the important mechanisms most commonly associated with the capability of PGPB to act as antagonistic agents (Glick et al. 2007; Abdel-Azeem et al. 2021). Furthermore, the production of antibiotics is used in the acquisition of genes coding for antibiotic resistance from transgenic plants by plant-associated bacteria (Montesinos 2003). Amongst PGPR, species belonging to *Pseudomonas* excrete a great variety of effective antibiotics such as 2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin, pyrrolnitrin, (Raaijmakers et al. 2002; (Singh and Yadav 2020; Yadav et al. 2020c). In addition, some species can also produce hydrogen cyanide (HCN) that is toxic to certain pathogenic fungi (Dowling and O'Gara 1994).

In soil, several metabolites from endophytic *Streptomyces* sp. have been characterized, which are associated with antibiotic activity (Castillo et al. 2003; Guan et al. 2005). Furthermore, endophytic fungus, *Acremonium zeae*, has been implicated in the protection of its host against *Aspergillus flavus* and *Fusarium verticillioides* (Wicklow et al. 2005).

2.4 Beneficial Effects on Crop Production and Yield

Plant-associated microbiomes play a pivotal role in plant biology, performing key functions in germination, growth, health and stress protection (Mendes and Raaijmakers 2015; Tiwari et al. 2021). An increasing number of studies have shown that plant-associated microbes improve plants' nutritional conditions, resistance to abiotic stresses and inhibit pathogens and pests (Vandenkoornhuyse et al. 2015). Importantly, rhizospheric microbes affect plant growth, development and stress resistance by diverse mechanisms (Lareen et al. 2016; Rai et al. 2020). Beneficial effects of some plant-associated microbes on crop productivity and yields have been listed in Table 2.1.

2.4.1 Seed Germination Enhancement

Seed germination is an important stage in the life cycle of plants (Song et al. 2005). In particular, seed-associated microorganisms can be essential for the germination process in different plant phyla (Jacquemyn et al. 2015). Effectively, PGPB can accelerate seed germination and improve seedling emergence (Souza et al. 2015). This is illustrated by seed treatment of legumes with Rhizobaceae that frequently leads to increase in yield (Thilakarathna and Raizada 2017). In addition, the application of beneficial microorganisms to seeds is an efficient mechanism for the placement

Table 2.1 Beneficial effects of plant-associated microbes on some crop productivity and yields

Associated microbes	Crops	Effects	References
Pseudomonas spp.	Soybean and wheat	Increased straw and grain yields; increased nutrient uptake: N, P, K, Zn and Fe	(Sharma et al. 2011)
Pseudomonas fluorescens	Rice	In field experiments, the occurrence of sheath blight and leaf folder insect incidence decreased by average 62.1% and 47.7–56.1%, respectively	(Commare et al. 2002)
Serratia marcescens strain SRM	Wheat	Significantly influence wheat seedling growth at cold temperatures	(Selvakumar et al. 2008)
Bacillus thuringiensis	Maize	Increase seed germination percentage up (94%), seedling growth to (36.08 cm/seedling) and vigor index (3391.52)	(Kassogué et al. 2016)
Bacillus subtilis	Tomato	Reduce substantially seedling mortality in inoculated plants, it (6.6%) is compared to high mortality in the control seedlings (51.6%)	(Cabra Cendales et al. 2017)
Azospirillum brasilense	Wheat and oat	Yield increase up to 27% in wheat and to 6% in oat	(Swędrzyńska 2000)
Streptomyces sp. KLBMP 5084	Wheat	Increase in germination rate, concentration of N, P, Fe and Mn, shoots grown under salinity stress	(Sadeghi et al. 2012)
Trichodermaatroviridae	Indian mustard	Bioremediation by influencing uptake and translocation of Ni, Zn and Cd	(Cao et al. 2008)

of microbial inoculum to soil and protection against soil-borne diseases and pests (O’Callaghan 2016).

The enhancement mechanism of seed germination is ensured via the production of different PGP traits. Seed treatment of cowpea with *Bacillus* sp. exhibiting multiple PGP attributes improved seed germination and yield parameters (Minaxi et al. 2012). Paul et al. (2011) reported IAA-producing bacterium *Azotobacter chroomcoccum*, particularly when co-inoculated with arbuscular mycorrhizal fungi improve seed germination.

2.4.2 Stimulation of Plant Growth

The positive response of different crops to microbial inoculation has been assessed in many experiments under greenhouse and field conditions (Calvo et al. 2014). It has been reported that specific guilds of taxa among the soil bacterial microbiome can be selected to modify plant traits and to coordinate changes in soil resource pools (Pfeiffer et al. 2017). Notably, plant growth-promoting rhizobacteria are beneficial microorganisms that help in promoting plant growth and significantly increase soil fertility (Kashyap et al. 2017). Some microorganisms when given the opportunity to inhabit plant roots become root symbionts. Such root colonization by symbiotic microbes can enhance crop yields by promoting the growth, nutrient uptake, fixation, resistance to pests, diseases and abiotic environmental stress conditions stresses (Harman and Uphoff 2019; Yadav et al. 2018).

2.5 Resistance to Abiotic Stress

Abiotic stress in soils includes extreme temperatures, pH, drought, water-logging and toxic metals (Wu 2017), salinity (Shrivastava and Kumar 2015) and some gases and nutrient deficiency or excess (Hayat et al. 2017). They are greatly affecting plant growth and agricultural productivity and cause more than 50% of worldwide yield loss of major crops every year (Jarvis et al. 2006; Kumari et al. 2019). These conditions often favor pathogens and negatively affect plant productivity and soil fertility (Dresselhaus and Hückelhoven 2018). Particularly, drought has affected 64% of the worldwide land area, salinity 6%, anoxia 13%, soil alkalinity 15%, mineral starvation 9% and cold 57% (Mittler 2006). For example, drought stress limits the growth and productivity of crops particularly in arid and semi-arid areas (Kramer and Boyer 1995).

Plant-associated microbiomes have a much greater evolutionary potential for dealing with abiotic stresses than the plant itself (Jones et al. 2019). Therefore, it is potentially more sustainable to manage abiotic stresses in a holistic and multifaceted manner. The microorganisms use indirect and direct mechanisms to promote plant growth and development during stress conditions (Kumar and Verma 2018). Some bacteria have sigma factors to change gene expression under adverse conditions to overcome negative effects (Gupta et al. 2013). Notably, microorganism communications with the plants incite a few fundamental responses that improve their metabolic mechanism for defense against abiotic stress conditions (Nguyen et al. 2016).

2.5.1 Bioremediation

Environmental pollution resulting from human activities has a great impact on the biodiversity and functioning of terrestrial and aquatic ecosystems and is a major threat to human health across the globe (Alava et al. 2017). Extensive pollution of terrestrial ecosystems with petroleum hydrocarbons (PHCs) has generated a need for hazardous and expensive physico-chemical remediation techniques. Alternatively, plant-associated bacteria and cooperation between these bacteria and their host plants allow for greater plant survivability and treatment outcomes in contaminated sites (Gkorezis et al. 2016). Such ecological microorganisms are expected to have multiple implications for maintaining pollutant decomposition and ecological services in terrestrial environments (Shi et al. 2018). Filamentous fungi including *Aspergillus* sp., *Mucor* sp., *Penicillium* sp. and *Trichoderma* sp. have been reported to possess capability to tolerate heavy metal stress (Ezzouhri et al. 2009; Oladipo et al. 2017). Mycorrhizal fungi, free-living or endophytic fungi are also known for their strong degradative capacities and are often applied during phytoremediation of organic pollutants (Deng and Cao 2017).

The basic principle of bioremediation involves reducing the solubility of environmental contaminants by changing pH, the redox reactions and adsorption of contaminants from the polluted environment (Jain and Arnepalli 2019). Especially, the in situ bioremediation processes have become an attractive way to rehabilitate various contaminated sites (Ayoub et al. 2010). More particular, phytoremediation is using plants and associated bacteria for the treatment of soil contaminated by toxic pollutants (Salt et al. 1998). Concerning plant-associated microbes, such as rhizospheric bacteria, implicated in “Rhizomediation”, it has been demonstrated that they lead to the decomposition of polluted soil by harmful organic elements and may enhance phytoremediation (Babalola 2010). These microbes’ capacity to cleave contaminants depends on the effectiveness of their development and various metabolic surrounding conditions, including appropriate pH, temperature and humidity (Verma and Jaiswal 2016).

2.5.2 Plant Disease and Pest Control

Plant infections typically happen in regions, forests or fields when different plant components (like leaves, fruits or flowers) are attacked (Sastry and Zitter 2014). They are principally treated mainly by chemical pesticides. Plant-related microorganisms may also serve as biological control agents due to their protective effect based likely on the synthesis of effective inhibiting enzymes and substances like hydrolases and antibiotics destruct the phytopathogenic cell wall (Kumar et al. 2017). Genera, including Gram-positive and Gram-negative bacteria such as *Burkholderia*, *Pantoes*, *Bacillus*, *Enterobacter*, *Paenibacillus*, *Streptomyces* and *Pseudomonas* were, in particular, mentioned for their involvement in pathogen suppression (Schlatter et al. 2017). Additionally, certain native plant epiphytic microorganisms could be employed in the suppression of agri-foodstuff phytopathogens (Lopez-Velasco et al. 2012), and at a less degree of endophytic bacteria.

2.6 Factors Affecting Crop Productivity and Yield

Crop productivity and yield can be influenced by many organisms as a community contributes efficient genome and chemical exchange to create a competitive metagenome, contributing to improved plants' production and to strengthen relationships with each other (Zorner et al. 2018). The nature and the quality of plant and microorganism interaction and soil microbial diversity can affect largely crop productivity and yields. Several experiments have also shown the direct effect of various plant species on the selection of rhizosphere populations (Marschner et al. 2004; Coleman-Derr et al. 2015). Nevertheless, other considerations are included like developmental stage or variety (Qiao et al. 2017) that may additionally affect their microbiome contents. In addition, microbiome balance and abiotic indicators can contribute to crop productivity and yield determination including soil structure, stability in wet aggregate, water supply potential, rigidity of the soil, pH, capability for nutritional element and cation exchange (Jeanne et al. 2019). Furthermore, crop productivity and yield are affected by environmental impacts of unhealthy soil via microbial activities that could not sequester carbon but cause emissions of methane, CO_2 and other greenhouse gases that harm ecosystems in turn. For example, the increased global temperature has led adversely to high greenhouse gasses (Saha and Mandal 2009). Similarly, soil microbial communities are impacted by meteorology (Terrat et al. 2017). Figure 2.3 illustrates the factors affecting crop productivity and yield including: Environmental factors, biotic and abiotic stresses and plants (species, genotype and stage development).

2.7 Conclusion and Future Prospects

The microbes associated with plants are much diversified and can eventually occupy all the plant parts during their all-development cycle; from seeds to maturation. These microbes can be both beneficial and harmful, leading to a loss of crop yields or countless beneficial effects for development and protection against various biotic and abiotic stresses, undoubtedly leading to an effective increase in crop productivity and yields. Furthermore, the variability and complexity of the interaction mechanisms between microbes, plants and soil always require more investigations; especially with regard to the overlap and simultaneous effects of interaction mechanisms such as the association of abiotic and biotic stress impacts on both plants and microorganisms, as well as the different strategies developed by each partnership in these specific and complex interactions.

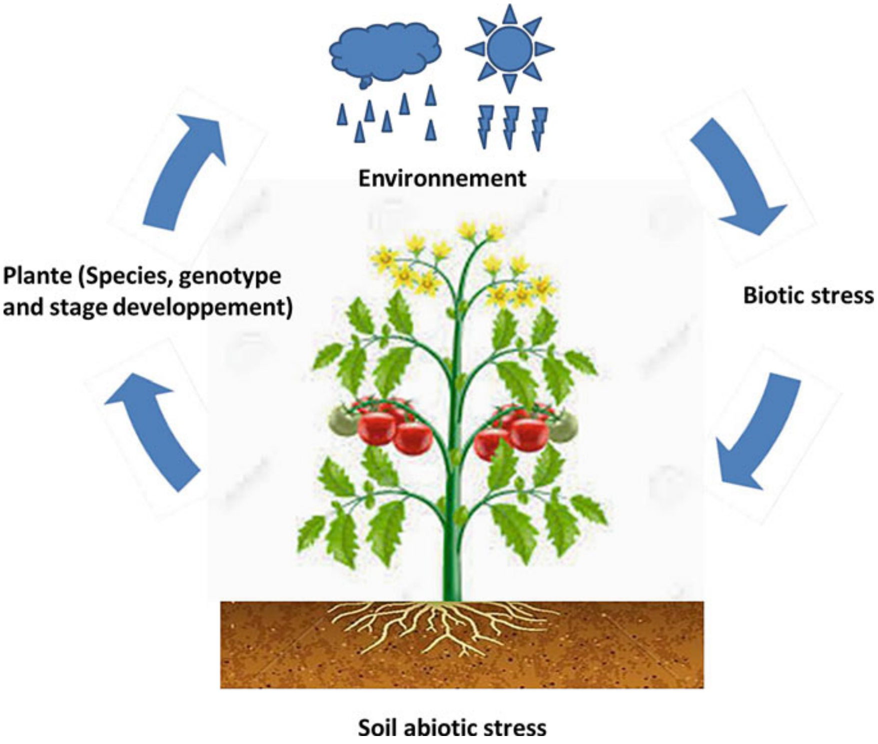

Fig. 2.3 Factors affecting crop productivity and yields

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Chapter 3
Soil Microbes with Multifarious Plant Growth Promoting Attributes for Enhanced Production of Food Crops

Yasaman Kiani Boroujeni, Vahid Nikoubin Boroujeni, Ali Asghar Rastegari, Neelam Yadav, and Ajar Nath Yadav

Abstract Fertility is the simplest yet most sophisticated word to describe a well-cultivated soil. Simply because it can, in general, make the most of the product available to everyone and complex because many aspects of its sustainable management are still unknown, even to experts in the field of soil science. In fact, fertility is a reflection of the intrinsic complexity of the plant's soil ecosystem, because of one of the characteristics of the various components of this vital system, as well as the numerous interactions between them. These components are affected and, as a result, they provide the sum of their effects in the capacity to support plant growth and crop production. Therefore, maintaining this capability at optimum crop production level requires steady, comprehensive management, and is aware of all the physical, chemical, and biological aspects that affect not only the quantity of production but also the quality and health of the soil and environmental resources. Microbial fertilizers and soil microorganisms play an important role in controlling plant diseases, eliminating plant pests, and converting part of the minerals to a usable form for plants. Chemical fertilizers are essential components of biocontrol and plant growth factors. The use of plant food-producing bacteria and the application of proper soil fertility and plant nutrition in addition to protecting the environment and human health also avoid the unnecessary and wasteful use of chemical fertilizers.

Keywords Biofertilizers · PGPR · Plant growth promoting attributes · Microorganisms · Soil

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3.1 Introduction

Microorganisms or microbes are the microbial organisms that are possible in the form of a single cell or a colony of the cells that would have existed. Recognition of beneficial soil microorganisms and their interactions with other microorganisms, plants, and soils are among the main topics of soil microbiology. Microorganisms play a key role in the decomposition of organic matter, elemental cycles, and other soil chemical changes (Kaur et al. 2019). In fact, the general measurements of soil microbial activity are synonymous with organic matter degradation. The decomposition of organic matter is usually controlled by heterotrophic microorganisms and leads to the release of elements (especially nitrogen (N), sulfur (S), and phosphorus (P)). Microorganisms also stabilize amounts of carbon and other elements in their cells. Therefore, all living microorganisms (microbial biomass) play a pivotal role as a source, reservoir, and regulator. They have changed the energy and nutrients of the soil. The remarkable diversity of microbial species and their ability to break a wide range of chemical bonds means that these organisms are responsible for many of the key soil functions in which areas (i) decomposition, organic matter available in soil matter, and plant or animal debris that releases nutrients (ii) changing chemicals from one form to another often leads to the formation of absorbent and active substances for the plant and prevents chemical wastes and (iii) the production of antibiotics that can help deter soil-borne diseases (Wardle 1992).

Synthetic biology in the last two decades and higher potential microorganisms for genetic engineering in the direction to increase their efficiency leading to dramatic changes in the has been created by microorganism's recombinant with industrial and medical purposes worldwide and have been used commercially in the manufacture of various products (Keasling 2012; Sarantinopoulos 2014). Recombinant microorganisms contain new genes that give them useful properties with greater efficiency for agricultural purposes. Including applications recombinant microorganisms in agriculture can produce high performance, recombinant microorganisms to control pests and diseases as well as create high-efficiency biofertilizers to produce various enzymes used in agriculture (Olson et al. 2012; Adrio and Demain 2014; Kumar et al. 2021; Singh and Yadav 2020). Production of recombinant antibiotics and drugs, biological receptors to detect soil and water pollution (Belkin 2003), bioremediation, and reduction of pollutants such as heavy metal treatment soil pointed (Kapoor and Rajagopal 2011; Sharma et al. 2021). Regarding increasing the performance of microbial agent's plant growth-stimulator (Biofertilizers) through genetic engineering also numerous studies it has happened over the past few years. For example, corn to nitrogen stabilizing recombinant bacteria (Rhizobium) with the bio-refining ability of soil heavy metals (Ike et al. 2007), *Anabaena* sp. with the growth-stimulating ability and higher nitrogen fixation (Chaurasia and Apte 2011) and *Azospirillum* with high auxin production capacity and indicated higher growth stimuli (Baudoin et al. 2010).

3.2 Soil

Soil is a very complex and heterogeneous ecosystem with high microbial diversity. Less than one percent of soil microorganisms is currently cultivable and identified in vitro (Whipps 2001). On the one hand, these organisms interact with other parts of the soil and, on the other hand, affect each other at different biological levels (Müller et al. 2002). Since ancient times, human beings inevitably seek to improve and expand agricultural crops by using different cultivation methods. Without considering the invisible microorganisms that play an important role in providing the materials needed for plant growth and development suppose, for example, that the clover was planted intermittently to enrich their fields without knowing the role of nitrogen-fixing microorganisms. Today, environmental microbiologists are well aware that many microorganisms play an important role in improving and expanding agricultural products, these include bacteria, *Actinomycetes*, fungi, algae, protozoa, viruses, and nematodes. Of which the role of bacteria is more prominent. Soil is a major source of nutrients for crops and supports plant growth in many ways. Understanding soil health and maintaining it is crucial to productivity. Soil health can be assessed through the quality and crops grown on it. This assessment is possible by farmers through physical, chemical, and biological analysis of soils. Plant nutrients such as Mg, Ca, K, P, N, and S are called nutrients while Fe, Zn, Cu, Mo, Mn, Br, and Cl are called micronutrients (Motsara and Roy 2008; Kaur et al. 2020). Plants need nutrients that are called essential elements and help the plant grow and reproduce. Nutrients are required for the plant in varying amounts and vary in the amount of mobility within the plant and soil. Knowing the relative amounts of nutrients is helpful in preparing and recommending fertilizer. Soil characteristics affect nutrient availability to plants and affect nutrient management (Table 3.1). There are more than 100 chemical elements, but scientists have found that only 17 of them are necessary for plant growth (Jones and Olson-Rutz 2016), and here we ask a question, what role do bacteria play in plants or in other words what do they provide for plants? A plant needs light, water, temperature, and nutrients to gro

3.2.1 Actinomycetes

Actinomycetes constitute about 4% of the soil bacterial population (Hopwood 2007). They are a group of gram-positive bacteria belonging to the branch of *Actinobacteria*. Antibiotics, vitamins, alkaloids, stimulants of plant-enzymes, and enzyme-inhibiting compounds can be named *Actinomycetes*. Approximately 85% of naturally produced and used antibiotics have been isolated from *Actinomycetes* and mainly by different *Streptomyces* species (Rothrock and Gottleib 1981). They are Soil bio buffer guides and contribute to crop production by decomposing organic matter (Shimizu et al. 2000). One of the characteristic features of this bacterium that makes it suitable for controlling some of the plant's damaging agents is the secretion of the enzyme

Table 3.1 Essential elements needed by plants

Element	Role in Plant	Source
Carbon (C)	Constituent of carbohydrates; necessary for photosynthesis	Air
Hydrogen (H)	Maintains osmotic balance; important in numerous biochemical reactions; a constituent of carbohydrate	Water
Oxygen (O)	Constituent of carbohydrates, necessary for respiration	Air/Water
Nitrogen (N)	Constituent of proteins, chlorophyll and nucleic acids	Air/Soil
Phosphorus (P)	Constituent of many proteins, coenzymes, nucleic acids and metabolic substrates; important in energy	Soil
Potassium (K)	Involved with photosynthesis, carbohydrate translocation, protein synthesis, etc	Soil
Calcium (Ca)	A component of cell walls; plays a role in the structure and permeability of membranes	Soil
Magnesium (Mg)	Enzyme activator, component of chlorophyll	Soil
Sulfur (S)	Important component of plant proteins	Soil
Boron (B)	Believed to be important in sugar translocation and carbohydrate metabolism	Soil
Chlorine (Cl)	Oxygen production	Soil
Copper (Cu)	Breathable catalysts	Soil
Iron (Fe)	Chlorophyll synthesis and electron transfer are involved	Soil
Manganese (Mn)	Controls oxidation reduction and photosynthesis	Soil
Molybdenum (Mo)	Stabilization of nitrogen and conversion of nitrate to ammonium	Soil
Nickel (Ni)	It is essential for proper enzyme function and seed germination	Soil
Zinc (Zn)	Regulation of metabolic activity	Soil

chitinase, which is the main chitin-degrading bacterium (Deshpande 1986). *Actinomycetes* are filamentous bacteria and are mainly aerobic (Almustapha et al. 2017; Saadoun et al. 2015). The importance of *Actinomycetes* lies in its ability to produce antibiotics and enzymes (Thirumalairaj 2015).

3.2.2 Fungi

All fungi are decomposers, breaking down the dead matter for nutrients, and they cannot produce their own food. Most fungi are multicellular, but others, such as yeast are single-celled A fungus is a eukaryote that digests food externally and absorbs nutrients directly through its cell walls (Abdel-Azeem et al. 2021). Most fungi reproduce by spores and have a body (thallus) composed of microscopic tubular cells called hypha. Fungi are heterotrophs and, like animals, obtain their carbon and energy from other organisms (Carris 2012; Yadav 2020).

3.2.3 Algae

Algae are a large and diverse group of simple, typically autotrophic microorganisms that can carry out photosynthesis since they capture energy from sunlight. Algae play an important role in agriculture where they are used as biofertilizers and soil stabilizers (Abdel-Raouf et al. 2012).

3.2.4 Protozoa

Protozoa are an unofficial term for protozoa, eukaryotes that are (non-parasitic) and/or parasites that feed on organic matter such as other microorganisms or residual organic tissues. Soil protozoa are divided into six groups (Fig. 3.1). Protozoa have about 1600 species in the soil and adapt to the soil environment. Protozoa have important functions in the decomposition and the growth cycle of plants and are valuable markers for natural and anthropogenic effects (Foissner 2014). The high number of protozoa and their rapid reproduction makes it possible to effectively control microbial growth. The rhizosphere is the focus of microbial and protozoan activities the presence of protozoa in the rhizosphere typically results in a 30–80% plant increase (Bonkowski et al. 2000). The role that protozoa play for plants is crucial in that they provide nutrients in minerals and access to plants and soil organisms. The protozoa help maintain an ecological balance in the soil. When they graze on bacteria, protozoa stimulate the growth of the bacterial population and decomposition rates, and soil aggregation. Protozoa help maintain ecological balance in the soil protozoa are important food sources for soil organisms (Hoorman 2011).

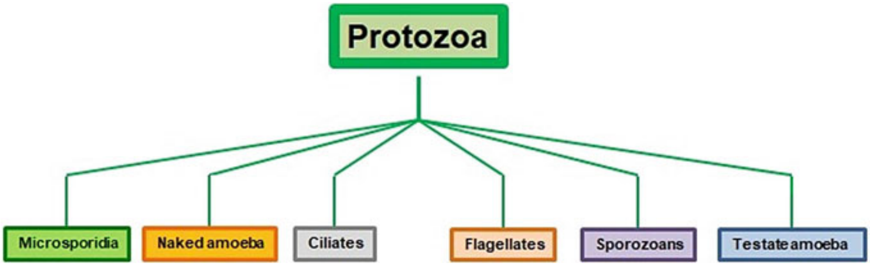

Fig. 3.1 Protozoa classification (Foissner 2014)

3.2.5 Viruses

Viruses cause many plant diseases and are responsible for much damage to the production and quality of crops and though they have no activity outside the body of the living being. When they enter the living organism's body using the genetic material of most viruses that DNA and RNA are able to encode host cell proteins (Lodish et al. 2000). Infected plants may have many symptoms depending on the disease. For example, to tarnish the entire plant, abnormalities in flower or fruit formation can be named. Even viruses can enter the microbial population and have a major impact on microbial mortality in the biological soil environment and by reducing the microbial community, nutrient concentrations for plants decrease and thus have a negative impact on vegetation (Johns 2017).

3.2.6 Nematodes

Nematodes are one of the most ecologically diverse animals on earth found in almost all habitats. The abundance of nematodes in different ecosystems has made them one of the best indicators to monitor environmental pollution. Among soil organisms, nematodes are one of the best biomarkers for identifying disturbances in the soil, including contamination of heavy metals (Yeates et al. 2009; Thakur et al. 2020). Nematodes play an important role in processes associated with most ecosystems. In the soil food web, nematodes transform organic matter into minerals absorbed by plants and play an important role in plant growth and crop production (Bongers and Ferris 1999). This group feeds on bacteria, fungi, algae, yeast, and diatoms. In addition, for invertebrates, vertebrates and plants are parasites. Feeding nematodes from bacteria and fungi release a high percentage of nitrogen during feeding, so they are responsible for providing more available nitrogen to the plant (Poinar 2014). *Caenorhabditis elegans* nematode is a model for genetic studies that are used to determine the association between gene expression and developmental stages. It is the first multicellular living organism to be sequenced. The diversity of nematodes in agricultural ecosystems and their relation to soil processes reflects the fact that they have the capability of the biodiversity index. One of these indices is plant-parasitic nematodes such as the families *Heteroderidae* and *Longidoridae.* The results show that the population of free nematodes in organic-rich soils is much higher than in other soils and this group acts as biodegrades in the soil. Examination of soil-derived nematodes revealed that among the nematodes that feed on bacteria, the *Cephalobidae* family is the most abundant group of soil nematodes (Bernard et al. 2017; Neher 2001).

3.2.7 Bacteria

Bacteria are a very broad group of prokaryotic single-celled organisms that exist in all earth's ecosystems. Bacteria are the smallest single-celled organisms living in the soil (Müller et al. 2002; Balasubramanian 2017; Johns 2017). These microorganisms, despite their small size, have a greater metabolic capacity than other groups of organisms. An important role in soil formation, organic matter degradation, contaminated soil remediation, biological deformations of nutrients in the soil and establish interactions between plants and pathogens (Müller et al. 2002; Yadav 2021). Bacteria are decomposing and they constitute the largest biomass of soil organisms. Bacteria have different types that focus more on the *Rhizobium* and *Actinomycetes* which is important for agriculture. Bacteria contribute to the carbon cycle through photosynthesis and decomposition and reside in water, soil, and radioactive waste, and also live in coexistence and parasitic relationships with plants and animals (Balasubramanian 2017). *Rhizobium* is one of the earliest known growth-promoting bacteria that atmospheric nitrogen in a form coexistence, with the roots of legume plants, stabilized and in the possession of the plant put (Zahir et al. 2004). *Rhizobium* is a gram-negative bacterium that is associated with the formation of root nodules in plants. This bacterium lives in coexistence with beans it extracts nitrogen from the atmosphere and transports it to the plant, helping it to grow in low nitrogen soils (Sawada et al. 2003).

3.3 Bacteria that Stimulate the Growth of Plants

In modern agriculture, the common use of chemical fertilizers, especially nitrogen and phosphorus, is common; this significantly contributes to soil and climate pollution. Overuse of these chemicals, in addition to exerting adverse effects on soil microorganisms, can affect soil fertility and cause environmental pollution (Youssef and Eissa 2014; Prasad et al. 2021). Long-term use of these fertilizers, especially nitrogen, often reduces soil pH and inaccessibility, inorganic elements for agricultural products (Joshi et al. 2006). Chemical fertilizers used in agriculture in addition to increasing crop yields they have negative effects on the ecosystem. Currently, public concern about the adverse effects of chemicals is causing increasing attention to the coexistence between plants and the microbial population in the rhizosphere (Rai et al. 2020). Therefore, the need to use biological fertilizers worldwide has been accepted. The use of biofertilizer and environmentally friendly, causing reduces the usage of chemical fertilizers, and improves soil fertility (Singh et al. 2020a). These changes are probably due to the presence of microbial populations in the soil or rhizosphere.

Increase soil microbial population by accelerating food cycle and food availability, maintaining root health during growth in competition with root pathogens, and increasing nutrient uptake will increase plant growth and consequently increase yield (Dey et al. 2004).

Biofertilizers not only improve the cycle of elements but also provides optimal plant access to water and nutrients and ultimately increases plant yield (Aliasgharzade et al. 2006). Biofertilizers are a variety of microorganisms that help plants grow through nutrients (Kour et al. 2020c). The types of biological fertilizers and their classification are shown in Table 3.2 (Datta et al. 2007). Useful soil bacteria that increase plant growth and so on are called growth-promoting bacteria, and they are the most important types of biofertilizers (Aliasgharzade et al. 2006). *Bacillus*, *Pseudomonas*, *Rhizobium*, *Azospirillum*, *Azotobacter* is among the bacteria that stimulate the growth of plants. *Azotobacter* and *Pseudomonas* bacteria are attracted more attention because of the ability to communicate with important crops like corn, sorghum, wheat. These bacteria are most commonly found near or even inside the root of the plant (Saleh-Rastin 2001). A rhizosphere is a place where the interactions between soil, plants, and micro-organisms occur. The bacteria in the rhizosphere are called rhizobacteria. The types of rhizobacteria that have positive effects on plant growth and function are called plant growth-promoting rhizobacteria (PGPR).

They are an important group of free-living bacteria that colonize the rhizosphere or, in other words, have beneficial effects on plant growth in the space around the root (Tilak et al. 2005; Kour et al. 2019). When used in seeds or crops, it promotes plant growth (Kloepper et al 1988). The term was first coined by Skrot and Cloper in 1978 and was used only for a variety of rhizosphere bacteria until later years. Indirectly through controlling plant pathogens and helping to maintain plant health, the conditions for plant growth were provided. Nowadays, direct mechanisms of the efficacy of various types of PGPR such as the production of phytohormones, ionophores, increased plant access to phosphorus through enzymatic and non-enzymatic dissolution, insoluble organic phosphates and mineral, the development of the root system, enzymatic activities such as ACC-deaminase and rhizobitoxin production to reduce the adverse effects of ethylene stress and increase nodulation and ultimately biological stabilization of molecular nitrogen, etc. have been demonstrated (Antoun and

Table 3.2 Classification of biological fertilizers and related groups

Groups	Examples
N2 Fixing biofertilizer Free-living, Symbiotic, Associative symbiotic	*Azotobacter, Rhizobium, Azospirillum, Frankia, Azospirillum, Mesorhizobium, Sinorhizzobium, Pseudomonas*
P solubilizing biofertilizer, P Mobilizing Biofertilizers	*Bacillus cirulans, Pseudomonas, Rhizobium, Serratia, Mycorrhiza*
Biofertilizers for mono-nutrients Silicates and zinc solubilizers	*Bacillus spp., Burkholderia spp., Pseudomonas*
PhytohormonesSiderophore	*Pseudomonas, Rhizobium, Bacillus, Azotobacter*
Bio-control Antifungal	*Streptomycetes, Bacillus, Pseudomonas*

Kloepper 2001; Yadav et al. 2020a; Dikilitas et al. 2021; Suyal et al. 2021; Yadav et al. 2021a). On the other hand, early studies of PGPR have focused only on root crops such as potatoes, radishes, and sugar beets, but subsequent studies cover a wider range of agricultural products, including cereals and legumes (Rodriguez and Fraga 1999).

Biological fertilizers are used to increase productivity. The importance of microbial communities is due to the important role that these communities play in biologically active processes in the soil that determine the level of plant production are, play. A bacterium called *Azospirillum*, in cooperation with the roots of cereal family plants such as wheat, stabilizes air nitrogen (Tilak et al. 2005). Also, the role of these bacteria in the rapid development of the root system, strengthening the vigor of most seedlings in the early stages of growth, increasing the germination percentage, increasing the green area of the farm, increasing plant tolerance to abnormal environmental stresses (drought, salinity, etc.) and living factors (many soil diseases) and ultimately increased crop yield has been demonstrated (Lucy et al. 2004). This bacterium, in combination with plants such as wheat, sorghum, and maize, showed a yield increase of about 10–30%, but this increase was attributed to the production of plant growth hormones including auxin in addition to nitrogen production. These bacteria increase the number and length of sub-lethal roots and lethal fibers and ultimately increase the root uptake which results in increased absorption of water and nutrients by the plant (Saleh Rastin 1999). Today, it is believed that the interactions between plant roots and soil organisms have been affected by human interventions through agricultural and industrial activities (Lynch 2002). So the quality of the soil is not only dependent on its physical and chemical properties, but also closely related to its biological properties (Ebhin Masto et al. 2006).

The application of biological fertilizers to maintain biological balance, soil fertility in order to maximize achieving optimal biological relationships of the system and minimizing the use of the materials and operations that disrupt these relationships, especially the use of chemical fertilizers, are of particular importance, although the use of biological fertilizers in agriculture It has great antiquity. In the past not so far, all the food consumed by humans has been produced using such valuable resources but the scientific exploitation of such resources, not recorded. The application of biological fertilizers, especially bacteria, stimulating plant growth, the most important strategy in management, integrated plant nutrition for sustainable agriculture system, in combination with the consumption of chemical fertilizers by using these bacteria are considered (Sharma 2003; Singh et al. 2020b).

3.3.1 The Mechanism of Action of Growth-Stimulating Bacteria

Increased plant growth by growth-promoting bacteria is a well-known phenomenon, and this growth is due to some traits and the specific properties of the growth-promoting bacteria. Growth-promoting bacteria induce plant growth directly because of their ability to supply nutrients (nitrogen, phosphorus, potassium, and essential minerals) or plant hormone production, also by reducing the effects of pathogens, the production of hydrolytic enzymes and siderophore production indirectly affects plant growth (Kloepper and Schroth 1981; Tiwari et al. 2020; Yadav et al. 2020c). Growth-stimulating bacteria by facilitating food absorption and increasing access to nutrients through nitrogen fixation, the dissolution of minerals, and the production of plant hormones directly increases plant growth (Bhardwaj et al. 2014). Direct and indirect effects of growth-promoting bacteria are shown in Fig. 3.2.

Plants, directly and indirectly, increase soil fertility, by increasing the amount of nitrogen and phosphorus, and other nutrients needed by the plant and synthesizing various phytohormones such as indole-3-acetic acid, which can promote plant growth (Saleem et al. 2007). And suppressing pathogens in the soil by producing hydrogen cyanide, siderophore and antibiotics help increase plant tolerance to drought, soil salinity, and metal toxicity according to Kloepper and Schroth (1981), plant growth is facilitated by PGPR by altering the microbial community in the rhizosphere wall through the production of various materials (Table 3.3) (Kloepper and Schroth 1981; Hesham et al. 2021; Tiwari et al. 2021).

PGPR is classified into two main groups: (i) extracellular PGPR, which exists in the rhizosphere or spaces between root cortical cells and (ii) intracellular PGPR, which exists within the root cells (e.g., *Bacillus*, *Pseudomonas*, and *Azotobacter*).

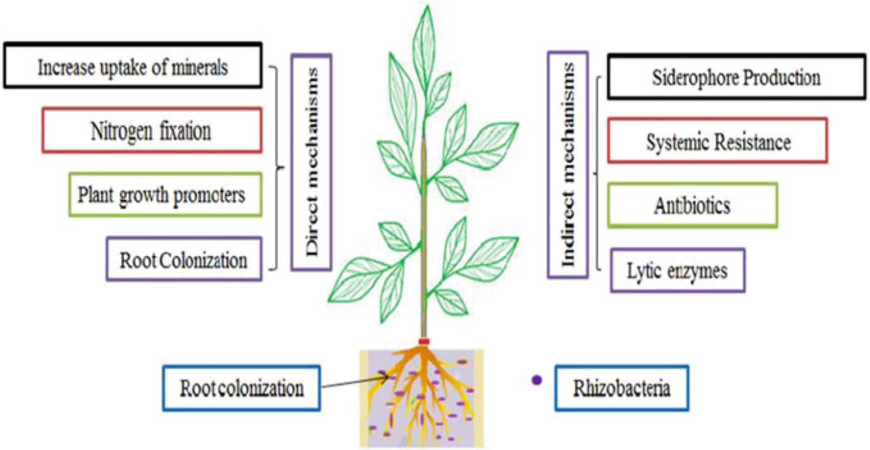

Fig. 3.2 Schematic representation showing direct and indirect effects of growth promoting bacteria on plants (Ngoma et al. 2012)

Table 3.3 Types of Growth promoting substances released by PGPR

PGPR	Plant growth-promoting traits	References
Pseudomonas putida	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2012a, 2012c) and Ahemad and Khan (2011c)
Pseudomonas aeruginosa	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2011a, 2011k) and Ahemad and Khan (2010d)
Klebsiella sp.	IAA, siderophores, HCN, ammonia exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2011b, 2011f, 2011g)
Enterobacter asburiae	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2010a, 2010b)
Rhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2012b), Ahemad and Khan (2011i), Ahemad and Khan (2010c) and Ahemad and Khan (2009b)
Mesorhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2012d), Ahemad and Khan (2010e, 2010h) and Ahemad and Khan (2009a)
Acinetobacter sp.	IAA, phosphate solubilization, siderophores	Rokhbakhsh-Zamin et al. (2011)
Rhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2011e, 2011j) and Ahemad and Khan (2010f, 2010g)
Pseudomonas sp. A3R3	IAA, siderophores	Ma et al. (2011a)
Psychrobacter sp. SRS8	Heavy metal mobilization	Ma et al. (2011b)
Bradyrhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2011f) and Ahemad and Khan (2011d, 2011h, 2011l)
Pseudomonas aeruginosa 4EA	Siderophores	Naik and Dubey (2011)
Bradyrhizobium sp. 750,	Heavy metal mobilization	Dary et al. (2010)
Bacillus sp. PSB10	IAA, siderophores, HCN, ammonia	Wani and Khan (2010)
Paenibacillus polymyxa	IAA, siderophores	Phi et al. (2010)

(continued)

Table 3.3 (continued)

PGPR	Plant growth-promoting traits	References
Rhizobium phaseoli	IAA	Zahir et al. (2010)
Stenotrophomonas maltophilia	Nitrogenase activity, phosphate	Mehnaz et al. (2010)
Rahnella aquatilis	Phosphate solubilization, IAA, ACC deaminase	Mehnaz et al. (2010)
Azospirillum amazonense	IAA, nitrogenase activity	Rodrigues et al. (2008)
Mesorhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2008)
Serratia marcescens	IAA, siderophore, HCN	Selvakumar et al. (2008)
Enterobacter sp.	ACC deaminase, IAA, siderophore, phosphate solubilization	Kumar et al. (2008)
Pseudomonas jessenii	ACC deaminase, IAA, siderophore, heavy metal solubilization, phosphate solubilization	Rajkumar and Freitas (2008)
Pseudomonas aeruginosa	ACC deaminase, IAA, siderophore, phosphate solubilization	Ganesan (2008)
Azotobacter sp., *Mesorhizobium* sp., *Pseudomonas* sp., *Bacillus* sp.	IAA, siderophore, antifungal activity, ammonia production,HCN	Ahmad et al. (2008)
Bradyrhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2007a)
Rhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2007b)
Mesorhizobiumciceri, Azotobacter chroococcum	IAA, siderophores	Wani et al. (2007c)
Pseudomonas, Bacillus	Phosphate solubilization, IAA and siderophores	Wani et al. (2007c)
Klebsiella oxytoca	IAA, phosphate solubilization, nitrogenase activity	Jha and Kumar (2007)

The beneficial effects of PGPRs on a wide range of crops including cereals, vegetables, oilseeds, and crops have been reported. Currently, these bacteria are used as biological fertilizers and controllers for agricultural production. Therefore, a fundamental understanding of the performance and diversity of microorganisms before using microbial soil technology in the rhizosphere is essential (Babalola 2010).

3.3.2 *The Influence of PGPR Bacteria on System Architecture and Root Structure*

The root system of most plants, in order to search for nutrients in the soil for survival and growth, they have found a special expansion. The root is a complex organ of the plant system from different parts like the tip of the root, meristem root, differentiation, and elongation area and emerging area of the lateral roots are composed (Sadafi et al. 2002). These areas have a special role and are in plants distinct. For example, hairy roots that are differentiated from specific epidermal cells play an important role in better nutrition of the plant, gene expression research (Viterbo et al. 2007), and measure the nutrients in the soil (Abdel-Latif et al. 2005).

An important feature of plants is their ability to perform useful interactions with microbial organisms in the soil. For example, in root tip legumes, the most important region is the onset of the uptake of *Rhizobacteria* and consequently the formation of root nodes. For example, in root tip legumes, the most important region is the onset of the uptake of *Rhizobacteria* and consequently the formation of root nodes. That by this interaction the plant can live and non-living environmental stresses better to endure and make more use of nutrients in the soil (Coventry et al. 2006). There are many capillary and lateral roots in the cereals that are the site of activity of PGPR plant growth-promoting *Rhizobacteria*. In fact, the plants utilizing these microbial agents have beneficial properties including development, and they find the expansion of capillary and lateral roots (Paulitz and Belanger 2001). Root system architecture (RSA) from root system topology, the spatial distribution of main and lateral roots, the number and size of roots are composed. Various factors include living and non-living beings affect the RSA. Including these agents are PGPR bacteria. These bacteria mainly change the root structure through hormonal interactions in favor of the plant (Suresh et al. 2010). These bacteria can stimulate root growth through the production of plant hormones, secondary metabolites, and enzyme balance and this way make the acquisition of foodstuffs and better root performance.

One of the most visible effects of them is the decrease in growth rate, early roots, and increase in number and length of lateral and capillary roots. PGPR bacteria with nitrogen fixation, phosphorus solubilization, and siderophore production, improve plant nutrition (Fig. 3.3) (Kour et al. 2021; Rana et al. 2019; Yadav et al. 2020b; Yadav et al. 2021b). These microbial agents also, with the change in gene transcription and the biosynthesis of metabolites in plant cells, cause changes in root physiology (Suresh et al. 2010).

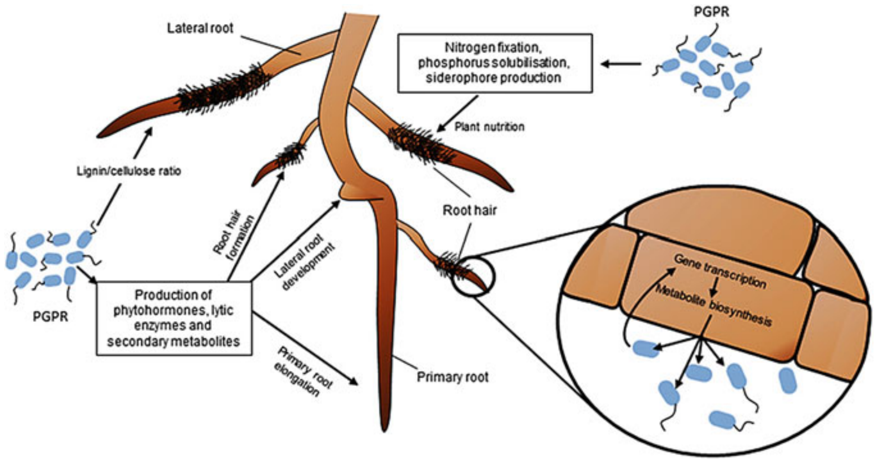

Fig. 3.3 Impact of PGPR bacteria on root system architecture (RAS) (Rubin et al. 2017)

3.4 The Most Important Plant Growth-Promoting Bacteria

3.4.1 Azospirillum

Bacteria of the genus *Azospirillum* are generally known as plant hormone-producing bacteria, polyamines, and amino acids in the culture medium. Plant hormones produced by the genus *Azospirillum* affect the rate of respiration, metabolism, and root growth and thus increase the uptake of water and nutrients in inoculated plants, which can increase growth performance (Mohammadi et al. 2010). A bacterium called *Azospirillum*, in cooperation with the roots of cereal family plants such as wheat, stabilizes air nitrogen (Tilak et al. 2005). Also, the role of these bacteria in the rapid development of the root system, strengthening the vigor of most seedlings in the early stages of growth, increasing the germination percentage, increasing the green area of the farm, increasing plant tolerance to abnormal environmental stresses (drought, salinity, etc.) and living factors (many soil diseases) and ultimately increased crop yield has been demonstrated (Lucy et al. 2004). This bacterium, in combination with plants such as wheat, sorghum, and maize, showed a yield increase of about 10–30%, but this increase was attributed to the production of plant growth hormones including auxin in addition to nitrogen production. These bacteria increase the number and length of sublethal roots and lethal fibers and ultimately increase the root uptake which results in increased absorption of water and nutrients by the plant (Saleh Rastin 1999).

3.4.2 *Azotobacter*

Azotobacter bacteria, *Azospirillum*, are the most important plant growth-promoting bacteria. In addition to the biological stabilization of nitrogen, by producing significant amounts of growth hormones, especially auxin, gibberellin, and cytokinin, it promotes the growth and function of crops (Zahir et al. 2004). *Azotobacter* is one of the most useful soil bacteria which due to its abundance and spreading propagation, has been considered more than other types of nitrogen stabilizers. Research has shown that *Azotobacter* as a seed inoculum is effective not only in nitrogen fixation, but also in the production of growth hormones, antifungal compounds, siderophore, and phosphate solubilization (Hokmalipour 2017).

Azotobacter is a gram-negative, aerobic, chemoorganotropic bacterium in rod, spherical and elliptic shapes. It belongs to the *Gamma-proteobacteria* and *Pseudomonads* family and has seven species. *Azotobacter* lacks sporulation ability, but usually forms cysts. Various species of *Azotobacter* are found from very hot and humid regions to Polar Regions in the range of pH 3–9. However, they are mostly found in neutral to alkaline soils. *Azotobacter* is able to stabilize molecular nitrogen in a non-symbiotic manner. It can synthesize a variety of amino acids, vitamins and plant growth hormones, and a variety of exopolysaccharides. The role of *Azotobacter* in plant growth is due to the production of growth hormones, soluble phosphate solubility, increased elemental uptake, nitrogen fixation, increased resistance to stress, and biocontrol of plant pathogens. Some *Azotobacter* strains have shown their potential in bioremediation of contaminated soils (Garrity et al. 2005). In sustainable agricultural systems, the application of biofertilizers is of particular importance in enhancing the production and maintenance of sustainable soil fertility. The term biofertilizers refers to organic matter derived from animal manure, plant residues, green manure, etc. as well as beneficial bacterial and fungal organisms. They are known for their activity and are the most important biological fertilizers for growing plant growth bacteria or so-called PGPR. This group of bacteria, in addition to increasing the bioavailability of soil minerals through biological nitrogen fixation, phosphorus and potassium solubilization, and inhibition of pathogens, affect crop yield through the production of plant growth regulating substances and hormones they put (Sturz and Christie 2003). Also, due to the effect of growth on the growth and development of crops, these bacteria are also called performance-enhancing bacteria (Vessey 2003).

Some species of *Azotobacter*, *Azospirillum*, and *Pseudomonas* are the most important species of PGPR in the root environment (rhizosphere) which, besides biological stabilization of nitrogen and solubilization of soil phosphorus by producing significant amounts of excitatory substances and hormones a variety of auxins, gibberellins, and cytokines affect the growth and function of crops (Zahir et al. 2004). Recent studies have indicated that the production of indole acetic acid and cytokinin by the use of tryptophan and basal adenine-secreted amino acids, hydrolysis of ethylene precursor, 1-amino cyclopropane, 3-carboxylic acid (ACC) by enzyme C-deaminase, and the production of hormonal and quasi-hormonal substances such as indole butyric acid, gibberellic acid, etc., are the most important mechanisms of these bacteria due to the reaction of nitrite with nitrate respiration with ascorbic acid (Zahir et al. 2004).

The root of the plant is a water-absorbing organ and nutrients from the soil and organs producing various compounds from including growth hormones is important for plant growth and development. Research has shown that the growth of maize root is due to auxin produced by *Azotobacter crococci* and also the growth of maize root and other crops is due to the release of gibberellic acid and cytokinin by *Azospirillum lipoferum* and *Pseudomonas putida* has been identified (Hall et al. 1996).

3.4.3 Phosphobacter

Phosphorus is an important nutrient for plant growth that is low in soil availability. Phosphorus is both organic and inorganic forms found in soil. Plant growth-stimulating bacteria or PGPR bacteria in the soil and rhizosphere are plants that help plant growth through different mechanisms (Kour et al. 2020a, b). The ability of some microsatellites to convert insoluble phosphorus into a usable form such as inorganic phosphate is an important feature of PGPR that enhances plant performance. The main mechanism for the dissolution of inorganic phosphate is the production of organic acids, and in the organic phosphorus degradation, phosphatases play a major role in soil. Food supply is a challenge as the population grows. The green revolution, although it has been able to help people with their food needs, with the growing trend of population and the need for more food, the need for another green revolution has been felt with greater respect for environmental principles and their sustainability. The green revolution that was created by the introduction and supply of chemical fertilizers, along with increased production, posed a threat to the environment and to humans.

Therefore, human beings have sought to use methods that are more environmentally friendly to preserve their basic production and sustainability through sustainable agriculture, with a greater emphasis on soil bio-potentials and capabilities. Turning to biofertilizers instead of chemical fertilizers seems to be a good alternative. Phosphate biofertilizers are used according to the importance and role of phosphorus in plant nutrition (Khan et al. 2007). Despite the abundance of phosphate compounds in the soil, plants absorb phosphorus in the form of phosphate anion ($H2PO_4^-$ or HPO_4^{2-}) from the soil solution (Ezawa et al. 2002). Phosphorus has the least mobility in soil and plants. Root development, stem consistency, flower and seed formation, fruit ripening, nitrogen fixation in legume plants, crop quality, and disease resistance are all directly related to phosphorus nutrition (Fageria 2009) (Rana et al. 2020). Phosphorus is one of the essential components of energy metabolism, part of nucleic acids, and biological membranes. Basic biochemical processes such as photosynthesis and respiration are activated by inorganic phosphate (Pi) or its organic derivatives (Raghothama and Karthikeyan 2005). Phosphorus is the second most important element in plant nutrition. Which has a significant role in many physiological and biochemical reactions of plants (Fageria et al. 2013). Phosphorus stimulates nitrogen fixation in legume plants and is essential for the production of sugars (Saber et al. 2005). Soil soluble phosphate concentrations are usually very low, with values of 1 mg kg-1 or less (Paul 2007). The very low levels of phosphate absorbed in the rhizosphere make it one of the most important growth-limiting factors in many ecosystems. Mineral fixation of phosphate in the soil and the formation of organic complexes is among the primary reasons for its low availability (Raghothama and Karthikeyan 2005). The dominant form of phosphate in alkaline conditions is tricalcium phosphate. Inorganic phosphate rocks such as fluorapatite and francolite are sources of calcium phosphate that are insoluble in soil and do not supply the plant's needs. Phosphate dynamics in the soil are affected by physicochemical (adsorption and desorption) and biological (non-motility and mineralization) processes (Fageria 2009; Paul 2007).

3.4.3.1 PGPR and Phosphate Solubilizing Bacteria

The microbial community of the soil produces its fertility through decomposition, mineralization, storage, and affecting nutrient release due to the release of about 40% of substances Photosynthesis in the plant rhizosphere has provided this environment with favorable conditions for the presence of the microbial population; plant growth-promoting bacteria or PGPR contain root-surrounding bacteria that promote plant growth. Today, PGPR are used as microbial biogenic fertilizers or controllers (Ping and Boland 2004). The mechanisms by which PGPR influences plant growth are divided into direct and indirect effects. The indirect effect is mostly through the production of microbial metabolites that have a negative effect on pathogens such as antibiotics, siderophores, or HNC and inhibit the growth of pathogenic microsatellites but increase their direct effects through pathways (Yadav et al. 2016). Synthesis of plant hormones facilitates nutrient uptake, nitrogen fixation, reduction of root membrane potential, synthesis of some enzymes such as (ACC deaminase) that modulate the levels of plant hormones (Rodriguez and Fraga 1999). And also the dissolution of inorganic phosphate and mineralization of organic phosphate can be used in plants (Rodriguez and Fraga 1999; Timmusk and Wagner 1999). Evidence of the role of rhizosphere microsatellites in dissolving inorganic phosphate has been presented in the year 1903 (Illmer and Schinner 1992). Microsatellites increase the availability of phosphorus to plants by mineralizing organic phosphorus and dissolved sedimentary phosphates (Chen et al 2006; Pradhan and Sukla 2005).

Bacteria are much more effective in phosphate solubilization than fungi and have a high population (Alam et al. 2002). Significant populations of phosphate solubilizing bacteria exist in the soil and in the rhizosphere of the plant which includes aerobic and anaerobic species with the predominance of aerobic species, and their populations in the rhizosphere were significantly higher than non-rhizosphere soil (Whitelaw 2000). Bacteria, *B. megaterium*, *B. circulans*, *B. subtilis*, *B. polymixa*, *B. sircalmous*, *P. striata*, and Enterobactercan be identified as the most important species (Kucey et al. 1989). Phosphate-solubilizing bacteria have been used since the year 1950 as biofertilizers. The relationship between plants and phosphate solubilizing bacteria is known as a synergistic or intensifying relationship in nature. Because, on the one hand, the bacteria provide soluble phosphate to the plant and on the other hand, the plant, through its root secretions, releases the carbon compounds needed most often (sugars) for bacterial growth (Pérez et al. 2007). Synchronous use of phosphate solubilizing bacteria with other beneficial rhizosphere microflora such as mycorrhizal fungi and nitrogen-fixing bacteria increase the growth of plants compared to when they are alone more stimulated (Zaidi et al. 2003; Perveenet al. 2002). The co-operation of microsatellites in the rhizosphere of plants can improve the uptake of available phosphates and also provide stabilized phosphate sources for the plant (Tao et al. 2008). Studies show that *Bacillus, Pseudomonas*, and *Rhizobium* are the most potent solvents are phosphates (Rodriguez and Fraga 1999). Organic phosphorus compounds such as phytic acid may account for 20–80% of the soil phosphorus. Almost half of the micronutrients in the soil and roots of the plants mineralize organic phosphorus with their phosphatase activity. Acidic and alkaline phosphatases Organic phosphate as a substrate becomes mineralized (Beech et al. 2001). Although the main mechanism in mineralization of organic phosphate soil produces acid phosphatases (Rodrıguez et al. 2000a). In addition, the release of organic anion and the production of siderophore can hydrolyze soil organic phosphorus (Yadaf and Tarafdar 2001). The degradability of organic phosphorus is largely dependent on the biochemical and physicochemical properties of the molecule, for example, nucleic acids, phospholipids, and phosphate sugars are readily degraded, while phytic acid polyphosphates decompose slowly (Rodriguez and Fraga, 1999). Phosphorus can be released from soil organic compounds by three enzymatic groups:

i–Non-specific phosphatases, which follow the dephosphorylation of phosphoester or phosphonidaride bonds in organic matter.

ii–Specific phosphatases such as phytases that release phosphorus from phytates.

iii–Phosphonatase and C-P Lias (Rodriguez et al. 2006).

Phytases (myo-inositol hexakisphosphate phosphohydrolase) belong to a specific group of phosphomonosides that are able to release phosphorus from phytates. Phytic acid was first discovered in 1903 and its salts are known as phytate (Mullaney and Ullah 2005). In Fig. 3.4 release phosphate from the phytate molecule by phytase enzyme.

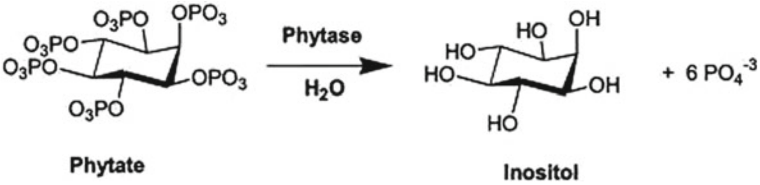

Fig. 3.4 Hydrolysis of phytate in presence of phytase enzyme (Haefner et al. 2005)

3.4.4 Bacillus

Bacillus bacteria have a wide range of potent antimicrobial metabolites such as surfactin, fengicycin, bacillin, deficidin, macrolactin produce, and control soil-borne plant pathogens (Pristchepa et al. 2006). These bacteria increase the growth and induction resistance of the plant. *Bacillus subtilis* Cohn 1872 by producing antifungal proteins, it has an inhibitory effect on growth plant pathogens in the culture medium (Leben 1987). *Bacillus subtilis* bacteria marketed under different brand names reduces 99% of superficial white matter disease cucumbers and squash. Also, bacteria *B. cereus* Frankland, *Bacillus lentimorbus* Dutky, *B. licheniformis* (Weigmann, & Frankland Emend, Gibson) by producing volatiles and degrading enzymes chitin and glucan, decay reduces potatoes. Bacillus bacteria due to their widespread presence in soil, tolerance of temperature changes, pH, environmental salinity, and the production of endospore resistant forms are considered as suitable agents in biological control. Species *Bacillus* is often found in soil and rhizosphere. These bacteria produce siderophores, produce enzymes, produce antibiotics, and induce systemic resistance to help control plant pathogens (Jacobsen et al. 2002).

3.4.5 **Pseudomonas** *in Biological Control*

Fluorescent *Pseudomonas* in the rhizosphere, due to the ability to protect plants against fungal, bacterial, and nematode pathogens is important (Gangwar 2013). These bacteria form the most important constituents of microflora beyond the root, plants are considered and because of their rapid growth, easier metabolism, and adaptability, they have been the focus of biological research (Vacheron et al. 2013). Fluorescent *Pseudomonas* species, especially the species *P. putida*, *Pseudomonas fluorescens* (Flugge) Trevisan are the most abundant bacteria in the rhizosphere. These bacteria through the impact on the growth of the pathogen and the production of siderophore since the late 1970s are of great importance in biological control (Baker and cook 1974). Mechanisms this group of bacteria is competition for iron through the production of siderophore production of hydrogen cyanide (Nejad and Johnson 2000). Secretion of extracellular enzymes such as chitinase, β 1,3 glucanases, protease, and lipase production of antibiotics, production of siderophore pseudobacteri, and povidorin (Jetiyanon et al. 2003) caused stimulate plant growth, competition for food, and occupy microbial sites in the area beyond the root and induce systemic resistance of the plant (Sun et al. 2010).

3.5 Conclusion

In today's world, alongside the problem of human societies providing food and producing more food, there are other important issues such as climate change and environmental problems, and the decline of genetic resources. The use of biological agents such as fertilizers and bio-pesticides in the direction to reduce the consumption of these hazardous compounds can have an important role in protecting the environment and agricultural fields. In addition to increasing the efficiency of these biological agents using new biotechnologies like genetic engineering can also increase their effectiveness. A lot of chemical changes in the soil, it is done by the soil microbial biomass. Thus, microorganisms have a major control role in the cycle, and loss of the nutrients is from the soil. Quantity and soil organic matter quality is one of the most important factors in controlling the abundance and activity are microorganisms and therefore the bedrock of many changes of microbial conversion in the soil is considered. Also, studies on the coexistence of growth-promoting bacteria with crops in stress and non-stress conditions indicate the role of these bacteria in enhancing the performance of host plants and their resistance to environmental stresses. So with the development of power usage growth-stimulating bacteria in agriculture, one can step towards sustainable agriculture and while producing acceptable performance, it prevented environmental pollution and contributed to the survival and sustainability of the ecosystem.

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Chapter 4
Phosphorus Solubilization: Mechanisms, Recent Advancement and Future Challenge

Zarrindokht Emami-Karvani and Zahra Chitsaz-Esfahani

Abstract Phosphorus deficiency is the limiting factor for crop productivity on more than 40% of arable lands worldwide and using fertilizers is counted as the most popular way to face this problem. The increasing food demand and searching for efficient, cost-effective, and environmental friendly approaches to sustainable agriculture made scientists and farmers take biofertilizers to account for a potent solution. Phosphate-solubilizing microorganisms (PSMs) with the potential of transforming insoluble forms of phosphate to soluble and bioavailable forms are good choices for promoting plant growth with increasing soil soluble P as a major limiting macronutrient. A variety of bacterial and fungal species belongs to PSMs. These organisms are either free organisms in the rhizosphere or live endophytic in external or internal parts of plant tissues. These organisms can act either as free organisms in the rhizosphere or live endophytic in external or internal parts of plant tissues. PSMs use several mechanisms for solubilization and mineralization of inorganic and organic phosphates such as organic acid production, chelation, siderophore production, and excretion of phosphatase and phytase enzymes. Phosphate-solubilizing microorganisms stimulate plant growth by several mechanisms including solubilization of organic P and mineralization of inorganic P, which release soluble P as a nutrient for plants, production of growth-promoting phytohormones such as Indole acetic acid (IAA), ACC deaminase, gibberline and cytokinins; and release of biocontrol agents such as siderophores, antifungal agents and antibiotic. Preparation of profitable microbial inoculants from PSMs, their field application, and challenges in the way of microbial biofertilizer application are from the contents discussed in this chapter. To prevent using biofertilizers failure, an appropriate amount of used inoculants for different plant-soil conditions and different microbial interactions between applied PSMs and other soil inhabitants should be investigated before application.

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4.1 Introduction

After nitrogen (N), phosphorus (P) is the most crucial key nutrition for plant growth which directly affects many fundamental metabolic processes in the plant such as photosynthesis, cell development, cell division, respiration, energy transfer and macromolecular biosynthesis (Shenoy and Kalagudi 2005; Yadav 2021). Despite the fact that phosphorus presents abundant in the soil in both organic and inorganic forms, this macronutrient is the most limiting factor for plant development (Kour et al. 2020c, 2021). The establishment of insoluble complex such as tricalcium phosphate in alkaline or neutral soils and aluminum phosphate and iron phosphate in acidic soils makes phosphorus unavailable to plants root uptake (Barber 1995). This phenomenon rapidly occurs after the application of phosphatic fertilizers (Chen et al. 2006) so that only 0.1% of soil phosphorous which contents 0.05% (w/w) of this is available for plants (Alori et al. 2017).

Regarding the mentioned problem and negative environmental effects of inorganic phosphate fertilizers such as wastewater eutrophication and groundwater contamination (Kang et al. 2011), scientists seek to investigate management strategies to solve the problem of phosphorus fertilization output, gain more crop yields and reduce environmental pollution (Alori et al. 2017).

A variety of bacterial species, mainly present in the plant rhizosphere called plant growth-promoting bacteria (PGPB), are known as lucrative microorganisms used instead of synthetic chemicals which can greatly improve plant growth by providing plant required nutrients and may overcome environmental health menace and help soil productivity (Esitken et al. 2010). There are plenty of biological processes containing the transformation of insoluble soil nutrients which results in solubilization and mineralization of insoluble soil phosphorus for plant use. Aside from chemical fertilization, this is the only practicable way to enhance plant-available phosphorus.

In the soil rhizosphere, there is a large number of microorganisms, effective at releasing phosphorus from different kinds of soil phosphorus through solubilization and mineralization (Bhattacharyya and Jha 2012), called phosphorus-solubilizing microorganisms (PSMs). These microorganisms enhance the bioavailability of soil insoluble P compounds for plant uptake (Sharma et al. 2013; Singh et al. 2020a) by solubilizing insoluble mineral phosphorus and mineralizing insoluble organic phosphorus (Alori et al. 2017). In some cases, the plant growth-promoting ability of PSBs has been exhibited by measuring siderophore and indole acetic acid production (Park et al. 2011). To explain the mechanisms of solubilization of the insoluble P, there are three valuable theories counting the sink theory, the organic acid theory and the theory of acidification through H^+ excretion (Zaidi et al. 2009a). This chapter especially focuses on the methods of phosphorus solubilization, its mechanisms, recent developments and future challenges.

4.2 Importance of Phosphorus for Agriculture

Adequate levels of soil nutrients always have been a crucial agricultural matter. Sustainable development of farming requires a vast investigation on all physical, chemical and biological processes affecting nutrients availability in soil for plant use (Pierzynski et al. 2005; Prasad et al. 2021; Sharma et al. 2021). Because of the restrictions of P availability, phosphorus is generally recycled to diverse extents in different ecosystems depending on soil type, climate, and ecosystem level (Filippelli 2002; Hesham et al. 2021). In this chapter, we especially focus on phosphorous as the most important key element for plant growth and agriculture after nitrogen. This element is necessary for all life on our planet. Dramatic growth of the human population during the twentieth century has made a big food demand which is directly dependent on the presence of phosphorus (Walan et al. 2014). It is interesting to know that based on investigations, P deficiency is the limiting factor for crop productivity on more than 40% of arable lands worldwide (Vance 2001) and using fertilizers is counted as the most popular way to face this problem.

4.3 Phosphate Resources and Reserves

There are a handful of P pools on earth, counting ocean sediments, land sources, mineral reserves and resources, terrestrial, oceanic and freshwater living organisms, seawater and freshwater (Yuan et al. 2018). Literally, about phosphate, resource refers to “Phosphate rock (PR) of any grade that may be produced at some time in the future, including reserves” and reserve is “Phosphate rock that can be economically produced at the time of the determination to make suitable products, reported as tons of concentrate” (Van Kauwenbergh 2010). While phosphate is found in various forms such as calcite, quartz, dolomite, apatite and other deposits or other primary minerals which are formed during the earth geological age, phosphate rocks are known as sedimentary (carbonate apatite) and igneous (fire-formed (F^- or C^- or OH^--apatite)) are used for producing fertilizers (Samreen and Kausar 2019). Although igneous is lower in grade (usually containing less than 5% P_2O_5), the ability to upgrade its concentration to 35–40% P_2O_5 makes igneous phosphate rock the reserve of 10–15% of phosphate fertilizers (Edixhoven et al. 2014). Sedimentary and igneous resources are mainly located in a handful of countries such as China, the U.S. and Morocco (Rodríguez and Fraga 1999), but its bioavailability for plants highly depends on pH and soil types, so that soil acidity steadily discharges plant-available P. After the U.S., respectively Morocco and China are the largest phosphate fertilizer producers (Rodríguez and Fraga 1999; Samreen and Kausar 2019; Van Kauwenbergh 2010).

Table 4.1 Common phosphorous (P) minerals found in acid, neutral and calcareous soils

S. N.	Minerals	Chemical formula
Acid soils		
	Strengite	$FePO_4{\cdot}2H_2O$
	Variscite	$AlPO_4{\cdot}2H_2O$
Neutral and calcareous soils		
	B-tricalcium phosphate	$Ca_3(PO_4)_2$
	Dicalcium phosphate	$CaHPO_4$
	Dicalcium phosphate dehydrate	$CaHPO_4{\cdot}2H_2O$
	Fluorapatite	$Ca_5(PO_4)_3F$
	Hydroxyapatite	$Ca_5(PO_4)_3OH$
	Octacalcium phosphate	$Ca_4H(PO_4)_3{\cdot}2\text{-}5H_2O$

Sources Yadav and Verma (2012)

Besides, counting P as a finite non-renewable resource, it is acknowledged that the world's known sources of superior phosphate rock may be exhausted, within the current century, if we continue its current rate of use (Cordell et al. 2009).

Phosphate plays a crucial role in plant growth. Although P is the 11th most abundant element on the earth surface, usually there are low levels of soluble P in soils; about 1 ppm or less (10 M $H_2PO_4^-$) because of its high reactivity which is due to the occurrence of francolite. Between different forms of phosphate, that plant should uptake, the greatest part of absorption belongs to the water-soluble forms of HPO_4^{2-} or $H_2PO_4^-$ (Krauss and Saam 1984; Rodríguez and Fraga 1999). Common phosphorous (P) minerals found in acid, neutral and calcareous soils are shown in (Yadav and Verma 2012) Table 4.1.

Water-soluble P (WSP) can easily mobilize to water-insoluble P after rebounding with soil ingredients such as Fe oxides or hydroxides and Al hydroxides in acidic soils and Ca carbonate in alkaline soils through chemical precipitation or physical adsorption. Consequently, a crop grown can recover only 10–30% of the applied phosphate fertilizer (Balemi and Negisho 2012). On another hand, using novel high-yielding crop fertilizer varieties which were introduced in the 1960s resulted in extracting much more nutrients from the soil, growing irrigation requirements and using more fertilizers. Besides, phosphate and consequently phosphate fertilizers price grow rapidly in 2007 (Walan et al. 2014). Thus, the mentioned facts and surface water eutrophication due to excessive P from soil surface runoff, made scientists investigate the alternative solutions (Chien et al. 2009).

4.4 Soil Phosphorus Cycle

There are a handful of main sources of mineral phosphorous in the world. The first one is an igneous rock in the lithosphere containing fluorapatite crystals. Another one is sedimentary rocks, in which P is mainly associated with carbonate-fluorapatite, then is sedimentary rocks in which P is mainly associated with carbonate-fluorapatite. Apatite minerals are dominated by sediments of ocean and freshwaters (Filippelli 2008; Stumm 1973; Yuan et al. 2018). As it is mentioned before, in apatite minerals phosphate presents in links with calcium cations. The reaction of carbonic acid with apatite minerals results in weathering of phosphate rocks through the following reaction:

$$\mathrm{Ca_5(PO_4)_3OH} + 4\mathrm{H_2CO_3} \leftrightarrow 5\mathrm{Ca^{2+}} + 3\mathrm{HPO_4^{2-}} + 4\mathrm{HCO_3^-} + \mathrm{H_2O}$$

This reaction, known as chemical weathering, is a consequence of preparing raw material by physical weathering. Physical weathering provides P, an unavailable form of phosphorus for biota through soil erosion. But this phenomenon produces fine raw materials whit large surfaces for chemical weathering which provides soluble forms of phosphate for biota (Filippelli 2008; Yuan et al. 2018). Ocean sediments are another large phosphor pool. Soils weathering and waterways runoff deliver phosphorus from land to the oceans. Meanwhile, riverine runoff, a very short part of P (only 0.5 ± 0.5 Tg P yr − 1) transports to the ocean via atmospheric transfer (Yuan et al. 2018).

Living organisms are the bridges between mineral and organic P cycles either in terrestrial or aquatic environments. The organic cycle consists of the transformation of P from soil to plants and animals through immobilization, and then returning to the soil through mineralization by microorganisms after their death. Organic tissues are oxidized by bacterial and fungal strains during mineralization, and resulted in P from this reaction is released to the soil as bioavailable phosphate. During mineralization, bacteria and fungi oxidize organic tissue and release P as bioavailable phosphate to soil (Yuan et al. 2018). Soil organisms and plants root participate in phosphate solubilization by producing $\mathrm{CO_2}$ and organic acids. Biochemical respiration is the phenomenon in which $\mathrm{CO_2}$ releases in the soil and provides an acidic area around degrading organic tissue (Schlesinger and Bernhardt 2013). This increase in soil acidity results in rapid dissolution of P-bearing minerals and releasing P to the soil for plant uptake. Secretion of phosphatase or making symbiotic lives with other organisms (such as mycorrhizae) are other tactics using by plants to increase soluble and bioavailable forms of phosphate around their roots (Yuan et al. 2018). The P concentration of the soil solution at equilibrium state will provide maximum P for plant uptake, highest at the slightly acidic to neutral pH range and are reduced considerably in strongly acidic or alkaline soil conditions (Arif et al. 2017) (Fig. 4.1).

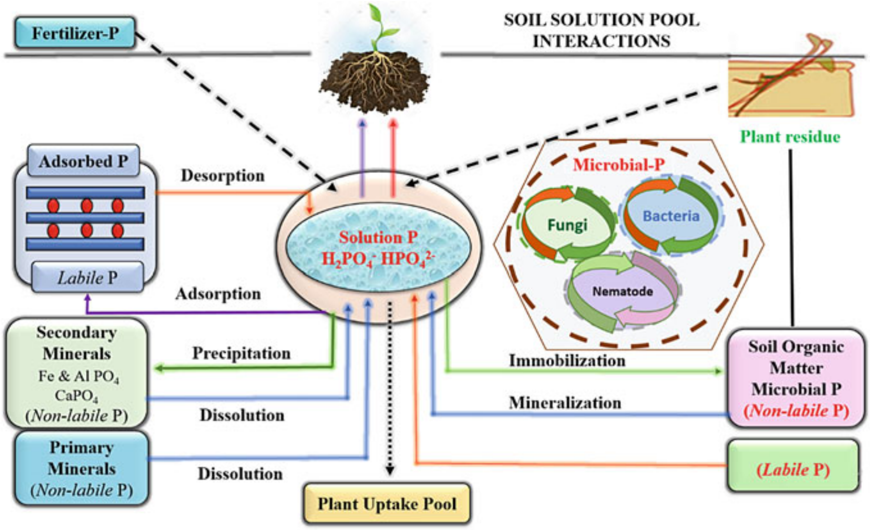

Fig. 4.1 Phosphorus cycle (Arif et al. 2017)

4.5 Different Strategies to Increase Soil Soluble Phosphate Requirement

Organic phosphate, obtaining from natural resources such as bones, vegetables and manures is the first used strategy in history. This form of P is a crucial source of immobilized P which accounts for 20–80% of phosphate in soils (Edixhoven et al. 2014). Since the 1940s, soil organic P has been widely researched (Condron et al. 2005). Organic P refers to P bonded with C in any way. The origins of soil organic P are animal and plant dead remains and another part is produced by soil organisms through their metabolism. Orthophosphate is the absorbed form of phosphate from the soil by microorganisms. The absorbed P covalently bonds to C moieties through some biochemical pathways (Goldwhite 1981). Depended on the type of P bond, we classify organic P compounds into three types of orthophosphate esters, anhydrides and phosphonates. Further, synthetic organic phosphate compounds could widely be applied to soil as plant growth regulators or pesticides and affect the P cycle of the soil (Condron et al. 2005). Specific aspects of soil organic P, organic matter include plants, manure and microbial P dynamics as a conceptual model is shown in Fig. 4.2.

Based on the information obtained from organic phosphate, the first fertilizer was produced in the laboratory by the germen chemist “Liebig” in 1840 through dissolving bones in H_2SO_4 to form super-phosphate that increased soil P bioavailability. Following this practice resulted in the restriction of bone supply very soon. In 1847, extraction of P from rocks was started to defeat this problem (Samreen and Kausar 2019). By 1853, England, the United States and Austria were the biggest super-phosphate producers worldwide (Russel and Williams 1977). These days in

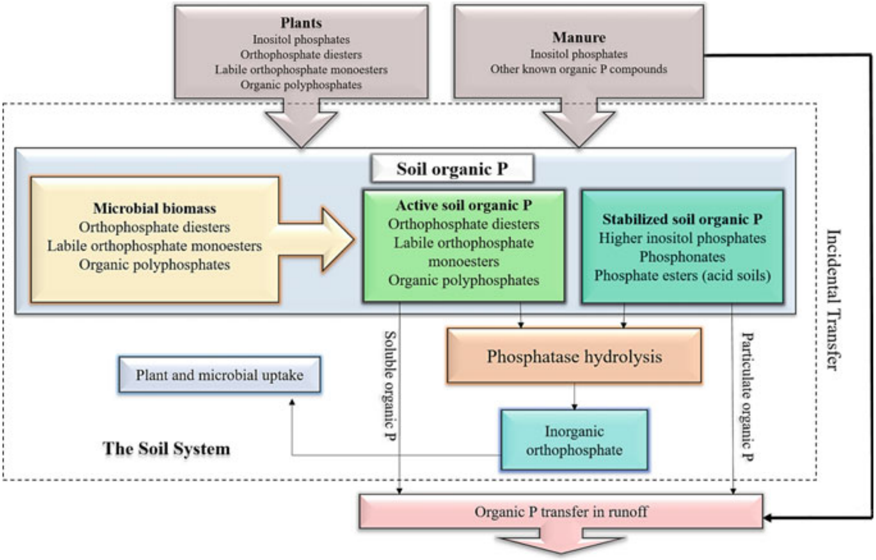

Fig. 4.2 Conceptual model of soil organic P dynamics (Condron et al. 2005)

most of the countries, farmers are recommended to use large amounts of inorganic phosphate fertilizers to achieve an insured level of bioavailable P in the soil so that avoid crop yield limitations due to phosphate shortage. From consequences of this inefficient insurance-based approach, we can name low rates of phosphate recovery in soil due to P fixation phenomenon, fluctuations in crop response to the applied fertilizer, large annual phosphate surpluses and this elements accumulation in soil which forms residual P and indispensable environmental hazard (Withers et al. 2014).

A routine procedure of soil test P known as STP is used for monitoring soil P fertility increase and maintenance. Using this method brings more efficient practices of P fertilizer (in case of timing, methods and amount of application) and noticeably reduces dependence on P fertilizers relying on investigations about soil potentials to reduce P demand, using inherent P present in soil, recycling and recovering it (Withers et al. 2014). To overcome these problems, many researches are done recently. For example, Heppell has recommended gaining more information about soil characteristics and predict fertilizer placement and the needed amount to apply using mathematical models. These models provide required analysis to evaluate strategies that cannot easily be gained at field scale experiments because of money, time and location-specific limitations (Heppell et al. 2016).

The wet method is called to treating phosphate rocks with sulfuric acid after mining and upgrading. Edixhoven has suggested using reactive phosphate rock as a more suitable form of PR because of its chemical composition (containing accessory minerals such as Ca) which helps rapid dissolution of P fertilizer in the soil. In their study, Morocco phosphate rocks were introduced as an effective source of P fertilizer, regarding its residual effects (Edixhoven et al. 2014). Further, this fact that agricultural dependence on phosphate fertilizers is very inefficient, regarding the depletion of global phosphate rocks, this method not only is increasingly costly and not able to respond to growing P demand, but also causes many environmental problems (Withers et al. 2014).

4.6 Environmental Problems of Chemical Fertilizers

Fertilizers are used to provide and certify required nutrients for crops and they are successful in this case. However, they may contain trace elements such as As, Cd, and Pb which can accumulate in the soil after repeated application of fertilizers. The further direct effect of this accumulation on soil quality, these trace elements harm human health by entering the food chain processes (Jiao et al. 2012; Tiwari et al. 2021; Patil et al. 2021) (Fig. 4.3).

The bioavailability of trace elements in the soils is affected by several factors such as soil pH, type of organic matter and cation exchange capacity (CEC). The number of factors such as soil pH, type of organic matters and cation exchange capacity (known as CEC) are effect trace elements bioavailability in soils. Long-term use of phosphate fertilizers influences these factors by a significant decrease in soil pH and increasing CEC. Besides, As accumulation in soils results in a competition between P and As in soil, for plant absorption and solid-phase binding sites. Therefore, an As accumulation is perceived in both shoot and root of wheat plants (Jiao et al. 2012). This repetitive application also leaves a legacy of phosphate accumulation in soils, wastes and sediments that easily gets into surface waters and causes widespread eutrophication (Withers et al. 2014) in a way that an estimate on 100 world's largest lakes showed that total P (TP) average loads during 2005–2010 were 7% higher than what it was during 1900–1995. It is interesting to know that in South America, this number reached 79% (Fink et al. 2016).

Eutrophication has several negative impacts on the fresh waters ecosystem. Phytoplankton species' dramatic growth is one of the most immediate impacts of this and in acute cases, harmful algal blooms (HABs), death of fishes and increased concentration of harmful metabolites which makes drinking water dangerous to use are observed (Jetoo et al. 2015; Yuan et al. 2018; Kumar et al. 2021). Further loss of biodiversity as a consequence of long-term eutrophication, there is also the occurrence of hypoxia in hypolimnia part of waters as a result of eutrophication. In a study, it has indicated that 20% of 365 lakes worldwide, met hypoxic condition since the middle years of the nineteenth century and is highly associated with total P release (Jenny et al. 2016; Vonlanthen et al. 2012; Yuan et al. 2018).

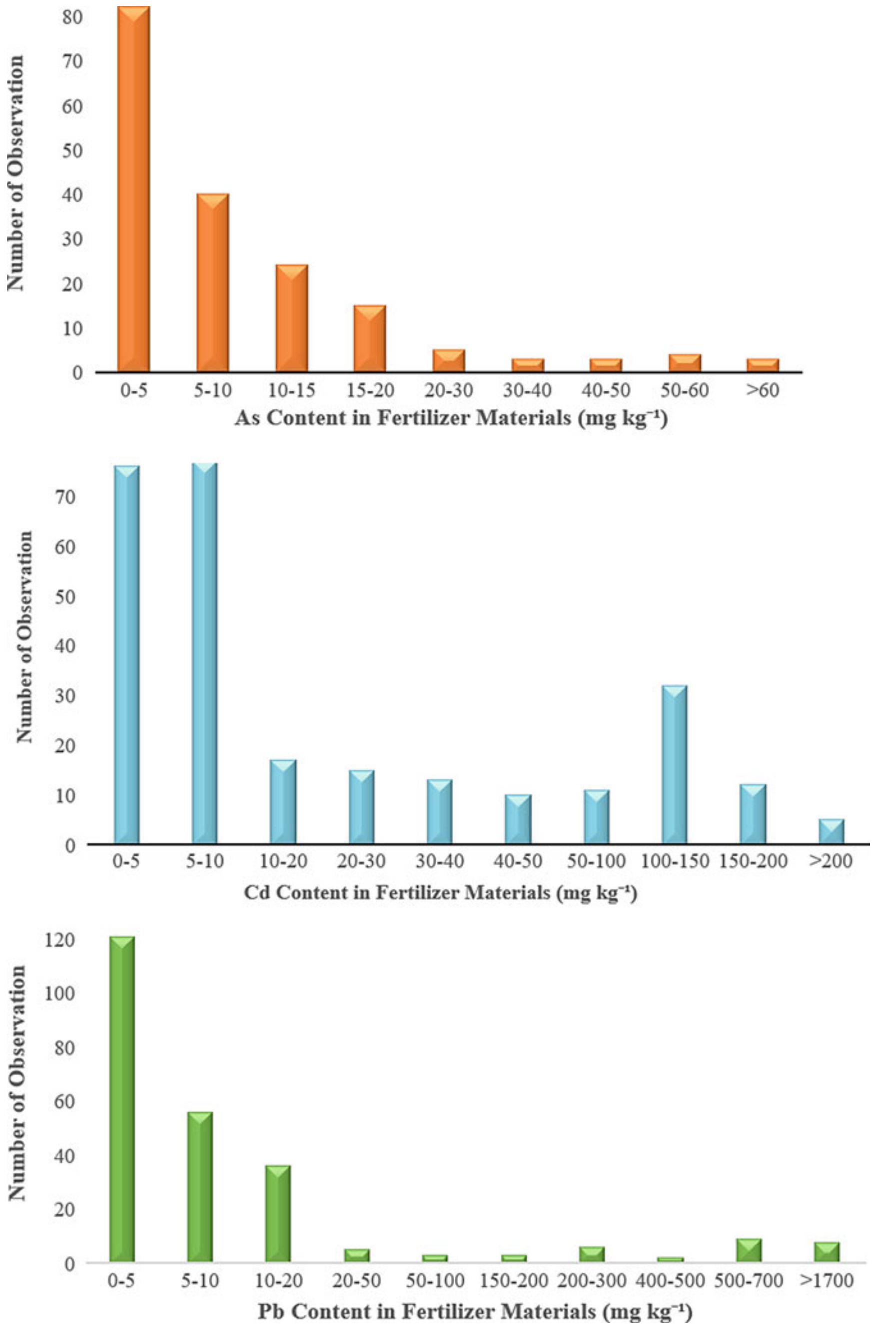

Fig. 4.3 Probability distribution of As, Cd and Pb content in commercial phosphate fertilizers in USA (Jiao et al. 2012)

4.7 Phosphate-Solubilizing Microorganisms

Phosphorus has a key role in many important biological processes such as energy production, respiration, photosynthesis, biosynthesis of macromolecules and nitrogen fixation (Khan et al. 2010; Yadav et al. 2020, 2021). But Phosphorus is a limited factor due to its non-availability in soluble forms in many agricultural soils. Soil microorganisms can affect the health of the soil and its nature by doing beneficial or harmful activities. Microorganisms living in the rhizosphere participate in certain processes, such as biodegradation, mineralization, decomposition, nutrient immobilization, nitrogen fixation and release of nutrient (Rai et al. 2020; Yadav et al. 2018). Phosphate-solubilizing microorganisms (PSMs) applies to some microorganisms include archaea, bacteria, actinomycetes and fungal strains that could liberate soluble phosphorous from insoluble soil P and making it available for other living organisms such as plants and other microorganisms (Pradhan et al. 2017; Saeid et al. 2018; Sujatha et al. 2020). It could be occurred by solubilization and mineralization of inorganic and organic phosphates in soil (Arif et al. 2017; Khan et al. 2016; Khan et al. 2007; Kumar 2016). A brief schematic model for the isolation of PSMs from different sources is shown in Fig. 4.4.

These microorganisms could be as an alternative to chemical phosphorus fertilizer which is better than them, because these PSMs promote plant growth by providing other plant requirements such as nitrogen via nitrogen fixation, phytohormones synthesizing, biocontrol of plant disease, producing 1-aminocyclopropane-1carboxylate (ACC) deaminase and reducing ethylene toxicity (Zaidi et al. 2009b; Dikilitas et al. 2021; Suyal et al. 2021). Phosphate-solubilizing bacteria (PSB) are also called phosphobacteria because they can increase the availability of orthophosphate to the plant by secreting P-hydrolyzing enzymes (Barra et al. 2018; Jorquera

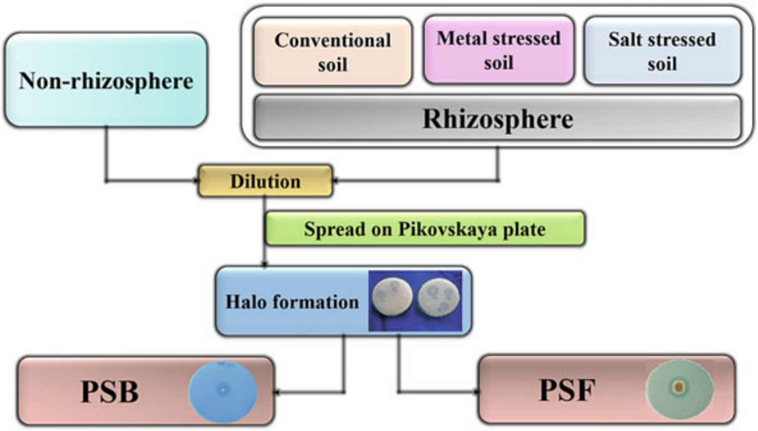

Fig. 4.4 A brief schematic model for isolation of PSMs from different sources. Adapted from (Zaidi et al. 2014)

et al. 2008; Patel et al. 2010) and organic acids (Sharon et al. 2016). Rock Phosphate (RP) is the most abundant form of phosphate worldwide. P-solubilizing microorganisms such as *Pseudomonas strita*, *Aspergillus awamori* and arbuscular mycorrhizae could be used effectively for RP dissolution (Kaur and Reddy 2017).

The interactions between plants and microorganisms and the ability of microorganisms to promote the growth of plants is agriculturally and environmentally important. This promotion can be caused by endophytic and rhizospheric bacteria and fungi. These microorganisms are termed as plant growth-promoting microorganisms (PGPM), plant growth-promoting bacteria (PGPB), plant growth-promoting fungi (PGPF), plant growth-promoting actinobacteria (PGPA) or plant growth-promoting rhizobacteria (PGPR) depending on the kind or the habitat of them. PGPMs can act either as free organisms in the rhizosphere or live endophytic in external or internal parts of plant tissues (Sujatha et al. 2020). Endophytes are microorganisms (mostly bacteria and fungi) that present asymptomatically in plants (White et al. 2019). Both organisms benefit during symbiotic association between plants and endophytes, and there is a mutualistic relationship between them (Rana et al. 2019b). The plant provides food for the colonizing of endophytes, and endophytes promote biosynthetic pathways to produce metabolites that are important in plant growth (Sujatha et al. 2020). PGPM can absorb nutrients from the soil and transfer them to the plant, stimulate plant development, increase plant resistance to various environmental stressors such as oxidative stress, saline stress and tolerance to heavy metals, reduce the pathogenicity of pathogens and increase plant resistance to disease and suppresses the growth of competitor plant species (White et al. 2019).

Some of PGPM that have the ability to dissolve phosphate from organic and inorganic forms are considered as PSMs (Ahemad and Kibret 2014; Barra et al. 2018; da Silva et al. 2018; Emami et al. 2020; Jorquera et al. 2008; Patel et al. 2010; Rana et al. 2012; Sindhu et al. 2014). The bioavailability of inorganic phosphorus by PSMs in the plant rhizosphere varies considerably due to plant species, soil conditions and the amount of nutrient in the soil (Khan et al. 2007). The production of different organic and inorganic acids is the main responsible mechanism for the phosphorus solubilization (Saeid et al. 2018). The most dominant and efficient PSMs strains in rhizospheric region include the P-solubilizing bacteria such as *Bacillus polymyxa* and *Pseudomonas striata* and among fungi are *Aspergillus niger*, *A. awamori* and *Penicillium digitatum* (Kaur and Reddy 2017).

Inoculating seeds, crops and soil with PSMs is an encouraging strategy to increase the potential of world food production. Plant growth promotion could be done by endophytic and rhizospheric microorganisms as microbial inoculants (da Silva et al. 2018). This strategy has not shown any environmental hazards. Because of significance role of inoculant in improving soil fertility, at the near future, the use of phosphorus-solubilizing microorganisms as inoculant could be instead of chemical fertilizers using conventionally in commercial agriculture (Alori et al. 2017). The phosphatic microbial inoculants, sometimes termed microphos are viable bacterial or fungal preparations that can be applied under different agro-ecological niches (Khan et al. 2016; Zaidi et al. 2009b, 2014). In this section, the types of microorganisms that can dissolve phosphorus and therefore can be used as fertilizer are introduced.

In the following, the mechanisms of solubilization of inorganic phosphorus by PSMs and mineralization of organic phosphorus will be discussed.

4.7.1 Phosphate-Solubilizing Fungi

Fungi are an important component of soil microbiota. In most soils, the biomass of fungi is higher than that of bacteria, depending on the depth of the soil and the nutrients condition. PSF have been isolated from different habitats such as agricultural soil, forest soil, rhizosphere of different crop plants, coffee plantation, saline soil, mine soil, terrestrial soil, hill soil, volcanic soils, arctic region, mangrove area, husk waste and vermicompost (Sahoo and Gupta 2014; Abdel-Azeem et al. 2021). According to their role and the region of colonization, fungi can be classified as pathogenic, epiphytic, endophytic and mycorrhizal fungi (Porras-Alfaro and Bayman 2011). Endophytic fungi belong to different genera include *Penicillium, Aspergillus, Trichoderma, Rhizopus, Fusarium, Cryptococcus, Paecilomyces, Cladosporium, Rhizoctonia, Curvularia, Rhodotorula, Cladosporium, Alternaria, Phaeomoniella, Ophiognomonia, Chaetomium, Acremonium, Geomyces, Phyllosticta, Colletotrichum, Berkleasmium, Glomus, Wallemia, Leptospora, Microdochium, Neotyphodium* and *Xylaria.* These PSF have been isolated from various host plants (Ameen et al. 2019; Elias et al. 2016; Islam et al. 2019; Noorjahan et al. 2019; Rojas et al. 2019; Sahoo and Gupta 2014; Sujatha et al. 2020; Rana et al. 2019a).

PSF can effect on phosphate solubilization in both free and endophytic forms. Among PSMs, plant growth-promoting fungal stains (PGPF), have the ability to solubilize insoluble P to soluble forms and make it available for plants by several methods such as organic acid production, ion exchange and chelation processes. They also could promote plant growth by different mechanisms (Khan et al. 2010; Sujatha et al. 2020) (Fig. 4.5). So application of PSF with rock phosphate seems to be a cost-effective method for phosphate availability in agriculture (Kaur and Reddy 2017).

Black Aspergilli and some of *Penicillium* species are filamentous fungi that produce organic acid and have been reported to solubilize rock phosphates. Some PSF and their habitat are shown in Table 4.2. One of the main responsible mechanisms for phosphorus solubilization in PSMs is the production of different organic and inorganic acids (Saeid et al. 2018). Organic acids produced by different PSF are shown in Table 4.3.

4.7.2 Phosphate-Solubilizing Bacteria (PSB)

Phosphate-solubilizing bacteria belong to different genera such as *Pseudomonas*, *Mesorhizobium, Azotobacter, Beijerinckia*, *Enterobacter*, *Acinetobacter, Erwinia*,

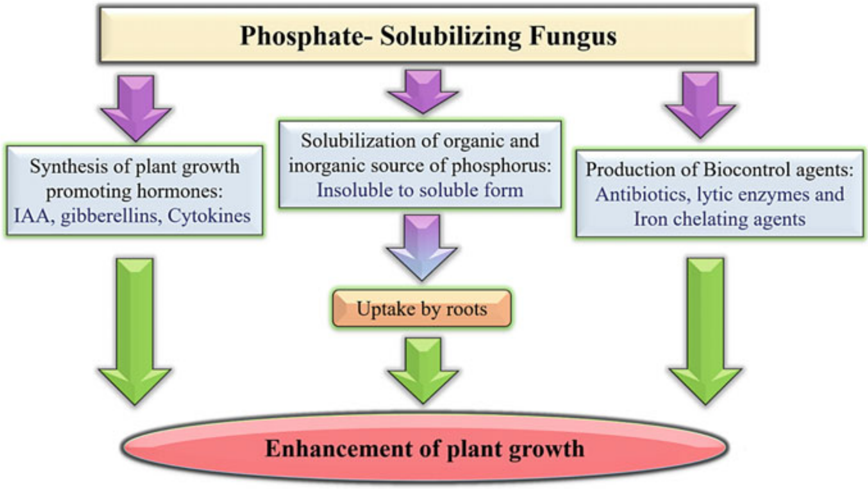

Fig. 4.5 Mechanisms involved in plant growth promotion by phosphate-solubilizing fungi. Adapted from Sujatha et al. (2020)

Serratia, Flavobacterium, *Burkholderia*, *Arthrobacter*, *Microbacterium*, *Bacillus*, *Rhizobium* and *Rhodococcus* (Kour et al. 2020b; Singh et al. 2020c; Verma et al. 2016; Yadav et al. 2015a). These PSB are used as biofertilizers to increase plant growth. Organic acid production is one of the most important mechanisms for phosphate solubilization (Yadav et al. 2015b). Different organic acids produced by PBS are shown in Table 4.4.

4.7.3 Phosphate-Solubilizing Actinobacteria

Among PSMs, actinomycetes produced different substances such as antibiotics, antifungi, anti-helminthes and phytohormones. On the other hand, these filamentous bacteria reproductive in very different soils and could be grown in extreme condition, because some of them could produce semi- resistance forms such as conidiospores and sporangiospores. Like PSFs and PSBs, PSA could produce some plant growth-promoting substances. Some researchers work on PSA and isolated different genus according to their habitat (Alper et al. 2020; Chukwuneme et al. 2020; Faried et al. 2019; Fatmawati et al. 2019; Mesta et al. 2018; Nandimath et al. 2017; Phạm et al. 2020; Putri et al. 2020; Wahyudi et al. 2019). The main mechanisms for phosphate solubilization by actinomycetes might be either due to organic acid secretion causing acidification of the surrounding medium or production of chelating agents such as siderophores to form a stable complex with phosphorus adsorbents (Faried et al. 2019).

Table 4.2 Some phosphate-solubilizing fungi and their habitat

P-Solubilizing fungi	Habitat	References
Aspergillus clavatus	Agricultural soil; saline soil	Chakraborty et al. (2010), Singh et al. (2012)
Aspergillus melleus	Agricultural soil	Chakraborty et al. (2010)
Penicilium purpurogenum	Agricultural soil	Scervino et al. (2010)
Penicilium citrinum	Hill soil; rhizosphere of sugarcane; rhizospheric soils	Sharma (2011), Yadav et al. (2011)
Penicilium. albidum *Penicilium frequentans*	Volcanic soils	Morales et al. (2011)
Penicilium restrictum	Volcanic soils; hills soil	Morales et al. (2011), Sharma (2011)
Penicilium mellini *Penicilium olivicolo* *Penicilium rugulosum*	Hill soil	Sharma (2011)
Penicilium notatum	Rhizospheric soil and roots	Malviya et al. (2011)
Aspergillus glaucus *Aspergillus sydowii*	Himalayan soil Himalayan soil, saline soil	Rinu et al. (2013), Singh et al. (2012)
Cylindrocarpon obtusisporum *Cylindrocarpon didymum,* *Paecilomyces marquandii,* *Penicillium janthinellum*	Coffee plants	Posada et al. (2013)
Aspergillus glaucus, *A. niger* *A. sydowii*	Himalayan soil	Rinu et al. (2013)
Aspergillus sp. *Penicillium* sp.	Rhizosphere of banana	Reena et al. (2013)
Aspergillus sp.	Rhizosphere soil of leguminous plant	Selvi (2013)
Aspergillus niger *Penicillium variable* *Trichoderma harzianum* *Fusarium*	Soil	Yasser et al. (2014)
Bipolaris tetramera	Rhizosphere	Fatima et al. (2015)
Penicillium bilaii	Sand soil	Ram et al. (2015)
Penicillium oxalicum *Aspergillus niger*	Maize Rhizosphere, Soybean rhizosphere	Li et al. (2016)
Aspergillus sp. *Penicillium spp* *Fusarium*	Rhizosphere soil	Elias et al. (2016)
Talaromyces aurantiacus *Aspergillus neoniger*	Rhizosphere soil	Zhang et al. (2018)

(continued)

Table 4.2 (continued)

P-Solubilizing fungi	Habitat	References
Aspergillus chevalieri *Fusarium moniliforme* *Trichoderma harzianum*	Rhizosphere soil, Agriculture soil	Abdel-Ghany et al. (2019)
Aspergillus niger *Penicillium oxalicum* *Talaromyces pinophilus*	Soil	Islam et al. (2019)
Aspergillus niger *Penicilium brevicompctum* Direx (Hs42)	Coffee plants	Rojas et al. (2019)
Glomus multisubtensum *Rhizophagus intraradices*	Rhizosphere soil	Nacoon et al. (2020)
Aspergillus niger	Different farm	Mazrou et al. (2020)
Penicillium oxalicum	Corn farm	Wang et al. (2020)
Aspergillus, Penicillium, Trichoderma, Piriformospora curvularia	Different farm	Sujatha et al. (2020)

Thermo-tolerant actinomycetes are more resistant to the high temperature of composting than mesophilic organisms, so they are a better choice for phosphate-solubilizing biofertilizer production which could be added to the biodegradation of complex macromolecules in composting (Nandimath et al. 2017). Because of their filamentous structure, such as filamentous fungi, they could save more water than other bacteria in their hyphae and alive in drought stress. Drought stress is alleviated by mediated drought-adaptive and phosphorus solubilizing actinomycetes (Chukwuneme et al. 2020; Kour et al. 2020a). The isolated strains under drought stress accumulate different osmolytes such as glycine, betaine, proline, sugars and decreased lipid peroxidation and increased chlorophyll content (Kour et al. 2020a). The isolated actinomycetes from different habitats are demonstrated in Table 4.5.

4.8 Mechanism of P-Solubilization

There are two major mechanisms for releasing P from different compounds by soil microorganisms. Solubilization and mineralization are effective mechanisms for releasing P from inorganic and organic compounds respectively. Another reaction that performed by soil microorganisms is P immobilization, which provides accessible P for uptake by plants. The notable mechanisms used by PSMs for P-solubilization from inorganic compounds are (i) organic and inorganic acids, protons, hydroxyl ions, CO_2 and siderophores production that dissolve or complex with inorganic compounds for release of P; and (ii) secretion of extracellular enzymes (Khan

Table 4.3 Organic acids produced by phosphate-solubilizing fungi

Microorganism	Organic acids	References
Penicillium rugulosum *Aspergillus niger*	Citric, gluconic, succinic	Reyes et al. (2001), Vazquez et al. (2000)
Aspergillus niger *Aspergillus clavatus* *Penicilium conescens*	Oxalic, citric, gluconic	Alam et al. (2002)
Aspergillus flavus Aspergillus niger, Penicillium canescens	Oxalic, citric, gluconic, succinic	Rashid et al. (2004)
Aspergillus flavus	Fumaric, gluconic, succinic, acetic, Oxalic, citric	Rashid et al. (2004)
Aspergillus flavus Aspergillus candidus, Penicillium oxalicum	Glutaric, malic, gluconic, oxalic	Shin et al. (2006)
Aspergillus niger *Aspergillus terreus* *Aspergilluswentii, Fusarium oxysporum* *Penicillium* sp. *Trichoderma isridae, Trichoderma* sp.	Lactic, maleic, malic, acetic, tartaric, citric, fumaric, gluconic	Akintokun et al. (2007)
Aspergillus niger, Penicillium bilaiae, Penicillium sp.	Oxalic, citric	Arwidsson et al. (2010)
Trichoderma flavus *Trichoderma helicus* *Penicilium purpurogenum,* *Penicilium janthinellum*	Acetic, butyric, citric, fumaric, gluconic, glucuronic, lactic, oxalic, propionic, succinic, valeric	Scervino et al. (2010)
Aspergillus awamori S19	Oxalic, malic, citric, succinic, fumaric	Jain et al. (2012)
Aspergillus niger FS1 *Penicilliumcanescens* FS23 *Eupenicillium ludwigii* FS27 *Penicillium islandicum* FS30	Citric, gluconic, oxalic	Mendes et al. (2013)
Aspergillus sp. *Penicillium* sp.	Acetic	Syamsia et al. (2015)
Burkgolderia	Acetic, oxalic, lactic, oxalic, butyric	Istina et al. (2015)
Aspergillus niger	Citric, oxalic	Li et al. (2016)
Aspergillus niger *Aspergillus terrus*	Itaconic	Hossain et al. (2019)
Aspergillus niger	Oxalic	Kang et al. (2020)
Trichoderma spp.	Lactic, fumaric, gluconic, citric, D-isocitric, ascorbic, D-malic, phytic acid	Bononi et al. (2020)

Table 4.4 Organic acids produced by different phosphate-solubilizing bacteria

Bacteria	Organic acids	References
Bacillus amyloliquefaciens, Bacillus licheniformis, Bacillus atrophaeus, Paenibacillus macerans, Pseudomonas aeruginosa	Lactic acid, isovaleric acid, isobutyric acid, acetic acid	Vazquez et al. (2000)
Enterobacter intermedium	2-ketogluconic	Hwangbo et al. (2003)
Pseudomonas fluorescens	Citric acid, malic acid, tartaric acid, gluconic acid	Fankem et al. (2006)
Bacillus, Rhodococcus, Arthrobacter, Serratia and one Chryseobacterium, Delftia, Gordonia, Phyllobacterium, Arthrobacter ureafaciens, Phyllobacterium myrsinacearum, Rhodococcus erythropolis, Delftia sp.	Citric acid, gluconic acid, lactic acid, succinic acid, propionic acid	Chen et al. (2006)
Burkholderia, Serratia, Ralstonia and Pantoea	Gluconic acid	Perez et al. (2007)
Burkholderia cepacia DA23	Gluconic acid	Song et al. (2008)
Pseudomonas corrugate (NRRL B-30409)	Gluconic, 2-ketogluconic acid	Trivedi and Sa (2008)
Citrobacter sp. DHRSS	Acetic and gluconic acid	Patel et al. (2008)
Arthrobacter sp. (CC-BC03)	Citric acid, lactic acid	Yi et al. (2008)
Pseudomonastrivialis (BIHB 769)	Gluconic acid, 2-ketoglutaric acid, lactic acid, succinic acid, formic acid, malic acid	Vyas and Gulati (2009)
Bacillus megatrium, Pseudomonas fluorescens	Gluconic acid, phosphoric acid, 2-ketogluconic acid	Sharma et al. (2011)
Enterobacter sp. Fs-11	Malic acid, gluconic acid	Shahid et al. (2012)
Bacillus sp.	Indoleacetic acid, oxalic acid. malic acid	Panhwar et al. (2012)
Pseudomonas sp.	Formic acid, butyric acid, propanedioic acid, gluconic acid	Chen et al. (2016)
Alcaligenes aquatilis, Burkholderia cepacia	Formic acid, gluconic acid, citric acid	Pande et al. (2017)
Firmicutes, Proteobacterium, Actinibacterium	Citric acid, lactic acid, succinic acid, acetic acid, formic acid, oxalic acid	Wei et al. (2018)
Leclercia adeearboxylata, Pseudomonas putida	Phosphoric acid	Teng et al. (2019)
Pantoea, serratia, Pseudomonas, Enterobacter	Oxalic acid, fumaric acide, gluconic acid, citric acid, succinic acid, acetic acid	Rfaki et al. (2020)

(continued)

Table 4.4 (continued)

Bacteria	Organic acids	References
Bacillus sp, Burkholderia sp, Paeni Bacillus sp	Gluconic acid, citric acid, succinic acid, acetic acid, tartaric acid, formic acid	Chawngthu et al. (2020)
Klebsiella variicola, Rhizophagus intraradies, Sphingobacterium thalpophilum, Ochrobactrum pseudogrignonense, Burkholderia tropica, Achrobacterium xylosoxidans, Pseudomonas aeruginisa	Phosphoric acid, gluconic acid, oxalic acid, acetic acid, marlic acid, lactic acid, tartaric acid, DL-marlic acid	Sabaiporn et al. (2020)
Agrobacterium sp	Fumaric acide, succinic acid, tartaric acid	Li et al. (2020)

Adapted Zaidi et al. (2009a, b)

Table 4.5 The isolated actinomycetes from different habitat

Habitat	Actinomycete genus isolated	References
Millet (Sorghum bicolour L.) under drought stress	*Streptomyces laurentii*	Kour et al. (2020a)
Olive tree Rhizisphere	*Streptomyces* sp.	Alper et al. (2020)
Maize plan	*Arthrobacter arilaitensis*	Chukwuneme et al. (2020)
Roots of acacia	*Fodinicola acaciae* sp.	Phạm et al. (2020)
Surface of the stone	*Gordonia, Microbactrium, Micromonospora, Nocardia, Streptomyces*	Putri et al. (2020)
Rhizosphere soil	*Streptomyces* sp.	Faried et al. (2019)
Forest soil, Rhizosphere soil	*Actinibacter* AH6, *Streptomyces.* sp.	Hamim et al. (2019)
Soybean Rhizosphere	*Streptomyces* sp. ASR46, *Streptomyces* sp. ASR58, *Streptomyces* sp. ASR75, *Streptomyces* sp. ASR76	Wahyudi et al. (2019)
Soybean Rhizosphere	*Streptomyces panaciradicis, Streptomyces recifensis, Streptomyces manipurensis, Streptomyces* spCAH7	Fatmawati et al. (2019)
Mongrove plants	*Rhizosphera mucronuta, Sunneratia caseoluris*	Mesta et al. (2018)
Thermo-tolerant	*Streptomyces flavissimus, Streptoverticillium olivoverticillatum, Streptomyces nogalater, Streptomyces longisporoflavus, Streptomyces cellulosae*	Nandimath et al. (2017)

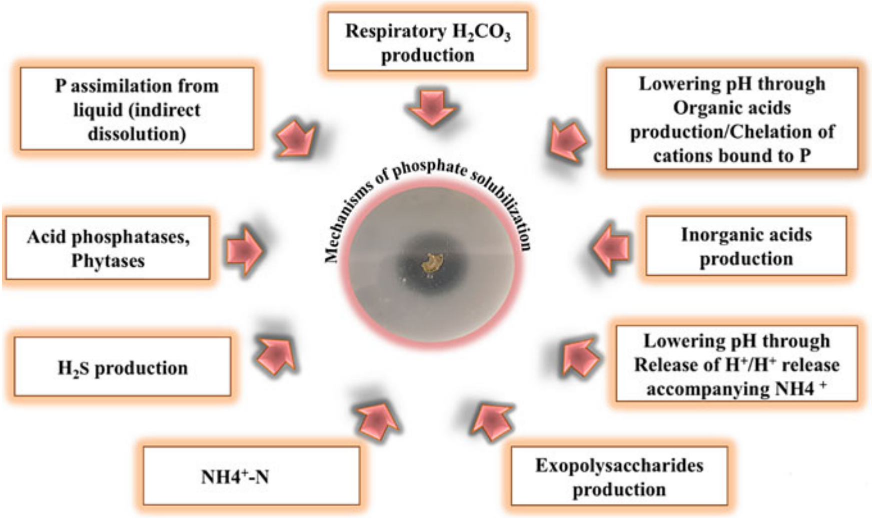

Fig. 4.6 Mechanisms for phosphate solubilization by PSMs. Adapted from Khan et al. (2010), Zaidi et al. (2009a, b)

et al. 2010; Zaidi et al. 2009b) Different mechanisms involved in the insoluble P-solubilization by natural soil microbial communities are briefly shown in (Fig. 4.6). There are three major processes in P cycle in the soil that microbial population play important role in them: facilitate mineralization to immobilization, dissolution to precipitation and sorption to desorption (Kaur and Reddy 2017).

4.8.1 Inorganic P-Solubilization

4.8.1.1 Acid Production and P-Solubilization

One of the most important mechanisms for solubilizing inorganic P is low molecular mass organic acids (OA) production. These acids mostly are the products of organic carbon sources metabolism by oxidative respiration or fermentation (Sharma et al. 2013). Organic acids generally separate into anion(s) and proton(s) in a pH-dependent equilibrium. By shifting the equilibrium of the dissolution, the H^+ ions prefer P-solubilization resulting in the release of more P into the solution. Organic acids also buffer the pH and continue to separate as protons. The major organic acids released by P-solubilizing microorganisms are gluconic, oxalic, citric, lactic, and tartaric and aspartic acids. Among these, gluconic acid and 2-ketogluconic acids seem to be the most frequent acids in P-solubilization (Kalayu 2019; Khan et al. 2010, 2016). OA produced by different fungal and bacterial PSM strains are listed in Tables 4.3 and 4.4 respectively. As shown in the Tables, the amount and type of organic acids are differing in different microorganisms. It seems that aliphatic acids are more effective than phenolic, fumaric and citric acids, and tri- or dicarboxylic acids efficiency in phosphate solubilization are more than monobasic and aromatic acids (Kalayu 2019).

By OA production, pH is decreased and cation chelations are increased and bring P into solution (Pradhan et al. 2017). In addition, organic acids have competed with P for adsorption sites on the soil and finally, by acidification of microbial cells and their surroundings, H^+ is substituted for metal ions such as Ca^{2+}, Al^{3+} or Fe^{3+} and release P-ions form insoluble metal salts such as tricalcium phosphate (TCP: $Ca_3)PO_4)_2$), aluminum phosphate ($AlPO_4$), iron phosphate (FePO4), etc., and phosphorus is released. So, in addition to the acidification process, in some PSMs, especially in fungi, chelation and reduction processes play important roles in P-solubilizing activity. Functional groups particularly carboxylic acid in chelating agents such as EDTA (Ethylene Diamine Tetra Acetate), DTPA (Diethylene Triamine Penta Acetic acid) and NTA (Nitrilo-2,2',2"-Tri Acetic acid) form a stable complex with metal ions of insoluble phosphate salts such as Ca^{2+}, Al^{3+} or Fe^{3+} and are influenced on P-solubilization.

Some of the inorganic acids such as HCl or nitric acid and sulfuric acid produced by chemoautotrophs and H^+ produced by proton motive force (PMF) during microbial metabolism could effect by the same way of OA in solubilizing the insoluble P. The inorganic acids convert TCP to di and monobasic phosphate which are more available for plants. According to the sink theory, in a liquid culture medium, P-solubilizing organisms release and assimilate P from the liquid and therefore, indirect dissolution of calcium phosphate compounds from liquid culture is activated by continuous removal of P (Sharma et al. 2013). H_2S production is another mechanism that reacts with $FePO_4$ and produces $FeSO_4$ with concomitant release of P. Another mechanism is H^+ production from $NH_4{}^+$assimilation that could be an alternative mechanisms of P-solubilization (Kumar 2016; Sharma et al. 2013).

4.8.1.2 Siderophores and P-Solubilization

Siderophores are low molecular weight agents secret by certain soil microorganisms to solubilize iron from insoluble organic or inorganic forms. In iron-limiting conditions, some microorganisms survive by secreting siderophores, which could effect on solubilizing iron from minerals or organic compounds by active transport carrier mechanism or mineralization (Arif et al. 2017; Kaur and Reddy 2017). Siderophores have wide applications in different areas including agriculture, microbial ecology, heavy metal bioremediation, biosensor technology and medicine (Saha et al. 2016).

In addition to iron, siderophores are chelate other ions by similar mechanisms (Karmakar et al. 2018). Many PSMs produce siderophores (Alori et al. 2017; Ameen et al. 2019; Chhabra and Dowling 2017; Chukwuneme et al. 2020; Saha et al. 2016). As mineralization of organic compounds such as ferric phosphate to extract Fe from them, P availability improves indirectly by siderophore producing PSMs (Kaur and Reddy 2017; Zaidi et al. 2009b).

4.8.1.3 Exopolysaccharides and P-Solubilization

Many microorganisms produce high molecular weight extracellular polymeric substances (EPS) around their cell wall. This non-enzymatic mucilage has special physicochemical characteristics and activities such as stability, suspending and gelling ability and the ability to store water, so, EPS producing microorganisms have many applications in various industries such as adhesives, pharmaceuticals, food and beverage industries, oil and metal recovery from ore and industries (Yi et al. 2008). EPS structural composition is heterogenous and mainly composed homo or heteropolysaccharides with various organic and inorganic substitutes (Arif et al. 2017). In addition to organic acids and protons, EPS is an important factor in the indirect dissolution of inorganic P such as TCP. In this process, P-solubilization homeostasis is changed toward P dissolution by EPS, because EPS is holding free P in the medium, therefore greater phosphorus is released from insoluble phosphate (Yi et al. 2008).

In addition to the above mechanisms, EPS is attached and formed complexes with soil metals and act as a chelating agent to release P from insoluble phosphates. Further studies are needed for understanding the relationship between phosphorus holding and EPS structure in different PSMs and its mechanisms.

4.9 Organic P-Solubilization

Organic P compounds and their mineralization play an important role in P cycling. There are several enzymes that released phosphorus from organic P compounds in the soil (Kaur and Reddy 2017):

(a) Phosphomonoesterases known as phosphatases are produced by different PSMs. These enzymes dephosphorylate phosphoester or phosphoanhydride bonds of organic matter. Acid phosphatases and alkaline phosphatases are different phosphatases that are more frequent in acidic and neutral or alkaline soils respectively. Plant roots are also produced acid phosphatases.

(b) Phytases release P from the phytate, the major organic P compounds in the soil that is the major form of P in plants. Phytases are a kind of phosphohydrolases. Phytate mineralization by soil microorganisms release P and make it available for plants root. Microbial phytases have led to the promotion of the plants grow during the supplementation exogenously, as well as the overexpression in different plants (Singh et al. 2020b).

(c) Phosphonatases and C-P lyases, which break the C-P bond of organophosphonates. The organophosphonates are biogenic and xenobiotic compounds characterized by the presence of a stable carbon to phosphorus (C-P) bond.

All the mechanisms including solubilization, immobilization and mineralization that effect on phosphorus bioavailability are shown in Fig. 4.7.

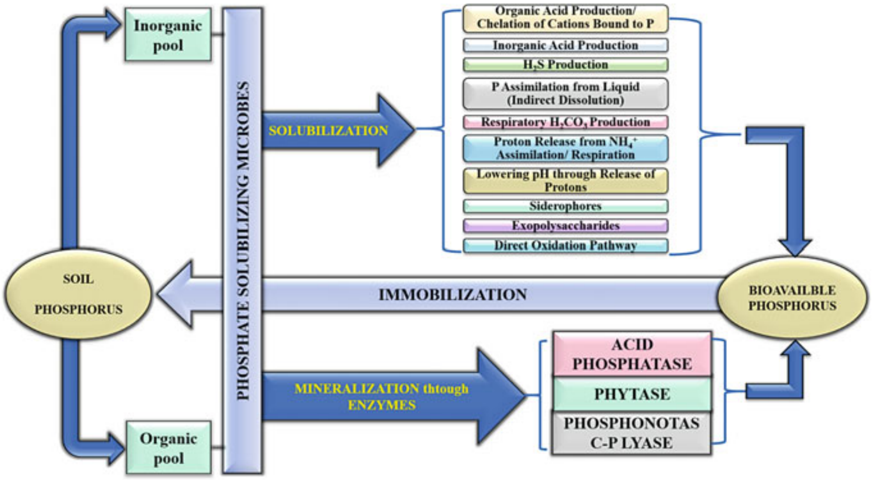

Fig. 4.7 Schematic representation of the mechanism of phosphate solubilization/mineralization and immobilization by phosphate-solubilizing microorganisms. Adapted from Kaur and Reddy (2017), Sharma et al. (2013)

4.10 Plant Growth Promotion by P-Solubilizing Microorganisms

Various mechanisms are used by PGPR to act as biofertilizers, phytostimulators, rhizoremediation agents or stress controllers (Lugtenberg and Kamilova 2009). Generally, these mechanisms can be categorized into two major groups of direct and indirect ways. Direct PGP methods include activities that cause improvements of mineral nutrients such as nitrogen fixation, phosphate solubilization, and iron sequestration by producing siderophores, production of organic plant growth regulators such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, auxins, cytokinin, gibberellins and ethylene. On another hand, indirect methods contain activities that result in inhibition of phytopathogenic microorganisms like, production of HCN, fungal cell wall degrader enzymes and a variety of antibiotic components (Arif et al. 2017; Kaur and Reddy 2017; Lugtenberg and Kamilova 2009) (Fig. 4.8).

In summary, phosphate-solubilizing microorganisms stimulate plant growth in the following ways (Fig. 4.9) (Khan et al. 2014; Sattiraju et al. 2019; Sharma et al. 2013):

- Solubilization of organic P and mineralization of inorganic P, which releases soluble P as a nutrient for plants
- Production of growth-promoting phytohormons:
  - Indole acetic acid (IAA): PSMs produced IAA that uptake by plants. IAA could effect on various stages of plant growth (Fig. 4.10).

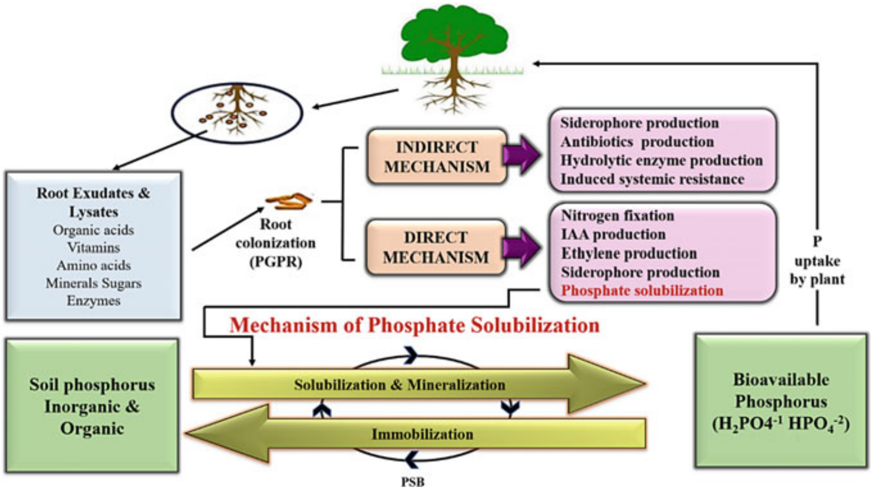

Fig. 4.8 Role of PGPR and mechanism of phosphate solubilization (Pradhan et al. 2017)

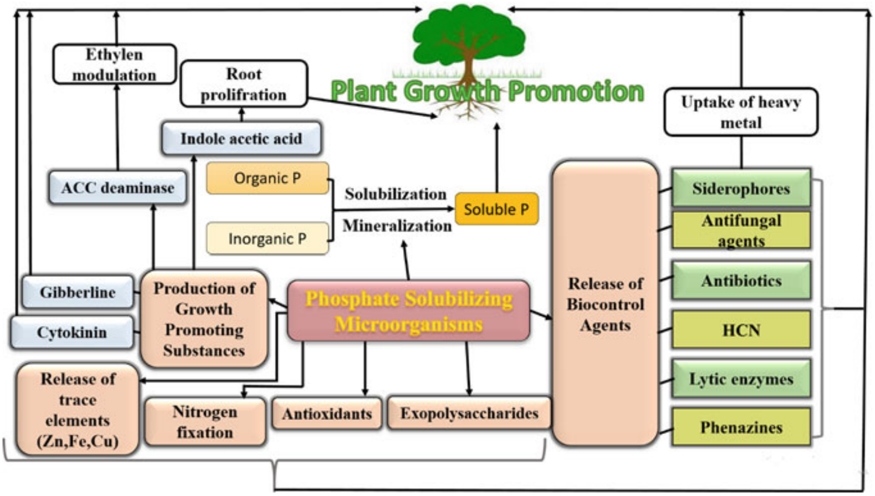

Fig. 4.9 Possible Mechanisms involved in plant growth promotion by PSMs. Adapted from Sharma et al. (2013)

- 1-aminocyclopropane-1carboxylate (ACC) deaminase: cleavage the ACC, the immediate precursor of ethylene by ACC deaminase will lead to reduced ethylene production in plants. Reduce the amount of ethylene increases plant growth (Fig. 4.11).
- Gibberellins: Some PSMs produce gibberline. Gibberlineis a growth regulator that affects seed germination, stimulates the growth of plants and delays aging.

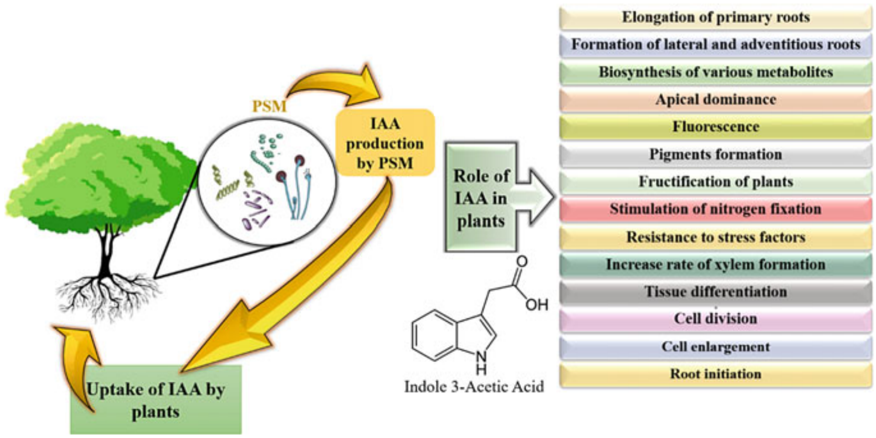

Fig. 4.10 Role of IAA in plant growth. Adapted from Khan et al. (2014)

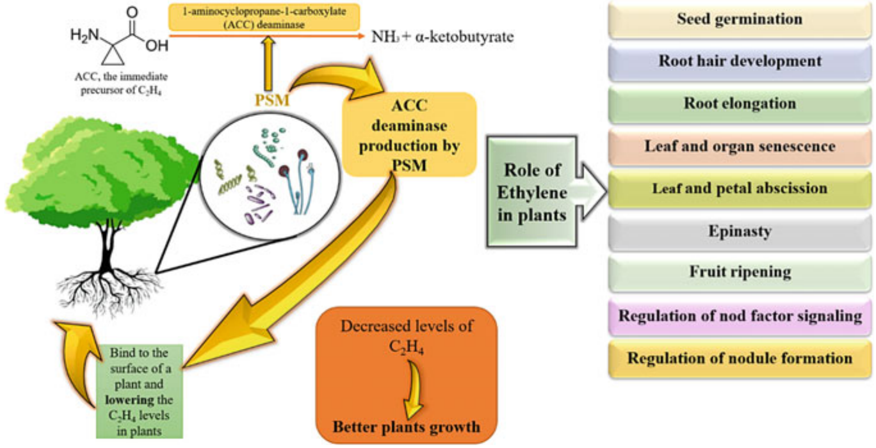

Fig. 4.11 The role of ACC deaminase in plant growth

  - Cytokinins: cytokinins produced by PSM influence both cell division and cell enlargement of plants and also affect seed dormancy, flowering, fruiting and plant senescence.

- Release of biocontrol agents: Biological control agents produced by PSM are generally considered more environmentally sound than pesticides and other antimicrobial treatments.
  - Siderophores: act as solubilizing agents for iron from minerals or organic compounds under conditions of iron starvation.

  - Antifungal agents: DAPG (2,4-diacetylphloroglucinol), Pyrrolnitrin and many other compounds are broad-spectrum antifungal metabolite that produced by some PSMs (Sattiraju et al. 2019).
  - Antibiotics: Oomycin A, pyoluteorin, pyrrolnitrin, tensin, tropolone, cyclic lipopepdes, oligomycin A, kanosamine, zwittermicin A, xanthobaccin, viscosinamideare some antibiotics that produced by some PSM (Sattiraju et al. 2019).
  - HCN: Hydrogen cyanide (HCN) blocks the cytochrome oxidase pathway and is highly toxic to all aerobic microorganisms at picomolar concentrations.
  - Lytic enzyme: microbial hydrolytic enzymes such as chitinase, β-1,3-glucanase, peroxidase, protease and lipase produced by PSM can effectively manage the plant pathogens and reduce them.
  - Phenazines: Phenazines are heterocyclic pigments that contain nitrogen which is produced by some PSM such as *Pseudomonas*, *Streptomyces*, *Burkholderia* and *Brevibacterium* species. They could be employed as biocontrol agents for phytopathogens (Sattiraju et al. 2019).

- Exopolysaccharide production
- Antioxidants production
- Nitrogen fixation
- Release of trace elements such as Zn, Fe and Cu.

Different growth-promoting substances produced by PSMs are shown in Table 4.6.

4.11 Genetic Manipulation of PSMs

So far several genes involving in phosphate solubilization have been reported and characterized. Through cloning and manipulation of these genes a higher capacity of phosphate-solubilizing activity by PSMs could be gained (Ingle and Padole 2017; Rodríguez et al. 2006). Expression of phosphatase encoding genes and both mineral phosphate solubilization and organic phosphate solubilization genes in for instance rhizobacterial strains has given a good perspective of using them in the development of sustainable agriculture (Zaidi et al. 2009a). The first step in this way was taken in 1987 by cloning of PS genes of *Erwinia herbicola* in an *E. coli* strain which gained PS ability after transformation (Goldstein and Liu 1987). Observing emerging the ability of gluconic acid production in the manipulated strain and sequencing of its related gene resulted in detecting involvement of pyrroloquinoline quinone (PQQ) synthase as an enzyme needed for producing a required co-factor for the formation of glucose dehydrogenase (GDH)-PQQ (Rodríguez and Fraga 1999). This approach continued by cloning of napA phosphatase gene driven from *Morganella morganii* in *Burkholderia cepacia* IS-16 (Fraga et al. 2001).

As time passed several other genes coding phosphate-solubilizing mechanisms were detected, analyzed and categorized which are shown in Table 4.7. These researches greatly helped to achieve modified PS strains with a high capacity of

Table 4.6 Growth-promoting substances released by phosphate-solubilizing bacteria

Phosphate-solubilizing bacteria	Plant growth-promoting traits	References
Pseudomonas sp., *Bacillus* sp.	IAA, siderophore	Rajkumar et al. (2006)
Mesorhizobiumloti MP6	HCN, IAA	Chandra et al. (2007)
Bacillus spp.	IAA, siderophores, ammonia production, HCN, chromium reduction, metal solubilization	Wani et al. (2007a, b)
Azotobacter sp., *Mesorhizobium* sp., *Pseudomonas* sp., *Bacillus* sp.	IAA, siderophore, antifungal activity, ammonia production, HCN	Ahmad et al. (2008)
Pseudomonasaeruginosa	ACC deaminase, IAA, siderophore	Ganesan (2008)
Pseudomonasjessenii	ACC deaminase, IAA, siderophore, heavy metal solubilization	Rajkumar and Freitas (2008)
Burkholderia	ACC deaminase, IAA, siderophore, heavy metal solubilization	Jiang et al. (2008)
Enterobacter sp.	ACC deaminase, IAA, siderophore	Kumar et al. (2008)
Acinetobacter sp., *Pseudomonas* sp.	ACC deaminase, IAA, antifungal activity, N2-fixation	Indiragandhi et al. (2008)
Pseudomonasfluorescens	ACC deaminase	Shaharoona et al. (2008)
Serratiamarcescens	IAA, siderophore, HCN	Selvakumar et al. (2008)
Bacillussubtilis	IAA, siderophore, antifungal activity	Singh et al. (2008)
Pseudomonas sp.	ACC deaminase, IAA, siderophore	Poonguzhali et al. (2008)
Dyellaginsengisoli, *Burkholderiakururiensis*, *Pandoraea* sp. strain ATSB30	Siderophore, IAA, salicylic acid, ACC deaminase	Anandham et al. (2008)

(continued)

Table 4.6 (continued)

Phosphate-solubilizing bacteria	Plant growth-promoting traits	References
Pseudomonasaeruginosa, *PseudomonasPlecoglossicida* and *Pseudomonasmosselii*	ACC deaminase, IAA, siderophore, heavy metal solubilization	Jha et al. (2009)
Pseudomonasaeruginosa PS1, *Klebsiella* sp. strain PS19	IAA, HCN, Siderophore	Ahemad and Khan (2011a, b)
Pantoeaagglomerance, *Burkholderiaanthina*	IAA, ammoni, HCN, siderophore	Walpola and Yoon (2013)
Dematophoranecatrix	IAA, HCN	(Mehta et al. 2013)
Enterobacterium sp. strain NIASMVII	IAA	Sorty et al. (2016)
Burkholderiacepacia, *AeromomashydrophilaBacillus* sp. *Pseudomonas* sp.	HCN, ammonium production IAA, siderophore	Chibani et al. (2016)
Klebsiella sp. strain M02, *Klebsiella* sp. strain M03, *Klebsiella* sp. strain M04 *Bacillusmegaterium* strain M06, *Bacillusmegaterium* strain M07, *Bacillusmegaterium* strain M08, *Paenibacillus* sp. strain M09, *Paenibacillus* sp. strain M010	IAA IAA, HCN IAA, HCN	Zhang et al. (2017)
Bacillus sp. strain STJP	IAA, siderophores	Prakash and Arora (2019)
Aneurinibacillus Acc02, *Paenibacillus* ACC06	ACC	Pandey and Gupta (2019)
Acinetobacter guillouiae	Nitrogenase activity, IAA	Rana et al. (2020)
Streptomycespseudovenezuelae, *Arthrobacterarilaitensis*	IAA, ACC	Chukwuneme et al. (2020)
Bacillussubtilis	Siderophore, IAA	Wang et al. (2020)
Bacillus sp., *Burkholderia* sp., *Paenibacillus* sp	IAA	Chawngthu et al. (2020)
Bacillussafensis, *Bacilluspumilus*, *Halobacillus*, *Pseudomonas*	HCN, IAA, siderophore, ACC deaminase, antifungal activity	Mukhtar et al. (2020)
Pantoea, *Pseudomonas*, *serratia*, *Enterobacter*	IAA, HCN, siderophore, antifungal activity	Rfaki et al. (2020)

Adapted from Zaidi et al. (2009b)

Table 4.7 Genes involved in phosphate solubilization

Microorganisms	Gene or plasmid	Features	References
Erwinia herbicola	Mps	Produces gluconic acid and solubilizes mineral P in *E. coli* HB101; probably involved in PQQ synthesis	Goldstein and Liu (1987)
Pseudomonas cepacia	Gab Y	Produces gluconic acid and solubilizes mineral P in *E. coli* JM109; No homology with PQQ genes	Babu-Khan et al. (1995)
Enterobacter agglomerans	pKKY	Solubilizes phosphate in *E. coli* 109; does not lower pH	Kim et al. (1997)
Rahnella aquatilis	pKIM10	Solubilizes phosphate and produces gluconic acid in *E. coli* DH5a	Kim et al. (1998)
Serratia marcescens	pKG3791	Produces gluconic acid and solubilizes phosphate	Krishnaraj and Goldstein (2001)
Mornanella morganii	napA, PRK293	Solubilizes phosphate and produces gluconic acid in *Burkholderia cepacia* IS-16 and *E. coli* Increase in the extracellular enzyme	Fraga et al. (2001)
Azospirillum sp.	pqq-GDH	Oxidation of glucose to gluconic acid	Vikram et al. (2007)
Enterobacter asburiae	gcd	Solubilizes phosphate and produces gluconic acid in *E. coli* AT15	Tripura et al. (2007)
Basillus subtilis CB8A	gdh, nifH	Solubilizes phosphate and produces gluconic, The ability of CB8A in wide range of temperature, pH and varying salt concentration can be exploited for developing multifunctional biofertilizer in apple orchards.	Mehta et al. (2013)
Erwinia herbicola, Pseudomonas fluorenscens, Acinobacter calcoaceticus	pqq-E	Solubilizes phosphate and produces gluconic in Herbaspirillum seropedicae Z67	Wagh et al. (2014)
Burkholderia tropica	PQQ-GDH	Glucose dehydregenes produces gluconic acid, solubilizes phosphate	Bernabeu et al. (2016)

(continued)

Table 4.7 (continued)

Microorganisms	Gene or plasmid	Features	References
Serratia sp. S119	pqq-E	Produces gluconic acid, solubilizes phosphate	Ludueña et al. (2017)
Aneurinibacillus aneurinilyticus CKMV1	gdh, nifH	Glucose dehydregenes solubilizes phosphate	Chauhan et al. (2017)
Burkholderia cenocepacia 71-2	recA	Solubilizes phosphate and produces gluconic acid in *E. coli*	Liu et al. (2019)

producing large clearing halos in plates and performing satisfying in field experiments. In addition, these genetic manipulations can help better the survival of inoculant species in competition with other microbial populations in the field by giving them the ability to obtain specific nutrients in a more efficient way (Zaidi et al. 2009a).

4.12 Industrial Production of PSMs as Biofertilizers and Their Application

4.12.1 Isolation of PSMs

For the first step, soil samples including numerous organisms should be collected from 12 to 15 cm deep in the soil and be kept in sterile bags. To determine microbial diversity, each microbial population should be isolated in their standard media through a specialized microbiological method (Fig. 4.4). Suitable culture mediums, their chemical composition and growth conditions for the assessment of microbial diversity are shown in Tables 4.8 and Table 4.9 respectively. It is needed to mention

Table 4.8 Recommended medium and growth conditions used for isolation and enumeration of microbial populations

Microbes	Medium	Incubation temperature (°C)	pH of medium	Incubation period (days)
Bacteria	Nutrient agar	28 ± 2	7 ± 0.2	1–2
Fungi	Martin's agar	28 ± 2	7 ± 0.2	3–5
Actinomycetes	Kenknight's agar	28 ± 2	7 ± 0.2	5–7
PSM	Pikovskaya agar	28 ± 2	7 ± 0.2	5–7
Azotobacter spp.	Ashby's agar	28 ± 2	7 ± 0.2	5–7
Rhizobia	YEM agar	28 ± 2	7 ± 0.2	2–5

Almas Zaidi et al. (2014)

Table 4.9 Chemical composition of media used for assessment of microbial diversity in soil

	Amount (g/l)			
Media component	Pikovskaya medium	NBRIP medium	Ashby's medium	Yeast extract mannitol agar
Dextrose	10.0	10.0	–	–
Mannitol	–	–	20.0	10.0
Yeast extract	–	–	–	1.0
$Ca_3(PO_4)_2$	5.0	5.0	–	–
$CaCO_3$	–	–	5.0	2.0
$MgCl_2{\cdot}6H_2O$	5.0	5.0	–	–
$MgSO_4{\cdot}7H_2O$	0.25	0.25	0.2	0.2
KCl	0.2	0.2	–	–
$(NH_4)_2SO_4$	0.1	0.1	–	–
K_2HPO_4	–	–	0.2	0.5
K_2SO_4	–	–	0.1	–
NaCl	–	–	–	–
Bromophenol blue (BPB)	–	0.025	–	–

Zaidi et al. (2014)

that for short time storage, the samples should be stored in 4 °C in sterile polythene bags (Zaidi et al. 2014).

4.12.2 Scaling up of PSMs

After isolating high-quality PSMs in their specific medium in a laboratory scale (50 mL capacity flasks), it is time to incubating them under shaking condition until the time we meet 10^9 CFU/ml of live microorganisms. Then, 1–5% of the medium should be transferred to a larger. The process should be continued in a similar way to the last step of scaling up to fermenter. Fermentation, a term driven from the Latin term “fervere”, refers to a process in which specific microorganisms, grown in specific medium construction are used to produce specific metabolites (Anand et al. 2016). For large-scale fermentation, there are two main types of processes. The first one known as batch fermentation is a discontinues method of culture whereby the culture is grown in a number of inoculums vessels and then producing microorganisms and nutrients are transferred to the concerned fermentor only once at the beginning of the fermentation. Afterward, the products and other tank containers will be taken out after a specific period of time (Ghaffar et al. 2014; Suthar et al. 2017). The second is continues fermentation in which substrates are continuously supplied to the culture at a regular rate and similarly products are driven from the tank. No wonder higher

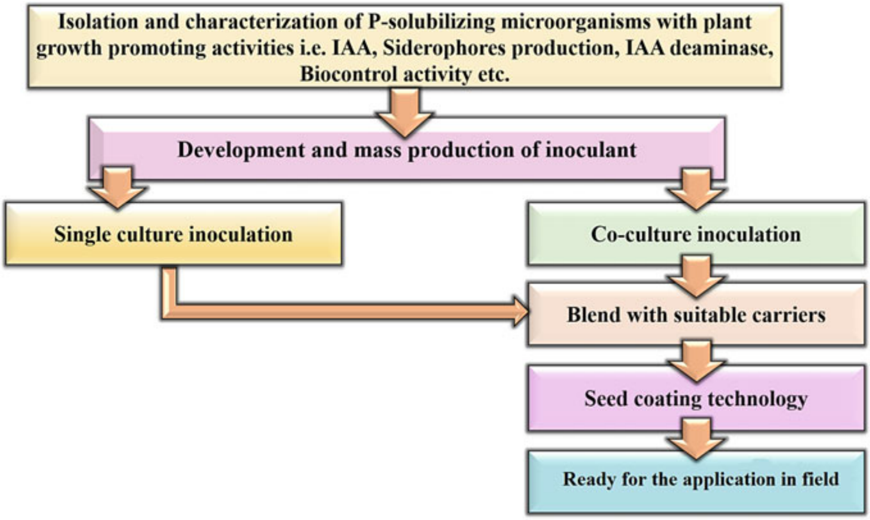

Fig. 4.12 Steps for preparation and application of phosphate-solubilizing microbial inoculants. Adapted from Sujatha et al. (2020)

productivity is achieved in this method and the process could be continued for a long time (Bakri et al. 2012; Ghaffar et al. 2014).

Dividing fermentation into two groups of SSF (solid-state fermentation) and SmF (submerged fermentation) is another type of classification depending on the type of substrate used. For biofertilizers production, substrates used in SSF method are usually bagasse, vegetable or fruit wastes, paper pulp and synthetic media and about SmF fermentation, materials commonly used are liquid synthetic media, vegetable or fruit extracts, dairy industries by-products, soluble sugar and wastewater (Suthar et al. 2017). The steps for inoculant preparation are shown in Fig. 4.12 and the process for the production of efficient biofertilizers containing phosphate-solubilizing microorganisms is demonstrated in Fig. 4.13.

Fermenter temperature, pH, contamination-free environment, aerobic or anaerobic conditions, incubation period and nutrient supply should be in an optimal condition for the strains. Until the quantity of organisms reaches 10^9 CFU/ml, fermenters should be checked on regular basis in case of probable contaminations and cell density. A standard specification of phosphate-solubilizing bacterial biofertilizers reported by FCO is shown in Table 4.10 (Suthar et al. 2017; Zaidi et al. 2014).

The next step is choosing and processing the suitable carrier material. Carrier material is used to keep microorganisms in a good physiological condition and transfer them from laboratory to rhizosphere or seed (Smith 1992). Among the variety of carriers commonly used in biofertilizers formula (categorized in Table 4.11), neutralized peat soil/lignite is counted as a more suitable carrier material (Zaidi et al. 2014). From the required characteristics of carriers we can name cost-effectiveness, being easy to mix and packaging, having the ability to keep organisms viable, the

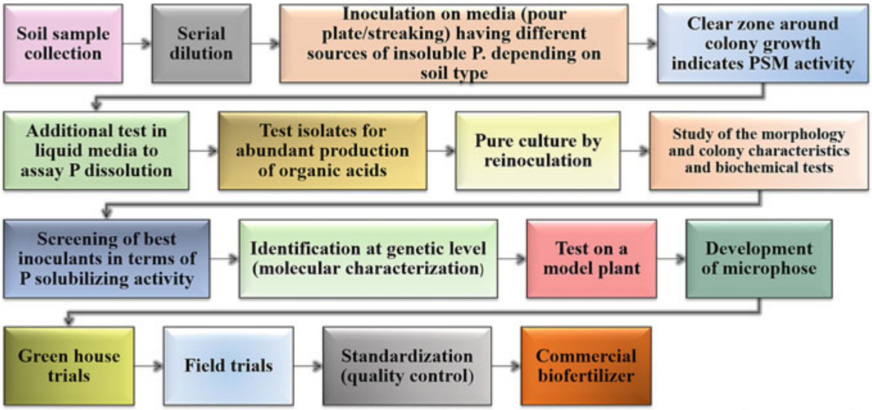

Fig. 4.13 Protocol for isolation and development of effective inoculants of PSMs-based biofertilizers. Adapted from Sharma et al. (2013)

Table 4.10 Standard specifications of phosphate-solubilizing bacterial biofertlizers (FCO 1985)

S. No.	Parameter	Requirements
i	Base	Carrier-based in the form of moist/dry powder or granules or liquid-based
ii	Viable cell count	CFU minimum 5 × 107 cells/g of powder, granules, or carrier material or 1 × 108 cells/ml of liquid
iii	Contamination level	No contamination at 105 dilution
iv	pH	6.5–7.5 for moist/dry powder, granulated carrier-based and 5.0–7.5 for liquid-based
v	Particle size in case of carrier-based material	All material shall pass through 0.15–0.212 mm IS sieve
vi	Moisture per cent by weight, maximum in case of carrier-based	30–40%
vii	Efficiency character	The strain should have phosphate-solubilizing capacity in the range of a minimum of 30%, when tested spectrophotometrically
		In terms of zone formation, a minimum of 5 mm solubilization zone in prescribed media having at least 3 mm thickness

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water-holding capacity of at least 50%, easy to sterilize by autoclaving (1 h in 121 °C) or gamma-irradiation and having the ability to remain in an unpolluted condition, being safe for plants inoculated microorganisms, being easy to adherence to seeds

Table 4.11 Different carriers used for inoculant production

Carrier material	Inoculant bacterium	Characteristics
Sterilized oxalic acid industrial waste	*Rhizobium*	Seed inoculation; Rhizobium multiplication in the carrier in ambient temperature up to 90 days; carrier sterilization resulted in a significant increase in grain yield, nodule number and N content
Alginate-perlite dry granule	*Rhizobium*	Soil inoculation; Rhizobium strains survived in dry granules beyond 180 days; the inoculant can be stored in a dry state without losing much viability
Composted sawdust seed	*Bradyrhizobium*, *Rhizobium* and *Azospirillum*	inoculation; good growth and survival of the inoculant strains
Agriperlite, expanded clay, kaolin, Celite, Diatom, porosil MP, MicroCelvermiculite	*Agrobacterium radiobacter* K84	Crown gall control. The screening was performed to find an improved formulation of K84 cells; the effect of carrier storage temperature and carrier water content on survival of K84 was examined
Cheese whey has grown cells in peat	*Rhizobiummeliloti*	Seed inoculation; better survival at various temperature during storage even under desiccation
Mineral soils	*Rhizobium*	Seed inoculants; Rhizobium survived better at 4 C than at higher temperature
Coal/charcoal	*Rhizobium*/PS bacteria	Seed inoculants
Granular inoculants amended with nutrients	*B. japonicum*	Soil inoculants; bentonite granules, illite and smectite granules, silica granules amended with glycerol, Na glutamate and inoculated with either peat or liquid *B. japonicum* inoculants; enhanced early nodulation of soybean and increased N content of grain

(continued)

Table 4.11 (continued)

Carrier material	Inoculant bacterium	Characteristics
Soybean oil or peanut oil added with lyophilized cells	*Rhizobium*	Seed inoculants; provide more protection than peat-based inoculants when rhizobia are inoculated on seeds and exposed to the condition of drought and high temperature
Perlite	*Rhizobium, Bradyrhizobium, Bacillus*	Seed inoculants; the combination of a sucrose adhesive with the perlite carrier gave better survival of bacteria on seeds; produced a similar number of nodules, nodule dry weight, crop yield and nitrogen content as peat-based inoculants
Wastewater sludge	*Sinorhizobium meliloti*	Seed inoculants; result showed the suitability of using sludge as a carrier because it had the same or a higher potential than peat to support the survival of *S. meliloti*
Wheat bran, sugar cane bagasse Soil	*Rhizobium/Bradyrhizobium* and PS fungus, *A. niger*	Inoculants; the number of microorganisms was the highest with peat, followed by bran and sugarcane bagasse
Nutrient-supplemented pumice	*Rhizobium*	Seed inoculants; good storage and handling properties and could be mixed directly with the seeds during the sowing process

Zaidi et al. (2014)

and having the ability of rapid release of organisms (Gomare et al. 2013; Zaidi et al. 2014).

Further solid-based biofertilizers (the group including mentioned carriers), there is another group of biofertilizers which are of interest in recent years. These are biofertilizers prepared by a liquid base for instance water, emulsion or oil. From advantages of this group we can name having more shelf life (about two years), having the ability to be stored at higher temperature (about 55 °C), having UV toleration, being less likely to get contaminated, requiring ten times lower dosage of application comparing with carrier-based fertilizers and being user friendly. After mixing well the inoculants with carriers, they become sealed, packaged and ready to use (Nehra and Choudhary 2015; Suthar et al. 2017).

4.12.3 Methods of Microbial Biofertilizers Application

The term “microphos” is used for a bio-preparation of viable and efficient PSMs, in a sufficient amount of organisms which used as biofertilizers (Zaidi et al. 2014). Mainly, there are three methods of biofertilizers application. The first and most traditional one is seed treatment in which plant seeds are coated by processed PSMs using non-toxic adhesive solutions. Sucrose solutions, gum arabic or vegetable oils are commonly used as adhesive solutions. The second is seeding root dip which is suitable for transplanted crops. In this method, microphos is mixed with water and then, for 5–10 min intended seedlings are dipped in the mixture before transplantation. Last method is main field/soil application. In this method, the chance of contact between plant roots and inoculants increases due to the direct placement of granular microphos into the groove under or beside the seed (Zaidi et al. 2014). Approaches used for microbial phosphatic biofertlizers production and their application are shown in Fig. 4.14.

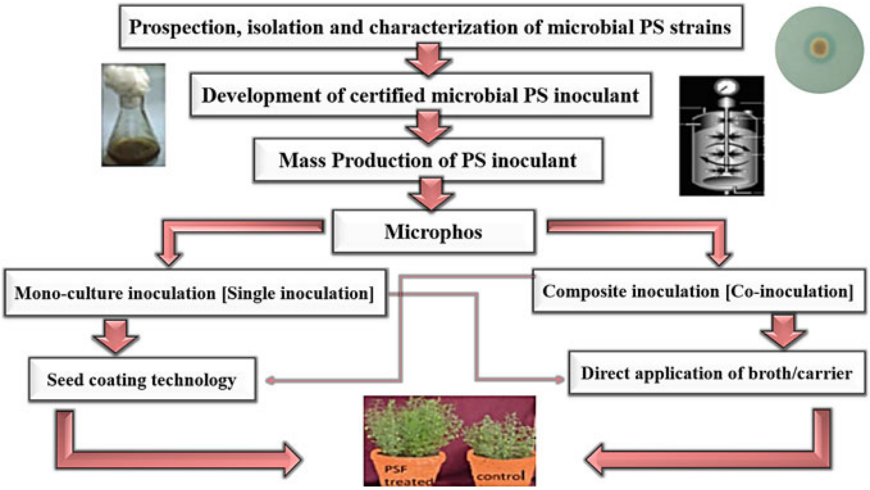

Fig. 4.14 Approaches used for microbial phosphatic biofertilizers production and their application (Zaidi et al. 2014)

4.13 Future Challenges in PSMs Application

Despite the satisfying effects of using PSMs to deal with soil P demand in laboratory or greenhouse experiments, farmers may face some challenges in field trails. Here we name some issues which should be considered by scientists and farmers for the development of microbial biofertlizers and their efficient application. First of all, complex interactions and competitions between inoculated strains and other microbial soil inhabitants should be taken into account to avoid their poor colonization or exclusion. Secondly, symbiotic associations with other potent and useful microbial species and their controlled co-inoculation could positively affect these biofertilizers efficiency. Next, regarding the fact that P solubilization and mineralization activities by microorganisms are affected by soil components and energy sources, understanding the type of P source present in the soil and the suitable PS mechanism based on the source would be very helpful for a profitable selection of PS isolates. Last, abundance and type of soil nutrients such as C and N and other soil physicochemical properties such as pH and temperature should be assessed before application because of its influence on phosphatases and phytases function and organic acids production (Eida et al. 2017; Khan et al. 2010; Scervino et al. 2011).

4.14 Conclusion

To enhance the soil bioavailable P, adding chemical phosphate fertilizers to the soil is the most popular way worldwide. But this method is not efficient and is expensive and poses serious risks to the environment. So scientists are looking for safety phytostimulators as better alternative solutions. But this method is inefficient, increasingly costly and is a serious threat to our environment in a way that made scientists investigate alternative solutions. Using phosphate-solubilizing microorganisms known as PSMs, not only reduces cultivation costs but also is environmental friendly and helps natural soil fertility. These biofertilizers can insure our food security without damaging soil dwellers by different mechanisms such as organic acids or enzyme production and ammonium assimilation. Agricultural dependence on synthetic fertilizers can strictly decrease with the application of PSMs because of their ability to supplying soluble phosphate to plants and increasing crop yield.

Regarding the fact that PSMs are abundant in soils, investigations on development of efficient methods to identify and isolate new and better agronomic PSMs is required. Moreover, functional processes of PSMs in different ecological niches should be recognized for more effective application and providing the conditions for beneficial genetic manipulations. The gap between in vitro experiments and the agricultural practice of these biofertilizers should be filled by the development of simple processes for mass production and popularizing the application. To prevent the failure of this method, the appropriate amount of used inoculants for different plant-soil conditions and different microbial interactions between applied PSMs and other soil inhabitants should be investigated before application. Further, researches on biocontrol potentials of these organisms are needed with the aim of substituting them with chemical pesticides under different farming systems to get the full benefit of these precious inoculants; and finally, to popularize and commercialize the application of microbial biofertilizers, development of technology advancements and innovative researches are needed to reach more cost-effective and user-friendly methods of production and application.

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Chapter 5
Potassium Solubilization: Mechanism and Functional Impact on Plant Growth

Chanda Vikrant Berde, Sonal Suresh Gawde, and Vikrant Balkrishna Berde

Abstract A major constituent as well as an essential nutrient of all living cells is potassium (K). This form of K in the soil, however, is not available for uptake by plants. Chemical fertilizers are added to agricultural fields to provide the required K but with negative impact on the environment. K-bearing minerals are solubilized by potassium solubilizing bacteria (KSB) and the insoluble K is converted to soluble K that is easily assimilated by plants. They solubilize K from insoluble forms like mica, fledspar, and others by mechanisms that involve formation of organic acids, siderophores, and also capsular polysaccharides. The diversity and abundance of KSB is dependent on numerous factors, including soil type, climatic conditions, etc. KSB are mostly found in the rhizosphere of plants. These PGPR can be utilized as biofertilizers for sustainable agriculture and can be an efficient substitute to chemical fertilizers.

Keywords Potassium solubilizing bacteria · Potassium · Plant growth · Bio-fertilizer · PGPR

5.1 Introduction

Feeding the increasing population will be the challenge in the future. Hence there is a need to increase the fertility of the soil in order to have higher yields. Plant nutrients that include nitrogen (N), phosphorus (P), and potassium (K) are supplied through chemical fertilizers (Glick 2012). This leads to temporary increase in fertility. Plants

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do not take up all the nutrients applied to the soil. The excess fertilizer remains in the soil or gets washed off. Excess unutilized fertilizers lead to increase in the salinity of the soil which makes it unfertile (Sharma et al. 2021). For sustainable agriculture, biofertilizers like phosphate solubilizing bacteria (PSB), potassium solubilizing bacteria (PSB), and nitrogen fixers should be used (Kour et al. 2020, 2021; Hesham et al. 2021; Yadav et al. 2021b).

Potassium is required for plant growth, for activation of numerous enzymes involved in different processes such as photosynthesis, and also involved in increasing the disease resistance and overcoming stress conditions (White and Karley 2010; Almeida et al. 2015; Gallegos-Cedillo et al. 2016; Hussain et al. 2016; Yang et al. 2015). Potassium being the most abundant element occurring in the range of 0.04–3%, however a very small percentage of this content is available to the plants for uptake (Sparks and Huang 1985). Various forms of K are available in the soil, including mineral, non-exchangeable, exchangeable and dissolved or solution, i.e., the ionic form. Thus, the K reserves in soil are ample but most of it being insoluble is unavailable for plant uptake. Plants can only directly take-up solution K. Potassium solubilizing bacteria (KSB) play a role in making K available to the plants in soluble form, thus playing a crucial role in agriculture under K-limited soils (Verma et al. 2017). With continued usage of KSB in the soil, the need for chemical fertilizers slowly becomes avoidable.

The efficiency of K solubilizing bacteria will depend on environmental conditions and also on the available source of K in the soil. Mostly KSB is added as a biofertilizer along with K containing minerals, to ensure the presence of K for the activity of the bacteria. Isolation, characterization, and K solubilizing mechanism studies of good K solubilizers are thus required for application of these bioinoculants in sustainable agriculture (Etisami et al. 2017).

5.2 Potassium in Soil

Potassium (K) is one of the essential macronutrients required for plant growth and development. In the soil, potassium (K) is present mainly in four different forms, namely, (a) K ions (K^+) in soil solution which is exchangeable cationic form, (b) form that is tightly held on the surfaces of clay minerals (illite) and organic matter, (c) tightly held or fixed form by weathered micaceous minerals, and (d) form present in the lattice of certain K-containing primary minerals (feldspar) (Sharpley 1989; Ahmad and Zargar 2009). Only forms that are utilized by the plants directly for their growth are the water-soluble and exchangeable K.

Mineral K makes up about 90–98%, which is again dependent on the soil type, and this pool is unavailable for plant usage (Sparks and Huang 1985; Goldstein 1994). Unavailability of K are also due to reasons such as exorbitant use of chemical fertilizers, increase in agriculture, loss of K from soil, and presence in bound form. Feldspar (orthoclase and microcline) and mica (biotite and muscovite) are examples of minerals containing K (McAfee 2008). The non-exchangeable form of K is found trapped in clay mineral sheets and making up about 10% of total soil K (Sparks 1987). K solution being the form that is soluble and can be assimilated by the plants, however, leaches out from the soil. The uptake is either directly or with the help of microbes. According to Sparks and Huang (1985), solution K in the soil ranges between 2 and 5 mg per L. Soil type plays a role in the release and in the availability of K concentrations.

K availability and release also depend on the soil type. K is found to be high in black soil; it is medium in red soil, while in the laterite soils, the K concentration is the lowest (Rehanul 2002). Over the course of time and continuous usage for agriculture, the soils rich in K can become depleted or deficit in the metal due to exorbitant usage. Other reasons for the depletion are wash-off, soil erosion, and leaching of the solution K. This depletion results in the non-exchangeable form being converted to exchangeable K (Sparks 1987; Sheng and Huang 2002; Prasad et al. 2021). According to the authors, the dynamic equilibrium and reactions involved in gaining kinetic energy affect the K solutions, i.e., the water-soluble exchangeable K proportions in soil. Hence, it is necessary to maintain K level in soils and find out ways of having sufficient K supply for sustainable agriculture (Sindhu et al. 2014).

5.3 Potassium Requirement for Plant Growth: Function and Deficiency

Crop production depends on the soil nutrient basin that gives mechanical support, micro and macro nutrients as well as water required for plant growth. It plays several significant roles, including production of plant enzymes, cell turgor maintenance, improves photosynthesis, and benefits in sugar and starch transport through the phloem (Usherwood 1985; Doman 1979; Marschner 1995; Pettigrew 2008). Potassium presence helps in nitrogen uptake by playing a role in nitrogen fixation and carries out the translocation of photosynthetic process taking place in the leaves to the roots that harbor root nodules (Savani et al. 1995). Water and nutrients transport via the xylem is another function of the metal. Potassium is also responsible for numerous properties related to crop yield, such as grain filling, weight of kernel, having good straw strength, and protection against plant pathogens by increasing resistance to pest and diseases. Presence of K enables the plants to resist abiotic and biotic stresses (Pettigrew 2008; Maqsood et al. 2013; Tiwari et al. 2021; Yadav et al. 2021a). Potassium also helps in protein synthesis and is involved in number of biochemical and physiological processes in plants. The most important role among these is the regulation of stomata opening and closing (Hawkesford et al. 2012). Apart from being responsible for enzyme activation, K is also involved in ATP synthesis. According to Brar and Tiwari (2004), K plays a significant role in transport of carbohydrates, photosynthesis, water uptake, pest and disease resistance, and helps to sustain balance between monovalent and divalent cations. Khawilkar and Ramteke

(1993) have elaborated on its significance in increasing the shelf life of crops apart from rendering the crops disease resistant.

Though K is absorbed by plants in huge amounts than the other minerals, the plant may suffer from deficiency symptoms if the uptake is not sufficient. Deficiency of essential elements is the limiting factor affecting agriculture (Xie 1998; Zord et al. 2014). Many workers have reported K deficiency in number of crops (Meena et al. 2015; Xiao et al. 2017).

Deficiency of K is seen throughout the plant starting with the yellowing of leaves in the lower parts of the plant which spreads upwards. It is called as yellow scorching or firing which is actually chlorosis, seen along the margin of the leaves. Effects of K deficiency are also seen in the roots which show poor and slow growth. The seed size is small and significant reduction in yield observed. These changes are usually not evident in the beginning and by the time symptoms become visible, the damage cannot be reversed (Khanwilkar and Ramteke 1993). There is tremendous loss of crop yield, and crop quality is also affected. Several factors are responsible for the depletion of K in the soil and this leads to shortage of K availability to plants. In order to overcome this problem, an alternative method of making K available to plants and maintaining K level in soil has to be adopted.

5.4 Potassium Solubilizing Microbes

Different types of microorganisms are present in the soil. The abundance of organisms is more in the rhizosphere where they help the plant in various ways. The rhizosphere consists of microflora that is able to carry out nitrogen fixation, phosphate solubilization, and potassium mobilization and also benefit the plants in other ways (Yadav 2021). Among these, the K solubilizers promote growth by converting insoluble K present in bound form to usable soluble form for the plants (Sperberg 1958; Zeng et al. 2012). Lot of research has been focused on methods to isolate the solubilizers, characterization of the selected strains and their application as biofertilizers for agriculture improvement (Table 5.1).

A number of bacteria carry out K solubilization, namely *Acidothiobacillus ferrooxidans*, *Bacillus mucilaginosus*, *Bacillus edaphicus*, *Bacillus circulans*, *Burkholderia* sp., *Pseudomonas* sp., and *Paenibacillus* sp. (Sheng et al. 2008; Singh et al. 2010; Liu et al. 2012; Basak and Biswas 2012). These bacteria are able to solubilize K minerals such as biotite, feldspar, illite, muscovite, and mica. Muentz (1890) gave the earliest evidence of microbial association in rock potassium solubilization. Another report by Archana (2013) describes the growth of the cultures *Aspergillus niger, Bacillus extroquens,* and *Clostridium pasteurianum* on muscovite, biotite, orthoclase microclase, and mica. Some bacterial species such as the silicate bacteria were reported to dissolve potassium, silicates, and aluminum from insoluble minerals (Aleksandrov 1967).

Certain microbial strains present in soil are capable of solubilizing the bound K from minerals, namely micas, illite, and orthoclases. KSB brings about the dissolution

Table 5.1 Potassium solubilization microbes from different host/habitats

Potassium solubilizing microbes	Host/sample	References
Acidithiobacillus ferrooxidans	Feldspar	Sheng and He (2006)
Agrobacterium tumefaciens	Tobacco rhizosphere	Zhang and Kong (2014)
Alcaligenes piechaudii	Wheat	Verma et al. (2015)
Aspergillus candidus	Alluvial soil	Banik and Dey (1982)
Aspergillus fumigatus	Rock powder	Lian et al. (2008)
Aspergillus niger	Heavy metals	Sperber (1958)
Aspergillus terreus	Feldspar	Prajapati et al. (2013a, b)
Azotobacter chroococcum	Sudan grass	Basak and Biswas (2010)
Bacillus altitudinis	Soil	Huang et al. (2013)
Bacillus amyloliquefaciens SVNM9	Mica mine	Gundala et al. (2013)
Bacillus coagulans PB16	Soil	Saiyad et al. (2015)
Bacillus edaphicus	Chillycotton	Sheng et al. (2003)
Bacillus globisporus	Soil	Sheng et al. (2008)
Bacillus megaterium JK3	Iranian soils	Keshavarz Zarjani et al. (2013)
Bacillus megaterium,	Pepper and cucumber	Han and Lee (2006)
Bacillus metallica	Soil	Saiyad et al. (2015)
Bacillus mucilaginosus MCRCp1	Groundnut	Sugumaran and Janarthanam (2007)
Bacillus subtilis KT7/2	Rhizospheric soil	Leaungvutiviroj et al. (2010)
Burkholderia cepacia	Tobacco rhizosphere	Zhang and Kong (2014)
Burkholderia cepacia GL13	Tobacco rhizosphere	Zhang and Kong (2014)
Burkholderia pyrrocinia	bamboo rhizosphere	Ruangsanka (2014)
Burkholderia ubonensis	bamboo rhizosphere	Ruangsanka (2014)
Enterobacter aerogenes	Tobacco rhizosphere	Zhang and Kong (2014)
Enterobacter asburiae	Tobacco rhizosphere	Zhang and Kong (2014)
Enterobacter cloacae	Soil	Zhang and Kong (2014)
Enterobacter hormaechei	Okra	Prajapati et al. (2013a, b)
Frateuria aurantia	Egg plant	Nayak (2001)
Frateuria aurantia	Brinjal	Ramarethinam and Chandra (2005)
Frateuria aurantia	Agricultural soils	Ramarethinam and Chandra (2006)
Klebsiella variicola	Soil	Zhang and Kong (2014)
Microbacterium foliorum	Soil	Zhang and Kong (2014)
Myroides odoratimimus JM19	Tobacco rhizosphere	Zhang and Kong (2014)

(continued)

Table 5.1 (continued)

Potassium solubilizing microbes	Host/sample	References
Paenibacillus glucanolyticus	Mica	Sangeeth et al. (2012)
Paenibacillus mucilaginosus	Illite	Liu et al. (2012)
Pantoea agglomerans	Tobacco rhizosphere	Zhang and Kong (2014)
Pseudomonas aeruginosa	Soil	Sheng et al. (2003)
Pseudomonas chlororaphis	Soil	Yu et al. (2012)
Pseudomonas putida	Tomato	Ordookhani et al. (2010)
Pseudomonas syringae	Maize	Nadeem et al. (2007)
Stenotrophomonas maltophilia	Wheat	Verma et al. (2015)
Stenotrophomonas sp. HHS2-27	Wheat	Verma et al. (2015)
Torulaspora globosa	Rock powder	Rosa-Magri et al. (2012)

of silicate minerals to release K by means of organic and inorganic acids, acidolysis, polysaccharides, complexolysis, chelation, and exchange reactions. Organic acids are reported to act directly on the rock K or chelate silicon ions from silica and release K in solution (Friedrich et al. 1991; Ullman et al. 1996; Bennett et al. 1998). This ability of the potassium solubilizing microorganisms (KSM) is exploited in agriculture for crops that require greater K levels (Vandevivere et al. 1994; Barker et al. 1998).

Reitmeir (1951) has reported the growth of *Aspergillus niger, Bacillus extroquens*, and *Clostridium pasteurianum* on muscovite, biotite, orthoclase, microcline, and micas, in vitro. Another report by Avakyan et al. (1986) and Li (1994) describes the isolation of KSB from different samples. *Bacillus mucilaginosus* is reported to produce organic acid for the solubilization of K minerals, such as micas, illite, and orthoclases (Friedrich et al. 1991; Ullman et al. 1996). In another study, Lin et al. (2002) showed an increase in uptake of K and P in tomato plants using *B. mucilaginosus* was significant as compared to control uninoculated plants. However, Hosseinpour and Kalbasi (2002) reported high levels of K being present in Iranian soils, thus making it advantageous for crops with high K demand. He and Sheng (2006) described illite and feldspar solubilization using organic aids and capsular polysaccharides produced by K solubilizers.

5.5 PGPR for Sustainable Agriculture

Plant growth promoting rhizobacteria (PGPR) has a very crucial role to play in fertility of soil and eventually in increasing plant growth (Ahmad et al. 2008). PGPR provide the plant the nutrients required for growth and production (Vessey 2003). PGPR includes the various microflora that function in nitrogen fixation, phosphate mobilization, and potassium-solubilization, which are used as biofertilizers to supply N, P, and K, respectively (Vessey 2003; Ekin 2010). A number of mechanisms have been described which allow the PGPR to directly enhance plant growth (Table 5.2). The mechanisms involved are solubilization of minerals, such as phosphorus, production of siderophores, hydrogen cyanide, and indole acetic acid (Yadav et al. 2018).

Table 5.2 Potential applications of potassium-solubilizing microorganisms for agricultural sustainability

Microorganisms	Crops	Increased parameters	References
Azotobacter chroococcum	Forage	Growth and acquisition	Basak and Biswas (2010)
Bacillus mucilaginosus	Forage	Growth and acquisition	Basak and Biswas (2010)
Bacillus edaphicus	Wheat	Growth and nutrient	Sheng and He (2006)
Bacillus edaphicus	Cotton rape	Growth, nutrients uptake	Sheng (2005)
Bacillus megaterium	Peppercucumber	Growth, uptake	Han and Lee (2006)
Bacillus mucilaginosus	Peppercucumber	Growth, uptake	Han and Lee (2006)
Azotobacter chroococcum	Maize-wheat	Growth, yield	Singh et al. (2010)
Bacillus mucilaginosus	Maize-wheat	Growth, yield	Singh et al. (2010)
Rhizobium leguminosarum	Soybean	Growth, yield	Fatima et al. (2006)
Rhizobium leguminosarum	Soybean	Growth, yield	Fatima et al. (2006)
Rhizobium leguminosarum	Soybean	Growth, yield	Fatima et al. (2006)
Bacillus megaterium	Chickpea	Nutrient uptake and yield	Rudresh et al. (2005)
Bacillus edaphicus NBT	Cotton	Nutrients uptake	Sheng (2005)
Bacillus mucilaginous	Sorghum	Nutrients uptake	Basak and Biswas (2009)
Frateuria aurantia	Egg plant	Nutrients uptake	Nayak (2001)
Bacillus edaphicus	Chillycotton	P and K contents	Sheng et al. (2003)
Bacillus mucilaginosus	Tomato	Uptake and biomass	Lin et al. (2002b)
Bacillus megaterium	Egg plant	Uptake, and yield	Han and Lee (2005)
Bacillus mucilaginosus	Eggplant	Yield	Han and Lee (2005)
Pseudomonas sp. 24	Maize	Yield	Chabot et al. (1996)
Rhizobium leguminosarum	Maize	Yield	Chabot et al. (1996)
Rhizobium leguminosarum	Maize	Yield	Chabot et al. (1996)

The indirect mechanism involves biological control (Ahmad et al. 2008). Thus the application of these microorganisms as biofertilizers sustainable agriculture could increase the uptake of nutrients by plants and lead to increased crop production (Meena et al. 2014a, b; Sindhu et al. 2014; Abdel-Azeem et al. 2021; Kumar et al. 2021). According to some reports, 72% of agricultural land in India has soil with medium and low K availability, thus requiring external K fertilizer supplementation (Ramamurthy and Bajaj 1969; Rehanu 2002). There are reports of use of KSB as K-biofertilizers in China and India, where the soil is deficient in K (Xie 1998; Basak and Biswas 2009).

There are numerous reports on the use of KSB as biofertilizer in agricultural practices for different crop cultivation. KSB has been used for cultivation of cotton, cucumber, groundnut, maize, pepper, rape, sorghum, Sudan grass, tea, wheat (Sheng 2005; Han and Supanjani 2006; Badr et al. 2006a; Sheng and He 2006; Sugumaran and Janarthanam 2007; Basak and Biswas 2009; Basak and Biswas 2010; Singh et al. 2010; Abou-el-Seoud and Abdel-Megeed 2012; Bagyalakshmi et al. 2012a, b).

According to Singh et al. (2010), maize and wheat when co-inoculated with KSB, served as a source of K for crop growth by solubilizing the waste mica (Singh et al. 2010). It has been reported that mobilization of K from relatively hard K minerals, i.e., hardness of more than 3 according to Mons' hardness index, was more challenging than mobilizing the relatively softer k minerals of hardness less than 3 (Sheng and Huang 2002). Most of the studies are therefore carried out with soft K-bearing minerals. Apart from providing the essential nutrients for plant growth, K solubilizing rhizobacteria produce antagonistic substances, biodegrade organic matter, and participate in nutrient cycling (Meena et al. 2013, 2014b).

5.6 Mechanism of Potassium Solubilization by Microorganisms

Microbial soil community can influence soil fertility through decomposition of organic matter, mineralization, and release of nutrients (Parmar and Sindhu 2013). Numerous microorganisms have been identified for their ability to solubilize K by various mechanisms (Table 5.3). Some of these mechanisms include the production of inorganic and organic acids, acidolysis, polysaccharides, complexolysis, chelation, polysaccharides, and exchange reactions (Gerke 1992; Rai et al. 2020; Yadav et al. 2020).

Most of the investigations describe the production of organic acids by bacteria that are responsible for making mineral K available (Alexander 1977; Prajapati et al. 2013a, b; Maurya et al. 2014; Meena et al. 2014b). A strain of *Bacillus megaterium* var *Phosphaticum* has been reported for higher crop yields via conversion of insoluble present in rocks in soluble forms (Bojinova et al. 1997; Schilling et al. 1998). Production of organic acids is a major mechanism for making K available. Organic acids produced by microorganisms include citric acid, formic acid, malic acid, oxalic

Table 5.3 Mechanisms of K solubilization by potassium solubilization microbes

Microorganisms	Mechanism of K solubilization	References
Aspergillus candidus	citric, oxalic	Banik and Dey (1982)
Aspergillus fumigatus	Oxalic, tartaric	Banik and Dey (1982)
Bacillus circulans GY92	Lipo-chitooligosaccharides	Lian et al. (2001)
Bacillus edaphicus	Production of organic acids	Sheng et al. (2008)
Bacillus megaterium	Citric, gluconic	Taha et al. (1969)
Bacillus mucilaginosus	Mica through organic acids	Basak and Biswas (2009)
Bacillus mucilaginosus	Illite solubilization	Han and Lee (2005)
Bacillus mucilaginosus	Oxalate, citrate	Sheng and He (2006)
Burkholderia glathei	Siderophores, organic ligands	Calvaruso et al. (2007)
Citrobacter freundii	Citric, gluconic	Taha et al. (1969)
Enterobacter hormaechei	Organic acids	Prajapati et al. (2013a, b)
Paenibacillus glucanolyticus	Organic acids	Sangeeth et al. (2012)
Paenibacillus mucilaginosus	Tartaric, citric, oxalic acids	Liu et al. (2012)
Paenibacillus mucilaginosus	Tartaric, citric, oxalic	Liu et al. (2012)
Penicillium frequentans	Oxalic citric	de la Torre et al. (1992)
Pseudomonas aeruginosa	Acetate, citrate, oxalate	Badr et al. (2006b)
Sphingomonas	Acidification, complexation	Uroz et al. (2007)

acid, acetic acid, etc. (Sheng et al. 2003). The organic acids act on the K compounds and bring about its dissolution by giving out protons and forming by Ca^{2+} complexes. Similarly, solubilization of K takes place by formation of organic acid complexes and complex formation with metal ions like Fe^{2+}, Al^{3+}, and Ca^{2+} (Styriakova 2003).

Grandstaff (1986) and Surdam and MacGowan (1988) report solubilization of aluminosilicate or quartz by producing organic ligands. Solubilization of K takes place by the action of inorganic and organic acids as well as capsular EPS by *Bacillus, Clostridium* and *Thiobacillus* (Groudev 1987). Similarly, Sheng and He (2006) have reported the release of K from feldspar and illite by organic acids like oxalate and tartarate by K solubilizing bacteria. The fungal species *Cladosporoides, Cladosporium*, and *Pencillium* sp. have been shown to bring about solubilization of clay silicates, mica, and feldspar by the action of protons, organic acids, siderophores, and organic ligands. The acids produced include citric, oxalic, and gluconic acids. The release of gluconic acid promotes dissolution of silicates such as albite, quartz, and koalinite (Argelis 1993). Hu (2006) describes several organic acids produced by the strain *B. edaphicus*. Oxalic acid caused dissolution of fledspar, while tartaric acid and oxalic acid brought about dissolution of illite.

5.7 Conclusions and Future Perspectives

Along with the minerals N and P, K is required essentially for plant growth. K fertilizers are added to soil to meet the plant's K requirements. However, the fertilizers are costly and also cause the lowering of soil sterility with overuse (Yadegari and Mosadeghzad 2012; Zhang et al. 2013). Over the time, it leads to harm being caused to the environment and eventually to mankind (Hu et al. 2010; Tuli et al. 2010). Nature-friendly, agriculturally profitable, and cost-effective solution for the problem is obtained in the form of potassium solubilizing bacteria (KSB). Applied as biofertilizer, the bacteria can solubilize insoluble minerals present in soil into soluble available forms, readily utilized by plants. Therefore, application of KSB as biofertilizer is thus an eco-friendly agriculture practice which acts with environment safeguard practice as the core and is the essence of conscientious farming.

More research is required to make the application of KSBs in agriculture a more rewarding and attractive venture. Research in the future should be focused on the following aspects:

(i) More field studies are needed with proper standardization of KSB application in situ. Application details and quantitated results of effects on yield, crop-wise should be available (Parmar and Sindhu 2013).
(ii) PGPR should be studied for all activities such as nitrogen fixation, indole acetic acid production, etc. along with K solubilization.
(iii) Study of the solubilization of other minerals along with K such as Fe, Mn, etc.
(iv) Laboratory and greenhouse conditions should be varied as per the conditions on field. Hence application procedure as per the field conditions should be available.
(v) Study of the genes involved in solubilization process and the genetic engineering of environmentally stable organisms with these genes could be a good strategy for having stable bioinoculants as K solubilizing agents.

Thus knowing the mechanisms as well as detailed research leaving no loopholes in the application of KSB for sustainable eco-friendly and profitable agriculture would be the fruit of all the efforts put in.

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Chapter 6
Fe Chelation and Zinc Solubilization: A Promising Approach for Cereals Biofortification

Upendra Kumar, Priyanka, Rashmi Malik, Prexha, Yogita, and Kamla Malik

Abstract Micronutrient deficiency, micronutrient malnutrition or hidden hunger is an increasingly severe global challenge for humankind. As wheat, rice and maize are the major staple food crops and are frequently consumed, it has become necessary to biofortify cereal crops with micronutrients, especially iron and zinc, in order to fulfill the requirements for better human health. Cellular and molecular mechanisms should be understood to maintain the homeostasis of micronutrients for increasing iron and zinc in plants. For metal ions uptake under deficiency conditions, plants have established strongly regulated two different strategies. Reduction-based strategy-I is followed by non-graminaceous monocots and dicots, whereas chelation-based strategy-II is followed by grasses. Strategy-II plants (graminaceous species) facing Zn, Fe and other micronutrient deficiency have mechanism of Fe chelation which depends on methionine derivative synthesis known as mugineic acid family phytosiderophores. Graminaceous plants also show quantitative and qualitative differences in MAs production. Wheat, rice and maize release only 2-deoxymugineic acid (DMA) in a very small fraction, thus due to low Fe availability these are reported as susceptible. Whereas, in low Fe availability, barley is reported more tolerant due to production of large amounts of different types of MAs, including MA, 3-epi-hydroxymugineic acid and 3-hydroxymugineic acid. In graminaceous plants, chelation and uptake of non-Fe metals are also facilitated by MAs, like Zn in

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the form of Zn (II)-MAs. Therefore, to solve the above problem, there is a requirement for alternative and eco-friendly technology such as plant growth-promoting rhizobacteria (PGPR) and organic farming practices to enhance zinc solubilization and its availability to plants.

Keywords Cereals · Fe and Zn deficiency · Chelation · Phytosiderophores · Biofortification

6.1 Introduction

The deficiencies of micronutrients or "hidden hunger" are a major concern in developing countries, mainly sub-Saharan Africa and South East Asia (Harding et al. 2018). These micronutrients mainly consist of vitamins and minerals. Iron, zinc, iodine, folate and vitamin A are crucial micronutrients that lack in the diets of developing countries populations. All these micronutrient deficiencies (MNDs) are responsible for poor growth, prenatal complications, intellectual impairments and increased risk of morality (Bailey et al. 2015; Kaur et al. 2020a, b). Among these MNDs, iron deficiency is the most common in the world; approximately more than 30% of the world's population, an estimated 2 billion people, are suffering from the iron deficiency diseases. The recommended daily iron intake varies between 8 and 18 mg/day according to age, gender and body weight, and 27 mg/day for pregnant women. WHO estimated that 50% cases of anemia are due to iron deficiency called iron deficiency anemia (IDA) (Picciano 2003; de Benoist et al. 2008). Iron deficiency anemia is very common in women because of menstruation cycle and child birth which results in heavy blood losses. Nutrition interventions made during pregnancy and early childhood (under two years of age) have the greatest impact in reducing vulnerability to disease and death due to poor nutrition.

To raise awareness about serious health problems such as iron deficiency anemia, every year November 26 is celebrated as Iron Deficiency Day. Vitamin A deficiency (VAD) causes blindness, xerophthalmia, night blindness and corneal ulcerations (Sherwin et al. 2012). The WHO estimated that because of VAD 250–500 million children are blind, and it is also common in pregnancy in lower-income countries with estimates ranging from 10 to 20%. Iodine is a trace mineral and plays a key role in thyroid hormone synthesis. When daily iodine intakes in diet are lower than 10–20 μg, hypothyroidism can occur and it is accompanied by goiter (Trumbo et al. 2001). Worldwide ~2 billion of people are estimated to have iodine deficiency (Andersson et al. 2012). Zinc deficiency is one of the primary causes of morbidity in developing countries (Hess et al. 2009). It leads to reduced growth, diarrhea, weak immune system, and increased the risks of respiratory diseases affecting ~2 billion people worldwide (Gibson 2012; Prasad 2013). Folate deficiency at the time of pregnancy can lead to neural tube defect in fetus, decreased deoxyribonucleic acid (DNA) methylation and cognitive problems (Martini et al. 2018).

In most of the parts of the world, malnutrition is present in the form of undernutrition, which is caused by a diet lacking adequate calories, protein and essential nutrients because of not enough food and/or of poor quality. Micronutrient deficiencies are affecting the health of over 2 billion people on the earth, and owing to poor diets almost 150 million children under the age of 5 years are stunted due to poor diets and 100,000 infants are born with preventable physical defects each year.

Even though deficiencies of micronutrients which are needed only in minute quantities (i.e. micrograms to milligrams per day), they are the significant cause of malnutrition and are associated with several health problems (World Health Organization 2009). It was found out that insufficient dietary intakes of these micronutrients can lead to malfunctioning of the brain, immune as well as reproductive systems and energy metabolism. These deficiencies lead to learning disabilities, deplete work capacity, serious illness and eventually death. Even modest levels of deficiency of these nutrients in diet (which can be detected by biochemical or clinical measurements) can cause serious detrimental effects on human health. MNM is a serious global affliction that limits the work capacity of people and seriously hinders economic development (Graham et al. 2000).

The most common deficient micronutrient found in the human diet is iron (Fe). Anemia caused by Fe deficiency has major detrimental consequences for human health. The children of anemic mothers have low iron reserves which lead to more requirement of Fe than supplied by breast milk to lower growth impairment cause by Fe deficiency. It is estimated that 800,000 deaths are attributable to Fe deficiency anemia annually (Mayer et al. 2008). An estimated four out of ten pre-school children in developing countries are anemic. Anemia affects an estimated 60% of the population in sub-Saharan Africa, 19% in Latin America and the Caribbean, 76% in South Asia and 40% in East Asia and the Pacific region.

Zinc (Zn) is essential for normal growth and reproduction of plants, animals and humans. While mild to moderate Zn deficiency is common throughout the world, one-third of the world's population is at high risk and lives in low-income countries, according to the International Zn Nutrition Consultative Group. Zn deficiency leads to impaired growth, immune dysfunction, increased morbidity and mortality, adverse pregnancy outcomes and abnormal neuro-behavioral development.

6.2 Key Problems Associated with Micronutrient Malnutrition

In low-income or developing countries, the daily calorie intake of poor people mainly constituted of carbohydrate-rich cereal-based food, which includes primarily cereal crops, i.e., rice, wheat and maize, while a diversified diet including vegetables, fruits, animal and fish products with high mineral content adds insignificant proportion. In developing countries, the rise in micronutrient deficiencies is linked to the shift in cultivation toward dominance by cereals as a consequence of green revolution.

Pressure on a fixed land base to produce more food has driven a shift in production toward cereals. The micronutrient content in cereal crops is inherently very low, compared with many other food crops, and has further reduced by various processing methods of crops such as milling and polishing during which nutrient-rich layer (aleurone) gets removed. The wheat aleurone layer is the most promising fraction from the outer layer of the grain with its unique benefits as described within the European Health Grain project. Hence, the food systems dominated by cereals are low in micronutrients (Graham and Welch 2000). Consequently, diet based only on staple cereals is not sufficient to provide the recommended dietary allowance (RDA). The wheat flour consumed contains a relatively poor amount of Fe and Zn, an average of only 11.7 mg/kg Fe and 7 mg/kg Zn (Herman et al. 2002) and polished rice contains an average of only 2 mg/kg Fe and 12 mg/kg Zn, whereas RDA for Fe is 10–15 mg/kg and 12–15 mg/kg for Zn (Impa et al. 2013). In cereal-based diet, the recommended amount of Fe and Zn for better nutrition is about 40–60 mg/kg, whereas in the present scenario, the available amount is in the range of 10–30 mg/kg (Cakmak et al. 2000).

The paradox for Fe is that in spite of the fourth most abundant mineral in earth crust, it is not readily available to the plants because Fe is present in insoluble form by making complexes of hydroxides, oxides and phosphates, hence their normal concentration in plants is only 0.005% (Welch and Graham 2002; Meng et al. 2005). Owing to high soil pH, nearly half of the world's cereal growing area is affected with Zn deficiency and one-third with Fe deficiency (Mori 1999).

6.3 Iron Uptake

In high pH and calcareous soils, Fe was found to be slightly soluble in aerobic conditions despite its abundance (Marschner 1995). It was reported by (Takagi 1976) that Fe-deficient graminaceous plants secreted Fe(III)-solubilizing molecules known as mugineic acids (MAs) family phytosiderophores. When Fe acquisition mechanisms in several plant species were reexamined by Romheld and Marschner, they placed them into two categories: Strategy-I in non-graminaceous plants and Strategy-II in graminaceous plants. These strategies have been identified that almost perfectly fit the model scheme proposed by Romheld and Marschner (1986) (Fig. 6.1).

This strategy is utilized by all the higher plants except graminaceous family. The dominated genes involved in these processes were ferric-chelate reductase oxidase (FRO2) gene and other iron-regulated transporter (IRT1) gene which were first cloned from *Arabidopsis* in 1990s. Since then, FRO2 and IRT1 homologous have been discovered and cloned from numerous plant species. Strategy-I also involved other processes that include excretion of proton and phenolic compounds from the roots into the rhizosphere, which helps to increase the solubility of ferric ions or support the reducing capacity of ferric Fe on the root surface. Among the various numbers of H+-ATPase genes (HA), some induced in Fe deficiency were thought to be functional in Strategy-I. In non-graminaceous plants, genes involved in phenolic secretion were

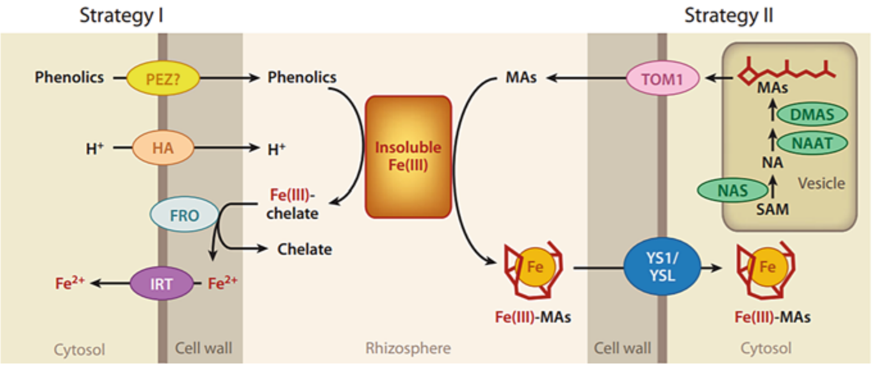

Fig. 6.1 Fe acquisition strategies in higher plants: Strategy-I in non-graminaceous plants (left) and Strategy-II in graminaceous plants (right). Ovals represent the transporters and enzymes that play central roles in these strategies, all of which are induced in response to Fe deficiency

not identified. With induction of these molecular components, other morphological changes in root architecture such as formation of transfer cells and extra root hairs were also seen under low Fe availability.

The Strategy-II response depends on biosynthesis and secretion of phytosiderophores, which are specific to graminaceous plants. Phytosiderophores are non-proteinogenic amino acid derivatives such as mugineic acid (Takagi 1976; Marschner et al. 1986; Marschner 1995; Ueno et al. 2009), mainly secreted at the root tip for a few hours after the onset of sunlight (Neumann and Romheld 2000). These chelates prefer to bind Fe but can also lead to binding Zn or copper. Fe is reabsorbed by roots in the chelated form as Fe—phytosiderophore through a specific transporter (Roemheld 1991; Von Wiren et al. 1993). Under severe Fe and Zn deficiency, the production and secretion of mugineic acids (may represent 50–90% of the exudates) rise enormously in wheat, rice, maize, sorghum and other graminaceous plants as well as correlated with the tolerance ability of plants to Fe deficiency chlorosis and necrosis (Brown and Jolley 1989; Cakmak et al. 1994; Curie et al. 2001). However, the distribution of Fe among different chelators depends not only on the affinity of the chelators toward Fe but also on their relative concentrations in solutions (Yehuda et al. 1996).

6.4 Molecular Components Involved in the Uptake of Micronutrients in Cereals

The graminaceous plants which are grown in conditions deficient in Zn, Fe and other micronutrients depend heavily on methionine derivatives synthesis known as mugineic acid family phytosiderophores (Mori and Nishizawa 1987) for Fe chelation mechanism. The first component which synthesized from methionine by

SAM synthetase is S-adenosylmethionine (SAM) (Shojima et al. 1989) and this enzyme activity is similar in both the conditions, i.e., Fe deficiency and Fe sufficiency (Takizawa et al. 1996). Therefore, constitutive SAM synthetase activity is likely to be sufficient for mugineic acid (MA) synthesis. After this, enzyme nicotianamine synthase (NAS) produces one molecule of nicotianamine by trimerization of three molecules of S-adenosylmethionine (Shojima et al. 1989). The mugineic acids synthesis is crucial for grasses only; in contrast, monocots and dicots share similar biosynthetic pathway up to NA. Thereafter, 3-keto intermediate is produced by transferring of an amino group to NA by enzyme nicotianamine aminotransferase (NAAT). Then by enzyme DMAS, 2′-deoxymugineic acid (precursor of all other MAs) is produced from NA by removal of an amino residue from it. Hence, NAAT and DMAS are critical enzymes in this pathway (Takahashi et al. 2001), as the expression of the genes encoding these enzymes is most crucial in biosynthetic pathway of MAs since it amplified MA, i.e., DMA (the first synthesized MA) (Curie and Brait 2003; Bashir et al. 2006).

Subsequently, other members of mugineic acids family were produced by hydroxylation of 2′-deoxymugineic acid, requirement of which varies with plant species (Bashir et al. 2006). Mugineic acid family phytosiderophores include mugineic acid (MA), 3-epihydroxymugeneic acid (epi-HMA), 3-epihydroxy-2-hydroxymugineic acid (epi-HDMA) and 2′-deoxymugeneic acid (DMA). Two barley cDNAs specifically expressed in Fe-deficient roots, HvIds2 and HvIds3 (iron deficiency-specific), were shown to encode dioxygenases involved in the production of 3-epihydroxy-2′-deoxymugineic acid and 3-epihydroxy-mugineic acid (Nakanishi et al. 2000; Kobayashi et al. 2001). DMA is converted into mugineic acid by enzyme dioxygenase that is coded by gene *Ids3*. MA is more commendable for internal mineral translocation because it is stable under mild acidic conditions (Kobayashi et al. 2009). The genes for NAS (Higuchi et al. 2001), SAM synthetase (Takizawa et al. 1996), NAAT (Takahashi et al. 1999), DMAS (Bashir et al. 2006), IDS2 (Okumura et al. 1994) and IDS3 (Nakanishi et al. 1993) have been cloned and characterized.

The varied differences in quantitative and qualitative production of MAs have been observed among graminaceae family. For instance, rice, maize and wheat secreted only 2-deoxymugineic acids in small fraction, thus because of low Fe availability, they are reported as susceptible. In contrast, barley is reported as tolerant in spite of low Fe availability due to secretion of large amount of different Mas, which include MA, HMA and epi-HMA (Singh et al. 1993). In graminaceous plants, MAs not only facilitate chelation and uptake of Fe but also non-Fe metals such as Zn in the form of Zn-III MAs (Suzuki et al. 2006).

After the chelation of Fe^{3+} by phytosiderophores (PS), a specialized transporter *YSL1* (Yellow-Stripe 1) located in the root cell's plasma membrane helps in the uptake of metal-PS complex in grasses. The *YSL1* maize mutants defective in Fe-PS uptake lead to interveinal necrosis (Curie et al. 2001) that signifies their role in mineral transportation.

In contrast to the biosynthetic pathway of mugineic acids, the molecular mechanisms of phytosiderophores secretion in the rhizosphere remain poorly understood. It has been suggested that vesicular transport may be involved, since the appearance of swollen vesicles in Fe-deficient barley roots correlates with phytosiderophores release. Therefore, at the molecular level, the present understanding reveals the core genes responsible for Fe uptake, translocation and subcellular translocation, and regulation in view of Fe shortage or excess in higher plants is listed in Table 6.1.

The severe yield loss and poor nutritional quality of grains in calcareous or salt stressed alkaline soils occurred due to inefficient uptake of these micronutrients in such conditions (Brown 1961; Cakmak 2008). According to requirement of plants, approximately 10^{-8} M Fe is needed, but calcareous soils or soils having high pH hold total soluble Fe below 10^{-10} M. As a result of this, most plants suffer Fe deficiency like leaf interveinal chlorosis because they lack active mechanisms for extracting and Fe uptake from soil (Kim and Geurinot 2007). Similarly, Zn deficiency symptoms can be observed in plants growing in very limited free Zn^{2+} ions in soils (Haydon and Cobbett 2007; Palmgren et al. 2008).

In case of cereals, the most useful micronutrients are present in husk, aleurone layer as well as embryo. Therefore, it is a major difficulty to make these stored nutrients bioavailable for human absorption. In addition, anti-nutritional factors such as fibers, polyphenols, hemagglutinins, phytic acid and certain tannins present in plant-based diets extremely reduce the micronutrients absorption (Kumar 2013). Another most important anti-nutritional factor is phytic acid (Bouis 2000), which causes reduction of the bioavailability of trace elements by chelation of minerals such as Fe, P, Ca, Mg, Zn and K (Ekholm et al. 2003). These anti-nutrients also cause detrimental losses in monogastric animals (like humans, pigs, fish and poultry) because they cannot utilize phytic acid by degradation due to lacking of microbial flora in their gut, whereas ruminants have possessed enzymatic degradation of phytic acid in their guts and release chelated minerals. It was also observed that phytate ion forms stable salts in seeds due to its high negative charge density and strong tendency to chelate metal cations (Brinch-Pederson et al. 2002). Hence, the presence of phytic acid further elevates deficiency of micronutrient in animal feeds and human diet and acts as a strong anti-nutrient. The level of phytic acid is highest in wheat germ and lowest in wheat flour (Ekholm et al. 2003).

There are certain organic acids, heme-protein, some amino acids, long-chain fatty acids, β-carotene that promote Fe and Zn bioavailability (Graham et al. 2001). Bioavailability of minerals is also dependent on the available forms of micronutrients present in human body such as Fe exists as Fe^{+3} ions within ferrite protein which is largely localized in leaves and amyloplasts of seeds. Ferritin-bound Fe has relatively high bioavailability. The profile of soil also plays significant role in micronutrient availability to plants. If the soil is deficient in Fe and Zn, the crop grown on such soil also observed to have deficiency of micronutrients. The micronutrient content in grains depends on the uptake of micronutrients by roots during grain development followed by remobilization and redistribution to grain from vegetative tissue across phloem. Movement of each element through phloem occurs differently. It has been observed that Mn and Cu show low movement, Fe shows intermediate movement and Zn shows good remobilization across phloem (Kochian 1991; Pearson and Rengel 1995). Also it has been reported that at maturity, only 4–5% of the shoot Fe is translocated in the grain of rice and wheat (Impa et al. 2013).

Table 6.1 Major genes responsible for Fe homeostasis in graminaceous plants

Name	Function	Fe deficiency response	References
TOM1	MAs efflux transporter	Induced (strong)	Nozoye et al. (2011)
YS1/YSL	Fe(III)-MAs transporter	Induced (strong)	Curie et al. (2001)
NAS	NA synthase	Induced (strong)	Higuchi et al. (2001)
NAAT	NA aminotransferase	Induced (strong)	Takahashi et al. (1999)
DMAS	Deoxymugineic acid synthase	Induced (strong)	Bashir et al. (2006)
IDS2	Putativeepihydroxymugineic acid synthase	Induced (strong)	Nakanishi et al. (2000), Okumura et al. (1994)
IDS3	Mugineic acid synthase	Induced (strong)	Kobayashi et al. (2001), Nakanishi et al. (1993, 2000)
SAMS/MAT	*S*-adenosyl-L-methionine synthetase	Induced (weak)	Kobayashi et al. (2005)
MTN	Methylthioadenosine/*S*-adenosyl homocysteine nucleosidase	Induced	Kobayashi et al. (2005), Rzewuski et al. (2007)
MTK	Methylthioribose kinase	Induced	Kobayashi et al. (2005), Sauter et al. (2004)
IDI2/MTI	Methylthioribose-1-phosphate isomerase	Induced	Suzuki et al. (2006), Yamaguchi et al. (2000a, b)
DEP	Methylthioriblose-1-phosphate dehydratase-enolase-phosphatase	Induced	Kobayashi et al. (2005)
IDI1/ARD	Acireductone dioxygenase	Induced	Yamaguchi et al. (2000a, b)
IDI4/AAT	Putative aminotransferase catalyzing the synthesis of methionine	Induced	Kobayashi et al. (2005)
FDH	Formate dehydrogenase	Induced	Suzuki et al. (1998)
APRT	Adenine phosphoribosyltransferase	Induced	Itai et al. (2000)
IDEF1	Positive transcriptional regulator	Constitutive	Kobayashi et al. (2007)
IDEF2	Positive transcriptional regulator	Constitutive	Ogo et al. (2008)
IRO2	Positive transcriptional regulator	Induced (strong)	Ogo et al. (2006)
IRO3	Transcriptional regulator (putatively negative)	Induced	Zheng et al. (2010)

Estimates of number of people affected by micronutrient malnutrition are high, with up to 5 billion people suffering from Fe deficiency. The fraction of developing country populations at risk of inadequate Zn intake is estimated to be 25–33% (Hotlz and Brown 2004). The Copenhagen Consensus Conference [Copenhagen Consensus 2008 (www.copenhagenconcensus.com)] ranked the alleviation of Fe and Zn deficiencies as a top priority. It is well established that plant product quality in the future must include an improvement of nutritional content and availability. In this context, it was proposed that feeding humans safely with enough Fe and Zn directly within their diet could become possible by using Fe and Zn fortified crops (Newell-McGloughlin 2008). Reaching such a goal requires an integrated knowledge of the establishment and control of micronutrient homeostasis in plants.

6.5 Zinc Solubilization

Zinc is a crucial micronutrient for plants which plays various important functions in their life cycle. The deficiency of zinc in the soil is one of the very common micronutrient deficiencies and results in decreased crop production. Majority of the agricultural soil is either zinc-deficient or contains zinc in a fixed form which is unavailable to plants; as a result, reflecting zinc deficiency in plants and soils. Therefore, to solve the above problem, there is a requirement for alternative and eco-friendly technology such as plant growth-promoting rhizobacteria (PGPR) and organic farming practices to enhance zinc solubilization and its availability to plants (Hesham et al. 2021; Yadav 2021). Zinc-solubilizing bacteria (Zn-SB) are promising bacteria to use for sustainable agriculture. Zn-SB have various plant growth-promoting (PGP) properties such as Zn solubilization, P solubilization, K solubilization, nitrogen fixation and production of phytohormones, like kinetin, indole-3-acetic acid (IAA) and gibberellic acid, besides production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase and siderophores, hydrogen cyanide and ammonia. Zn-SB secretes different organic acids that solubilize the fixed form of zinc to available form, which enhances plant growth promotion, yield and fertility status of the soil (Yadav et al. 2020b, 2021).

6.6 Mechanism of Zinc Solubilization by PGPR

Zn-solubilizing PGPR were studied extensively to explore their mechanisms. In general, PGPR use acidification, chelation, exchange reactions and release of organic acids to solubilize the micronutrients (Chung et al. 2005; Hafeez et al. 2005). The mobilization mechanism of Zn and Fe may possibly involve the siderophore production (Burd et al. 2000; Wani et al. 2007; Tariq et al. 2007; Saravanan et al. 2011; Abdel-Azeem et al. 2021; Yadav et al. 2020a) gluconate or derivatives of gluconic acids, e.g., 5-ketogluconic acid (Saravanan et al. 2007a, b), 2-ketogluconic acid (Fasim et al. 2002) and other organic acids by PGPR (Di Simine et al. 1998; Tariq

Table 6.2 Biofortification of micronutrients using the plant growth-promoting rhizobacteria

Microbes	Micronutrient	Crops	References
Anabaena sp.	Zn, Fe, Cu, Mn	Wheat	Rana et al. (2012a)
Bacillus anthracis	Zn	Soybean	Khande et al. (2017)
Bacillus aryabhattai	Zn	Maize	Mumtaz et al. (2017)
Bacillus cereus	Zn	Soybean	Khande et al. (2017)
Bacillus pumilus	Zn	Rice	Jha (2019)
Bacillus sp.	Fe	Wheat	Rana et al. (2012b)
Bacillus subtilis	Zn	Maize	Mumtaz et al. (2017)
Bacillus sp.	Zn	Rice	Shakeel et al. (2015)
Bacillus sp.	Zn	Maize	Mumtaz et al. (2017)
Brevundimonas sp.	Fe	Wheat	Rana et al. (2012b)
Calothrix sp.	Zn, Fe, Cu, Mn	Wheat	Rana et al. (2012a)
Enterobacter cloacae	Fe, Cu, Mn	Soybean	Ramesh et al. (2014)
Enterobacter cloacae	Zn	Rice	Krithika et al. (2016)
Pantoea dispersa	Fe	Mungbean	Patel et al. (2018)
Providencia sp.	Zn, Fe, Cu, Mn	Wheat	Rana et al. (2012a)
Providencia sp.	Fe	Wheat	Rana et al. (2012b)
Pseudomonas fluorescens	Zn	Black gram	Sirohi et al. (2015)
Pseudomonas pseudoalcaligenes	Zn	Rice	Jha (2019)
Pseudomonas putida	Fe	Mungbean	Patel et al. (2018)
Pseudomonas sp.	Zn	Wheat	Rehman et al. (2018b)

Source Kaur et al. (2020), with permission)

et al. 2007; Wani et al. 2007). PGPR-mediated biofortification can be achieved by using various PGPR microbes isolated from several crops (Table 6.2).

It was found that soil–plant–microbe interactions are complex in nature and there are various processes which affect the outcome that can influence the crop vigor and yield (Hafeez et al. 2002; Pieterse et al. 2003). In broader scenario, the precise mechanism still not completely understood through which PGPR promote plant growth (Hafeez et al. 2014).

6.7 Biofortification

Biofortification is a method for increasing the availability of essential elements in the edible portions of crops through agronomic or genetic and genomic interventions. Biofortification is a novel method to fulfill the daily micronutrients requirement of people. The major approaches used till date for biofortification of staple food crops are: agronomic biofortification, conventional plant breeding and genetic engineering.

Some of biofortified staple crops are: Vitamin A biofortified maize, cassava, sweet potato, iron biofortified pearl millet, beans and zinc biofortified maize, rice and wheat (Nestel et al. 2006). Biofortification has multiple advantages over supplementation and food fortification (Ottaway 2008). First, it fulfils the daily required amount of micronutrients in the diet as staple foods are dominantly consumed by poor people and people living in rural areas have limited/less access to the fortified food available in the market. Second, one-time investment is required for development of biofortified seeds, and these seeds are used by farmers for many years. Therefore, it is a cost-effective approach as it reduces the use of expensive fertilizers. Third, biofortified crops are highly sustainable (Rajendra 2009).

Among the various interventions to improve nutritional status of deprived human beings, biofortification of the crops is the most promising, widely accepted, cost-effective and easily affordable method (Zimmermann and Hurrel 2002; Lonnerdal 2003). Biofortification refers to the process of developing genetically improved food crops that were rich in bioavailable micronutrients, either through genetic modification via conventional breeding or molecular approaches. Various micronutrient initiative programs are running worldwide and Harvest Plus is one of them which was started to challenge micronutrient malnutrition with the objective of improving nutritional status in staple food crops with Zn, Fe and vitamin A by using plant breeding strategy (Pfeiffer and McClafferty 2007). During the first phase of this program, priority was given to rice, wheat, maize, sweet potato, cassava and beans, while in the second phase to potato, barley, cowpeas, groundnuts, lentils, millets, plaintains, sorghum, pigeon peas and yams. The biofortification of cereals is achieved through combined techniques of conventional breeding, molecular breeding and genetic engineering (Bouis 2000; Nestel et al. 2006). The simplest method of fortification relies on the addition of the required micronutrient as an inorganic compound to the fertilizer but its applicability depends on various factors such as soil composition, mineral mobility in soil, in plant and its accumulation site. Two other approaches involved genetic engineering and conventional molecular breeding methods for nutritional enhancement wheat, rice and maize (India Biofortification Program).

6.7.1 Agronomic Biofortification

Agronomic biofortification is also termed as ferti-fortification as it involves fertilizing crops with micronutrients (Bindraban et al. 2015). In this, the amount of micronutrient in the food crop is enhanced by physical application of mineral fertilizers that mainly consist of iron, zinc and selenium. These mineral fertilizers can be applied directly to the soil, seeds, foliar spray or by dipping seedlings into the solution of fertilizers. By conducting various studies, it was found that foliar application is highly effective in increasing micronutrient concentration in edible parts of crops compared to their soil application (Cakmak et al. 2010). On the other side, soil application is highly effective in enhancing the grain yields (Aro et al. 1995). This approach is simple and easy to apply as it does not require any technical learning, but needs attention while choosing the source of nutrient, application method and effects of fertilizers on the environment (Rengel et al. 1999). A major drawback of applying mineral fertilizers is their repeated and regular application in every season, and thus less cost-effective to poor farmers. In addition to application of mineral fertilizers, soil microorganisms like Rhizobium, Azotobacter, Bacillus, Pseudomonas etc. can also be used which can increase the nutrients uptake and their mobility from the soil to the edible parts of the crops, and thus improve their nutritional value (Smith and Read 2010). The nutritional status of different crops has been enhanced through agronomical biofortification.

6.7.2 Breeding Approach Toward Biofortification

Biofortification using plant breeding approach involves improvement of micronutrients concentration and their bioavailability in staple food crops with the use of conventional breeding and current biotechnological methods such as marker-assisted selections (Mayer et al. 2008). Biofortification with the use of conventional breeding is one of the most accepted methods of biofortification, as it involves crossing between natural crop varieties. Sufficient genotypic variation for the trait of interest is the primary need of conventional breeding. Conventional breeding involves crossing between donor parent (contain high amount of micronutrient) and recipient parent (into which desired trait have to be transferred) over several generations to generate plant with desired micronutrients. Therefore, production of desired variety can take up to 6–7 years (Stein et al. 2007). Due to less availability of natural genetic variation, another method, that is mutational breeding, can be used to biofortify staple crops. This technique enhances crop variety by creating genetic variability with chemical mutagens such as ethyl methyl sulfonate (EMS), ethyl nitrosourea (ENU) or irradiation that involves gamma rays, X-rays, UV rays etc. Recent breeding approach being used worldwide is molecular breeding, also known as marker-assisted breeding. This modern biotechnology technique uses the molecular marker (a segment of DNA) linked to a particular trait of interest in order to screen nutrient-rich crop varieties. It speed up the breeding process by selection of desired crop varieties at early stages of development. The use of molecular breeding is increasing gradually, both by seed companies and plant breeders. Using this approach multiple genes from different varieties which code for different traits can also stack into single variety (Pray and Listman 2006).

6.7.3 Biofortification Through Genetic Engineering

Genetic engineering is now being used as one of the most advanced weapons to fight against micronutrient deficiency by generating transgenic by transferring genes directly to elite genotypes. Improved knowledge about DNA has facilitated scientists for speedily exploiting the hidden secrets and benefits of different genes. However, for the development of transgenic for nutrient biofortification, two criteria need to be considered; first, the selection of widely adapted genotype of economically important crop, and second, accumulation of nutrient in the edible portion of the crop plant without having adverse effects on their physiological and developmental characteristics (Vanderschuren et al. 2013). Genetic engineering approach has been used in various crops for nutritional enrichment by focusing on increasing the uptake and utilization efficiency of crop through modulation of reporter's expression, and reducing the concentration of anti-nutritional factors (Garg et al. 2018). Transgenic iron and zinc rice has been developed and tested in confined field trials that can provide 30% of the EAR for both nutrients (Trijatmiko et al. 2016). Golden rice, which contains β carotene, is capable of providing more than 50% of the EAR for vitamin A. Despite being available as a prototype since early 2000, however, golden rice has not been introduced in any country, in large part due to highly risk-averse regulatory approval processes (Wesseler and Zilberman 2014). This has been reported that by improving the Fe, Zn and Se content of crops by utilizing the information regarding plant genetic makeup and applying transgenic approach we could definitely solve the problem of micronutrient malnutrition but it's very expensive and will require a lot of time. However, once these crops are being developed, there are no more utilization of resource because the changes have been made permanent directly at genetic level (Bilski et al. 2012). Although using genetic approaches we are able to get desirable results, but using it for production of transgenic is not well accepted due to acceptance issues related to transgenic crops. Moreover, recently it was found that editing in plants is possible through various genome editing tools, like CRISPR-Cas, ZFN, TALLEN, etc. and these tools can be further exploited to get our desirable results (Jaganathan et al. 2018).

Various transgenic strategies for nutritional fortification of cereals included alteration in metabolic pathway for either increasing the amount of desirable compound, decreasing the number of competitive compounds or extension of the biosynthetic pathway for the production of novel product used by various workers. It also involved expression of recombinant proteins that make minerals to be stored in trivalent form such as ferritin. This is a Fe storage protein consisting of 24 subunit shell around a 4500-atom Fe core. Ferritin resisted the denaturation during gastrointestinal digestion and also protected it from chelators during digestion, thus enhances Fe absorption. Ferritin gene expression has been demonstrated in a variety of plants, including *Arabidopsis*, soybeans, beans, cowpeas, peas and maize. Transgenic rice with 3 to 4.4 times higher grain Fe level than wild type has been reported (Goto et al. 1999). In another study constitutive promoter along with soybean ferritin gene resulted in elevated Fe level in the leaves of transgenic rice and wheat plants. Six-fold Fe and 1.6-fold Zn content was increased by transgenic approach for overexpression of the Fe storage protein ferritin *soyferH2,* overexpression of *HvNAS1* for the overproduction of the natural metal chelator nicotianamine, and iron(II)-nicotianamine transporter *OsYSL2* under the control of an endosperm-specific promoter and sucrose transporter promoter (Masuda et al. 2008). Two to six-fold increase in Fe content of endosperm of rice seed was observed in genetically transformed rice where nicotianamine synthase genes (NAS) and ferritin genes were expressed independently or in conjugation for this increase.

Another aspect of biofortification and alleviation of malnutrition is bioavailability. Even after achieving higher micronutrient content in edible tissue, how much of these get absorbed by human gut. It was observed that phytic acid present in food chelates metal cations such as Fe^{2+}, Zn^{2+} and Ca^{2+} and forms phytin, thus reduces their absorption in the human gut and acts as an anti-nutritional factor. Reduction in phytic acid could be achieved through development of low phytic acid mutants and development of thermostable phytase enzyme for solubilizing phytic acid. Low phytic acid mutants have been identified in rice, barley, maize (Shi et al. 2008), wheat and soyabean. Expression of phytase and reduction of phytate biosynthesis increased the bioavailability of Fe and Zn in cereals grain. Nearly 55–60% reduction in phytic acid phosphorus was reported in these low phytic acid mutants. In tortillas made by *lpa* maize, 49% increase in Fe bioavailability has been observed as compared with wild-type maize. Stable transgenics may be used for hybrid production in maize and rice with improvement in phosphorus availability. In rice, the gene controlling MIPS was under the control of *RINO1* gene expressed in developing rice seeds specifically in aleurone and embryo. Using antisense *RINO1* technology, transgenic rice with 68% lower phytic acid, normal seed weight, and germination and plant growth has been produced.

Production of transgenic seeds with higher phytase activity might also result in enhanced minerals absorption. Maize seeds expressing phyA2 gene showed 2,200 units of phytase activity per kg seeds which was nearly 50-fold increase over non-transgenic maize. Transgenic crops containing phytase genes from various *Aspergillus* species have been produced in tobacco, soybean, alfalfa, wheat, rice and canola seeds (Brinch-Pedersen et al. 2002). Differential gene expression, coding sequence and copy numbers resulted in post zygotic sterility. In spite of some advances with transgenic approach, there are certain constraints associated with it. Stability in the expression of transgenic plants from one generation to next generation is a key concern for biofortification program. Other problem refers to various socio-economical and socio-political concerns related with the acceptance of transgenic crops by farmers and common people. Issue associated with licensing and intellectual property rights also creates troubles in popularization of these biofortified crops and ultimately, they didn't reach to the neediest people.

6.7.4 Molecular Breeding Techniques for Biofortification

Molecular markers are very useful tools for crop improvement and to reduce the time required in varietal development in crop improvement programs and being utilized in almost all the important crops. Cereals such as rice, wheat, maize and millets are very poor source of micronutrients. Wheat cultivars had very low Fe and Zn content in grains, which largely distributed in embryos and the peripheral tissue of bran (Welch and Graham 1999). In contrast to this, non-progenitor species wheat is having good genetic variability for Fe and Zn concentration, which ranged 2–3-fold higher than that of wheat cultivars (Cakmak et al. 2000; Chhuneja et al. 2006; Rawat et al. 2009; Kumar et al. 2015). Similarly, genetic variability for grain Fe and Zn concentrations is present in various wild relatives of rice. The Fe concentration in brown rice samples ranged from 6.3 to 24.4 ppm with a mean value of 12.2 ppm, whereas for Zn, the range was 13.5–58.4 ppm with a mean of 25.4 ppm. Some traditional varieties of rice such as Jalmagna, Zuchem, XuaBueNuo, Madhukar were reported to have twice the Fe and Zn content than that of elite cultivars. This variability was utilized for developing biofortified varieties through plant breeding.

Useful variability of *Aegilops kotschyi* and other non-progenitor wheat was screened (Chhuneja et al. 2006) and used for wheat biofortification for Fe and Zn through classical and molecular breeding (Tiwari et al. 2010). Addition and substitution derivatives of *Ae. kotschyi* group 1, 2 and 7 chromosomes had been developed for high grain micronutrients (Fe and Zn) by molecular breeding (Tiwari et al. 2010; Rawat et al. 2011). Variability from *Ae. peregrina* for high Fe and Zn was also utilized (Neelam et al. 2011). Scientists at CIMMYT, Mexico have used synthetic hexaploid wheat from crosses between *T. durum* and *Ae. tauschii* with high Fe and Zn contents in breeding programs and developed wheat lines with higher level of these micronutrients which were tested at agricultural fields in India, Pakistan and other countries (Calderini and Monasterio 2003). However, the level of enhancement of Fe and Zn using wheat synthetics has not been very impressive because of the limited variability for Fe and Zn in the progenitor wild parents. Therefore, screening of non-progenitor species for additional variability for micronutrients was required and considered very important.

6.8 Biofortification of Wheat for Fe and Zn

Wheat (*Triticum* sp.) is the second major staple food crop of the world in terms of food source and cultivated area. Various progenitor and non-progenitor species were screened for utilization of their useful variability (Chhuneja et al. 2006) and used for wheat biofortification for Fe and Zn by molecular breeding (Tiwari et al. 2010). In contrast to wheat cultivars, one of the species, *Aegilops* had possessed a unique and distinctive genetic system for the micronutrient uptake, translocation and sequestration. They secrete 3–4 times high amount of phytosiderophore than wheat cultivars in both nutrient-deficient and sufficient conditions (Neelam et al. 2012). Since then, numerous alien addition, substitution and translocation lines in wheat had been produced via transfer of variability through their several related wild progenitor and non-progenitor species (Raupp et al. 1995; Friebe et al. 1996, 2000; Qi et al. 2007). Wheat-*Aegilops* addition lines were reported to had higher content of Fe and Zn than hexaploid wheat but lower than *Aegilops* species (Schlegel et al. 1998). Variability from *Ae. peregrina* was utilized by Neelam et al. (2011) for high Fe and Zn content. Wheat-*Ae. kotschyi* addition/substitution derivative lines with 2S and 7U chromosome and wheat-*Ae. peregrina* addition/substitution derivative lines with 4 and 7 group chromosomes were developed and reported to have high grain Fe and Zn content in comparison to elite wheat cultivar (Tiwari et al. 2010; Neelam et al. 2011). Additionally, 5B, 6A and 6B chromosome substitution lines had also been reported to have high grain Fe and Zn content compared to their recipient parental line. Using wild and synthetic parents, durum wheat was also fortified for Zn and Fe content (Cakmak et al. 2010).

Moreover, amphiploids ($\mathrm{AABBS^{l}S^{l}}$) of *Ae. longissima* and *T. turgidum* also had been developed possessing high Fe and Zn content (Tiwari et al. 2008). Synthetic amphiploids of *T. aestivum* cv. Chinese Spring (Ph^{I}) and WL711 with different accessions of *Ae. kotschyi* (UUSS) were generated by using colchicine treatment of sterile hybrids (Rawat et al. 2009). Scientists at CIMMYT, Mexico have utilized synthetic hexaploid wheat in breeding programs from crosses between *T. durum* and *Ae. tauschii* with higher Fe and Zn content, and the developed wheat lines containing increased level of these micronutrients were then tested in agricultural fields of India, Pakistan and other countries (Calderini and Monasterio 2003). However, enhancement level of Fe and Zn using synthetic wheat has not been as expected due to limited variability for Fe and Zn in the progenitor wild parents. Therefore, the requirement of screening of non-progenitor species for additional variability for micronutrients is very important step, for the development of biofortified varieties through plant breeding.

Therefore, the addition/substitution lines possessing genetic material of *Aegilops* species with high Fe and Zn are very crucial, but because of associated linkage drag, these cannot be utilized directly. Previously, a number of genes have been introgressed showing resistance against various pests and diseases into wheat from related species and exploited commercially (Marais et al. 2005; Kuraparthy et al. 2007; Schneider et al. 2008). Similarly, to reduce linkage drag different methods have been used for the precise transfer of potential gene (s) from the alien chromosomes.

6.8.1 Utilization of ph1b Mutant

The homoeologous pairing in wheat was prevented by *ph1* gene which in contrast allows pairing of homologous chromosomes. The manipulation of *ph*-gene system, therefore, allows pairing of alien chromosomes with wheat chromosomes. Numerous approaches were developed and used for manipulating *ph1* gene for induced homoeologous recombination. One of them involves elimination of the *Ph1* gene either through use of nullisomy for 5B or using deletion mutants spanning the *Ph1* locus such as *ph1b* and *ph1c* (Sears 1977; Giorgi et al. 1983). Another alternative is Ph^{I} gene, transferred from *Ae. speltoides* to *T. aestivum* (Chen et al. 1994). Mutant for *ph* was developed by irradiating the pollen by X-ray and pollinating them on mono 5B plants (Sears 1977). Alien additions, substitutions, translocations, deletions, monosomes, ditelosomes and nullisomes of wheat were developed using *ph1b* line. The wheat *ph1b* mutation, which allows meiotic pairing between homoeologous chromosomes, was deployed to induce recombination between wheat chromosome 2B and goat grass 2S chromatin using a backcross scheme which is favorable for induction and detection of the homoeologous recombinants with introgression of small goatgrass chromosome segments (Niu et al. 2011). Translocation lines of wheat were generated with stem rust resistance that have *Sr39* gene conferring resistance to seven stem rust races (Yu et al. 2010).

6.8.2 Utilization of Mono 5B Line

Development of mono 5B lines can also be used for manipulating *ph1* gene as 5B chromosomes of wheat had *ph1* gene on long arm (5BL) (Holm 1988). Formation of multivalent and random pairing between homologous and homoeologous chromosome can occur due to absence of 5BL chromosome (Hobolth 1981) which allowed pairing and recombination between the chromosome of wheat and related species and therefore, introduce alien genetic variation into wheat. Examples of such alien transfer were wheat-rye crosses (37%) and wheat-Aecolumneris crosses (50%) (Lacadena 1967). Advanced lines of durum wheat where homoeologous D genome replaced B genome were created by Joppa and Williams (1988). These lines were used for homoeologous pairing. Homoeologous recombination was also observed in triploids of Festuca arundinaceae var multiflorum (LmLmLmLm) hybrids using GISH (Morgan et al. 2001).

6.8.3 Radiation-Induced Gene Transfer

The major barriers of alien gene transfer among wheat were hybrid sterility and lack of recombination between alien chromosomes and wheat. Various strategies were deployed for transferring alien segments that were smaller than the complete chromosome arms. Irradiation treatments of various types have been used for fine gene transfer from alien chromosomes into recipient lines (Michalak et al. 2008). Pollen irradiation had also been used to obtain gene transfer (Snape et al. 1983). X-ray irradiation at the dose of 2, 3 and 5 krad was used for transfer of genes or chromosome fragments in wheat (Snape et al. 1983). Grain quality and reduced plant height was achieved by gamma rays at the rate of 10, 20, 30 and 40 krad (Singh and Balyan 2009). However, it was observed that use of pollen irradiation for transfer of gene was more precise. It was also found that dose of irradiation determines fragment length to be transfer, i.e., higher the dose, smaller the fragment transferred.

Aegilops germplasm has been utilized extensively for the wheat improvement, and various addition, substitution, translocation lines for different chromosomes of *Aegilops* species have already been reported by many workers (Schneider et al. 2008). A number of genes have been introgressed into wheat from related progenitor and non-progenitor species (Friebe et al. 2000; Marais et al. 2005; Sears 1956) transferred *Lr9* from *Ae. umbellulata* to wheat using irradiation. Since then various workers have utilized wild wheat germplasm for different purposes of wheat improvement. Some of the examples are *Yr8* from *Ae. comosa* (Riley et al. 1968), wheat streak mosaic resistance from *Agropyrone longatum* (Sebesta et al. 1972), *Pm13* from *Ae. longissima* (Ceoloni et al. 1988), *Lr35* and *Sr39* from *Ae. Speltoides*, *H21* and *H25* (Hessian Fly resistance) from rye, *Pm29* from *Ae. geniculata* (Stoilova and Spetsov 2006), *Lr57* and *Yr40* from *Ae. geniculata* (Kuraparthy et al. 2007), *Lr58* from *Ae. truncialis* (Kuraparthy et al. 2007) and *Pm19* and *Pm35* from *Ae. tauschii* (Miranda et al. 2007). Powdery mildew resistance locus *Pm21* was transferred from *Haynaldia villosa* to wheat using female gametes irradiation-induced transfer (Chen et al. 2012).

Genes for yield and quality improvement have also been transferred from wild species to cultivars (Hajjar and Hodgkin 2007). Alien introgression of *Lr57/Yr40* from *Ae. geniculata* and *Lr58* from *Ae. triuncialis* to wheat was achieved without linkage drag (Gill et al. 2008). Various cytological and molecular techniques have been utilized to analyze the introgressed alien chromosomes and precise fragments from wild germplasm to wheat. Recently, the 2S chromosomal fragment(s) of *Aegilops kotschyi* ($2S^k$) have been transferred into the bread wheat genome in the direction of developing biofortified wheat with high grain Fe and Zn content (Verma 2014).

6.9 Conclusion

Micronutrient deficiency, micronutrient malnutrition or hidden hunger is an increasingly severe global challenge for humankind. As wheat, rice and maize are the major staple food crops in temperate countries and is frequently consumed in developing countries, it has become necessary to biofortify cereal crops with micronutrients, especially iron and zinc, in order to fulfil the requirements for better human health. With increase in knowledge about molecular and cellular mechanisms establishing micronutrient homeostasis understood at most levels alleviates uptake of Fe and Zn from soil, transport within plant, subcellular compartmentation and storage in edible parts. On the other hand, different approaches like biofortification using radiations, transgenics and other methods for alien gene transfer further enhance the prospect of high percentage of micronutrients in cereal crops. Use of PGPR for the improvements of micronutrients deficiency is promising due to its ecological, economic and eco-friendly nature. The net increase in nutrient contents and yield has been reported by the recent studies in the last decades for different grain yielding crops.

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Chapter 7
Soil Microbes in Plant Growth Promotion and for Mitigation of Abiotic Stress of Drought

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Abstract A large proportion of world's agricultural land is becoming less productive or completely unproductive due to different environmental factors. Drought is one of the major agriculture constraints which is caused by insufficient rainfall, prolonged and frequent dry spells or changes in rainfall patterns. Drought impairs growth, water relations and water use efficiency of plants, which further alters their morphological, physiological and biochemical activities. Crop growth models predict that occurrence and intensity of drought will be more severe in future. In the current scenario, to meet global food demands, various strategies have been formulated to cultivate the crops under drought-affected area. Among them, the use of different microbial community could be a viable strategy, which enables plants to combat with water stress through various direct and indirect ways. The use of microbial inoculation for drought stress management is considered as cost-effective and more eco-friendly approach than traditional methods. Various rhizospheric soil microbes, including arbuscular mycorrhizal (AM) fungi, N-fixing bacteria and plant growth promoting microbes (PGPMs), help in stress resistance and better plant performance. PGPMs represent a broad range of archaea, bacteria and fungi, which are having excellent root association ability to produce different enzymes and metabolites for various

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abiotic stress tolerances. In the present chapter, the exploration of potential soil and root microbiome and their mechanism of actions for drought tolerance in relation to better plant growth and development have been discussed.

Keywords Drought · Phytohormone · Proline · PGPM · Rhizobacteria

7.1 Introduction

Drought or moisture stress is one of the devastating environmental tremors that has expanded its frequency throughout in the last 25 years and has severely affected food and nutritional security of the earth. Drought stress disturbs majority of the agricultural lands in the world, and poses serious agriculture challenges by limiting plant growth and productivity. Climate change has an extremely aggravating impact on occurrences of drought. Lesk et al. (2016) estimated that drought stress could decline 9–10% in grain productivity and by 2050, >50% crop productions under global agricultural areas are adverse effect by water stress (Vinocur and Altman 2005). In agriculture, drought mainly occurs due to shortfall in precipitation along with a higher evapotranspiration rate (Mishra and Cherkauer 2010) which limits the accessibility of water for plant growth and development to accomplish normal life cycle (Manivannan et al. 2008). However, by 2050, it is projected that global human population reaches >9 billion and that will require a sustained increase in food production to ensure nutritional safety (Foley et al. 2011; Gatehouse et al. 2011). Therefore, a renewed interest to find out alternative ways to water deficit-related problems, i.e., drought and its impact on food and nutritional security gain priority. In addition, solutions have to be pursued to improve plant tolerance under drought environment and allow proper crop growth to meet the nutritional needs under reduced water supply (Editorial 2010; Mancosu et al. 2015).

At any stage of growth, deficit water supply has harmful effects on crop production. Restricted water supply decreases cell size, membrane toughness, induces O^{3-} species (ROS) and encourages defoliation, which results in lower plant growth and development (Tiwari et al. 2017). Despite this, plants experience a range of physiological and molecular changes during water deficiency, such as increased ethylene level, greenness index, disruption of leaf mesophyll cells and interruption in photochemical reaction (Lata and Prasad 2011). Water-deficit environment also leads to the accretion of O^{3-} species that stimulate an alteration in cell membrane activity, tertiary and quaternary protein binding, and peroxidation of lipid molecules that ultimately cause cell expiry (Tiwari et al. 2016). The crops have evolved many strategies that help them to survive under water-deficit condition (Foyer and Noctor 2005), which includes development of some specialized bio-chemical pathways inside the protoplasm (Apel and Hirt 2004; Gill and Tuteja 2010). Therefore, metabolic re-orientation happens in cells (Shao et al. 2008; Bolto 2009; Massad et al. 2012) to expedite regular catabolic and anabolic activities regardless to water stress situation (Mickelbart et al. 2015). Globally, extensive research is underway to establish tactics in dealing with water insufficiency, such as drought-resistance crops, planting calendar changes, water management techniques, etc. (Venkateswarlu and Shanker 2009), and many of them are expensive. Apart from this, another approach to reduce the adverse impact of water insufficiency on plants requires application of microbes, namely bacteria or arbuscular mycorrhizal fungi (AMF) (Forchetti et al. 2010; Marulanda et al. 2010).

Recent research suggests that plants are facilitated to alleviate the load of environmental stress by the use of microbes in their inhabitants (Turner et al. 2013). Research on biochemical, physiological and molecular interactions between plants and microbes has shown that microbial interactions mostly control plant responses toward abiotic and biotic stresses tolerance (Fig. 7.1) and boost up the crop productivity (Marulanda et al. 2010; Yang et al. 2009; Farrar et al. 2014). Nowadays, an attempt has been made to utilize such useful microscopic organisms for better plant growth promotion under the shifting environment (Yang et al. 2009; Nadeem et al. 2014). Among these plant–microbes association, AMF (Aroca and Ruiz-Lozan 2012; Azcón et al. 2013), N_2-fixing microbes (Lugtenberg and Kamilova 2009) and PGPR (Kloepper et al. 2004; Glick 2012) are well known. An advantageous community of microbes colonizes the endo- and exo-rhizospheric region of the crops and stimulates crop productivity by a combination of diverse mechanisms (Shahzad et al. 2017) which include various kinds of low molecular weight organic compounds that assist crops to survive under changing climate (Pineda et al. 2013; Chauhan et al. 2015). In the present chapter, we have explored the potential microbial-mediated mechanisms to mitigate drought stress in relation to plant growth and development.

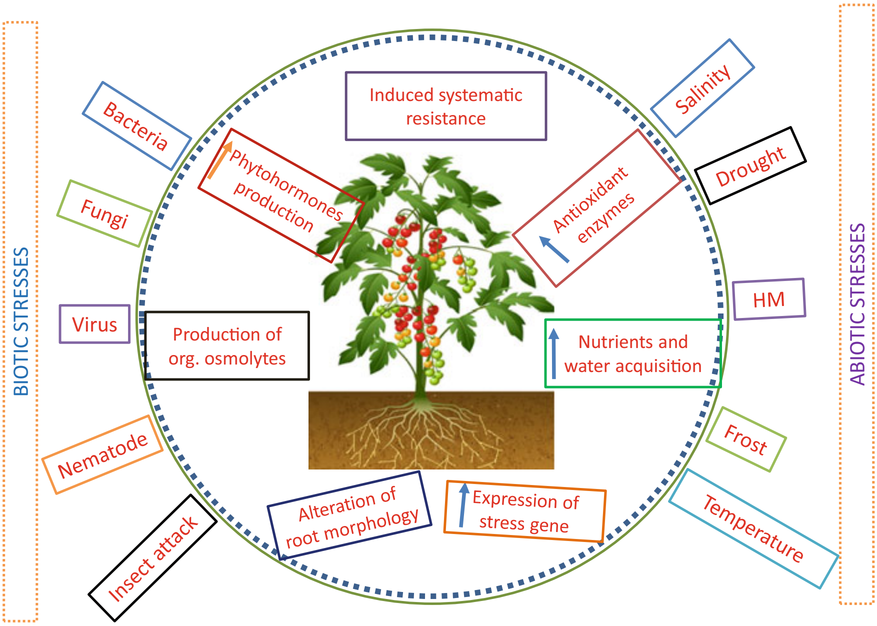

Fig. 7.1 Microbes-mediated mechanism of biotic and abiotic stress tolerance

7.2 Drought Stress and Plant Performance

Drought is the main constraints for higher agricultural productivity and is likely to increase further (Kour et al. 2020a; Yadav et al. 2021a; b). The environmental changes are responsible for drought-like conditions. Thus, all the living beings will be affected by drought, particularly plants, which don't have organs that permit them to move elsewhere when water and food become scarce. As a result, diverse terrestrial ecosystems will therefore be harshly influenced by drought stress. Drought, the most common devastating environmental stress, has led to serious impact on crop productivity in virtually all parts of the world.

In the current decade, drought condition has emerged as a severe problem in low rainfall area (Hossain et al. 2013). Extreme drought is responsible for the modification in physiological, vegetative and other metabolic activities in plant (Maqsood et al. 2012; Yadav et al. 2020). However, there are many defense mechanisms in plant which could be beneficial for the plant in response to drought stress. Drought condition adversely influenced the plant morphology, photosynthesis and antioxidant enzymes activity; however, the severity of changes depends on plant growth stage (Maqsood et al. 2013). In addition, plant root system is also a major organ against the abiotic stress, as it absorbs available water and nutrients from the soil solution (Cseuz et al. 2009) and plays a key role to alleviate the drought stress. Influence of drought on root is reflected in several aspects, such as root morphology and further on plant production. Du et al. (2020a) reported that drought stress enhances the root/shoot (R/S) ratio in soybean seedlings and this might be due to upregulation of soluble sugar and starch contents in soybean roots under soil moisture stress.

Under drought condition, plant leaves help in water utilization and contribute significantly in survival and growth of plant (Grzesiak et al. 2013). Plants react to drought stress at biochemical, morphological and molecular levels from the seed emerging stage to harvest stage (Tiwari et al. 2017). Drought stress influences water potential to turgor pressure and interferes with normal plant functions (Hsiao 2000) by changing physiological characteristics of the plants. Furthermore, drought stress also affects transport and availability of nutrients present in the soil solution, as it decreases diffusion and mass flow of NO_3^-, SO_4^{2-}, Ca, Mg and Si (Selvakumar et al. 2012). According to Rucker et al. (1995) drought can reduce effective leaf area, which subsequently reduces the photosynthetic rate. Moreover, number, size and longevity of leaf per plant can be shrunk by water stress. Aboveground portions of vegetable are more susceptible to drought stress than counterparts. Under water-deficit condition, plants respond by shrinkage area and spiraling of leaves. However, reduction in leaf size lowers down the photosynthetic activity (Farooq et al. 2009). Drought also influenced the biochemical composition of plants, like lower nitrate reductase (NR) activity, because of lower nitrate uptake from the soil system (Caravaca et al. 2005).

Drought can also cause pollen sterility, grain shrinkage, build-up of ABA in spikes of drought-susceptible genotypes and abscisic acid (ABA) synthesis in the anthers. It also decreases the biosynthesis of ethylene, which influences the growth and development of plants through several mechanisms. Under drought stress, plants exhibited several changes such as lower straw yield, altered root morphology, decreased photosynthesis, transpiration rate and stomatal regulation with higher oxidative enzyme activity (Conesa et al. 2016). Drought stress reduced soybean seed weight by reducing biomass accumulation on organs and decreased biomass allocated to seed (Du et al. 2020b). In rose, water deficiency reduced the photosynthetic activity, shoot length, weight and leaf surface, while it induced flowering in the early stages (Shi et al. 2019).

7.3 Microbes-Mediated Drought Tolerance in Plants

The below ground microbial communities substantially reduce the impact of drought stress and enhance the persistence ability of various plant species (Table 7.1). This could be achieved by altering the plant root system, through forming a diverse microbial culture that affects crop development and yield (Schmidt et al. 2014). Structural modifications of crop-linked microbial populations in root zone under water stress condition help crops to adapt during water-deficit condition and develop tolerance against stressors (Schmidt et al. 2014; Cherif et al. 2015; Hartman and Tringe 2019). The responses of crops toward the drought-specific microbe could be an evolutionary adaptation; however, frequent drought spells had contributed to the development of sustainable crop-microbial interrelation which enhances both host and microbe endurance ability. Soil attenuation is an alternate way to obtain drought-tolerant community; in such cases, microbial communities develop resistance under drought-exposed soils, and therefore the plants might have only one option to appoint these useful microbes.

Lau and Lennon (2011) reported that plants grown under previously stressed soils were more adaptable to survive in drought condition. Furthermore, plants grown repeatedly in the same soil can improve their performance under water stress conditions due to the recruitment of beneficial bacteria that persist in the soil and may increase resistance against drought for other members of their species (Zolla et al. 2013; Nadeem et al. 2019). Compared to control soil, pepper plant (*Capsicum annuum* L.) grown under arid conditions revealed a complex community of drought-tolerant microbial population in the endosphere, rhizosphere and root surrounding soil (Marasco et al. 2012). *Piper nigrum* plants associated with microbial (bacterial) strain from desert demonstrated greater resistance under drought stress over non-inoculated plants which might be explained due to root enlargement of ~ 40% that increased water absorption capacity (Marasco et al. 2013). Brassica rapa cultivated in complex soil microbial communities showed increased chlorophyll content, flowers and fecund compared to soil grown in control condition (Lau and Lennon 2011).

Under unfavorable conditions, plant growth and survival can be improved by adding stress-tolerant bacteria, plant growth promoting microbiome (PGPM) and AMF (Nadeem et al. 2014). Microbes use indirect and direct pathways to facilitate growth and development of plants under stress situations. Furthermore, microbes use various biochemical and molecular processes to promote growth and development.

Table 7.1 Effect of various microbes on drought tolerance in various crops

Microbes	Crop	Results	References
Trichoderma atroviride	Maize	Increase fresh and dry weight of maize roots	Guler et al. (2016)
Trichoderma harzianum	Rice	*T. harzianum*-rice plant interaction alleviate drought stress by modulating proline, SOD, lipid peroxidation, growth attributes and molecular interaction	Pandey et al. (2016)
Trichoderma harzianum	Rice	Decreases proline, MDA (malondealdehyde) and H_2O_2 contents, and increases phenolics concentration, MSI (Membrane Stability Index), root and seedling growth	Shukla et al. (2012)
Bacillus amyloliquefaciens and *Azospirillum brasilense*	Wheat	Improved homeostatic mechanism of the plant	Kasim et al. (2013)
Mixture of *Rhizobium tropici, Paenibacillus polymyxa* and *P. polymyxa*	Bean (*Phaseolus vulgaris*)	Increases plant growth, nitrogen content and nodulation	Figueiredo et al. (2008)
Sinorhizobium medicae or Sinorhizobium meliloti	*Medicago truncatula*	Significant delay in drought-related leaf senescence in inoculated relative to non-inoculated plants and increases osmolytes concentration during drought	Staudinger et al. (2016)
Bradyrhizobium (*B. japonicum*) *and Rhizobium* (*R. leguminosarum*)	Sorghum (*Sorghum bicolor* L.)	Significantly increases yield and yield attributes of the plants	Rashad et al. (2001)
Glomus intraradices	Tomato	Significantly increases uptake of N and P in both roots and shoots; also increases shoot dry matter and the number of fruits	Subramanian et al. (2006)
Glomus intraradices	Soybean	Increase osmotic adjustment in roots and alleviate oxidative stress	Porcel and Ruiz-Lozano (2004)

(continued)

Table 7.1 (continued)

Microbes	Crop	Results	References
Azospirillum lipoferum	Maize (*Zea mays* L.)	Seed and rhizosphere inoculation with *A. lipoferum* increases plant height by 43.89% and 35.33%, respectively	Bano et al. (2013)
Azospirillum spp.	Maize (*Zea mays* L.)	Provides better response against water deficit	García et al. (2017)
Bacillus subtilis	Timothy (*Phleum pratense* L.)	*B. subtilis* inoculation increases shoot biomass and root volume by 26.6 and 63.8% and photosynthesis and stomatal conductance by 55.2 and 214.9%, respectively	Gagné-Bourque et al. (2016)
Pseudomonas putida and Bacillus amyloliquefaciens	Chick pea (*Cicer arietinum* L.)	Significant increase in biomass of the plant, and modulate enzymes activity and microbial diversity	Kumar et al. (2016)
AMF species with *Bacillus thuringiensis*	*Lavandula dentate*	Increase plant growth and nutrition while decrease the plant oxidative damage of lipids	Armada et al. (2016)
Bacillus spp.	Sorghum	Inoculation increases growth in terms of shoot length and root biomass with higher chlorophyll content than un-inoculated plants	Grover et al. (2014)
Bacillus subtilis	*Platycladus orientalis* (oriental thuja)	Thus, inoculation of cytokinin-producing PGPR ↑ shoot dry weight of normal and drought seedlings by 34.85 and 19.23%, and root by 15.445 and 13.99%, respectively	Liu et al. (2013)

(continued)

Table 7.1 (continued)

Microbes	Crop	Results	References
Pseudomonas aeruginosa	Mung bean (*Vigna radiata* L.) R. Wilczek)	Inoculated plants showed increase in growth attributes, relative water content and upregulation of drought stress-responsive genes in comparison to non-inoculated control	Sarma and Saikia (2014)
Pseudomonas putida	Chickpea (*Cicer arietinum* L.)	Promotes plant growth	Tiwari et al. (2016)
Various strain of *Pseudomonas entomophila*	Maize	The strain GAP-P45 was found superior in terms of influencing the biochemical, physiological and growth parameter of the seedlings under drought stress	Sandhya et al. (2010)
Azotobacter strains	Maize	Significantly increases plant growth and nutrient concentration	Shirinbayan et al. (2019)
Bacillus megaterium, *Enterobacter* sp., *Bacillus thuringiensis*, and *Bacillus* sp.	*Lavandula dentata* and *Salvia officinalis*	*B. thuringiensis* influences nutritional (increase K content), physiological (decrease stomatal conductivity) and metabolic (decrease cellular oxidative damage) plant activities	Armada et al. (2014)
Pseudomonas libanensis EU-LWNA-33	Wheat	Positively prompting the growth and physiological attribute	Kour et al. (2020b)
Streptomyces laurentii EU-LWT 3-69; *Penicillium* sp. EU-DSF-10	*Sorghum bicolour* L.	Improving build-up of diverse osmolytes such as glycine betaine, proline, sugars, increased greenness index, and declining lipid peroxidation	Kour et al. (2020a)
Acinetobacter calcoaceticus EU-LRNA-72 and *Penicillium* sp. EU-FTF-6	*Setaria italica* L.	Efficiently alleviated the antagonistic influence of stress in foxtail millet by build-up of glycine betaine, proline, sugars, and declining lipid peroxidation	Kour et al. (2020c)

Rhizobacteria-mediated induced drought endurance and resilience (RIDER) is an effective intervention that includes changes in plant physiological and biochemical processes. Physiological pathways include improvements in phytohormone concentrations, antioxidant protection mechanisms and development of exopolysaccharides (EPS), whereas these when related with bio-chemical modifications entail aggregation with many organic compounds (such as amino acids, sugars and polyamines) and, moreover, synthesis of dehydrins and volatile organic compounds (VOCs) (Ngumbi and Kloepper 2016; Vílchez et al. 2016; Kaushal and Wani 2016). During occurrence of drought, crops enhance osmolytes concentration and thus improve the osmotic balance inside the protoplasm (Farooq et al. 2009). Interestingly, those osmolytes include substances exudates by microbes in the root zone. Osmo-tolerant bacteria synthesize glycine betaine which functions along with crop and synthesize glycine betaine under water deficiency to improve resistance against water stress situation (Kour et al. 2019). These osmo-tolerant microbes generate indole-3-acetic acid (IAA), which is another important compound to enhance plant growth and development. This hormone is likely to cause increase in root proliferation under microbial-inoculated drought-stressed plants (Yuwono et al. 2005), which promotes water absorption. Under severe stress situation the positive effects of osmolyte-producing rhizobacteria on plants were more immense. Yuwono et al. (2005) documented that under severe drought circumstance, bacteria associated *Oryza sativa* plants recorded higher root and shoot dry weight and number of tillers over the control. Bacteria that live on root surfaces that produce 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase are said to alter the leaves and roots development response to drought, possibly through affecting ethylene sensing. *Achromobacter piechaudii* inoculation in tomato and pepper significantly improved the fresh and dry weights under drought spell and this might be due to production of ACC deaminase through the bacteria (Mayak et al. 2004).

It has been also stated that bacterial inoculation prevents a substantial drop in water content, and promotes root growth, leaf biomass, leaves surface area and formation of proline in roots and leaf (Casanovas et al. 2002). Maize seedlings under drought stress condition, associated with *Azospirillum brasilense* reported higher water content, compared to control treatments. Moreover, these results were more profound as water supply was decreased by 75% over 50% (Casanovas et al. 2002). Creus et al. (2004) revealed that wheat cultivated under water stress environment with *Azospirillum* inoculation recorded higher concentration of Mg, K and Ca in grain but contrastingly decreases the crop productivity. Therefore, content and potential of water, relative water content and apoplastic water fraction improved under inoculated wheat plants. In the same experiment, measurement of cell wall elasticity indicates that an ‘elastic adjustment’ is critical for increasing water stress mitigation (Creus et al. 2004). It was widely believed that the inoculation of *Azospirillum* alters the host plant’s root morphology, and thus enhanced drought tolerance potential. However, at present it is not clear that how the microbes alter in crop root structure though it was believed that bacteria secretes hormone-like chemicals, which played a crucial part in this method (Dobbelaere et al. 1999; Cassán et al. 2001). Moreover, recently discovered that bacteria produce nitric oxide (NO) gas, which acts as signaling molecule in

IAA-mediated route for root proliferation (Creus et al. 2005; Molina-Favero et al. 2008). They reported that tomato plants inoculated with *Azospirillum* produces nitric oxide, which helps to develop the lateral root and root hairs. Belimov et al. (2009) stated that under water-deficit condition, *Variovorax paradoxus*-inoculated pea plants recorded higher growth, yield and water-use efficiency over un-inoculated plants and this might be due to synthesis of ACC deaminase by the bacteria. TerHorst et al. (2014) showed that Brassica rapa plants exposed to drought stress environments were reported to increase microbial abundance and diversity around the root system compared to plants grown under normal environment. Ullah et al. (2019) isolates two thermophilic bacterial strains, i.e., Chloroflexi and Gemmatimonadetes which thrives well under water stress condition and helps cotton plants to sustain various physiological functions under drought stress.

For mitigating water stress in plants, fungal association played a vital role. AMF symbiosis modifies hormonal synthesis, which alters plants physiological activity, and thus alleviates water-deficit stress. This also increases photo-chemical reactions performance to produce nutritional substances in drought stress situation (Ruiz-Lozano et al. 2016). Shukla et al. (2012) reported that rice plants inoculated with Trichoderma harzianum enhanced root proliferation under drought stress, thus enhancing plants survival ability under water-deficit situation. In lettuce and tomato plants, strigolactone level also reported to alleviate water-deficit situation by forming a symbiotic association among crop-fungi (Ruiz-Lozano et al. 2016).

Inoculation of plants with PGPM encourages plant growth in water-deficient conditions by controlling hormonal and nutritional equilibrium, by generating crop hormonal regulators, and moreover, encouraging tolerance against biotic and abiotic stress (Spence and Bais 2015; Dikilitas et al. 2021; Tiwari et al. 2021). In addition, microbes stimulate crop productivity by capturing atmospheric N_2, mobilization of P, and by releasing hormones (Ahmad et al. 2011; Hesham et al. 2021). Plants adopted few more pathways to cope with the unfavorable environment, such as solubilization of nutrients, synthesis of exopolysaccharide, rhizobitoxine etc. (Vardharajula et al. 2011). Under drought stress situation, rhizobitoxine encourages plant growth and development by preventing the synthesis of ethylene (Kumar et al. 2009). Plant growth promoting bacteria (PGPB) mediated drought tolerance in tomato (Solanum lycopersicum L.) was studied by inoculation with *Bacillus cereus* AR156, and enhancement in growth responses was documented (Wang et al. 2012). Conjoint use of silicon (Si) and PGPB strain improved crop performances under water-deficit situation relative to their individual application (Ullah et al. 2016). In tomato, Si and PGPB inoculation increased absorption of K^+, Ca^{2+} and Mg^{2+}, relative water content and reduced electrolyte outflow. However, more field-based investigations need to be performed to expose the morphological and physiological feedbacks induced by PGPB, such as improvements in root architecture and drought tolerance. The association of PGPR could promote maize productivity via the synthesis of plant hormones by microbes in root zone that would improve root formation, leading to improved water and nutrients uptake (Lin et al. 2020).

7.4 Mechanism of Drought Tolerance by Soil Microbiome

There are several mechanism followed by beneficial soil microbes to mitigate the drought stress as described in Fig. 7.2. This includes phytohormone production, synthesis of volatile compounds by soil microbes, morphological alteration of the root, 1-aminocyclopropane-1-carboxylate deaminase action, osmolytes accumulation, exopolysaccharide performance, antioxidant resistance and molecular approaches (Fig. 7.2).

7.4.1 Alteration of Phytohormones Production in Plants

Phytohormones (indole acetic acid, gibberellic acid, cytokinins, abscisic acid and ethylene) are essential for the growth and development of plants (Egamberdieva 2013; Qu et al. 2020). Phytohormones play a significant role in the escape or survival of stressful conditions in plants (Fahad et al. 2015; Abdel-Azeem et al. 2021; Yadav 2021). PGPRs such as *Azospirillum lipoferum*, *Bacillus thuringiensis* and *Phyllobacterium brassicacearum* are capable of synthesizing phytohormones (indole-3-acetic acid, cytokinin, abscisic acid and gibberellins) that stimulate cell growth, cell division, increase water and nutrients uptake, as well as the stress transduction signal pathways which lead to decrease leaf transpiration in various crops (Arzanesh et al. 2011; Armada et al. 2014; Kaushal and Wani 2016). Some PGPR isolates produced IAA that increased the root volume of the seedlings to mitigate drought

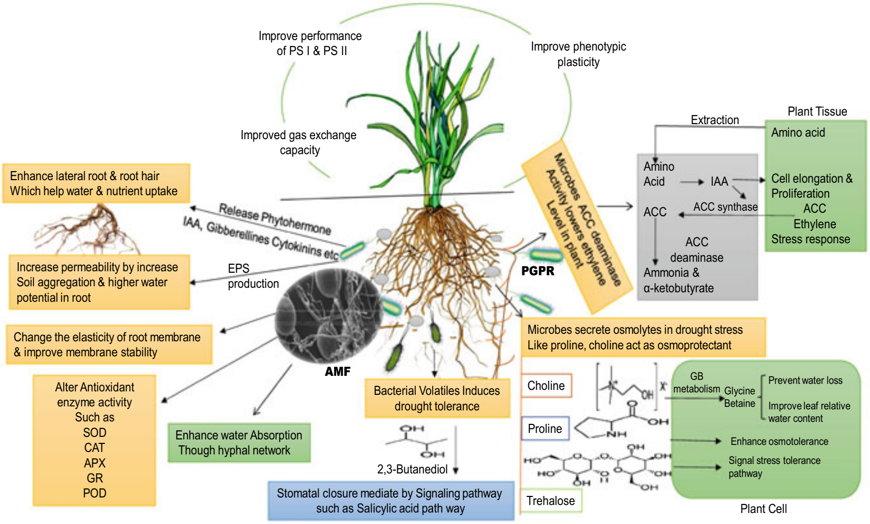

Fig. 7.2 Mechanism of drought tolerance by soil microbiomes

stress (Hussain et al. 2014; Liu et al. 2020). Asghari et al. (2020) and Jochum et al. (2019) informed *Bacillus* sp. (12D6) and *Enterobacter* sp. (16i) metabolized indole-3-acetic acid (IAA) and salicylic acid (SA) under drought stress, significantly altering root morphology and promoting growth in crops of wheat (*Triticum aestivum*) and maize (*Zea mays*).

7.4.2 Functions of Volatile Compound

Accumulation of volatile compound occurs when plant are subjected to various stresses (Holopainen and Gershenzon 2010; Raza and Shen 2020; Loreto and Schnitzler 2010). These volatile compounds stimulate signals for different metabolic reactions both inside and in neighboring plants (Niinemets 2010; Poltronieri et al. 2020). When *Pseudomonas chlororaphis* was present at rhizosphere of the *Arabidopsis* plant, it induced drought tolerance by producing 2R, 3R-butanediol, volatile metabolite that prevents water loss by inducing stomatal closure in the plant through an SA-dependent mechanism, whereas no tolerance mechanism has been shown in the absence of bacteria (Cho et al. 2008). Rhizobacteria emitted various volatile organic compounds that cause similarly increased tolerance to abiotic stress (Garbeva and Weisskopf 2020).

7.4.3 Modification in Root Morphology

Bacteria-mediated modifications in the root cell membrane elasticity was one of the first measures in improved resistance toward drought stress (Dimkpa et al. 2009). Plant growth-promoting rhizobacteria significantly increases the cell membranes integrity by stimulating the antioxidant defense mechanism and mediate drought tolerance (Gusain et al. 2015).

7.4.3.1 ACC Deaminase Productions

In ethylene metabolic pathways, s-adenosyl methionine (S-AdoMet) is converted into 1-aminocyclopropane-1-carboxylate (ACC) by 1-aminocyclopropane-1-carboxylate synthase (ACS) which acts as a precursor to ethylene. Ethylene maintains plant homoeostasis in an endogenous way during drought, by controlling plant growth and development (Gontia-Mishra et al. 2020). The sequestered plant ACC was depleted by bacterial ACC deaminase to provide nitrogen and energy to bacteria. Lower ACC content in the plant eliminates the negative impact of ethylene and encourages plant growth under drought stress conditions (Glick 2005; Singh et al. 2020). In pot and field trials, ACC producing bacteria abolished the influence of drought stress on the yield and yield attributes ripening of peas (Arshad et al. 2008). Similarly, *Bacillus licheniformis* K11 inoculated pepper released ACC deaminase and six separate stress proteins, which were detected by two-dimensional polyacrylamide gel electrophoresis (2D-PAGE) to alleviate drought stress (Hui and Kim 2013). In tomato plants, ACC deaminase producing Rhizo SF 48 provides greater resistance against oxidative damage under moisture stress condition and promotes plant growth (Gowtham et al. 2020).

7.4.3.2 Osmolytes Production

Plant drought tolerance is associated with metabolic modifications which lead to the accumulation of several ideal electrolytes/osmolytes such as choline, carbohydrates, proline, betaines, polyamines, quaternary ammonium compounds, and polyhydric alcohols and other amino acids and water stress proteins such as dehydrine (Yancey et al. 1982; Close 1996; de Vries et al. 2020). Under drought stress conditions, PGPR secretes osmolytes that are synergistic with plant-produced osmolytes. It promotes plant growth and development (Paul et al. 2008). *Pseudomonas putida* GAP-P45 inoculation improved dry matter weight (DMW), relative water content of leaf (RWC) and leaf water efficiency due to greater proline accumulation in plants under moisture stress (Sandhya et al. 2010 and Gusain et al. 2015). Like proline, the metabolism of trehalose in rhizobacteria is important for sensing plant growth, productivity and tolerance to abiotic and biotic stresses, and its handling had a major agronomic effect on crops (Rodriguez et al. 2009). Evident studies on *Bacillus subtilis* GB03, *Klebsiella variicola* F2 (*Arabidopsis*) and *Pseudomonas fluorescens* YX2 (maize) mediated dry tolerance function by biogenesis and production of choline as a precursor to glycine betaine metabolism, increases RWC and DMW (Zhang et al. 2010; Gou et al. 2015). Moreno-Galván et al. (2020) observed that the induction of glutathione reductase activity and proline accumulation were primarily responsible for drought stress in Guinea grass.

7.4.3.3 Productions of Exopolysaccharide

The synthesis of EPS by rhizobacteria defends them from extreme climates and allows them to thrive (Vives-Peris et al. 2020). Rhizobacteria releases EPS in soil as capsular or slime materials that adsorbed to soil colloidal surfaces by forming cation bridges, H-bonding, Waals forces and adsorption mechanism, and improves soil aggregate stability (Tisdall and Oades 1982; Sandhya et al. 2009). EPS offers a microenvironment that holds available water and prevents the environment from drying out, thereby protecting microorganism and roots against drought stress (Hepper 1975, Selvakumar et al. 2012). Plants inoculated with EPS-producing bacteria have shown increased accumulation of organic osmolytes under water-deficit stress (Khan and Bano 2019).

7.4.3.4 Antioxidant Enzymes

Under drought stress, reactive oxygen species (ROS) are formed in plants. ROS interacts with plant metabolites such as oligonucleotide, polysaccharide, protein, lipids and DNA, which induce oxidative damage and disrupt the normal function of the plant cells. In order to mitigate these effects, PGPRs application might be helpful to enhance the resistance against drought by modifying the function of antioxidants during water stress (Gusain et al. 2015). Gusain et al. (2015) recorded that combined inoculation of *Pseudomonas jessenii* R62, *Pseudomonas synxantha* R81 and *Arthrobacter nitroguajacolicus* strain YB3 enhanced plant dry matter content and increased stress-related enzymes such as superoxide dismutase (SOD), common antioxidant enzyme (CAT), peroxidase, ascorbate peroxidase (APX) and malondialdehyde in Sahbhagi and IR-64 rice cultivars (*Oryza sativa* L.) under drought stress compared to control.

7.4.4 AMF-Mediated Drought Tolerance

Drought is susceptible to soil degradation and poses severe challenges to agriculture. Most of the research in the past few years was focused on the symbioses mechanism of AMF to defend plants from drought, showing that symbiotic relationship often results in increased osmoregulator sequestration, nutrient uptake, water use efficiency and dry matter production (Zhao et al. 2015). AMF induced drought tolerance in the plant by the following mechanism.

7.4.4.1 Biochemical Changes

The AMF works against drought conditions and promotes crop growth through regulating their biochemical pathways. The first mechanism includes direct uptake of water through hyphae and its transport to the root system and scavenging the ROS generation such as hydroxyl radicals (OH) and singlet oxygen (Huang et al. 2017). The second mechanism involves the synthesis of enzymatic antioxidant (catalase, superoxide dismutase and ascorbate peroxidase) and non-enzymatic antioxidants (tocopherol, glutathione, carotenoid, ascorbate and flavonoids) because of mutual interaction (Bahmani et al. 2018; Xie et al. 2018). For example, AM symbiosis minimized the oxidative stress in maize under droughts and benefitted the plants from non-systematic oxidative stress (Barzana et al. 2015). Mutual symbiosis starts with the transition of biochemical signals between the symbionts by physical interaction, which induces preparatory reactions in the other symbionts (Ruiz-Lozano et al. 2016). The molecular dialog begins with a carotenoid-based plant hormone, i.e., strigolactones, released from plant, which regulates different plant developmental processes (Lopez-Obando et al. 2015). The host plant initially secreted a labile rhizospheric signaling molecule (Strigolactones) to stimulate AMF to recognize its host.

AsAMF recognizes strigolactones; it activates oxidative metabolism, which promotes mycelium production, and help to develop physical contact between the AMF and the host plant (Mori et al. 2016; Peng et al. 2020). Phytohormone and ABA level rises in AMF-colonized plants under drought to deal with the stress. Simultaneously, plant increases the expression of genes encoding D-myositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF), which are found to be involved in ABA signaling transduction, and in the activation of 14-3-3 proteins and aquaporins in *Rhizophagus intraradices*. Such results indicate that IPS and 14-3GF co-expressions are responsible to perform the synergistic acts by symbiotic partners to improve plant tolerance to drought (Li et al. 2016; Martin-Rodriguez et al. 2016). Zhang et al. (2020) reported that jujube seedling inoculation with *Pseudomonas lini* and *Serratia plymuthica* provides excellent protection against drought stress by regulating IAA and ABA synthesis with lower ROS production which improves plant growth and production. Under circumstances of drought, plants modify water connections by synthesizing well-suited solutes (e.g., starch, proline, protein) to retain turgor pressure and cellular functions for sustaining metabolic functions (Ouledali et al. 2019; Boutasknit et al. 2020).

7.4.5 By Altering Root Morphology

The AMF enhances the ability of the plant to respond against drought condition. It has demonstrated its capacity to restore water supply and increase the uptake of plant nutrients by mycelium elongation under drought. Furthermore, improved water content may result in greater root activity and hydraulic conductivity (Zou et al. 2017). In addition, AMF has the capacity to perform the task of anastomosis (the capacity to cause inter-individual fusion of vegetative cells) which is considered to be an essential mechanism for AMF persistence under dry conditions; in particular anastomosis of damaged mycelium to regenerate the boundary after water-deficit stress (Avio et al. 2006).

7.4.6 AMF-Mediated Water and Nutrient Uptake

Water movement occurs primarily through a gradation-driven movement across plasma membranes, a mechanism induced and regulated by water channels called aquaporins (AQPs) (Quiroga et al. 2017). Plant aquaporins play a significant part in AM symbiotic relationship and can react directly to stress (Marjanovic et al. 2005). Expression patterns of AQP genes coding with AMF and drought stress are observed in plant roots for certain plasma membrane-intrinsic proteins (PIPs) (Aroca et al. 2007). Expression levels of AQP genes have continuously become documented in both root cortical cells that contain arbuscules and extraradical mycelia, while molecular mechanism involves water and nutrients uptake through extraradical hyphae and improved root morphology (Zou et al. 2015). The AMF improves the water and nutrients uptake to the plants under water-deficit situation and it could be achieved by extending root outreach (Bagheri et al. 2018; Bahadur et al. 2019). Le et al. and Boutasknit et al. (2020) documented that AMF inoculation has strengthened the nutrient deficit under sustained moisture stress by encouraging the absorption of essential macro- and micro-nutrients, organic solutes, stomatal conductance and resistance against oxidative harm during drought and regeneration, primarily phosphate.

7.4.7 Challenges to Use Microbial Bio-inoculants

Microbial bio-inoculants provide various benefits to the plants either by augmenting plant growth through solubilization of nutrients or production of substances which enhance plant performance, as well as resistance, under drought stress condition. In addition to improving plant nutrients, beneficial bio-inoculants restore the soil fertility without polluting the environment and dissimilar conventional chemical fertilizers are utilized in crop fields; thus, they are environmental-friendly (Kour et al. 2020b). In addition, when carrying out these roles, certain bio-inoculants often limit the environmental stresses, such as drought or moisture stress. Despite these benefits, there are some challenges regarding availability, applicability and commercialization of beneficial microorganism for sustainable agricultural production. However, many microbial products are available in the markets (Table 7.2) but the effectiveness of these microbes is also influenced by various soil physical properties (texture, structure) as well as pH and chemical characteristics.

Another limitation is the lack of mass exploitation of these favorable microbes for crop production. Furthermore, under stressed environments, extreme temperature may distress the effectiveness of particular inoculants strains, except root colonizing endophytic microbes having ability to produce biofilms. High temperatures could also reduce the beneficial microorganisms in the soil since the microbe inoculum do not have any defensive support.

However, certain strains perform excellently when applied solely but not necessarily provide good results when used as consortium due to poor compatibility with other microbes. Lastly, an appropriate carrier has to be used for the bio-formulation of PGPR. To popularize these bio-inoculants among end-users, certain characteristics, such as cost, presence of toxic elements, physical appearance, viability, effective propagules density etc., need to be evaluated carefully.

7.5 Conclusion and Future Prospects

In order to enhance agricultural production, management of various biotic and abiotic stresses is an important strategy. Therefore, use of soil biota such as PGP microbes

Table 7.2 List of various microbial products available in the market

Microbial product	Mechanism	Application rate	Suitable crops	Country
MaxMicrobe	Increase N_2-fixation, systemic resistance, iron availability and produce vitamins	1-2 mL/Gallon for both growth and bloom phase	All crops	USA
EM-1 Microbial Inoculant	Increase seed germination, root development, nutrient availability, microbial activity and improve drought tolerance	One ounce per gallon (2 TBS)	All crops	USA
Bio Yield® Biostimulant	Promotes growth by increasing P and providing better plant defense	Seed or furrow application within 14 days of planting	Corn/Maize	USA
Mycorrcin	Improve plant immune through induced systemic resistance (ISR) pathway	For crops and fruits: 2–4 L/ha sprayed onto the soil; For vegetables: At planting apply 6 L/ha sprayed onto the soil	Mainly fruits, vegetables, sugarcane and other crops	New Zealand
Soil activator	Improves nutrient availability soil microbial activity and suppresses disease	Vegetables: 5–10 L/ha every 1–2 weeks from emergence/transplant; Fruit and nut trees: 5–10 L/ha monthly; Broad-acre crops and pasture: 3–6 L/ha 1–3 times during the season	Vegetables, vines, fruit and nut trees and pasture crop	Australia
Humigene	Improves soil and plant condition and microbial activity	Foliar spray: 2-3 mL/L, soil application: 1 L/acre and seed treatment: 10 mL/kg	All crops	India
Zaena Stress Relief Bacterial Consortium	Alleviate plant stress and stimulates the plant immune system against phytopathogens	Soil application or seed treatment: (10–20 mL/kg) or spraying or drenching (10 mL/L)	All crops	India
Fitomare®	Increases drought tolerance and reduces oxidative damage	Foliar application	Tomato	Spain

(continued)

Table 7.2 (continued)

Microbial product	Mechanism	Application rate	Suitable crops	Country
Plantsorb	Improve plant vitality and growth through alleviating drought stress	Planting: 20 g/L, surface application: 500 g/m^2 and volume application: 100 g/L	All crops	Czech Republic

could be a potential option to alleviate the plant stresses including drought stress. Soil microbes follow various mechanisms such as production of the phytohormones, solubilization of nutrients, production of ACC deaminase, siderophore, and various compatible organic osmolytes and by increasing the availability of water to manage the stress condition. More specifically, under stress environment, soil microbes influence the plant growth either directly or indirectly. Direct effect includes delivery of certain microbe-based metabolic products or greater availability of soil nutrients or water. While indirect mechanism includes the preventive measures against plant pathogenic organism. Overall, we conclude that soil microbes have a great potential to enhance the agriculture production under stress environment but their proper exploitation through molecular and biotechnological approaches is required for further identification and development of novel and efficient bio-products. In addition, development of mechanistic understanding with multidisciplinary approach and extensive research is required to unlock the full potential of soil microbiome in drought and other stress management.

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Chapter 8
Thermotolerant Soil Microbes and Their Role in Mitigation of Heat Stress in Plants

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Abstract A growing worldwide population, urbanization and industrialization are expanding the pace of transformation of arable land into no-man's land. Providing food to an ever-expanding populace is perhaps the greatest test that agriculturalists and plant researchers are now facing. Ecological anxieties make this circumstance much graver. In spite of the enlistment of a few resilience components, touchy plants regularly neglect to make due under natural limits. New mechanical methodologies are basic. Customary rearing techniques have a restricted potential to improve plant genomes against ecological pressure. As of late, hereditary building has contributed hugely to the advancement of hereditarily altered assortments of various harvests, for example, cotton, maize, rice, canola and soybean. The distinguishing proof of pressure responsive qualities and their resulting introgression or overexpression inside delicate yield species is presently being broadly done by plant researchers. The design of significant resilience pathways, similar to cell reinforcement chemicals, osmolyte amassing, layer limited transporters for effective compartmentation of harmful particles and aggregation of fundamental components and opposition against irritations or microorganisms is additionally a territory that has been seriously investigated.

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In this chapter, the role of microbial biotechnology for mitigation of heat stress in plants are discussed.

Keywords Heat stress · Plant responses · Adverse impacts · Thermotolerant soil microbes · Mitigation of heat stress

8.1 Introduction

Biodiversity is a significant component of ecological preservation and is vital to horticulture creation. Dangerous atmospheric deviations and their related impacts can result in forced abiotic stresses; for example, limits of temperature ranges, dry seasons and flooding, that will undoubtedly affect food creation. Environmental change influences horticulture and the food creation framework from multiple points of view (Godfray et al. 2011). Harvest creation is influenced by climatic factors, for example, rising temperatures, changing precipitation systems and expanded barometrical CO_2 levels. It is likewise influenced by natural factors, for example, the lengths of the harvest development periods and the yield cycle. Over the course of the twentieth century, fabulous increments in horticultural yields spared over a billion people from starvation. Because of accomplishments in the Green Revolution (Pingali 2012), it appeared that the world's food requirements could be met; however, in spite of the fact that the quantity of undernourished individuals has diminished consistently throughout the most recent decades, around 795 million individuals stay undernourished around the world, the greater part of whom live in developing nations. In any event, recognizing the advantages of the Green Revolution in helping to adjust populace development and food creation, it became apparent before long that the increase of horticulture through the selection of agro-advancements by ranchers had prompted the debasement of delicate agroecosystems, due to the loss of soil fruitfulness, disintegration, natural lopsided characteristics, and contamination. These issues were the outcome of the foolish and unbalanced utilization of the advances created inside the Green Revolution, exacerbated by shallow formative arrangements (Rahman 2015). Lamentably, almost fifty years after it began, the critical heritage called the Green Revolution has in numerous areas turned into the debasement of agricultural regular environments, and a significant part of the populace have not received the guaranteed end-of-hunger rewards on those innovations.

Today, new ideal models have emerged, and one specifically—practical strengthening—has increased wide acknowledgment. As per Pretty and collaborators (2011), feasible strengthening alludes to delivering more yields from a similar zone of land while lessening the negative ecological effects and simultaneously expanding commitments to regular capital and the progression of natural administrations. This idea was received by universal strategy and examination associations like the CGIAR, SDSN, World Economic Forum, FAO, and the Montpellier Panel (Tittonell 2014). One conceivable approach to accomplish horticultural increase without genuinely trading off other biological system capacities, is to appropriate and sufficiently use a frequently dismissed asset—the dirt microbiome. Truth be told, organism-based innovations have more than once been shown to increment horticultural profitability and manageability without hurting nature (Velivelli et al. 2014). For that requirement, the inoculants of microbes are becoming progressively mainstream, and speak to a genuine option in contrast to manufactured agrochemicals. Soil organisms of numerous sorts: parasites, microorganisms, protists, nematodes, and also bacteria flourish in the zone-encompassing roots of plants, as well as being affected by root affidavits: "rhizosphere." Indeed, natural particles discharged by roots of plants, such as flavonoids, amino acids, carbohydrates and so on, are able to pull microorganisms of the soil (Zhang et al. 2014). Some of these rhizospheric microbes advance plant development and improvement, the most important ones (Mendes et al. 2013) being known as plant development advancing microorganisms. These can be grouped into a few classes: those ready to hinder or alienate plant microorganisms are designated biocontrollers or bioprotectants; others discharge phytohormones, metabolites, and advance development legitimately (biostimulants); numerous microbes can become activated by using mineral supplements, as nutrients were synthetically inaccessible (biofertilizers); another group may enact plant resistance frameworks (bioelicitors); and last, numerous microbes can synthetically change poisonous xenobiotics working as bioremediators (Glick 2012).

Intriguingly, a portion of these microorganisms can show creepy-crawly pathogenicity, in this way functioning as bioinsecticides ready to shield plants from root-taking care of creepy-crawlies (Kupferschmied et al. 2013). As it has been over and again affirmed, a similar microorganism may show a few of these attributes at the same time (Ahemad and Kibret 2014). Some current acts of practical agribusiness depend on the utilization of plant growth promoting microbes (PGPMs). The most popular case of this are the nitrogen-fixing (NF) microorganisms. These fix N_2 in the root nodules of vegetables, which results in improvements to their development and yield (Herridge et al. 2008). By 2012, biofertilizers dependent on NF microbes were the most utilized far and wide, representing practically 80% of worldwide biofertilizer requests.

Phosphate-soluble microscopic organisms are another group of PGPMs which are accepting expanding consideration. This can promptly and successfully solubilizes P sparingly dissolvable the hydroxyapatite, minerals and phosphatic salts, through the arrival of natural acids such as gluconic acid and citrus acid (Sharma et al. 2013; Kour et al. 2021; Yadav et al. 2021b). These naturally occurring acids are likewise assemblages of oxides phosphorus (P), aluminum (Al), iron (Fe), especially bountiful in acidic soils, by productively chelating the metal particles (Johnson and Loeppert 2006). Considerably less successive is the utilization of naturally occurring phosphorus microorganisms, capable of hydrolyzing natural types of anhydrides, phosphonates, and phosphate esters, by methods for explicit compounds (essentially phosphatases) to discharge PO_4^{2-} (Richardson and Simpson 2011). These take into account the fact that natural types of P can establish up to 95% of the all-out soil minerals, and that assets of salt of phosphates, appropriate for manure creation, are diminishing, and what's more, will be drained in the midterm (Scholz and Wellmer 2016). A few microbes can be soluble in inorganic P, and also can mineralize natural

P at the same time. Other than microscopic organisms, a few parasites are additionally extremely proficient at advancing plant development. Arbuscular mycorrhizal growths were the most popular and contemplated. These are the growth of cells underlying foundations of where they build up their trademark structures which permit supplement trade between accomplices.

In the present chapter plant responses to heat stress, its adverse impacts and the role of thermotolerant microbes are addressed for a sustainable crop production.

8.2 Plant Responses to Heat Stress

Stress due to temperature influences the vegetative and reproductive growth of plants to a great extent (Tiwari et al. 2021; Dikilitas et al. 2021). Nowadays, under the changing climatic scenario, this has become a major challenge to agricultural scientists. As per the IPCC (Intergovernmental Panel on Climate Change 2007), day–night temperature is going to increase by 1.8–5.8° by the end of the twenty-first century. Such drastic changes not only cause heat stress to the plants, but also it will cause sudden occurrences of drought, floods, and emergences of new pests and diseases. This increasing trend in annual temperatures might be facilitated the drought situation by escalating the evapo-transpirational losses from the crops which would negatively impact on the performance of cereals at the flowering stage (Ihsan et al. 2016). Over the last fifty years (1961–2014), there were losses in cereals, oilseeds, pulses, fruit and vegetable production to the tune of 1.4, 0.5, 0.6, 0.2, 0.09%, owing to having drought vis-à-vis heat stress (Mehrabi and Ramankutty 2017). Heat stress can be defined as an extreme temperature episode which is of a higher range than the optimal temperature range in plants (Yadav et al. 2021a). Recently, there have been many approaches such as field experimentation, crop simulation modeling, big data analysis as well as using various statistical tools, etc., to realize the adverse effects of high stress due to heat on plants (Asseng et al. 2011). Heat stress in the plant causes many abnormalities; among these are the development of infertile pollen, restricted pollination, moreover, failure in embryo development—all major concerns. Booting to grain filling are vital growth phases of wheat that show vulnerability to heat stress (Alghabari et al. 2015, 2016).

8.2.1 Heat Stress on Plant Physiology

Critical physiological activities of crops like the germination of seeds, photosynthesis, transpiration, respiration, assimilate production and grain maturity are controlled by the temperature (Zhao et al. 2013). Thus, temperature has a pivotal role in crop production. All the crops require a certain range of temperature for their optimal growth and development. Both primary and secondary metabolism rates are largely altered by heat stress. The plant defense mechanism is stimulated by such adverse changes in the primary as well as secondary metabolites, and production of these metabolites can give a good idea of the extent of stressfulness. The metabolic processes of plants are influenced by temperature, and abrupt change of temperature may cause poor performance in terms of growth and development of crops (Table 8.1). Under high temperatures, the concentration of free radicals at cellular levels and reactive oxygen species (ROS) are generally amplified. Such increments result in some of the abnormalities found in plants, such denaturation of enzymes, irregular organelles shape, protein assembly and denaturation of enzymes (Ihsan et al. 2019).

8.2.1.1 Photosynthesis

Changes in temperature have a massive impact on photosynthesis in plants. Both the dark as well as light reactions of photosynthesis is controlled by heat-sensitive components. Photosystem II (PS-II) is the heat labile component of the electron transport chain and a critical site to damage (Allakhverdiev et al. 2008). A rise of temperature beyond 45° Champers PS-II. However, at mild heat stress, PS-I may be affected very much (Haque et al. 2014). In wheat, heat stress causes losses in chlorophyll content as well as disproportion in chlorophyll a/b (Shanmugam et al. 2013). With most of the cereal grains, high temperature at the grain-filling phase ultimately reduces yield along with quality of the crops (Fahad et al. 2016a; Farooq et al. 2011).

8.2.1.2 Plant Development

Heat stress in plants accelerates their biochemical reactions; thereby crop development becomes faster and this phenomenon ultimately reduces the LGP (length of growing period) (Fahad et al. 2016b, c). Optimal vegetative growth of the plant is highly correlated with the formation of generative organs, because proficient photosynthesis as well as the buildup of stem reserves during this phase determines the development of said organs. Optimum productivity can be accomplished by taking into consideration the entire physiological and metabolic processes of each grain type. This demands appropriate plans that concern every developmental phases concurrently (Ihsan et al. 2019).

8.2.1.3 Pollens and Pollination in Crops

Heat stress affects the pollen grains the most (Wassmann et al. 2009). Pollen production and its viability are decreased rapidly when the mean temperature is elevated at 5 °C above the optimal in rice. Similarly, in maize, extreme heat stress (38 °C) reduces pollen viability, kernel number, and ultimately lowers the yield of the crop (Otegui 1995). In case of mustard, temperatures above 29 °C resulted in raceme sterility. However, pollens are remaining viable up to 33 °C (Morrison et al. 2016).

Table 8.1 Impact of thermo-stress on the growth, physiology and yield of cereal crops

Cereal crops	Length of stress period	Temperature (°C)	Crop physiological/yield parameters	Interpretations	Sources
Maize	15 h	33–40	Kernel weight	High temperature at early grain filling phase resulted in 23% reduction	Edreira et al. (2014)
	15 × 2 h	33–40	Kernel number	Heat stress at silking and anthesis reduced kernel number plant^{-1} to the tune of 75 and 52%, respectively	Rattalino-Edreira and Otegui (2013)
	15 × 3 h	33–40	Kernel weight	Heat stress at initial grain filling reduced weight of the kernel about 23%	Edreira et al. (2014)
	16 – 18 h	–	Harvest index (HI)	High temperature decreased HI to a great extent, from 46 to 20%	Ordóñez et al. (2015)
Wheat	1 h	35	Water-soluble carbohydrate	Considerable loss in carbohydrate content (26%) was recorded due to heat stress	Talukder et al. (2014)
	2 + 5 h	40	Photosystem II (PSII)	Quantum yield (F'_q/F'_m) as well as photochemical efficiency (F_v/F_m) of PSII was hampered	Haque et al. (2014)
	15 h	38	Oxidative stress	Toxic compound like H_2O_2 concentration was increased	Iqbal et al. (2015)
Sorghum	10 h	40	Ethanol production	High temperature stress during seed filling stage decreased ethanol production about 9%	Ananda et al. (2011)

(continued)

Table 8.1 (continued)

Cereal crops	Length of stress period	Temperature (°C)	Crop physiological/yield parameters	Interpretations	Sources
Barley	30 min	45	Gene transcription	Transcription of following genes in leaves; Cu/Zn-SOD, HvAPX, HvCAT2, HSP18, HSP17 and HSP90 were induced	Faralli et al. (2015)

Cereal crops are especially vulnerable to heat stress during their seed-filling phase. Thus, high temperatures above normal minimizes sizable quantity in crop productivity. Under high temperature stress, the biosynthesis of auxin is reduced. Therefore, pollens become sterile (Sakata et al. 2010).

8.2.1.4 Fertilization and Grain Yield

Fertilization and the development of the embryo and endosperm are largely influenced by thermo-stress and this declines crop productivity. Yield attributing characters such as the number of grains and weight of the grains are reduced due to heat stress (Farooq et al. 2011). In addition, owing to affecting physiological and metabolic activities of the plant, temperature stress causes sharp reductions in crop yield (Suyal et al. 2021) (Table 8.1). The periodicity and length of stress also regulate the quantity of productivity, and results in inferior quality. Maize yield was reduced by about 23% at a temperature range of 33–44 °C during the early grain-filling phase (Edreira et al. 2014).

8.2.1.5 ROS (Reactive Oxygen Species) Production

Normal cellular homeostasis becomes disrupted due to high temperature stress, which sometime causes death of the plant. The main reason behind this is formation of ROS which are accumulated in large amounts in the body of the plant in response to signals of heat stress (Cvikrova et al. 2012). Thus, the defense mechanism of the plant under thermo-stress, i.e., production of ROS, damages the cellular compounds and alters the cellular metabolic processes (Ihsan et al. 2019). Higher concentrations of ROSin plants results in the break-off of water via-a-vis ion homeostasis, and this phenomenon eventually decreases the growth and development of the plant.

8.3 Heat Stress Impacts on Crops

The impact is observed in growth and development. High temperature above the threshold level with excessive radiation may harm the apical growth by scorching of twigs and leaves. The typical symptoms such as sunburn may be observed, with early senescence of leaves, less photosynthate production, retardation of growth and staining of fruits (Fahad et al. 2017a; Vollenweider and Gunthardt-Goerg 2005). Poor germination and inferior plant stand are also observed because of heat stress. Seed filling is inclusive of different metabolic processes such as assimilate production and translocation and biosynthesis of seed reserves, and heat impacts greatly on these. Heat stress influences the seed yield by reducing the number and size of seed, the test-weight and quality (Akter and Rafiqul Islam 2017; Nguyen et al. 2016; Sehgal et al. 2018). Temperature rises alter the water content in plant tissue, and under soil moisture deficit conditions the reduction of water from plant tissues may create serious problems in physiological and metabolic activities in plants (Machado and Paulsen 2001). In general, both above- and below-ground plant parts are adversely affected by water scarcity (Huang et al. 2012). Due to the reduction of root growth in heat stress, nutrient uptake by plants is reduced (Basirirad 2000; Giri et al. 2017) and activity of nitrate reductase declines, hampering the metabolism of nutrients (Rennenberg et al. 2006; Yuan et al. 2017). Chlorophyll synthesis in plants is reduced under high temperatures, resulting in less assimilate production (Dutta et al. 2009; Wang et al. 2018). Different enzyme activities are also changed due to thermo-stresses, causing an adverse impact on metabolism (Bita and Gerats 2013; Morales et al. 2003; Nievola et al. 2017; Schulte 2015; Vu et al. 2001). The economic yield of crops is reduced due to the improper conversion of sink from source (Farooq et al. 2009; Kim et al. 2020; Taiz and Zeiger 2006). Various crops respond differently, but temperatures below or above the normal threshold levels impact on plant physiology and metabolism, and ultimately growth and development processes are altered.

8.3.1 Cereals

In tropical climates heat stress is a common phenomenon and various cereal crops respond to heat stress. The congenial climatic condition for rice (*Oryza sativa*) is a warm temperature (20–30 °C) (Yoshida 1981). But when temperatures increase (to above 35 °C), alterations in physiological and metabolic processes may occur. The high temperatures cause spikelet sterility, chaffy grains and low yield (Nguyen 2012). In rice, the rise in temperature decreases the flourishing of reproductive organs in plants (Prasad et al. 2006). In general, the flourishing of yield-attributing characters of rice is hampered due to thermo-stress and yield is reduced. When night temperatures reach beyond the threshold, level tillering in rice is reduced, damage is caused to chlorophyll content, N content in leaves is decreased with blockage of the PSII reaction center, and an electron flow results (Fahad et al. 2016a). The temperature range for germination of wheat (*Triticumaestivum*) seed is considered as 12–25 °C and the critical temperature for grain filling in rice is 35.4 °C (Porter and Gawith 1998). An increase in temperature beyond the threshold level is harmful in wheat productivity also (Luo 2011; Zhao et al. 2017). Higher temperatures also enhance transpiration and accelerates crop phenology (Eduardo et al. 2013). Heat stress during the growth stage negatively impacts crop growth and assimilate production (Lobell and Gourdji 2012). The ideal temperature for wheat was optimum at 20–30 °C and declined beyond 30 °C in an experiment (Wardlaw 1974). Vegetative growth and production of photosynthates are troubled in maize under high temperatures (Wahid and Close 2007). The optimum temperature for growth is considered for maize as 34 °C (Kiniry and Bonhomme 1991) and above 35 °C the temperature is sensitive for pollen viability (Dupuis and Dumas 1990). In sorghum (*Sorghum bicolor*), seed set is hampered in high temperature stress (Prasad et al. 2006).

8.3.2 Pulses

A rise in temperature caused decreased productivity in common beans (*Phaseolus vulgaris*) (Rainey and Griffiths 2005). Heat stress causes floral and pod abortion, poor fertilization, pod set and seed filling, resulting in smaller yields (Sita et al. 2017). High temperatures also cause early senescence and reduced life cycles leading to decrease in seed yield by 50% (Gowda et al. 2013). The threshold temperatures of lentil (*Lens esculenta*) are >33 and <15 °C and beyond these temperatures terminal heat stress (THS) is pronounced. Due to THS lentils show reduced biomass production, poor pod set and fewer yields (Agrawal 2017; Bhaduri et al. 2017; Delahunty et al. 2016). Temperatures of over 35 °C cause inferior pollen viability, pod set, small seed, reduced seed weight and poor productivity in chickpeas (*Cicer arietinum*) (Basu et al. 2009; Devasirvatham et al. 2010; Kumar et al. 2012; Wang et al. 2006).

8.3.3 Oilseeds

In the groundnut (*Arachis hypogea*), temperature influences the growth of the crop and above 35°C growth of the crop is halted (Sreekanth et al. 2013). Thermo-stress is known to decline yields of groundnuts as reported by Vara Parasad et al. (1999). Temperature impacts on the formation of unsaturated fatty acid. In flax (*Linum usitatissimum*), sunflower (*Helianthus annuus*) and canola (*Brassica napus*) low temperature increases unsaturated fatty acid (Schulte et al. 2013). An increase in temperature enhances the formation of oleic acid, but decreases linoleic and linolenic acid formation in soybeans (*Glycine max*), sunflower and canola (*Brassica napus*) (Schulte et al. 2013). In Brassica species erucic acid synthesis is temperature dependent (Zohara and Schafferman 1995). Safflower (*Carthamus tinctorius*) is known as a thermotolerant crop, but low temperature during the reproductive stage is harmful, and a temperature above 38 °C is also not beneficial (Sreekanth et al. 2013). Sesame is a warm-season crop, but pollination and capsule formation is disturbed when temperatures rise above 40 °C (Sreekanth et al. 2013).

8.3.4 Cotton

Temperature is a variable climatic parameter which impacts on the growth and productivity of cotton (Hodges et al. 1993). Cooler temperatures enhance vegetative branches, while warm temperature triggers fruiting branches (Reddy et al. 1992). However increased temperature reduces metabolites accumulation and reduction of crop duration (Reddy et al. 1996). High temperature also causes reduced boll size, low lint content inside the boll, malformation and shedding of bolls (Oosterhuis 1999, 2002). Pollination and fertilization are crucial stages when high temperature stress does harm (Snider et al. 2009). High temperature damages pollen, hampers growth of the pollen tube, cause pollen indehiscence (Snider et al. 2009; Zahid et al. 2016), decreases boll and seed numbers (Kakani et al. 2005), disturbs boll development (Gokani and Thaker 2002; Gou et al. 2007; Singh et al. 2007), declines quality of fiber (Haigler 2007; Murtaza and Shah 2007; Wang et al. 2014), adversely effects length, strength and micronaire value of fiber (Bowman and Gutiérrez 2003; Gokani and Thaker 2002) and reduces yield (Gutierrez et al. 2015; Reddy et al. 1996; Xu et al. 2017). The mean daily temperature congenial for the development of fiber in cotton bolls is 26 °C (Dai et al. 2015; Murtaza and Shah 2007) and if it exceeds 30 °C, the quality of fiber is degraded (Murtaza and Shah 2007). However, the photosynthetic ability of cotton decreased with mean daily temperature at 32 °C or more (Crafts-Brandner and Salvucci 2000).

8.3.5 Sugarcane

Heat stress causes disturbance in growth and assimilate production and reduction of water in tissues (Wahid and Close 2007; Morales et al. 2003; Srivastava et al. 2012) reduces the intermodal length of sugarcane (*Saccharum officinarum*) (Ebrahim et al. 1998; Bonnett et al. 2006) and cane yield (Warland et al. 2006). In a study in Australia, it was noted that under high temperatures (>32 °C) sugarcane produced lower sucrose content (Bonnett et al. 2006). Further, high temperature adversely influenced sprouting (Johkan et al. 2011), lower sucrose content in juice (Bonnett et al. 2006) and damage of leaf margin and tip followed by the appearance of necrosis and drying (Omae et al. 2012). But with low temperature, there was enhancement in juice acidity (Pathak et al. 2018). Temperature also has a great impact on ripening, and low temperature is favorable for ripening (Gawander 2007). Further, low temperature is known to disrupt the structure of chloroplast and reduces photosynthesis (Li et al. 2018).

8.3.6 Vegetables

High temperatures during stolon formation and tuberization cause yield loss in potatoes (*Solanum tuberosum*) (Li and Zhang 2020; Shimoda et al. 2018) because of changes in physiological and metabolic processes (Camejo et al. 2005; Dahal et al. 2019). For tuberization an average temperature of 15–20 °C is considered as optimum (Lovatt et al. 1997a, b). However, for tomatoes (*Lycopersicum esculentum*), ideal temperature ranges for fruit set are 18° to 24 °C (Lovatt et al. 1998). Fruit weight decreases with rise of temperature above 25 °C (Peetet al. 1997; Adams et al. 2001). Fruit set is hampered at a temperature less than 14 °C (Adams et al. 2001; Higashide 2009). Sato et al. (2006) reported that pollen viability and fruit set was adversely affected by abnormal temperature. Vegetative growth of tomatoes is also hampered due to decrease in water content and root conductance (Morales et al. 2003) and reduction of chlorophyll (Han et al. 2017). Under protected cultivation, the growing of tomatoes with mean daily temperatures of 25–26 °C were ideal in the in the Mediterranean summer season (Harel et al. 2014; Sato et al. 2006). The growth of fruit of the capsicum (red pepper) (*Capsicum annuum*) was hampered above a temperature of 30 °C, and above 33 °C deformities in fruits were noted, plus a reduced number of fruits (Erickson and Markhart 2002). High temperature after anthesis caused smaller fruits (Pagamas and Nawata 2008). In general, the temperature required for germination for cucarbitaceous crops ranges from 15 to 38 °C (Bannayan 2017; Ellis et al. 1985; Pacheco et al. 2017). A rise in temperature above 35 °C negatively influenced the development of floral parts and pollen viability in pumpkins (*Cucurbita moschata*) (Iapichino and Loy 1987; Loy 2004). For cucumbers (*Cucumis sativus*), high temperature stress disturbed the biosynthesis of chlorophyll (Dalal and Tripathy 2012; Tewari and Tripathy 1998). Further decreased photosynthate production and starch content was noted in cucumbers due to high temperature stress (Ding et al. 2016). In celery, stress due to high temperature reduces the biosynthesis of chlorophyll (Sharma et al. 2019a, b).

8.4 Thermotolerant Soil Microbes

The present scenario of climate change is no longer limited to research papers. The IPCC (2014) has already stated that the negative effects on crop productivity due to climate change are no longer negligible, and that the negative impacts are expected to intensify over the coming years, as per several model-based studies (IPCC 2013). It has been suggested by several workers that extreme climatic events will become more and more frequent due to the changing climate scenarios (Gibelin and Déqué 2003; IPCC 2014; Swain et al. 2014). Drought and heat waves are some of the extreme events that are progressively becoming more and more common in the agricultural systems. Such events severely affect the plants as well as the microbial communities growing in the soil. The effect of the changes in the mean soil temperature over the mesophilic range on the soil-dwelling microbes is not fully known at the present time (Hamdi et al. 2011). However, a range of studies have been conducted in recent decades, especially on rhizospheric microbes, to study the effect of changing temperatures as well as water regimes.

Soil is a dynamic body and a very complex biophysical system. Microbes constitute the major biological part of the soil and might be held responsible for most dynamic transformations in the soil. Researchers such as Thiele-Bruhn et al. (2012), Pulleman et al. (2012) and many others have emphasized how microbial biodiversity is central to the proper functioning of the soil–plant systems. Climatic events affecting soil microflora are thus expected to induce significant changes in soil dynamics, besides directly affecting agricultural systems.

Heat stress in the soil may often appear with the soil moisture stress. Events of heat waves are thus characterized by high temperatures above 45 °C, coupled with moderate to severe drought conditions. Plants are not only affected by heat waves that persist for few days or weeks, but also by other events in the increment of the soil temperatures, especially surface temperatures over the optimum for extended periods. Loss of vegetative cover, low organic matter and little to no residue over the soil surface can introduce soil to harsh weather conditions, and temperatures even may touch 74 °C momentarily in several places. These conditions remain hugely detrimental for the majority of soil microbes as most of them are mesophilic in nature.

Long exposure to soil temperatures modifies the soil microbial community, replacing the native soil organisms with thermophilic ones. However, short-term heat exposure may be tolerated by some groups of microbes through genophytic as well as phenophytic heat acclimations. A recent study reveals that thermotolerant strains of soil microbes are quite ubiquitous in nature (Kumar and Verma 2018).

High temperatures may induce severe loss of cell water content and dehydration of the cells of microbes. Temperatures above 50 °C may also induce damage to the genetic material as well as to the protein structures, including enzymatic activities which can be lethal to the microbes. Thermotolerant microbes employ several defensive strategies to defy the detrimental effects of thermo-stress. Production of Heat Shock Proteins (HSPs), DNArepair mechanisms, use of molecular chaperons and EPS-based biofilm production are some of the well-studied mechanisms of heat tolerance in microbes. Microbes may opt for sporulation to produce dormant spores. Pettersson and Baath (2003) reported that the changes induced in the soil microbiome community in the course of increasing temperature over a long period are quite persistent, and did not volatilize on the omission of heat stress. Hartley et al. (2008) also reported similar findings, and they concluded that microbial response to soil warming is considerably faster than for soil cooling. A fungus is universally more vulnerable to heat stress to bacteria.

In the present context of rising global mean temperatures as well as increasing events of high soil temperatures, it has become increasingly useful to study thermotolerant soil microbes. In the recent past, several thermotolerant microbial strains were identified worldwide. *Aliclyvlobacillus acidoterrestris, Pseudomonas cerdrina, Pseudomonas putida, Pseudomonas aeruginosa, Brevundimonas terrae,* *Anthrobacter nicotiniae, Burkholderia phytofirmans, etc.*, are some of the identified thermotolerant organisms (Bensalim et al. 1998; Yadav et al. 2014; Meena et al. 2015). The ubiquitous presence of bacteria from genus *Geobacillus* and related genera can grow up to 70 °C under laboratory environments. These bacteria are common in soils in the mesophilic range as vegetative spores (Marchant et al. 2008; Portillo et al. 2012; Santana et al. 2013). Khan et al. (2020) revealed positive impacts of thermotolerant *Bacillus cereus* on the heat tolerance of soybeans. Actinomycetes belonging to the genera *Actinokinespora* have been identified from China that can tolerate temperatures up to 55 °C (Tang et al. 2012). Phosphate solubilizing activities of thermotolerant soil bacteria such as *Bacillus coagulans* C45, *B. licheniformis* A3, *B. smithi* F18 were found up to 75 °C in lab conditions. Fungus *Aspergillus fumigants* O4 and NTU-132 strains were reported to be active up to 65 °C with all enzymatic activities intact (Chang and Yang 2009).

In the complex ecosystem of soil and plant, the microorganisms can play important roles in the soil nutrient dynamics, plant growth promotion and stress tolerance activities. Proper and in-depth knowledge of such organisms may help to cope with the temperature stresses being experienced and yet to be experienced in the near future worldwide. With the advent of the widening horizons of knowledge about rhizospheric organisms, thermotolerant microbes may be proven a boon from nature toward a sustainable agricultural system in changing climatic scenarios.

8.5 Role of Thermotolerant Soil Microbes in the Mitigation of Heat Stress

The rhizosphere is a limited soil volume within the close vicinity of plant roots. It is the site of very important soil biological activities by microbes (Yadav et al. 2020; Yadav 2021). The complex chemical matrix of the root rhizosphere selectively allows for the growth of certain colonies of the microbes within a specific plant–soil environment (Haldar and Sengupta 2015). Microbial populations within the rhizospheric zones are largely shaped by root exudates, signaling molecules in most of the plants including crops like peas, maize, wheat, sugar beet, etc. (Canarini et al. 2019; Singh et al. 2020). Chaparro et al. (2013) have found a significant correlation of the expression of microbial genes with the presence and absence of a wide variety of root exudates at different stages of crop growth. Such relations suggest that not only can a plant exert influence over the colonization of the microbes in the root vicinity, but also can greatly modify its functions.

The influence of the root microbiome on the suppression of disease-causing organisms has been exhaustively studied for many years. However, recent advancements in knowledge have revealed the significant roles of soil-dwelling microbes in abiotic stress mitigation. Several organisms have already been identified that help the plant in combating abiotic stress conditions. Some of the recent findings are presented in Table 8.2. Out of several biotic and abiotic stresses mitigated by soil microbes,

Table 8.2 Involvement of soil microorganisms in the impartation of stress tolerance to several crops

Crop	Stress	Microbes involved	References
Rice	Salt	*Pseudomonas pseudoalcaligens, Bacillus pumilus*	Jha et al. (2011)
	Heavy metal	*Bacillus subtilis, Bacillus megaterium*	Asch and Padham (2005), Terre et al. (2007)
	Osmotic	*Achromobacter brasilense*	Cassán et al. (2009)
Wheat	Salt	*Aeromonas hydrophilia, Bacillus insolitus*	Ashraf et al. (2004)
	Drought	*Azospirrilum* *Burkholderia phytofirmans*	Creus et al. (2004), Naveed et al. (2014)
	Osmotic	*Azospirrilum*	Pereira (2019)
	Temperature	*Pseudomonas fluorescens, Pantoea agglomerans, Mycobacterium* sp. *Bacillus amyliliquefaciens* *Pantoea agglomerans*	Abd El-Daim et al. (2014), Egamberdiyeva and Höflich (2003), Mukherjee et al. (2019)
Maize	Salt	*Bacillus megaterium, Azospirrilum, Pseudomonas syringae, Enterobacter aerogenes*	Marulanda et al. (2007), Meziane et al. (2005), Nadeem et al. (2007)
	Drought	*Pseudomonas* sp. *Achromobacter brasilense*	Casanovas et al. (2003), Sandhya et al. (2009)
	Nutrient	*Azotobacter chroococcu, Azospirrilum brasilens* *Pseudomonas putida* *Bacillus lentus* *Burkholderia* sp. *Streptomyces platensis* *Bacillus polymixa Mycobacterium phlei Pseudomonas alcaligenes*	Adesemoye et al. (2008), Egamberdiyeva (2007), Oliveira et al. (2009)
Soybean	Temperature	*Aeromonas hydrophilla* *Serratia liquefaciens* *Serratia proteamaculans*	Feng et al. (2002)
	Salt	*Pseudomonas* sp.	Kasotia et al. (2012)
Potato	Temperature	*B. phytofirmans*	Bensalim et al. (1998)
	Osmotic	*Bacillus* sp.	Gururani et al. (2013)
Tomato	Flooding	*Enterobacter cloaceae* *Pseudomonas putida*	Glick (2014)
	Drought	*Achromobacter piechauli*	Mayak et al. (2004)
Lettuce	Drought	*Bacillus* sp.	Arkhipova et al. (2007)
Groundnut	Salt	*Pseudomonas fluorescens*	Saravanakumar and Samiyappan (2007)

(continued)

Table 8.2 (continued)

Crop	Stress	Microbes involved	References
Bean	Drought	*Ensifer meliliti* *Rhizobium tropici* *Paenibacillus polymixa*	Figueiredo et al. (2008)

Source Adapted from Dimkpa et al. (2009), Carmen and Roberto (2011), Choudhary (2012)

heat tolerance induced by thermotolerant microbes as a measure of plant heat stress mitigation, is reviewed in detail in the scope of this chapter.

8.5.1 Heat Stress in Plants and the Thermotolerant Microbiome

Abiotic stresses are great constraints for production of crops all over the world. Under the present context of global warming and climate change, these stresses have become more frequent in causing crop damage, and threaten food security in many places. Heat stress, sometimes in combination with drought, often appears as a menace to crop production (Fahad et al. 2017a; Hesham et al. 2021; Sharma et al. 2021). Changing patterns of rainfall and temperature regimes, and global warming, etc., have aggravated such problems to a serious extent. Several optimistic reports estimate that about 21–40% yield loss in staple crops like wheat and maize is due to such stresses (Daryanto et al. 2016). Global wheat yield has been predicted to decline by at least 6% with the enhancement of each degree Celsius rise in the atmospheric mean temperature (Asseng et al. 2015).

Heat stress not only affects plants and crop production in indirect ways, but it also impacts on soil microbial communities. Most mesophilic microbes undergo severe stress under high temperature conditions in the upper soil layers coupled with low water potentials in the soil. However, this naturally selects that only the tolerant microbes can survive in the soil where these events are more frequent. Recent studies have found a significant contribution of this thermotolerant microbiome in the impartation of heat tolerance in the plants growing on the soil. This constitutes a symbiotic relation with the rhizo-organisms with the host plants. Actually, the growth and performance of the microbial community are dependent on the easy carbon source provided by the plant root exudates. The survival and proper functioning of the plant favors the survival of microbial communities under stress conditions.

8.5.2 Heat Shock Proteins and Heat Shock Transcription Factors Mediated Heat Tolerance

Though the exact mechanisms on how microbes can impart thermotolerance to plants are not yet exhaustively studied, some links have successfully been identified. Those links may pose great opportunities for the development of a fair understanding of the underlying facts and mechanisms. Heat Shock Protein 90 (HSP90), a molecular chaperon, is confirmed to be this type of useful molecular link in the cross-talks between plants and microbes, and imparts some degree of tolerance to plants (Picard 2002; Pratt and Toft 2003; Young et al. 2001). Altered levels of HSP90 in the plants have been found to respond differently to environmental cues, especially temperature and light (Queitsch et al. 2000). Several other studies have successfully demonstrated that manipulations in the levels of HSP90 may result in phenotypic changes as well as heritable genetic changes, due to epigenetic modification in the organisms (Queitsch et al. 2002; Sollars et al. 2003; Yeyati et al. 2007). Such dramatic changes in the HSP90 buffering can be caused by several environmental cues, as well as with several HSP90-specific small molecules released by microorganisms, such as several fungal strains that may inhibit or may promote the function of HSP90 (Sangster and Queitsch 2005; Turbyville et al. 2006). McLellan et al. (2007) have mentioned that the thermotolerant rhizospheric fungus *Paraphaeosphaeria quadrisepata* induced heat tolerance in *Arabidopsis* and wheat plants through modulation of the HSP90 chaperon with HSP90-specific inhibitor monocillin I (MON) and radiciol (RAD). Inhibition of HSP90 invariably leads to the up-regulation and expression of major heat responsive elements such as HSP70 and HSP101. The same mechanism was also found to be successful in young maize plant subjected to temperature stress by Gomes et al. (2003).

8.5.3 Plant Growth Regulator Mediated Heat Tolerance

Plant growth regulators (PRGs) play a great role in the responses of plants to environmental conditions, including stresses. Plants' response to stresses may act as the thin silver lining between plants' survival and death under severe stress conditions. All of the major plant growth regulators such as auxin, gibberellin, cytokinin, ethylene, ABA and brassinosteroid, as well as signaling molecules such as salicylic acid and jasmonic acid, take an active part in the heat tolerance of plants (Ahammed et al. 2016; Xia et al. 2015). Among PGRs, the role of auxin as a thermo-protectant has recently gained much attention. A significant interaction of auxin with HSPs and plant heat stress transcription factors had already been found in *Arabidopsis* (Wang et al. 2016). A reduction in the GA levels results in the inhibition of growth and consequently enhanced stress tolerance due to accumulation of DELLA proteins (Hedden and Thomas 2012). Cytokinins help in the promotion of cell division, maintenance of the meristematic activity and regulation of redox potentials during heat stress

(Gupta and Rashotte 2012; Werner et al. 2010). There are also roles of cytokinin in the maintenance of stomatal conductance which enhances the transpirational cooling to the plant (Macková et al. 2013). Cytokinins also have defined roles in dictating HSPmetabolism and are found to be involved in imparting heat tolerance in *Passiflora* (Sobol et al. 2014). ABA act as signaling molecules, induce heat shock factors, HSPs and act as growth moderators to induce heat tolerance in plants (Hu et al. 2010; Islam et al. 2018; Li et al. 2015). ABA is also known to have a role in stomatal operation in plants (Gong et al. 1998; Hsieh et al. 2013; Hu et al. 2010; Tang et al. 2008).

Several microbial organisms are identified to produce plant growth-regulating compounds that may help in the acquisition of thermotolerance in several plants. A bacterial strain named *Azospirillum brasilense* Sp245 was reported to impart heat tolerance in wheat under heat and drought stresses due to maintenance of better tissue water status and impartation of phenotypic plasticity due to production of auxins and cytokinins (Choudhary 2011; Choudhary et al. 2016). A strain of *Achromobacter piechaudii* ARV8 was reported to produce ACC deaminase enzyme which moderated ethylene metabolism, and ultimately resulted in better heat tolerance as well as salt tolerance of pepper (Gururani et al. 2013) (see Fig. 8.1). Removal of ACC by ACC-deaminase reduces the deleterious effects of overproduction of ethylene (Mayak et al. 1999). Khan et al. (2020) had demonstrated how a thermotolerant bacterial strain *Bacillus cereus* SA1 isolated from roots of *Echinochloa cruss-galli* imparts thermotolerance on soybean plants through moderations in the auxin and

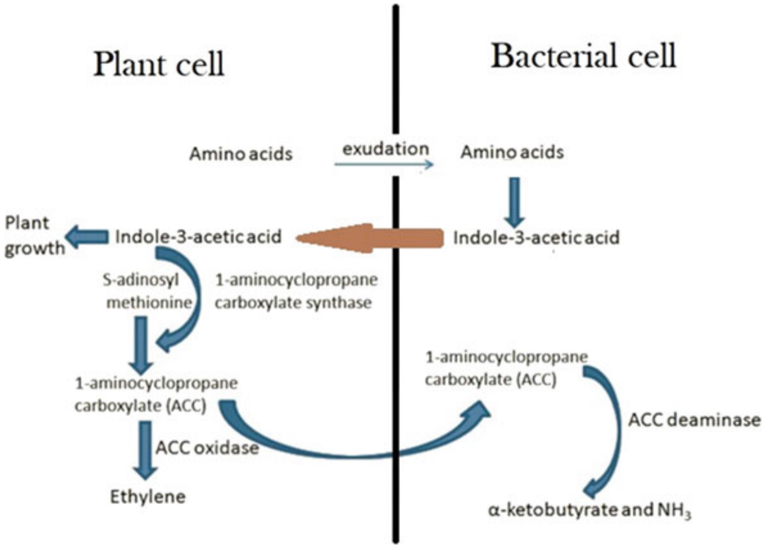

Fig. 8.1 Role of rhizobacteria in ethylene metabolism of plants. *Source* Adapted from Choudhary et al. (2016)

gibberellin levels. They had also found that the strain yielded no significant difference in the plants' hormonal balance under normal conditions. The effects were only realized when the plants were subjected to heat stress. Such microbial strains are non-pathogenic to the plants, and these situation-specific actions make them worthy candidates for use in commercial biofertilizers or PGPR formulations to alleviate heat stress from target plants.

8.5.4 Microbial Mediation of ROS

ROS stands for Reactive Oxygen Species and includes a range of active radicles such as hydroxyl radicles, peroxide radicles, singlet oxygen, superoxide radicles and so on (Gupta et al. 2017; Kalia et al. 2017). ROS are mainly the side products of the plant's natural metabolism under normal conditions, and plants have good management of such radicles so that significant harm can be avoided (Apel and Hirt 2004). Under different stress conditions, the production of ROS exceeds the optimum levels, resulting in cell damage, lipid peroxidation, membrane leakage, denaturation of proteins, the degradation of pigments and storage food materials, and so on (Bose et al. 2013; Li et al. 2018; Martínez et al. 2017; Van Ruyskensvelde et al. 2018). Such damage significantly reduces the plant's performance under stress as well as reducing the plant yield (Park et al. 2017). ROS have been broadly studied in animal systems and microbes for a long time. Recent developments in biology have extended the study area for ROS to the higher plants. Studies have found important roles of ROS as signaling molecules in plant systems (Lopes et al. 2016). However, such ROS productions above plants' antioxidative defenses may cause severe harm to plants' internal structures and functions (Afzal et al. 2014; Guan and Lan 2018; Maritim et al. 2003; Pisoschi and Pop 2015).

Studies suggest that the involvement of rhizospheric microbes is actively involved in the ROSmetabolism of the plants under stressed environments (Kohler et al. 2009). Plants inoculated with thermotolerant strains like *Pseudomonas mendoina* impart greater thermotolerance than control groups of plants in terms of lesser membrane damage due to increased SOD, POX, APX, etc., antioxidant enzymes (Bianco et al. 2009). Drought-tolerant strains of *Pseudomonas entomophila, P. putida, P. montelii* and *P. stutzeri* had been found to improve the oxidative stress as indicated by low oxidative damage, cell leakage, etc., in maize crops (Sandhya et al. 2010b). Inoculation with *Azospirrilum brasilense* showed lower heat as well as salinity stress in barley plants in a similar way (Omar et al. 2009). Improved performance of *Medicago* inoculated with IAA-overproducing heat-tolerant rhizobacteria has also been reported and found well correlated with plants' antioxidant activities (Bianco et al. 2009). Thermotolerant strains of *Azospirrilum brasilense* NO40 and *Bacillus amyloliquefaciens* UCMB5113 have resulted in greater antioxidant activities in heat-stressed young wheat seedlings (Abd El-Daim et al. 2014). The microbial moderations in the molecular level as well as the genetic level to improve plant performance in the oxidative stress, may be of great use as these stresses are general in almost every abiotic stress conditions including heat and drought as well as salinity stress (Carmen and Roberto 2011).

8.5.5 EPS or Biofilm-Based Defense

EPS or exopolysaccharides are natural active components of the soil organic matter (Gouzou et al. 1993). EPS constitutes a significant part of the extracellular environment for the microorganisms and often range from 40 to 95% of the total cell weight in the case of bacteria (Flemming and Wingender 2001). Some of the rhizosphere-dwelling organisms, viz., bacteria and fungi, produce EPS as cell exudates for their defense, such as *Pseudomonas* (Sandhya et al. 2009, 2010b). Microbial EPS are nearly 97% water in a complex polymer matrix which is very helpful for the organism to achieve desiccation tolerance (Bhaskar and Bhosle 2005; Hunter and Beveridge 2005). Studies reveal such EPS production peaks under stress conditions such as heat, salinity or drought in the soil. Such polysaccharides are known to physically impact soil properties under the microenvironment. It has been seen that soil structure improves with EPS due to the excellent binding properties of the polysaccharides (Bashan et al. 2004). A well-structured soil holds more water and dries more slowly, delaying the onset of water stress. EPS also works as a biofilm and creates a congenial microenvironment within its boundaries (Sandhya et al. 2009). Higher water potential in the soil is much desired, especially in cases of heat stress. If the water balance of the plant is properly maintained, transpirational cooling may work, and the deleterious effects of heat stress may be avoided. Water stress acts as an environmental cue for ABA signaling for stomatal closure and thus worsens the condition of heat-stressed plants. A well-maintained cell turgor may thus keep the stomatal function optimum for the continuation of the plant's cooling system.

Thermotolerant strains of *Bacillus ceres* P2 and *Planomicrobium chinense* P1 have been found to produce enough EPS to positively impact on the rainfed wheat under drought and temperature stress (Khan and Bano 2019). In a study conducted by Naseem and Bano (2014), strains of tolerant rhizobacteria such as *Proteus penneri* PP1, *Pseudomonas aeruginosa* PA2 and *Alcaligens faecalis* AF3 were found to form mucilaginous EPS materials in the rhizosphere of drought- and heat-stressed maize plants. They also claimed that such microbial consortia may be used in future to combat drought as well as heat stress in commercial crops. Bensalim et al. (1998) noted that plants treated with EPS-producing strains of *Azospirrilum* expressed more resistance than the control group under combined water stress. Under conditions of severe drought, EPS-producing bacterial strain YAA34 resulted in an increase in the root tissue in sunflowers, due to lubrication provided to the root tips, and better moisture retention in the rhizosphere (Alami et al. 2000).

8.5.6 Protective Molecules Moderation

Several studies have confirmed the roles of different small and large molecular weight compounds within the plant's system to be actively involved in stress response and mitigation. Most of them are nitrogenous compounds, small organic molecules, non-protein amino acids, etc. (Parida and Das 2005). Accumulation of proline and glycin-betaine were reported to have active roles in the stress response of the plants by multiple workers (Kishor et al. 2005; Szabados and Savouré 2010; Verbruggen and Hermans 2008). Inoculation of thermotolerant PGPR has been reported to enhance proline and glycine-betaine in the plants, either through direct absorption of microbial origin compounds, or by up-regulation of the genetic control for higher production of such molecules through several signaling molecules under stress (Barka et al. 2006; Jha et al. 2011; Kohler et al. 2010; Sandhya et al. 2010a). However, the exact mechanisms of how microbes moderate the synthesis of plant origin protective molecules remains largely as hypotheses based on the state of current knowledge.

8.5.7 Nutrient and Water Uptake

Often environmental stresses are in complex form rather than a single separated event (Anisman and Merali 1999). For example, heat stress often appears with water stress and both of these result in oxidative stress and nutrient deficiency (Sattar et al. 2020; Zhou et al. 2017). Photosynthesis is one of the earliest processes hampered under thermo-stress (Sharma et al. 2019a, b). Plants deprived of new photosynthates combat the stress with already-available resources. In such conditions, energy-consuming processes like active uptake of nutrients are nearly halted. Further developments of water stress in the soil also reduces nutrient availability to the plant roots (Bista et al. 2018; Prasad et al. 2021). Under severe stress, root cells also loses their integrity to uptake nutrients properly. Besides the actual stress, plants suffer from nutritional deficiencies which significantly affects the plant's performance as a whole. Several researchers have revealed that the plant's nutritional status has a great role in the determination of the plant's performance under stress conditions (Heidari and Jamshid 2010; Munns and Tester 2008). Several rhizobacteria and fungi have the capability of making nutrients more available to plants even under stressed conditions. The role of thermotolerant bacteria in the availability of soil phosphorus to plants has drawn attention in recent days. Thermotolerant strains of *Erwinia, Bacillus* and *Rhizobium,* and *Pseudomonas* are reported to be involved in phosphorus mineralization through the production of organic acids (Rodríguez and Fraga 1999). Thermotolerant strains of *Bacillus smithi, Bacillus coagulans, Bacillus licheniformis, Aspergillus fumigatus,* and *Streptomyces thermophiles* were so good at phosphate solubilizing activity that they were found suitable for commercial biofertilizers for high-temperature soils (Chang and Yang 2009). Other groups of auxin-producing rhizo-organisms may be attributed to the extended root growth and better uptake of nutrients and water. The roles of mycorrhizae in nutrient and water absorption have long been known. Some of the root dwellers are also involved in the secretion of siderophores, and thus increase the availability of iron and zinc (Carmen and Roberto 2011).

8.6 Use of Thermotolerant Soil Microbes for Agricultural Sustainability

The sustainability of agricultural ecosystems is challenged by several factors today (Zhao et al. 2008). Out of such factors, erratic climatic events are of huge concern. Drought and heat stress have become frequently occurring events under the changing climatic scenarios (Raza et al. 2019). Such abiotic stresses cause huge losses in the agricultural productivity of different crops (Fahad et al. 2017b). Further, it has been well predicted that an increase in the annual mean temperature by 1.5–2.0 °C may result in a catastrophic situation for agricultural production, and the worst hit will be staple crops like wheat, maize, rice, etc. (Gornall et al. 2010; IPCC 2013, 2014). In particular, under-developed and developing countries have a higher risk of facing climate-induced havoc on the agricultural systems (Abdallah et al. 2014).

Drought as well as heat-stressed plants in the agricultural systems can be managed wisely to get optimum benefits out of a stressed system. Rhizospheric management is one of the many suggested ways to mitigate thermo-stress and ensure the healthy performance of crops. Thermotolerant microbes pose several positive points for their adoption under stressed as well as normal conditions (Sandhya et al. 2009, 2010b). Most of the thermotolerant genera of microbes found to have a positive impact on the plant system are also found to be involved in the soil nutrient dynamics. The role of strains such as *Azotobacter, Azospirrilum* and *Rhizobium* in biological nitrogen fixation is well known. Other strains like *Aspergillus, Pseudomonas,* and *Burkholderia*, etc., have active roles in phosphorus and potassium dynamics in the soil (Bargaz et al. 2018). EPS-producing microbes are involved in the betterment of soil physical structures. These rhizo-organisms have also been reported to have suppressive effects on the pathogenic organisms. Induction of the systemic response of the plants through various bio-signaling has also been reported by multiple workers in recent times. Thermotolerant microbes need a special mention for their preferable use as a compost enrichment, as they are able to withstand high temperatures (Chen et al. 2007; Etesami and Adl 2020; Kumar et al. 2016). These microbes do not lose their activities in the high-temperature regime and keep the soil biological rhythm optimal, besides helping the host plants to survive and withstand environmental stress. Biofertilizers enriched with these organisms can be produced for drier regions. Even though extensive knowledge about the thermotolerant soil microbes and their roles in the agro-ecosystem is not very clear, it is quite obvious from current knowledge that thermotolerant microbial diversity has a great potential to revolutionize the vulnerable, fragile agricultural system for a food-secure and sustainable future.

The plant microbiomes (epiphytic, endophytic and rhizospheric) have the capacity to advance plant development, are alluded to as plant development advancing microorganisms. The plant microbiomes which have been sifted through from assorted sources have a place with every one of the three domains of archaea, microscopic organisms and growths. Among three area frameworks, the individuals from space microorganisms are all around described and announced as from various abiotic stresses, for example, basic soil, saline soil, acidic soil, low temperature, high temperature and drought. Among every one of the three space microorganisms, there are not many reported on archaea as plant development advancement; for example, halophilic archaea, including the following, having the qualities of phosphorus solubilization under hypersaline conditions.

- *Haloterrigena*
- *Halobacterium*
- *Halostagnicola*
- *Halococcus*
- *Halolamina*
- *Haloferax*
- *Haloarcula*
- *Natronoarchaeum*
- *Natrialba*
- *Natrinema*

The microorganisms related to the plant rhizosphere are named as rhizospheric organisms and rhizospheric *actinobacteria* are generally predominant in nature. In the investigation of various microbial assorted varieties in types of plant microbiomes, it may very well be that the individuals from phylum *actinobacteria* have been accounted for from various genera. These are as follows:

- *Streptomyces*
- *Sanguibacter*
- *Rhodococcus*
- *Pseudonocardia*
- *Propionibacterium*
- *Nocardia*
- *Mycobacterium*
- *Micrococcus*
- *Microbacterium*
- *Frankia*
- *Corynebacterium*
- *Clavibacter*
- *Cellulomonas*
- *Bifidobacterium*
- *Arthrobacter*
- *Actinomyces*
- *Acidimicrobium*

Actinobacteria have been an enormous segment of soil microbiomes in the plant root frameworks. The Actinobacteria have been detached from various sources study. These are as follows:

- chickpeas (*Cicer arietinum*)
- maize (*Zea mays*)
- peas (*Pisum sativum*)
- rice (*Oryza sativa*)
- soybeans (*Glycine max*)
- sugarcane (*Saccharum officinarum*)
- sunflowers (*Helianthus annuus*)
- wheat (*Triticum aestivum*)

The gram-positive living beings with a high guanine and cytosine content have a place within the phylum *Actinobacteria*, and establish probably the biggest phylum inside the area of microscopic organisms, comprising six classes, and are as follows:

- *Thermoleophilia*
- *Rubrobacteria*
- *Nitriliruptoria*
- *Coriobacteriia*
- *Actinobacteria*
- *Acidimicrobiia*

Among 3900 unmistakable types of *actinobacteria*, thirty genera are as follows:

- *Streptosporangium*
- *Streptomyces*
- *Saccharothrix*
- *Saccharopolyspora*
- *Rhodococcus*
- *Pseudonocardia*
- *Nonomuraea*
- *Nocardiopsis*
- *Nocardioides*
- *Nocardia*
- *Mycobacterium*
- *Micromonospora*
- *Microbacterium*
- *Leucobacter*
- *Kribbella*
- *Kocuria*
- *Kitasatospora*
- *Gordonia*
- *Geodermatophilus*
- *Corynebacterium*
- *Cellulomonas*

- *Brevibacterium*
- *Brachybacterium*
- *Bifidobacterium*
- *Arthrobacter*
- *Amycolatopsis*
- *Agromyces*
- *Actinoplanes*
- *Actinomyces*
- *Actinomadura*

Among all genera, *Streptomyces* have been generally prevailing with 961 distinct species followed by *Mycobacterium* (186 species). Nineteen microbes and their applications as bioinoculants have systems to expand the current yields for practical farming. Microorganisms as bioinoculants and biopesticides are an option in contrast to synthetic composts to diminished natural contaminations. The microorganisms have plant development-advancing properties, for example, nitrogen obsession and other plant development-advancing characteristics like the solubilization of P, K and Zn, and the creation of Fe-chelating mixes, phytohormones. *Microbacterium, Microbacterium* FS-01 and *Pseudonocardia dioxanivorans* CBI190 have been secluded from the rhizosphere of different harvests, which contribute fixed nitrogen to the related plants. Phosphorus is a basic component for the foundation and advancement of plants since it improves the whole root framework, thus improving the shoot. Phosphate solubilization is a typical quality among microorganisms, for example, archaea, microbes and organisms. There are numerous reports on PGP *Actinobacteria* with phosphate solubilizing traits and huge quantities of P-solubilizing microorganisms have been accounted for which incorporate individuals having a place with *Streptomyce djakartensis* TB-4 and *Streptomyces sp* (Yadav and Yadav 2019).

In bioformulations, bacterial cells ought to have the option to endure numerous ominous circumstances, for example, parching and extremely hot conditions. The microscopic organisms ought to support high endurance rates and have the ability to upgrade plant development during delayed timespans. For endurance, microorganisms utilize different methodologies: for example, arrangement and capacity of osmolytes or polyhydroxyl alkanoates (PHAs). Osmo-changed cells that hold osmolytes, for example, trehalose or glycine betaine, show a lot more grounded ability to manage drying out than non-osmomodified organisms, altogether improving their plant advancement potential (Bonaterra et al. 2005). Microorganisms with over-the-top PHA levels can endure harsh conditions better than those with lessened levels, as PHAs offer cells the capacity to endure different antagonistic physicochemical burdens (Morel et al. 2012). The perfect organism plant mutualistic affiliation incorporates a diazotrophic microbial relationship with the developing plant. Diazotrophs convert environmental nitrogen to alkali. Certain diazotrophs and different PGPBs (Pseudomonas and Bacillus) likewise yield phytohormones, siderophores, and phosphate-solubilizing atoms, among different edifices (Morel and Castro-Sowinski 2013). Added substances and metabolites assume crucial jobs in making bioformulations progressively solid and powerful. Flavonoids are primer biomolecules utilized in conjunction with rhizobial inoculants to advance nodulation. The expansion of flavonoids to rhizobial inoculants improves nodulation, N2 obsession, and the ability to battle abiotic stresses. Nodulation happens through discharge of single LCO mixes by root-nodulating microscopic organisms called rhizobia. The relationship among rhizobia and vegetable roots is known to be harmonious in nature, and LCO biomolecules are crucial in this affiliation, affecting the harvest yield emphatically (Oldroyd 2013).

8.7 Conclusion

Plant diseases can be usefully managed by creating and using biocontrol methods. Bioformulation is one of these methods and is savvy and naturally benevolent. Bioformulations from opposing microorganisms and other biocontrol specialists are increasingly gaining credible significance and consideration universally, especially in nations where soil-borne ailments present serious issues. The ideal plan and viability of biocontrol specialists are major parts for the suitability of bioformulations. Plans that have been created and broken down can be useful for smothering plant infections and conceivably other plant–microbe blends. These bioformulations have extraordinary potential as characteristic pesticides and can supplant substance fungicides. A bioformulation can support item security, shield microscopic organisms against various natural conditions, and furthermore, provide an underlying food source. Use of PGPRs either to advance crop well-being or to control plant diseases relies upon the creation of business that keep up the feasibility of the microorganisms for a considerable timeframe. It is imperative to gauge the endurance of the immobilized microorganisms in various transporters, and furthermore their ability to hold the characteristics required for plant development advancement.

Utilization of consortia containing multitrait plant development advancing microorganisms might be valuable in definition of novel bioinoculants that can offer modest, sensible, and engaging substitutes for expensive agrochemicals. The inoculant business is confronting various difficulties to improve quality definitions that offer a long timeframe of realistic usability and progressively reasonable and resistive cells in rhizosphere environmental factors. More examination to investigate the common-sense parts of large-scale manufacturing and definition are required so as to create viable, steady, more secure, increasingly practical, and novel bioformulations.

The need of the present world is for high agricultural yields, and upgraded creation of the harvest, and especially enrichment of the soil, obtained through eco-accommodating means. *Actinobacteria* need to be investigated for the utilization of bio-inoculants for various yields suffering under abiotic stresses, for example, temperature, pH, drought and salt levels. Taking into account the clinical, biotechnological and natural significance of the *Actinobacteria*, a comprehension of the developmental connections among individuals from this huge phylum, and what remarkable biochemical or physiological attributes recognize types of various classes of *Actinobacteria* is of extraordinary significance and criticalness. The individuals from *Actinobacteria* can be applied for biofortification of minerals for various grain crops just as numerous most predominant *Actinobacteria* can be utilized as probiotics as practical nourishments for human well-being.

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Chapter 9
Microbiomes of Hypersaline Soils and Their Role in Mitigation of Salt Stress

Salma Mukhtar, Dalaq Aiysha, Samina Mehnaz, and Kauser Abdulla Malik

Abstract Soil salinity is an important abiotic factor because of that crop yield is reduced more 40% globally every year. With the increase in world food production, it is very important to increase crop production and develop transgentic crops which can grow in saline and arid soils. Salinity is a continuously increasing problem in different parts of the world. Halophyte-associated microbial communities can be explored to characterize halotolerant and halophilic plant growth-promoting bacteria that can be used for the non-halophytic crops grown in saline conditions. Salt tolerant PGPRs have the potential to stimulate plant growth and productivity by increasing the availability of nutrients to the plants, production of phytohormones and nitrogen. These bacteria also produce disease resistance in plants against bacterial, fungal, or protist pathogens. This chapter gives an overview of halotolerant and halophilic PGPRs isolated and characterized from the rhizosphere of different halophytes. Here, we also discuss various direct and indirect methods of plant growth promotion used by halotolerant and halophilic bacteria. This study also illustrates that halotolerant PGPRs from hypersaline soils can be used as effective inoculants for different non-halophytic crops such as wheat, rice, maize, and sugarcane grown in salt-affected agricultural soils.

Keywords Soil salinity · Halophilic PGPR · Mineral solubilization · ACC deaminase · Phytohormones · Exopolysaccharides

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9.1 Introduction

Salinization is the main problem that adversely affects the agricultural areas globally. Salinity-affected lands comprise more than 6% of the total area of the world (Bui 2013; Rengsamy 2002). In Pakistan, about 6.5 million hectares of agricultural land are affected by drought, salinity, and sodicity (Mukhtar et al. 2016, 2018a, 2019a, b; Qureshi et al. 2008). Plant growth is usually reduced by an increase in soluble ion concentrations in soil and photosynthesis and transpiration rate is reduced. High salt concentration also affects the nutrients availability and plants metabolic pathways and ultimately had bad effects on their growth. It also reduces the soil aeration and permeability (Flowers and Colmer 2015; Munns 2005; Munns and Tester 2008; Nassar and Horton 1999). Due to salinity stress, about 70% yield of economically important crops such as wheat; rice, maize, barley, and sugarcane have decreased (Acquaah 2007; Hasegawa et al. 2000; Sobhanian et al. 2011).

Various chemical and biological approaches have been used to utilize salt-affected agricultural lands. The use of PGPRs (plant growth-promoting bacteria) to grow different crops in these areas is an important approach (Hesham et al. 2021; Yadav 2021). Extremophilic PGPRs have unique proteins and enzymes that enable them to survive under harsh conditions and promote plant growth (Flowers and Colmer 2015; Parida and Das 2005; Suyal et al. 2021; Yadav et al. 2021a). Salt tolerant plants such as *Urochloa mutica*, *Salsola stocksii, Kochia indica, Suaeda fruticosa*, and *Atriplex hortensis* have an important role in food supply, fuel production, and finer content and as fodder crops (Ashraf et al. 2009; Khan 2003; Mukhtar et al. 2016, 2017a, 2018a). Halophytes can be used as fodder crops especially in areas where agriculture is salinity affected and cannot be used for crop production and may be considered as desert or barren land (Ahmad et al. 2009; Bui 2013; Bauder and Brock 2001).

Microorganisms living in hypersaline environments have specific enzymes and proteins and they can grow at different salt concentrations due to specific modifications in their metabolic pathways (Olsen et al. 1994; Pitman and Lauchi 2002; Podell et al. 2013). Plant growth-promoting bacteria and ectomycorrhizal fungi play a vital role in the physiology and metabolism of the halophytes (Smith et al. 2015; Upadhyay and Singh 2015; Tiwari et al. 2021; Yadav et al. 2021b). The root and rhizosphere of salt-tolerant plants harbor a variety of PGP microorganisms that potentially increase the availability of minerals and nutrients from rhizosphere through plant roots and shoots (Khan et al. 2017; Mukhtar et al. 2019b; Rodriguez and Fraga 1999). PGPR genera including *Bacillus*, *Klebsiella, Pseudomonas, Enterobacter, Burkholderia*, and *Serratia* are also known as facultative bacterial strains that can reside inside plant cells and form a mutual beneficial relationship (Gray and Smith 2005; Mukhtar et al. 2019d; Ruppel et al. 2013; Singh and Jha 2016; Vokou et al. 2012). A number of studies on hypersaline soils reported that Actinobacteria, Proteobacteria, and Firmicutes are the most abundant bacterial phyla in the hypersaline environments (Bodenhausen et al. 2013; Mukhtar et al. 2019d; Singh and Jha 2016).

A number of studies have previously reported the physiological and genetic modifications of salinity resistance in the halophytes, but only a few studies have focused on soil microbiomes from hypersaline environments. So, our main focus is on diversity and functions of soil and root microbiomes of salt-tolerant plants growing in hypersaline environments. In this chapter, we also explain about 1. Various strategies of halophilic microorganisms use to survive under hypersaline environments, 2. The role of soil microorganisms in salinity tolerance, and 3. the role of PGPRs and pathogenic bacteria that are associated with the halophyte rhizosphere and root endosphere.

9.2 Adaptations to High Salinity by Halophytes

Halophytes can grow in salt-affected areas by using different strategies, e.g., they usually use exclusions or inclusion of salts from their tissues to main their internal osmotic balance. They use energy to exclude the excessive salts from their cells and tissues and protect themselves (Bittel and Robatzek 2007; Meng et al. 2018; Mansour et al. 2008). Halophytes tolerate high salt concentrations by some basic strategies, either by salt inclusion or exclusion (Chen et al. 2007). Concentrations of sodium and chloride ions in plant cells usually range from 13 to 31 mM. A number of sodium or hydrogen ion antiporters can create a proton gradient in these cells, and this phenomenon helps halophytes cells to maintain their internal osmotic stress (Nuccio et al. 1998; Queirós et al. 2009; Silva and Gerós 2009). Some salt-tolerant plants use their vacuoles for sequestration of salts (Fig. 9.1). These plant cells have more vacuolar space as compared to normal plant cells to store the excessive salts (Flowers and Colmer 2015). Halophytes also utilize compatible solutes or small molecules such as betaine, ectoine, proline, and trehalose to survive under high salt concentrations (Maurel 1997). These osmolytes can be categorized according to their structure and composition, e.g., they may be zwitterionic solutes, anionic solute, and non-charged ions or solutes. Salt-affected plants also use special glands to survive in saline environments (Fig. 9.1). These glands evaporate water and form crystals of salts on leaf surface (Dou and Zhou 2005). Plant proteins such as aquaporins have an important role in osmoregulation of halophyte plant cells. These proteins control the movement of water and osmolyte molecules across the cell membrane of plant cells (Bittel and Robatzek 2007).

9.3 Hypersaline Soil Microbiome

Hypersaline environments such as large Salt lakes, the Dead Sea, and the Khewra Salt Mine are populated with salt-tolerant bacteria and archaea that have ability to develop and maintain their osmotic balance even at high salt concentrations. The soil microbiome of hypersaline environments plays an important role in nutrient cycling

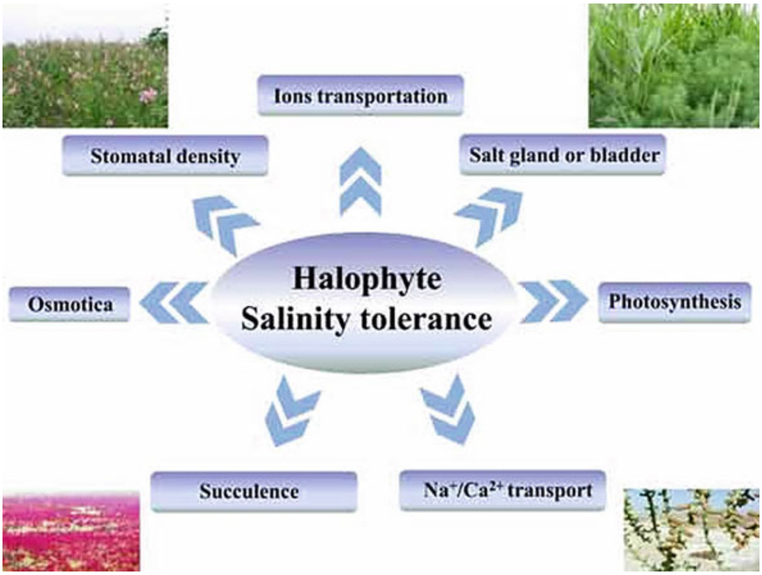

Fig. 9.1 Salinity tolerance mechanism of halophytes. Adapted from Xu et al. (2016)

and physicochemical properties of soil. Halophiles can survive under hypersaline conditions, and they are able to grow at different NaCl concentrations (Amoozegar et al. 2016; Dang et al. 2009; DasSarma and DasSarma 2015; Zamioudis et al. 2013). Halophilic bacteria and archaea have ability to degrade pollutant compounds and help the phytoremediation of contaminated soils in the hypersaline environments (Biswas and Paul 2013; Irshad et al. 2014; Sánchez-Porro et al. 2003). The advancement in sequencing techniques and different bioinformatics approaches help us to better understand the microbial diversity and plant-microbe interactions from different extreme environments including hypersaline and arid environments. The internal osmotic balance of halophilic microorganisms has been affected by a change in pH, salt concentration, temperature, and availability of different nutrients (Boutaiba et al. 2011; Qin et al. 2016; Janssen et al. 2015; Weyens et al. 2015).

Halophilic microorganisms usually use two strategies to adapt to hypersaline environments (Fig. 9.2). Mostly halophiles can utilize small molecules or osmolytes to maintain their internal osmotic balance. This is known as ‘compatible solute strategy’ and osmolytes include betaine, glutmate, ammino acids, sugars and some other molecules. Anaerobic halophilic and archaea use ‘salt in strategy’ to survive at high salt concentrations. They have ability to accumulate inorganic ions specially Cl^- and K^+ (DasSarma and DasSarma 2015; Gupta et al. 2015; Koh et al. 2015; Ventosa 2006; Ventosa et al. 2012). Halophilic archaeal cells also have various pigmented molecules, such as bacterioruberins that provides energy to the cells from sunlight and help the cells to exclude the salts from the cytoplasm. Halophilic archaea and bacteria have plasmids that play an important role in osmoregulation of these organisms.

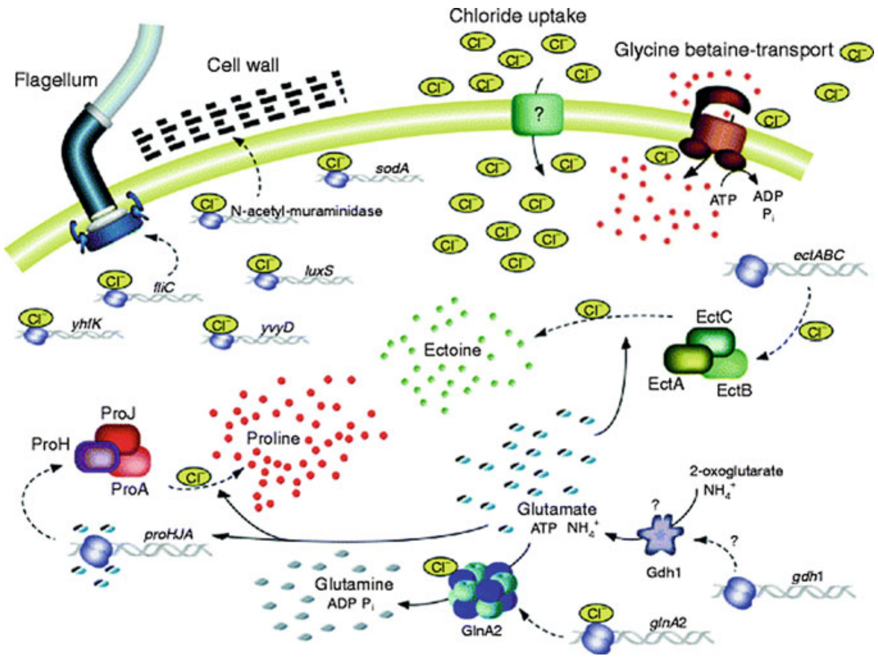

Fig. 9.2 Various strategies used by halophiles to grow at high salt concentrations. Adapted from Hänelt and Müller (2013)

Genes encode different traits include resistance for antibiotic and heavy metals, adaptation to abiotic stresses, virulence, plant tumors, nitrogen fixation, and root nodulation are present on the plasmids (Dziewit et al. 2015; Mukhtar et al. 2019c; Youssef et al. 2014; Xin et al. 2000). These plasmids encode also different pigmented molecules, e.g., cytochromes, enzymes, and phenotypic traits (Mukhtar et al. 2019c). Halophiles usually use two-component systems to regulate their metabolic functions, i.e., osmosensor and osmoregulatory enzymes and proteins. They have ability to control the change in ion concentrations in and out of the cells (Delbarre-Ladrat et al. 2014; Foo et al. 2015).

9.4 Role of Hypersaline Soil and Halophyte Microbiomes in Salinity Tolerance

The soil regions around plant roots or rhizosphere influence the plant growth by secretion of various compounds from roots. A great variety of organic molecules and inorganic ions, such as amino acids, vitamins, sugars, hormones, and growth factors are produced by root cells (Beneduzi et al. 2012; Goswami et al. 2016).

These root exudates affect the microbial communities from the phyllosphere, endosphere, and rhizosphere of plants (Gonzalez et al. 2015; Mukhtar et al. 2018b, 2019a, b; Shi et al. 2012; Prasad et al. 2021). Microorganisms reside in the endosphere and rhizosphere also depends on the plant types and it also changes with the different developmental stages of plant (Chaparro et al. 2013; Chaparo et al. 2014; Dimkpa et al. 2012; Mukhtar et al. 2018c). Microbiome of the same plant may vary with the change in soil physicochemical properties and development stage of the plant. Plant soil or rhizosphere harbors more microbial diversity as compared to root and leaf endosphere microbiomes (Figs. 9.3 and 9.4). PGPRs have the potential to stimulate the plant growth by providing the essential nutrients and minerals, production of phytohormones (cytokinins, auxins, gibberellins, absicisic acids, and ethylene) and siderophores in salinity-affected agricultural lands (Amoozegar et al. 2008; Bodenhausen et al. 2014; Browne et al. 2009; Gonzalez et al. 2015; Mehnaz et al. 2010; Mukhtar et al. 2019b; Susilowati et al. 2015).

PGPR bacteria from the hypersaline soils have potential to change atmospheric nitrogen to nitrate compounds that can be easily used by the plants (Figs. 9.3 and 9.5). Some bacteria including *Bradyrhizobium, Mesorhizobium, Azospirillum, Salinibacter, Pseudomonas, Bacillus,* and *Serratia* are the best examples of nitrogen fixers (Ahemad and Kibret 2014; Antón et al. 2002; Glick 2012; Kuan et al. 2016; Martínez-Hidalgo and Hirsch 2017). Some endophytic bacterial genera from the root and leaf can produce a variety of antifungal and antibacterial compounds and can be used

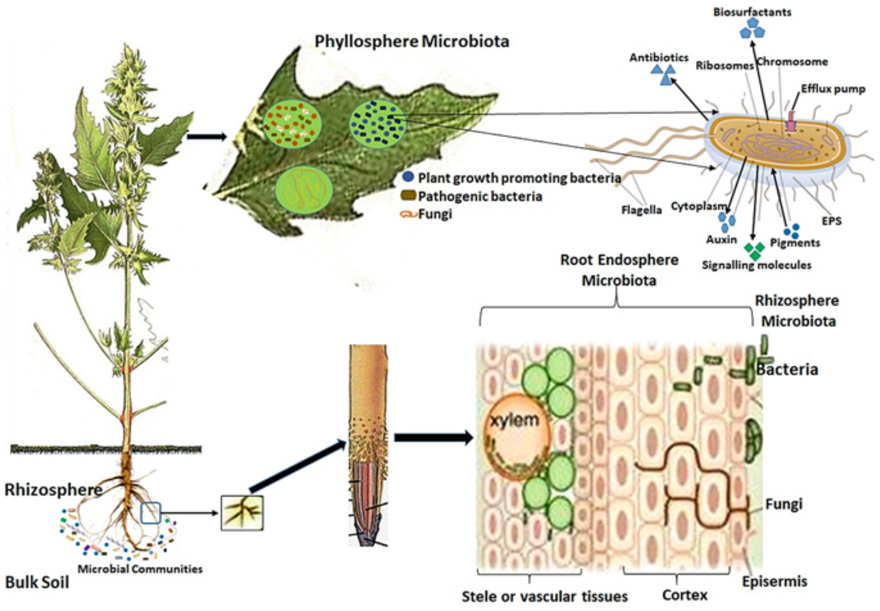

Fig. 9.3 The rhizosphere, phyllosphere, and endosphere microbiomes of salt-affected plants and overview of their functions. Adapted from Mukhtar et al. (2019b)

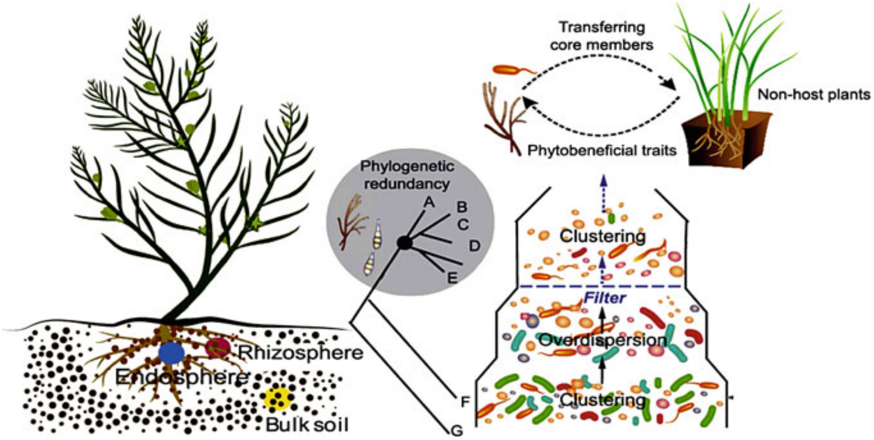

Fig. 9.4 Changes in composition of microbial communities in the soil samples around the plants (BS), rhizospheric soil samples (RS), and root endosphere samples (R). Microbial diversity may be lost or reduced from the rhizosphere or soil part to aerial parts of the plants and this is due to the decrease in nutrient availability and various abiotic factors at the rhizosphere and root cells interface. Adapted from Mukhtar et al. (2019b)

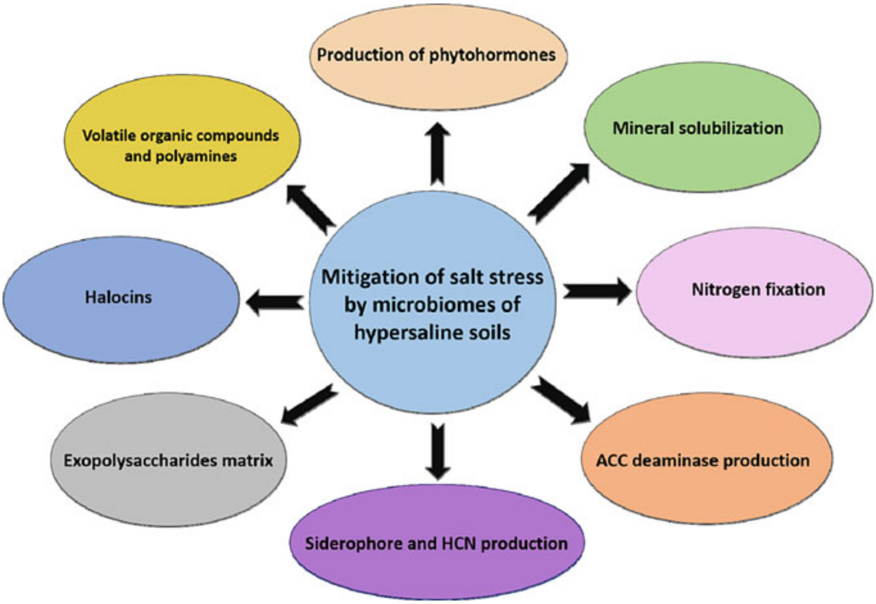

Fig. 9.5 PGPRs strains isolated from different salt-affected soils and plants and their plant growth-promoting traits, such as phosphate solubilization, production of phytohormones, HCN, siderophores, ACC deaminase, nitrogen fixation, exopolysaccharides, volatile organic compounds, and halocins

as biocontrol agents (Jaisingh et al. 2016; Mukhtar et al. 2019d). Halotolerant and halophilic *Bacilli* and other bacterial genera also produce hydrolytic enzymes like chitinase, protease, cellulase, amylase, and lipase (Biswas and Paul 2013; Gupta et al. 2015; Mukhtar et al. 2017b, 2018a; Shi et al. 2012). These PGPR strains also help the plants to suppress the fungal pathogens like *Alternaria* spp., *Aspergillus flavus,* and *Fusarium* spp. (Table 9.1).

9.4.1 Phytohormones Production

Halotolerant and halophilic bacteria produce a number of phytohormones including auxins, abscisic acid, cytokinins, gibberellins, and ethylene. These bacteria promote plant growth under salt-affected areas (Dodd and Perez-Alfocea 2012). Indole acetic acid (IAA) produced by halophilic PGPRs enhances plant growth and length of roots and shoots directly by increasing the cell differentiation and division processes (Desale et al. 2014; Gauthier et al. 1992; Mukhtar et al. 2017a). PGPR genera including *Bacillus, Halobacillus, Enterobacter, Pseudomonsas, Halomonas, Micrococcus*, and *Serratia* improved salt tolerance in economical important crops, such as maize, wheat and sugarcane and increase the activity of various enzymes including catalase and peroxidase, also increase the different nutrients and amino acids to the plant roots (Bari and Jones 2009; Gontia et al. 2011; Mukhtar et al. 2017a, 2019d; Susilowati et al. 2015). *Halobacillus* strains isolated from the hypersaline soils can produce cytokinins and have an important role in increase shoot biomass under salinity-affected conditions (Fig. 9.5 and Table 9.1). The cytokinin signaling in plant cells especially in root cells is reduced because of abscisic acids' production in shoot and leaf cells (Arkhipova et al. 2007; Bari and Jones 2009; Goswami et al. 2016; Ilangumaran and Smith 2017; Susilowati et al. 2015).

9.4.2 Mineral Solubilization

Halotolerant and halophilic PGPR can directly promote plant growth by increasing nutrients supply to the roots (Figs. 9.4 and 9.5). A number of PGPR strains, including *Bacillus, Halobacillus, Halomonas, Enterobacter, Micrococcus, Pseudomonas, Virgibacillus, Pantoea*, *Rhizobium*, and *Serratia* have the potential to change inorganic forms of some important minerals into solubilize forms, e.g., P, K, and Zn (Jaisingh et al. 2016; Mukhtar et al. 2017b; Richardson et al. 2009; Sharma et al. 2013). These strains change inorganic phosphates into available organic phosphates and can be used as biofertilizers for various crops like rice, sugarcane, maize, wheat, cotton, and barley (Heyndrickx et al. 1998; Goswami et al. 2016; Mukhtar et al. 2019d, 2020a; Nautiyal 1999; Ramaekers et al. 2010; Siddikee et al. 2011; Sgroy et al. 2009). PGPR strains, e.g., *Pseudomonas*, *Bacillus,* and *Enterobacter,* produce organic acids including citric acid, oxalic acid, acetic acid, and lactic acid,

Table 9.1 Halotolerant and halophilic bacterial strains identified from various salt-affected environments and their potential for plant growth promotion

Halophilic bacteria	Host halophyte	PGP activity	References
Halobacillus	*Psoralea corylifolia*	Production of IAA, solubilization of phosphate, and ACC deaminase production	Mukhtar et al. (2019d), Sorty et al. (2016)
Halomonas	*Salsola stocksii* and *Triticum aestivum*	Mineral solubilization, IAA, siderophore, and HCN production	Orhan (2016), Mukhtar et al. (2019a)
Micrococcus	*Arthrocnemum macrostachyum*	N2 fixation, IAA production, and mineral solubilization	Navarro-Torre et al. (2017)
Planococcus	*Salsola stocksii*	Mineral solubilization, production of IAA, ACC deaminase, and siderophore	Mukhtar et al. (2019a)
Oceanobacillus	*Atriplex amnicola*	Mineral solubilization, production of IAA, HCN, and siderophore	Mukhtar et al. (2019a, d)
Marinococcus	*Salicornia europaea*	Nitrogen fixation, phosphate solubilization, IAA, siderophore, and HCN production	Zhao et al. (2016)
Marinobacter	*Salsola stocksii*	Nitrogen fixation, solubilization of phosphate, IAA, HCN, and ACC deaminase production	Mukhtar et al. (2019d)
Virgibacillus	*Atriplex amnicola* and *Arthrocnemum Macrostachyum*	Mineral solubilization, production of IAA and siderophore	Mukhtar et al. (2019a)
Halovibrio	*Aster tripolium*	Mineral solubilization, production of IAA, siderophore, and biocontrol Activity	Szymanska et al. (2016)
Acinetobacter	*Psoralea corylifolia*	Auxin production, HCN, and siderophore production	Sorty et al. (2016)
Variovorax	*Salicornia europaea*	Auxin production and siderophore production	Sharma et al. (2016)

(continued)

Table 9.1 (continued)

Halophilic bacteria	Host halophyte	PGP activity	References
Dietzia	*Suaeda salsa*	Auxin production and nitrogen fixation	Yuan et al. (2016)
Pseudomonas	*Suaeda fruticose*	Nitrogen fixation, IAA, and siderophore production	Ullah and Bano (2015)
Salinivibrio	*Salsola stocksii* and *Atriplex amnicola*	IAA, HCN, and siderophore production	Mukhtar et al. (2019a, d)
Serratia	*Aster tripolium*	Nitrogen fixation, mineral solubilization, production of IAA, HCN, and siderophore	Amoozegar et al. (2008), Szymanska et al. (2016)
Arthrobacter	*Atriplex leucoclada*	Mineral solubilization, production of IAA and siderophore	Ullah and Bano (2015)
Rhizobium	*Psoralea corylifolia*	Nitrogen fixation, phytohormone production, and siderophore production	Martínez-Hidalgo and Hirsch (2017)
Enterobacter	*Psoralea corylifolia*	Production of IAA, HCN, and siderophore	Mukhtar et al. (2020a), Qin et al. (2014)
Agrobacterium	*Salicornia bigelovii*	Induction of plant stress Resistance; mineral solubilization, auxin production	Zhang et al. (2013)
Nesterenkonia	*Salicornia strobilacea*	Nitrogen fixation, mineral solubilization, production of phytohormones and siderophore	Mapelli et al. (2013)
Brachybacterium	*Salicornia brachiata*	Mineral solubilization and IAA production	Jha et al. (2012)
Pantoea	*Suaeda salsa*	Nitrogen fixation, auxin production, HCN, and siderophore production	Siddikee et al. (2011)
Brevibacillus	*Limonium sinense*	Mineral solubilization, auxin production, and biocontrol activity	Qin et al. (2014)
Haererohalobacter	*Salicornia brachiata*	Nutrient uptake, production of HCN, IAA, and siderophore	Susilowati et al. (2015)

(continued)

Table 9.1 (continued)

Halophilic bacteria	Host halophyte	PGP activity	References
Lysinibacillus	*Prosopis strombulifera*	Nutrient uptake, auxin production, and siderophore production	Mukhtar et al. (2019a), Sgroy et al. (2009)
Cronobacter	*Salicornia sp.*	Nutrient uptake and production siderophore	Shukla et al. (2012)
Azospirillum	*Kallar grass*	Nitrogen fixation, antioxidant defense enzymes production, auxin, and siderophore production	Reinhold et al. (1987)
Azotobacter	*Kallar grass*	Nutrient uptake, nitrogen fixation, auxin production	Malik et al. (1997)

when they solubilize inorganic phosphate into organic forms (Berendsen et al. 2012; Sharma et al. 2013).

Some PGPR strains such as *Bacillus*, *Pseudomonas, Burkholderia, Brevibacillus,* and *Gluconacetobacter* isolated from the saline environments have ability to solubilize inorganic zinc and increase the availability of zinc to the plants as shown in Table 9.1 (Fasim et al. 2002; Impa and Impa 2012; Navarro-Torre et al. 2017; Parmar and Sindhu 2013; Qin et al. 2014). These bacteria directly promote plant growth and act as chemo-attractants to the plant roots (Desai et al. 2012; Gandhi and Muralidharan 2016; Zhao et al. 2016). Among the PGPR strains, potassium solubilizing bacteria including *Bacillus, Acidothiobacillus, Paenibacillus, Azospirillum, Marinococcus, Serratia, Streptomyces,* and *Azotobacter* have gained attraction as biofertilizers for potassium deficient agricultural soils (Badar et al. 2006; Zhang et al. 2013; Zarjani et al. 2013; Zhang and Kong 2014). These bacteria have ability to increase the K availability in soils and thus decrease the use of inorganic or chemical fertilizers. A number of studies have reported the use of potassium solubilizing bacteria as biofertilizers for the growth, improvement of different crops including rice, wheat, maize, sugarcane, and cotton (Etesami et al. 2017; Shakeel et al. 2015; Shukla et al. 2012; Zeng et al. 2012).

9.4.3 Biological Nitrogen Fixation

Halophilic PGPRs have the potential to convert nitrogen gas into different nitrates compounds that can be easily used by plants. Nitrogen fixation is considered as an important plant growth-promoting trait (Fig. 9.5 and Table 9.1). Bacterial genera including *Azotobacter, Rhizobium, Mesorhizobium, Bradyrhizobium, Pseudomonas Azospirillum, Bacillus,* and *Serratia* are famous nitrogen fixers (Glick 2012; Malik et al. 1997; Martínez-Hidalgo and Hirsch 2017; Reinhold et al. 1987). These bacteria can enhance plant growth through nitrogen-fixing process, production of various phytohormones and siderophores. These bacteria can also suppress the plant diseases caused by various bacterial and fungal pathogens (Wu et al. 2009; Mukhtar et al. 2020b). Rhizosphere-associated nitrogen-fixing bacteria genera including *Azospirillum, Enterobacter, Azotobacter, Klebsiella, Pseudomonas,* and *Xanthobacter* have been characterized from a number of hypersaline environments. These bacteria have been used as biofertilizers for economically important crops, such as maize, rice, wheat, barley, and sugarcane (Brusamarello-Santos et al. 2012; Susilowati et al. 2015).

9.4.4 ACC Deaminase Production

PGPR strains including *Oceanobacillus, Bacillus, Achromobacter, Halobacillus, Halomonas, Micrococcus, Virgibacillus,* and *Planococcus* can decrease the concentrations of ethylene because of ACC deaminase (1-aminocyclopropane-1-carboxylic acid) (Fig. 9.5 and Table 9.1). Bacterial strains with a potential to produce ACC deaminase can enhance plant growth in different abiotic stress conditions, e.g., water logging, drought, salinity, and contaminated soils. The enzymes including ACC synthetase change *S-adenosylmethionine* in ACC deaminase and ultimately this will be converted into ACC oxidase oxidase (Glick 2012; Goswami et al. 2016; Mukhtar et al. 2020a; Qin et al. 2014). These bacteria can decrease the concentration of ethylene because of the ACC deaminase activity. PGPRs usually lower the concentration of ACC outside the plant cells and helps them to maintain balance between their internal and external ACC deaminase levels. They also play a role in the good growth of plant roots by decreasing the ethylene inhibitory effect (Kim et al. 2007; Mukhtar et al. 2020a; Sorokin and Tindall 2006).

9.4.5 Siderophores and Hydrogen Cyanide Production

Iron is an important micronutrient that is required for different biochemical processes such as photosynthesis, respiration, and nitrogen fixation. In saline and sodic soils, iron availability is very low (Abbas et al. 2015; Kobayashi and Nishizawa 2012; Singh et al. 2015; Yousfi et al. 2007). A number of PGPR bacterial strains produce small, high-affinity Fe(III)-chelating compounds which as known as siderophores (Fig. 9.5 and Table 9.1). Siderophore production by halotolerant and halophilic PGPRs such as *Halobacillus, Bacillus, Halomonas, Pseudomonas, Halovibrio, Klebsiella,* and *Rhizobium*have been reported from various saline environments (Bhattacharyya and Jha 2012; Haas and Défago 2005; Mirza et al. 2006; Vacheron et al. 2013).

Some halotolerant PGPRs including *Aeromonas, Rhizobium, Bacillus, Halomonas, Acinetobacter, Pseudomonas,* and *Enterobacter* have the ability to produce antibacterial and antifungal metabolites such as HCN (hydrogen cyanide), 2,4-diacetylphloroglucinol, pyrrol-nitrin, gliotoxin, pyoluteorin, and tensin (Bhattacharyya and Jha 2012; Drogue et al. 2012; Howell et al. 1993; Shen et al. 2013; Singh et al. 2015). These plant-associated bacteria help plants to produce resistance against a number of bacteria and fungi (Fig. 9.5 and Table 9.1). HCN producing bacteria have been identified and characterized from a number of environments (Barea et al. 2005; Szymanska et al. 2016; Taunton et al. 2000). Recent studies on minerals from nation soils and rocks have reported that HCN producing bacteria help plant roots to mobilize various minerals like P, K, and Zn in soil (Frey et al. 2010; Lapanje et al. 2012; Wongfun et al. 2014). In acidic soils, HCN not only plays a role in iron sequestration but, mainly contributes to the mobilization of phosphate in the soil and increases its availability to plants (Howell et al. 1993; Lanteigne et al. 2012; Ström et al. 2002; von Rohr et al. 2009).

9.4.6 Exopolysaccharides Matrix

A number of halotolerant PGPR strains including *Halomonas, Halobacillus, Pseudomonas, Corynebacterium, Nesterenkonia, Acinetobacter,* and *Planococcus* secrete exopolysaccharides (EPS) which can be used for the attachment of soil particles or root surfaces (Fig. 9.5 and Table 9.1). These bacteria play a major role in cellular associations among microorganisms, plant-microbe interactions and protect plants from bacterial, fungal and protist pathogens (Abd_Allah et al. 2018; Delbarre-Ladrat et al. 2014; Llamas et al. 2012; Mapelli et al. 2013; Sorty et al. 2016). Exopolysaccharides have a role in stabilization of soil structure, composition, and soil particles' water-holding ability. EPS producing halotolerant and halophilic bacteria can be used as biofertilizers for crops such as sugarcane, maize, wheat, and chickpea under salinity-affected areas (Kumar et al. 2016; Mukhtar et al. 2019d; Oren 2015).

9.4.7 Halocins

Halophilic archaea and bacteria produce small proteinaceous bacteriocins which are known as halocins (Fig. 9.5 and Table 9.1). These compounds are classified into two types; peptides or microhalocins with a size of about 10 kDa or less and the large proteins with bacteriocin properties and they have a size larger than 10 kDa. These compounds have different functions. They play a crucial in protection of plants against various fungal and bacterial pathogens in hypersaline environments (Besse et al. 2015). They help to maintain plant-microbe interactions. They can function as RNA or DNA endonucleases, affect transcription and translation processes, formation of pores and bacterial cell lysis (Meknaci et al. 2014; Subramanian et al. 2016). Growth of some archaea and bacteria can be inhibited by a number of halocins. A halo zone or inhibition zone is formed around the bacterial growth on the agar plate to show the effect of halocins. Halophilic archaeal strains such as *Haloferax, Halobacterium,* and *Halococcus* have different halocins including H4, R1, A2, G1, H6, and C8. They are well-studied halocins from different hypersaline environments (Quadri et al. 2016; Vurukonda et al. 2016). Using metagenomic and metatranscriptomic analyses, a number of new halocins have been discovered recently. Some bacterial strains such as *Bacillus, Pseudomonas,* and *Halomonas* also produce a variety of halocins and affect the growth of plant when inoculated as biofertilizers under salinity-affected lands. These compounds also change the plant proteome and affect the energy metabolism pathways of plants (Mohan and Dubnau 1990; Zhang et al. 2008).

9.4.8 Polyamines and Volatile Organic Compounds

Many halotolerant PGPR strains such as *Bacillus, Stenotrophomonas, Pseudomonas, Halomonas, Serratia, Variovorax,* and *Arthrobacter* release volatile organic compounds that can be used for plant protection against bacterial and fungal pathogens and indirectly promote plant growth (Fig. 9.5 and Table 9.1). Inoculation of PGPR strains *Bacillus, Serratia* and *Pseudomonas* increased photosynthesis rate and the plant biomass of maize, wheat and sugarcane and reduce the emission of volatile compounds (Park et al. 2015; Tahir et al. 2017; Raza et al. 2016; Sharma et al. 2016; Zhuo et al. 2016). *Bacillus volatiles* and *Bacillus subtilis* produce volatile compounds that enhance the resistance against *Ralstonia solanacearum* induced bacterial wilt in salt-stressed tobacco and *Arabidopsis* (Aslam et al. 2011; Tahir et al. 2017; Xie et al. 2014). The volatile compounds secreted by halotolerant PGPR promote the growth of plants by increasing the chlorophyll content and proline and decreasing root Na^+ ions accumulation. Polyamines produced by certain halotolerant and halophilic bacteria also enhance the plant growth (Mukhtar et al. 2019d; Ullah and Bano 2015). Inoculation with *Bacillus megaterium* BODC15 strains and *Bacillus subtilis* OKA105 strain positively affect the growth of plant and increase the plant length and biomass by mediating the increase in cellular polyamines in *Arabidopsis* (Kadmiri et al. 2018; Zhang et al. 2007; Zhuo et al. 2016).

9.5 Conclusion and Future Prospects

Halophyte microbiome functions in a more eco-friendly and promote the plant growth in salinity-affected agricultural areas. Halotolerant and halophilic PGPRs play a vital role in the maintenance of biogeochemical cycles. The composition of microbial communities associated with the rhizosphere of halophytes changes with the increase in soil salinity. Halotolerant and halophilic PGPRs have ability to survive under hypersaline conditions because these microorganisms have special genetic and physiological modifications for their survival. PGPRs isolated from the saline soils, rhizosphere, phyllosphere, and endosphere of halophytes have the potential to stimulate plant growth by phytohormones hormones production, mineral solubilization, nitrogen fixation, siderophores, HCN, ACC deaminase and volatile compounds production and biosynthesis of exopolysaccharides. These PGPR traits affect the metabolic pathways in plants and act as signals to different abiotic stress responses. So, in this way, they help the plants to grow well under hypersaline conditions. These microorganisms can be potentially used as reclamation and plant protection of salt-affected soils. Halotolerant PGPR bacteria and fungi can be used for growth promotion of plants and also improve the yield of non-halophytic crops that are grown under salinity stress conditions. Halotolerant PGPR-based biofertilizers can be considered as a better strategy for sustainable crop production under salinity-affected agricultural lands. Co-inoculation of halotolerant PGPR bacteria and fungi for a long time period (at least 3 years) can improve the plant growth and yield under different abiotic conditions.

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Chapter 10
Psychrotrophic Soil Microbes and Their Role in Alleviation of Cold Stress in Plants

Yachana Jha, Anjali Kulkarni, and R. B. Subramanian

Abstract The psychrotrophic microbes having plant growth-promoting ability is used to enhance the ability of plant to develop tolerance against different stresses including cold stress, but the real mechanism behind such improved tolerant ability for protecting the host plant is not clearly known till date. The effect of plant-associated psychrotrophic bacteria has been studied in the maize, on the nutrient status, lipid profile of cell wall and lignin content to establish a correlation between lipid profile and cold stress tolerance. The cold stress also results in cell dehydration due to frizzing effect on cell content, which will block all the cell biochemical activities. So the effect of psychrotrophic bacteria on the osmotic and oxidative stress in cold stressed maize plant has been studied to minimize the adverse effect of stress. The study showed that psychrotrophic bacteria is capable to change lipid profile as well as the cell membrane properties of plant under cold stress and help plant to better survive under stress.

Keywords Alleviation · Cold stress · Psychrophiles · Psychrotolerant

10.1 Introduction

The production of crop plant has been affected by a multitude of environmental factors including abiotic and biotic factors, and it further get exacerbated with the increasing human population (Yadav et al. 2020). These factors include drought, salinity, flooding, heat, low temperature, high radiation, extreme pH, deficient or excess of essential nutrients, and gaseous pollutants (Kour et al. 2020b; Hesham et al. 2021; Yadav et al. 2021a). These abiotic factors have multidimensional effect on

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plant growth as generation of osmotic stress, oxidative stress, disturbed homeostasis of the cell, and cell death (Kour et al. 2019). Among these, low temperature stress is the most common stress in hill regions and the main abiotic factors that badly reduced the production of crop by imparting direct or indirect effect nearly on all aspect of the plant life by altering the plant physiology and metabolism (Pandey et al. 2017; Yadav et al. 2015; Dikilitas et al. 2021). To minimize the effect of cold stress responses in plants, there is multilayer effect—the primary effect is plant cell membrane rigidification—for the protection of intracellular organelle.

The secondary effect of cold stress results in reduced enzyme activity due to altered protein complexes and stability of enzymes such as enzyme of photosynthesis, respiration, and ROS scavenging enzymes (Yadav et al. 2016). They ultimately affect important functions like photosynthesis, respiration, photo-inhibition due to considerable membrane damage (Jha 2019a; Kumar et al. 2019). Finally, cold stress alters the enzymes activity and expression of gene, to induce the conformational change in RNA. Cold stress has been divided into two groups as chilling stress and freezing stress and freezing stress has more damaging effect on plant than chilling stress. The most damaging effect of freezing stress is formation of intracellular ice crystals, which induce water efflux, leading to cell dehydration, may cause plant death. Plants being sessile have to modify their metabolic pathway for better survival under such stress. Most temperate plants have developed cold adaptation, but till date several crops having great economic importance lack the ability of cold acclimation. There are several cold stress signal transduction pathways such as lipid signaling cascades, protein kinase, Ca^{2+}, protein phosphatase, and generation of ROS. So the need of hour is to develop climate-smart crops, flexible to climate change, require a multiplicity of physiological interactions. During cold acclimatization, plant develops cold tolerance ability by induction of protective metabolite likes proline, soluble sugar, and LEA, etc. (Hussain et al. 2018).

Microorganisms are early forms of life, which are competent to carrying several important metabolic reactions for other organisms like plants, animals. Higher eukaryotes would be able to survive and flourish due to past microbial association and activities that help in degradation of complex bio-molecule, incorporation of important organic matter, or recycling of key minerals. Microorganisms have diverse action on other organisms as they may be pathogenic, or produce antimicrobial agents or enzymes. Also microorganisms are able to grow on a wide range temperature and divided into three groups on the basis of its temperature requirement for their growth. The microorganisms are able to grow on ambient temperature between 20 and 45 °C are mesophiles, survive at a temperature between 50 and 70 °C are thermophiles and found at temperature range between −16 and 40 °C are psychrotrophs or psychrophiles (Torsvik and Øvreås 2008). Such psychrotrophic microbes directly or indirectly help host plant in cold adaptation in diverse agricultural conditions due to their versatility and can have biotechnological potential applications in agriculture practice (Suyal et al. 2021) (Tiwari et al. 2021).

10.2 Isolation and Inoculation of Psychrotrophic Bacteria in Maize

Earth has very diverse environment range from polar sea ice (−89.2 °C) to heat desert (+54 °C), but prominently our earth is a cold, marine planet. About 20% of the earth's surface is covered with snow consisting of polar ice sea, glaciers, ice sheets, permafrost soils, and 70% of the earth consists of the ocean's water having temperature of −1 to +5 °C. So the earth is habitats for large proportion of cold-adapted microorganisms from diverse groups of bacteria and fungi like *Mucoromycota*, *Bacteroidetes*, *Proteobacteria*, *Actinobacteria*, and blue green algae, etc. Psychrotrophic is a group of bacteria that has the ability to grow and multiply at extremely low temperature at the range of 0 to −20 °C and reside even in permanently cold regions like deep sea and at polar regions (Yadav et al. 2019). The plant able to grow at low temperature has several adaptations including association with psychrotrophic microbiomes with plant. Such associations are mostly symbiotic in which fungus or bacteria physically reside within the plant tissue without causing any detrimental effect to the plant host (Jha 2019b).

Common multifunctional PGP attributes of the plant psychrotrophic bacteria comprise solubilization of insoluble mineral nutrients, siderophores production, and modulation of phytohormones, to enhance the ability of host plant to acquire tolerance against the abiotic and biotic stress (Gaiero et al. 2013; Verma et al. 2015). Some plant-associated psychrotrophic bacteria also has gene to convert the dinitrogen gas into ammonium and nitrate form to be used by the host plant for its growth.

In this study, such favorable plant-associated psychrotrophic bacteria are isolated from the roots of *Suaeda nudiflora* plant from the different sites of mount Abu hill station near Gujarat Rajasthan border in the month of December (Jha and Subramanian 2011). Serial dilution technique has been used for isolation of bacteria in semi-solid NFb medium with Fluconazole (0.015% w/v), then transferred on NFb agar plate with Fluconazole and bromothymol blue. After plating the plates are incubated in BOD incubator for 96 h at 15 ± 1 °C and isolated pure culture are maintained at 4 °C. The selection of the psychrotrophic bacteria for further experiment has been done on the basis of its growth temperature range and plant growth promotion ability. The identification of the isolates of interest is carried by morphological, cultural characteristics, biochemical tests, and molecular analysis. The molecular analysis of the isolates has been done by sequencing of 16S rDNA gene followed by BLAST analysis and phylogenetic profiling. The obtained sequences are submitted to gene bank having Gene Bank accession number: HM756642 has been identified as *Lysinibacillus fusiformis* strain YJ4 and HM756643 as *Lysinibacillus sphaericus* strain YJ5.

The ability of these root residing psychrotrophic bacteria in plant growth and modulation of metabolites to provide protection to host plant in cold stress has been studied on maize plant. The maize seedling has been inoculated with selected psychrotrophic bacteria as per our published method (Jha and Subramanian 2013). The seed of selected maize variety Pioneer 30 V92 has been obtained from the Main

Maize station Gujarat. The healthy seed has been properly surface sterilized and the seed completely free from contamination has been further inoculated with selected psychrotrophic bacteria. The co-inoculation of sterilized maize seeds with isolated psychrotrophic bacterial inoculums has been carried out in 20 ml Hoagland's nutrient medium in culture tube and tubes are placed in culture room at 27 °C at 12 h light–dark cycle for a week (Jha et al. 2012).

The root association of psychrotrophic bacterial with maize has been confirmed by root staining with 2, 3, 5-triphenyl tetrazolium chloride stain overnight (Jha and Subramanian 2018). The presence of psychrotrophic bacteria in the root has been observed in the cross sections of the stained root under an image analyzer microscope (Carl Zeiss) as red-colored cells. The effect of the psychrotrophic bacteria on maize growth promotion has been analyzed in green house, and the result of the study shows the positive effect of the psychrotrophic bacteria as in Table 10.1. Common effect of low temperature on plants is low rate of seed germination, poor growth, appearance, less number of tillering, but inoculation with both the psychrotrophic bacteria reduced the effect of cold stress in maize. But the cold stress also has effects on the reproductive stage results in delayed heading and pollen sterility, which is responsible for reduced crop production (Suzuki et al. 2013). Such psychrotrophic bacteria has positive effect on plant growth and also has the ability to act as biological

Table 10.1 Effect of psychrotrophic bacteria on plant growth parameter of maize under cold stress ($n = 5$)

Treatment	Germination %	Root length (cm)	Shoot length (cm)	Dry weight (gm Plant^{-1})
Normal				
No inoculation	74.2^{d}	1.81^{cd}	39.2^{d}	2.02^{d}
Inoculation with *L. fusiformis*	82.1^{bc}	2.13^{c}	41.5^{c}	2.13^{c}
Inoculation with *L. sphaericus*	91.3^{b}	2.35^{ab}	43.6^{ab}	2.32^{ab}
Inoculation with *L. fusiformis* + *L. sphaericus*	96.2^{a}	2.33^{a}	45.1^{a}	2.41^{a}
Cold stress				
No inoculation	52.2^{cd}	1.34^{cd}	28.1^{cd}	1.43^{d}
Inoculation with *L. fusiformis*	63.4^{c}	1.41^{c}	31.4^{c}	1.49^{bc}
Inoculation with *L. sphaericus*	67.3^{b}	1.49^{ab}	34.2^{ab}	1.58^{b}
Inoculation with *L. fusiformis* + *L. sphaericus*	69.3^{a}	1.53^{a}	35.3^{a}	1.62^{a}

For each Parameter, values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

control agent against different pathogens under cold stress, so psychrotrophic bacteria can be used as an eco-friendly tool for crops production at its full potential cultivated under the cold stess (Yadav 2017).

10.3 Effect of Cold Stress on Physiological Response of Plants

Low temperature is responsible for major injuries caused in plant which limits plant growth and yield. However, low temperature stress has been categorized into freezing stress (temperatures below 0 °C) and chilling stress (temperatures above 0 °C) having different effects on plant cell. In freezing stress, cell aqueous content gets converted into ice crystals within the cell, which cause metabolic dysfunction as well as mechanical damages to plants cell (Li et al. 2018; Yadav et al. 2021b). While chilling stress generally causes cellular membrane damages, leaf wilting, chlorosis, necrosis, reduction in photosynthesis, oxidative stress, and finally reduced plant growth (Verma et al. 2017). However, plants develop tolerance toward freezing and chilling stress by evolving multilayer mechanisms as accumulation and production of osmoprotectant such as soluble sugars, amino acids, carbohydrates, and cold-induced stress-related proteins. All ecological stresses including cold stress are initially recognized by specific receptor on the cell membrane of the plant cell and are transduced signal for the activation of related downstream signaling pathways cascade for the induction of protection mechanism. Plasma membrane is chief barrier between the plant cell and external environment and first to experience the deleterious effects of cold stress. Cold stress generally results in alteration in lipid composition of the plasma membrane and alters the fluidity of the membrane to protect the plant cell from chilling stress. But lipid composition of plasma membrane has crucial role in maintaining the stability and function. The major function of cell membrane is not only in protection, metabolism, homeostasis, but it also has function in signal recognition and signaling cascades for protein-lipid interactions as a main regulatory activity under stress condition (Sunshine and Iruela-Arispe 2017).

Plant under stress can able to survive by the multilayer modifications starting from morphological, physiological, biochemical, and molecular level. After sensing stress plant signal molecules like enzyme kinase, phosphatase, ROS, lipid, and calcium signaling cascades get activated to induce the transcription factors for the stress-responsive genes of major targets of the stress. Such specificity is achieved by timely and combined activity of several related signaling pathways. Calcium is a secondary messenger for the activation/ inactivation of specific transcriptional factor by initiating a phosphorylation/dephosphorylation cascade. Transcriptional factor has the ability to regulate the expression of function of specific gene for the survival and adaptation of plant under stress (Hoang et al. 2017).

10.3.1 Effect of Psychrotrophic Bacteria Nutrient Availability for Plant in Maize Under Cold Stress

Plant nutrient dynamics is directly related to worldwide climate change of various types of extremities like drought, cold, salinity, etc. The acquisition, assimilation, and distribution of important nutrient in the plant depend on the availability of nutrients in the soil and disturbed by change in climatic factors (Jha 2019c). The climatic factor-like cold stress affects the plant nutrient dynamics in different plant parts, including mobilization from senescing leaves or transportation to important organs. The redistribution of mineral nutrients, water fluxes, and assimilation of food is badly affected by cold stress.

The psychrotrophic bacteria are plant growth promoters having different multifunctional growth promotion attributes such as ability for biological nitrogen fixation to produce siderophores, phytohormone, and solubilize phosphate and potassium, resulting in an increased availability of important major mineral nutrient ions for the plant's growth (Singh and Yadav 2020; Kour et al. 2021). The association of psychrotrophic bacteria with plant under cold stress and their effect on the biological growth response is complex. Among major mineral nutrient, nitrogen and potassium are the most important nutrient for the plant and are required for synthesis of amino acids and functioning of proteins. So, in this study, the isolation of psychrotrophic bacteria which has been done on the NFb media indicates that these isolates have nitrogen fixation potential. The use of such N_2-fixing psychrotrophic bacterial association for enhanced plant growth and yield is a sustainable technique under cold stress as well as in normal condition. The foliar contents of K, P, Ca, and N have been estimated in the leaves of maize inoculated with psychrotrophic bacteria. The foliar concentration of K, P, Ca, and N has been determined by digital flame photometry using specific filter after digesting 1 g plant material in tri-acid mixture in the ratio of 9:3:1. The plant associated with psychrotrophic bacteria has significantly higher foliar concentration of K, P, Ca, and N under normal and cold stress conditions. The plants treated with psychrotrophic bacteria always show elevated levels of foliar N and K (Table 10.2).

Potassium is an osmotically active solute; it contributes to water retention and absorption in the plant cell for maintaining central metabolic activity of cold stressed plant (Jha 2018a). Also potassium is one of the important cofactor for many metabolic enzymes necessary for central metabolic pathway. The psychrotrophic bacteria that reduced the uptake of cations in the inoculated maize plant under cold stress is the most interesting result of this study. Cations like Na^+ and Ca^{2+} adversely affect the properties of plant cell membrane and membrane transport, which ultimately change the cytoplasmic Ca^{2+} activity. All such effect collectively alters the plant physiology, as water and ion transport, nutrition uptake and photosynthate distribution under cold stress. So the selection and inoculation of psychrotrophic bacterial consortium can confer tolerance to plant against adverse environmental condition and also improve other nutrient availability. The use of microbial bioinoculants or biofertilizers of such psychrotrophic bacteria with diverse multifunctional plant growth promotion

Table 10.2 Effect of psychrotrophic bacteria on minerals concentration of maize under cold stress ($n = 5$)

Treatment	N(mg kg^{-1})	P(g kg^{-1})	K(g kg^{-1})	Ca(g kg^{-1})
Normal				
No inoculation	22.3^{cd}	1.72^{d}	53.1^{d}	15.2^{a}
Inoculation with *L. fusiformis*	23.1^{c}	1.83^{bc}	56.3^{c}	13.4^{cd}
Inoculation with *L. sphaericus*	24.5^{b}	1.93^{b}	57.4^{b}	13.8^{bc}
Inoculation with *L. fusiformis* + *L. sphaericus*	25.4^{a}	2.11^{a}	59.2^{a}	14.1^{b}
Stressed				
No inoculation	17.3^{d}	1.43^{cd}	45.2^{d}	16.4^{a}
Inoculation with *L. fusiformis*	18.2^{c}	1.54^{c}	46.3^{bc}	14.2^{cd}
Inoculation with *L. sphaericus*	19.6^{ab}	1.59^{b}	47.2^{ab}	13.3^{bc}
Inoculation with *L. fusiformis* + *L. sphaericus*	20.1^{a}	1.61^{a}	47.8^{a}	14.2^{b}

For each Parameter, values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

attributes is required for enhancing or maintaining the current rate of crop and food production for sustainable agricultural agroecosystems (Woo and Pepe 2018).

10.3.2 Effect of Psychrotrophic Bacteria on Photosynthetic Parameters in Maize Under Cold Stress

Plants being sessile are regularly exposed to different environmental stresses, which affect their growth and production. Environmental stress is one of the important parameters for crop production as it directly affects the physiological processes related to stress injury. Tolerance to environmental stress is an organized integrated event coordinates between various levels of anatomical, biochemical, cellular, morphological, and physiological events. One of the most important physiological and metabolic activities of plant is photosynthesis for the synthesis of carbohydrate and is highly sensitive to low temperature (Hajihashemi et al. 2018). Photosynthesis is the principal process on the earth carried out by the plant for the production of food due to the presence of chlorophyll. The photosystem I (PSI) and photosystem II (PSII) of chlorophyll have the ability to trap light energy to generate redox potential for the production of ATP. Low temperature that result in limited photon density induces the reduced photosynthetic capacity of stressed plant. Cold stress rapidly reduced chloroplasts equilibrium by inducing imbalances in the antenna complexes and PSII. To maintain the photon density, stressed plant typically hoards higher concentration of ancillary pigments like carotenoids and chlorophyll a/b under cold stress. Carotenoids also help in protection of photon sequestering protein complex from changing temperature-induced injuries (Banerjee and Roychoudhury 2019). The effect of psychrotrophic bacteria on the concentration of carotenoids and chlorophyll pigment in maize under cold stress has been determined by chlorophyll extraction method from 0.5 g fresh leaves. The supernatant of the extract has been taken to determine the concentration of carotenoids and chlorophyll a/b by taking absorbance at 470, 663, and 645, respectively. The result of the study showed that cold stress has remarkable effect on the concentration of light-harvesting pigments, but psychrotrophic bacteria significantly increase the chlorophyll content in the inoculated plant compared to untreated control (Table 10.3).

Cold stress primarily results in loss of membrane fluidity of plant cell. Plants under cold stress that are not able to maintain fluidity of membrane resulted in membrane

Table 10.3 Effect of psychrotrophic bacteria on the total chlorophyll content, chlorophyll a, chlorophyll b, carotenoid content and rate of photosynthesis of maize under cold stress ($n = 5$)

Treatment	Total chlorophyll content (g kg^{-1})	Chlorophyll a (g kg^{-1})	Chlorophyll b (g kg^{-1})	Carotenoid (mg kg^{-1})	Photosynthesis (µmol m^{-2}s^{-1})
Normal					
No inoculation	1.83 ^{cd}	6431^{d}	6372^{d}	1.76^{d}	24
Inoculation with *L. fusiformis*	1.97^{c}	6781^{c}	7844^{bc}	1.87^{c}	27
Inoculation with *L. sphaericus*	2.12^{ab}	7646^{ab}	8192^{b}	2.01^{ab}	27
Inoculation with *L. fusiformis* + *L. sphaericus*	2.42^{a}	7813^{a}	8613^{a}	2.22^{a}	29
Stressed					
No inoculation	1.22^{d}	2124 ^{cd}	3243^{d}	0.92 ^{cd}	18
Inoculation with *L. fusiformis*	1.34^{c}	2243^{c}	3462^{bc}	1.04^{c}	20
Inoculation with *L. sphaericus*	1.39^{ab}	2342^{ab}	3581^{ab}	1.13^{b}	21
Inoculation with *L. fusiformis* + *L. sphaericus*	1.42^{a}	2397^{a}	3525^{a}	1.26^{a}	23

For each Parameter, values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

damage of cell and organelles including chloroplast, having deleterious effect chlorophyll content, electron transport in membrane, thylakoid structure, photosynthetic enzyme activities and stomatal closure. The cold stress that limits the stomatal conductance resulted in reduced rate of photosynthesis for sugar production. The effect of psychrotrophic bacteria on stomatal conductance, photosynthetic rate, and sugar accumulation has been analyzed by an open-system portable photosynthesis meter (Li-Cor 6400) in the maize plant under cold stress. The result showed that all the photosynthesis-related parameters like stomatal conductance, photosynthetic rate, and sugar accumulation in maize are adversely affected by cold irrespective of psychrotrophic bacteria inoculation as shown in (Table 10.3). The observation showed that stomatal conductance, rate of photosynthesis, and sugar accumulation are significantly higher in maize plants inoculated with psychrotrophic bacteria under normal condition, but under cold stress also it has positive effect. Cold stress has multiple metabolic and physiological effects and all these combined effect on reduced photosynthetic efficiencies of plant under cold stress and this reduction in photosynthetic capacity generally accompanied with augmented accumulation of sugar (Jha 2019f), which act as osmoprotectant to provide protection to plant against low temperature (Slama et al. 2015) and help in maintaining the fluidity of membrane require to increase the unsaturated fatty acids content for proper function of chloroplast.

10.3.3 Effect of Psychrotrophic Bacteria on Membrane Permeability–Electrolyte Leakage and Malondialdehyde Content

Plant cell membrane is one of the most dynamic structures and is the main targets of environmental stresses like cold stress, having numerous biophysical and biochemical activities. Cold stress generally results in changes in membrane fluidity, decrease in enzymatic activity, alteration of metabolic processes as well as reduction of photosynthetic capacity. The major adverse effect of cold stress is damage of plasma membrane of the plant cell, which further gets argument due to cold stress-induced dehydration. The lipids and protein are the two major component of plasma membrane, having two types of lipid, i.e., unsaturated and saturated fatty acids. And there is direct relation between concentration of concentration of unsaturated and saturated fatty acids and temperature. Higher concentration of unsaturated fatty acids provides membrane fluidity, whereas higher concentration of saturated fatty acids is responsible for membrane rigidity. Cold stress also causes changes in the lipid and fatty acid composition of higher-plant membranes (Barrero-Sicilia et al. 2017). Such alteration in the fatty acid composition results in enhanced proportion of unsaturated fatty acids like linolenic acid/galactolipids under cold stress. For low-temperature acclimation accumulation of high concentration of unsaturated fatty acid like phosphatidilglycerol, protect the major membrane phase transition and also reduced the phase transition temperature of the membrane lipid content, ultimately enhance the membrane stability index under cold stress.

Such alterations in the fatty acid composition also alter the permeability and integrity of the membrane, as well as cell compartment, which affect the rates of solute and electrolyte leakage. The intracellular electrolyte leakage rate act as an indicator for the cold stress-induced cell membrane damage. Leakage points domain representing alters lipid configurations due to cold-induced changes in cell membrane. The effect of psychrotrophic bacteria on membrane stability index, electrolyte leakage, and malondialdehyde (MDA) accumulation in maize leaf has been analyzed under cold stress. The thiobarbituric acid is the end product of lipid peroxidation reaction that has been used to determine the malondialdehyde (MDA). Cold-induced changes in cell membrane are indicated by the extent of cell membrane lipid peroxidation in plant cell membrane as malondialdehyde (MDA). Membrane stability index (MSI) has been estimated by using fresh leaves (0.1 g) in two sets of 10 cm^3 of double-distilled water. The electrical conductivity has been recorded for both the sets, subjected to 40 °C for 30 min (C1) and at 100 °C for 10 min (C2) and are considered by formula

$$(\mathrm{MSI}) = [1 - (\mathrm{C1}/\mathrm{C2})] \times 100$$

Plant response to stress is accompanied by electrolyte leakage, which is directly related to K^+ efflux from the stressed cell. The electrolytic K^+ efflux is mediated by plasma membrane cation conductance and will result in irreversible loss of K^+ ion from the plant roots under influence of stress response. Cold stress remarkably increases the MDA content and decreases membrane stability index in maize, but inoculation with psychrotrophic bacteria decreased the lipid peroxidation and increases the membrane stability index in maize under cold stress as a decrease in MDA content has been observed (Figs. 10.1 and 10.2). Cell membrane is the first component of plant cell that gets exposed and damaged by cold stress and peroxidation of polyunsaturated fatty acids which takes place resulted in malondialdehyde (MDA) production in the plant cell. So malondialdehyde (MDA) can serve as an important indicator of damage of cell membrane and deterioration of cellular metabolism. The entire physiological and biochemical processes including cell membrane function of the plant get affected due to coexistence of osmotic and cold stress. The altered cell permeability that causes leakage of ions out of the cell indicate massive damage in cell membrane and has been used as an important parameter to analyze the stress tolerance ability of the plant (Jha 2018b).

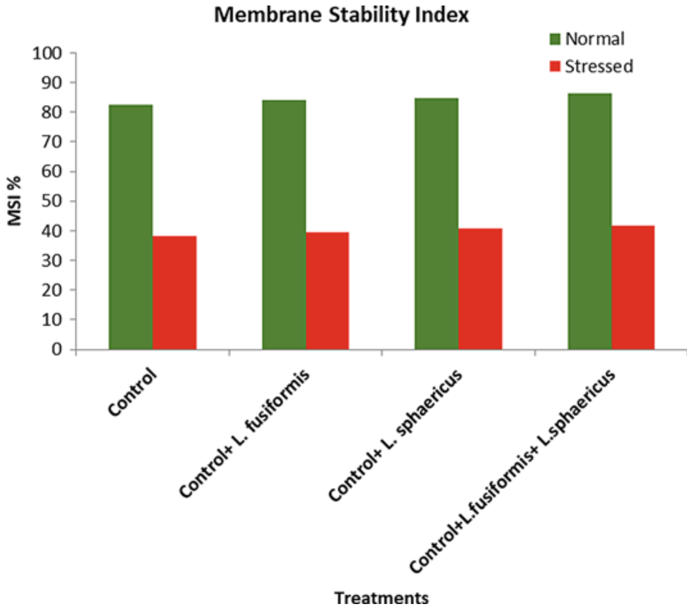

Fig. 10.1 Effect of psychrotrophic bacteria on membrane stability index maize under cold stress ($n = 5$)

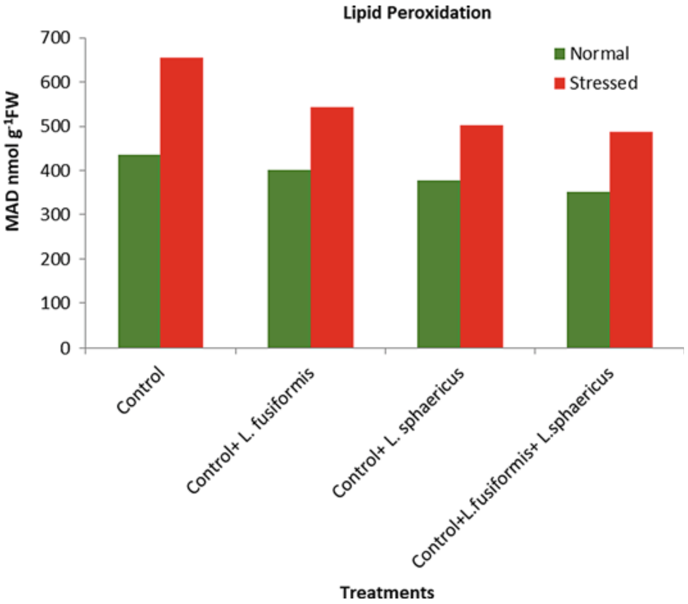

Fig. 10.2 Effect of psychrotrophic bacteria on lipid peroxidation in maize under cold stress ($n = 5$)

10.3.4 Effect of Psychrotrophic Bacteria on Phytohormones Modulation Under Cold Stress

Every living organism including plant has ability to sense the external and internal stimuli and respond accordingly for its proper growth and development (Wolters and Jurgens 2009). Different group of chemical signal molecules produced in very low concentration by the plant to adjudicate the plant responses toward such stimuli is phytohormones, which play a major role in inducing plant acclimatization according to surrounding environments by allocation of nutrient and source/sink transitions to maintain growth its development. However, the phytohormones that are one of the most important endogenous substances have ability to regulate the biochemical, physiological as well as molecular activity of the plant in response to stress. Phytohormones are considered as a critical regulator bio-molecule for the survival of plant under changing environment. Phytohormones like gibberellins, cytokinins, auxin, abscisic acid, jasmonic acid, and ethylene have key function in the elastic growth and development (Yadav 2021).

The psychrotrophic microbes growing optimally at warmer temperatures that have also ability to grow and remain functional at extreme low temperature has its own significant role for agroecosystems at high-altitude. At high-altitude, there are cold conditions having transitional in nature. The plant's root growing in any environment mostly remains crowded by variety of microbes for acquiring nutrient. The association of such microbes promotes the growth of host plant by multiple mechanisms like siderophore production, induction of systemic resistance toward plant pathogen (Jha 2019d), as well as reduced production of ethylene. The psychrotrophic bacteria having ACC demaniase activity facilitate the deamination of the precursor molecule for ethylene production as well as able to produce many other important stimulatory phytohormones in the plant root cell. The phytohormone auxin and cytokinin produced by psychrotrophic bacteria induce denser root hair, which enhance the uptake of mineral nutrients and water from soil.

The pytohormone produced by the plant has a critical role in the growth and development of plant which is of different types having different functions as well as work in different concentrations at different sites (Egamberdieva et al. 2017). The pytohormone like indole acetic acid, gibberellins, cytokinins, indole acetic acid, abscisic acid, and ethylene are accountable for the synchronized corresponding development of plant as per its genetical potential. The pytohormone produced by the plant, helps plant to respond to environmental stimuli by modifying the physiological and metabolic activities for the survival of the plant in response to changes in the environment. Plant hormone like auxin is responsible for root initiation and delayed plant senescence (Jha 2020). Bioactive gibberelline involved stem elongation, flowering, leaf expansion, and plant growth. Cytokinins are basically involved in cell enlargement, cell division and also in nutrient mobilization, chloroplast biogenesis, leaf senescence and regulate stomatal closure under cold stress.

In this study, both the psychrotrophic bacteria have the ability for the auxin and gibberellic acid production in tryptophan containing medium and an increase has been recorded with time (Table 10.4). The plant inoculated with phytohormone producing plant-associated psychrotrophic bacteria can help plant to survive and deal with water scarcity as well as to grow at its full genetic potential in cold stress, by stimulating modification of root architecture for enhanced uptake of mineral nutrient and water. Plant stress hormone like abscisic acid can influence the different processes such as seed dormancy, germination rate, senescence in leaves, and cell division. Critical signaling is carried out by jasmonic acid (JA) for different developmental processes and defense responses, while salicylic acid (SA) is involved in broad range of abiotic stresses. The plant hormone ethylene and Abscisic acid have directly and indirectly involved in a wide range of abiotic stress including cold stress (Jha and Subramanian 2020).

The production of ethylene starts with precursor 1-aminocyclopropane-1-carboxylate (ACC) and the plant hormone ethylene endogenously regulates plant homoeostasis under stress, having detrimental effect on plant growth (Rana et al. 2020). The immediate precursor of ethylene that has been degraded by the enzyme ACC deaminase resulted in reduced level of ethylene in plant. Several psychrotrophic bacteria have the ability for the production of ACC deaminase and are responsible for the degradation and sequestion of plant ACC, to acquire nitrogen and energy for its

Table 10.4 Effect of psychrotrophic bacteria on Auxin, Gibberelline, ACC deaminase, proline and glycine-betaine content of maize under cold stress ($n = 5$)

Treatment	Auxin (μg ml^{-1})	Gibberelline (μg ml^{-1})	ACC deaminase (μg ml^{-1})	Proline (μg mg^{-1} FW)	Glycine-betaine (μ mol g^{-1} FW)
Normal					
No inoculation	0.562^{cd}	0.862^{cd}	0.534^{d}	0.23^{d}	0.876^{cd}
Inoculation with *L. fusiformis*	0.624^{c}	0.915^{ab}	0.574^{cd}	0.28^{c}	0.927^{abc}
Inoculation with *L. sphaericus*	0.647^{ab}	0.978^{bc}	0.634^{ab}	0.33^{ab}	0.989^{ab}
Inoculation with *L. fusiformis* + *L. sphaericus*	0.704^{a}	1.013^{a}	0.686^{a}	0.37^{a}	1.213^{a}
Stressed					
No inoculation	0. 322^{d}	0.624^{cd}	0.762^{a}	0.27^{c}	0.936^{d}
Inoculation with *L. fusiformis*	0.447^{c}	0.656^{c}	0.794^{ab}	0.31^{ab}	0.969^{bc}
Inoculation with *L. sphaericus*	0.463^{b}	0.693^{b}	0.762^{abc}	0.36^{a}	0.983^{b}
Inoculation with *L. fusiformis* + *L. sphaericus*	0.496^{a}	0.711^{a}	0.744^{d}	0.36^{a}	1.017^{a}

For each Parameter, values in columns followed by the same letter are not significantly different at ($P \leq 0.05$)

growth and establishment. The psychrotrophic bacteria reduce the harmful effect of ethylene by degrading the immediate precursor of ethylene and promote plant growth (Jha et al. 2014). Abscisic acid is other important stress phytohormone, which considerably increases in plant under cold stress to develop stress tolerance and to adapt in such stressful condition (Ng et al. 2014; Tiwari et al. 2020). By increasing water influx into roots and decreasing leaves transpiration, abscisic acid is able to alter the turgor pressure. The phytohormones like gibberellic acid, auxin, ACC deaminase, and abscisic acid have been produced by both the isolate in this study. And under continuous stress, the production of abscisic acid and ACC deaminase activity also increases both the isolates (Table 10.4).

10.3.5 Effect of Psychrotrophic Bacteria on Osmotic Stress Management of Plants Under Cold Stress

All stress directly or indirectly reduced the crop yield by 50–80%, depending on the type of crop and stress period. Both biotic and abiotic factors are responsible for different types of stress on the agricultural crops (Subrahmanyam et al. 2020). One of the most important abiotic factors is cold or low temperature and the average minimum temperature over 64% of the total land area on Earth is less than 0 °C (Rihan et al. 2017). SO cold stress adversely affects plant growth and development and decreases crop yields worldwide. Plant growing in such condition may develop a sequence of comprehensive metabolic and physiological events to withstand in cold stress. Plant induce production of protective substances or proteins, such as cold-resistance proteins, soluble sugars, proline and other osmoprotectants to regulate osmotic potential, the stability of cell membranes, turgor pressure, reactive oxygen species (ROS) scavenging and ice crystal formation.

The accumulation of low molecular weight organic compounds to maintain the osmotic pressure of the plant under osmotic stresses is osmoprotectants. It has no net charge at physiological pH, highly soluble and nontoxic even at high concentrations, responsible for maintaining driving gradient for turgor pressure and water uptake. Osmoprotectants not only help in osmotic adjustment, but also having chaperone-like activity, helps in metabolic detoxification and scavenging of reactive oxygen species (ROS) (Jha 2019e). It also plays a major role in stabilizing membranes and proteins during oxidative stress. Osmoprotectants are chemically divided into three groups—quaternary ammonium compounds, amino acids, polyols, and sugars. Chemically osmoprotectants are classified into three category quaternary ammonium compounds (e.g., glycine-betaine), polyols or sugars (mannitol, trehalose, fructans, d-ononito) and amino acids (e.g., Proline). However, in plant accumulation of mannitol, proline and glycine-betaine in cytosol and chloroplast has been commonly reported under osmotic stress, but with increase in stress it has also been reported in the few other organelles. Proline as an organic osmolyte remains widely distributed in plants and act as the most common protection material. Free Proline stabilize cellular structures and maintain osmotic balance in plants under cold stress. For osmotic adjustment in plant under cold stress, proline and betaine are well known compatible solutes that helps in osmotic adjustment for the proper metabolic activity. But some important crops are not able to accumulate osmoprotectants like proline and glycine-betaine due to deficit in the enzymes involved in its biosynthesis cannot withstand such stress (Kour et al. 2020a).

The effect of psychrotrophic bacteria on accumulation of osmoprotectant like glycine-betaine and proline has been studied. The result of the study showed that important crop like maize develop the potential for osmoprotectants like glycine-betaine and proline after getting inoculated with isolated psychrotrophic bacteria (Table 10.4), to promote the survival of plant under stress (Jha 2017a, b). An increase in proline and glycine-betaine content has been reported in the maize plant and the concentration of non-conjugated like glycine-betaine and proline has been remarkably high in the seedling under cold stress. Psychrotrophic bacteria play an essential role to save plant under cold stress by regulating the metabolism to develop tolerance against such stress. With continuous increase in world population and limited agricultural land, its need of the hour to make use of frost covers soil for cultivation by using novel stain of such psychrotrophic bacteria, which play an essential role in improving crop growth under osmotic stress.

10.3.6 Effect of Psychrotrophic Bacteria on ROS Scavenging Activity in Plants Under Cold Stress

Plant growing under cold stress needs improved production of heat for its survival, which is fulfilled by enhanced rate of respiration. Increased respiration directly increases oxygen consumption and generation of a group of free radicals and reactive ions derived from molecular oxygen is known as ROS. Generation of ROS causes alteration of the redox state, cellular oxidative damage and change several metabolic activity by affecting activity of metabolic enzymes (Jha et al. 2014). About one percent of oxygen consumed by the plant is used for the production of ROS in different subcellular loci such as chloroplasts, peroxisomes, and mitochondria. ROS have dual role in plants, i.e., beneficial and harmful according to its concentration. ROS play the role as second messenger for intracellular signaling cascades for regular response of the plant, when generated at low/moderate amount, whereas at concentration it has deleterious effect on surrounding bio-molecules. ROS have multifunctional roles in cell under normal condition, therefore the threshold level of ROS needs to be maintained in the regular cell activity, which needs a tight equilibrium between ROS production and scavenging. And detoxification of excess ROS in plant has been carried out with the help of efficient antioxidative system including enzymic and nonenzymic antioxidants. The enzymatic antioxidants comprise catalase, peroxidase, superoxide dismutase, and nonenzymic antioxidants which include ascorbate, glutathione, carotenoids, tocopherols, and phenolics within the plant cell.

ROS have been generated in both stressed and unstressed cells at diverse locations in cell organelles. The expected leakage of electrons from the electron transport chain of mitochondria, chloroplasts and plasma membranes results in generation of ROS and ROS is also produced as a byproduct of different metabolic activities that take place in different cellular compartments. To avoid oxidative stress production and removal of ROS need to be strictly regulated and when its level exceeds the threshold level that resulted in oxidative stress in that cell. Reactive oxygen when generated in excess amount will randomly react with important bio-molecule of the cell.

The ester linkage between the fatty acid and glycerol and unsaturated (double) bond between two carbon atoms of fatty acid is potential target of ROS attack on the lipid molecules. The plasma membrane of cell contains polyunsaturated fatty acids in its phospholipids that are the common site for attack by ROS. The attack of ROS on proteins may cause modification of proteins directly and indirectly. Direct modification involves modulation of a protein's activity through carbonylation, disulphide bond formation, glutathionylation, and nitrosylation. Indirect modification involves conjugation with breakdown products of peroxidation of fatty acid. The most important bio-molecule DNA is also a potential target for ROS-induced damage in cell and DNA encoded information for the proper functioning of cell. Any alteration in DNA resulted in corresponding change in the information, which seriously affects the cell function and ultimately the organism. Excessive ROS also react with lipid and protein component of cell and cell membrane and affect the inherent properties of cell membrane like protein cross-linking, ion transport, membrane fluidity as well as loss of enzyme activity, inhibition of protein synthesis, which finally resulted in cell death of the stressed plant exposed toward the cold stress.

There is a need of an hour to determining the roles of antioxidant enzymes on the tolerance of cold stress is by determining the response of the antioxidant genes for its up or down-regulation in plant under cold stress. Such response may be due to differential induction of gene responsible for production of enzymes or due to change in the chromosome locus responsible for regulated activity of antioxidant genes or due to physical distinction among the genes of antioxidant enzymes or due to differential response of the multigene of antioxidant enzymes family or due to nucleotide difference ORF in the genes of antioxidant enzymes under cold stress. The function of antioxidant enzymes in cold acclimation biochemically is due to contribution of signal transduction pathway. The excessive ROS generated under cold stress are effectively neutralized by antioxidant enzymes to alleviate cold stress-induced injury in plant. There are several reports on the over-expressing a variety of antioxidant enzymes like catalase, peroxidase, superoxide dismutase which increased the stress tolerance ability of the plant against the abiotic stress and protect various important cell organelle like peroxisomes, chloroplasts, endoplasmic reticulum, plasma membranes and plasma membranes for ROS activity at such site (Jha and Subramanian 2015).

10.4 Conclusion

Cold stress-induced damage of the agriculture crop is not a problem of a particular geographic location, but also persists significantly in temperate regions, which results in remarkable economical loss in throughout the regions. To develop technique for better tolerance against the cold stress in agricultural crop is need of hour to meet the increasing food demand in the existing situation of continuous environmental alteration for the increasing world population. The microbes are the most versatile organism and able to grow in all environmental condition in association with organism growing in that environment. So isolation of indigenous psychrotrophic bacteria is associated with plant having plant growth promotion ability from the stress-affected region, to be used as biological option for sustainable crop production under cold stress is an eco-friendly tool. The vast microbial diversity which is highly promising option for use of competent and favorable soil microbes in the agriculture field is the latest possibility for sustainable organic production, and cold-adapted microbes are concerned a special attention among the agricultural scientist due to their enhanced ability for adaptation toward the low temperature with high plant growth promotion potential.

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Chapter 11
Strategies for Abiotic Stress Management in Plants Through Soil Rhizobacteria

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Abstract Soil is among the most challenging ecosystems for microbiologists in terms of microbial diversity and community size. Prokaryotes are the most abundant organisms in the soil and constitute the largest component of the soil biomass. In their native ecosystem, microorganisms live under different kinds of interactions that decide their survival and functioning. Both positive and negative interactions may operate under natural conditions. While negative interactions are inhibitory for microbial growth and development; positive ones are among the beneficial and sometimes obligatory for the growth of some other microorganisms. Therefore, these soil microbial communities may affect plant growth and development in several ways. They may have a direct or indirect role in plant growth and development through the synthesis of different chemical regulators in the rhizosphere's proximity. Under direct mechanisms, they help the plants in macro/micronutrient uptake as well as by modulating plant hormone levels. Indirectly microbes may boost plant health by declining the detrimental effects of the biotic as well as abiotic stress. Among them,

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understanding the microbe-mediated abiotic stress tolerance mechanisms in plants is one of the major challenges in the field of agricultural research. Abiotic stresses like chilling injury, drought, high temperature, heavy metal toxicity, and salinity pose a major constraint to plant growth and crop production under natural field conditions. Because of the global food demand and limited resources, it becomes essential to generate deeper insights into the stress-alleviating mechanisms and the approaches employed by the plants, so that they can be explored for sustainable agricultural plants.

Keywords Abiotic Stress · Agriculture · Microbes · Omics · Plant

11.1 Introduction

Plant-microbes interactions have been realized of greatest importance by the natural selection of microbial populations most suited to its growth. Since plants of agricultural importance are required to be adopted in diverse agroclimatic zones for sustainable harvest, therefore, it becomes necessary to characterize new bio-inoculants more precisely adopting new and advanced molecular biology and other specified tools (Verma et al. 2017; Yadav 2021). Soil rhizosphere forms the connecting link between plant and microbe interaction. These interactions may be harmful (as in the case of plant-pathogen interaction) or can be beneficial (as in the case of mycorrhiza-plant root interaction) (Suyal et al. 2015a; Tomer et al. 2017; Dash et al. 2019). It is the ecologically most diverse niche in soil profile inhabiting numerous microorganisms (bacteria, fungi, algae, protozoa, nematodes, viruses, and archaea), which significantly influences plant growth (Yadav et al. 2021b). Among all these microorganisms, bacteria are the most abundant microbes found in the rhizosphere and also they have a greater influence on different plant physiological processes, which is termed as beneficial (Tomer et al. 2016; Goel et al. 2017a; Jeyakumar et al. 2020; Kour et al. 2019). It has been reported that the bacterial population is 10–1000 times higher in the rhizosphere as compared to bulk soil because plant root secretes many metabolites (in form of organic acids, sugars, amino acids, vitamins, sterols, phenolics, and plant growth regulators), which serve as nutrients for bacterial growth (Goel et al. 2017b, 2018a; Kumar et al. 2019; Yadav et al. 2020d). Due to the rich availability of nutrients, a healthy competition arises among different bacterial genera for colonizing the root rhizosphere. Not only they help in the uptake of several nutrients from the soil but they also help in plant growth promotion activities by producing several chemicals like hormones, siderophores, antibiotics, bacteriocins, and enzymes. Besides acting as biocontrol agents, these bacteria are also helpful in the alleviation of abiotic stresses (Giri et al. 2015; Joshi et al. 2017; Goel et al. 2018b; Kour et al. 2020c, d).

11.2 Abiotic Stresses in the Plants

In the recent past, several diversified and promising "omics" technologies have emerged that have proved persuasive for elucidating how the plants modify themselves at the molecular level for facing the abiotic stresses. For example, drought is known to impose oxidative stress on the plants that arise from the reactive oxygen species (ROS) formation due to inadequate CO_2. It thus disrupts the photosynthetic machinery of the plants (Kumar et al. 2017; Meena et al. 2017; Kour et al. 2020b; Yadav and Yadav 2018).

11.3 Mitigation of Abiotic Stresses

The plants involve several genes and enzymes to overcome abiotic stress (Tiwari et al. 2021). Conventional breeding approaches are frequently used to transfer the stress-associated genes among the plants. However, alternatively, microorganisms can also be used to improve stress tolerance (Dikilitas et al. 2021; Hesham et al. 2021; Yadav et al. 2021a). Several plant growth-promoting rhizobacteria (PGPR) have been studied for their role to mitigate the abiotic stress. The term plant growth-promoting rhizobacteria (PGPR) defines soil bacteria that colonize the rhizospheric region of plants, living in, on, or near plant tissues that vitalize the growth of the plant by various mechanisms. Although, a plant has rich micro-biodiversity associated with it, supplementing the rhizosphere of crop plants with plant growth-promoting rhizobacteria has shown remarkable improvement in crop health and subsequently its productivity. Since that time, there has been tremendous development in the field of PGPR and numerous microorganisms have been identified that have significant positive effects on various crops (Kumar et al. 2014, 2018; Rajwar et al. 2018; Joshi et al. 2019; Rai et al. 2020).

PGPR affects the health of the plants in two ways. First is the direct association of PGPR with its beneficial effects on the host plant and second is the indirect way of antagonizing plant pathogens. Direct stimulation includes several mechanisms such as the production of 1-aminocyclopropane-1-carboxylate (ACC)-deaminase to reduce ethylene levels in the roots of developing plants; production of regulators which directly enhance the plant growth like auxins, gibberellins, cytokines, and various volatiles; biological nitrogen fixation (symbiotic and non-symbiotic); solubilization of insoluble mineral-like phosphorus and other nutrients (Yadav 2017) (Singh et al. 2020). Rhizospheric microorganisms facilitate the uptake of specific trace elements such as iron by secreting siderophores. Furthermore, several microorganisms are known to alleviate abiotic stress, viz. cold stress in plants (Suyal et al. 2014a, b; Rawat et al. 2019; Yadav et al. 2020b). Biocontrol is the indirect stimulation, which includes antagonistic and inducing plant systemic responses to phytopathogenic microorganisms and interfering in the bacterial Quorum Sensing (QS) systems, etc. (Dash et al. 2019). *Trichoderma* has emerged as a very successful biocontrol agent, which is commercially available and is in wide use (Sharma et al. 2019).

Microorganisms employseveral strategies to mitigate abiotic stresses (Meena et al. 2017). Among them, stimulation of root growth through the production of indole acetic acid (IAA) and/or nitric oxide under drought, nutrient deficiency, and salinity; production of ACC deaminase to reduce plant's ethylene level under stress conditions, and modification in the cell wall and membrane during stress are the most common (Yadav et al. 2020c). A list of abiotic stresses and the microbe-mediated tolerance mechanism is mentioned in Table 11.1.

The beneficial microbes including PGPR and microbial endophytes have been isolated and characterized using culture-based and culture-independent metagenomics techniques. Unculturable microbes for sustainable agriculture have been reviewed in the recent past (Goel et al. 2017b, 2018a). In addition to the rhizosphere microbiome, root and root compartments (Rhizoplane and Endosphere) associated microbes reported having an important role in plant growth development and tolerance to various biotic and abiotic stresses (Goel et al. 2017a, 2018b; Rana et al. 2020; Subrahmanyam et al. 2020).

11.4 Salinity, Alkali Stress, and Acidic Stress

Soil salinity and alkalinity often exist meanwhile because of the complexity of soil property. Salinity stress is an important yield-limiting factor that poses a significant threat to agriculture worldwide. It involves a huge accumulation of salts near the root zone/surroundings, which causes an osmotic effect followed by specific toxicity (Visser et al. 2005; Sharma et al. 2021; Yadav et al. 2020a). It is important to understand the genetic variations that exist in a plant in response to salinity stress and their linked traits are crucial for improving the adaptation of plants to the saline environment (Pareek et al. 2020). Studies have been conducted to identify the key proteins, enzymes, TFs involved in the stress perception and adaptation and found involvement of roles of receptor-like kinases, membrane-bound histidine kinases, calcium channels, aquaporins, and mechano-sensitive phospholipase Cas osmosensors in stress perception (Nongpiur et al. 2020). Microbial communities associated with plants have successfully been applied for enhancing crop production and stress tolerance in the plants (Yang et al. 2009; Yadav and Saxena 2018).

The available report showed the inoculation of rhizospheric and endophytic bacteria can modulate the effect of salt stress. Inoculated *Azospirillum* in maize showed modulation of salt stress by increasing the higher K+ /Na+ ions ratio (Hamidia et al. 2004). Similarly, inoculation of *Bacillus sp.* TW4 to pepper led to aid from osmotic stress (Sziderics et al. 2007). *Arabidopsis thaliana* inoculated with *Micrococcus yunnanensis* and *Paenibacillus yonginensis* showed more abiotic stress tolerance than the uninoculated plants (Sukweenadhi et al. 2015). Recently, the saline-alkaline stress tolerance capability of the plants was found to enhance significantly by *Bacillus licheniformis* and other PGPR. It was concluded that certain signal

Table 11.1 List of various microbial genera reported for their ability to mitigate plant abiotic stresses

S.No	Microbes	Name of the abiotic stresses	Host plant	Mechanism of action for tolerance	Reference
	Bacillus cereus, Serratia sp.	Drought	Cucumber (*Cucumis sativa*)	Production of monodehydroascorbate, proline, and antioxidant enzyme, expression of genes	Wang et al. (2012)
	Burkholderia phytofirman	Drought	*Wheat* (*Triticum aestivum L.*)	Increase in mineral contents and reduction of oxidative stress	Naveed et al. (2014)
	Azotobacter chroococcum	Drought	Tomato (*Solanum lycopersicum*)	Increased nutrient availability and enhanced water retention	Viscardi et al. (2016)
	Sinorhizobium medicae	Drought	*Medicago* (*Medicago truncatula*)	Root nodulation and nutrient acquisition of nutrient during drought stress	Staudinger et al. (2016)
	Pseudomonas putida	Drought	Chickpea (*Cicer arietinum* L.)	Osmolyte accumulation, ROS scavenging ability, and stress-responsive gene expressions	Tiwari et al. (2016)
	Pseudomonas fluorescens	Drought	Foxtail millet (*Setaria italic* L.)	Improved seed germination and seedling growth	Niu et al. (2018)
	Bacillus amyloliquefaciens and *Pseudomonas aeruginosa*	Drought	Pepper (*Capsicum annum* L.)	Increased nutrient uptake, chlorophyll content, and biomass production	Gupta et al. (2019)
	Pseudomonas koreensis	Salt	Soybean (*Glycine max* L.)	Increasing level of potassium ion and decreasing level of sodium ions	Kasotia et al. (2015)

(continued)

Table 11.1 (continued)

S.No	Microbes	Name of the abiotic stresses	Host plant	Mechanism of action for tolerance	Reference
	Pseudomonas simiae	Salt	Soybean (*Glycine max* L.)	Improving seed germination and production of quinoline	Vaishnav et al. (2016)
	Microbacterium oleivorans, Brevibacterium iodinum, Rhizobium massiliae	Salt	Pepper (*Capsicum annum* L)	By Increase in plant height, fresh weight, dry weight, and total chlorophyll content	Hahm et al. (2017)
	Arthrobacter woluwensis, Microbacterium oxydans, Bacillus megaterium	Salinity	Soybean (*Glycine max* L.)	Increased production of IAA, gibberellin, and siderophores and increased phosphate solubilization	Khan et al. (2019)
	Azospirillum brasilence and *Bacillus amyloliquefaciens*	Heat	*Wheat* (*Triticum aestivum* L.)	Activation of heat shock TFs and modifying metabolome andROS	Timmusk et al. (2014)
	Burkholderia phytofirmans	Cold	Grape (*Vitis vinifera* L.)	By Modulating carbohydrate metabolism	Fernandez et al. (2012)
	Pseudomonas sp	Chilling	Tomato (*Solanum lycopersicum*Mill.)	Activation of their antioxidant capacity	Subramanian et al. (2015)
	Glomus intraradices	Osmotic stress	Common bean(*Phaseolus vulgaris*)	increased active solute transport through roots	Aroca et al. (2007)
	Bacillus megaterium	Osmotic stress	Maize (*Zea mays*)	Increased root expression, High hydraulic conductance	Marulanda et al. (2010)
	Pseudomonas brassicacearum	Zn toxicity	Mustard (*Brassica juncea*)	Metal-chelating molecules IAA	Adediran et al. (2016)

(continued)

Table 11.1 (continued)

S.No	Microbes	Name of the abiotic stresses	Host plant	Mechanism of action for tolerance	Reference
	Staphylococcus arlettae	Arsenic toxicity	Mustard (*Brassica juncea*)	Increased soil dehydrogenase, phosphatase, and available phosphorus	Srivastava et al. (2013)

transduction pathways of the plants helped them to adapt to adverse conditions (Zhou et al. 2017).

11.5 Drought Stress

Drought causes accumulation of ROS, which leads to oxidative damage in plants. Furthermore, it may reduce the crop yield and causes monetary losses to the farmers. Rhizospheric microorganisms have shown a great potential to reduce drought stress in plants. As plant health is associated with the diversity and community structure of the phytobiome (Berg et al. 2017), the strong root microbiome under drought stress will have significant consequences on plant health (Kour and Yadav 2020). It has been observed that Gram-positive to Gram-negative bacteria ratio is likely to increase during drought stress (Chodak et al. 2015). Further, Fuchslueger et al. (2014) have analyzed the effect of drought stress on soil microorganisms and plants. Inoculated plants have shown enhanced growth and development. The term “microbe-mediated Induced Systemic Tolerance (MIST)” can be used to reveal the chemical and physical changes in the plants which have been induced by the microorganisms under drought tolerance. Further, the production of phytohormones, viz. abscisic acid (ABA), ACC deaminase, cytokinins, and indole-3-acetic acid (IAA) also contribute to stress tolerance. 1-aminocyclopropane-1-carboxylate (ACC) deaminase-producing microorganisms can regulate plant ethylene levels and thus offer drought stress tolerance to the plants (Raghuwanshi and Prasad 2018). This enzyme hydrolyzes the 1-aminocyclopropane-1-carboxylic acid (ACC), which is a precursor of ethylene in the plants (Raghuwanshi and Prasad 2018; Kour et al. 2018). Furthermore, this activity can ameliorate the harmful effects of ROS(Ojuederie et al. 2019). *Achromobacter piechaudii* was found to produce ACC deaminase to alleviate the effect of oxidative stress on tomato and pepper crops (Mayak et al. 2004). Similarly, inoculation of *Bacillus* spp. and *Enterobacter* spp. significantly enhanced the drought stress tolerance by reducing the accumulation of ACC in *Mucuna* plants (Saleem et al. 2018).

Another term “RIDER” (rhizobacteria-induced drought endurance and resilience) can also be used to represent the morphological, biochemical, physiological, and molecular adaptations to produce the stress alleviation associated antioxidants, enzymes, and the proteins to survive under stress conditions (Gupta et al. 2019; Kour et al. 2020a). Microbes-mediated alleviation of drought stress have been reported in several crops. Vurukonda et al. (2016) reported that the PGPR inoculated crops under stressed conditions have produced higher biomass, proline, free amino acid, and sugars. Similarly, in soybean crops, *Pseudomonas putida* inoculation has enhanced plant growth and development by alleviating drought stress (Kang et al. 2014). Bacterial mediated adaptation of plants to drought tolerance has been studied at the molecular level and by overexpressing bacterial polysaccharide synthesis (EPS) gene of *Rhizobium* sps in sunflower (Alami et al. 2000) and trehalose-6-phosphate synthase in rhizobia in common bean (Suárez et al. 2008) showed enhanced tolerance to drought stress.

11.6 Cold Stress

Cold is a major class of physical stress that influences most of the parameters of a living cell including enzyme kinetics, macromolecular interactions, membrane fluidity, and solute diffusion rates.

11.6.1 Mechanisms of Bacterial Cold Adaptations

Adaptations in bacteria refer to the evolution of the molecular mechanisms to carry out the vital processes of life under the changing physiochemical conditions as consequences of environmental stress. Microorganisms growing in extreme habitats are equipped with long-term adaptations and are so adapted to the environment that those cannot grow without a stressed environment. Bacteria also have to evolve for the other additional stresses which are associated with low temperature.

Cold stress affects the stability of the secondary structure of nucleic acid hence affecting the vital process of transcription, translation, and RNA degradation (Suyal et al. 2018, 2019b). During this cold stress, bacteria modify their cellular physiology and biochemistry. Low temperature triggers the cold shock response in which bacteria adapt to the cold stress (Kumar et al. 2020; Suyal et al. 2021; Yadav et al. 2017). During the initial cold response, growth arrest is observed for 3–6 h. This phase of growth arrest is termed as the acclimation phase, where only the cold-inducible proteins (CIPs) are expressed and the rest of the protein expression is downregulated. After the acclimation phase, the cell down-regulates the expression of cold-inducible proteins, resumes the expression of the other proteins and starts dividing normally.

CIPs prevent secondary structure formation and facilitate the degradation of structural RNA. Among the CIPs, some proteins from the small acidic protein family of 7.4 kDa are most strongly induced under cold stress and are termed as cold shock proteins (CSPs). CSPs bind to only single-stranded RNA or DNA and not to the double-stranded conformation. All CSPs have nucleic acid binding domains termed as cold shock domain (CSD), which facilitates their binding to the nucleic acid (Phadtare and Inouye 2008). Binding of CSPs to RNA maintains the single-stranded conformations thus protecting the cell from cold-induced secondary structure formation. In mesophilic organisms, CSPs are transiently induced during cold shock and soon after the acclimatization, their expression is downregulated (Hebraud and Potier 1999). However, in psychrophiles, they are constitutively expressed and act as cold adaptive proteins (CAPs) (D'Amico et al. 2006).

Induction of the CSP expression in bacteria under cold stress is complex and does not have a specific sigma factor as present in other types of stress adaptations.

Immediate expression of the CIPs due to cold response is based on the selective ability of CIPs mRNA to change the conformation under low temperature so that they are accessible to translational machinery. The most commonly studied CSP is the Csp A, which is the major protein formed under cold acclimatization. It is reported that about 13% of the total cell proteins under cold stress is Csp A (Barria et al. 2013). At a temperature of more than 15 °C cspA, mRNA has the conformation which is not translated and easily recognized by the cellular RNA degrading machinery. However, at 15 °C and lower temperature, cspA 5' untranslated region (5'UTR) undergoes the structural rearrangements and escapes the cellular RNA degradation mechanism and gains accessibility to the translation by exposing the translation initiation region (Barria et al. 2013).

Moreover, all psychrophilic microorganisms do not have CSPs. Antarctic psychrophilic archaea, Methanococcoides burtonii, have small RNA chaperones proteins that were found to be upregulated under cold stress (Cavicchioli et al. 2000). These RNA chaperones function similarly to the CSPs and have nucleic acid binding TRAM domain instead of the CSD domain (Williams et al. 2009). Thus, these RNA chaperones are referred to as Ctr (cold-responsive TRAM domain) proteins which are major cold adaptive proteins in psychrophilic archaea (Zhang et al. 2017).

Further production of antifreeze proteins (AFPs) and accumulation of compounds that inhibit ice-crystallization are other means of cold adaptation in bacteria (Gilbert et al. 2004). AFPs are a diverse group of proteins with the ability to modify ice-crystals via Van der Waals interactions and/or hydrogen bonds. During cold acclimatization, many psychrophiles are known to accumulate antifreeze proteins. Moreover, the bacterium survived freezing temperatures ranging from −20 °C to −50 °C and could secrete an antifreeze protein into the growth medium at 5 °C.

11.6.2 Membrane Adaptation in Psychrophiles

Membrane permeability and fluidity both are reported to decrease at low temperatures. In response to the low-temperature elastic liquid, cell membrane turns into a rigid gel-phased state which influences the membrane transport and several other functions negatively (Phadtare 2004). Dysregulations of the membrane proteins were reported soon after the exposure to the low temperature, suggesting the role of membrane proteins in sensing the cold stress (Shivaji and Prakash 2010). Further, low temperature causes the phase separation of the phospholipids in the cell membrane which increases the membrane permeability and decreases membrane fluidity. The lipids of psychrophilic bacteria contain polyunsaturated fatty acids or other long-chain hydrocarbons with multiple double bonds. These fatty acids remain more flexible at low temperature than saturated or monounsaturated fatty acids (Allen et al. 2009). Bacteria increases the unsaturation of lipids in their cell membrane by the biosynthesis of unsaturated fatty acids or by decreasing the pre-existing saturated fatty acids. Several-fold overexpression of the desaturase gene has been reported in *Exiguobacterium sibiricum* (Rodrigues et al. 2008). The high proportion of unsaturated fatty acid has been documented previously in *Colwellia, Marinomonas, Moritella*, *Psychromonas*, and *Shewanella* (Margesin and Miteva 2011). Carty et al. (1999) observed the increase in unsaturated palmitoleate over laurate under cold stress. In M. burtonii, desaturase is absent hence in this bacterium lipid biosynthesis is altered under the cold stress resulting in fewer saturated isoprenoid lipids.

11.6.3 Transcription and RNA Degradation/stabilization Under Cold Stress

The majority of the CIPs are involved in the metabolism of RNA, which regulates the stability of RNA and transcription process. Differential expression of the CIPs under cold stress is due to the low-temperature-induced negative supercoiling of the DNA. This induction is the result of the activity of histone-like HU protein (HupB) and gyrase (GyrA). Exogenous expression of the DNA gyrase inhibitors showed the decreased expression of the CIPs (Prakash et al. 2009). However, how HupB and gyrase GyrA sense the low temperature is least explored. CSPs were also reported in the maintenance of chromosome structure (Chaikam and Karlson 2010).

Low-temperature-induced RNA metabolism up-regulates the expression of nucleic acid chaperones. CspA and CspE act as transcription anti-termination by inhibiting the RNA hairpin formation thus preventing premature termination (Barria et al. 2013). Similarly, NusA is reported to function as an anti-terminator under cold stress (Li et al. 2013). Transcription factor RpoS, a stress-induced protein was also reported to regulate the gene expression under cold temperatures (White et al. 2008). Small RNA-binding proteins (Rbps) are the other class of CIPs other than CSPs, which help in cold adaptation and majorly found in cold-adapted cyanobacteria and rare in bacteria**.** Rbps have a single glycine-rich RNA-binding motif, which is previously reported to regulate the transcription terminations. Osmotic stress and cold stress both reduce the availability of free water thus Rbps are expressed in both stresses.

Under cold stress, RNA degrading enzymes are upregulated in psychrophilic bacteria. Previously, overexpression of RNases was reported in the psychrophilic bacteria *Psychrobacter arcticus* and *Methanococcoides burtonii* were isolated from the permafrost environment (Allen et al. 2009). This strategy conserves the biosynthetic precursors and also functions as quality control for the degradations of irreparably damaged RNA and proteins.

Several cold-induced proteins are molecular chaperones that are inevitable for the stability of mRNA under low temperatures. Csp A is a major chaperone that maintains the mRNA in linear form thus facilitating RNA degradation through ribonucleases. However, Csp E works exactly the opposite of the CspA, thus protecting the RNA from degradation (Van Assche et al. 2015). CspE has been reported to bind to the

RNA and interfering with the degradation by PNPase and RNA internal cleavage by RNase E. Previously, ATP-dependent DEAD-box RNA helicases (DeaD) were reported to unwind the secondary structure of RNA formed under low temperature, which then, in turn, is further degraded by the PNPase and RNase R exoribonuclease (Bernstein et al. 2004). DEAD-box helicase (DeaD) of E. coli has been studied to be incorporated in the degradosome complex under cold stress (Iost and Dreyfus 2006). Under in vitro studies, DeaD was reported to interact with the CspE. Thus both DeaD and Csp E work together in association. Further, DeaD was also reported to have helicase activity and shown to affect the ribosome maturation under cold stress. In vivo deletion of the DeaD leads to the depletion of the 50S ribosomal subunit thus affecting the ribosomal turnover.

Under cold stress, PNPase increases twofold in the cell and plays a crucial role in cell survival. PNPase inhibits the expression of the CSPs soon after the cold acclimatization phase. The high concentration of Csps was found even after the acclimatization phase in the mutants lacking PNPase and DeaD helicase. These findings suggested the Csp mRNA degradation functions of these proteins. Moreover, RNase R exoribonuclease is the only ribonuclease of *E. coli* that can complement the DeaD deletion phenotype. This is the only ribonuclease in *E coli* without the helicase activity which can degrade the secondary structure of RNA. The cold shock domain of the RNaseR assists in the unwinding of the secondary structure of the RNA. Thus RNase R is important for the degradation of the secondary structure of RNA under cold temperature.

11.6.4 Translational Regulations Under Cold Stress

Low temperature inhibits the translation of protein except for the cold-inducible proteins. This block on translation is induced through the binding of Py protein to the 30S subunit of ribosomes. Thus ribosomal units remain sequestered with the Py proteins and the functional ribosomes capable of forming 70S initiation complex decrease.

Further, temperature-induced secondary structure formation in the mRNA hides the Shine Dalgarno sequence on the mRNA, thus negatively affecting the translation process. However, under the cold shock response, IF3 stimulates the translation of only cold shock mRNA with the help of IF1. IF3 preferentially stimulates cold shock mRNA translation and IF1 enhances the effect of IF3 without influencing translational specificity. Besides this, IF3 is also reported to have some role incorrect protein folding. The evolution of this mechanism is the basic requirement for cold adaptation.

Under cold stress stability of tRNA is one of the major factors determining the rate of translation. Dihydrouridine is reported to enhance the flexibility and stability of tRNA in some cold-adapted archaea and bacteria (Saunders et al. 2003). Further, trigger factor (TF), assists in cotranslational protein folding, which is evident by the fact that *E. coli* cells overexpressing this protein are more resistant to cold stress than the TF mutants (Castanie et al. 2014).

11.6.5 Protein Adaptation to the Cold

Proteins from psychrophilic microorganisms have higher activity in cold temperatures compared to the mesophilic and thermophilic homologs (Siddiqui and Cavicchioli 2006). Psychrophilic organisms exhibit a wide range of adaptations (Yadav et al. 2019). They contain cold-active enzymes that show greater amounts of α-helix and lesser amounts of β-sheet secondary structure than mesophilic counterpart because β-sheet secondary structures tend to be more rigid than α-helices. The greater α-helix content of cold-active enzymes provides greater flexibility for catalyzing the biochemical reactions at cold temperatures.

To retain the functional enzyme activity at low-temperature psychrophilic enzymes have a specific amino acid composition, which leads to the different secondary, tertiary, and quaternary structural properties (Saunders et al. 2003). Cold-active enzymes contain more polar amino acids, lesser hydrophobic amino acid, lower arginine/lysine ratio, weaker interdomain and intersubunit interactions, more and longer loops, decreased secondary structure content, more glycine residues, fewer prolines in loops, more prolines in α-helices, fewer and weaker metal-binding sites, fewer disulfide bridges, fewer electrostatic interactions (H-bonds, salt bridges, cation-pi interactions and aromatic-aromatic interactions than their mesophilic and thermophilic counterparts. Proteins of psychrophilic archaea contain more noncharged polar amino acids (especially Gln and Thr), lesser hydrophobic amino acids (particularly Leu) and increased exposure to hydrophobic residues (Siddiqui and Cavicchioli 2006).

11.7 Heavy Metal Stress

Rhizoremediation is a process where degradation of hazardous pollutants occurs by bacteria surrounding the rhizosphere plant roots (Kingsley et al. 1994). It is a natural process but it can also be improved by cautious manipulation of the rhizosphere which can be accomplished by using suitable plant–microbe pairs (Mackova et al. 2006), which in turn supplement to phytoremediation process (Kuiper et al. 2004; Kumar et al. 2019). Rhizoremediatioin also represents an interactive consortium between plant and rhizobacteria which comprises two important processes, i.e., phytostimulation and photodegradation. A successful rhizoremediation process is the resultant of various factors like plant age, chemical stress in soil (Yee et al. 1998), the composition of root exudates containing organic photosynthates as the carbon source for the microbe. Among these, alcohols, amino acids, sugars, proteins, organic acids, nucleotides, flavanones, phenolic compounds, certain enzymes are good examples

(Kuiper et al. 2004; Pilon-Smits 2005**),** which ultimately affect the metabolic activities of rhizospheric microbes. These plant-produced carbon compounds are utilized by microbes to maintain plant nutrient recycling, resistance against plant microbial diseases, and tolerate toxic compounds.

Though the associative roles of rhizospheric microflora on the enhancement of different metal uptake by plants have been reported in past decades, the detailed mechanism of selective metal reclamation is still unclear. In the verge of finding possible mechanism underlying heavy metal such as arsenic (As) tolerance, detoxification, and accumulation, different ecotypes of *Pterisvittata*, a hyperaccumulator fern has been studied (Lei et al. 2012; Wang et al. 2012). Small biomass and slow growth rates of such hyperaccumulating plants made the scientific community to come up with an alternative heavy metal bioremediation process by exploiting the mutualistic symbiosis between rhizobium and legume (Carrasco et al. 2005), which can equally effective in restoring heavy-metal-contaminated sites (Teng et al. 2015) as well as cost-efficient (Checcucci et al. 2017).

International Agency for Research on Cancer (IARC) and the US Environmental Protection Agency (EPA) have declared arsenic as a toxic carcinogenic metalloid. The two major plants acceptable inorganic form of arsenic are the reduced form, arsenite (As^{3+}), and the oxidized form, arsenate (As^{5+}) (Cullen and Reimer 1989). Rhizobacteria-mediated chemical and microbial transformation of the two forms of arsenic (Han et al. 2017) results in arsenic accumulation in plants (Jia et al. 2014), which affects the bioavailability of the As in the rhizospheric soil, translocation in the plants (Shrivastava et al. 2016) and consequently As phytotoxicity (Sarkar et al. 2016).

Plant growth-promoting (PGP) bacteria secrete substances like siderophores, phytochelatins, and many other compounds which may hinder metal availability and complex formation by binding them with their anionic functional groups (Tomer et al. 2016) thus, attracting researchers to study the effect of the association between PGP bacteria and plant to alleviate metal toxicity (Kong and Glick 2017). Arsenic an example of which Guarino and Sciarrillo (2017) experimented by taking *Acacia saligna* along with rhizospheric bacteria which aided the phytostabilization of heavy metals in the roots of *Eucalyptus camaldulensis*. The results reported by Sun et al. (2017) regarding the microbe-assisted phytoremediation i.e., rhizoremediation was astonishingly higher than either of phytoremediation and microbial bioremediation alone which also influenced soil fertility positively due to enzymatic exchanges that took place between the plant and microbes. The increasing phytoextraction and phytostabilization resulted from this association between plant and plant-surrounded rhizobial population allowed the plants to thrive on metal contaminated soils (Kong and Glick 2017) by trace metal mobility and availability to the plants (Idris et al. 2004). Bacterial responses to metal ions such as biosorption, precipitation, and enzymatic metal transformation replaced traditional remediation methods that do not provide acceptable environmental restoration for the removal of metals from soils.

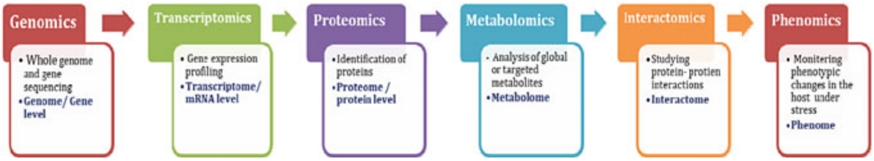

Fig. 11.1 Multi-omics approaches for addressing the impact of abiotic stresses on host and their mitigation strategies using microbial approaches

11.8 Omics Strategies

The "omics" approaches, viz. genomics and metagenomics, transcriptomics and metatranscritomics, proteomics and metaproteomics, metabolomics, and phenomics help to unravel the interactions of the microorganisms with the plants. Moreover, they are useful in real-time monitoring of the cellular processes. Nowadays, next-generation sequencing technologies are contributing to these studies (Kumar et al. 2019). The description of some omics approaches is given in Fig. 11.1.

11.9 Genomics and Metagenomics

The genomics and metagenomics facilitate detailed studies of microbial diversity and community structure. However, the majority of the microorganisms on the planet Earth are unculturable. In any environmental sample only 1–2% of microorganisms can be cultivated in the laboratory; the remaining 98–99% of the microorganisms cannot be cultivated by routine cultivation techniques and referred to as unculturable (Soni et al. 2016; Suyal et al. 2019a, c). Microbial diversity can be measured using techniques such as traditional plate counting and direct counting, molecular-based methods, and fatty acid analysis. However, the culture-dependent methods are not a good choice for the analysis of microbial diversity, because only 1–2% of the bacterial diversity in soil can be recovered by plate counting. To circumvent the problems of the genomics approaches, the culture-independent methods, especially metagenomics can be employed for understanding the diversity, population structure, and ecological roles of unculturable microorganisms in detail. The groundbreaking work of Carl Woese, which reported the 16S rRNA genes as evolutionary chronometers, created a new branch of microbial ecology referred to as metagenomics. Sequencing of the 16S rRNA gene started the new era of microbiology as even the unculturable microorganisms could be identified through metagenomics without culturing them (Suyal et al. 2015a, b).

"Metagenomics" is defined as the functional and sequence-based analysis of the collective microbial genomes present in an environmental sample (Handelsman 2004). Different environments including soil, fresh and marine aquatic habitats, feces, oral cavity, rumen, glacier ice and cold deserts have been the focus of the metagenomics (Kodzius and Gojobori 2015; Soni et al. 2016; Suyal et al. 2019a). With the development in the sequencing facilities and enormous potential of the technique, hardly any ecosystem is left within the human access which is not studied through metagenomics. Thus, metagenomics has enormous potential in microbial diversity analysis, which helps to answer the fundamental questions of microbial ecology.

Metagenomics plays a vital role in agriculture. The microbial communities in the soil are responsible for the health of plants and thus make a direct impact on yield. The manipulation by selecting the ideal combination of the microbes and crops will help to increase the yield parameter. Further, metagenomics studies on different phosphate solubilizers (Rajwar et al. 2018) and nitrogen fixer and siderophore producers (Joshi et al. 2019) and other microbial communities take part in biogeochemical cycling also seem to be very productive about microbial ecology and ecosystems.

Although metagenomics has the prospective to generate marvelous amounts of information, and this information needs to be decoded by bioinformatics explanation. Of course, recovered sequence information is made available via public databases, but this is often in a less useful form than the original datasets. Opening up metagenomic datasets for examination by a large group of researchers, whose interests span a greater breadth of microbial functions, seems to be a fairly easy step that could greatly amplify the understanding gleaned from large-scale metagenomics initiatives. Recent studies have been reported to use Metagenomics approaches in analyzing microbial diversity and functions (Kumar et al. 2019).

11.10 Transcriptomics

Transcriptomics can be defined as the analysis of the transcriptome, that is, the transcripts produced by the genome under a given set of conditions. This technique has shown a high potential to identify the patterns of gene expression by a cell under two different conditions. Wang et al. (2012) have used this approach to understand the role of *Rhizobium* in drought tolerance in different crops. Similarly, transcriptomics of *Stenotrophomonas rhizophila* has identified a plant growth regulator spermidine during abiotic stress tolerance (Alavi et al. 2013). Further, Mark et al. (2005) have shown the influence of sugar beet exudates on *Pseudomonas aeruginosa* transcriptome. One important attribute is response traits that define an organism's response towards the environment fluctuation and is measured across the environments. Furthermore, Defez et al. (2016) have performed next-generation RNAsequencing studies on *Sinorhizobium meliloti* and revealed that the abiotic stresses induces the IAA overproduction in the cells.

11.11 Proteomics

All the protein complements expressed in a cell under certain physiological conditions at a particular time are referred to as the proteome. The proteome is much more complex than the transcriptome and genome. The comprehensive analysis of expressed proteins from a cell, a multicellular system, an extracellular environment, and/or a large set of recombinant clones IS known as proteomics. Traditional techniques of proteome analysis were complex, less sensitive, and time-consuming. Presently mass-spectrometry-based proteomics is high throughput and widely used for the complete protein characterization (Suyal et al. 2014b, 2017). Thus, high-throughput proteomics deals with the protein characterization with reduced time and with increasing depth of proteome coverage. Proteomics is an excellent methodology for a better understanding of the regulation of biological systems by identifying several proteins as a signal of changes in physiological status due to stress or elements/factors responsible for stress alleviation (Soni et al. 2016). Mass spectrometry has emerged as one of the most sensitive tools for protein characterization, quantification, and post-transcriptional modification (PTM) studies (Suyal et al. 2018, 2019b). The development of mass spectrometers that can ionize and precisely determine the mass of peptides is what made it possible to link proteins with genome data. Traditionally, the characterization of proteins in the complex samples was done through the protein separation in two-dimensional polyacrylamide gel electrophoresis (2D PAGE) followed by the identification of the protein spots through mass spectrometric techniques (Soni et al. 2016; Kumar et al. 2017). However, this method is labor-intensive, time-consuming, and has poor resolution, thus not suitable for the high-throughput analysis. Further, proteins expressed in a very low amount cannot be detected by 2D PAGE, thus their identification remains obscure through traditional techniques of proteome analysis. Online linking of liquid chromatography to mass spectrometer provides a high-throughput solution for protein characterization. In high-throughput LC–MS technique, the power of liquid chromatography (LC) provides a better separation of thousands of proteins in a complex sample, whereas the mass spectrometer provides the subsequent protein identification with higher sensitivity and precision (Suyal et al. 2018, 2019b).

Several previous studies documented the bacterial cold adaptation through the proteomics approaches (Williams et al. 2009; Suyal et al. 2014b, 2019b). The proteome of several cold-adapted PGPR has been analyzed, viz. *Pseudomonas migulae* S10724 (Suyal et al. 2014b); *Pseudomonas palleroniana* N26 (Soni et al. 2015; Suyal et al. 2018); *Dyadobacter psychrophilus* B2 (Suyal et al. 2017); *Pseudomonas jessenii* MP1 (Suyal et al. 2017), and *Rhodococcus qingshengii* S10107 (Suyal et al. 2019b) under cold stressed conditions. Moreover, high-throughput proteomics has been widely used for the biomarker development of the various biological pathways (Lu et al. 2016; Suyal et al. 2019b). However, very few high-throughput proteomics studies were conducted on the psychrophilic bacteria, previously. Therefore, the comparative proteomic study of the psychrophilic bacteria could reveal the novel cold-adapted proteins expressed under cold stresses.

Environmental proteomics or metaproteomics is a special tool for the analysis of the structure and function of the proteins associated with the plant–microbe interactions that are directly extracted from the environment. It might be useful in the comparative protein analysis of the stressed as well as non-stressed plants. Furthermore, it may be explored to unravel the microbial metabolism, enzymes, metabolic pathways, and protein networking involved in signal transduction (Wang et al. 2012). The proteins of *Piriformospora indica* associated with drought stress by higher antioxidant production in barley were analyzed (Ghabooli et al. 2013). Further, the elucidation of the proteins expressed during the association with the diazotroph *Gluconacetobacter diazotrophicus* and sugarcane under drought stress revealed that bacterial inoculation was able to activate the signaling genes and confer drought resistance in sugar cane (Vargas et al. 2014). Nevertheless, Heyer et al. (2013) have conducted metaproteome analysis for revealing the mechanisms of microbial functioning in the biogas plants.

11.12 Metabolomics

Metabolomics is the identification and characterization of the metabolites produced by the organism under a particular set of conditions. Plant–microbe-soil interactions involve the exchange of chemical compounds for metabolism, signaling, and symbiosis. Therefore, metabolomics becomes an important research tool to characterize the metabolites and their mechanisms involved in plant growth promotion and development under abiotic stresses (Jorge et al. 2016). This branch of science explores different analytical techniques, viz. chromatography, mass spectrometry, and spectroscopy to generate a profile of the metabolites under given conditions. This technique also quantifies the abundance of the metabolites and thus can be useful in diagnosing plant diseases also. Moreover, it also offers an excellent way to characterize the novel metabolites. Abiotic stress may alter the metabolism of the living organisms, which further results in a change in the secretion pattern of metabolites. Metabolomics can also be used with metagenomics to predict the functions of the genes. Contreras-Cornejo et al. (2009) have showed that *Trichoderma* spp. produces auxins under stressed conditions and helps in plant growth promotion. Recently, Kang et al. (2019) have explored metabolomics to characterize the metabolic behavior and physiological changes in the wheat genotypes under drought stress conditions.

11.13 Phenomics

Phenomics is a documentation of phenotypic variation within an organism in response to a given condition. It is the result of the interactions among different genetic/genotypic elements of the organism with the environmental factors, viz.

developmental stages, temperature, salinity, drought water, or nutrient limitation. It is an important tool to unravel the interactions among the organisms that can be explored for crop management. Novel imaging techniques and their advancements have made it possible to analyze several phenotypic traits. Hassani et al. (2018) have discussed the significance of phenomics in correlating microbial communities and plant health. Moreover, Rouphael et al. (2018) have developed high-throughput phenotyping to characterize the effect of bio-inoculants. However, phenomics needs lots of advancements in terms of high-throughput and high-dimensional technologies to employ it at a global scale.

11.14 Conclusion

Multi-omics strategies can be explored to address the challenges that arises due to abiotic stresses in the plants. Moreover, keeping in mind the sustainability issues, microbial applications are financially savvy, renewable, and globally recommended. This chapter besides providing an insight into the various stresses, gives an overview of the role of omics technologies in abiotic stress tolerance. Further, the identification and characterization of stress-tolerant bio-inoculants will remain the priority to achieve agricultural sustainability under stress conditions.

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Chapter 12
The Omics Strategies for Abiotic Stress Responses and Microbe-Mediated Mitigation in Plants

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Jagadish Jena, and Tanmoy Shankar**

Abstract An abundance of metabolomics information on the plant stress reactions has been collected and countless metabolic pathways are proposed to be directed in different abiotic stresses. Be that as it may, there are fewer evidences that metabolites and pathways tentatively demonstrated to work in abiotic stress resilience. A profile of metabolites doesn't predict precisely whether there is any related metabolic pathway which can be upregulated or downregulated since both the responses can prompt the buildup of a metabolite. Those may be illuminated by contrasting the information on the metabolomics that can be derived from either transcriptomic or proteomic or both investigation and exercises of explicit proteins. Quality to metabolite administrative systems of glucosinolate blend and essential digestion under sulfur-and nitrogen-restricted conditions were likewise finished up. Furthermore, the guidelines of the information on the omics pathway in different abiotic stresses have been summerized. The examinations utilizing proteomics along with secretomics and metabolomics are moderately uncommon in the reaction field of plant stress. A portion of the varieties communicated as alterations of cytogenetical and phenotypical in plants was recovered from the culture by callus tissue. Cell culture and tissue culture conditions can limit or boost the degree of somaclonal varieties. Throughout the years, numerous varieties as changes in the genomes of plants have been normally advanced.

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12.1 Introduction

Plants are considered to biosynthesize specific (customarily called auxiliary) metabolites to adjust to ecological burdens, for example, biotic and abiotic stresses. Most specific metabolites incited by abiotic stress typically display antioxidative action in vitro, but their capacity in vivo is to a great extent yet to be affirmed (Yadav et al. 2020b). In this chapter, the late advances in the distinguishing proof of the job of abiotic stress-responsive particular metabolites with an accentuation on flavonoids have been featured. Coordinated "omics" examination, focused on metabolomics with a progression of plant assets varying in their flavonoid aggregation, indicated tentatively that flavonoids assumed a significant job in antioxidation in vivo. Moreover, the outcomes additionally recommend the job of flavonoids in the vacuole. To get more inside and out bits of knowledge, compound and organic provokes should be tended to for the recognizable proof of obscure specific metabolites and their in vivo works. Natural stresses, for example, biotic and abiotic are not kidding dangers to agricultural crops (Lobell et al. 2014).

Most outstandingly abiotic stresses are dry spell, saltiness, cool, high light/UV-B, heat, air contamination, overwhelming metal, mechanical injury and nourishing lack (Dixon and Paiva 1995; Vickers et al. 2009; Kumar et al. 2019b; Suyal et al. 2021) that bring about a worldwide decline in yields prompting poor return from crops (Suzuki et al. 2014). To comprehend and improve harvests, researchers have concentrated on the flagging observation, transcriptional guidelines, and articulation of useful proteins in the pressure reaction instruments utilized by plants against abiotic stresses (Hirayama and Shinozaki 2010). Furthermore, post-translational, post-transcriptional, and epigenetic guidelines have been examined. The amassing role of little atoms with antioxidative movement in vitro has regularly been talked about, or the role they play in alleviating the collection of receptive oxygen species (ROS) actuated by abiotic stresses. This conversation has advanced under the guess that the response in vitro may happen in vivo. Incorporated "omics" examination focused on metabolomics (coordinated metabolomics) can be a ground-breaking procedure to recognize the elements of qualities associated with the metabolic procedures of plants (Saito 2013). Logical systems for narrowing down expected qualities and distinguishing their capacities are moderately developed and transcriptome coexpression investigation and untargeted examination in metabolomics utilizing freak lines have become typical (Saito et al. 2008). The subsequent stage is to recognize the capacity of particular metabolites, which is a demanding task. Further, the ongoing advancement in the understanding of the capacity of abiotic stress-responsive particular metabolites with an accentuation on flavonoids as a delegated case of such mixes is also an important consideration in this regard.

Abiotic stresses are caused because of the inconvenient consequences for endurance, biomass creation, collection, and yield of most harvested grains. They are found to be the prime reason for misfortunes in numerous crops around the world (Athar and Ashraf 2009). Dry season, saltiness, elevated metal levels in soil, and outrageous temperatures have found to be the major natural variables among all abiotic stress factors that cutting-edge agriculture needs to remain alive (Kour et al. 2020c; Kumar et al. 2019a; Tiwari et al. 2021; Yadav et al. 2020a). Around 50–70% yield decrease in significant harvest is brought about by them. The crop species, growth stages, and duration of stress periods are important concerns in this regard (Jaleel et al. 2008). The most normal reactions that are activated in plants exposed to various abiotic stresses remember to change for quality articulation, anatomical and morphological alterations, diminished productivity of photosynthesis, decreased N digestion ability, modified exercises of many identified chemicals and also plasma film attributes, cell metabolic modifications, excess production of metabolites, and expanded blend of stress-incited novel proteins. Among all these abiotic stresses, drought or water deficit is the most intense and answerable for declined crop productivity around the world. Water stress impacts plants in various ways such as plant development and plant improvement, loss of layer respectability, stomatal conclusion, shade content, osmotic adjustments, water relations, limit photosynthetic movement by lessening CO_2 deluge, osmolytes proline, aggregation of abscisic acid (ABA), sorbitol, mannitol, arrangement of radical searching mixes (glutathione, ascorbate, a-tocopherol, and so on), amalgamation of newly found mRNAs, and proteins (Osakabe et al. 2014), just as the reduction in an electron transport chain and carboxylation exercises of the chloroplasts situated inside the cells of mesophyll (Feller and Vaseva 2014). Salinity has been found to be the second most harming stress after drought that diminishes crop growth and productivity. High salt focus can invade unfavorable consequences like germination of seeds, seedling vigor, vegetative development, blossoming and natural product set, and at the end cause poor yield. The ionic stress and osmotic pressure are the two significant impacts prompted by salinity (Munns and Tester 2008).

Plants respond to different abiotic stresses variously, and the impact of stresses is observed in the growth and developmental processes of different crops. Recovery from the stresses is important for the optimum flourishment of plants, and there are possible mitigation and adaptation options. The chapter deals in the omics strategies for abiotic stress response and microbe-mediated mitigation in plants.

12.2 Abiotic Stress Response in Plants

12.2.1 Salinity Stress

Globally in all agro-climatic regions, salt-affected lands are found. They also occurr at various altitudes, from below sea level to 5000 m above the soil surface of rising mountains like the Tibetian Plateau (Singh and Chatrath 2001). About 800 million ha of arable area is globally exaggerated by salinity (Munns and Tester 2008). Soil salinity is such a condition when soil consists of more concentrations of soluble salts, viz., chloride and sulfates of Sodium (Gaba et al. 2017). When the electrical conductivity (EC) of the soil is ≥4 dS/m which creates an osmotic pressure of 0.2 MPa, it is called saline soil (USDA-ARS 2008). In saline soils, because of sodium ion accumulation, necrosis and chlorosis appear in plants which are actually ion toxicity (Munns 2002). Generally, all soils and irrigation water contain some dissolved salts (Kotuby-Amacher et al. 2000), but in dry regions salinity is a great threat to crop production (Acosta-Motos et al. 2017). Salts originate in many ways like mineral weathering, non-judicious use of irrigation water, chemical fertilizers, and soil amendments (e.g., organic manures and gypsum). Under mild salinity, very less or no impact has been observed on crop growth (Maggio et al. 2001).

During the last two decades, the salinity of soil and water became more problematic due to faulty land and water management (Cirillo et al. 2016; Munns et al. 2015). Most of the plants are glycophytes and cannot flourish under high soil salinity and even died with 100–200 mMNaCl. Glycophytes under salt stress tend to exclude the salt, and halophytes accumulate salts by measuring ion content in the plants (Zhu 2007). But euhalophytes can gather salt up to a certain extent in the cell sap when the osmotic potentials remain less than that in the soil moisture. The stress response to salinity is noted in the root system of plants, and growth is checked due to water and nutrient shortage (Munns 2005). Under salinity conditions, plants show greater absorption of sodium and chlorine ions, and deficiency of calcium and potassium is noted leading to nutrient unbalances (Marschner 2005); thus, salinity causes ionic toxicity and osmotic stress. Further, salinity causes oxidative stress mediated by reactive oxygen species (ROS) (Isayenkov 2012) and ultimately harms crops (Hernández et al. 2003; Mittova et al. 2004).

The impact of stress due to soil salinity on plants can be explained in two ways: more concentration of salt within the plant itself causes toxicity and alters different physiological and metabolic activities like nutrient uptake and assimilation, and more amount of salt in soil affects moisture extraction by roots (Isayenkov and Maathuis 2019; Munns 2002). Greenway and Munns (1980) stated that saline soil consists of more chloride, which caused identifiable symptoms like leaf blade scorching, whereas leaf mottling and leaf necrosis were the symptoms of accumulation of sodic salts. Accumulation of excessive quantity of salts in plants affects the transpiration that ultimately causes a reduction in plant growth (Hanin et al. 2016). The rate of leaf expansion reduces due to salinity stress, and it also closes leaf stomata causing a reduction in photosynthesis. This actually occurs due to the shortage of soil moisture because of the osmotic stress (Rahnama et al. 2010). The toxic concentration of Na^+ accumulates in leaves and reduces the longevity of photosynthetic tissues which results in growth retardation (Munns 2002; Tavakkoli et al. 2010). Further, soil salinity brings down the photosynthetic pigments in plants and reduces photosynthesis (Misra et al. 2006; Murillo-Amador et al. 2007; Sultana et al. 2000; Taffouo et al. 2010; Tort and Turkyilmaz 2004). Another effect is an increase or decrease of protein content in plants which is influenced by the change in salt concentration

(Chen et al. 2007; Kapoor and Srivastava 2010). There are variations in salinity tolerance among the monocotyledonous and dicotyledonous plants; however, dicot plants show better salinity tolerance than monocot ones. Among all cereal crops, barley is highly tolerant and rice is sensitive to soil salinity (Byrt et al. 2018; Zagorchev 2014).

12.2.2 Drought Stress

The effect of drought stress on plants depend on the duration and intensity, including the time period of a plant's life cycle (Kocoń 2015). Drought stress causes 30–50% yield reduction because of high temperature, which results in high evapotranspiration, low humidity, increased respiration, and enzyme activity in the plants (Bagheri 2009; Fahad et al. 2017; Lamaoui et al. 2018; Kour et al. 2020b). Most of the plants absorb nutrients from the upper horizon of the soil profile, which is reduced due to drought (Rasmussen et al. 2020; Schoonover and Crim 2015). Drought stress is also to some extent related to stress due to salinity on plants, as salts and ions are accumulated on the topsoil around the rhizosphere induceng ion toxicity and osmotic stress (Kamran et al. 2020). Due to drought, mesophyll cells become dehydrated and the abscisic acid is stored in the chloroplast, synthesized more in guard cells and mesophyll cells (Christmann et al. 2005; McAdam and Brodribb 2018). With the loss of guard cells, stomata closes during drought (Daszkowska-Golec and Szarejko 2013; Malcheska et al. 2017; Kour et al. 2020a). Dehydration in plants causes discoloration of leaves and increases leaf stomata numbers and trichomes (Bagheri 2009; Christophe et al. 2011). Drought causes a decrease in carbon assimilation via photosynthesis (Flexas and Medrano 2002; Wang et al. 2018). Compared to the vegetative stage, drought stress is more important for the reproductive stage (Kabiri 2010; Sehgal et al. 2018; Yang et al. 2019). Drought influences on plant nutrition as nutrient uptake decreases due to water shortage (Bista et al. 2018; Cramer et al. 2009; Ge et al. 2012; Mariotte et al. 2020; Waraich et al. 2011; Kour et al. 2021).

There are several reasons for decline of nutrient uptak and these are reductions of nutrient supply through mineralization (Sanaullah et al. 2012; Schimel and Balser 2007; Prasad et al. 2021) and because of lessening mass flow and diffusion in the soil (Chapin 1991; Lambers et al. 2008). There are adverse impacts of stress due to drought on vegetative growth of the plants such as a decrease in plant height and a reduction in leaf area and plant dry weight (Apel and Hirt 2004; Farooq et al. 2009; Nadeem et al. 2019; Zheng et al. 2016). Water deficit inhibits water flow from the xylem to other growing tissues and declines plant cell turgidity resulting in decreased cell elongation and leaf area (Nonami 1998; Schuppler et al. 1998; Saradadevi et al. 2017; Taiz and Zeiger 2003). Under drought stress, starch is converted into sugar (Du et al. 2020; Hong-Bo et al. 2006; Sircelj et al. 2005; Thalmann and Santelia 2017). Further, the synthesis of different amino acids (arginine, proline, lysine, histidine, glycine, etc.) and polyamines is also affected by drought (Rabe 1990; Majumdar et al. 2016).

12.2.3 Submergence and Flood Stress

Flooding can be further classified based on the height of the water stagnation (covers only the root) and submergence (when water covers some portion of the shoot also) (Sasidharan et al. 2017), and movement of oxygen from the air to plant tissues is inhibited (Lee et al. 2011). Sasidharan et al. (2017) reported that naturally a hypoxia condition is created at <21% O_2. Under anaerobic conditions, both photosynthesis and translocation of carbohydrates are diminished (Kramer and Kozlowski 1979). Total mineral nutrient absorption and concentration of primary nutrients like N, P, and K in plants decline in flood intolerant species under inundated conditions (Kempen et al. 2017; Liu et al. 2014; Trought and Drew 1980a, b). In alkaline soil, P availability is less due to high soil pH. But flooding results in a change in soil pH and improves P availability to plants (Tian et al. 2017). Prolonged flooding increases P availability but reduces the total uptake as roots decay (Ruiz et al. 2020; Zhang et al. 2017a, b). Submergence alters phytohormone synthesis in plants leading to an increase in ethylene (Lee and Yoon 2018), auxins (Nakayama et al. 2017; Wample and Reid 1979), and abscisic acid (Peres et al. 2019; Shaybany and Martin 1977). Synthesis of these phytohormones in shoots in more quantity ultimately reduces the synthesis and translocation of gibberellins and cytokinins (Binenbaum et al. 2018; Park et al. 2017).

Flooding stress on plants impacts root growth more than the shoot (Fukao et al. 2019). Further, flooding results in the inhibition of seed germination, leaf initiation and proliferation, internode elongation, cambial growth, and root growth (Vishal and Kumar 2018). Various types of unwanted compounds gather in inundated soil which may cause phytotoxicity. Sulfides, CO_2, soluble iron, and manganese are produced by the roots (Pires et al. 2018). The anaerobic microbial metabolism produces methane, ethane, propylene, unsaturated acids, hydroxy and dicarboxylic acids, fatty acids, aldehydes, diamines, ketones, and heterocyclic compounds. Ethylene is formed by flooded plants and as a result of microbial metabolism in soil (Ravanbakhsh et al. 2018). Plants under flooded condition maximize ethylene synthesis that increases cellulose activity leading to aerenchyma tissue development (Steffens and Rasmussen 2016). Under flooding conditions, many woody and herbaceous plants regenerate new roots on both submerged roots and stems (Zhang et al. 2017a, b).

12.2.4 Heat Stress

Heat stress can be explained as the rise in temperature above the threshold level to cause an adverse effect on the permanent growth and development of plants (Wahid et al. 2007). Heat stress depends on intensity, duration, and temperature rise. Heat stress can be considered when there is a quick increase in 10–15 °C above typical, ambient temperature. Soil temperature rises when air temperature is more with the water deficit due to drought (Sekhon et al. 2010; Simoes-Araujo et al. 2003). In general, air temperature above 30 °C results in water shortage and limits plant growth and sustainable agriculture (Farooq et al. 2012; Mittler 2006; Rojas-Downing et al. 2017). In maize, photosynthesis is inhibited at a high leaf temperature above 38 °C, when the temperature is increased suddenly than gradually (Crafts-Brander and Salvucci 2002; Qu et al. 2018). Both heat stress and drought stress cause hindrance in nutrient uptake and photosynthesis. Wheat crop in both late and early sown conditions affects different developmental stages like tillering, jointing, booting, anthesis, and grain filling (Lamaoui et al. 2018; Hossain 2013a). In rice, the high temperature causes spikelet sterility, chaffy grains, and low yield (Nguyen et al. 2012). In Uttar Pradesh, India, there was a rise of minimum temperature during the monsoon season by 0.06–0.44 °C over a decade which adversely affected rice yield, particularly when the temperature prevailed more than 35 °C during the reproductive stage of the crop (Bhatt et al. 2019). Both drought and heat stresss together cause rapid water loss from plant and soil surfaces (Wahid et al. 2007), while inadequate water supply to fulfill the demand of evaporation can also cause heat stress (Koop and Tadi 2020; Pei et al. 1998).

12.2.5 Low Temperature Stress

Low temperature stress including chilling and freezing temperature exposure of plants severely disturbs the plant community and ecosystem biodiversity limiting plant quality and yield as well as their economic value (Chen et al. 2014). Low temperature stress, i.e., 0–15 °C mainly causes cellular damage that limits the productivity and distribution (Theocharis et al. 2012; Yadav et al. 2017, 2020d). Low temperature stress influences crop growth and development badly limiting crop productivity (Zaynab et al. 2017). Low temperature mainly affects plant growth in two ways, i.e., sub-optimal temperature and cellular dehydration due to freezing of the cellular water content (Beck et al. 2007). Sub-optimal temperature and sub-freezing temperature also affect cell division and elongation, photosynthesis, water transport, hormonal balance, etc., negatively impacting the yield (Khan et al. 2015a, b). They also affect the metabolic processes, i.e., change in enzyme and antioxidant activity, membrane fatty acid composition, and gene regulation (Kazemi-Shahandashti et al. 2014). One of the sensitive features is the damage of the cell membrane through electrolyte leakage and during low temperature stress. The actively dividing cell numbers and mitotic index of apices and basal part of young leaves declines (Lukatkin et al. 2012). Strauss et al. (2007) reported that the inhibition of cell growth significantly modifies plant developmental structures.

Cold temperature stress hampers the growth and development of plants by declining the action of enzymes, accumulating ROS, damaging membrane integrity, inhibiting chlorophyll biosynthesis, and ultimately impairing the photosynthetic activity (Liu et al. 2011; Xia et al. 2009; Dikilitas et al. 2021; Yadav et al. 2019). Khan et al. (2019) reported that there is a significant decrease in net assimilate production, transpiration rate, stomatal conductance, and internal carbon dioxide concentration of plants due to cold stress. Cakmark et al. (2005) mentioned that the minimization of photosynthetic transport, sink activity, and senescence-related enzyme activity were also affected by low temperature stress. It also affects and inhibits the D1 precursor necessary for PSII complex activation and repair (Kanervo et al. 1997). Higher activity of Catalase and Peroxidase activity were observed in cold-resistant plants (Luo et al. 2001). In wheat, the increase in catalase activity was observed in low temperature stress conditions (Khan et al. 2015a, b; Zhang et al. 2010a). At cold temperature, enhanced production of ROS leads to lipid peroxidation (Maeda et al. 2005). Khan et al. (2015a, b) reported that increased activity of antioxidant enzymes, i.e., SOD, CAT, and POX, and a lowered activity of lycopene and beta carotene content in *Lycopersicon esculantum* fruit are observed under low-temperature exposure. The low-temperature treatment also causes an increase in H_2O_2 content (Khan et al. 2015a, b). An increase in α-tocopherol activity was also noted in maize under cold stress (Leipner et al. 2000).

Cold acclimation triggers signaling pathways activating genes that make changes in the composition of sugar, proteins, prolines, membrane lipid compositions, osmolytes, and peroxides (Askari-Khorasgani et al. 2019). Cold acclimation also induces enzymes and antioxidant activity, stabilizes cellular components, macromolecules that prevent chilling and freezing injury, dehydration, and spread cold tolerance and existence rate (Kwon et al. 2007; Ouellet and Charron 2013; Strimbeck et al. 2015). Acclimation of plants to low temperature stress is also characterized by the increase in the potential of plants to produce more quantity of osmolytes, i.e., alcohols and soluble sugars as well as the nitrogenous compounds, namely glycine betaine and proline (Peng et al. 2008; Thomashow 1999). Stress-induced coldregulated proteins (CORs), i.e., dehydrins contribute to stress tolerance by ABA-dependent pathway (Agarwal et al. 2006; Choi et al. 2000; Uno et al. 2000) and maintain ionic homeostasis by ROS removal and membrane stabilization (Agarwal et al. 2006).

12.2.6 High Light Stress

Solar radiation has the primary importance with respect to crop growth, yield, and quality. The duration and intensity of solar radiation cannot be managed and modified in an open field, and the plant should adapt to light stress. Acclimation toward light is a dynamic process that involves the response of plants to light at various time scales in many cell compartments (Dietz 2015). Light intensity directly disturbs the crop growth and allocation of photosynthates (Kromdijk et al. 2016). High light intensity is responsible for photo-oxidation, photo-inhibition, and photo-damage resulting in early maturity and reduction in productivity (Tian et al. 2015). After the saturation light intensity, photosynthetic activity is severely reduced (Mathur et al. 2014). High light intensity may lead to ROS formation that increases photo-damage of chlorophyll molecules (Foyer et al. 1994; Trivellini et al. 2017) and in response to which plants must increase the production of carotenoid concentration to protect chlorophyll molecules from high light stress (Horton and Ruban 2005). High light intensity with high temperature often results in the damage of photosystems (Chen et al. 2017). Tikkanen et al. (2014) and Widiastuti et al. (2015) reported that the PSII is mostly susceptible to photo-inhibition under extraordinary light stress, and the D1 protein is the primary target of the photo-inhibition process (Adir et al. 2003). To sustain photosynthetic activity, D1 turn-over mechanism should be activated (Keren and Krieger-Liszkay 2011).

There is a report of an increase in both soluble sugar and anthocyanin accumulation under high light conditions. Albert et al. (2009) reported enhancement in leaf anthocyanin up to 3 mg g^{-1} under a high light intensity of 750 μmol m^{-2} s^{-1}. Kataoka et al. (2004) reported doubling of leaf sucrose content under high light exposure of *Phalaenopsis*. Jaipargas et al. (2016) observed increased peroxule-mitochondria interactions in plants under high light intensity. Lee and Back (2018) mentioned that the expression of melatonin-induced genes and melatonin content are increased under high light stress. Perez-Lopez et al. (2018) recorded increased phenolic compound concentration under high light intensity with raised CO_2 concentration. Lu et al. (2017) reported a significant decrease in RUBISCO activity, net photosynthetic rate, electron transport, maximal photochemistry efficiency, and an increase in PSII energy dissipation under high temperature and high light stress in the tomato plant. High light intensity directly or indirectly affects chlorophyll fluorescence (Maxwell and Johnson 2000) which is one of the three processes of energy directing by chlorophyll molecules, i.e., dissipation as heat, energizing photosynthesis, and fluorescence remission (Müller et al. 2001). It is also reported that in high light intensity, the non-photochemical quenching (NPQ) increases significantly (Miyake et al. 2005). It was also reported about increase in anthocyanin and carotenoid concentration in high light stress conditions by Gould et al. (2000) and Hatier and Gould (2008). An increase in F_0 and decrease in variable to maximal florescence (F_v/F_m) were reported during full stress conditions by Maxwell and Johnson (2000).

12.2.7 Soil Acidity Stress

Among different abiotic stresses, soil acidity stress ranks second after drought adversely affecting the growth and development of plants. Globally, a wide extent of arable land is under acidic soil reaction (Kochian et al. 2004). The benefits of agricultural systems in tropical regions are often limited with soil acidity that reduces macro-nutrient availability and microbial activity (Lambridge et al. 2007) and also creates problems of Mn and Al toxicity (Churka Blum et al. 2013). When the pH value of soil comes below 5.0–5.5, the soil reaction is said to be acidic and it is quite critical for the normal growth and development of most of the crops (Edmeades et al. 1995). Lower the soil pH results due to increase in H^+ ion concentration directly shows the toxic effect for most of the plants (Kidd and Proctor 2001) linked with biochemical and morpho-physiological plant attributes (Felle et al. 2009; Hinsinger et al. 2003), increase in aluminum toxicity (Kochian et al. 2015; Rao et al. 2016; Sairam et al. 1998) causing reduced root growth (Hiscox and Isrealstam 1979; Sairam 1994), and limiting the availability of different soil nutrients (Menconi et al. 1995) with reduced plant growth (Hernandez et al. 1993). Acidic soil reaction also disrupts germination (Deska et al. 2011; Lee et al. 1998), water uptake, nutrient uptake, and assimilation (Bahrami et al. 2012; Bian et al. 2013).

At the cellular level, low pH affects the integrity of plasma membrane, cytoskeleton structure, cell division, DNA synthesis, signal transduction pathway, etc., (Garcia-Oliveira et al. 2013), impaired activity of enzymatic antioxidants (Nahar et al. 2017) and enzymes, i.e., esterase, phosphatases, and glucosidase (Taranishi et al. 1974). There is a positive correlation found between acidic pH and the availability of micronutrients like Fe, Cu, Al, Mn, and Zn in toxic amounts (Ginocchio et al. 2009). Along with Al toxicity in low pH, plants respond to Fe and Mn toxicity. Tolerant cultivars can precipitate excess Fe in their roots and facilitate essential nutrient absorption and assimilation (Ayeni et al. 2014; Sikirou et al. 2016). Mn toxicity disrupts chloroplast structure and hampers transpiration and CO_2 fixation due to stomatal dysfunction (Havlin et al. 2005; Hong et al. 2010). Production of excess ROS due to low pH stress causes oxidative damage including degeneration of biomolecules and programmed cell death (Hasanuzzaman et al. 2018). Low pH also seems to alter the enzymatic antioxidant activity, i.e., activity of SOD, CAT, APX, MDHAR, DHAR, GR, GPX, GST, POD, and non-enzymatic antioxidant activity, i.e., AsA, GSH of the cell (Hasanuzzaman et al. 2012).

12.2.8 Heavy Metal Stress

Heavy metals are elements of higher density and cause toxicity at a low concentration (Kao 2015; Khan et al. 2015a, b). The contamination of heavy metals in agriculture is mainly due to injudicious fertilizer and agro-chemical application and improper management of sewage and sludge, smelter dust and effluents from industries, and so on (Herawati et al. 2000). Lead and cadmium substitution in biomolecules leads to the inhibition of growth resulting from metabolic disturbances (Farooq et al. 2016). In response to adaptation mechanism for tolerance to heavy metals, some mechanism gets activated in plants, that is, protein repairing, metal chelation, subcellular compartmentation, cell wall binding, and metal pumping (Herawati et al. 2000; Hall 2002; Farid et al. 2017b). The examples of heavy metal stress are DNA damage in leaf and root tip of *Vicia faba* (Lin et al. 2008), DNA damage by Cd interfering transcription (Sarkar 1995), damage in a photosynthetic protein complex, and decreased Hill reaction on increasing Ni concentration in *Zea mays* (Ghasemi et al. 2012), injury to macro-molecules on the formation of ROS (Emamverdian et al. 2015; Lombardi and Sebastiani 2005), alteration in chloroplast structure and activity of PSII (Ventrella et al. 2011; Khan et al. 2016a, b) due to dissociation of O_2-evolving complex, reduction in chlorophyll molecule with more concentration of Zn (Li et al.

2013), unstructural changes in chloroplast due to Cr toxicity, decreased WUE and rate of photosynthesis due to Pb toxicity (Ahmad et al. 2011), etc.

Heavy metal contaminated soil and water affect crops and cause damage to photosynthetic apparatus, cellular organelles, cell membranes, disrupt electron transport chain, and generate ROS (Farid et al. 2017a; Per et al. 2016; Yadav 2010). ROS in plant physiology is also considered as a "double-edged sword" (Mittler 2017), as it causes oxidative damage to the tissues as well as signals important developmental processes, i.e., polar growth (Mangano et al. 2016), cell wall modification (O'Brien et al. 2012), transcriptional activities (Xu et al. 2014a), and protein kinase cascade (Pitzschke and Hirt 2009). The basic response of plants to heavy metal stress is the production of ROS (Rizwan et al. 2016) in excessive amounts and to mitigate the effect of ROS and maintain cellular homeostasis. Plants also activate certain enzymatic antioxidants (SOD, CAT, APX, GR) and some non-enzymatic antioxidants (AsA, GSH, α-tocopherol, ascorbic acid, proline, phenolics, carotenoids, flavonoids, etc.) (Akram et al. 2017; Anjum et al. 2012; Mahmood et al. 2010; Sofo et al. 2010) under heavy metal stress conditions. Glutathione plays a major role in heavy metal tolerance, i.e., synthesis of metal-binding phytochelatins (Mohamed et al. 2012; Zhang et al. 2010b) and acts as a promising regulator for detoxification of reactive oxygen species in different heavy metal contaminations (Khan et al. 2016a, b; Nakamura et al. 2013; Noctor et al. 2011). To cope with the heavy metal stress in plants, genetic activation is observed as beneficial as the *AtNramp* cDNA gene isolated from Arabidopsis which is found responsible for Cd resistance (Thomine et al. 2000). There are other genes, i.e., PC synthase gene (Moffat 1999) and the cDNA *GmhPCS1* gene encoding homophytochelatin synthase in soybean (Oven et al. 2002). GSH has a major role in gene-level detoxification response of heavy metal contamination, i.e., mRNA level gene participation in GSH synthesis (Semane et al. 2007), removal of excess H_2O_2 by AsA-GSH cycle (Noctor and Foyer 1998), and optimal GSH/GSSG ratio for optimal growth (Szalai et al. 2009).

12.3 Physiological and Molecular Response of Plants Against Stress

Plants respond to different environmental conditions by sensing, managing or adapting the situation and their responses to abiotic factors that comprise some collaborative crosstalk of physiological and metabolic processes in miscellaneous biosynthetic pathways (Haldar and Sengupta 2015; Meena et al. 2017; Yadav 2021). Adaptation, defense, acclimation, and repair are important mechanisms of stress response (Sun and Zhou 2018). Roots remain in close contact with soil and are highly sensitive to abiotic stimuli and on the basis of nature and degree of stress, react accordingly (Khan et al. 2016a, b). The response of plant stress by roots is a very complicated phenomenon in which physiological, cellular, metabolic, and genetic changes may occur (Atkinson and Urwin 2012). In case of stress due to high temperature, drought, salinity, and frost, water deficit is observed in plant cells which leads to phenotypic, molecular, and biochemical changes in plants against these abiotic stresses (Xu and Zhou 2006; Yadav et al. 2020c). Under open environment conditions, plants face a number of stresses due to abiotic factors individually and in combinations of these stresses. Plants respond to these stresses by specific gene expression and complex metabolic processes (Haak et al. 2017a; Ma et al. 2020). Plant growth stage and biotic factors also influence in responding to abiotic stresses to express tolerance or susceptibility (Pandey et al. 2017; Rizhsky et al. 2004).

Many agricultural crops are grown under sub-optimal environments that create hindrance in the expression of exact genetic potential (Bailey-Serres et al. 2019; Bray et al. 2000). In case of stress due to water deficit, the occurrence of peroxidation influences adversely the metabolism of antioxidants (Xu et al. 2014b). Under water stress, with the application of irrigation water, peroxidation is decreased leading to stomatal opening and regrowth of plants (Mamnabi et al. 2020; Xu et al. 2010), but simultaneously H_2O_2 accumulation in roots occurs (Bian and Jiang 2009; Huang et al. 2017). Variation in response to water stress among plant species and the enzyme superoxide dismutase (SOD) play an important role in the metabolism of antioxidants (Xu et al. 2015; Laxa et al. 2019). Salinity is another threat (Isayenkov and Maathuis 2019; Voesenek and Pierik 2008) and causes oxidative stress to plants in the presence of ROS (Isayenkov 2012). The adverse effect of salinity is observed in terms of ion-independent growth reduction by stomatal closure, shyness of cell enlargement (Rajendran et al. 2009), and enhancement of cytotoxic ion, resulting in premature senescence, lowering metabolic activities, and ultimately causing cell death (Roy et al. 2014). The gene expression pattern in salinity stressed cells is changed (Dinneny et al. 2008; Kurotani et al. 2015; Munns 2005; Razzaque et al. 2019).

In soils with elevated salinity, osmotic potential is decreased resulting in ion toxicity to plants. The situation negatively impacts seed germination and poor seedling vigor, facilitates early senescence of leaves, and causes the death of plants (Acosta-Motos et al. 2017; Flowers and Colmer 2015; Stepien and Johnson 2009). Salinity reduces amino acids, namely methionine, cysteine and arginine, and productivity in arid and semi-arid conditions (Sadak et al. 2015). Under salinity stress conditions, the Salt Overly Sensitive (SOS) stress signaling pathway is observed (Hasegawa et al. 2000; Park et al. 2016; Rolly et al. 2020). Proline accumulation is known as a mitigation strategy against salinity stress (Chun et al. 2018; Evelin et al. 2019). Variation of hormones, presence of nitric oxide (NO), accumulation of glycine betaine, and stimulation of antioxidant enzymes are some changes commonly noted in salt-stressed plants (Ahmad et al. 2016; Gupta and Huang 2014; Sharma et al. 2019). All these ultimately hamper growth and productivity mainly due to the non-availability of fresh water and nutrients from the soil.

Climate change and global warming are ongoing problems that rise atmospheric temperature and badly impact physiological, biochemical, and morpho-anatomical activities of plants (Kaushal et al. 2016; Menezes-Silva et al. 2019). Besides, some genetic changes may occur due to thermostress (Meena et al. 2017; Raza et al. 2019). High temperature adversely affects germination; assimilating production and membrane permeability (Raza et al. 2019). Some more prominent responses of heat stress are changes in phytohormone (Sharma et al. 2019; Prerostova et al. 2020) and metabolite concentration (Austen et al. 2019; Escandón et al. 2018), enhancement in production of ROS (Choudhury et al. 2017; Huang et al. 2019), aggregation and denaturation of protein (Huang and Chenping 2008; Wang et al. 2004), augmentation in heat shock expression (Hemantaranjan et al. 2014; Guo et al. 2016), greater protein disposal and degradation (Haq et al. 2019), and shyness of protein synthesis (Altschuler and Mascarenhas 1982) and enzymes (Kaushal et al. 2016; Yuan et al. 2017). Further, excess light intensity also causes stress to plants by prompting photo-oxidation that increases the production of ROS to effect enzyme activities (Jalil and Ansari 2018; Koini et al. 2009; Li et al. 2009).

A combination of different stresses is less harmful than individual stress to plants and in nature generally, a combination of different stress factors occurs (Pandey et al. 2017). Combined stresses may reduce the adverse effects of each other and in this way, ultimate stress to plants is decreased (Ramegowda and Senthil-Kumar 2015). To minimize the adverse effects of stress, phytohormones play important roles (Egamberdieva et al. 2017; Sytar et al. 2019). Different signals given by proteins for tolerance of stress are controlled by hormones (Priya et al. 2019; Verma et al. 2016). Further, beneficial microbes influence the response to abiotic stresses, and the study of omics clearly indicates the kind of interaction between plants and microbes.

12.4 Role of Microbiomes in Plant Defense and the Immune System Against Stress

Microbes play a pivotal role in the adaptation of different abiotic stresses in plants, and both plants and microbes get the benefit to combat the stresses (Yadav et al. 2021). Researchers investigated the importance of microbes in easing abiotic stress in plants (Abd El-Daim et al. 2019; Bulgari et al. 2019). Because of inherent genetic and metabolic capabilities, microbes alleviate stresses to plants (Enebe and Babalola 2018; Hartman and Tringe 2019; Ojuederie et al. 2019). Different Rhizobacteria bring alteration in hormones, proteins, antioxidants, enzymes, and polysaccharides that help the plant to recover the abiotic stresses (Ilangumaran and Smith 2017; Khan et al. 2018a, b; Vurukonda et al. 2016) and the phenomenon is known as Rhizobacteria-induced drought endurance and resilience (RIDER) (Jalil and Ansari 2018; Kaushal 2019; Meena et al. 2017). Other than bacteria, fungi also perform in abiotic stress recovery to plants (Lata et al. 2018; Kollist et al. 2019; Millar and Bennett 2016). A brief account of the role of microorganisms in abiotic stress mitigation is presented in Table 12.1.

Table 12.1 Role of microbiomes in plant defense and the immune system against stress

Abiotic stress	Micro-organism	Role	Plant	Sources
Salinity	*Bacillus subtilis* GB03	Tissue-specific regulation of sodium transporter HKT1	Rockcress (*Arabidopsis thaliana*)	Allard-Massicotte et al. (2016), Zhang et al. (2008)
	Pseudomonas simiae- 4-	Nitroguaiacol and quinoline promote soybean seed germination	Soybean (*Glycine max*)	Vaishnav et al. (2016)
	Pseudomonas syringae DC3000, *Bacillus sp.* strain L81, *Arthrobacter oxidans*	SA-dependent pathway	Rockcress (*Arabidopsis thaliana*)	Barriuso et al. (2008)
	Root-associated plant growth-promoting *rhizobacteria*	Expression of salt stress-related RAB18 plant gene	Rice (*Oryza sativa*)	Jha et al. (2014)
	Cyanobacteria and *cyanobacterial extracts*	Phytohormones as elicitor molecule	Rice (*Oryza sativa*), wheat *(Triticum aestivum),* maize *(Zea mays),* and cotton *(Gossypium hirsutum)*	Singh (2014)
	Pseudomonas koreensis strain AK-1	Reduction in NaCl level and increase in KC level	Soybean *(Glycine max)*	Kasotia et al. (2015)
	Glomus etunicatum	Increased root but decreased shoot proline concentrations	Soybean *(Glycine max)*	Sharifi et al. (2007)
	Burkholderia, Arthrobacter, and *Bacillus*	Increased accumulation of proline	Grape *(Vitis vinifera),* Chili *(Capsicum annuum)*	Barka et al. (2006)
	Azospirillum brasilense strain Cd	Stimulation of persistent exudation of flavonoids	Kidney bean *(Phaseolus vulgaris)*	Dardanelli et al. (2008)
	Pseudomonas putida Rs-198	Prevent salinity-induced ABA accumulation in seedlings	*Cotton (Gossypium hirsutum)*	Yao et al. (2010)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
	Glomus intraradices BEG121	Reduced concentration of ABA	Lettuce *(Lactuca sativa)*	Aroca et al. (2008)
	Bacillus subtilis	Decreased root transcriptional expression of a high-affinity KC transporter (AtHKT1) decreasing root NaC import	Rockcress (*Arabidopsis thaliana*)	Zhang et al. (2008)
	Glomus clarum, Glomus etunicatum	Decreased NaC in root and shoot and incresed concentration of KC in root	Mung bean *(Vigna radiata),* Chili *(Capsicum annuum),* Wheat *(Triticum aestivum)*	Daei et al. (2009), Kaya et al. (2009), Rabie (2005)
	Glomus intraradices BAFC 3108	Decreased root and shoot NaCl accumulation and enhanced root KC concentrations	Deerweed *(Lotus glaber)*	Sannazzaro et al. (2006)
	Glomus intraradices	Accumulation of carbohydrates	Soybean *(Glycine max)*	Porcel and Ruiz-Lozano (2004)
	Glomus fasciculatum	Accumulation of carbohydrates	Ditch reed *(Phragmites australis)*	Al-Garni (2006)
	Bacillus subtilis	Root-to-shoot cytokinin signaling and stimulation of shoot biomass	Lettuce *(Lactuca sativa)*	Arkhipova et al. (2007)
	Azospirillum brasilense and *Pantoea dispersa* (Co-inoculation)	High stomatal conductance and photosynthesis	Chili *(Capsicum annuum)*	del Amor and Cuadra-Crespo (2012)
	Pseudomonas simiae	4-nitroguaiacol and quinoline promote seed germination	Soybean (*Glycine max*)	Vaishnav et al. (2016)
	Acinetobacter sp. and *Pseudomonas* sp.	Promote plant growth	Barley (*Hordeum vulgare*) and Oats (*Avena sativa*)	Chang et al. (2014)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
	Pseudomonas koreensis AK-1	Reduction in Na^+ level and increase in K^+ level	Soybean (*Glycine max*)	Kasotia et al. (2015)
	Co-inoculation of *Azospirillum brasilense* and *Pantoea dispersa*	High stomatal conductance and photosynthesis	Chili *(Capsicum annuum)*	de Zelicourt et al. (2013)
	Pseudomonas fluorescens	Enhanced ACC deaminase activity	Groundnut *(Arachis hypogea)*	Saravanakumar and Samiyappan (2007)
	Azospirillum	Restricted Na^+ uptake and increased K^+ and Ca^{2+} uptake along with increased nitrate reductase and nitrogenase activity	Maize *(Zea mays)*	Hamdia et al. (2004)
	Pseudomonas pseudoalcaligenes and *Bacillus pumilus*	Increased concentration of compatible solute	Rice (*Oryza sativa*)	Jha et al. (2011)
	Frankia	Plant growth, shoot, root, and total dry weight, proline, and chlorophyll contents	Sheoak (*Casuarina glauca*) and Australian pine (*Casuarina equisetifolia*)	Ngom et al. (2016)
	Endophytic diazotrophic Enterobacter sp. EN-21	1-Aminocyclopropane-1-carboxylate (ACC) deaminase activity is efficient	Sugarcane (*Saccharum officinarum L.)*	Kruasuwan and Thamchaipenet (2018)
	Arbuscular mycorrhizal fungi	Enhance growth, photosynthesis, root morphology, and ionic balance	Lemon (*Citrus limon*)	Wu et al. (2010)
	Arbuscular mycorrhizal fungi	Alter photosynthetic and antioxidant pathways	Desert grass *(Panicum turgidum)*	Hashem et al. (2015)
	Azospirillum brasilense	Improved salt tolerance of plant during the rooting stage	Jojoba *(Simmondsia chinensis)*	Gonzalez et al. (2015)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
Osmotic stress	*Bacillus megaterium*	High hydraulic conductance, increased root expression of two ZmPIP isoforms	Maize *(Zea mays)*	Marulanda et al. (2010)
	Glomus intraradices BEG 123	High osmotic root hydraulic conductance due to increased active solute transport through roots	Kidney bean *(Phaseolus vulgaris)*	Aroca et al. (2007)
Submergence and Flood	*Anabaena azollae* *Arthrobacter* spp.	Nitrogen fixation in soil	Mosquito fern (*Azolla filiculoides*)	Carrapico (2002), Stirk and van Staden (2003)
	Mesorhizobium loti	Nitrogen fixing	Yellow water-lily (*Nuphur spp.*)	Wagner (2012)
	Sinorhizobium meliloti P221	IAA production in roots	Rooted macrophytes	Golubev et al. (2009)
Drought	*Rhizobium tropici* and *Paenibacillus polymyxa* (Co-inoculation)	Upregulation of genes involved in stress tolerance	Kidney bean *(Phaseolus vulgaris)*	Figueiredo et al. (2008)
	Pseudomonas chlororaphis O6	Production of 2R,3R butanediol- a volatile compound	Rockcress (*Arabidopsis thaliana)*	Cho et al. (2008)
	Pseudomonas putida strain GAP-P45	Epoxypolysaccharide production	Sunflower *(Helianthus annuus)*	Ali et al. (2009)
	Bacillus cereus AR156, *B. subtilis* SM21, and *Serratia* sp. XY21	Production of monodehydroascorbate, proline, and antioxidant enzyme, expression of genes	Cucumber *(Cucumis sativus)*	Wang et al. (2012)
	Bacillus licheniformis strain K11	Stress-related genes and proteins	*Chilli (Capsicum annuum)*	Lim and Kim (2013)
	Burkholderia phytofirmans *Enterobacter sp.* FD17	Increased photosynthesis, root and shoot biomass under drought conditions	Maize *(Zea mays)*	Naveed et al. (2014)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
	Bacillus thuringiensis AZP2	Production of volatile organic compounds	Wheat *(Triticum aestivum)*	Timmusk et al. (2014)
	Arbuscular mycorrhizal fungi inoculation	Enhance prolin	Soybean (*Glycine max)*	Pavithra and Yapa (2018)
Heat	*Curvularia proturberata* isolate Cp4666D	Colonization of roots	Woolly rosette grass *(Dichanthelium lanuginosum), Tomato (Solanum lycopersicum)*	de Zelicourt et al. (2013)
	Bacillus amyloliquefaciens, Azospirillum brasilence	Reduced regeneration of reactive oxygen species, preactivation of heat shock transcription factors, changes in metabolome	Wheat *(Triticum aestivum)*	El-Daim et al. (2014)
Cold	Plant Growth Promoting Bacteria (PGPB)	Influence plant growth	Grape *(Vitis vinifera)*	Andrews and Harris (2003), Barka et al. (2006)
	Rhizobium leguminosarum bv. *trifolii*	Affect the nodulation and yield of host legumes	legumes	McKay and Djordjevic (1993)
	Pseudomonas ssp.	Enhance the seed germination, root and shoot lengths of wheat seedlings	Wheat *(Triticum aestivum)*	Mishra et al. (2008, 2009)
High light intensity	White color *Fusarium graminearum*	Control of defense gene expression to the mycotoxin deoxynivalenol	Wheat *(Triticum aestivum)*	Ansari et al. (2014)
	UV-*Botrytis cinerea*	Resistance to Botrytis cinerea via the sinapate pathway	Rockcress (*Arabidopsis thaliana)*	Demkura et al. (2010)
	UV-*Cochliobolus heterostrophus*	High bacterial diversity and reduced resistance to Southern leaf blight disease	Maize *(Zea mays)*	Balint-Kurti et al. (2010)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
	UV-*Phakopsora pachyrhizi*	Resistance to Phakopsora pachyrhizi through epicuticular wax	Soybean *(Glycine max)*	Young et al. (2012)
	Blue-*Botrytis cinerea*	Reduced development of gray mold disease	Grape *(Vitis vinifera)* Lettuce *(Lactuca sativa)*	Ahn et al. (2015), Kook et al. (2013)
	Blue-Mosaic virus	Inhibition of virus spreading	Tobacco (*Nicotiana tabacum),* Cucumber *(Cucumis sativus)*	Chen et al. (2015)
	Blue-*Botrytis cinerea*	Reduced development of gray mold disease	Tomato *(Solanum lycopersicum)*	Xu et al. (2017)
	Red-*Pseudomonas syringae*	Resistance to Pseudomonas syringae	Rockcress (*Arabidopsis thaliana*), Tomato *(Solanum lycopersicum)*	Islam et al. (2008)
	Green-*Pseudomonas cichorii*	Reduced disease caused by Pseudomonas cichorii	Tomato *(Solanum lycopersicum)*	Nagendran and Lee (2015)
Soil reaction (pH)	Rhizobia	Formation of the root nodules	Chickpea (*Cicer arietinum*) and lentil (*Lens culinaris*)	Weese et al. (2015)
	Mycorrhiza	Protect plant root systems against stresses ranging from nutrient depletion to drought and disease	Wheat *(Triticum aestivum)* and Chickpea (*Cicer arietinum*)	Seguel et al. (2013)
Heavy metal and eutrophication	Arsenic toxicity *Staphylococcus arlettae*	Increased soil dehydrogenase, phosphatase and available phosphorus	Mustard *(Brassica juncea)*	Srivastava et al. (2013a, b)
	Pb/Zn toxicity *Phyllobacterium myrsinacearum*	Resistance to 350 mg/L Cd, 1000 mg/L Zn, 1200 mg/L Pb	Stone crop *(Sedum plumbizincicola)*	Ma et al. (2013)

(continued)

Table 12.1 (continued)

Abiotic stress	Micro-organism	Role	Plant	Sources
	Zn toxicity *Pseudomonas aeruginosa*	Improved biomass, N and P uptake and total soluble protein	Wheat *(Triticum aestivum)*	Islam et al. (2014)
	Cd, AS, Cu, Pb, and Zn toxicity *Pseudomonas koreensis*	AGB-1 ACC deaminase, IAA production	Chinese silver grass *(Miscanthus sinensis)*	Babu et al. (2015)
	Zn toxicity *Pseudomonas brassicacearum, Rhizobium leguminosarum*	Metal-chelating molecules	Mustard *(Brassica juncea)*	Adediran et al. (2016)
	Hg toxicity *Photobacterium* spp.	IAA, mercury reductase activity	Ditchreed *(Phragmites australis)*	Mathew et al. (2015)

12.5 Omics Approaches for Mitigation of Abiotic Stress

In nature, plants are found to be the most unpredictable, sessile living beings and are subsequently uncovered to various ecological stresses from the post-regenerative to the vegetative stage (Jakab et al. 2005; Mosa et al. 2017; Parida et al. 2018). These ecological elements have been found to have a detrimental influence on plant development, advancement, and efficiency. Due to these stresses, there are serious decreases in the yield and efficiency of the plant because of the physiological, molecular and cellular developments (Singh et al. 2018; Xiong and Zhu 2002). These ecological factors are commonly isolated into two classes, biotic and abiotic stresses. The abiotic stress factors incorporate differences in temperatures, higher irradiance, different heavy metals, drought, salinity, and ultraviolet (UV) light and hypoxic conditions (Singh et al. 2018). The profound term, i.e., biotic pressure includes primarily viruses, bacteria, fungi, nematodes, rodents, insects, and so on. In the current situation, abiotic stresses are ready to generate unfavorable conditions as they seriously diminish the yield of crops and profitability. Intergovernmental Panel on Climate Change (IPCC) has already clearly reported on that (http://www.ipcc.ch). This may presume sooner rather than later abiotic stresses obviously will decrease of the yields as a result of an unnatural weather change, water consumption, anthropogenic activities, and deforestation (Singh et al. 2018). During the last two decades, it has already been found that other integrative "omics" approaches have profoundly picked up energy in the research field of plant sciences, peptide sequencing to nucleic acid sequencing, computational molecular biology, innovation in mass spectrometry (MS) and statistical analysis (Fig. 12.1).

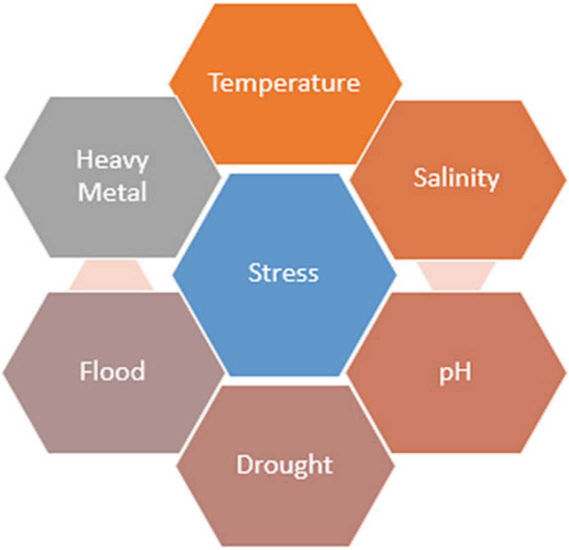

Fig. 12.1 Stress conditions in plants

Approaches of omics have risen as basic devices to detect and comprehend the atomic frameworks of the plants and their capacities, pick up experiences into natural systems, and advance the translational examination (Kumar and Shanker 2018; Parida et al. 2018). These approaches have been planned for describing the pool of plant's biomolecule in light of the fact that these particles assume jobs in keeping up homeostasis just as flagging reactions to modifying conditions. Albeit at first much work advanced in genomics, it turned out to be certain performed basic methodology including the investigation of different levels of omics that include proteomic, metabolic, and transcriptional profiles, and the transition appropriations of those are fundamental for an increasingly exhaustive comprehension (Shen et al. 2018). Because specialized advances were found in the exploratory conventions, information examination, representation methods, the articulation, and movement of any quality, their associating accomplices and controllers in the entire framework can be learned whenever (Sussman et al. 2009). This coming of omics-based methodologies has in this way prompted examinations on naturally significant examples moving to a great extent from the "theory-driven" to the "information and information-driven" approaches (Mousavi et al. 2016; Zhang et al. 2017a, b). The "Omics" study can be divided into many issues which are been described in Fig. 12.2.

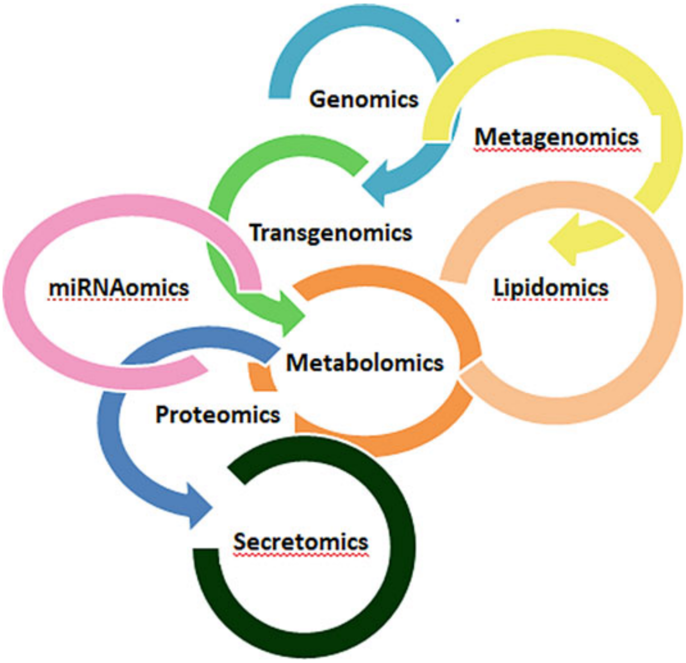

Fig. 12.2 The omics strategies for abiotic stress responses in plants

12.5.1 Genomics

Nowadays, the largely available genomic data of genes of plants are provided globally. Almost all partial or maybe complete sequences of complementary DNA (cDNAs) mostly provide the dimension of the transcriptome on a firm basis. There are three important databases, which are as follows.

- National Center for Biotechnology Information (NCBI)
- The Institute for Genomic Research (TIGR) Gene Indices, www.tigr.org; Sputnik, http://mips.gsf.de/proj/sputnik.
- Unigenes, http://www.ncbi.nlm.nih.gov/.

These serve to organize the available data from different resources, the plant expression sequence tags (ESTs), along with the characterization of genes which are non-redundant clusters of genes.

Genomics has been found to be the basic part of "omics" that manages all the genomic investigation and uncovers significant information about the living organisms (Gilliham et al. 2017). Some analysts have distinguished groupings of quality and intragenic conditions, and structures of qualities (Duque et al. 2013). This development of the studies of genomics have immensely helped by fast advancements in the innovation of the sequencing of the genome that has started in the year 1970s (original), proceeded into the mid-1990s and what's more, at present uses third-age sequencing advancements (El-Metwally et al. 2013, 2014). This investigation of genomics includes a progression of steps counting DNA extraction, intensification, sequencing, gathering, quality appraisal, and above all, basic and practical comment of the genome. This entire system gives significant information on the structure of the genomes of living beings. Utilitarian genomics has been effectively used in recognizing different qualities associated with the plant abiotic stress reactions (Govind et al. 2009; Ramegowdaet al. 2013, 2014; Zhang et al. 2017a, b; Wang et al. 2018). A large number of those qualities were effectively being used to creating abiotic stress open-minded harvest botanicals (Agarwal et al. 2014; Chen et al. 2012; Gilliham et al. 2017; Shankar et al. 2013). Moreover, the immense online genomic information created in time serve as an establishment for genome editing, transcriptomics, and proteomics (Alter et al. 2015; Mochida and Shinozaki 2010, 2011).

The investigation of ESTs created from cDNA libraries of focused study on the salinity of rice by Bohnert et al. (2001) demonstrated that there was an expansion in identified transcripts with cell salvage, protection, transport, vitality, and digestion, yet most of the stress-inducible qualities couldn't be appointed a capacity. In an examination performed to recognize salt pressure-inducible ESTs got from the polymerase chain reaction (PCR) deduction in salinity-independent rice, 384 qualities have been distinguished as salt responsive, approximately 5% of which were additionally established by Northern blotting investigation. Practically, half of these qualities were recognized for association in the stress reaction, detoxification, development, and improvement (Shiozaki et al. 2005). Furthermore, countless ESTs identified with abiotic stress in rice have been distinguished (Babu et al. 2002; de los Reyes et al. 2003; Sahi et al. 2003, 2006).

12.5.2 Metagenomics

The quantity of different microorganisms that are found to be colonized in plants can also reach in the density of a cell, a lot higher than the quantity of a plant cell. So also, the quantities of microbial qualities present in the plant rhizosphere are higher than the quantity of qualities present in a plant. The individuals from the microbiome rhizosphere and exhibit noteworthy impact on seed germinations, seedlings vigor, development and other advancements of plants, frequency of sicknesses and by and large efficiency by method of supporting supplement take-up, applying resistance against abiotic and biotic stresses and guideline of the plant insusceptible framework (Bakker et al. 2013; Berendsen et al. 2012; Berg et al. 2014; Lakshmanan et al. 2014; Mendes et al. 2013; Perez-Jaramillo et al. 2016; Turner et al. 2013). There are reports accessible where it was found that in just hardly any case of the normal determination in plants helps in gaining the obstruction against subterranean pathogens and the plant to a limited degree relies on the rhizospheric microorganisms for its protection against pathogens (Cook et al. 1995). The additional reports have mentioned that the particular microbial consortia present in the soils secure the plants from contamination by pathogens or are borne into them. Consequently, the plants gracefully have the carbon resources from which the rhizospheric microorganisms may be fed and thus decide their structure (Berendsen et al. 2012; Nelson 2004).

It was reported that two Open Reading Frames (ORFs) demonstrated a match with phasin and Clps, while these two shortened ORFs demonstrated a match with permease and poly-3-hydroxybutyrate synthase. Association of these particular ORFs appears in an encoded protein indicated to coordinate with almost 81% character to ATP-subordinate ClpS from *Erythrobacter sp.* NAP1 and Clp protease connector protein. These had moderated areas of the ClpS family (pfam02617, COG2127, PRK13019, PRK00033). Another found encoded protein indicated to coordinate with almost 55% character, phasin from *Erythrobacter sp.* SD-21 and this had monitored spaces of COG5490, pfam09361, the Phasin2 family. While another small encoded protein demonstrated a match with almost 63% personality to poly-3-hydroxybutyrate synthase from *Erythrobacter sp.* SD-21, it had shortened saved areas for PHA_synth_I, PhaC Poly (3-hydroxyalkanoate) synthetase (COG3243), PHA_synth_II, poly(R)-hydroxyalkanoic corrosive synthase, class II (TIGR1839) and poly(R)-hydroxyalkanoic corrosive synthase, and class I (TIGR01838). Another shortened encoded protein appeared coordinate with almost 78% personality to anticipate as permease, (YjgP/ YjgQ) from *Novosphingobium aromaticivorans* DSM 12444. This had shortened spaces for anticipated permease YjgP/YjgQ family (pfam03739) and anticipated permeases (COG0795) from permease YjgP/YjgQ family.

12.5.3 Transgenomics

Non-specific cleavages, causing alleged "askew" changes, can happen during genome altering and speak to a test that must be survived, particularly for clinical applications and in crop rearing. A few methodologies planned for dispensing with askew impacts and improving the explicitness of CRISPR/Cas9 were found to be reported (Fu et al. 2014; Ran et al. 2013). These blends of a changed adaptation of Cas9 (D10A, Cas9 nickase; Cas9n) and deliberately planned gRNAs (guide RNA) can work excellently in the explicitness of CRISPR/Cas9 (Jinek et al. 2012; Ran et al. 2013) and are powerful in staying away from askew effects (Mali et al. 2013; Pattanayak et al. 2013). The gRNAs, shortened at the 5′ end (17–18 nucleotides), can likewise diminish ask mutations (Fu et al. 2014). Further, it has also been accounted for that advancement of gRNA and Cas9 articulation levels can increment specificity (Fu et al. 2014; Pattanayak et al. 2013; Ran et al. 2013). In plant genome altering, askew effectiveness has been assessed utilizing Cas9 nickases (Fauser et al. 2014; Schiml et al. 2014), whereas off-targets may be maintained at a strategic distance by utilizing two nearby sgRNA target successions to manage the Cas9 nickases to produce a DNA twofold strand break (DSB) at the objective locus. In any case, these remaining parts form a region where further examinations are as yet expected to dispense with askew impacts in plant genome altering.

Plasma film proton (H^+)-ATPases are assumed to perform a significant job in the age of proton slopes in plant cells, enacting different auxiliary transporters including the take up of particles and metabolites (Osakabe et al. 2014; Palmgren 2001). There are 11 individuals from the plasma film H^+-ATPases in *Arabidopsis*, AHA1–AHA11 (Baxter et al. 2003), which are made out of N-terminal and C-terminal spaces in the cytoplasm and a transmembrane area comprising 10 helices including phosphorylation and nucleotide-restricting sites (Pedersen et al. 2007). The C-end is the major administrative space associated with the hindrance of H^+-ATPase, and enactment is constrained by phosphorylation in this locale and resulting connection with 14-3-3 proteins (Svennelid et al. 1999). Two predominant changes in the ost2 locus annul stomata react to abscisic acid (ABA), prompting constitutive movement of the proton pump (Merlot et al. 2007).

12.5.4 Proteomics

Proteomic examinations have given the recognizable proof of different responsive proteins of abiotic stress from those some of them may lead to be downstream regulators of the translation factors distinguished at the level of transcription. In addition, proteomics based on Mass Spectroscopy permit isoform explicit protein distinguishing proof, and thus can isolate explicit and imparted probabilities in a particular protein family. The degree of location is regularly monitored in transcriptomic examinations. Therefore, proteome-wide distinguishing proof and practical examination of proteins have turned out as an extra experience into the discoveries which are being acquired at the level of transcription and thereby profound superior comprehensive pathways of the abiotic stress reaction in plants. It has been summed up that different proteomic examinations have been performed with underlying foundations of various plant species developed under dry spell high saltiness, flooding or cold conditions.

Abiotic stress researches in plants are profound with an extraordinary scope of proteomic and transcriptomic examinations which give far-reaching data on adjustment articulation quality and profile of proteome during and following the condition of stress (Hakeem et al. 2012; Mizoi et al. 2012). At the level of transcripts, the reaction of abiotic stress was mostly concentrated from 30 min to 1 day after the acceptance of stress (Kilian et al. 2007). Precisely, the examinations done with near approaches in proteomics have been performed regularly on plants given to a specific pressure or for one day. This proteomic and trascriptomic time slips have been considered to be most likely to be dependent on the required time for the process of interpretation in the eukaryotes (Berthelot et al. 1973). Roughly, the qualities found to be receptive to flood are nearly half; extraordinary temperatures and salinity have been found to encode the controllers of transcription (Kilian et al. 2007; Mizoi et al. 2012). In this manner, translation factors have massively featured as abiotic stress controllers at the level of RNA investigations (Jaglo-Ottosen et al. 1998; Kasuga et al. 1999; Seki et al. 2001).

The effect of the invasion of salt on relative phosphoprotein enrichement has been considered by Kwon et al. (2006). Some of the activities have identified that there is a change in the post-translational improvement of some obstruction of citrus to salt stress (Tanou et al. 2009). The data have been found in addition to maintaining some agreement (Wu et al. 2013). Many researchers have also analyzed the proteome of the extracellular structure of drying out concentrated on the plants of rice (Pandey et al. 2010). Some articles indicated that the proteins related to hailing alterated sugar absorption and modified Reactive oxygen species (Pandey et al. 2010). In *A. thaliana*, *Brassica juncea*, *Glycine max L.*, and *Linum usitatissimum*, various researchers have commented to allude to get the understanding of the effect of the utilization of techniques in proteomics in Cadmium stress (Alvarez et al. 2009; Hradilova et al. 2010; Semane et al. 2010; Hossain et al. 2012; Ahsan et al. 2012). Different researches, furthermore, surveyed the effect of Aluminum, Boron, and Chromium (Alves et al. 2011; Duressa et al. 2011; Sharmin et al. 2012; Wang et al. 2013). On a similar note, *A. thaliana,* has been pondered by Yanguez et al. (2013) that the understanding of micro-RNAs efficiency under the temperature stress on the seedlings which were being used the genome-wide examination. In addition, the chickpea proteomic profile presented to cold stress conditions and also had been surveyed being completed (Heidarv and Amiri 2013). Moreover, considering the profile of protein in the nuclear of chickpea presented in the condition of drought (Subba et al. 2013). There are also researches that considered nuclear proteome relevant to this (Jaiswal et al. 2014). This found efficiency of sub-deadly ROS weight on the micro RNAs which was moved using the ribosome impressions arranging and it was done in the species *A. thaliana* (Juntawong et al. 2014). The research considered that under the drought conditions, there was an upregulation in some phosphorylated proteins, transporters, chaperones, and interpretation factors in the left phosphor proteome of wheat (Zhang et al. 2014). It has also dismembered that the tips of roots of soybean for nuclear phosphor proteome during the flood condition, uncovered about of different twenty seven phospho-proteins (Yin and Komatsu 2016). The uncovered proteins like H-2, 3 and 4 were controlled differently by critical chromatin upgrading. Wang et al. (2016) have found the different isoforms of S-adenosylmethionine synthetase in soybean in drought conditions and flooding also. The fibrillins proteins were conveyed differently under the drought stress (Kosmala et al. 2012; Urban et al. 2017). The researchers have thought to isolate the proteome from the leaf of chickpea. Besides, it also has been shown under the conditions, for instance, stresses related to temperature, dry season, and salinity on the leaf proteome (Santisree et al. 2017). They point around the proteins situated in the position of 590,797 and 248 were controlled differently, with the comparison of free imprint quantitative approaches of proteomics. It has also been reported that the proteome of chloroplast of dry season concentrated on tomato plants has been declared the crosstalk between the proteins from chloroplast with nuclear hailing proteins (Tamburino et al. 2017).

12.5.5 Metabolomics

Metabolomics is one of the promising methodologies which gives a biochemical preview of a life form’s phenotype. Metabolomics permits the orderly recognizable proof and evaluation of low-atomic weight particles that are firmly connected with significant toxicological and wholesome attributes. Information on qualities, proteins, and transcriptomes are insufficient to distinguish a cell totally; it is important to contemplate the wide scope of essential and optional metabolites present in a cell. Various investigations have been performed to comprehend the job of metabolites under high saltiness and drought conditions in plants. Methods like Gas Chromatography-Mass Spectrometry (Kaspar et al. 2011), CE-MS (electrophoresis-Mass spectrometry (Lee et al. 2012a, b), and NMR (Schripsema et al. 2010) have been utilized to read metabolites for stress reaction in plants. In many cases, the studies showed both abiotic and biotic stress reactions, among them there are no definite solutions for abiotic stresses.

In five cultivars of cherry tomato assortments, water stress came about in diminished shikimate and phenolic mixes (Sánchez-Rodríguez et al. 2011). Low oxygen stress can be actuated by capacity of foods grown from the ground under a closed environment. In another examination, the metabolic reaction of plant organs to low oxygen levels was analyzed and refined tomato cells were utilized for the metabolic examination to low oxygen. It was uncovered that low oxygen stress modified the metabolic profile of tomato cells by collecting the glycolysis intermediates notwithstanding expanded lactate and sugar alcohols (Ampofo-Asiama et al. 2014). The mix of metabolomics, linkage planning considerations, and metabolome-based genome-wide affiliation considerations (mGWAS) give thorough understanding into the degree of common variety in digestion and its hereditary and biochemical control in tomato (Zhu et al. 2018). As of late, Nunes-Nesi et al. (2019) led an examination to recognize leaf mQTL in tomato that were conceivably significant as for stress reactions and plant physiology. The examination recognized 42 positive and 76 negative mQTL which were engaged with the guideline of leaf essential carbon and nitrogen digestion (Nunes-Nesi et al. 2019). In reality, metabolomic concentrates in tomato have expanded comprehension of a few metabolite systems and pathways identified with numerous financial attributes. The utilization of metabolomics to consider abiotic stress will help to explain hidden atomic components related with stress.

Carbon/nitrogen digestion-related proteins, for example, α-mannosidase, trios phosphate isomerase, malate dehydrogenase, UDP-sugar pyro phosphorylase, phosphoglucomutase, NADP-malic catalyst, and UDP-glucose-6-phosphate dehydrogenase, were accounted for to be increasingly bountiful in foundations of soybean (Toorchi et al. 2009; Alam et al. 2010; Mohammadi et al. 2012), the wild watermelon (Yoshimura et al. 2007), and grape seed (Mohammadi et al. 2012) one day after dry season treatment. These has been mirrored an expanded vitality request just as improved cell exercises in the root tissues at this phase of the pressure. At the same time, local increment in root development rate was watched, which was additionally upheld by the bounty of development of root related to little G-protein relatives, for example, Ran GTPases (Yoshimura et al. 2007). This root lengthening can be the sign of an exertion by the root to ingest water from profound soil layers.

In plants, 250,000 metabolic substances were being seen (Kim et al. 2010). In this different condition of stress in plants, the number of absolutes, focus, and the metabolites have been essentially improved. These changes in quality articulation are legitimately reflected in the plant metabolite profiling. Picking up information on the significant metabolites that assume a fundamental job in the development, advancement, endurance, and their tweaking in the beginning of different abiotic stresses were exceptionally significant. These opened the degree for different distinguishing proof of practical markers of metabolomics which were found to be significant for abiotic stress (Freund and Hegeman 2017; Lafitte et al. 2006; Obata and Fernie 2012; Kumar et al. 2016; Parida et al. 2018). Different scientists have utilized the omics of metabolisms for dealing with the study of the profiles of metabolics in the plants in the named conditions (Bowne et al. 2012; Muthuramalingam et al. 2018; Shen et al. 2018; Skirycz et al. 2010; Srivastava et al. 2013a, b; Urano et al. 2009; Witt et al. 2012; Yang et al. 2014). Subsequently, it turned into a key apparatus in understanding the sub-atomic component hidden pressure reactions. Urano et al. (2009) oppressed the plants, *Arabidopsis thaliana,* to stress in the high temperature and uncovered collection of a few metabolites, such as proline, raffinose, the family of gamma-aminobutyrate, oligosaccharides, and a few metabolites of tricarboxylic acid cycle. Also, researchers exhibited that the transcriptional guideline of subordinated of ABA was answerable to the actuation of metabolic stress-related pathways. It has been contemplated that the transient profile changes putrescine, erythritol, proline by oppressing *A. thaliana* to gentle osmotic pressure (Skirycz et al. 2010). They additionally announced a normal connection between metabolites, the transcriptional reaction. Also, Verslues and Juenger (2011) uncovered osmolytes amassing during a dry season pressure reaction.

The researchers certified the capacity of beta chain amino acids as good osmolytes in different tissues of plants under pressure conditions. This aggregation of different proteins depends on the drying-up seriousness. This was affirmed by the amino acid profiling of maize and wheat submerged drying up (Bowne et al. 2012; Witt et al. 2012). In contrast, Colmsee et al. (2012) set up an information asset stage, in particular, OPTIMAS-DW to respond to various inquiries of maize science. It very well may be utilized to handle various information spaces as well with respect to the reconciliation of transcriptomics, metabolomics, proteomics, and ionomics information.

Amiour et al. (2012) utilized the coordination of proteomics, transcriptomics, and metabolomics studies to distinguish factors directing the control of digestion of nitrogen. So also, Srivastava et al. (2013a, b) archived an investigation on the quality of superoxide dismutase in the transgenic plant, Populus. Studies have given information on the handling stage that produced framework data on the level of ROS digestion. Some study area was focused to understand the uses of different omics approaches of the optional digestion (Yang et al. 2014). AbdElgawad et al. (2019) announced a-tocopherol improvement in the shoot of maize and also lofty decreament of ascorbic acid in the wake of exposing plants to salt stress.

Moreover, Wang et al. (2015) affirmed that in the seedlings of virginia, there was an upgradation of level of proline in the condition of saltiness. Shen et al. (2016) detailed the quick decreament in carbohydrate metabolism pathway, i.e., glycolysis in the grain under salinity. Besides, they watched in the peach plant that the collection of proline was presented in high temperature. As of late, Sun et al. (2018) evaluated the distinctions in the metabolome of maize with subsequent exposing to various stresses like heat, salinity, and dry spells. They concluded that the impact of individual stresses is unique in relation to the mix of stresses dependent on the metabolomics information. Khan et al. (2018a, b) evaluated an impact on chickpea of dry season on the metabolome of assortments utilizing untargeted innovation of the profiling of metabolics. The research revealed the huge decrease in relative water, development, dry weight, and content of chlorophyll. It has also revealed that a critical upgradation to the allantoin and expanded amino acids chains declined the sweet-smelling aspartic levels, amino acids, and also glucosamine.

12.5.6 Transcriptomics

Since the improvement of NGS, transcriptomes have been generally concentrated to pick up bits of knowledge into the atomic instruments by which plant species adjust to their conditions. Right now, transcriptome information investigations of plants act in different life forms under assorted conditions, including introduction to abiotic stresses. Most transcriptomes consider including abiotic stresses that have been acted in model plants, with a couple of studies looking at crops rewarded with a couple of various worries at a specific plant advancement stage (Cohen and Leach 2019; Coolen et al. 2016; Kang and Yeom 2018; Liu et al. 2015; Ma et al. 2017a, b; Rasmussen et al. 2013). Accordingly, similar restricted transcriptome investigations for plants reacting to various abiotic stresses have been performed.

Numerous investigations have uncovered subtleties of the signal transduction pathways that are actuated by individual stresses (Haak et al. 2017b). For instance, abscisic acid (ABA) and related pathways are actuated by dry spell stress, the ICE-CBF-COR flagging pathway is started by cool obstruction, and the SOS pathway is instigated by salt stress (Chinnusamy et al. 2007; Jiet al. 2013; Shinozaki and Yamaguchi-Shinozaki 2006). Besides, comparable administrative segments including shared quality articulation designs, physiological markers, and phenotypic attributes have been demonstrated to be associated with dry season, cold and high-saltiness stresses. In some plant species, the acceptance of cold opposition additionally advances dry spell obstruction and high-saltiness resilience, which is predictable with an expansion in the degrees of osmotic pressure mixes and anti-carcinogenic agent catalyst activities (Hossain et al. 2013b). In different investigations, a cover between the articulation examples of stress-responsive qualities in citrus (Oliveira et al. 2011), grape (*Vitis vinifera*) (Zandkarimi et al.2015), poplar (*Populus sp.*) (Yoon et al. 2014), tea (*Camellia sinensis*) (Wang et al. 2017a, b), *Arabidopsis thaliana* (Seki et al. 2002), maize (*Zea mays*) (Li et al. 2017a, b), and other plant species were seen after dry spell, cold and high-saltiness stress enlistments.

Overexpression of stress opposition qualities engaged with one kind of stress can improve protection from different burdens, further recommending complex cross-guidelines of various pressure-flagging pathways. For instance, the overexpression of DREB2a, which has been recognized as a dry spell obstruction quality, in transgenic *A. thaliana* and Lotus corniculatus rummage plants, brought about improved resilience to both dry season and salt stresses. Under stress, the transgenic plants were taller and had longer roots, raised degrees of solvent sugars and a lower substance of malondialdehyde contrasted (Zhou et al. 2012). Antioxidase GPX3, ordinarily thought to be a crucial forager of responsive oxygen species (ROS), additionally assumes a significant job in ABA-intervened stomatal conclusion under dry spell worry because of the oxidation of ABI1 and ABI2 by GPX3 (Miao et al. 2006; Zhou et al. 2013). Past investigations have uncovered qualities and pathways that were associated with different abiotic stresses and possibly helpful contender for hereditary building to improve numerous pressure resistance.

Transcriptome examination has been broadly applied to investigate and recognize differentially communicated qualities (DEGs) engaged with plant development, natural product improvement and stress hormone regulation (Kumar et al. 2016; Wang et al. 2017a, b; Rehman et al. 2018). The accessibility of the apple draft genome grouping gives a chance to definite investigation of stress opposition qualities and their interpretation; notwithstanding, as opposed to *A. thaliana* (Matsui et al. 2008; Sham et al. 2014), maize (Shan et al. 2013), and rice (*Oryza sativa*) (Rabbani 2003), little has been accounted for about transcriptome changes in apple in light of dry spell, cold and high saltiness. Here, we depict RNA-seq examinations of apple plants developed under dry spell, cold or intense high-saltiness stress to distinguish shared administrative pathways, key useful qualities or sign transduction segments engaged with the mentioned burdens.

Muthusamy et al. (2017) broke down the guideline of transcriptions and articulation levels difference of warmth stun wheat protein 20 (HSP20) relatives under dry spell, salt, or warmth stress. One research was carried out in cassava with a wide genome transcriptome examination and anticipated around 299 putative individuals from myeloblastosis (MYB) quality family (Ruan et al. 2017). Also, they announced the differential articulation of numerous MYB qualities exposed to conditions of dry and cold spells. Researchers stated that four individuals from a superfamily reacted on the treatment of ABA. In addition, it was found that in dry conditions, MeMYB2 went about as a negative control and in cold resistance utilizing RNAi innovation (Ruan et al. 2017). Some studies have distinguished and assessed in cotton plants, the differential articulation example of around 17 individuals from the family of PIN efflux. Moreover, it was announced the qualities of containing salicylic and the response of auxin components in those advertiser areas. In another occurrence, Shen et al. (2018) utilized innovation of genomic studies for evaluating the levels of articulation of HD-Zip quality plant, tea, and five unique medicines. As of late, Wang et al. (2013) distinguished around 95 grape essential helix-circle helix (bHLH) qualities utilizing a wide genomic investigation which considered a difference of bHLH family. Moreover, the 22 and 17 bHLH qualities were found and that were prompted under osmotic pressure and the cold pressure, individually. Three different qualities were identified with optiomal metabolite amalgamation utilizing GO work explanations. These quality advertisers can contain G-box components that assume the job of recognization (Wang et al. 2017a, b).

12.5.7 Lipidomics

Lipidomics has been utilized to describe living thing types and their metabolic movement over expanded time scales. Biogeochemistry, one of the most well-known regions of ecological lipidomics to date, is the investigation of changes across time; what's more, space in the dissemination of concoction components (e.g., C, O, N, S, and P) instigated by creature action. Deciding the huge scope effects of biological systems on the earth requires a comprehension of the metabolic procedures that move substance components from one sub-atomic structure to another, and consequently, influence essential vehicle and capacity. Lipids can be saved in fossilized substrates, silt, and icy masses, in this way giving significant data on biological system forms and their impact at geographical time scales not realistic by means of visual assessment of fossil records (Ouahabi and Grimalt 2017). Without a doubt, unsaturated fats, specifically soaked species, can stay flawless for hundreds of a huge number of years (Nes 2012).

At the point when *Chlamydomonas reinhardtii* starved for nitrogen in fixed stage within the sight of exogenous acetic acid derivation, those cells experience a 15-overlap increment in lipid body creation inside 48 h, and these lipid bodies comprise 90% triacylglycerol and 10% free unsaturated fat (Liu et al. 2013). A difference in starch/lipid proportion with expanded lipid creation was seen under nitrogen hardship conditions, even in a hereditarily starchless freak *C. reinhardtii* (Li et al. 2010a). RNA-seq and hereditary examination illustrated that three acyltransferases, namely DGTT1, DGAT1, and PDAT1, were found to have a job in triacylglycerol collection in *C. reinhardtii* under nitrogen starvation (Boyle et al. 2012). Sulfur, phosphorous, zinc and iron lack likewise brought about expanded lipid content in *C. reinhardtii* and the other numerous algal species (Guschina and Harwood 2006; Khozin-Goldberg et al. 2006; Kropat et al. 2011; Reitan et al. 1994; Urzica et al. 2013). In any case, intense and complete nitrogen hardship additionally stops development of algal biomass. An ongoing metabolic building report presumed that shunting carbon antecedents from the starch union pathway is more compelling for expanded triacylglycerol combination than adirect control of lipid pathways (Li et al. 2010b). In the meantime, encompassing temperature has a noteworthy impact on the intracellular unsaturated fat of green growth, for example, *Chlorella vulgaris* and *Botryococcus braunii;* be that as it may, there was no impact on the substance of acidic lipids sulfo-quinovosyl-diacyl-glycerols and phosphatidyl-glycerols in *C. reinhardtii* when temperature changed (Sato et al. 2000; Sushchik et al. 2003). Light can likewise influence the lipid digestion in green growth. Normally, when green growth developed at various light power, it can incite the development of various types of lipids (Fabregas et al. 2004; Khotimchenko and Yakovleva 2005).

Most as of late, it was indicated that under fractional nitrogen hardship, biochemical rebuilding of pathways empowers *C. reinhardtii* cells to hold typical paces of cell division with a considerably more adjusted guideline of lipid biosynthesis (Lee et al. 2012a, b). This report had just dissected the guideline of biosynthetic catalysts and essential metabolites (Lee et al. 2012a, b), yet not the impact of halfway supplement weight on the redesigning of complex lipids. We along these lines presently supplement this investigation by thoroughly breaking down the family member creation of complex lipids in *C. reinhardtii* utilizing shotgun lipidomics, a technique that has been demonstrated to be an amazing asset in worldwide lipid investigation in an assortment of animal types and organs (Han et al. 2005; Schwudke et al. 2007). Shotgun lipidomics utilizing triple quadrupole mass spectrometry with direct mixture as of now gives 158 clarified lipid species in plant extricates (Welti et al. 2005).

Such focused-on techniques are an exact, however, may miss novel or unreported lipid species. In particular, the lipid structure of *C. reinhardtii* had been concentrated with increasingly great instruments, for example, slight layer chromatography (Giroud et al. 1988; Giroud and Eichenberger 1989; Vieler et al. 2007; Li et al. 2012) and hardly any examinations with chromatography coupled mass spectrometry (Vieler et al. 2007; Liu et al. 2013). Many lipid species were identified including digalactosyldiacylglycerols (DGDG), phosphatidylglycerols (PG), phosphatidylinositols (PI), monogalactosyldiacylglycerols (MGDG), l, 2-diacylglyceryl-3-O-4′- (N, N, Ntrimethyl)-homoserine (DGTS), phosphatidylethanolamines (PE), sulfoquinovosyldiacylglycerols (SQDG), and triacylglycerols (TAG).

12.5.8 Micromics

The class of noncoding ribo nuclic acids, micro RNAs (miRNAs), that control the endogenous post-transcription. They are assumed to have roles in each part of flagging (Sharma et al. 2017), improvement (Hernandez and Sanan-Mishra 2017), and natural reactions (Hernandez and Sanan-Mishra 2017). Suggesion has been given on the originated reaction of micro-RNAs association with abiotic stress (Jones-Rhoades and Bartel 2004). These are being announced that in *Arabidopsis*, the upregulation of miR395, specifically during starvation of sulfate. This particular miRNA was seen as focusing on the sulfate compounds which acted as tansporters in osmosis (Jones-Rhoades and Bartel 2004). A short time later, numerous analysts additionally announced the job of different miRNAs in abiotic stress resilience (Chauhan and Kumar 2016; Hivrale et al. 2016; Khaksefidi et al. 2015; Song et al. 2017). Almost 400 micro RNAs are being accounted for in the stress of abiotic conditions in different species of plants from various families like *Solanaceae, Apocynaceae, Poaceae, Papaveraceae, Rosaceae, Amaranthaceae,* etc. The micro RNAs react in tissue protein, related to stress, genes of genotype, and micro-RNA-subordinate way (Zhang 2013) to abiotic condition.

The micro-RNA development works on plants varies in pathway since they do not have a Drosha homolog. Rather, the RNase III chemical DICER-LIKE 1 (DCL1), which is homologous to creature Dicer, is required for miRNA development (Papp et al. 2003; Park et al. 2002; Reinhart et al. 2000; Xie et al. 2004). In plants, DCL1 is limited in the core and can make both the principal pair of cuts made by Drosha and the second pair of cuts made by creature Dicer. As for creature Dicer, a dsRNA-restricting area protein accomplice, HYL1, has been ensnared in DCL1 work in plant miRNA development (Papp et al. 2003; Vazquez et al. 2004). The subsequent miRNA/miRNA* duplex is traded from the core by HASTY (HST), the plant ortholog of Exportin 5, furthermore, finishing its get-together into the RISC in the cytoplasm (Park et al. 2005; Peragine et al. 2004). Not all creature miRNAs ended with free 2 and 3 hydroxyl gatherings as they had a methyl bunch on the ribose of the last nucleotide. The terminal methyl bunch is included by the S-adenosyl methionine (SAM)-subordinate methyltranferase HEN1, and the change of the miRNA by HEN1 either shields the miRNA from further change or debasement, or then again may encourage its gathering into the RISC (Boutet et al. 2003; Yu et al. 2005). In plants, RNA-subordinate RNA polymerases may utilize little RNAs as preliminaries to blend twofold abandoned RNA from deviant single-abandoned transcripts, raising the likelihood that the terminal methoxy alteration on miRNA serves to forestall miRNA from going about as preliminaries.

12.6 Conclusion

Plants are presented to an assortment of abiotic stresses all through their lifetime on earth. Be that as it may, people began to consider abiotic stress reactions and resilience following the training of economically important plant species to boost crop yield. Numerous upsetting conditions cause aggregation of low atomic weight natural mixes, perfect solutes or osmolytes, stress-explicit proteins, LEA proteins, heat-stun proteins, phytochelatins and metallothioneins, and bring about actuation of numerous detoxification chemicals. Albeit totally extraordinary plant species have variable limits for pressure resilience, and a couple of them can effectively endure extreme burdens and still total their life cycles, most developed yield plant species are exceptionally delicate and either bite the soil or experience the ill effects of efficiency misfortune in the wake of being presented to extensive stretches of stresses. Accordingly, the understanding and improvement of stress resistance in crops present a difficult fundamental examination issue as well as have noteworthy effect on rural efficiency. Although significant endeavors have been made during this course, a few examination holes should be satisfied.

Genome altering is reforming crop rearing to the cutting edge for its few valuable highlights, for example, usability, exactness, straightforwardness, high particularity, and okay objective impacts. Genome altering as a progressed sub-atomic science strategy can create absolutely focused changes in any plant yield. It has given accessibility to an assortment of alterations of genome in various ways, and these are critical for thinking about an ideal framework. In various advancements previously reported to the improvement of genome-altering instruments and the improvement of new achievements, genome altering vows may get on quickening reproduction and achieving the expanding worldwide food interest. Additionally, change in environmental issues plays incredible adaptability, also in the development flexibility of crops and creation frameworks. For the utility of genome altering devices to improve in the harvest, the resistance of plant for abiotic stress, yield upgradation, quality of crops, healthy benefits, and another significant agronomic characteristic will be unmistakable work zones. All the work is being done by utilizing genome altering innovations where been primer and does need other improvement for using this effectively in all stages which prompts expanding to the track adequacy, along these lines the worldwide food security for the developing population in the whole world.

Framework science approaches have given an increasingly all-encompassing perspective on the atomic reaction in plants once presented to abiotic stress, and furthermore, the incorporation of different omics to have uncovered another zone of communications and guidelines. The joining of numerous omics innovations and coexpression association investigation of qualities will be useful in quickening abiotic stress resistance research soon. Coexpression examinations are helpful in which they have uncovered key administrative centers that can be controlled to deliver various phenotypes. The linkage of key administrative center points to phenotypic qualities will be taken into consideration increasingly for fast advancement in the hereditary control and yield output of harvest plants. Framework science is in a creating stage but then the future appears to be extremely optimistic as it offers a stage to help the worldwide exploration endeavors devoted to gathering data about every single segment of a given framework. The job of formal numerical and computational models in frameworks approaches renders the job of bioinformatics progressively significant for framework science research. Subsequently, it can be securely anticipated the framework that will turn out to be considerable in progressively inescapable in future.

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Chapter 13
Plant Probiotics: Technical Challenges and Emerging Solutions for Enhancing Food Crops

Ramna Zia, Malik Nawaz Shuja, Muhammad Ali, and Muhammad Sohail Afzal

Abstract The increased and non-judicious use of pesticides and fertilizers has associated complications on the human, animal and plant health. They may accumulate in water and soil to reduce diversification of croplands, limit nutrients availability and diminish genetic diversity of the associated microbes, flora and fauna. Chemical pesticides and fertilizers are also known to impart global warming, insect, animal and human genetic disorders and diseases. Plant probiotics, thereby enhancing plant health, growth and production, not only reduce/minimize the use of chemical pesticides and fertilizers but also are helpful reclaiming the soil beneficial for all living organisms. However, there are certain shortcomings and challenges associated with the use of plant probiotics. This chapter circumvents the studies covering, in general, the origin, classification, mechanism of action, and in specific, the perspectives and challenges using plant probiotics.

Keywords Biofertilizer · Phytohormone · Plant growth promoting rhizobacteria · Rhizobiome · Siderophores

13.1 Introduction

Lack of resources to feed the continuously increasing human population of the world is a major problem. In this scenario, agriculture is one of the main resources of food production, and through this we may overcome the problem by the production of enough food and nutrients. But the reality is not the same as as per our expectations. Rigorous agriculture has increased the pests and disease occurrence and promoted the use of pesticides. This wide-ranging agriculture is based upon the practice of

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increased levels of fertilizers (Devi et al. 2020b). These pesticides and fertilizers contaminate the ecosystem affecting the humans, animals, plants and accumulate in the water and soil (Thakur et al. 2020; Kumar et al. 2021; Sharma et al. 2021). So many problems are associated with the intensive agriculture, including reduction of the diversification of croplands, shortage of soil nutrients, genetic diversity loss, contribution to global warming etc. These issues are becoming more serious in those areas where population is increasing day by day, like in Asia and Africa (Pimentel et al. 2012). With the advent of different food production procedures, food safety and eminence, the consumers have become more mindful and conscious (Trienekens and Zuurbier 2008).

Probiotics are considered as useful live bacteria of gut and yeast which are beneficial for the digestive system. Also, these probiotics are good for plants and soil too. Specifically, when the harmful microorganism overcomes the useful microbes then disease may occur. The same case applies to the plants and the soil. In contrary to the microbes stealing the nutrients and infect the soil, probiotics are the microbes that not only help the plants against harmful microbes but also convert the organic materials for the growth and health of plants.

Probiotics are usually useful microorganisms, especially the bacteria. They are recommended for the treatment of almost every disease, starting from digestion and even includes depression. But the probiotics are not only useful for the animals or humans, they also maintain the balance among useful and harmful bacteria in soil and plants. Useful microbes help the plants to grow healthier, attain larger size and stronger defense mechanism (Kour et al. 2021; Yadav et al. 2021b). Plant probiotics are the microorganisms which produce beneficial effects on the plants when they are administered to plants in specific amounts (Bashan and De-Bashan 2005; Jiménez-Gómez et al. 2016). In addition, they also belong to the bacterial group plant growth promoting rhizobacteria (PGPR) as they can colonize the plant roots (García-Fraile et al. 2017; Güneş et al. 2014; Kour et al. 2019; Yadav 2021).

Plant growth promoting bacteria (PGPB) and rhizobacteria (PGPR) promote plant growth by performing various activities, while probiotics (for life) have been defined as live microorganisms which, when administered in adequate amounts, confer health benefits to the host according to the World Health Organization (WHO). By definition, the term plant probiotics should replace PGPB or PGPR, but these terms are well established among the researchers in the last two to three decades. The term PGPR or PGPB as plant probiotics do not make any big difference. The question that arises here is why one want to do this?? Just to make it catchy for the consumers (i.e. farmers), many biofertilizer companies are already doing this, or to attract the researchers working with gut microbes toward the plant–microbe interactions study, as the former considered being bit low-ranked research in comparison to later. So, we can say that PGPB and PGPR are quite informative and simple terms to address the group of bacteria which improves plant growth, health and productivity. PGPB and PGPR are well-known terms and informative enough. Earlier, they were plain biofertilizers, and then bioinoculant arrived and now slowly the plant probiotic. For example, taking picture of self with auto click camera was very much there earlier, but suddenly, a ‘selfie’ using cell phone is rage. Who knows, a change of word could attract more customers to biofertilizers, hopefully.

Some plant probiotics are endophytes microbes living inside the plant cell. Plant endophytes perform similar functions for plants as probiotics do for humans in enhancing resistance against disease. Many endophytes like the bacteria that fix nitrogen (N) help the plants to absorb nitrogen from soil and air (Rana et al. 2020).

According to recent studies, the crop production has increased many folds by using different bacterial strains. It has shown that these strains not only increased yield/production of plants, they also have many nutritional benefits associated with it. The microorganism-based products reported recently include, but not limited to using, *Pseudomonas*, *Azotobacter* and *Bacillus* (product name Phylazonit MC®) having positive effect on tomato yield (Le et al. 2018), *Azospirillum brasilense*, *Pseudomonas fluorescens* (product name Rhizoflo premium Maìz™) for increased maize grain yield (Di Salvo et al. 2018), *Paenibacillus mucilaginosus* for N, phosphorous and potassium mobilization in soybean (Ma et al. 2018), *P. fluorescens, Pseudomonas* sp., *Serratia* sp., and *Enterobacter* sp. for increased crop height and arial/pod biomass in oilseed rape (Lally et al. 2017), *Bacillus siamensis* in sweet pepper improved N use efficiency (Pastor-Bueis et al. 2017a), *Pseudomonas oryzihabitans* and *Bradyrhizobium japonicum* increased soybean plant growth (Kuzmicheva et al. 2017), *Azorhizobium* sp., *Azoarcus* sp. and *Azospirillum* sp. (product name TripleN®) wheat crop resilience to environmental stresses (Dal Cortivo et al. 2017), *Serratia marcescens, Microbacterium arborescens,* and *Enterobacter* sp. increased wheat growth and yield, *Pseudomonas aeruginosa* for N uptake efficiency in sunflower (Arif et al. 2017), *Pseudomonas rhodesiae, Paenibacillus polymyxa, Rahnella* sp., and *Serratia* sp. for improved crop height of switch grass (Shanta et al. 2016). For extensive lists on the efficacy and significance, see Marcia et al. (2019); Stamenković et al. (2018); Olivares et al. (2017); Glick (2015) and Ferreira et al. (2019).

The role of bacteria in improving the food and crop quality is also reported in different studies. In order to achieve the benefits to the plants, specific and efficient PGPR is selected. And for this selection, the relation and interaction among plants, bacteria and different environmental factors are considered. The environmental factors are deeply associated intense with the growth and efficiency of bacteria (Trivedi et al. 2012). Plant probiotics help the plants to live in stressful environmental conditions. Like these microbes help the plants to survive with less water, hotter weather and in saltier soil, the types of stresses which are becoming common nowadays. To conclude, the microbial communities which are associated with plants depend on the ecosystem development factors. The objective of this chapter is to analyze the importance of plant probiotics in the context of changing agriculture trends and the growing world population, while considering environment, health and sustainability.

13.2 Overview of Plant Probiotics

13.2.1 Origin of Plant Probiotics

The term plant probiotic bacteria (PPB) was first introduced by the Haas and keel to indicate a group of useful microbes benefiting plants. These microorganisms mainly help the plants in the following main three ways: (i) Increasing efficiency in niche establishment, (ii) the capability to generate induced systemic resistance (ISR) in the host, and (iii) defending against incompatible pathogens. This term PGPB was proposed by Kloepper and Schroth (1980) (Kloepper et al. 1980a). PGPB are naturally occurring soil bacteria having the ability to increase productivity and immunity in plants in a beneficial way (Prasad et al. 2021). The main roles of these bacteria are, but not limited to:

(a) Supplying nutrients to the plants
(b) Initiating the plant growth by the production of phytohormones
(c) Reduce the activity of plant pathogens
(d) Improvement of soil structure
(e) Bioaccumulation or microbial stealing of the inorganic compounds to form soil.

13.2.2 Classification of Plant Probiotics

Plant probiotic bacteria are classified into two subgroups based on their relationship and interaction with the host plants:

i. ***Free-living rhizobacteria*** that live outside the plant cell, thereby increasing the plant cells growth with the help of metabolites that they release in rhizosphere.
ii. ***Endophytes*** that live inside the plant cells that directly exchange the metabolites with the host cells, thereby increasing the growth of plant effectively.

Endophytic bacteria lives within the plant tissues or the intracellular spaces (Gray and Smith 2005; Hardoim et al. 2015). But in some cases, they penetrate inside the host cells by forming a true mutualistic relationship with host. Rhizobia are the best-known mutualistic symbiotic bacteria to fix the N for host plant. They form the symbiotic association with the leguminous plants in a specialized root structure called root nodules (Brewin 1991). A large number of microorganisms especially bacteria are present in rhizosphere. They have symbiotic and non-symbiotic relationship with the plants by which they not only benefit the plants but also get nutrients for their own survival. That's why rhizosphere is called as the “House of microbes” due to the presence of a large number of microbes and microbial activities. Rhizobiome is the community of microorganisms which are linked with the plant roots. Their composition differs according to the stages of growth of plant roots. These microbes can be pathogenic and beneficial too (Kundan et al. 2015). Plants probiotic bacteria benefit the plant by nutrient uptake through different ways:

(a) Changing the nutrients of soil
(b) By making nutrients accessible to plants
(c) By increasing the plants access to those nutrients (Menendez and Garcia-Fraile 2017).

Along with these, the plant probiotic bacteria also have many other features to promote the plant growth, for instance, the phytohormone biosynthesis (Menendez and Garcia-Fraile 2017).

13.3 Mechanism of Action of Plant Probiotics

Plant growth can be improved by rhizobacteria with the help of different mechanisms, which are basically divided according to their mode of action (Fig. 13.1) given as below:

i. The synthesis of the elements which are taken directly through plants

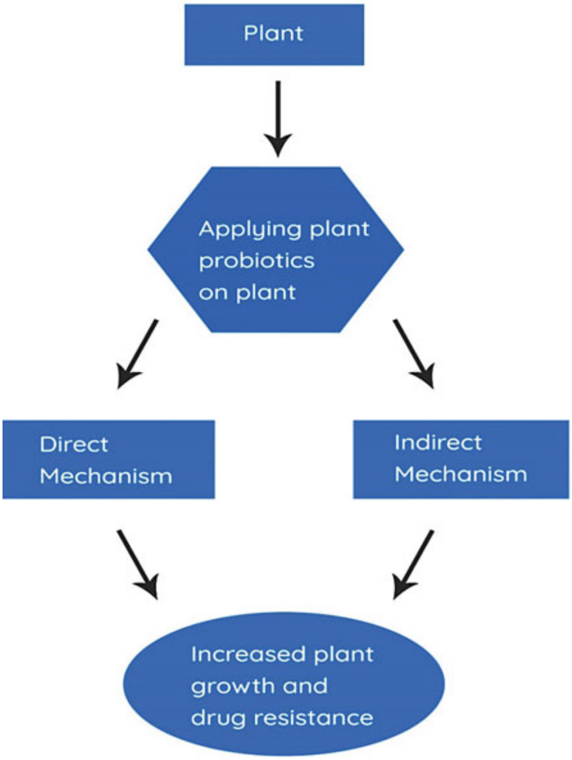

Fig. 13.1 Mechanism of action used by the plant growth promoting bacteria in plants

ii. The measure of the nutrients
iii. The initiation of the resistance against plant stress
iv. Inhibition of plant diseases.

The plant probiotics have two types of mechanism of actions which are direct and indirect. They are described in detail as follows.

13.3.1 Direct Mechanism of Action

In the direct method, those bacterial traits are used which help in the direct growth of the plants. They include the production of auxins, N fixation, ACC deaminase (1-aminocyclopropane-1-carboxylate deaminase), cytokinin, gibberellin, phosphorus solubilization and sequestration of Fe by the bacteria siderophores (Mondal et al. 2020; Hesham et al. 2021). These mechanisms help the plant to improve their growth and quality directly, but these actions vary from species to species on different plants. Organic compounds which stimulate and improve the plant growth are called as the plant growth regulators. At very low concentration, they stimulate plant growth by interacting with the physiological and morphological processes. Some direct methods are explained in the following sections.

13.3.1.1 Nitrogen Fixers

N is quite abundant on the Earth. But it is required in very less amount to the plant for the formation of proteins and synthesis of amino acids. Some prokaryotes have the ability to convert the atmospheric nitrogen directly into organic nutrients which are taken up by plants. Nitrogen fixation is the process in which atmospheric nitrogen is converted into the utilizable nitrogen that changes to ammonia. Biological nitrogen fixation usually takes place at mild temperatures with the help of nitrogen-fixing bacteria (Rana et al. 2019b). The complex of enzymes which help in the N-fixing process is called as "Nitrogenase complex". Along with the free-living *rhizobacteria*, members of the genera *Azospirillum, Azotobacter, Beijerinckia, Bacillus, Paenibacillus, Burkholderia, Gluconacetobacter* and *Herbaspirillum* are also N-fixing microorganisms. The members of genus *Azospirillum* are found in the temperate zones and linked with the cereals by growing their crop yield. They are also related to the sugarcane and leguminous plants (Sahoo et al. 2014; Tejera et al. 2005). Members of genus *Azotobacter* are involved in N fixation in the rice crops as well as some species of this genus has also been involved in several cereals, like oat, barley, wheat, rice, oil plants and other plants as the biofertilizers to improve their growth rate (Wani et al. 2013). Some species from the genera *Gluconacetobacter*, *Azospirillum* and *Herbaspirillum* are elaborated as the endophytes in the sugarcane plant for N fixation. The members of the genus *Herbaspirillum* are also involved as the endophyte in several crops for N fixation, and these traits make them suitable for application. Many species also live inside the root tissues and form connection with the root nodules and fix the nitrogen, for example, symbiosis between rhizobia and legumes and cyanobacteria and cycads (Chowdhury et al. 2015; Kao et al. 2003).

13.3.1.2 Phytohormone Biosynthesizer

Phytohormones are the chemical messengers that play important roles in the growth. They are organic molecules involved in many processes of the plant development at different stages. These phytochromes help in shaping the plant, affect the seed growth, senesces of leaves and flower sex is determined by them. They also affect the gene expression, levels of transcription method, cell division and growth of cell. During the plant growth, all the major activities like flower formation, seed development, cell division, ripening of fruit and response to stress all are controlled by phytohormones (Tiwari et al. 2020). Under many stressful conditions, PGPB helps in altering the levels of phytohormones in response. Many endophyte bacteria have the ability to synthesize these phytohormones. Biosynthesis of the phytohormones by different microorganisms may cause the plant pathogenesis. But many beneficial bacteria have the ability to produce these hormones for the positive growth of the plants (Trewavas 1981; Tiwari et al. 2020). Some beneficial phytohormones involved in the plant growth and development include auxins, cytokinin, gibberellins and ethylene.

Auxins are the phytohormones which are produced by different bacteria and these hormones help in coordination between different activities in plant cell body. Indole-3 acetic acid (IAA) is one of the well-known auxins which is most active in plants (Spaepen et al. 2007). Cell elongation, cell division, differentiation and extension are the major roles of the IAA in the cell. Members of *Bacillus* sp., which produce auxin in plants exert the positive effects on the development of several crops, like in potato and rice. IAA is synthesized by different pathways and is mostly produced in the buds and young leaves. It also plays a broader role in leaf and stem abscission and is known to help in DNA synthesis. Tryptophan plays an important role in the production of IAA as a negative feedback process (Suman et al. 2016).

Cytokinins also play an important role in the cell division of roots and shoots of plants. They usually help in improving the cytokinesis in plant cells (Kour et al. 2020). They also increase the sensitivity of vascular cambium and enhance the vascular differentiation and apical dominance in root cells so that farmers use the cytokinin for increasing the overall growth of plants (Arkhipova et al. 2007). Members of the *Bacillus* sp. also produce cytokinin in different plants, like in cucumber. In the same way the thuja seedlings which are inoculated with the cytokinin have more resistance against stress than simple seedlings.

Gibberellins are naturally produced by plants and mostly increase the seed germination in plants (Rai et al. 2020). They are also involved in stem and leaf growth, as well as in the flower induction process. They also help in the fruit development process and enhance the process of seed germination, sex expression and stem elongation (Bottini et al. 2004). *Bacillus cereus* enhances the growth rate in red pepper plants by producing gibberellins.

At the end, ethylene is the simplest molecule known for the regulation of several processes in the plant. It induces many different physiological changes in plant cells during growth. Ethylene increases the fruit ripening and flower blooming process. It also helps in the leaf abscission. Moreover, it also helps in the seed germination process as well as in the formation of secondary root and elongation of root hairs too. According to the species of plants and the types of tissues, the production of ethylene also varies. By the breakdown of methionine, which is present in all plant cells, the ethylene is formed. Mostly in the darkness it is produced in dividing cells. The most important effect of ethylene is fruit ripening and that's why it is also called as aging hormone in plants. Ethylene has a simplest structure and it is produced in plants during the extreme conditions like extreme temperature, flooding and radiations exposure etc. (Tiwari et al. 2021; Yadav et al. 2021a) (Suyal et al. 2021). Some bacteria produce ACC deaminase in stressed conditions to regulate the production of ethylene. To obtain ammonia and α-ketobutyrate, the ethylene precursor (ACC) is hydrolyzed. This obtained ammonia and α-ketobutyrate is then used for N and carbon source in plants. Therefore, bacteria maintain the ethylene level in the plant cells to prevent the plants from negative effects of high concentration of ethylene. Ethylene which is produced as a result of stressed conditions is called as "stress ethylene" (Sharaff et al. 2020). ACC deaminase was first obtained from the *Pseudomonas* and they help the wheat seedlings in growth. *Rhizobia* and related species also produce ACC deaminase. However, by using the ACC deaminase in combination with *Rhizobium* increases the growth and quality of mung beans under saline stress conditions. In the same way, when *Serratia* and *Pseudomonas* ACC deaminase are used in combination, they increase the product yield of wheat plants under saline conditions (Zahir et al. 2009).

Genus *Paenibacillus, Enterobacter* and related *Enterobacteriales* and *Rhizobia* all of them are known as phytohormones producers in different crops, like rice, barley, wheat, pepper, tomato, red carnation, wheat plant crops, lettuce, carrot etc. (Yanni et al. 2001, 2016).

13.3.1.3 Nutrient Mobilizers

Plant probiotic bacteria usually act as the phosphorus (P) and potassium (K) solubilizers in the plant cells. They also help in the siderophores production within pant cells. After N, P is the second largest essential nutrient required in plants for their growth. Due to its insolubility in soil, this element is provided to plants exogenously in the form of chemical P fertilizers. But it becomes insoluble rapidly when this is applied as fertilizer and plants can't uptake it (Yadav et al. 2020). Since most of the soils don't have phosphorus in adequate amounts and farmers cannot afford the expensive phosphate fertilizers, therefore, the P-solubilizing bacteria (PSB) are a great replacement of these toxic and environment destructive P fertilizers. To solubilize the phosphate, bacteria mainly use two methods, that are:

a. Releasing the organic acids and affecting the mobility of phosphorus by ionic interaction
b. By release of phosphatases which unbind the phosphate group from the organic compounds.

Many of the soil bacteria like genera *Micrococcus, Pseudomonas, Bacillus, Paenibacillus, Deftia, Azotobacter, Klebsiella, Pantoea* and *Flavobacterium* are the common bacterial species which act as the efficient phosphate solubilizers. Many other species of plant probiotic bacteria also act as the beneficial microbes and improves the growth of strawberries, ornamental plants, legumes, tomato and pepper (Peix et al. 2001; Schachtman et al. 1998).

The third most demanding essential nutrient for plants is K after N and P. Insoluble K forms are also available produced by some forms of rhizobacteria (Verma et al. 2017). Many types of K-solubilizing bacteria are present in nature. Along with *Firmicutes*, there are many examples of K-solubilizing bacteria including the genera *Bacillus* and *Paenibacillus. Bacillus* increased K uptake in wheat plants. *Paenibacillus* is known to increase the dry weight of the black pepper. In the same way, the plants inoculated with *Bacillus* and *Paenibacillus* showed more growth rate and increased plant biomass. Plants with the K-solubilizing bacteria also have more chlorophyll in their leaves. Moreover, in the cucumber, eggplant, pepper, groundnut, tea plants and in the tobacco plants the K-solubilizing bacteria shows the positive effects on growth and development. By increasing the K content in the plants increases the process of translocation. A higher volume of fruits is obtained through the translocation of carbohydrates from leaves to the fruit (Bagyalakshmi et al. 2012; Zhang and Kong 2014).

Iron is one of the most abundant elements, but it is not available to plants in adequate amount. It is present mostly as ferric ions which are not soluble in water. However, plants require the large amount of iron for their growth. Siderophores are the small iron chelating peptide molecules with low molecular weight (~400–1000 Da) and they have side chains with which ferric ions can bind easily. In case of Fe^{3+} deficiency, these siderophores fulfill the deficiency with the help of soil microbes. In stress conditions, they are known to help plants to cope with stresses. Furthermore, they could be species-specific. The mechanism of supplying the Fe to plant cells through the soil microbes is not known yet. The strains of *Rhizobia* are well-known siderophores and they improve the health and growth of carrot, lettuce, pepper, tomato, strawberry, red carnation and chickpea. Siderophores like *Phyllobacterium endophyticum* (promotes strawberries production), strains of genera *Micrococcus* and *Stenotrophomonas* (improve the growth of canola and maize) and *Chryseobacterium* (supplies Fe to famished tomato) help in improving the growth and production of plants (Maheshwari et al. 2019; Radzki et al. 2013).

13.3.2 Indirect Mechanism

Disease control through the application of microorganisms is an environment-friendly approach (biological control). The biocontrol bacterial ability is known to help improving plant growth indirectly. This indirect use is of considerable interest in (i) the development of understanding these primary mechanisms and which biocontrol bacteria is used, and (ii) use of the biocontrol bacteria commercially instead of chemical pesticides.

13.3.2.1 Antibiotic and Antifungal

In the indirect methods, the plant growth promoting bacteria involves the ability to lessen the harmful effects of certain plant pathogens on the plant growth. The production of antibiotic and lytic enzymes is the main feature of the plant growth promoting bacteria. This production of antibiotic compounds prevents the propagation of fungal and other pathogenic components in plants. They can also reduce the deleterious effect of plant pathogens on the growth rate. Lytic enzymes, like chitinase, cellulases, 1,3-glucanases, proteases and lipases, can lyse the cell walls of many harmful bacteria. In the same way, many antibiotics are also produced in resistance to many propagating pathogens in the plants (Kundan et al. 2015; Devi et al. 2020a).

But the main disadvantage of depending too much on antibiotics producing bacteria as biocontrol agents is the development of resistance against the specific antibiotics. To prevent this, scientists have applied the hydrogen cyanide producing biocontrol strains and one or more antibiotics at a time. This method is so useful because due to much less bioactivity of hydrogen cyanide, it acts with bacterially encoded antibiotics synergistically. Bacteria also act as the antagonistic agents by the production of more than one type of antibiotics against the phytopathogens and fungi, including *Botrytis cinerea*, *Sclerotium rolfsii*, *Fusarium oxysporum, Phytophthora* sp., *Rhizoctonia solani,* and *Pythium ultimum* (Frankowski et al. 2001; Glick et al. 2007; Kim et al. 2008).

13.3.2.2 Induced Systemic Response

PGPB also have the ability to trigger another phenomenon in plants which is called as induced systemic resistance (ISR) and it is phenotypically likely for the process of systemic acquired resistance (SAR). SAR occurs when defense system initiates in response to an infection by pathogens in plants (Pieterse et al. 2009).

ISR is the mechanism in which at some particular sites of plants (where infection occurs) the resistance increases many times than other parts. In the process of ISR, the defense occurs only when pathogens attack on plants and only ISR positive plants react faster against the pathogenic attack. ISR is considered as the first line of defense as it is not generalized response and is not specific any particular pathogen. Within the plant, ISR involves the jasmonate and ethylene signaling, and these hormones activate the defense system of host against the attack of different pathogens (Verhagen et al. 2004).

13.3.2.3 Production of Siderophores

Another mechanism is the production of siderophores to prevent the plants from some pathogens by reducing the amount of iron which is available to pathogens. Siderophores are the small peptide molecules having side chains and functional groups for binding with ferric ion. They act as iron chelators and iron carriers (Rana et al. 2019a). They have high affinity for some ligands. Large number of siderophores have been screened and used by microbes and they might be species-specific too. PGPB which secrete the siderophores prevent the plants by proliferation of pathogens through the production of siderophores with a high affinity for iron. These siderophores bind to most of the Fe^{+3} into the host plant. This prevents the pathogens from attaining the iron for their growth. So, pathogens can't thrive into host due to lack of iron because this lack of iron cause them to lose the ability to act as pathogen. The effectiveness of this method is based on the reason that PGPB siderophores have much higher affinity for iron than fungal siderophores (Kloepper et al. 1980b).

13.3.2.4 Competition

Although it is not easy to demonstrate but some evidences show that competition among PGPB and pathogens reduces the chances of disease and infection sternness. For example, non-pathogenic microbes which are present abundantly colonize rapidly on plant surfaces and use most of the available plant nutrients. This makes difficult for pathogens to grow efficiently. Like in the series of experiments, scientists showed that when plants are treated with leaf bacterium *Sphingomonas* sp., it prohibited the bacterial pathogen *Pseudomonas syringae* from triggering the pathogenic effects (Innerebner et al. 2011).

13.3.2.5 Quorum Quenching

For the detection of similar bacteria in the environment, bacteria follow the process of quorum sensing. In the growing bacterial cells, when they acquire the desired cell density, the mature bacterium senses the cell density through chemical signaling and starts altering the metabolism through turning on the different related genes. In this way, the proximally corresponding bacteria start working in a coordinate way (Cornforth et al. 2014).

Mostly, bacteria synthesize low molecular weight chemical molecules called auto inducers which are secreted outside the cell. By the increase of bacterial cell population, the level of auto inducers also increases. It increases to a threshold level and at this level they bind to the bacterial cell receptors and causes change in gene expression of bacteria. Through this change, the pathogenic bacteria become more virulent at a specific cell density. By disturbing the quorum sensing, the increase in virulence of pathogens can be decreased or stopped to inhibit plant growth (Chan et al. 2011).

For the quorum quenching, there are many methods. One of them is using lactonase producing PGPB. Lactonase degrades the plant pathogens which produce autoinducers. Seedlings are also pre-treated by these PGPB to avoid the pathogens. This clever trick is successful in laboratory till now but haven't applied in field yet (Glick 2015).

13.3.2.6 Phage Therapy

The lysis of some bacterial pathogens can be done easily by using the bacteriophages. And this process of treating bacterial infection with the phages is called as phage therapy. This process is used against plant pathogens in case of plant wilt diseases. It can also be done by the use of bacterial viruses (Álvarez and Biosca 2017). The bacterial phytopathogen must be identified well to make this trick successful. It is also possible to isolate such bacteriophages which can lyse the only targeted strain and won't disturb the other strains. In this method, a mixture of two or three different types of bacteriophages which are against the targeted pathogen is sprayed over the diseased plant. We use the mixture of two or three different strain to avoid the risk of formation of bacteriophage resistant mutants of the targeted pathogen. It might happen due to the presence of different binding sites of bacteriophages on the target cell surface (Glick 2015).

Bacteriophages are sprayed onto the targeted plant in the dusk when UV light intensity is so low because bacteriophages are so sensitive to UV light. And with such precautionary measures, bacteriophages needed to spray daily, weekly or monthly to avoid the pathogenic attack on the plant (Buttimer et al. 2017). Recently, few bacteriophages have been licensed as biocontrol against bacterial spot of pepper and tomato causing bacterial pathogen *Xanthomonas campestris pv. Vesicatoria*, cancer disease causing pathogen *Pseudomonas syringaepv. Actinidae* in kiwi fruit, and bacterial speck causing pathogen *Pseudomonas syringae pv. Tomato* in tomato crops (Linus et al. 2017; Peitl et al. 2017; Yu et al. 2016).

13.4 Plant Probiotics and Plant Nutrient Content

Nowadays, scientists are working on different methods to improve the quality of food for a better and healthy life. They are trying to improve food quality by getting food with more nutrients in different ways, just like vitamins are essential for life and their deficiency in food and body can result in many severe issues. Due to importance of vitamins the WHO presented a proposal to improve the essential vitamins and nutrients in the food to overcome such malnutrition problems.

Vitamins are the most essential nutrient and are highly recommended to intake in daily dose. Berry crops are considered as one of the good sources of the vitamins in our diet. Berry crops also have the anticarcinogenic and antimutagenic properties. By introducing the plant (PGPB) in berry crops the amount of vitamin B9 increases to the double level and makes the fruit nutrient filled. According to the literature, it is also revealed that some vitamins have the antioxidant properties. For instance, strawberries are a good source of antioxidants, specifically due to their anthocyanin contents. By inoculating the plant growth promoting bacteria in combination with mycorrhizal fungi results in increased level production of anthocyanin in the strawberries.

Tomatoes are the best-known antioxidants. They are one of the most cultivating crops in the world which are used for such studies. The amount of vitamin C and phenols increases in the tomatoes when they are cultivated with the induction of *B. licheniformis.* Basil is a medicinal plant and used worldwide for cooking. Its antioxidant activity increases when it is treated with three bacterial species: *Pseudomonas* sp., *Bacillus lentus* and *Azospirillum brasilens.* Also, a noteworthy change in leaf chlorophyll is also observed. Peppers are economically significant agricultural crop and they are also well-known antioxidants. Peppers show higher antioxidant properties when they are introduced with *Rhizobium leguminosarum* (Silva et al. 2014).

Carotenoids play an important role in the prevention of plants from the photooxidative damage and maintain the structure of the plant. A red-colored carotenoid named lycopene is present in tomatoes and act as anticarcinogenic compounds in human diet. Nowadays, scientists are trying to increase the carotenoids in crops (due to their importance) by using the biofertilizers which are based on bacteria.

PGPB have acquired multiple ways through which they facilitate the plants through nutrients availability and absorption, and further enhance quality and growth. For example, they fix N, solubilize phosphate and produce phytohormones for nutrients uptake and improving absorption in plants. By using the PGPB, the usage of chemical fertilizers can be reduced to protect our environment and can increase the plant growth (Bhardwaj et al. 2014).

Vegetables, rich in dietary nutrients, fibers and phytohormones can also be improved by using the PGPB. For example, broccoli vegetable is full of dietary nutrients and phytohormones and is used widely all over the world. By applying the PGPB (*Bacillus cereus, Brevibacillus reuszeri* and *Rhizobium rubi*) to the roots of broccoli increases the yield rate of it. As well as, these bacteria also increase the amount of nutrients (N, P, K, Ca, S, Zn, Mg, Fe and Cu) and chlorophyll in the vegetable (Yildirim et al. 2011). In the same way, the strains of *Azospirillum brasilense* Sp7 and *Bacillus sphericus* can be used as biofertilizers to increase the nutrients content (N, P, K, Ca and Mg) and they also increase their growth and product yield rate (Vayssières et al. 2009).

13.5 Plant Growth Promoting Probiotics and Omics Technologies

Different advanced technologies have empowered us to gain familiarity about structure and functioning of microbes which are associated with plants growth. For the selection of efficient bacterial strains having improved traits like uptake of nutrients and biotic and abiotic tolerance, the advancements in omics technologies are helping a lot by exploring the metabolic and regulatory network in plant–PGPB interactions. Omics technologies help to disclose the whole accompaniment of DNA, RNA, proteins and metabolites of the soil microbes which affect the plant development and help in stress lenience. Microbiome affects those plant traits which are involved in growth and development. This microbiome is shaped by various factors involving temperature, pH and exudates from microbes (Lakshmanan et al. 2014). Potential PGPB can be linked with enhancement of plant health with the help of multiple data taken from bioinformatics, statistical tools and in silico models. Association of a specific group of bacteria with a treatment group can be enabled by the statistical tools (Rebollar et al. 2016).

For the management of microbiome to heighten plant functioning and increase the soil health, omics technologies play an imperative role in the rhizosphere engineering (Fig. 13.2). Through rhizosphere engineering the bacteria are engineered by known signaling networks and players which are tangled in plant–PGPB interaction and this led to negligible or no environmental impacts (Baltrus 2017; Quiza et al. 2015). The identification of novel mechanisms which are involved in the interactions among plants and PGPB can be done by massive genomic sequencing. Many of the plant and pathogen species are completely sequenced, assembled and annotated. For example, the two bacterial species, *Pseudomonas* and *Xanthomonas,* contribute to plant–microbe interaction expressively (Quirino et al. 2010). Proteins which are involved in plant innate immunity are identified by the extracellular proteome map of PGPB *Bacillus amyloliquefaciens* FZB 42 and it plays an important role in the establishment of plant–microbe interaction (Kierul et al. 2015).

Growth of microbes is enhanced by the specific plant genotypes. Now the rhizosphere can be re-engineered by inoculation with microbes with the help of new tools. These inoculating microbes form a connection with innate microbiome which is vanished due to unnecessary use of chemical fertilizers (Wallenstein 2017). For example, the main molecule surfactin which acts as a signaling molecule for communication with other microorganisms and stabilizes the metabolism of carbon and synthesis of fatty acids is released by *Bacillus amyloliquefaciens* strain. To understand the mechanisms of biotic and abiotic stress tolerance in PGPB-inoculated plants, the comparative proteomic studies can be helpful (Zhi et al. 2017).

Metagenomics and meta-transcriptomics provide the ability to study the common microbial functions that are based on the individual microbial population and exist in a microbial community. A latent approach to screen the communication between different strains at the molecular level is the system-wide omics technology paired with computational approaches (Müller et al. 2016). Machine learning approaches

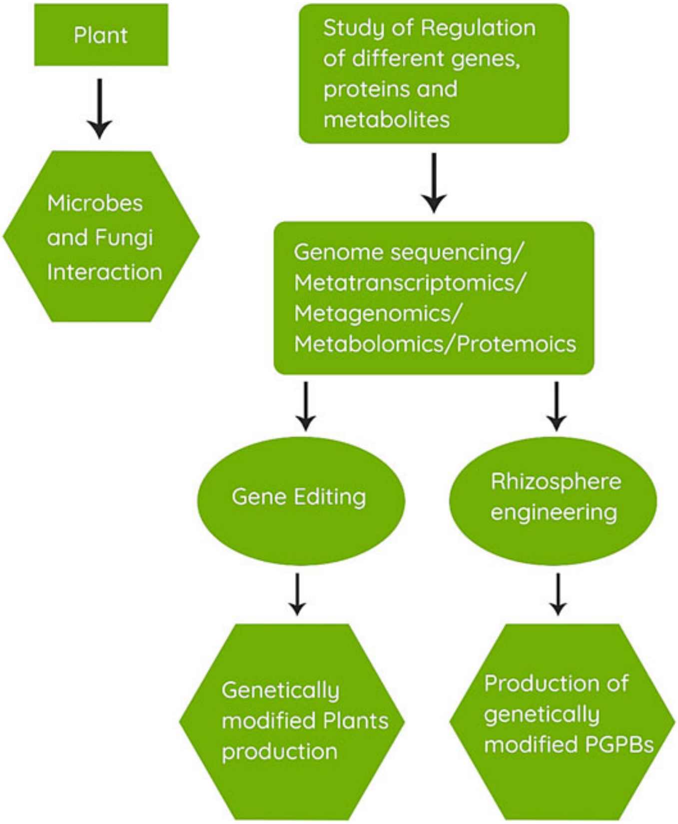

Fig. 13.2 Applications of OMICS technologies and plant probiotics

can also be used to predict the ratio of productivity which is based on PGPB composition (Chang et al. 2017).

Metabolomics offers comprehensive information concerning biological pathways which are involved in each experiment. It also gives evidences about gene to metabolite interaction. For example, *Streptomyces hydrogenans* strain, which is a soil microbe, produces a compound which acts against the *Meloidogyne incognita* and fungal phytopathogens as the potential nematicidal agent (Kaur et al. 2016). For the prediction of gene function and regulatory networks, metabolomics has provided many tools with the help of other omics like transcriptomics and proteomics. Overall proteomics and metabolomics can be used for the screening of those significant PGPB strains which can be used for the crop management and commercialization of bioformulations (Urano et al. 2010).

To analyze the protein–protein and protein–metabolite interactions and for the construction of gene networks, the data from transcriptomics, metabolomics and proteomics can be used widely. Similarly, next-generation techniques are also used to study efficient significance of the PGPB antibiotic resistance and its significance to plant growth endorsing activity. Omics technologies not only help in finding out the protein and biological pathways for crop growth improvement but also unveil the PGPB working and their interaction with host plant and soil in different environmental conditions (Crofts et al. 2017; Pretali et al. 2016).

13.6 Perspectives and Challenges of PGPB Applications

Development of PGPB on the commercial scale was initiated more than 100 years ago. In the beginning of 1900s, *Bacillus thuringiensis* was the very first commercial asymbiotic which was discovered as an insect pathogen. The first commercial biopesticide was the Sporeine, which is a compound based on *B. thuringiensis.* In 1983, it was available in France. In the 1960–1970s, the serious development of industrial products started which were based on *B. thuringiensis.* Due to tremendously increased practice of chemical fertilizers, the damage to natural environment has increased to a hazardous level. Because of this unsafe usage of chemical fertilizers and the increased knowledge about plants and soil relationship, it has increased the development and use of biofertilizers on large scale. The progression has also initiated the segregation and assortment of best plant growth promoting competences by direct or indirect methods to improve the plant growth.

Since 1950s in many countries, new types of fertilizers based on PGPB have been available due to their positive and best effect on agricultural growth. The process of development of PGPB is so complex as it requires highly trained and experienced specialists of various fields. On the commercial scale the product must be produced on large scale, well preserved and formulated in a way to ensure the biocompatibility for commercial delivery (Fig. 13.3).

13.6.1 The Global PGPB Market

The markets of biofertilizer and biopesticide are divided on the basis of type of product, active ingredients on the product, application method, geography and type of crops. The PGPB are commercially used as biofertilizers and biopesticides. According to the Transparency Market Research report that up to 2014 the market value of global pesticides was US $1.72 billion. It is expected to touch US $4.17 billion by the year 2023. Out of the total chemical market, the biofertilizers market is representing only 5% currently. It is due to dominance of N-fixing organisms over the global biofertilizer market because nitrogen is an essential compound for the plants. According to survey, in 2013 the North American region had the highest demand for biofertilizers. Also, it is reported that the highest growth for biofertilizers in the years 2013–2019 is in the region of Asia Pacific (Yaish et al. 2016).

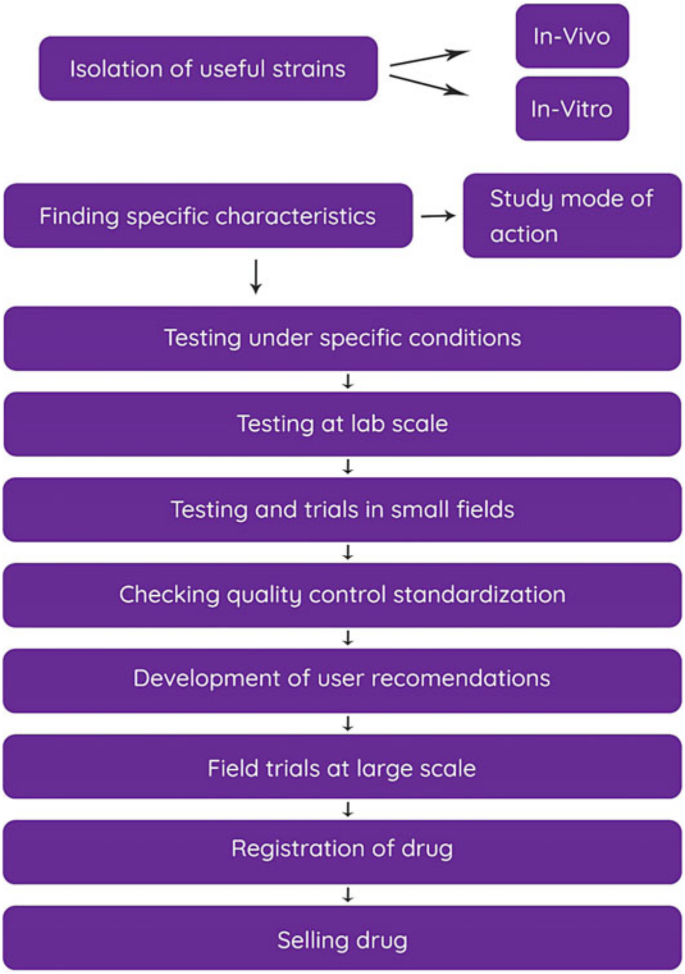

Fig. 13.3 Stages of development of plant probiotics at commercial scale and in laboratory

13.6.2 Challenges with Commercial Application of PGPB Products

According to literature study, the use of PGPB as biofertilizers and biopesticides is increasing day by day in agriculture. In many developing countries, bacteria are used effectively mainly due to the additional benefits, like they produce renewable environment-friendly compounds that may enhance soil fertility as well as activate the soil biology. Furthermore, PGPB also can reduce the load of abiotic stress in the soil (Bharti et al. 2016; Sharma et al. 2016; Timmusk et al. 2014, 2015; Timmusk and Wagner 1999).

One of the main points is the specificity of the PGPB, as the conventional chemicals for agriculture are broad spectrum products and have effects on multiple types of organisms. But on the other hand, PGPB are highly targeted and specific. This can result in variable results by efficiency and eminence of the product. Several new approaches will be required to apply the PGPB products for the growth, shipping, storage and application of these products when they are taken out of laboratories and greenhouse to field and large-scale commercialization field. In the same way, one popular myth is that bacteria are not good for health and they only cause diseases. That's why before the commercialization this must be addressed widely so that society could accepts the positive aspects and benefits of PGPB in agriculture.

13.6.3 Challenges in Product Registration

The process of regulation and documentation of the PGPB products is not without complications and is time taking. Any PGPB product cannot be used commercially without registering it with the health department. The active agent within the biofertilizer must be registered and authorized by directorate general for health and consumer affairs. This process may take from months to several years. Different countries respond with the different requirements according to their soil fertility and climate. High fees are implemented, and this differs country wise.

13.6.4 Antibiotic Resistance of PGPB

Many of the bacterial strains isolated from the soil are used in the greenhouse conditions and as inoculants to improve the plant growth. But these bacterial species have the antibiotic resistance genes (ARGs). These ARGs are more dominant in the Proteobacteria and Bacteroidetes and may create hurdles in the application of PGPB in the field (Crofts et al. 2017; Kang et al. 2017). Overuse of the antibiotics in the animals farming and in the pharma engineering is the main cause of spreading of ARGs in the soil. Many of the known PGPB contain more than one chromosomal and plasmid-borne ARGs, based on genome sequencing data. In some soil, bacteria plasmids contain the *bac* gene which persuades the resistance against bacitracin produced by *Bacilli* (Li and Ramakrishna 2011).

In the major groups of reported PGPB, antibiotic resistance associated with these microbes is ignored widely. So, there is an imperative need to contemplate these adverse facets before applying them into the field. To exploit the advantageous features which are linked with PGPB, various methods are used. It includes the use of microbes having a little of ARGs and optimization of metabolite production for the plant growth in the PGPB. In the same way to avoid antibiotic resistance, genome editing tools like CRISPR/Cas9 can also be used (Perron et al. 2015; Van Goethem et al. 2018).

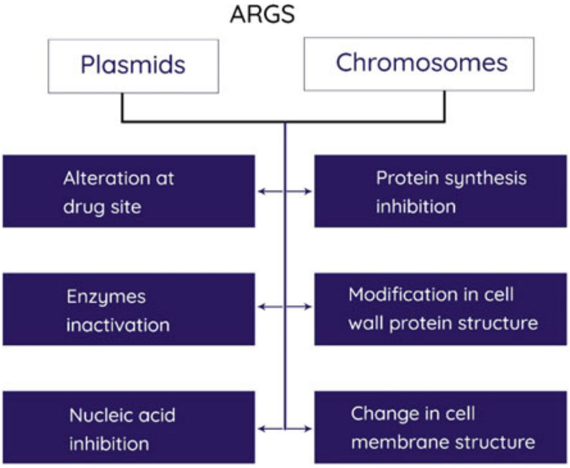

Fig. 13.4 Mechanisms involved in the antibiotic resistance of plant probiotics

In the soil bacteria, modern anthropogenic activities are also contributing in antibiotic resistance. In these strains such types of genes are present which deliberate the resistance against tetracycline, penicillin, carbapenem, cephalosporin, beta-lactam, aminoglycoside and chloramphenicol, as they are naturally produced by soil bacteria. In the antibiotic resistance different mechanisms are involved including interference with cell wall synthesis (e.g., β-lactams and glycol-peptides), cell membrane inhibitors (polymyxins and daptomycin), protein synthesis inhibitors (tetracycline, chloramphenicol, aminoglycosides) and nucleic acid synthesis inhibitors (fluoroquinolones and rifampicin). Many bacteria also show the intrinsic resistance against antibiotics (Fig. 13.4). For example, many gram-negative bacteria show intrinsic resistance to antibiotics because they cannot cross the outer membrane. As in the case of vancomycin, which targets the D-Ala-D-Ala peptides involved in the peptidoglycan cross linking is only effective in gram-positive bacteria and not in the gram-negative bacteria (Cytryn et al. 2017; Koskiniemi et al. 2011). It is not clear yet either antibiotic resistance is due to exposure of antibiotics in PGPB or due to production of antibiotics by PGPB. But some evidences indicate that the reason for this resistance is the presence of ARGs.

13.7 Conclusion and Future Prospects

The main objective of PGPB application is the production of important properties like biological activities to target the plant. This needs advanced approaches so that the product can find the targeted location easily. In the last decade, technology has provided us advancements to comprehend the interaction between PGPB and crop plant. Due to increasing costs of agrochemicals and demand for green technologies in the society, there is a high demand of the PGPB, and it is increasing day by day.

According to an estimate, about 12% increase per year in PGPB has been reported in the global market (Calvo et al. 2014).

Insights into the mechanism by which PGPB improves plant growth have revealed an understanding about different angles of disease suppression by these biocontrol agents. But despite of these researches and knowledge, the results are not always the same as expected when applied to the field. So, there is a need to find out the natural microbiome of each plant and then design the PGPB only specified to that plant which will be based on plant's needs and environment. The productive efficiency of a PGPB must be more enhanced by considering the soil conditions. At present, the commercial production is achieved by using many PGPB like *Burkholderia, Pseudomonas, Rhizobium, Azospirillum, Azotobacter, Bacillus and Serratia* sp. in a large scale. But under the field conditions, the main holdups are consistency, shelf life and efficiency of the PGPB. For example, gram-negative bacteria have shorter life span compared to the gram-positive bacteria. So more basic research is needed in future to maximize the shelf life of PGPB while enhancing the plant colonization. Some of the PGPB are also reported as the opportunistic human pathogens like *Burkholderia cepacia and Pseudomonas aeruginosa.* These PGPB cause risks for human health ecologically. Before the manufacturing of such kind of PGPB at the commercial scale they must be addressed appropriately. Another aspect which needs to be highlighted is the optimization of the fermentative process to produce microorganisms at industrial scale. The cost of growth media to produce microbes must be cheap and feasible and for that residues can also be used (Pastor-Bueis et al. 2017b).

As PGPB can provide multiple benefits including high production rate of crops, pathogen control and soil remediation, there is a need and potential to identify the new PGPB specifically from the extreme environments for their downstream applications. Further advancements in the high throughput technology to identify, characterize and find out the production of microbes will lead to efficient and increased utilization of PGPB in the field. The future of PGPB is based on its acceptance as a green technology. Green technology provides better commercial and ecological paybacks as compared to the chemical manures. Now as a main player of the green technology, there is a window for PGPB to be successful in the upcoming days. But it is the one side of the coin. On the other side of coin, the possible negative impacts of PGPB due to antibiotic resistance and the lack of long-term studies on the effect of PGPB on the soil microbes can be seen clearly. At present this facet of the PGPB is unheeded by the scientists fully with the available knowledge which is not adequate and equivalent to the tip of an iceberg.

Finally, these apprehensions can be addressed by directing the field trials of PGPB for several years. Theoretically, it is possible to achieve multiple responses by applying microbes onto plants. However, it is sometimes difficult to observe the same effects of microbes onto plants in the field even if it is observed in lab under controlled conditions. Also, by considering the changes in plant growth and PGPB by using the omics technologies which is tailed by the study of targeted biomacromolecules (genes, proteins and metabolites) the future of PGPB can be revolutionized (Ramakrishna et al. 2019).

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Chapter 14
Biofertilizers: Microbes for Agricultural Productivity

Fatemeh Salimi and Javad Hamedi

Abstract The world has witnessed explosive population growth, which requires an efficient food supply. To this end, various efforts have been performed in agriculture among which the applying chemicals with anti-pest and fertilizing activity was a strategy of choice. However, implementation of such compounds has shown to have serious drawbacks, from the reduction of naturally occurring organisms which control the pests to the concerns arisen from environmental pollution. Therefore, the discovery and development of biological strategies have attracted much attention. Accordingly, there are well-known plant growth-promoting microorganisms (GPMs) with great potentials in improving the growth of plants via providing nutrition and alleviating biotic and abiotic stresses. Herein, a comprehensive study was performed to gather together the most updated knowledge on these mechanisms.

Keywords Agricultural applications · Biofertilizers · Microbiomes · Sustainability

14.1 Introduction

Different soil properties such as its texture, structure, and nutritional ingredients directly influence plant growth, among which, the latter property shows great importance. There are non-minerals (hydrogen, oxygen, and carbon), and minerals (macronutrients and micronutrients) obligatory for the growth and development of plants. Carbon dioxide and water provide non-minerals for the plant (Taiz 2010), while the latter is obtained from the soil. Since plants consume large amounts of some macronutrients such as nitrogen, phosphorus, and potassium, these components exist

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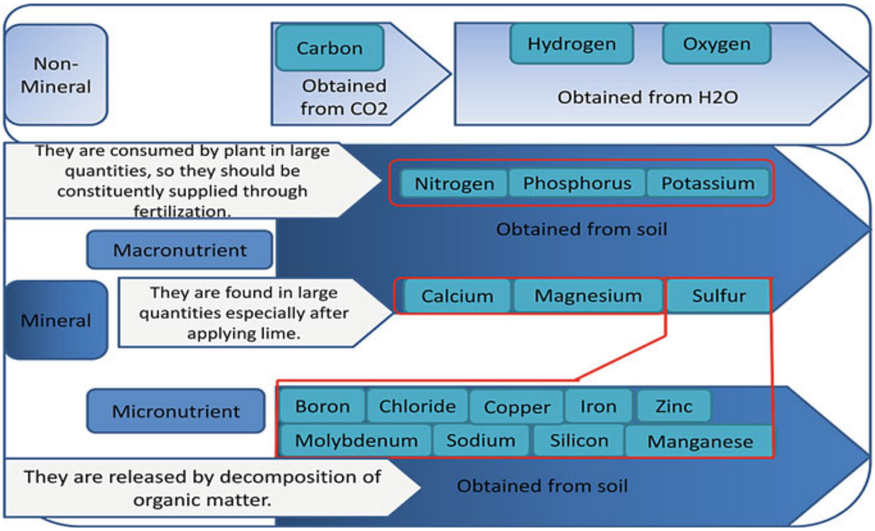

Fig. 14.1 Essential mineral and non-mineral nutrients for plant growth

in very low quantity in nutrient-depleted soil, while other macronutrients like calcium and magnesium are found abundantly in the soil under normal conditions, especially whenever lime is applied to reduce soil acidity. Macronutrients, e.g., sulphur, and micronutrients including boron, copper, iron, chloride, manganese, molybdenum, and zinc are released by the slow procedure of organic matter decomposition (Hänsch and Mendel 2009; Yadav et al. 2021) (Fig. 14.1).

Bioavailability of these nutrients for plants is dependent on their amounts in the soil, the soil composition, as well as its physicochemical characteristics like nutrient and water retention, and oxygen content of the soil which are influenced by soil texture, the proportion of soil ingredients or components like sand, silt, clay and organic matter (Bronick and Lal 2005). High content of clay and organic matter leads to a considerable level of nutrient and water retention, and in some cases, it results in waterlogged soil and thus depletion of oxygen content. In this condition, aerobic respiration and nitrate production are ceased. On the other hand, nutrient uptake becomes difficult in soil containing a high level of sand, due to their leaching and entering to groundwater (Galloway et al. 2008). Soil structure, aggregation of soil particles, determines productivity; because it directly affects the movement of water and oxygen, availability of nutrient, and microbial activity within the rhizospheric regions of plants (Bronick and Lal 2005). Soil pH is also an influential factor in the bioavailability of nutrients. The macronutrients and micronutrients show less bioavailability at high and low pH levels. The slightly acidic pH range due to promoting root growth, nitrogen fixation, and sulfur conversion to sulfate, releasing minerals, and increasing carbonates, sulfates, and phosphates solubility, is suitable for plant growth (Taiz 2010). In sum, the soil contains essential elements, and its physical, chemical, and biological characteristics influence plant growth (Fig. 14.2).

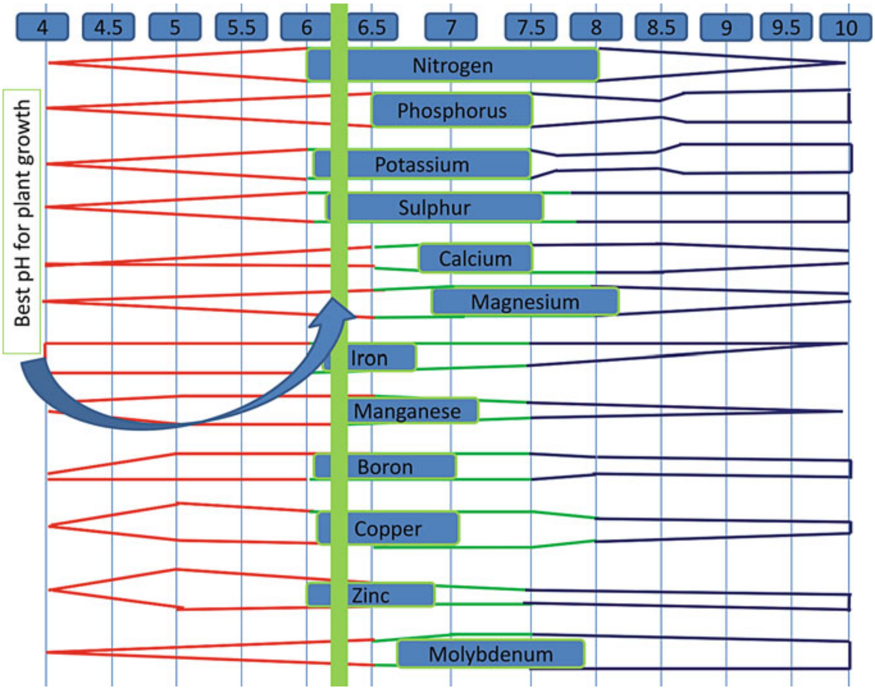

Fig. 14.2 Availability of macro and micronutrients in various pH. Distance of upper and lower lines indicates its bioavailability for living organisms

14.2 Fertilizers as Plant Growth Boosters

It has been predicted that the world population will be undoubtedly increased to 10 billion around 2050, with an annual increase of 97 million (Conway 2012). Therefore, the inevitable increasing demand for food and the falling ratio of cultivable lands will be a serious challenge. According to FAO, an unacceptably high portion of people are undernourished (FAO 2010). To ameliorate this need, fertilizers and pesticides have been consumed to achieve enhanced productivity through promoting plant growth and preventing product loss due to pests.

14.2.1 Chemical Fertilizers

Chemical fertilizers, cost-effective formulation of nitrogen, phosphate, and potassium, have been widely used over centuries. These fertilizers provide nutrition in the form of bioavailable organic/inorganic salts, and their application appeared as a quick improvement in plant growth. In addition to nutrients including, phosphate, nitrate, ammonium, and potassium salts, heavy metals like Hg, Cd, As, Pb, Cu, Ni, and Cu; natural radionuclides like ^{238}U, ^{232}Th, and ^{210}Po also exist in chemical fertilizers. Netherlands, Egypt, Japan, China, UK, Germany, France, USA, Italy, India, Greece, Indonesia, and Turkey are using 665.5, 624.8, 373.2, 301.5, 287.5, 205.4, 180.1, 160.8, 126.4, 121.4, 115.4,106.9, and 100.4 kg per hectare chemical fertilizer ($N + P + K$), respectively (Savci 2012).

Over time, it has been revealed that prolonged usage of chemical fertilizers has resulted in the gradual loss of their effectiveness and corresponding environmental problems were also emerging (Kumar et al. 2021; Sharma et al. 2021; Xiang et al. 2012). In this situation, more chemical fertilizers should be applied to achieve the same productivity. Also, the production process of chemical fertilizer results in the release of hazardous substances including sulfur oxides, nitric oxides, and fluorine compounds into the environment. Continuous application of chemical fertilizers can profoundly modify the salinity and pH of the soil, decline soil mineral and its water retention capacity, which can lead to gradual deterioration. It has been observed that extended or continuous supply of a considerable amount of nitrogen fertilizer can cause plant tissue softening, leading to increased sensitivity of plants to pests and diseases (Adesemoye et al. 2010; Chen 2006).

Whenever excessive amounts of chemical fertilizers are applied, and plants cannot assimilate them; several physical and chemical procedures are activated to decrease their concentrations in soil. Rinsing out, leaching, volatilization, immobilization, replacement, precipitation, and microbiological conversions are some of these strategies which may lead to the dispersion of hazardous chemicals into the air and aquatic ecosystems and cause long-lasting serious environmental problems, e.g., eutrophication of waters.

Considerable rate (50–70%) of nitrogenous contamination is due to nitrogenous fertilizer. Unabsorbed nitrogenous fertilizers are converted to nitrate through microbial nitrification. Generated soluble nitrate reaches the depth of soil and enter the groundwater due to its high solubility and negative charge. Leached nitrate, reactive nitrogen species, nitrites, and nitrosamines in ground and surface waters are some of the life-threatening compounds. High levels of nitrates, nitrites, and nitrosamines can aggregate in crops and adversely impose human and animal health. High-level nitrate (more than 50 mg NO^{3-}/L) in drinking water cause inflammation of the digestive and urinary systems, methemoglobinemia, and some related diseases in infants and ruminant animals. Also, it increases the risk of metabolic diseases including cancers, respiratory disorders, cardiovascular ailments, goiter, congenital disabilities, digestive system disease, and the rate of infections with West Nile virus, malaria, and cholera (Galloway et al. 2008).

High buffering feature of soil has resulted in less obvious effects of chemical fertilizers on it; however, over time its deterioration occurs, and in turn, leads to decreased soil quality, normal structure, and composition due to losing its buffering potential. Also, the accumulation of toxic substances in the soil is lethal for living organisms, like microorganisms and earthworms. This biologically passive soil possesses negligible organic matter and less liberation of nutrients as much as biologically active soil, and because of this, interactions of living organisms are disrupted in this condition (Chandramohan et al. 2013). Prolonged consumption of nitrogen fertilizers like ammonium sulfate, which produces acid, dramatically reduces soil pH. Also, the diversity of microbial species in the rhizospheric regions are changed in acidic soil. In this condition, activities of plant growth-promoting microorganisms like decomposition of organic matter and symbiotic interaction with plants are reduced or inhibited. Ammonium sulfate fertilizer extremely acidifies the soil, and its extensive use will result in Mg deficiency (Fageria et al. 2010).

One of the most problematic matters during applying chemical fertilizers is groundwater contamination (Galloway et al. 2008). Nitrates are generated from the breakdown of nitrogen fertilizers, and because of their water-solubility feature, they easily move within the soil and can persist in that position for a long time leading to ecosystem deterioration (3).

Besides detrimental effects on human and animal life, terrestrial and aquatic ecosystems are affected by the extensive use of chemical fertilizers. For instance, large fractions of nitrogen fertilizers are oxidized, and nitrogen monoxides and nitric oxides are generated through denitrification process, which results in the depletion of the ozone layer and increases the probability of skin cancer. Also, nitric acid can be created after using urea and ammonium salt, the most current forms of ammonium, and in combination with sulphuric acid leading to the generation of acid rains which adversely affects ecosystems and results in erosion and depletion of the soil. High levels of water-soluble potassium impose an adverse effect on the soil pH and structure as well as seed germination. In this condition, uptake of other minerals and nutrients is ceased and the quality of the crop is declined (Savci 2012).

Rampant fertilization using phosphorous fertilizers disrupts its balance and leads to the accumulation of phosphorous in sites of application. Applied ammonium phosphates and superphosphates containing calcium phosphate, readily relocate under acidic conditions and plants could consume them as the phosphorous source. While in alkaline conditions, phosphorous compounds are potently attached in the phosphorus retarded reactions between soluble phosphates, and aluminum, iron, manganese, and calcium ions. The result of these reactions (including phosphate sorption, adsorption, retention, precipitation, or immobilization) is the production of insoluble and unleachable salts. Therefore, they cannot travel within the soil tissue. Therefore, these processes profoundly decrease the availability of plants to phosphorous. This process makes the continuous application of phosphate fertilizers inevitable. Excessive and accumulated phosphates accelerate eutrophication in terrestrial and aquatic ecosystems, which can impose lethal effects on their inhabitants.

Eutrophication creates an oxygen-free environment that is not suitable for drinking and profoundly reduce living species in the marine ecosystems as well as causes proliferation of unwanted species and unfavorable odor (Chislock et al. 2013). In addition, trace amounts of cadmium, chromium, lead, uranium, and radium exist in phosphate fertilizers. The prolonged application of this fertilizer can enhance the concentrations of these pollutants. These hazardous compounds pollute the soil and water, and whenever they enter the surface water or are absorbed by plants, can, in turn, enter into the human body through the food chain and create life-threatening problems (Fig. 14.3) (Khan et al. 2018).

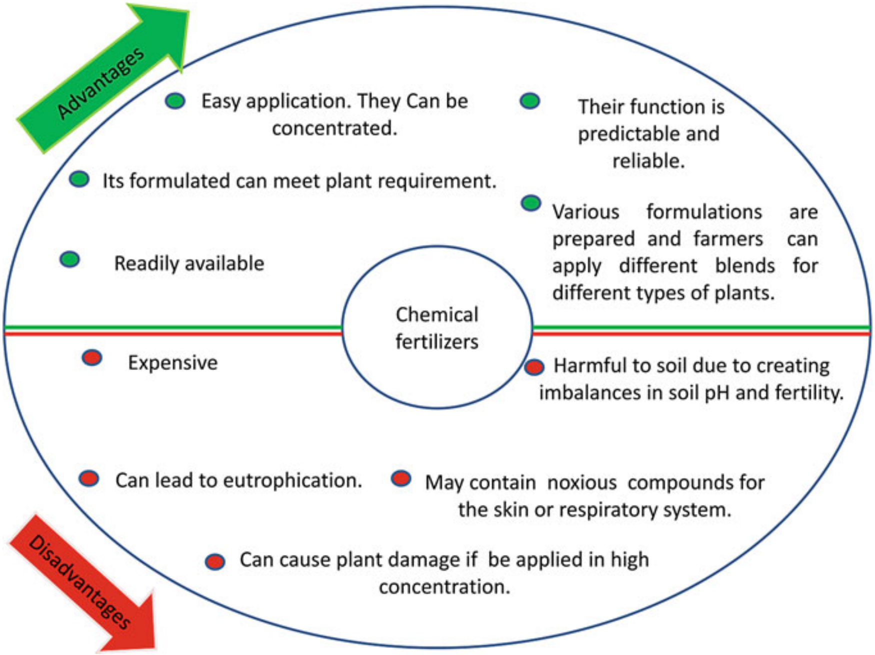

Fig. 14.3 Advantages and disadvantages of chemical fertilizers

Although extensive usage of chemical fertilizers has adverse effects on human and animal health and ecosystems, the inevitable need for chemical fertilizers by the agriculture industry is obvious. Lack of their use can lead to insufficient nutrients for the world population. Therefore, there is a pivotal need for alternative fertilizers which sustainably and eco-friendly flourish agricultural yield.

14.2.2 Organic Fertilizers

Conventional agriculture via chemical fertilizers and devastating agricultural imposes adverse effects on human and animal health, microbial habitats, and beneficial insects. It leads to the deterioration of soil and terrestrial ecosystems, and ozone layers. Also, it has been proven that its efficiency is unsustainable (Fricke and Vogtmann 1993; Mäder et al. 2002). Therefore, alternate farming methods are being applied to recover soil quality and ameliorate environmental degradation. One of these new eco-friendly approaches with self-sustainability features is organic agriculture. FAO/WHO has defined organic agriculture as a comprehensive production management system which uses it, the health of agro-ecosystem that is characterized by improved biodiversity, balanced biogeochemical cycles, and enhanced animal and microbial activities in soils. In organic agriculture, sustainable management practices

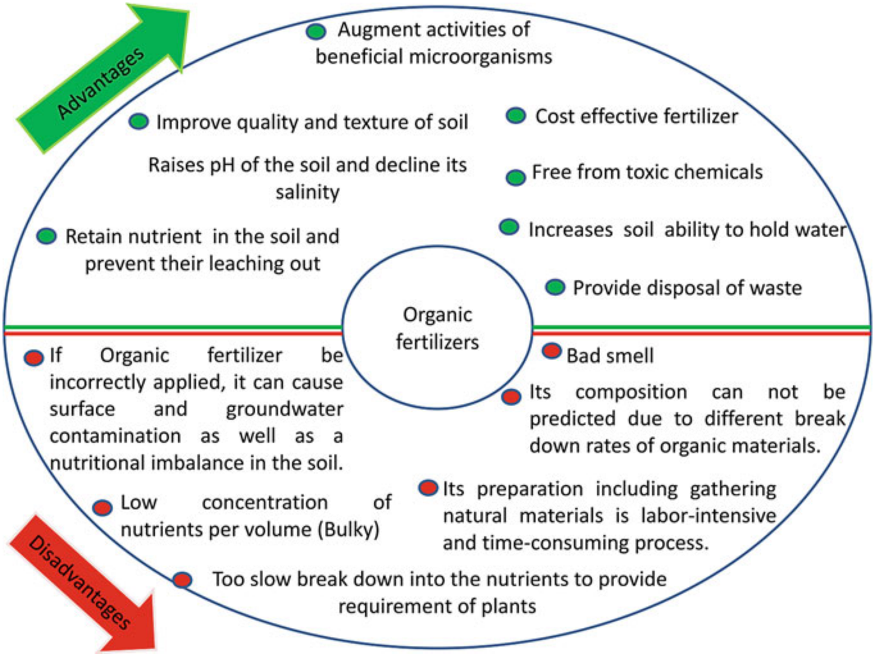

Fig. 14.4 Advantages and disadvantages of organic fertilizers

in all aspects of farm management by considering regional conditions and applying locally adapted systems such as agronomic, biological, and mechanical methods should be implemented (FAO/WHO 2015).

In this regard, natural means like growing cover crops, mainly leguminous species, are applied. Organic fertilizers like composts and manure act in a different way in comparison to chemical fertilizers, e.g., they supply nutrients in a lower concentration (like potassium) (Fricke and Vogtmann 1993; Hernández et al. 2010) and slower release rate (like nitrogen because of low rate of mineralization) (Hernández et al. 2010). In sustainable agriculture, maximum yield cannot be achieved by solely relying on organic fertilizers. Therefore, through the combined usage of chemical–organic fertilizer along with biofertilizers, production yield can be maximized in a sustainable approach (Qin et al. 2015; Shafi et al. 2012; Song et al. 2015). The advantages and disadvantages of organic fertilizers are presented in (Fig. 14.4).

14.2.3 Biofertilizers

Applying manure, crop rotation with legumes, and water managing to increase soil's nutrient content through their naturally occurring microorganisms are some of the ancient strategies to improve the fertility of lands (Franche et al. 2009; Morrison and Cozatl-Manzano 2003; Suthar et al. 2017). Microbial fertilizers were developed and commercialized in the late nineteenth century for the first time (Bashan 1998; Kilian et al. 2000) to ameliorate the unfavorable aspects of excessive usage of chemical fertilizers. Applying biofertilizer results in a reduced application of chemical fertilizer (Singh and Adholeya 2003).

Biofertilizers and green manure, intercrop, or organic supplemented chemical fertilizers are not the same concepts (Bhattacharyya and Jha 2012; Halpern et al. 2015). They are formulated with different types of beneficial microorganisms or their latent forms, which once applied, colonize the rhizospheric region or the inner parts of the plant and perform agriculturally-important activities including conversion of nutritionally critical nutrients from unavailable to bioavailable form (nitrogen and phosphate), mineralization of sulphur, zinc, potassium, and iron, producing degrading enzymes, antibiotics and phytohormones, induction of resistant mechanisms in the plants, secretion of growth hormones through which enhance crop yield up to 10–40% (Ahemad and Kibret 2014; Bhardwaj et al. 2014; Bhattacharjee and Dey 2014; Gaur 2010; Kour et al. 2019b, 2021; Lugtenberg and Kamilova 2009; Mishra et al. 2013a; Owen et al. 2015). Since the biofertilizers have low cost and renewable properties, they can be supplied along with chemical fertilizers to cut down their use, intensify their beneficial activities, and reduce their deteriorating activity on the ecosystem. Biofertilizer provides various inorganic substances with low bio-availability. Therefore, this strategy is more cost-effective for farmers than synthetic fertilizers (Kour et al. 2020). Co-application of phosphate solubilizing bacteria and bacteria with potassium solubilizing activity along with rocks containing low soluble phosphate and potassium enhanced yield and assimilation of nitrogen, phosphate, and potassium by various plants in phosphate and potassium limiting conditions (Han and Lee 2005; Han et al. 2006; Vassilev et al. 2006a). There are several types of biofertilizers, including microorganisms with the ability of nitrogen fixation, phosphate solubilization, phosphate mobilization, and promotion of plant growth (Mondal et al. 2020; Yadav 2021). It is proven that combined application of chemical, organic, and biofertilizers can meet the increasing need of enhancing world population to foods at a time when agriculture-based industries are facing various environmental concerns (Suthar et al. 2017).

However, despite the tremendous application of biofertilizers, their application is limited due to many factors such as the unpredictability of results, difficult identification, and traceability of microbial strains in the field, limited knowledge about interactions among microbial cells and plants, and the technical process of large scale production (Bashan et al. 2014; Lucy et al. 2004; Owen et al. 2015). In addition to bacterial grazers, especially naked amoeba, nematodes can also modify the effectiveness of microbial inoculum (Malusa et al. 2010). One of the important obstacles in applying biofertilizers is that behavioral characteristics of microorganisms are changed in a microbial community compared to a situation that they exist in pure culture. These constraints are encouraging reasons to conduct extensive and comprehensive studies on biofertilizers (Fig. 14.5).

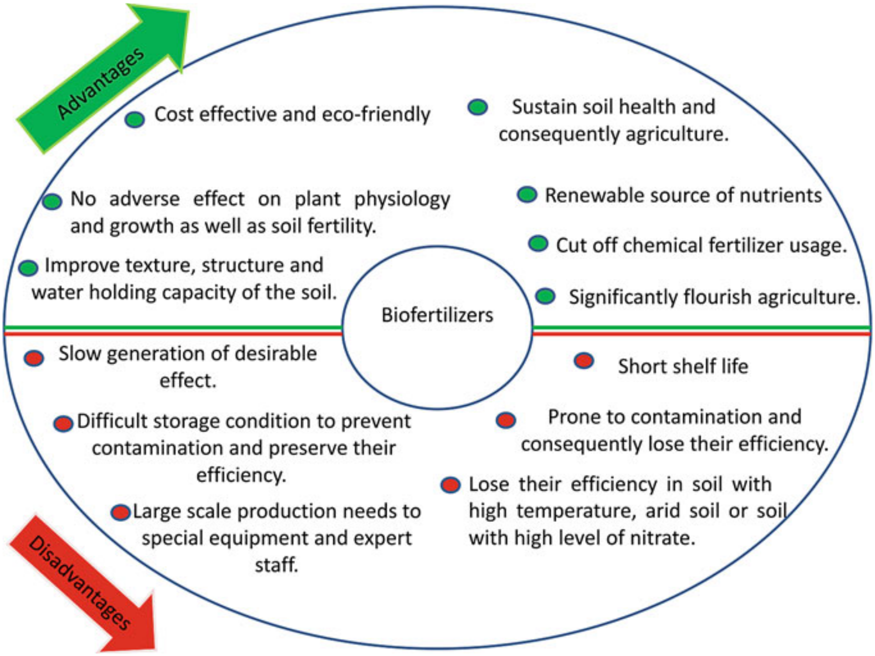

Fig. 14.5 Advantages and disadvantages of biofertilizers

14.2.3.1 Major Constituents of Biofertilizers

Each type of biofertilizer contains various beneficial microorganisms, including plant growth-promoting rhizobacteria, fungal strains like mycorrhiza and cyanobacteria (Table 14.1). These microorganisms can suppress the adverse effects of phytopathogenic organisms and abiotic stresses on plant growth and development via various strategies such as facilitating nitrogen, phosphate, iron, zinc, and potassium acquisition, modifying phytohormone levels, which, in turn, can flourish agriculture in an eco-friendly manner (Kour et al. 2019a; Singh et al. 2020; Thakur et al. 2020; Tiwari et al. 2020, 2021). According to the mechanisms by which biofertilizers augment plant growth, they are divided into various groups including biofertilizers containing microorganisms with nitrogen fixation ability (*Rhizobium, Bradyrhizobium, Azospirillum,* and *Azotobacter*), phosphate mobilization ability (*Mycorrhiza*), growth promotion activity (*Pseudomonas*), phosphorous solubilization capability (*Bacillus, Pseudomonas, Aspergillus*, *Penicillium*, *Fusarium, Trichoderma*, *Mucor*, *Ovularopsis*, *Tritirachium,* and *Candida*), and biofertilizers with compost enriching activities (*Humicola fuscoatra*, *Aspergillus flavus*, *Aspergillus nidulans*, *Aspergillus niger*, *Aspergillus ochraceus*, *Fusarium solani*, and *F. oxysporum*).

Biological fertilizers can be made either by a single microorganism or a mixture of them. Results would be better if applying single microorganism which shows simultaneous mechanisms to promote plant growth, e.g., simultaneous capability of

Table 14.1 Active agents in various types of commercial biofertilizers

S. no.	Commercial biofertilizers
1	Nitrogen-fixing biofertilizers containing *Rhizobium, Bradyrhizobium, Azospirillum* or *Azotobacter*
2	Phosphate solubilizing biofertilizers containing *Bacillus, Pseudomonas* or *Aspergillus*
3	Phosphate mobilizing biofertilizers containing *Mycorrhizae*
4	Plant growth-promoting biofertilizers containing *Pseudomonas* sp.
5	Phospho-bacterium and *Mycorrhizae*
6	*Rhizobium* and phosphobacterins
7	Cyanobacteria
8	*Aspergillus niger* 1107 phosphate solubilizing fungus
9	*Bacilluscereus* strain RS87
10	*Azoarcus* and *Zoogloea*
11	*Vesicular arbuscular mycorrhiza*
12	*Azospirillium brasiliense*
13	*Azospirillium amazonense*
14	*Acetobacter diazotrophicus*
15	*Derxia gummosa*
16	*Torulospora globasa*
17	*Thiobacillus*
18	*Trichoderma* sp.
19	*Paecillomyces* sp.
20	*Pseudomonasfluorescens*

Source Mahanty et al. (2017)

phosphate solubilization and biological control of filamentous fungi (Vassilev et al. 2006a), simultaneous ability to solubilize phosphate and biological control of *Trichoderma* strains (Altomare et al. 1999), simultaneous assimilation of both inorganic and organic nitrogen along with phosphate or other micro- and macro-elements by arbuscular mycorrhiza fungi (AMF) (Hawkins et al. 2000; Smith and Read 2008) have been reported. On the other hand, biofertilizers containing mixed microbial inoculum can promote plant growth through various strategies. These microbial strains are produced in individual fermentation processes and then mixed with each other (De Roy et al. 2014). For instance, the co-application of *Penicillium* spp. and AMF, *Penicillium* and *Rhizobium* spp., AMF with rhizobia, *Rhizobium* and phosphate solubilizing bacteria, AMF/Rhizobium/phosphate solubilizing fungus can be named, which leads to enhanced growth of cereals (Babana and Antoun 2006; Kucey 1988) and legumes, respectively (Alagawadi and Gaur 1988; Downey and Van Kessel 1990; Rice et al. 2000; Wang et al. 2011).

In some cases, the yield of fertilized plants by biofertilizer containing arbuscular mycorrhiza fungi and free-living bacteria with nitrogen fixing ability or various

PGPR was equal to plants which were fertilized with chemicals (Adesemoye et al. 2008; Malusa et al. 2007; Wu et al. 2005; Xavier and Germida 2003). Biofertilizers with several plant growth-promoting mechanisms can obtain more acceptance from farmers and markets who prefer to use multifunctional products and present a product for several purposes, respectively (Vassilev et al. 2006b).

Plant Growth-Promoting Rhizobacteria (PGPR)

Rhizospheric bacteria are divided into three groups according to their interaction with plants, including commensal, parasite, and beneficial association (Rai et al. 2020). In commensalism, bacteria harmlessly colonize on the root surface (Verma et al. 2017). No observable effect is imposed on the physicochemical properties of plants (Beattie 2007). Phytopathogenic rhizobacteria establish a parasitism interaction with host plants through producing phytotoxic substances which adversely affect the physicochemical properties of plants. Beneficial rhizobacteria are considered an available part of the rhizospheric reign. They grow in the vicinity of host plants and stimulate their growth through multifaceted activities like solubilizing the nutrients, fixing atmospheric nitrogen, producing phytohormones and lytic enzymes, stimulating the growth of beneficial microorganisms like mycorrhizae, limiting phytopathogens, acting as biocontrol agents (Franco-Correa et al. 2010), removing phytotoxic substances or alleviating salinity, drought, and flooding stresses (Bashan and De-Bashan 2010; Khalid et al. 2004), thus they are identified as plant growth-promoting rhizobacteria (PGPR).

A few of their characteristics like high adaptability to various environmental conditions, fast growth rate, and considerable ability to degrade an extended spectrum of natural and xenobiotic compounds lead to their successful competition with autochthonous, and especially phytopathogenic microorganisms. Rhizobacteria with aggressive root colonization potential, ability to stimulate plant growth, and biocontrol activities can be considered as PGPR (Vessey 2003).

According to their association with root cells of the plants, PGPR are divided into extracellular plant growth-promoting rhizobacteria (ePGPR) and intracellular plant growth-promoting rhizobacteria (iPGPR) (Martínez-Viveros et al. 2010). ePGPR frequently exist within the rhizoplane or in the spaces between the cells of the root cortex, while iPGPR are exclusively present within the specialized nodular structures of root cells. ePGPR belong to *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium, Micrococcus*, *Pseudomonas,* and *Serratia* genera (Gray and Smith 2005), while iPGPR belong to *Frankia*, *Allorhizobium*, *Azorhizobium* (*Azorhizobium caulinodans*) (Dreyfus et al. 1988), *Bradyrhizobium* (*Bradyrhizobium japonicum*) (Guerinot and Chelm 1984), *Mesorhizobium* (*Mesorhizobium chacoense* (Velázquez et al. 2001), *Mesorhizobium pluriforium* (de Lajudie et al. 1998), *Sinorhizobium* (*Sinorhizobium arboris* (Nick et al. 1999), *Sinorhizobium fredii* (Chen et al. 1988), and *Sinorhizobium medicae* (Rome et al. 1996)), and *Rhizobium* (*Rhizobium cicero* (Nour et al. 1994), *Rhizobium etli* (Segovia et al. 1993), *Rhizobium fredii* (Scholla and Elkan 1984), *Rhizobium galegae* (Lindström 1989), *Rhizobium gallicum* (Amarger et al. 1997), *Rhizobium giardinii* (Amarger et al. 1997)) genera.

Fungi

Fungal biofertilizers comprise a single fungus or mixture of fungal strains and through direct or indirect mechanisms improve the growth of plants and yield of crops (Devi et al. 2020). Mycorrhizal hyphae extend into the soil through infecting plants growing in their vicinity and impose their improving effect on plant growth by penetrating nutrient depletion zone and increasing bioavailability or mobility of elements (Chiariello et al. 1982).

A mycorrhiza, a fungal distinct morphological structure, generates mutualistic association with roots of host plants like herbs, shrubs, trees, aquatic, xerophytes, epiphytes, hydrophytes, many crops, and forest tree species (Rai et al. 2013). In this association, roots of host plants are intracellularly or extracellularly colonized, either by endomycorrhizal fungi or ectomycorrhizal fungi, respectively. Applying biofertilizers containing mycorrhizal fungi probably results in carbon storage in soil via altering kinetic properties of the root, improving its ability to uptake nutrients which consequently leads to improved quality of soil organic matter to support more agricultural productivity (Smith and Smith 1997).

They are various endomycorrhiza, they are categorized into arbuscular, ericoid, arbutoid, monotropoid, and orchid mycorrhizae. Arbuscular mycorrhizal (AM) fungi are frequent in the terrestrial ecosystem from the arctic to the tropics (Gerdemann 1968). Studies have shown their high occurrence in symbiotic association. They possess high diversity due to the diversity of plant species, soil characteristics, and seasonal conditions (Smith and Smith 2012). They belong to the Glomeromycota phylum (Schuessler et al. 2001). *Gerdemannia*, *Acaulospora*, *Scutellospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Archaeospora*, *Geosiphon*, *Paraglomus*, and *Sclerocystis*are AM forming genera. After arbuscular mycorrhiza colonization on the root cortex, highly branched structures like arbuscules are formed inside the cells where nutrient exchange occurs between plant and fungus (Balestrini et al. 2015).

Fungi alleviate biotic stresses like parasitic fungi and nematodes (Duchesne et al. 1989) and abiotic stresses due to drought, salinity, and flooding and enhance the resistance of plants against heavy metals, promote plant productivity and agricultural productivity mainly in low-nutrient and stressful conditions through mobilizing P, supplying macro and micronutrients like P, Ca, Zn, S, N which are inaccessible to plant roots (Augé et al. 2015; Meier et al. 2015; Porcel et al. 2012; Rana et al. 2019a; Sharma et al. 2019). It has been revealed that AM symbiosis induces the expression of Pi transporters in plants (Walder and van der Heijden 2015; Xie et al. 2013). Fungal hyphae have a higher penetration ability than plant roots which able them to obtain nutrients which are away from plant roots. In turn, plants supply carbohydrates for AM fungi (Allen 2011).

Trees with ectomycorrhizal (ECM) fungi inoculated roots due to rapid absorbing and accumulating nitrogen, phosphorus, potassium, and calcium show better growth parameters than nonmycorrhizal plants. These fungi accelerate the degradation of the complicated minerals and organic matter in the soil and their transmission to the tree. Also, they enhance the tolerance of trees to biotic and abiotic stress including, drought, high temperatures, extreme pH of the soil, and toxins. *Pisolithus tinctorius* and *Piriformospora indica* are ECM fungi with multifaceted plant growth-promoting activities (Schwartz et al. 2006). There are many fungal biofertilizers such as fungal species which exert their plant growth improving effects through solubilizing phosphorous (*Aspergillus* spp., *A. tubingensis*, *Penicillium* spp., *Fusarium* spp., *Trichoderma* spp., *Mucor* spp., *Tritirachium* spp., and *Candida* spp.), solubilizing potassium (*Aspergillusfumigates*, *A. niger*, *A. terreus*, and ectomycorrhizal fungi), solubilizing zinc (*Saccharomyces* spp., *Oidiodendron maius* and *Aspergillus niger*, *Penicillium simplicissimum*), mobilizing phosphate (ectomycorrhiza and *Arbuscular mycorrhiza*), and enriching compost (*Trichoderma* spp., *Penicillium* spp., *Aspergillus* spp., *Pleurotus* spp., *Chaetomium* spp., *Humicola fuscoatra*, and *Fusarium* spp.) (Lian et al. 2008; Whitelaw 2000; Raj 2007).

Cyanobacteria

Biofertilizers containing microalgae, especially cyanobacteria promote plant growth and soil condition via various strategies. They improve the nutrient quantity of soil through secreting phytohormones like auxin (*Nostoc*, *Hapalosiphon*), gibberellin, vitamins like vitamin B12 (*Cylindrospermum* sp. *Tolypothrix tenuis*, *Nostoc muscorum*, and *Hapalosiphon fontinalis*), amino acids (Rodríguez et al. 2006a, 2006b; Roger and Pierre-Adrien 1982), fixing nitrogen and releasing nutrients after their death and decomposition. *Anabaena azollae* with lignolysis ability release phenolic compounds once applyied as biofertilizer. *Nostoc linkia*, *Anabaena variabilis*, *Aulosira fertilisima*, *Calothrix* sp., *Tolypothrix* sp., and *Scytonema* sp. are nitrogen-fixing cyanobacteria, which can be utilized for rice cultivation (Prasad and Prasad 2001). *Anabaena* fixes nitrogen (up to 60 kg/ha/season) in association with water fern *Azolla* and enhances organic matter content in the soils (Moore 1969).

Cyanobacteria contain considerable amounts of macro and micronutrients, as well as amino acids. They can be considered as a suitable alternative for chemical fertilizers to alleviate their environmental polluting effects (MM 2001). Algae via producing organic acids can increase the bioavailability of soil phosphate. The physicochemical properties of soil can be improved via algal biofertilizers. They enhance water holding capacity and aeration of soils through their jelly structure and filamentous structure, respectively. Soil salinity is reduced after their application. They can act as viable biocontrol agents by preventing the growth of weeds. Since cyanobacteria are capable of degrading various kinds of pollutants and possess simple growth requirements, they can be applied to rehabilitate deteriorated ecosystems (Subramanian 1996).

14.2.3.2 Biofertilizer's Mechanism of Action

As mentioned, microbial cells in biofertilizers improve plant growth via various mechanisms which will be discussed hereafter (Tables 14.2, 14.3, and 14.4) and (Fig. 14.6) also summarized these mechanisms.

Table 14.2 Plant growth-promoting activities of microbial cells by increasing bioavailability of nutrients

Microorganisms	Mechanism of action for plant growth improvement
Azoarcus sp.	Nitrogen fixation
Azorhizobium	
Azospirillum sp.	
Azotobacter sp.	
Beijerinckia sp.	
Burkholderia sp.	
Frankia sp.	
Gluconacetobacter diazotrophicus	
Herbaspirillum sp.	
Bacillus polymyxa	
Cyanobacteria	
Paenibacillus sp.	Potassium solubilization
Bacillus sp.	
Aspergillus fumigates, Aspergillus niger, Aspergillus terreus	
Acidothiobacillus ferrooxidans	
Phyllobacterium sp.	Phosphate solubilization
Rhizobium leguminosarum	
Mesorhizobium mediterraneum	
Bradyrhizobium sp.	
Bradyrhizobium japonicum	
Arthrobacter sp.	
Burkholderia sp.	
Enterobacter asburiae	
Acinetobacter sp.	
Flavobacterium sp.	
Microbacterium pseudomonas	
Rhodococcus sp.	
Erwinia sp.	
Aspergillus tubingensis, *Aspergillus niger*, *Aspergillus terreus*, *Aspergillus awamori*, *Aspergillus fumigates*, *Aspergillus tubingensis*, *Aspergillus melleus*	

(continued)

Table 14.2 (continued)

Microorganisms	Mechanism of action for plant growth improvement
Penicillium bilaji, *Penicillium albidum*, *Penicillium italicum*, *Penicillium simplicissimum*, *Penicillium frequentans*, *Penicillium oxalicum*, *Penicillium rubrum*, *Penicillium expansum*, *Penicillium citrinum*	
Fusarium moniliforme, *Fusarium udam*	
Trichoderma viridi, *Trichoderma harzianum*, *Trichoderma virens*, *Trichoderma asperellum*	
Mucor ramosissimus, *Mucor mucedo*, *Mucor hiemalis*	
Tritirachium album, *Tritirachium egenum*	
Candida krissii, *Candida scotti*	
Ectomycorrhiza	Phosphate mobilizing biofertilizer
Arbuscular mycorrhiza	
Acaulospora spp.	
Scutellospora spp.	
Enterophospora, *Gerdemannia*, *Gigaspora* sp.	
Saccharomyces spp.	Zinc solubilising biofertilizers
Oidiodendron maius	
Penicillium simplicissimum	
Aspergillus niger	

Sources Hayat et al. (2010), Meena et al. (2017)

14.3 Making Nutrient Available for Plants

Biofertilizers augment plant growth through enhancing the bioavailability of nutrients in the rhizospheric regions gradually. They increase nutrient availability and prevent nutrient leaching out via fixing nitrogen, solubilizing phosphate, potassium, and zinc and producing siderophores as well as decompose organic material (Prasad et al. 2021).

14.3.1 Fixation of Nitrogen

Nitrogen is a critical macronutrient for plant growth and productivity, which plants require to construct macromolecules like proteins and nucleic acid. Most portion of nitrogen (78%) exists in the atmosphere as N_2 which is an unavailable form for plant assimilation. N_2 should be converted to bioavailable organic form (ammonia) to

Table 14.3 Plant growth-promoting activities of microbial cells by producing or modulating phytohormones

Microorganisms	Mechanism of action for plant growth improvement
Azobacter sp.	Cytokinin synthesis
Bacillus sp.	
Rhizobium leguminosarum	
Bacillus sp.	Auxin synthesis
Bacillus sp.	Gibberelin synthesis
Sphingomonas sp.	
Paenibacillus polymyxa	
Pseudomonas fluorescens	
Rhizobium leguminosarum	
Paenibacillus sp.	Indole acetic acid synthesis
Rhizobium leguminosarum	
Aeromonas veronii	
Agrobacterium sp.	
Alcaligenes piechaudii	
Azospirillum brasilense	
Azotobacter sp.	
Comamonas acidovorans	
Enterobacter cloacae, *Enterobacter* sp.	
Bradyrhizobium sp., *Bradyrhizobium japonicum*	
Mycobacterium sp.	
Kluyvera ascorbata SUD 165	
Serratia mercescens	
Azospirillum brasilense	
Bacilluscirculans P2, *Bacillus* sp. P3, *Bacillusmagaterium* P5 *Bacillus*. sp. Psd7	
Streptomycesanthocysnicus	
Azospirillumlipoferum strains 15, *Pseudomonasaeruginosa* Psd5 *Pseudomonaspieketti* Psd6, *Pseudomonas fluorescens* MTCC103	

Sources Hayat et al. (2010), Meena et al. (2017)

Table 14.4 Plant growth-promoting activities of microbial cells by inhibiting phytopathogens and increasing resistance of plant

Microorganisms	Mechanism of action for plant growth improvement
Bacillus sp.	Siderophore production
Chryseobacterium sp.	
Phyllobacterium sp.	
Pseudomonas fluorescens	
Rhizobium sp.	
Streptomyces sp.	
Mesorhizobium loti MP6	
Pseudomonas tolaasii	
Serratia mercescens	
Kluyvera ascorbata SUD 165	
Rhizobium meliloti	
Bradyrhizobium sp.	
Bradyrhizobium japonicum	
Pseudomonas sp.	ACC deaminase synthesis
Rhizobium sp.	
Alcaligenes sp.	
Bacillus pumilus	
Enterobacter cloacae	
Pseudomonas cepacia	
Pseudomonas putida	
Pseudomonas sp.	
Variovorax paradoxus	
Bacillus sp.	Induction of plant stress resistance
Mycobacterium sp.	
Pseudomonas sp.	
Rhizobia sp.	
Rhizobia sp.	Hydrogen cyanide production
Bacillus sp.	Antibiotic production
Pseudomonas sp.	
Pseudomonas sp.	Chitinase and β-glucanases production
Sinorhizobium sp.	

Sources Hayat et al. (2010), Meena et al. (2017)

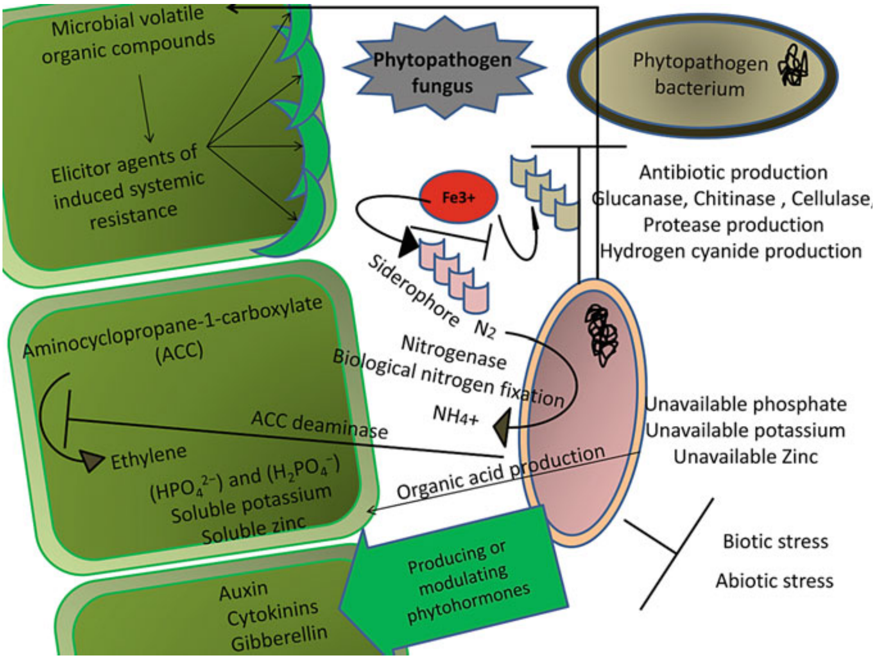

Fig. 14.6 Various mechanisms by which microbial cell forming biofertilizers improve plant growth

compensate the loss of N from soils or ecosystems by a well-known process known as biological nitrogen fixation (Tairo and Ndakidemi 2013). This process, exclusively, can be performed by nitrogen-fixing organisms, also known as diazotrophs, including bacteria and cyanobacteria through an oxygen-sensitive enzymatic complex known as nitrogenase system (Rana et al. 2020; Smith and Newton 2013). A considerable amount of ammonia (2.5×10^{11} kg) is annually produced through this system (Schlesinger and Bernhardt 2013). The amount of biologically fixed nitrogen can be affected by environmental conditions or different plant-microbe combinations. Biological fixation of nitrogen tremendously declines volatilization, leaching, and denitrification process. Biological nitrogen fixation can be done via free-living and symbiotic microorganisms. Some nitrogen-fixing microorganisms possess intimate endophytic associations with host plants and some nitrogen fixers, who live in close association in the rhizospheric region, and do not form intimate endophytic symbioses.

The nitrogen fixing ability of Rhizobia species like *Rhizobium*, *Allorhizobium Sinorhizobium*, *Bradyrhizobium*, *Azorhizobium*, and *Mesorhizobium*), as endophytes of leguminous plants, have been extensively studied (Gopalakrishnan et al. 2015; Laranjo and Oliveira 2014; Rana et al. 2019b). N_2-fixing endophytes are highly found in the legume class, but are not restricted to this class (Carvalho et al. 2014). Recently, many investigates have reported the isolation of endophytes from various non-leguminous plants. Restriction of a specific compartment has not been observed in the endophytes of non-legumes. It has been observed that they colonize in various parts of plants, including, roots, stems, and leaves. The obligative or facultative association among these microorganisms and host plants can be created. The stomata or cracks at the site of lateral root emergence are sites through which these microorganisms can enter into various tissues of plants (Glick 2015; Gaiero et al. 2013). Entering endophytes into the plant's tissues caused a more favorable environment for the plant in the rhizospheric region (Reinhold-Hurek 2011). Since, they easily access to nutritional elements and low concentration of oxygen needed for nitrogenase activity. In return, the endophytes encourage the productivity of the host plants by fixing nitrogen and supplying compounds with growth-promoting activity. In recent years, the number of identified endophytic diazotrophs has been significantly enhanced. Various bacteria belonging to different genera, such as *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus*, and *Serratia*, have been reported to augment the growth of plants via various strategies (Glick 2015)

Nitrogen-fixing microorganisms can be either symbiotic or non-symbiotic. Symbiotic microorganisms (*Rhizobium*, *Frankia,* and *Azolla*) form a symbiotic relationship with leguminous and non-leguminous plants (Ahemad 2010; Glick 2015), while asymbiotic nitrogen fixers are free-living (*Azotobacter*, *Beijerinckia*) or endophytic (*Gluconacetobacter*, *Azospirillum,* and *Herbaspirillum*) microorganisms (Bhattacharyya and Jha 2012). There are many nitrogen-fixing microorganisms including *Achromobacter*, *Alcaligenes*, *Arthrobacter*, *Acetobacter*, *Azomonas*, *Beijerinckia*, *Bacillus*, *Clostridium*, *Enterobacter*, *Erwinia*, *Derxia*, *Desulfovibrio*, *Corynebacterium*, *Campylobacter*, *Herbaspirillum*, *Klebsiella*, *Lignobacter*, *Mycobacterium*, *Rhodospirillum*, *Rhodopseudomonas*, *Xanthobacter*, *Mycobacterium,* and *Methylosinus* which are associated with non-legumes(Wani 1990).

Some symbiotic bacteria with nitrogen fixing ability have been extensively studied, which includes *Rhizobia, Bradyrhizobium*, and *Frankia.* A large portion (70–80%) of biological fixation of nitrogen is performed by symbiotic microorganisms (Ishizuka 1992). Below are the descriptions of some symbiotic nitrogen fixers.

14.3.1.1 Rhizobium

Rhizobium is the best-known group of microorganisms which via symbiotic relationship with legume crops fixes nitrogen (50–100 kg/ha) and belongs to *Rhizobiaceae* family which consists of *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium*, *Rhizobium*, *Sinorhizobium*, *Devosia, Methylobacterium, Ochrobactrum,* and *Phyllobacterium, Burkholderia,* and *Cupriavidus* genera. Commercial rhizobial fertilizers, for legume crops, were first introduced in the 1890s. *Rhizobium* is an aerobic, non-sporulating, Gram-negative, rod-shaped, and fast-growing bacterium which forms nodules in the leguminous plant (Allito and Alemneh 2014; Lindström et al. 2006; Lindström and Martinez-Romero 2007).

Plant roots attract the rhizobia via their exudates. They colonize the roots of leguminous plants. An infection thread passes the root cortex toward a cluster of dividing cells that will become a plant root primordium. In this symbiotic relationship, the plant produces flavonoids that induce rhizobial nod genes and subsequently signal nodulation through the expression of *nod, nol, and noe* genes, leading to nodule formation, wherein nitrogen is biologically fixed. Besides N_2-fixing activity, rhizobia augment plant growth through mobilizing inorganic and organic P. In selecting biofertilizers, the high ability of their strains to fix nitrogen and compete with phytopathogens microorganisms should be considered. Under unfavorable conditions (acidic or basic soil) in which the population of symbiotic rhizobia is low (100 rhizobia per gram of soil), inoculation with compatible rhizobia is likely to prove highly advantageous. While in the presence of high densities of the rhizobial population, the inoculation is likely to be unnecessary, and investment in inoculation practice might be wasted (Abdel-Lateif et al. 2013; Abiala et al. 2013).

14.3.1.2 Bradyrhizobium

One important group of the symbiotic nitrogen fixers is *Bradyrhizobium.* They are slow-growing soil-dwelling microorganisms which fix nitrogen, and in turn, use carbohydrate derived from plants in a symbiotic association. It has been shown that nodule formation and availability of nutrients in the soil can be enhanced once the application of inoculum consists of *Bradyrhizobium* and certain PGPRs probably due to auxins and siderophores production which consequently promote plant growth and increase its tolerance to the phytopathogens (Youssef and Eissa 2014).

14.3.1.3 Frankia

Many commercial drugs are derived from these bacteria. Recent investigations have revealed the significant importance of actinobacteria in producing medically (Salimi et al. 2018a, b, 2019), industrially (Imanparast et al. 2018), and agriculturally important compounds or enzymes (Hamedi and Mohammadipanah 2015). One of these outstanding genera is *Frankia. Frankia,* a N2-fixing actinobacteria, fix nitrogen via nodulation of actinorhizal plants (more than 280 species of woody plants) including the Elaeagnaceae, Casuarinaceae, Datisticaceae, Coriariaceae, and Myricaceae families, whereas nodulation occurs occasionally in Betulaceae, Rhamnaceae, and Rosaceae (Benson and Clawson 2000). These plants are woody trees or shrubs except for *Datisca* and can impose a pivotal role in agroforestry and land reclamation. The *Frankia* genus belongs to the family Frankiaceae. These bacteria produce differentiated structures, vesicles, where nitrogen is biologically fixed. Some parameters like the age of the microbial inoculum, its concentration, and preservation strategy may greatly affect inoculum efficiency.

Plant survival and performance can be improved through inoculation and nodulation before seedling transplanting (Prat 1992). They infect host plants through two various strategies: intracellular and intercellular root invasion (Wall and Berry 2007). Earlier occurs via the signal exchange between *Frankia* and the host plant which results in root curling and invagination of *Frankia* growing filaments into them and their subsequent encapsulation by a cell wall deposit. Besides nitrogen fixation, *Frankia* via releasing plant growth regulators, hydrogen cyanide, siderophores or increasing availability of phosphate improves plant growth. *Frankia* inoculum can be preserved as lyophilized or frozen in glycerol (Fontaine et al. 1986; Franche et al. 2009).

14.3.1.4 Gluconoacetobacter Diazotrophicus

Gluconoacetobacter diazotrophicus also known as *Acetobacter diazotrophicus*, fixes nitrogen in a symbiotic association with sugarcane as the host plant. It belongs to the Acetobacteriaceae family. Its inoculation leads to cut off chemical N fertilizer usage for at least two successive years (Muthukumarasamy et al. 2002).

14.3.1.5 *Cyanobacteria* and *Azolla*

Nitrogen can be fixed in plant roots via associate interaction by heterocystous cyanobacteria, including *Nostoc* and *Anabaena.* A significant amount of nitrogen (36% of global N2 fixation) is symbiotically fixed via an aquatic cyanobacterium, *Trichodesmium* (Gallon 2001). Cyanobacterial nitrogen fixation in heterocysts fulfills the nitrogen requirement of plants, and in turn, the plant supply carbohydrates derived from their photosynthetic activity. Asymbiotic association can be generated among cyanobacteria and fungi, liverworts, ferns, as well as flowering plants (Roychowdhury et al. 2014). Until the end of the 1970s, symbiosis of *Azolla–Anabaena* was the crucial nitrogen source to cultivate rice in China. Also, it can serve as an applicable source of nitrogen. It imposes its growth-promoting on plants via producing phytohormones like auxin, indole acetic acid, and gibberellic acid and providing a considerable level of iron, zinc, phosphorus, potassium, molybdenum, and other micronutrients. It has been reported inhibitory effects of three cyanobacteria including *Anabaena oryzae*, *Nostoc calcicola*, and *Spirulina* sp. on galls and egg masses (Al Abboud and Alawlaqi 2014; Mishra et al. 2013).

The effect of microorganisms, that non-symbiotically fix nitrogen, on agricultural productivity and yield is tremendous. Non-symbiotic nitrogen fixers compensate their access to plant derived nutrients decreasing their distance from the host (rhizoplane) or entering into the plants (endophytes). *Azotobacter* sp., *Azospirillum*, *Azoarcus* sp., *Gluconacetobacter diazotrophicus*, *Herbaspirillium* sp., *Achromobacter*, *Acetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhodospirillum, Rhodopseudomonas,* and *Xanthobacter* are non-symbiotic nitrogen fixers (Saxena and Tilak 1998). In the following, some of these non-symbiotic nitrogen fixers are presented in detail.

14.3.1.6 Azotobacter

Free-living microorganisms like *Azotobacter, Clostridium*, *Rhodospirillum,* and *Klebsiella* which are known as asymbiotic nitrogen fixers are present in the rhizospheric region. *Azotobacter*, as a well-known asymbiotic nitrogen fixer belongs to the family *Azotobacteriaceae*, establishes a mutual relationship with plants in which they fix nitrogen and absorb organic compounds from plant exudate. It has been reported that *Azotobacter* through producing and releasing vitamin B and various plant hormones like gibberellins, naphthalene acetic acid (NAA), promotes root growth and minerals uptake and simultaneously inhibits root pathogens (Mathivanan et al. 2015). The *Azotobacter* has been found in the rhizospheric region of some crop plants like vegetables, sugarcane, rice, maize, bajra, and plantation crops. *A.chroococcum*, via multiple mechanisms other than nitrogen fixation like production of vitamin, growth substance, antifungals, and siderophore (Martinez-Toledo et al. 1988), promotes plant growth. *Azotobacter indicum* through producing a lot of antifungal compounds inhibits some pathogenic fungi in the rhizosphere hence considerably decreases the seedling mortality (Martin et al. 2011). Occurrence of *Azotobacters* has been reported in soils with neutral or alkaline pH. *A. chroococcum* is a common species in arid soils. Other reported species include *A. vinelandii*, *A. beijerinckii*, *A. insignis*, and *A. macrocytogenes.* A sizable proportion of root colonized *Azotobacter* penetrates the root tissues and lives in an associate relationship with the host plants. However, any visible nodules or outgrowth on root tissue is not created (Bhat et al. 2015).

14.3.1.7 Azospirillum

Azospirillum with ten species including *A. lipoferum, A. brasilense*, *A. amazonense*, *A. halopraeferens*, *A. irakense, A. largimobile, A. doebereinerae, A. oryzae,* and *A. melinis* is one of the non-symbiont nitrogen-fixing bacterial genus (20–40 kg/ha) (non-nodule forming bacteria), belong to the *Spirilaceae* family and colonizes a great variety of annual and perennial plants (Mehnaz 2015). In these microorganisms, nitrogen fixation occurs under microaerophilic conditions. These bacteria have an interrelationship with roots of corn, wheat, sorghum, and other grasses (Montañez et al. 2012) especially plant with C4 dicarboxylic pathway of photosynthesis which their growth and nitrogen fixation occurs in the presence of the aspartic and malic acid as well as the organic salts (Mishra and Dash 2014). It seems that *Azospirillum* is not limited to a specific plant and can be considered as a general root colonizer; therefore, they are suitable for pearl millet, sorghum, maize, sugarcane, etc. *Azospirillum* can increase the growth of different crops including, sunflower, carrot, oak, sugarbeet, tomato, eggplant, pepper, cotton, wheat, and rice due to fixing nitrogen, as well as producing growth-promoting compounds including, IAA, gibberellins, and cytokinin by which development of root and nutrient (N, P, and K) uptake are enhanced. It has been shown that maize inoculation with *A. brasilense* sp. 245 enhanced the production of various phytohormones which had been led to a substantial enhancement of maize growth. It has been shown that commercial production and field application of *Azospirillum*is simple. Its inoculum can be cost effectively produced and applied as peat formulation (Steenhoudt and Vanderleyden 2000).

14.3.1.8 Nitrogen-Fixing Endophytes

There is increasing evidence which proves the presence of endophytic nitrogen-fixing bacteria (10^8 CFU per g of dry weight). They cause no disease and damage. Nitrogen-fixing endophytes are bacteria belonging to *Azoarcus*, *Gluconacetobacter,* and *Herbaspirillum* genera. These bacteria successfully multiply and spread within plant tissues (Rana et al. 2019c). They colonize on the root cortex of host plants like rhizospheric bacteria. Then, using hydrolytic enzymes, they penetrate endodermis to colonize the steel, from which they may be subsequently translocated to the aerial parts, and in turn, will systemically spread in xylem vessels and shoots. Endophytic diazotrophs colonize the apoplast, like the intercellular spaces, the xylem vessels, and lignified xylem parenchyma, as well as dead cells, such as those comprising lysigenous aerenchyma in rice and kallar grass. *G.diazotrophicus* and *H. frisingense* are some examples of endophytic nitrogen-fixing bacteria in sugar cane and C4- gramineous plant *Miscanthus sinensis*, respectively (Franche et al. 2009). *Azoarcus*, is also an endophytic nitrogen fixer, which can enter into the host plant (*Leptochloa fusca* L Kunth) and live endophytically. Biofertilizer containing *Azoarcus* can efficiently be used under salinity stress in soils with low fertility.

14.3.2 Phosphate Solubilizing Activity

Phosphate is the second indispensable macronutrient for growing plants. The low frequency of its soluble form limits the growth of terrestrial plants that require phosphate to synthesize macromolecules and perform the transfer of energy, respiration, photosynthesis, and signal transduction (Hesham et al. 2021; Khan et al. 2010; Subrahmanyam et al. 2020). Phosphate abundance is 400–1200 mg kg^{-1} of soil. Phosphate application can deeply affect crop yield due to its fundamental role in the growth and reproduction processes of plants. In general, chemical phosphatic fertilizers are applied to supply phosphates to the soil. Studies have shown that a low portion of phosphatic fertilizers (30–35%) is utilized by the plants, while its significant portion (65–70%) is turned into insoluble, immobilized, or precipitated forms and consequently unavailable to the plants. Therefore, available phosphate is less than plant requirement (Angus 2012). Aluminum and iron phosphates, as well as calcium phosphates, are most of the insoluble phosphate forms in acidic and alkaline soils, respectively. The insoluble forms are found as inorganic material like apatite or organic forms such as phosphomonoesters, phosphotriesters, and inositol phosphate (Mahdi et al. 2012). The abundance of phosphate in soluble form is usually very negligible (1 ppm) (Goldstein 1994).

Monobasic phosphoric acid (HPO_4^{2-})] and dibasic [dihydrogen phosphate ($H_2PO_4^-$)] are less frequent, soluble, and bioavailable forms of phosphate in the soil. Insoluble phosphate compounds (both organic and inorganic) should be converted to bioavailable form to avoid continuous usage of phosphate chemical fertilizer and its degrading effect on the ecosystem and also to elevate agricultural yields in soils with less bioavailable phosphorous. This crucial requirement can be provided using a biofertilizer containing phosphate solubilizing microorganisms (Rodríguez et al. 2006a, 2006b). Acidification of soil via producing low molecular weight organic acids like glycolic acid, citric acids, gluconic acid, 2-ketogluconic acid, malonic acid, oxalic acid, succinic acid, and propionic acid which make inorganic phosphorus into their soluble form occur by the activity of these bacteria. They play a crucial role in providing phosphorus to the plants. Hydroxyl and carboxyl groups are existing organic acids with low molecular weight. They can chelate the cations bound to phosphate and convert insoluble phosphorous to its bioavailable form (Glick 2012).

Phosphate solubilizing bacteria belong to various genera including, *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Acetobacter*, *Flavobacterium*, *Arthrobacter*, *Enterobacter*, *Beijerinckia*, *Microbacterium*, *Rhizobium*, *Mesorhizobium*, *Flavobacterium*, *Rhodococcus*, *Serratia*, *Phyllobacterium*, and *Erwinia*cansolubilize insoluble and inorganic phosphate compounds such as rock phosphate, dicalcium phosphate, tricalcium phosphate, hydroxyl apatite (Goldstein 1986; Otieno et al. 2015; Rodriguez and Fraga 1999a). Higher frequency of bacteria with phosphate solubilizing activity is commonly found in the rhizospheric regions in comparison with nonrhizosphere soil due to a higher amount of organic substrates in rhizospheres which attract phosphate solubilizing bacteria (PSB) (Youssef and Eissa 2014). In addition, PSB augment the growth of plants via inducing biological nitrogen fixation by nitrogen-fixing microbial cells (Mohammadi and Sohrabi 2012).

Also, various P containing organic substances can be applied as a promising P resource for requirements of plants after mineralization process where organic P is hydrolyzed to its inorganic form by means of enzymes like phosphatase (phosphohydrolases) (Rodriguez and Fraga 1999), phytase (Richardson 1997), phosphonoacetate hydrolase (McGrath et al. 1998), D-α-glycerophosphatase (Skraly and Cameron 1998), and C-P lyase (Ohtake et al. 1998). A considerable level of acid phosphatases is created by rhizospheric microorganisms like bacteria belong to *Rhizobium* (Abd-Alla 1994), *Enterobacter*, *Serratia*, *Citrobacter*, *Proteus,* and *Klebsiella* (Thaller et al. 1995), as well as *Pseudomonas* (Gügi et al. 1991) and *Bacillus* genera (McComb et al. 2013).

14.3.3 Potassium Solubilizing Activity

Potassium (K) is the third essential element necessary for the growth of plants. Orthoclase, mica, illite, and muscovite are the insoluble source of K in soil. Soluble potassium exists in very low concentration in the soil (Parmar and Sindhu 2013; Yadav et al. 2020b). In soluble-potassium limiting conditions, plant growth and production rate significantly declined. To enhance the bioavailability of potassium to plants, a combination of high K containing clay mineral with K solubilizing bacteria can be applied to meet the K requirement of plants in the agricultural industry (Shrivastava et al. 2016). These microorganisms via producing organic substances solubilize potassium, thus enhance the concentration of soluble K in soil solution. *Frateuria aurantia*, *Bacillus edaphicus*, *Paenibacillus glucanolyticus*, *Bacillus mucilaginosus*, *Acidothiobacillus* sp., *Pseudomonas* sp., *Burkholderia* sp., and *Paenibacillus* sp. are well-known as potassium mobilizing microorganisms (Prakash and Verma 2016; Priyadharsini and Muthukumar 2016; Raghavendra et al. 2016; Rawat et al. 2016). Also, these microorganisms produce diverse amino acids, compounds with plant growth-promoting activity (IAA and gibberellic acid), and vitamins, by them plant growth and productivity are increased (Dotaniya et al. 2016)

14.3.4 Zinc Solubilization

Zn is one of the crucial elements which is required in low amount. Deficiency of zinc declines the growth and yield of crops. Hence, Zn containing fertilizers, with soluble zinc sulfate ($ZnSO_4$), are currently used. On this matter, applying Zn solubilizers extremely affect the reproduction and quality of crops. The reaction of used zinc fertilizers with soil constituents converts them into bioavailable. Several events, including cation exchange of acidic soil, chemisorption in alkaline soil ($Zn\text{-}CaCO_3$) or making a complex with organic ligands immobilize the zinc in soil and decline its abundance in soil. Most well-known biofertilizers contain microorganisms which supply significant macronutrients like nitrogen, phosphate, and potassium, while the unmet need to micronutrient like Zn also negatively affects plant growth, development, and productivity. Therefore, biofertilizers containing Zn solubilizing microorganisms like *B. subtilis*, *Thiobacillus thiooxidans*, and *Saccharomyces* sp. are severely required. It has been shown that better responses can be achieved through co-application of these strains with Zn fertilizers or Zn containing oxides (Zinc oxide, Zinc carbonate, and Zinc sulfide) (Samoon et al. 2010).

14.3.5 Iron Sequestration

Iron is one of the pivotal growth elements for nearly all living organisms, including animals plants, bacteria, and fungi (Rajkumar et al. 2010). In the presence of oxygen, iron mainly presents as ferric iron (Fe^{3+}) and probably generate insoluble hydroxides and oxyhydroxides. Therefore, a large amount of the iron is not in bioavailable form for plant and bacterial assimilation (Rajkumar et al. 2010). The low abundance of bioavailable iron in terrestrial ecosystems creates an extreme competition. Plants frequently produce and excrete water-soluble organic compounds (siderophores) with low molecular weight, that chelate Fe^{3+} and maintain it in solution. The root surface receives Fe^{3+} from siderophores and reduces it to Fe^{2+} and consequently absorbs it. Also, bacteria produce and release siderophores, high-affinity iron chelator, to scavenge iron by the formation of soluble Fe^{3+}complexes. They can be considered as agents with iron solubilizing activity from minerals or organic compounds in iron-limiting conditions (Ahemad and Khan 2011; Rajkumar et al. 2010). They can be categorized into two types including extracellular and intracellular iron chelators. Enterobactin is one of the strongest siderophores (Hider and Kong 2010).

Microbially derived siderophores also can be applied by plants; hence they can augment the growth of plants under iron limited condition. Plants can assimilate iron provided by microbial siderophores via diverse strategies like chelating and releasing iron, direct uptake of siderophores-Fe complexes, or ligand exchange reaction (Thomine and Lanquar 2011). Several isolates belonging to *Pseudomonas*, *Enterobacter*, *Bacillus*, and *Rhodococcus* genera are siderophore producing microorganisms. Siderophores producing *Phyllobacterium* strain, *Pseudomonas fluorescens* C7, and *Chryseobacterium* sp C138 promote the growth and quality of strawberries and *Arabidopsis thaliana*, respectively (Parray et al. 2016). More importantly, biofertilizer containing siderophore producing microorganisms like *Pseudomonas, Bacillus* sp. and *Streptomyces* can be applied as biological agents for biocontrol. They limit the reproduction and activity of phytopathogens via producing high iron affinity siderophores. Through this mechanism, phytopathogens like *Fusarium oxysporum* cannot meet their iron requirement, and therefore, their reproduction will be limited (Bashan and De-Bashan 2005; Saraf et al. 2014).

14.3.6 Production of Volatile Organic Compounds

Producing volatile organic compounds (VOCs) is one of the interesting strategies which is applied by biofertilizers to promote plant growth and its resistance towards fungal pathogen and pathogenic nematodes as well as abiotic stresses. Acetoin, 2,3-butanediol cyclohexane, 2-(benzyloxy) ethanamine, benzene, methyldecane-1-(*N*-phenylcarbamyl)-2-morpholinocyclohexene, dodecane, benzene(1-methylnonadecyl), 1-chlorooctadecane, tetradecane, 2,6,10-trimethyl, dotriacontane, and 11-decyldocosane are some of these compounds (Effmert et al. 2012; Kanchiswamy et al. 2015; Ryu et al. 2003).

Rhizobacterially-produced VOCs act as signaling molecules to trigger the plant responses and form plant–microbe interactions and elicitor agents of induced systemic resistance (Ryu et al. 2003; Sharifi and Ryu 2016). Reported VOC producing microorganisms are *Bacillus subtilis* GB03, *B. amyloliquefaciens* IN937a, *Pseudomonas*, *Serratia*, *Arthrobacter*, and *Stenotrophomonas* and *Enterobacter cloacae* JM22. It has been reported that some of these VOC producing microorganisms can promote the growth of *Arabidopsis thaliana* (Choudhary et al. 2016).

Some rhizospheric microorganisms including *Rhizobium*, *Pseudomonas*, *Bacillus*, and *Aeromonas* genera can produce hydrogen cyanide (HCN), a bioactive compounds with an adverse effect on the reproduction of phytopathogens or weeds whose usage will protect the host plants (Ahmad et al. 2008; Das et al. 2017; Flury et al. 2017; Nandi et al. 2015; Sivakumar et al. 2012; Zachow et al. 2017). It has been found that HCN production is common in *Pseudomonas* (88.89%) and *Bacillus* (50%) genera (Ahmad et al. 2008). Since, produced HCN has no adverse effect on host plants, HCN producing microorganisms can act as biocontrol agents. In most cases, these microorganisms also produce compounds with antibiotic activity or cell wall degrading enzymes which along with HCN can synergistically suppress the growth of phytopathogens. On the other hand, low level of HCN cannot effectively prevent the proliferation of most fungal phytopathogens (Ramette et al. 2006) but can prevent phytopathogens to become resistant (Olanrewaju et al. 2017). HCN impose its toxicity effect due to the inhibitory effect on cytochrome c oxidase and other critical metalloenzymes (Nandi et al. 2017). Recently, it has been revealed that promoting the activity of HCN on the growth of plants is mostly related to its role in increasing the bioavailability of phosphate for the pioneer plants (like French sorrel) living in oligotrophic alpine environments (like granite-based substrate) (Rijavec and Lapanje 2016).

14.3.7 Production of Hydrolytic Enzymes

Many microorganisms can improve plant growth by suppressing the growth of their pathogens. Production of hydrolytic enzymes such as chitinase, glucanase, protease, and cellulase (Suyal et al. 2021; Yadav et al. 2016). Producing hydrolytic enzymes are one of the critical strategies by which microorganisms control pathogen growth (Jadhav and Sayyed 2016; Jadhav et al. 2017). A wide range of polymeric compounds like chitin, proteins, cellulose, and hemicellulose in the cell wall of the targeted phytopathogens can be hydrolyzed via these enzymes (Mabood et al. 2014).

14.3.7.1 Chitinase Production

Chitin is an insoluble unbranched β-1,4-β-linked polymer of *N*-acetyl-D-glucosamine (C8 $H_{13}O_5N)_n$ and is the second most plentiful naturally occurring polymer (Huang et al. 2005). Chitinase producing microorganisms can be considered as promising biological control agents and prevent fungal related plant diseases. Chitinase producing fluorescent *Pseudomonas* and *Streptomyces* sp. isolates can control ragi blast disease and sheath blight disease in rice, respectively (Chaiharn et al. 2018; Negi et al. 2017). Chitinasescategorized into three classes according to their mode action: β-1,4-*N*-acetyl-glucosaminidases, endochitinases, and exochitinases. Chitin degradation can be achieved through endochitinases via randomly cleaving at internal sites of chitin micro-fibril orexochitinases via progressive release of diacetylchitobiose in a stepwise manner without releasing monosaccharide or oligosaccharides (Harman et al. 1993; Manocha and Balasubramanian 1994).

14.3.7.2 Glucanase Production

β-1,3-Glucanases-producing microorganisms like *Paenibacillus terrae* NK3-4 can efficiently degrade another important cell wall component of fungi and yeasts, β-1,3(1,6)-Glucans (Simmons 1994; Yu et al. 2019). This polysaccharide consists of a β-1,3-linked backbone with some branches via β-1,6-linkages. They are classified into two groups, according to their mode of action: sequent removing of glucose residues from non-reducing end or randomly breakdown of linkage at random sites and releasing smaller oligosaccharides can be conducted via exo- or endo-β-1,3-glucanases, respectively. (Jadhav and Sayyed 2016).

14.3.7.3 Cellulase Production

Bacillus cereus, *Bacillus subtilis*, *Bacillus thuringiensis,* and *Streptomyces* sp. can impose their biocontrol activity via degrading the 1,4-β-D-glucosidic bonds in cellulose (Patagundi et al. 2014; Sadeghi et al. 2017). Cellulose consists of β-D-glucose units which are bonded via 1,4-β-linkages. These microorganisms also play a pivotal role in nature through the recycling of this abundant polymer. The rigid, insoluble, crystalline cellulosic microfibrils are formed via abundant intra- and intermolecular hydrogen bonds. Various hydrolytic enzymes including endoglucanases, exo-glucanases, and β-glucosidases are involved to completely degrade cellulose into β-glucose (Lynd et al. 2002).

14.3.7.4 Protease Production

Protease or proteinase plays a crucial role in degrading the cell wall of phytopathogenic fungi. This enzyme degrades the protein matrix where chitin and/or fibrils of β-glucan (major components of the cell walls) are present. The polymer is hydrolyzed to peptide chains and/or their amino acids by this enzyme. Also, several proteases via inactivating extracellular enzymes of phytopathogenic fungi, suppress their growth (Al-Askar et al. 2015; Jadhav and Sayyed 2016).

14.3.8 Production of Hormones

Phytohormones, plant hormones, are organic substances that affect physiological, biochemical, and morphological characteristics in plants including growth, differentiation, and development of cells, tissues, and organs (Damam et al. 2016; Peleg and

Blumwald 2011). These compounds can be considered as chemical signals to communicate cellular activities in higher plants (Voß et al. 2014), and their synthesis is tightly regulated. Some well-known examples are auxins, ethylene, gibberellins, abscisic acid (ABA), and cytokinins, which play a critical role at very low concentrations (<1 mM). They are active in plants in a short period of time and are mainly produced in special parts of the plant and transferred to another part. Since these chemical compounds affect the growth of the plant, they are also recognized as regulators of plant growth. Under stress conditions, plants or their rhizospheric microorganisms produce or modulate phytohormone levels to coordinate various signal transduction pathways and consequently ameliorate the adverse effects of environmental stresses (Kazan 2015).

Microbial produced phytohormones are known as exogenous phytohormones. Microbial production of plant hormones such as auxin and cytokinins are reported by a lot of rhizospheric microorganisms (Ahemad and Khan 2011). Also, phytohormones improve defense response of plants through stimulating cell division, extension, differentiation, photosynthesis, and pigment formation, inducing seed and tuber germination, increasing the development rate of xylem and root (Gupta et al. 2015; Ljung 2013; Spaepen and Vanderleyden 2011). *Azospirillum* is a well-known plant growth-promoting bacterium with the ability to excrete phytohormones including gibberellins, cytokinins, and auxins (Tien et al. 1979).

Root surface area and its length can be enhanced by microbial IAA, which enables the plant to achieve more nutrients from the soil (Ahemad and Khan 2012b). The plant cell wall is affected by rhizobacterial IAA and its loosening lead to facilitated exudation of plant exudates, which assure sufficient bacterial growth (Ahemad and Khan 2012a). Inoculating auxin-synthesizing *Bacillus* spp. positively affects the growth of *Solanum tuberosum* (Ahmed 2010). Seed germination, floral induction, development of flower and fruit, and growth of leaf and steam are affected by another pivotal phytohormone, gibberellin. Gibberellin-producing *Sphingomonas* sp. LK11 positively affects plant growth characters (Khan et al. 2014). It has been reported that cytokinin-producing *Bacillus subtilis* strains caused draught resistance of inoculated plants. It has been shown that *Bacillus amyloliquefaciens* RWL-1, an endophyte, synthesize ABA. Hence, it has the ability to enhance the salinity tolerance of *Oryza sativa*. Biofertilizers containing phytohormone producing or modulating microorganisms can offer economic and ecological advantages to boost agricultural production (Shahzad et al. 2017).

Ethylene is a significant phytohormone that affects the ripening of fruits and the abscission of leaves (Reid 1981). Elevated level of aminocyclopropane-1-carboxylate (ACC) synthesis, that is, the precursor of ethylene, is observed in plants under stress conditions like low temperature, drought, flooding, infections with pathogens, and the presence of heavy metals which creates physical or chemical perturbation in various tissues of plants (Li and Glick 2005), and for this reason, wounding hormone is its other name (Salisbury 1992). Increased level of ethylene halts the growth of stem and root, fixation of nitrogen in legumes, and causes premature senescence and consequently decreases the yield. In this regard, there are some rhizospheric microorganisms which produce aminocyclopropane-1-carboxylate deaminase, a pyridoxal phosphate-dependent enzyme. This enzyme can hydrolyze the precursor of ethylene, ACC, to ammonia and α-ketobutyrate then use them as nitrogen and carbon sources. Therefore, ACC deaminase producing microorganisms via reducing the level of ethylene precursor, ACC, improve the growth of plants in the presence of biotic and abiotic stresses (Glick 2014). So, plant growth-promoting microorganism's ability to hydrolyze ACC possesses profound significance in declining the adverse effect of environmental stressors.

Synthesis of this enzyme is induced in the presence of ACC. ACC deaminase is encoded by *AcdS* gene which is found in Actinobacteria, Deinococcus-Thermus, three classes of α, β, and γ Proteobacteria, various fungi belonging to Ascomycota and Basidiomycota, and in some Stramenopiles (Nascimento et al. 2014). Of possessing microorganisms, different bacteria (*Alcaligenes* sp., *Bacillus pumilus*, *Pseudomonas* sp., and *Variovorax paradoxus,* as well as *Azoarcus*, *Azorhizobium caulinodans*, *Azospirillum* spp., *Gluconacetobacter diazotrophicus*, *Herbaspirillum* spp., *Burkholderia vietnamiensis.*) and some yeast (*Hansenula saturnus* and *Issatchenkia occidentalis*) (Minami et al. 1998; Palmer et al. 2007), as well as fungi (*Penicillium citrinum*, *Trichoderma asperellum*, and *Phytophthora sojae*) (Jia et al. 1999; Singh and Kashyap 2012; Viterbo et al. 2010) and archaea like *Pyrococcus horikoshii* (Fujino et al. 2004; Singh et al. 2015) can be considered. Also, it has been known that even certain plants like *Arabidopsis thaliana* (McDonnell et al. 2009) are ACC deaminase producing organisms.

These ACC deaminase producing microorganisms efficiently augment the growth rate, physiological characteristics, and quality of plants, especially in presence of salinity stress. ACC deaminase synthesizing *Pseudomonas putida* UW4 reduced post-submergence ethylene production. Therefore, it has been concluded that plant response to environmental stressors can be modified by rhizospheric bacteria (Ravanbakhsh et al. 2017). According to other studies, a salt-tolerant bacterium with ACC deaminase activity, *Enterobacter* sp., was isolated from the rice field and was reported to promote rice seedling growth in salinity stress (Sarkar et al. 2018). In another study, ACC producing endophyte, *Pseudomonas migulae* 8R6, limited phytoplasma-induced damages, and consequently *Flavescence dorée* disease in periwinkle (Gamalero et al. 2017).

It has been revealed that a salt-tolerant endophyte SMR20 with the capability to produce ACC deaminase, *Brachybacterium paraconglomeratum*, isolated from *Chlorophytum borivilianum* reduced salt stress-induced damage in the host plant and delayed chlorosis and senescence and improved yield. In addition, this bacterium modifies the levels of indole-3-acetic acid and abscisic acid in plants (Barnawal et al. 2016).

14.4 Environmental Stress Relief

Various biotic (bacterial and fungal phytopathogens, pests, and herbivores) and abiotic stresses (hostile conditions of ecosystem like drought, water logging, extreme temperatures, salt stress, oxidative stress, air pollution, heavy metals, pesticides, and unfavorable soil pH) affect plant growth and its productivity during their growth and development which lead to a reduction of agricultural yield (Rastegari et al. 2020a, 2020b; Suman et al. 2016; Yadav et al. 2020a). Reactive oxygen species (ROS) including H_2O_2, O_2^-, and OH^- radicals are generated in stress conditions and their elevated level created oxidative stress, which consequently imposes its deleterious effect on plants (CH 2018). They can alleviate this oxidative stress through various strategies like producing and accumulating poly-sugars, proline, glycine-betaine, abscisic acid, and up-regulating enzymatic and nonenzymatic antioxidants, like superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, ascorbic acid, α-tocopherol, and glutathione (Agami et al. 2016).

In these conditions, plant inoculation by biofertilizers can provide more protection against these stresses through microbial activities, including the release of substances that can improve soil structure, inhibiting the causative agents of biotic stress via modulating phytohormones and inducing systemic resistance (Yang et al. 2009). In addition, beneficial microorganisms can ameliorate the toxic effect of heavy metal on plants through various strategies like binding mechanisms. It has been reported that *Pseudomonas putida* and *Pseudomonas fluorescens* alleviate the toxic effect of cadmium contamination on barley plants through their ability to scavenge cadmium ions from soil (Baharlouei et al. 2011).

Microbial induced modifications lead to increased survival and productivity of plants. Some examples have validated the protective effect of biofertilizers, e.g., *Azospirillum* inoculation enhanced the growth of wheat and faba beans under saline stress. One group of microbial substances which alters the structure of soil, and imposes an improving effect on the growth of plants in the presence of water stress is a microbial polysaccharide. For example, inoculation of sunflower and wheat plants with exopolysaccharide producing *Rhizobium* sp. and *Pantoea agglomerans* resulted in better growth parameters in comparison with uninoculated plants. It has been reported that *Pseudomonas* strains via enhancing the assimilation of Mg^{2+}, K^+, and Ca^{2+}, declining uptake of Na^+, and enhancing the synthesis of endogenous indole acetic acid have improved asparagus seedling growth and seed germination in presence of water and salt stresses. Several reactive oxygen species generated during water stress cause injury to the photosynthetic mechanisms of the plant (Heidari and Golpayegani 2012). In this regard, biofertilizer containing *Pseudomonades*, *Bacillus lentus*, and *Azospirillum brasilense* through increasing expression of enzymatic antioxidants and enhancing the amount of chlorophyll in leaves ameliorate this stress. Therefore, biological fertilizer can augment the photosynthetic activity of the plant, and improve its physiological properties in presence of unfavorable conditions (Heidari and Golpayegani 2012).

Improving leaf water status, especially in the presence of salt and drought stresses, is another strategy to improve plant growth (Ahmad et al. 2013; Naveed et al. 2014). Biofertilizers via improving stomatal conductance of plant leaf enhance its ability in utilizing water and surviving under drought conditions. *Pseudomonas aeruginosa* has improved the growth of *Vigna radiata* plant in drought conditions (Naveed et al. 2014; Sarma and Saikia 2014). It has been demonstrated that *Bacillus megaterium* and *Pantoea agglomerans* enhanced the ability of maize roots to absorb water under salinity stress (Gond et al. 2015; Marulanda et al. 2010). *Azospirillum brasilense* also has enhanced the salt resistance of the jojoba plant rooting (Ahmad et al. 2013; Gonzalez et al. 2015; Naveed et al. 2014)

Biotic stresses impose their deleterious effect on co-evolution, dynamics of population, nutrient cycling in the ecosystem, ecology of natural habitat, and health of horticultural plant (Gusain et al. 2015). *Bacillus* spp. (like *Paenibacillus polymyxa* strains B2, B3, and B4, *Bacillus amyloliquefaciens* strain HYD-B17, *B. licheniformis* strain HYTAPB18, *B. thuringiensis* strain HYDGRFB19, *P. favisporus* strain BKB30, and *B. subtilis* strain RMPB44) and *Pseudomonas* sp. Decrease the growth and activity of phytopathogens by their antimicrobial metabolites or competition.

Pseudomonas sp. and rhizobacteria produce antimicrobial compounds and proteins with toxic properties against *Gaeumannomyces graminis* var. tritici (inducing wheat take-all) and crop insect pests, respectively (Strange and Scott 2005).

Phenazines, phenazine-1-carboxylic acid, phenazine-1-carboxamide, pyrrolnitrin, pyoluteorin, 2,4diacetylphloroglucinol, rhamnolipids, oomycin A, cepaciamide A, ecomycins, viscosinamide, butyrolactones, N-butylbenzene sulfonamide, pyocyanin are antifungal agents produced by *Pseudomonas* strains also produce antibacterial compounds (pseudomonic acid and azomycin), antitumor antibiotics (cepafungins and FR901463). Karalicine is an antiviral derived from *Pseudomonas* (Ramadan et al. 2016). Surfactin, iturins, and bacillomycin are antibacterial compounds derived from *Bacillus* sp. (Wang et al. 2015).

B. cereus UW85 and *B. thuringiensis* subsp. *kurstaki* HD-1 can be applied as biological agents to control the damping-off of alfalfa and gypsy moth, respectively (Broderick et al. 2000; Handelsman et al. 1990). *Photorhabdus* and *Xenorhabdus* inhibit harmful insects. *Pseudomonas* sp. and *Bacillus subtilis* produce siderophores that can be considered as biocontrol agents, which limit fungal pathogens like *Fusarium* wilt that is produced by *Fusarium oxysporum* in potato (Haggag et al. 2015).

Tolerance of plants to the attack of herbivores can be elevated by symbiosis with rhizobacteria. It is likely that these bacteria via supplying additional nitrogen make synthesizing cyanogenic defense compounds possible. These synthesized compounds repel leaf-chewing herbivores (Godschalx 2017). Also, chitinases and β-glucanases-producing microorganisms like *Sinorhizobium fredii* KCC5, *Pseudomonas fluorescens* LPK2, and *Pseudomonas spp.* via degrading chitin and β-1,4-*N*-*N*-acetylglucosamine inhibit *Fusarium udum* (causative agent of fusarium wilt), *Rhizoctoniasolani,* and *Phytophthoracapsici* (destructive crop pathogens), respectively (Ramadan et al. 2016).

14.5 Factors Influencing the Efficiency of Biofertilizers

One of the considerable properties which has resulted in limited application of biofertilizers is their unpredictable function under different agro-environmental conditions, which may seriously reduce their plant growth promotion potential. There are some less investigated factors including the production process of biofertilizers, interaction of host plant and microbial strains, competition condition of the soil, which involved in this phenomenon (Bashan 1998; Owen et al. 2015). Reducing the unfavorable properties of the biofertilizers and improving the influential factors on biofertilizer efficiency can encourage the farmers to use them. Biofertilization program by selecting strains according to their high root colonization, abundant sporulation, or growth augmentation in pot experiments without considering affecting factors like field conditions can lead to non-conclusive results.

14.5.1 Effect of the Plants on the Efficacy of Biofertilizers

One of the determinant factors on biofertilizer efficiency is the interaction of microbial biofertilizers with plants. Crop species and environmental conditions of the field are two main factors that govern the interaction between microorganisms and plants (Dodd and Ruiz-Lozano 2012). Promoting and inhibitory effects of plants are significantly depending on their phenological growth phase and physiological and nutritional status. These situations directly affect the release of compounds from the roots. These compounds in plant exudates impose quantitative and qualitative modifications in the rhizospheric region due to the growth promotion or inhibition of specific rhizospheric bacterial communities (Dennis et al. 2010; Hartmann et al. 2009; Uren 2000; Van Overbeek and Van Elsas 2008). In P-deficiency, plants stimulate hyphal branching and colonization of AM fungi through releasing inducing chemicals (Akiyama et al. 2002; Akiyama et al. 2005). Genistein, a phenylpropanoid compound, and phenolic acids are influential compounds in root exudates that stimulate AMF root colonization and change soil microbial communities, respectively (Cesco et al. 2010; Qu and Wang 2008).

14.5.2 Effect of Soil Conditions on the Efficacy of Biofertilizers

Another critical factor in successful biofertilizer establishment is the soil in which microbial cell is introduced. Chemical (pH, nutrient content) and physical (texture) properties of soil profoundly affect biofertilizer establishment, colonization, and plant growth-promoting activities (Fierer and Jackson 2006; Girvan et al. 2003; Lauber et al. 2008). Acidic soils have a less diverse microbial community in comparison to neutral soils because of the narrow pH growth tolerance of bacterial taxa (Fierer and Jackson 2006; Rousk et al. 2010). *Acaulospora* species are exclusive to acidic soils in the tropics. Therefore, broad-range microbial species like *Glomus intraradices* can assure the efficiency of biofertilizers. Because it has been adapted to an extended range of environmental conditions, especially harsh situations including, unfavorable pH and temperature and less available nutrients (Antunes et al. 2011).

14.5.3 Effect of Interaction of Soil Microorganisms with Autochthonous on the Efficacy of Biofertilizers

Successful fertilization can be achieved by characterizing microorganisms, their activities, and the interrelationship between them and soil particles. However, there is limited knowledge about the ecological interactions of autochthonous soil microorganisms and microorganisms derived biofertilizers (Malusà et al. 2016). Once microbial cells forming biofertilizers are introduced in the soil, they are faced with an extreme competition condition due to the presence of indigenous microorganisms. Therefore, the exact evaluation of ecological interactions among indigenous soil microorganisms and introduced microbial inoculants is so critical in determining the biofertilizer's efficiency in the short- and long-period of time. For this purpose, various indicators of soil microorganisms, including their biomass, activity, community structure, and diversity should be comprehensively analyzed (Trabelsi and Mhamdi 2013).

It must also be noted that the observed relationships between inhabitant and inoculant microorganisms would depend considerably on the methods used to show the dynamics of terrestrial microbial communities (Trabelsi and Mhamdi 2013). Simultaneous use of metagenomic approaches and culture-dependent methods can lead to the identification of a number of microbial taxa. However, identification of their related function is still very complicated. The evaluation of coding genes of significant enzymes or main genes in the interaction process between the introduced and native microorganisms may help to gain such information.

It has been revealed that diverse taxonomical or functional classes of autochthonous soil microorganisms are affected by complex inoculum through various strategies. Roots colonization of biofertilizers can be achieved through successful competition with indigenous microorganisms. In these competitive conditions, the ability to produce biofilm or having motility can be advantageou for colonizing root and competition. Therefore, to use these beneficial characteristics, a sufficient amount of microbial cells should be present to produce specific chemicals and consequently gain these properties through turning on quorum sensing (Gera and Srivastava 2006). Some of the soil habitants like protozoan grazing, bacterial grazer, fungi, and insects in soil adversely affect biofertilizer efficacy through reducing their number and colonization ability (Finlay 1985). It has been observed that the population of nematodes has been increased after applying biofertilizers (Malusá et al. 2012). Colonization of wheat rhizosphere by *Pseudomonas* species and *Bacillus subtilis* was greatly declined by nematode species (e.g., *Caenorhabditis elegans*, *Acrobeloides thornei*, and *Cruznema* sp.) (Knox et al. 2003).

14.5.4 *Effect of Farmers' Practices on the Efficacy of Biofertilizers*

Another important factor in biofertilizer efficacy is the overall fertility or nutritional conditions of the soil. Some microbial inocula like *Glomus* are more mostly found in fertile soils, with a great amount of nutrients (Hayman and Stovold 1979). In most cases, applying a large amount of chemical fertilizers for a long term increases the nitrogen, phosphorus, and/or potassium accumulation in the soil, modifies interaction of plant and microbial cells, and simultaneously imposes adverse effects on colonization, establishment, and activities of soil microbial communities including autochthonous soil microorganisms and biofertilizer microbial cells (Gosling et al. 2006). For example, low levels of AMF colonization have been observed in maize, soybean, and wheat which were grown on chemically fertilized soils (Duan et al. 2010). The genera *Scutellospora*, *Acaulospora,* and *Gigaspora* are more frequent in soils with low level of nutrients (Hartmann 2006; Johnson et al. 2005; Mäder et al. 2002; Oehl et al. 2004). Long-term applications (10 or 90 years) of chemical phosphate fertilizers or irrigation with wastewater result in P-accumulation in the soils, which declined colonization and population of AM fungi (Cheng et al. 2013; Ortega-Larrocea et al. 2001). Moreover, in the presence of sufficient bioavailable nitrogen and phosphate, the growth of AM fungi is more likely suppressed, they show mutualistic symbiosis in soil with sufficient bioavailable nitrogen, along with limited P (Johnson et al. 2010).

Therefore, it has been proposed that to achieve efficient colonization of microbial inoculum and their corresponding activities, the quantity of applied chemical fertilizers must be reduced (by 20–50%) (Adesemoye et al. 2009; Jeffries et al. 2003). It was shown that most efficiencies of biofertilizer, which consists of two strains of *Pseudomonas fluorescens* on wheat, were achieved when it is applied via 25% of recommended NPK fertilizers dose (Shaharoona et al. 2008).

In most cases, organic fertilizers like manure, compost, stillage, and vermicompost extract stimulated colonization and growth of several microbial communities via plant growth-promoting activities (Canfora et al. 2015; Esperschütz et al. 2007; Toljander et al. 2008). Although some organic fertilizers reduce AMF richness like sewage sludge (Esperschütz et al. 2007; Toljander et al. 2008), application of some agrochemicals such as aliette, ridomil, benomyl, and benlate has some adverse effects on AM fungi development (Sukarno et al. 1996).

14.5.5 *Other Factors Affecting the Efficacy of Biofertilizers*

It has been shown that colonization and mycorrhiza-mediated nutrient uptake are detrimentally influenced by tillage, monoculture, and intensive agriculture detrimentally (Perron et al. 2001). Method of inoculum application has a significant role in its efficiency (Date 2001; Deaker et al. 2004). To achieve the best results, new machines are developed or existing machines are adapted to efficiently applying various physical forms of biofertilizers in specific conditions, e.g., inoculation of horticultural crops or big trees by liquid biofertilizer containing AMF is performed (Malusà et al. 2016; Malusa and Sas 2009).

Biofertilizers can be introduced through the foliar application, treating seeds, mixing with soil or organic matter like vermicompost, spraying through hydraulic atomization system (Bhattacharjya and Chandra 2013; Świechowski et al. 2012). Each of these strategies has a considerable effect on biofertilizer efficiency.

The number of delivered spores and their efficacy is influenced by water volume and adjuvants (Bailey et al. 2007). According to the possible recovery period of PGPR (30–40 days after inoculation), it has been suggested that it is suitable to repeat biofertilizer inoculation (2–4 times) during the growing season, with an interval of 3–4 weeks (Bashan et al. 1995).

In some cases, the activities of biofertilizers are slower than that of chemical fertilizers. The activity of a biofertilizer depends on various factors including inoculant delivery system, skill of farmers, viability of biofertilizer under adverse climatic, transport condition, and storage management. Generally, developing biofertilizers needs high investment costs. Moreover, occurring mutation during the production process is deemed as a major limitation of biofertilizers. It must also be noted that low awareness of the farmers can cause poor resource generation by the industries (Singh et al. 2016).

14.6 Production Process

As mentioned previously, biofertilizers can have one or more microbial strains. Preparing the microbial inoculum has a considerable effect on the final product efficiency and quality (Bashan et al. 2014; Stephens and Rask 2000). Recently, the application of complex microbial consortia in diverse annual and horticultural crops has attracted more attention due to favorable results on legumes and non-legume plants. For example, rhizobia with arbuscular mycorrhizal fungi (Alagawadi and Gaur 1988), (AMF), Rhizobium and phosphate solubilizing bacteria (Wang et al. 2011), Rhizobium and a phosphorus solubilizing bacteria (Prasad and Chandra 2003), AMF with free-living bacteria with a nitrogen-fixing ability (Adesemoye et al. 2008; Barea et al. 2002) and biofertilizer simultaneously containing AMF and various PGPR for diverse annual and horticultural crops (Malusa et al. 2007) are successful examples of biofertilizer with complex inocula. In selecting strains to prepare a consortium for a biofertilizer, it should be noted that the applied strains not only should not inhibit the growth of each other, but also coapplication of them must lead to higher colonization (Vestergård et al. 2008).

In designing a biofertilizer for a specific agrogeographical condition, adaptation of the microbial cells to ecosystem conditions should be investigated (Malusá et al. 2012; Zoppellari et al. 2014). Along with the selection of suitable and efficient microbial cells, the type of fermentation process which profoundly affects the shelf life of a biofertilizer is also important. In this period, the microbial cells in inoculant should preserve their survival and plant growth-promoting activities at an acceptable level (Bashan et al. 2014). One of the critical involved factors in biofertilizer shelf life is a multistep process, which is called formulation.

A suitable formulation containing additives (Bashan et al. 2014; Herrmann and Lesueur 2013; Malusá et al. 2012) which by protecting microbial cells during storage and transportation enhance their persistence in soil or even improve the microbial cell efficacy using nodulation elicitors (Legume biofertilizers) (Smith and Smith 2012) and colonization and establishment inducing metabolites like strigolactones assures biofertilizer efficiency (Manikandan et al. 2010; Skorupska et al. 2010). It has been shown that biofertilizer in the shape of granular inoculants represents better results under unfavorable conditions of the soil (Rice et al. 2000). Easier distribution of microbial cells in liquid inoculants can lead to their shorter shelf life (Bashan et al. 2014; Date 2001; Stephens and Rask 2000). Encapsulation of PGPR in alginate or other polymers with various compositions and structures was introduced (Vassilev et al. 2005); however, limit industrial application was seen (Bashan et al. 2014; John et al. 2011).

14.7 Fermentation Process

In order to commercialize a biofertilizer, suitable and efficient microbial strains should be selected and characterized. Large-scale production of these strains should be performed and the desired inoculants must be prepared (Sethi and Adhikary 2012). Mass production of microbial cells for biofertilization can be produced through fermentation processes including, submerged fermentation (SmF) and solid state fermentation (SSF) (De Roy et al. 2014).

Selecting a suitable and affordable nutrient medium is an essential prerequisite for a successful biofertilizer production process. Cost-effective substrates like liquid synthetic media, vegetable extracts, soluble sugars, fruit and dairy by-products, and wastewater can be used in submerged fermentation for large-scale production of biofertilizers (Subramaniyam and Vimala 2012). Low-cost substances or even industrial waste like agro-industrial wastes can be used as the substrate to mass production of microbial cells for biological fertilizers through SSF. In this fermentation, microorganisms are grown on solid materials such as sterilized peat or calcinated clay without the presence of free water (Gowthaman et al. 2001). In this strategy, tight contact between microorganisms and agro-industrial wastes provides the highest substrate concentrations for fermentation.

Also, fertilizers can be produced without a complicated formulation process by mixing microbial cells with agricultural by-products. Industrial wastes, like whey, molasses, bagasse, paper pulp, wheat bran, rice, and rice straw, vegetable and fruit wastes can be efficiently applied as low-cost substrates to solubilize insoluble, inorganic, and low-grade phosphate rocks by various fungi in solid state fermentation (Mendes et al. 2015; Pandey et al. 1999). Prepared biofertilizer using agro-industrial waste materials through solid state fermentation can enrich the soil with organic substances, minerals, and bioactive compounds. It has been revealed that a mixture inoculum of bacterial and fungal microorganisms accelerates the mineralization process of solid waste and their action results in the highly nutrient-rich final product (Cariello et al. 2007; Singh et al. 2011).

Agricultural residues which are treated by microorganisms have a significant ability to reinstate fertility and microbial diversity of disturbed soils. Some fermentation parameters, including pH, temperature, and incubation period, should be optimized in a pilot-scale study to achieve the best production yield.

14.8 Biofertilizer Formulation

The formulation process is a crucial multistep approach in commercializing new biofertilizers and directly affects their efficiency, stability, and quality (Bashan et al. 2014). During the formulation process, microbial cells (one or more strains) are mixed with certain carriers which preserve the cells and their activities under not optimized storage conditions (unfavorable temperature and light exposure) (Herrmann and Lesueur 2013). Good formulation assures successful multiplication of microbial cells, extending their shelf life, and enhances their activity to a higher rate after inoculation to the host plants (Arora et al. 2010). Since formulated biofertilizer largely consists of substances as carriers, they significantly affect the success or the failure of the inoculation.

Being non-toxic, non-pollutant, biodegradable, and biocompatible are critical prerequisites of carriers for formulation. They should be stable and preserve microbial survival under harsh conditions, having adjustable pH, sufficient shelf life, fine grinding in order to mix with other constituents (nutrients, adjuvants), and consist of low-priced substances (Catroux et al. 2001; Herrmann and Lesueur 2013). In desirable formulation, controlled release of microorganisms into the soil can be achieved. Also, applying this formulation can be performed via standard seeding machinery (Malusá et al. 2012). Adherence of microbial cells on the seeds can be improved by using adhesive material, which is known as stickers. Organic, inorganic, or synthetic substances can be used as carriers. Generally, they are categorized into four key classes including soils (inorganic soil peat, clays, coal, and lignite), herbal waste (farmyard manure, wheat bran, charcoal, composts, cellulose, soybean meal, soybean and peanut oil, press mud, and corn cobs), inert materials (ground rock phosphate, vermiculite, perlite, bentonite, calcium sulfate, polyacrylamide, and alginate), and lyophilized microbial cultures and old dried bacteria (Bashan 1998).

It is possible that a formulated biofertilizer be made from a mixture of mentioned carriers. Besides, the carriers and stickers, some macro- and micronutrients such as carbon or mineral resources, hormones, and fungicides, which are known as additives may be added during biofertilizer formulation (Arora and Mishra 2016). Additives, like skim milk (Vassilev et al. 1997), xanthan (Lorda et al. 2007), or sodium alginate (Tittabutr et al. 2007) provide nutrient and moisture, as well as inactivate toxic compounds, delay inoculant desiccation and improve its quality, stability, and shelf life (Manikandan et al. 2010).

Five formulations are currently used for biofertilizers, including peat formulations, liquid formulations, granules, and freeze-dried powders as well as the most recent strategy of stabilization (Bashan 1998).

14.8.1 Peat Formulations

Peat is composed of partially decayed vegetation that is accumulated for a long time. Microbial cells can successfully grow on it as a nutrient-enriched and protective environment (Bashan et al. 2014). Used peat in the formulation process should have acceptable content of organic matter and water retaining capacity. They must be free from toxic substances for microorganisms, plants, animals, and humans), should be cost-effective, highly adsorptive, and simply sterilizable. Peat processing steps include drainage, sieving, and drying (~5%). Drying must be performed at the lowest possible temperatures to avoid the release of hazardous compounds. After the drying process, they are passed through a 250-μm sieve, and their pH is adjusted at pH 6.5–7.0 by liming (Roughley 1976). Then sterilization of the prepared peat is conducted, and a sufficient quantity of liquid inoculum is added to the peat to achieve a final moisture content of 40–55%. Microbial inoculated peat is incubated for a period of time to allow bacterial multiplication in the carrier which is known as maturing or curing and has a tremendous effect on bacteria survival during storage and on seeds (Okon and Baker 1987). In order to increase the uniformity of biofertilizer coverage on seed, sticking agents including polymeric materials like polysaccharides (like Arabic gum or carboxymethylcellulose), polyalcohol derivatives, or caseinate salts are incorporated into the peat (Albareda et al. 2008; Stephens and Rask 2000). These adhesive agents should be free from hazardous compounds for plant seed or microorganisms, be dispersible in water, and improve microbial cells' survival rate and adherence to the seeds.

Microbially treated peat is generally applied on-site on the seeds just before sowing. The seed coating by microbial inoculated peats can be performed using cement mixers, and mechanical tumbling machines (Schulz and Thelen 2008). Some peat characters like its undefined and complex content, which are source-dependent, poor controllability on the quantity of microorganisms applied per seed, its costly processing, and probable release of toxic substances during its sterilization interfere in the consistent quality of peat formulations and influence the growth and survival of microbial cells (Bashan et al. 2014; Tittabutr et al. 2007). Extensive use of peat poses an adverse impact on the environment and ecosystem where it has been extracted (John et al. 2011). Cork industry derived compost by better ability in preserving the survival of various microbial cells in rhizospheric soil or on the seeds can be a suitable alternative to peat (up to six months) (Albareda et al. 2008).

14.8.2 Liquid Formulations

Easy handling and application either on seeds or in soil are some of the properties which make liquid formulations popular. These are various types of these formulations including, aqueous (broth cultures), mineral or organic oils, oil in water, or polymer-based suspensions (Herrmann and Lesueur 2013). Its physical form makes adding nutrients and cell protectants, including sucrose, glycerol, and Arabic gum, possible, which can improve its performance (John et al. 2011; Sahu and Brahmaprakash 2016). In comparison to peat formulations, they are easily sterilized, compatible with machinery on large farms, and eventually, these features enhanced their field efficacy (Bashan et al. 2014). Biofertilizer in liquid formulations needs more specific storage conditions (cool temperatures) (Stephens and Rask 2000).

14.8.3 Granule Formulations

Another formulation can be made using marble, calcite, and silica grains. For this purpose, created granules are wetted with an adhesive and coated with the microbial cells (Bashan et al. 2014). To have a high-quality end product, a microbial culture containing suitable microbial cells should be prepared (Herrmann and Lesueur 2013). Being less dusty and easier and controllable handling and application are some of the granule advantages compared to peat formulation, although the bulkier size of granules allows cost-effective transport and storage. To avoid direct contact of microbial cell coated granules with the chemicals or pesticides, they are put in a furrow near to the seed to facilitate lateral root interactions (Bashan et al. 2014; Herrmann and Lesueur 2013). Granular inoculants have more survival rate under unfavorable soil conditions such as soil acidity, moisture stress, or cool, wet soils than other formulations (Rice et al. 2000).

14.8.4 Freeze-Dry Formulations

Biofertilizers can be formulated in shapes of freeze-dried powders using various nontoxic and cost-effective, organic, inorganic, or synthetic carriers (Bashan et al. 2014). These carriers physically or nutritionally through supplying a protective surface or a specific substrate, respectively, provide temporarily niche for microbial cells of biofertilizers in soil. Therefore, they have an enormous significance (Arora et al. 2010). These carriers should have high moisture absorption capability, pH buffering capacity, and being sterilizable to assure delivering the right number of viable cells in good physiological condition (Bashan et al. 2014).

14.8.5 Cell Immobilization Formulations

Cell immobilization is a new promising approach which has also been implemented in the formulation of biofertilizer preparations (Jain et al. 2012; Stockwell et al. 2011). In this approach, microbial cells are attached, entrapped or immobilized into a matrix through various strategies including flocculation, adsorption on surfaces, covalent bonding to carriers, cross-linking of cells, and encapsulation in a natural or synthetic polymer gel-like polysaccharides, a protein material, polyacrylamide and polyurethane (Cassidy et al. 1996). Chemical compounds should have the ability to interact with other constituents for encapsulation. Polyacrylamide and alginate are the two commonly used chemicals in preparing encapsulated biofertilizers. Among these, alginate is a naturally occurring polymer with biodegradability and nontoxic feature. To perform encapsulation using alginate, microbial cells should be dispersed into the alginate solution and the microbial cells incorporated alginate matrix is prepared through dropping mixed solution into cationic solution. Shelf life and inoculation efficacy can be extended via adding nutrients and other additives (Malusá et al. 2012). Then dried beads are packaged (Date 2001). Many strategies including spray drying, solvent extraction/evaporation, coacervation, extrusion, emulsion technique, thermal gelation, pre-gel dissolving methods have been presented to precisely define the size, shape, and texture of the beads (Park and Chang 2000).

Encapsulation through protecting cells (bacteria, fungal spores, or small fragments of hypha) in a nutritive shell against mechanical and environmental stresses (like unfavorable pH, temperature, organic solvent, or toxins), as well as predators, assures biofertilizer efficiency (Bashan 1998; Jain et al. 2012; John et al. 2011) and contamination can be minimized through providing aseptic conditions. PSB encapsulation enhanced their efficiency in P solubilization (Jain et al. 2012). Due to a concentrated situation, low volume, and extended shelf life of encapsulated biofertilizers, their transportation, and storage (room temperatures) are easier than other formulations (John et al. 2011). Once the introduction of the encapsulated microbial cell into the soil occurs, they slowly degrade the capsules, which gradually released into the soil (Bashan 1998). In these regards, smaller beads (microencapsulation) enhance the application efficacy via providing direct contact with seeds (John et al. 2011). High production costs and technical handling are the limitations of this formulation. Gels consist of chemical components like fluidized bed, magnesium silicate, or cellulose-based gel revealed some promise, but none have been adopted on-farm (Jawson et al. 1989).

14.9 Advances in Formulation

It has been revealed that limited formulations cannot meet the need of diverse microorganisms to present new biofertilizers with better efficiency, stability, shelf life, lower cost, easier application, handling, and storage. Therefore, an extended range of materials including organic (water sludge, composts, sawdust, sugarcane bagasse, whey, coal, or enriched agro-industrial residues) and inorganic substances (clays, lapillus, volcanic pumice, or diatomite earth) are being evaluated to develop new carriers (Albareda et al. 2008; Malusá et al. 2012). Some of them have many drawbacks, e.g., sludge wastewater due to the presence of hazardous heavy metals (Malusá et al. 2012).

Various formulated biofertilizers can be applied through different routes. For instance, the seed can be directly inoculated by dry biofertilizers or be soaked with water, then mixed with peat powder (sprinkle method). In another approach, suspended biofertilizer can be added to the seeds and mixed with them (slurry method). Biofertilizer with peat formulation can be suspended in water and sprayed into the furrow during sowing. Moreover, biofertilizer and adhesive can be supplied as slurry to seeds and coated with ground material like lime. Finally, soil can directly be treated by biofertilizers (Bashan 1998).

14.10 Packaging and Quality Control

The nature of the packaging material for biofertilizers can affect its quality. These materials should allow the exchange of oxygen while limiting the water passage. The packaging should minimize biofertilizer contamination during storage and transportation (Roughley 1976). Unfavorable quality and unreliable efficiency under field conditions are the critical factors in biofertilizer failure to gain farmer's acceptance (Herridge 2008; Tarbell and Koske 2007). For example, it has been revealed that 90% of all commercial legume biofertilizers have no practical effect on the legume production yield (Catroux et al. 2001). Contamination is another extensive problem in commercialized biofertilizers. Herrmann and Lesueur (2013) analyzed 65 commercial biofertilizers among which only 37% are containing "pure" and the remaining products (63%) were contaminated with one or more bacterial strains (Herrmann and Lesueur 2013). It has been reported that a significant portion of the commercialized biofertilizers (40%) do not contain pure strains or do not have the claimed strains. Lack of facilities to produce and store high-quality inoculants generates these problems and often leads to inconsistent field results (Bashan 1998). In this regard, systems of quality control are greatly required for ensuring that efficacious biofertilizers are entered into the markets. Quality control and quality assurance systems remove low-quality inoculants from markets. Therefore, consistent results can be obtained in field conditions and better global acceptance can be achieved (Bashan 1998; Bhattacharyya and Jha 2012).

In addition, sufficient information including the name of the microorganisms, guaranteed numbers, nutrients, and other used components content, registration information, lot number, expiry date, dosage and method of application, instructions for disposal, precautions of use of commercialized biofertilizers should be represented on its label to evaluate the quality and the efficacy of a biofertilizer by farmers and make sure to purchase an effective product (Gemell et al. 2005; Husen et al. 2016).

Accordingly, there is a great need to educate manufacturing workers and farmers to assure the quality requirements and a successful crop inoculation, respectively. To prepare biofertilizers with a stable and reproducible efficacy under a wide range of field conditions, it should contain pure isolates and contains no opportunistic pathogens for human, animals, and plants and possesses long term shelf life and its microbial cells should be potently propagated under an extended range of environmental condition (Catroux et al. 2001; John et al. 2011; Lupwayi et al. 2006). A list of several commercial biofertilizers is presented in (Table 14.5).

14.11 Conclusion and Future Prospects

Since the emergence of civilization, 10,0000 years ago, increasing the quality and quantity of agricultural products is one of the main concerns of humans. To achieve these goals, chemical fertilizers have been extensively used; however, their unfavorable effects were revealed on ecosystems. Although organic fertilizers have no adverse effect on soil and its organisms, their labor-intensive and time-consuming preparation makes them unsuitable for application on large scale as a commercial approach. Therefore, it needs promising, safe, and commercial alternatives without environmental adverse effects. Biofertilizers can be considered as cost-effective fertilizers that act in an eco-friendly manner without imposing adverse effects on plant growth and terrestrial and aquatic micro- and macro-organisms, improve soil fertility and its texture, and therefore, can flourish agriculture-related industries. But effective large-scale production and storage strategies should be invented and applied to produce biofertilizers that can be resistant and effective in a wide range of environmental conditions like high temperature and aridity.

Table 14.5 Commercial biofertilizers, their company and microbial strains

Product	Company	Microbial strains
Cell-Tech	Novozymes	Rhizobia
Nitragin Gold	Novozymes	Rhizobia
TagTeam	Novozymes	rhizobia + *Penicillium bilaii*
Accomplish	Loveland Products, Inc	PGPR + enzymes + organic acids + chelators
Nodulator	BASF Canada Inc.	*Bradyrhizobium japonicum*
NodulatorN/T	BASF Canada Inc.	*Bacillus subtilis MBI 600* + *Bradyrhizobium Japonicum*
Nodulator PRO	BASF Canada Inc.	*Bacillus subtilis* + *Bradyrhizobium japonicum*
Nodulator XL	BASF Canada Inc.	*Rhizobium leguminosarum biovar viceae 1435*
Bioboots	Brett-Young Seeds	*Delftia acidovorans*
Bioboots (soybean)	Brett-Young Seeds	*Delftia acidovorans* + *Bradyrhizobium* sp.
EVL coating	EVL Inc.	PGPR consortia
Nitrofix	LabiofamS.A.	*Azospirillum* sp.
Bioativo	Institutode Fosfato Biológico (IFB) Ltda.	PGPR consortia
VitaSoil	Symborg	PGPR consortia
Azotobacterin	JSC "Industrial Innovations"	*Azospirillum brasilense* B-4485
Mamezo	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (in peat)
R-Processing Seeds	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (coated legume seeds)
Hyper Coating Seeds	Tokachi Federation of Agricultural Cooperatives (TFAC)	rhizobia (coated grass legume seeds)
Life	Biomax	PGPR consortia
Biomix	Biomax	PGPR consortia
Biozink	Biomax	PGPR consortia
Biodine	Biomax	PGPR consortia
Grotop PSB Powder	MD Biocoals Pvt. Ltd.	Phosphate Solubilizing Microorganisms (*Bacillus* sp.), Powder 10^7–10^9 cfu g^{-1} and Liquid 10^9 cfu ml^{-1}

(continued)

Table 14.5 (continued)

Product	Company	Microbial strains
Bio Promoter	Mani Dharma Biotech Private Limited, Tamil Nadu	*Bacillus megaterium* + *Aspergillus niger*
Multiplex Nalapak	Multiplex Bio-Tech Pvt. Ltd., Karnataka	Homogenous mixture of *Azotobacter* + *Azospirillium* + phosphate solubilizer + potash mobilizer
Ambiphos	Ambika Biotech & Agro Services, Madhya Pradesh	Phosphate solubilizing microorganism (*Aspergillus niger*)
Biophos	Biotech International Limited, Delhi	*Bacillus megaterium* var. *Phosphaticum*
BioP-P	Sundaram Overseas Cooperation, Gujarat	Phosphate solubilizing microorganism (2×10^8 CFU g^{-1})
PSM	Shree Biocare India, Shree Biocare Solution Pvt Ltd, Gujarat	Phosphate solubilizing microorganisms
Multiplex Sagar (Compost Poly Culture)	Multiplex Bio-Tech Pvt. Ltd., Karnataka	Homogenous mixture of *Azospirillum* + *Trichoderma* + *Pleurotous*
Enriched compost Culture	Organic Biotech Pvt Limited, Maharastra	*Trichoderma harzianum* + *Aspergillus* + *Penicillium*
Bio-manure Culture	Uno Natural and Greens Private Limited, Tamil Nadu	*Trichoderma harzianum* + *Aspergillus*
LignoBiocompost Culture	Peak Chemical Industries Limited, West Bengal	*Trichoderma resei*, *Phanerochaete chrysosporium* and *Aspergillus awamori*

Sources Kabaluk et al. (2010), Pal et al. (2015)

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Chapter 15
Biopesticides: Microbes for Agricultural Sustainability

Fatemeh Salimi and Javad Hamedi

Abstract The human population is growing over time. In this regard, the agricultural yield should be improved and effective strategies must be intended to minimize crop loss to meet the food demand of this population. One of the detrimental groups that adversely affect agricultural yield is pest. Therefore, pesticide application can be considered as a promising approach in diminishing pests corresponding to damages to agricultural yield. Although improper and extensive usage of non-biodegradable chemical pesticides can adversely affect ecosystem and health of human, animal and non-target organisms. Therefore, alternative strategies should be considered to augment plant growth, preserve agricultural yield and compensate for reduced consumption of chemical fertilizers. The most suitable substituent for chemical pesticides is biopesticides. They are formulated pesticides containing various microorganisms (nematodes, bacteria, fungi and viruses) or plant, animal, bacteria and fungi-derived compounds that ecofriendly control insect, weed, nematode and plant disease by various mechanisms and, therefore, gaining importance all over the world. Some of the biopesticides have equal efficiency comparing with chemical pesticides while having no pathogenicity or toxicity on non-target micro- and macroorganisms, so they can be applied near harvesting time. In addition, due to their decomposability feature, they do not remain in agricultural products and do not compromise air, groundwater and soil quality. Microorganisms in biopesticides impose their effects via producing antimicrobial compounds, lytic enzymes or compete with phytopathogens for uptake nutrients, attachment, establishment, and colonization on plants. Interfering in communication of pathogens via degrading of chemical signal messenger or inducing resistance in plants are other strategies which are applied by biofertilizers. In this chapter, we reviewed the types of biofertilizers,

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their mode action and their limitation as well as molecular and culture-based monitoring strategies, fermentation procedures by which microbial cells are multiplied, types of formulation, their advantages and limitation are also discussed.

Keywords Agricultural applications · Bacteria · Biopesticides · Fermentation · Formulation · Fungi

15.1 Introduction

Agricultural productivity can be enhanced through applying high-yielding varieties, optimum irrigation, managing fertilization and minimizing pest-associated losses. In best condition, a meaningful portion of agricultural productivity is lost because of the influential effect of the pests. It has been estimated that pests cause a dramatic reduction in rice (51%), wheat (37%), maize (38%), potato (41%), cotton (38%), soybean (32%), barley (32%) and coffee (29%) (Sharma et al. 2001). According to Food and Agriculture Organization (FAO), pests, weeds and phytopathogens are responsible for a significant loss (20–40%) of the world's potential crop production annually (Fao 2012). Therefore, effective crop protection strategies should be intended to minimize crop loss in the field (pre-harvest losses) and during storage (post-harvest losses) (Oerke 2006). It seems that two-thirds of all crops will be lost if not using pesticides (Deedat 1994). Before the development of chemical pesticides, natural enemies of those specific pests were considered as a crucial strategy to biologically control pests and their corresponding damages to agricultural yield. Pesticide usage has profoundly improved the yield and quality of agricultural production.

According to FAO definition, the pesticide is any pure compound or their mixture, which is applied to prevent, destroy, repel or mitigate insect pests (insecticides), plant diseases, weeds (herbicides), rats, fungal infections (fungicides) or other unwanted organisms and interfering agents in the critical process of production, processing, storage, transportation or marketing of food and agricultural commodities to increase crop yield. They can act as a regulator of plant growth, defoliant, desiccant or preservation compounds, which preserve the agricultural products from spoilage during storage and transport. Pesticides are divided into two groups: chemical and biological pesticides according to their origins (Thakur et al. 2020). However, they can be also categorized into distinct classes according to their target organism (insecticides, herbicides, fungicides, rodenticides and fumigants), chemical structure, physical state, mode of action and application route. Chemical fertilizers that act very effective, affordable and rapid play an undeniable role in the yield of agriculture to meet the enhancing requirement of increasing world population to the food. Meanwhile, the use of biofertilizers is promising and increasing due to the limitations of chemical fertilizers.

Improper and extensive usage of non-biodegradable chemical pesticides including chlorinated hydrocarbons, organophosphates and carbamates can impose deleterious effect on human and animal health (neurological, psychological, behavioral and immune system dysfunctions and hormonal imbalances, reproductive system defects, genotoxicity and blood disorders) as well as ecosystems via enhancing hazardous residue through food chain, contaminating soil and groundwater (Barnawal et al. 2016; Sharma et al. 2021), destroying soil quality and fertility, creating hard water, emerging pesticide-resistant insects, mites, pathogenic fungi, pathogenic bacteria, pathogenic nematodes and weeds (which is due to modification of their target receptors involved in pesticide activity and results in consecutive failures of the commercial controlling agents to gain an effective rate of control when applied based on the label recommendations and necessitate new pesticide) (Kogan et al. 1982), reducing biodiversity as well as beneficial microbial activities like nitrogen fixation and disturbing biological balances by their non-specific effect on non-target organisms and acute poisoning (Carvalho 2017). In addition, through their non-specific action, it is possible that they induce a harmful effect on non-target organisms like insects/pests predators or parasites. Therefore, alternative strategies should be considered to augment plant growth, preserve agricultural yield and compensate for reduced consumption of chemical fertilizers like organochlorine, organophosphate, carbamate, pyrethroid, halogenated insecticides (Smith and Gangolli 2002) through inhibiting the growth of detriment pests. Biological pesticides are environmentally friendly alternatives to chemical pesticides (Gupta and Dikshit 2010; Kumar et al. 2021; Yadav 2021).

By revealing various adverse effects of chemical pesticides, a lot of studies are conducting to find and introduce efficient and safe biocontrol agents as biopesticides. Biopesticides are formulated pesticides containing various microorganisms (nematodes, bacteria like *Bacillus thuringiensis* and *Bacillus sphaericus*, fungi like *Trichoderma* and virus-like nucleopolyhedrosis) or plant, animal, bacteria and fungi-derived compounds that ecofriendly control insect, weed, nematode and plant disease by non-toxic mechanisms and, therefore, gaining importance all over the world for turf, field crop, orchard and garden (Grewal et al. 2005). A lot of bacterial (>100), entomopathogenic fungal (>800), viral (>1000) and protozoan species (>1000) have been known as insect pathogens. Biopesticides are frequently used along with other controlling substances like chemicals (Senthil-Nathan 2015).

Biopesticides have equal efficiency comparing with chemical pesticides while having no pathogenicity or toxicity on non-target macroorganisms (including predators, parasitoids, pollinators, animals and humans), beneficial microorganisms, communities and ecosystems as they have a narrow activity spectrum (target-specific) and their toxic action is mostly specific on pest of interest; also they can be applied near harvesting time. In addition, they have no residue problem that is an issue of substantial concern for consumers. They are usually effective in very small quantity and, therefore, biofertilizer application leads to lower exposures of non-target organisms and minimized pollution problems. In some cases, the establishment of biopesticides in a pest population or their habitat assures efficient control of pest in subsequent generations or seasons. Biopesticides can promote plant growth and agricultural yield by acting at the same time as biofertilizers and improving the growth of plant roots and beneficial microorganisms (Hesham et al. 2021; Yadav et al. 2021). They do not decline air, groundwater and soil quality because of their naturally and quickly decomposability feature. Finally, they can be considered as a constituent of integrated pest management (IPM) (Usta 2013).

The introduction of live organisms or their derived compounds as a commercial pesticide requires comprehensive investigations including systematic studies on biological agent properties, its pesticide mechanism and its probable pathogenicity on non-target macro- and microorganisms. Ecological investigations on the dynamics of diseases in pest population of interest should be conducted due to the significant effect of environmental factors on disease outbreaks; also a wide range of studies should be evaluated biopesticides persistence and dispersal potential. High-qualified technologies should be considered for large-scale production of viable agents or their derived products to make biopesticides without contamination.

Since the formulation tremendously affects biopesticide efficiency and shelf life, extensive studies should be performed to design a suitable formation. In this regard, dry formulations are preferred comparing to liquid ones. In addition, the speed of killing pests should be improved to meet farmers' requirements.

Co-application of biopesticides along with chemical pesticides may be inappropriate, in some cases due to incompatibility occurrence, which includes the adverse effect of chemical compounds on the living organism. There are some physicochemical conditions like heat, desiccation or exposure to ultraviolet radiation, which deactivate biopesticides. Formulation and storage procedures can profoundly affect the efficiency of biopesticides. Since applying one biopesticide cannot control several pests due to their pest-specific activity, it is possible that their potential market be limited. Also, complicated production, formulation, and storage processes of biopesticides lead to their high cost in comparison with chemical pesticides (Fig. 15.1).

15.2 Classification of Biopesticides

According to active ingredients in the biopesticides or their origin, they can be divided into three categories including microbial pesticides (bacterial, fungal, viral, nematode, protozoan), biochemical pesticides including compounds derived from animals or plants and plant-incorporated protectants, which are the results of incorporation of pesticide coding genes into the plant's genetic material.

15.2.1 Microbial Pesticides

It has been estimated that the portion of bacterial, fungal, viral, predator and other biopesticides from global biopesticide market is 74%, 10%, 5%, 8% and 3%, respectively (Thakore 2006). Active ingredients in microbial pesticides, whether the microorganism itself or its product, maybe native or genetically engineered. Currently, 73 active microbial ingredients with significant pesticide activities have

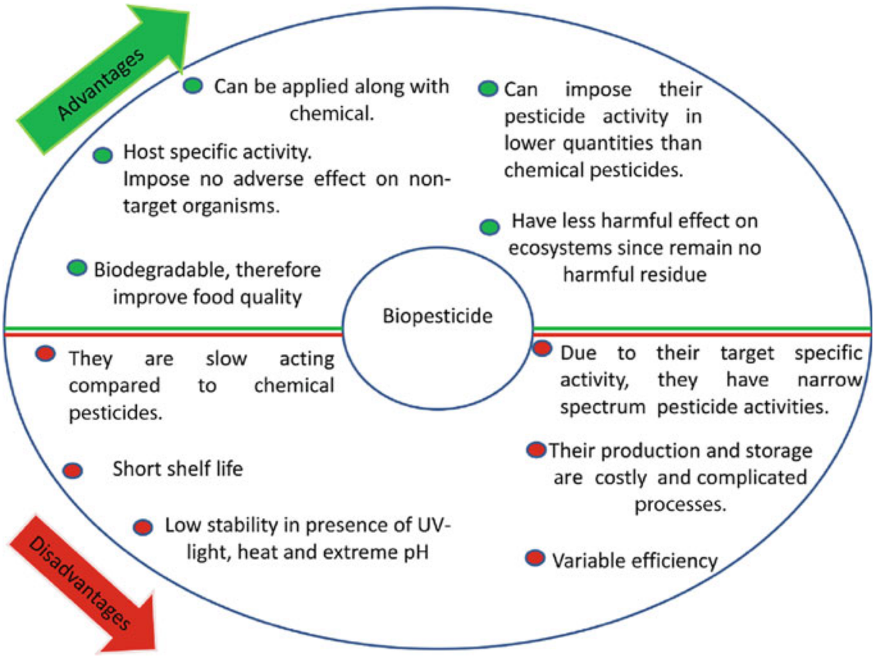

Fig. 15.1 Advantages and disadvantages of biopesticides

been registered by the United States Environmental Protection Agency (US EPA). Microbial pesticides include mainly biofungicides (*Trichoderma*, *Pseudomonas*, *Bacillus*), bioherbicides (*Phytophthora*) and bioinsecticides (*Bacillus thuringiensis*) (Gupta and Dikshit 2010). They inhibit pests through synthesizing specific toxic, antibacterial or antifungal bio compounds, blocking attachment, establishment and colonization of other microbial cells via parasitism or competition. Insecticides usually have specific activity on various species of moths, butterflies, beetles, flies and mosquitoes. A lot of microbial insecticides can preserve their bioactivities in the presence of synthetic chemicals, which make their usage as a mixture possible to achieve better pest management (Kachhawa 2017).

Microorganisms through producing various antimicrobial compounds like cyclolipopeptides, phenolic compounds, bacteriocins or degrading enzymes against pathogenic bacteria and fungi limit their growth. Production of fengycins (produced by *Bacillus subtilis*) (Fan et al. 2017), pyrrolnitrin (produced by *Pseudomonas cepacia*) (Cartwright et al. 1995) herbicolin, pantocins (produced by *Pantoea agglomerans* and *Pantoea vagans*) (Ishimaru et al. 1988; Smits et al. 2010; Wright and Beer 2001) and lytic enzymes (produced by some yeast and fungi like *Trichoderma harzianum*) (Batta 2004) are some examples for this strategy, which are applied by several microorganisms. In another strategy, they compete with plant pathogens for assimilation of nutrients, attachment, establishment and colonization on plants

(Sharma et al. 2009). Some microorganisms like *Pichia* and *Trichoderma* via interfering in communication of pathogens through degrading of chemical signal messengers (which are essential for communication through quorum sensing e.g. acyl-homoserine lactones) (Molina et al. 2003) or inducing resistance in plants (through producing either elicitors or messenger molecules e.g. salicylic acid) (Spadaro and Gullino 2004) limit the unfavorable effect of pests on plants (Harman et al. 2007). Viral-based biopesticides that containing fungal, bacterial or insect viruses can limit the growth of phytopathogens through parasitism and lysis of pathogenic bacteria, fungi or insects (Ghabrial and Suzuki 2009).

15.2.1.1 Bacterial Pesticides

Bacterial pesticides are the most common and cost-effective pesticides. These pesticides are usually applied as biological agents to kill insects, insecticides; also they can also be used to control unwanted bacteria, fungi or viruses. Producers mostly belong to *Bacillaceae*, *Pseudomonadaceae*, *Enterobacteriaceae*, *Streptococcaceae* and *Micrococcaceae* genera (Tanada and Kaya 2012). Bacterial pesticides colonize various organs of plants including roots and leaves to obstacle phytopathogen attachment, establishment, colonization and finally pathogenesis (O'Brien et al. 2009). Microbial insecticides specifically kill particular species of moths and butterflies or species of beetles, flies and mosquitoes. For this purpose, they should come into contact with pests of interest or be ingested by them. In this regard, bacteria via producing endotoxins specifically damage the digestive system of insects.

Most commercial microbial pesticides are produced by the subspecies and strains of the *Bacillus* genus, which frequently exist in soil and possess wide genetic biodiversity. They can create spores that are tremendously tolerant dormant forms able to resist extreme temperatures, pH, drought and starvation. Therefore, they could be significant sources of potential microbial biopesticides (Piggot and Hilbert 2004).

Almost 90% of commercial pesticides in the USA are *B. thuringiensis* (Bt) containing pesticides (Kumar and Singh 2015). *B. thuringiensis*is an aerobic, Gram-positive, spore-producing soil bacterium whose biopesticides are extensively applied to control agriculturally and medically important insects (Mazid et al. 2011). Its biopesticide action is based on the production of crystalline inclusions that contain δ endotoxins or cry proteins during sporulation. They have no toxicity to other organisms, including vertebrates and beneficial insects. A different mixture of proteins is produced by each strain of *B. thuringiensis*, which are capable to particularly destroy one or a few related species of insect larvae. The generated toxin can bound to the receptors of larval gut, so lead to its starvation. Whenever the insect feeds on the *B. thuringiensis* contaminated foliage, Cry proteins are hydrolyzed in the midgut of insect and consequently an active endotoxin is produced and its attachment to receptor sites on epithelial cells in the gut is resulted in ionic disbalance of the cell via forming transmembrane pores or ion channels. This event leads to cell lysis due to osmotic shock. Paralysis of the insect's mouthparts and gut is considered as subsequent symptoms (Lambert et al. 1992). High efficiency and environmental safety of

B. thuringiensis and cry proteins make them suitable alternatives to chemicals with pesticide activity to kill insect pests (Roy et al. 2007).

The extensively applied microorganisms with effective biopesticide activity are strains of *B. thuringiensis.* They can efficiently kill three genera of mosquitos including, *Culex*, *Culiseta* and *Aedes*. *B.thuringiensis* var. *tenebrionis* strain Xd3 (Btt-Xd3) also exhibited biopesticide activity on *Agelasticaalni* (Eski et al. 2017). It has been proved that the bacteria can survive for a considerable time. Five percent of applied *B. thuringiensis* can survive after a year in the form of spores. Nowadays, using genetic engineering, insect-resistant crops such as cotton, maize, potato and rice have been produced through transferring coding genes of the insecticidal crystal proteins into their genetic material. The first developed *B. thuringiensis* insecticidal agent was a mixture of *B. thuringiensis* spores and its toxin. *B. thuringiensis*-based formulated pesticides are present in solid (powdery or granulated) or liquid forms. These products contain spores and toxin crystals and are used on feeding sites of larvae like leaves (Usta 2013).

Another *Bacillus* with larvicidal characteristics is *B. sphaericus.* This bacterium is frequently found in the soil and has been applied to biologically control *Culex* and *Anopheles* populations in diverse geographical regions. Although there are *B. sphaericus* resistant insects like *Psorophora*, *Aedesaegypti* and *Ae. albopictus.* It is first isolated from *Simulium* in Nigeria with low larvicidal activity. *B. sphaericus* 1593, which was isolated from dead mosquito larvae in Indonesia exhibit a significantly higher mosquitocidal activity on *Culexquin quefasciatus.* This strain has been applied as an insecticide in the field as part of vector control programs (Kellen et al. 1965). This bacterium produces a fetal pro-toxin during its sporulation, which is causative agent of fatal cellular alterations in the cells of insects. It has been revealed that some toxins may be located in several parts of the cell like cell wall but the spore possesses the most concentration of the toxin (Brownbridge and Margalit 1987; Charles et al. 1993). Vectolex is a commercial biopesticide with a larvicidal activity, which contains *B. sphaericus.*

Pseudomonas syringae Van Hall with the commercial name of Bio-Save has been used to control fungal infection in various fruits like apples, pears and citrus (Koul et al. 2001). Antinsectan compounds derived from actinobacteria and some fungal strains (e.g. milbemycins, actinomycin A, nikkomycin, piericidins, aplasmomycin, avermectins, citromycin, spinosyns, various cyclic peptides, etc.) and other bacteria (e.g. aminolevulinic acid, thiolutin, thuringiensin, xenorhabdins) are compounds with antifeedants, toxic, growth inhibitory effect and physiological disrupter activities on various pests (Dowd 2001; Kirst 2010; Koul and Dhaliwal 2003). In this regard, avermectins and spinosyns are some of the commercialized compounds (Tables 15.1, 15.2, 15.3 and 15.4).

15.2.1.2 Fungal Pesticides

Fungal biopesticides are containing fungal strains, which are capable of controlling insects, pathogenic fungi or bacteria, nematodes and weeds (Table 15.5). These

Table 15.1 Biopesticides derived from bacteria belonged to *Bacillus* genus

Microorganisms	Trade name	Host range
Bacillus thuringiensis var. kurstaki(Bt)	Bactur, Bactospeine, Bioworm, Caterpillar Killer, Dipel, Futura, Javelin, SOKBt, Thuricide, Topside, Tribactur, Worthy Attack, Lepidocid, Rokur, Bio-Dart, Biolep, Halt Taciobio-Btk, Imperial, Tuneup, Gumulmang, Biobit, Bychung, Bigule, Samgong BT, Shuricide, Youngil BT	Larvae of moths and butterflies
Bacillus thuringiensis subsp. *Kurstaki* ABTS 351, PB 54, SA 11, SA12, and EG 2348	Batik, Delfin	Lepidoptera pests
Bacillus thuringiensis subsp. *kurstaki* BMP 123	BMP 123 Prolong	Lepidoptera pests
Bacillus thuringiensis subspp. *Aizawai* and *kurstaki*	Agree	Lepidoptera larvae
Bacillus thuringiensis subsp. *Israelensis*	VectoBac, Tacibio, Technar, Aquabee, Bactimos, Gnatrol, LarvX, Mosquito Attack, Skeetal	Mosquito, Lepidopteran pests, Sciarids, larvae of Aedes and Psorophora mosquitoes, black flies, and fungus gnats
Bacillus thuringiensis var. tenebrinos	Foil, M-One, M-Track, Novardo, Trident	Larvae of Colorado potato beetle, elm leaf beetle adults
Bacillus thuringiensis var. aizawai	Certan, Biocan, Salchungtan, Scolpion Solbichae, Tobagi	Wax moth caterpillars and Lepidopteran pests
Bacillus thuringiensis subsp. *Aizawai* GC-91	Turex	Lepidoptera pests
Bacillus thuringiensis subsp. *Tenebrionis* NB 176	Novodor	Coleoptera pests
Bacillus popilliae and *Bacillus lentimorbus*	Doom, Japidemic, Grub Attack	Larvae of Japanese beetle
Bacillus sphaericus	Vectolex CG, Vectolex WDG	Larvae of *Culex*, *Psorophora*, and *Culiseta* mosquitos, larvae of some *Aedes* spp.
Bacillus subtilis	Defender, Bibong, Ecogent, Ecosmart Topsaver, Teras, Holeinone, Ibsalim Greenall, Cillus, Shootingstar, Jaenotan Gamair SP, Alirin-B, Phytosporin	Powdery mildew, gray mold, *Alternaria* blight, large patch, brown patch, *Pythium* blight, *Phytophthora* blight, Root rot, mildew, bacterioses, phytophtorosis, seed molds anthracnose and microsporiosis
Bacillus subtilis 101	Shelter	Root and leaf diseases

(continued)

Table 15.1 (continued)

Microorganisms	Trade name	Host range
Bacillus subtilis 102	Artemis	Root and leaf diseases
Bacillus subtilis 246	Avogreen	Root and leaf diseases
Bacillus subtilis QST 713	Serenade	*Botrytis* spp.
Bacillus subtilis WG6-14	Bactophyt SP	Bactophyt SP
Bacillus subtilis IPM-215	Bactophit	Mildew, root rots
Bacillus pumilus	Ecosense	*Phytophthora* blight
Paenibacillus polymixa	Topseed	*Phytophthora* blight and powdery mildew

Source Usta (2013)

Table 15.2 Biopesticides derived from bacteria belonged to *Pseudomonas* genus

Microorganisms	Trade name	Host range
Pseudomonas fluorescens	ABTEC Pseudo, Biomonas, EsvinPseudo, Sudo, Phalada 104PF, Sun Agro Monus, Bio-cure-B, PlanrizKS	Root rots, mildew, bacterioses, anthracnose phytophtorosis and microsporiosis
Pseudomonas chlororaphis	Cedomon, Cerall	*Pyrenophora teres, Pyrenophora graminea, Tilletia caries, Septoria nodorum* and *Fusarium* spp.
Pseudomonas syringae	Pentafag–M	*Erwinia amylovora, Pseudomonas* spp., *Xanthomonas* spp.
Pseudomonas sp. DSMZ 13134	Proradix	Root rots
Pseudomonas chlororaphis MA 342	Cerall	Cereal diseases
Pseudomonas aureofaciens	AGAT-25, Pseudobacterin 2Z, Agat 25K, Gaupsin	Root rots, mildew, septoriosis, brown rust, ear fusariosis, cercosporosis, pseudoperonosporosis and larvae of harmful insects, scrub, mildew, fruit rots

Table 15.3 Biopesticides derived from bacteria belonged to *Streptomyces* genus

Microorganisms	Trade name	Host range
Streptomyces colombiensis	Mycocide	Powdery mildew, gray mold, brown patch
Streptomyces kasugaensis	Safegrow	Sheath blight, large patch
Streptomyces griseoviridis K61	Mycostop	*Fusarium* wilt, *Botrytis* grey mold, root rot, stem rot, stemend rot, damping off, seed rot, soil-borne damping off, crown rot, *Rhizoctonia*, *Phytophthora*, wilt, seed damping off and early root rot

Table 15.4 Biopesticides derived from bacteria belonged to other genera

Microorganisms	Trade name	Host range
Agrobacterium radiobacter	Crown Gall Inoculant	Crown gall
Aureobasidium pullulans	*Aureobasidium pullulans*	Fire blight and postharvest diseases in apples
Klebsiella oxytoca and *Bacillus mucilaginosus*	Kleps	Enhance resistance to root diseases
Flavobacterium, *Phytobacteriomycin*	Phytoflavin-300	Bacterioses and fungal diseases
Salmonella enteriditis subsp. *Danysz* (LABIOFAM 101-04)	BioratG	Rats
Actinomyces levendula	Phytobacteriomycin	Root rots and bacterioses
Pseudomonas fluorescens, *Streptomyces albus,* and *Micrococcus roseus* bacterial complex	Bactophil	Seed germination diseases
Achromobacter album	Albobacteryn	Sprouting inhibition

fungi kill and control various pests via producing antimicrobial compounds, enzymes or parasitism e.g. *Trichoderma* produces and releases cell wall degrading enzymes (Kawalekar 2013; Kumar 2015; Sharma et al. 2019).

Insect-associated fungi are known as entomopathogenic fungi (also known as mycoinsecticide agents) and classified into four main groups including *Laboulbeniales*, *Pyrenomycetes*, *Hyphomycetes* and *Zygomycetes* (Sharma 2012). These fungi have commensalism or symbiotic relationship with insects (Pucheta and Navarro 2016). They attack, infect and consequently kill the interested insects and regulate their population. Entomopathogenic fungi control sucking pests including aphids, thrips, mealybugs, whiteflies, scale insects, mosquitoes and mites via their infecting and killing. *Beauveria bassiana, Metarhizium anisopilae, Nomuraearileyi, Paecilomyces farinosus* and *Verticillium lecanii* are some of the most widely used entomopathogenic fungi. They penetrate through integument (cuticle), ingestion wounds or trachea and then enter to hemolymph and generate toxins (Meadows 1993). They are regarded as crucial agents in controlling insect populations. There are a lot of obligate and facultative fungal pathogens for insects (90 genera and almost above 750 species). The first commercial mycoinsecticide ‘Boverin’ contained *Beauveria bassiana*, white muscardine fungus, along with the declined amount of trichlorophon has been successfully applied to inhibit the second-generation outbreaks of *Cydiapomonella* L. (Ferron 1971). Various studies have been conducted on *B. bassiana.* Spores of this fungal strain germinate, grow and proliferate in the body of insects and via producing lethal toxins and draining nutrients lead to their death (Wakefield et al. 2010). Insect-pathogenic fungus *Metarhizium anisopliae* can successfully control the population of adult *Aedesa egypti* and *Aedesa lbopictus* through reducing their

Table 15.5 Commercial fungal biopesticides

Microorganisms	Trade name	Host range
Fungi		
Beauveria bassiana	Botanigard, Mycotrol, Naturalis,Myco-Jaal, Biosoft, ATEC Beauveria, Larvo-Guard, Biorin, Biolarvex, Biogrubex Biowonder, Veera, Phalada 101B Bioguard, Bio-power, Bb Plus, Bb weevil, Sparticus, Ceremoni, Boverin	Aphids, fungus gnats, mealybugs, mites, thrips, whiteflies, coffee berry borer, diamondback moth, thrips, grasshoppers, whiteflies, aphids, codling moth larvae of most pest mosquito species, thrips, greenhouse whitefly, two-spotted spider mite, insect pests, larvae of Colorado potato beetle
Beauveria bassiana strain GHA and *Bacillus thuringensis*	Bitoxibacillin	Colorado potato beetle
Metarhizium anisopliae	Green Muscle, ABTEC, Verticillium Meta-Guard, Biomet, Biomagic, Meta, Biomet, SunAgroMeta, Bio-Magic	Locust, Coleoptera and lepidoptera, termites, mosquitoes, leafhoppers, beetles, grubs
Paecilomyces fumosoroseus	Nemato-Guard Priority Bangsili	Whitefly, two-spotted spider mite, greenhouse whitefly
Paecilomyces fumosoroseus Apopka 97	Preferal WG	Greenhouse whiteflies (*Trialeurodes vaporariorum*)
Paecilomyces fumosoroseus Fe9901	Nofly	Whiteflies
Monacrosporium thaumasium	Ddangumi	Root knot nematode
Lecanicillium muscarium	Mycotal, Vertalec	Whiteflies, thrips, aphids (except the Chrysanthemum aphid: *Macrosiphoniella sanborni*)
Paecilomyces lilacinus	Bio-Nematon, Yorker, ABTEC, Paceilomyces, Paecil, Pacihit, ROM biomite, Bio-Nematon	Nematodes and Whitefly
Paecilomyces lilacinus 251	PL Plus	Nematodes

(continued)

Table 15.5 (continued)

Microorganisms	Trade name	Host range
Trichoderma harzianum	Eco-77, Eco-T, Promot, Romulus, Rootgard, Trichoplus, Trykocide, TrianumP, Trichodex, Rootshield, Gliocladin, Biozim, Monitor, Trichoguard, NIPROT, Bioderma Biovidi, EswinTricho, Biohit Tricontrol, Ecoderm, Phalada 106TV Sun Agro Derma, Defense SF Mycofungicyd, T-Gro	Root diseases *Botritiscinerea, Collectotrichum* spp.*, Fulviafulva, Monilialaxa, Plasmoparaviticola, Pseudoperonospora cubensis, Rhizopus stolonifer, Sclerotinia Sclerotiorum*
Trichoderma aspellerum (ICC012) (T25) (TV1) (formerly *T. harzianum*)	Tenet	Fungal infections (*Pythium, Phytophthera, Botrytis* and *Rhizoctonia*)
Trichodermaatro viridae	Binab T Pellets, Esquive	*Botrytis cinerea,* pruning wound infection *Chondrostereum purpureum*. Fungal infections (*Pythium, Phytophthera, Botrytis, Rhizoctonia*)
Trichoderma gamsii	Remedier	Fungal infections (*Pythium, Phytophthera, Botrytis, Rhizoctonia*)
Verticillium lecanii	Verisoft, ABTEC, Verticillium, Vert-Guard, Bioline, Biosappex, Versitile Ecocil, Phalada 107 V, BiovertRich ROMVerlac, ROMGurbkill, SunAgroVerti, Bio-Catch, Mycotal	Whitefly, coffee green bug, homopteran pests Whitefly, thrips, scale insects, Mealybug
Verticillium albo-atrum (WCS850) (formerly *Verticillium dahliae*)	Dutch Trig	Dutch elm disease
Ampelomyces quisqualis	Bio-Dewcon	Powdery mildew due to fungal pathogens
Coniothyrium minitans C ON/M-91-05	ContansWG	*Sclerotinia sclerotiorum, Sclerotinia minor*

(continued)

life span (Shi and Feng 2004). Now, there are many commercial fungal biopesticides mostly from Zygomycota, Deuteromycota (Samson et al. 1988), Oomycota and Chytridiomycota (Barr 2001).

Fungal spores germinate on the integument surface and begin an infection, then they deteriorate the insect's cuticle via excreting various degrading enzymes like proteases, chitinases, quitobiases and lipoxygenases and accelerate the penetration process through mechanical forces, which is initiated via a specialized structure formed in the germinative tube, appressorium. The emergence of hyphal bodies in

Table 15.5 (continued)

Microorganisms	Trade name	Host range
Gliocladium catenulatum J1446	Prestop, PrestopMix	Damping off, gummy stem blight, grey mold, root rot, stem rot, wilt, storage diseases, foliar diseases, seed rot
Pseudozyma flocculosa PF-A22 UL	Sporodex	Powdery mildew
Pythium oligandrum	Polyversum	Polyversum
Coniothyrium minitans CON/M/91-08	Contans	*Sclerotinia*
Arthrobotrys spp.	Nematophagin	Nematodes
Chaetomium spp.	Chetomic	Root molds, grey and white molds, fusariosis, common and silver scrub and rhizoctoniosis
Ampelomyces quisqualis	Cufect	Powdery mildew
Yeast		
Candida oleophila O	Nexyl	Post-harvest diseases

Source Usta (2013)

insect body, which disseminate through the hemocoel, is accompanied with their invasion to various muscle tissues, fatty bodies, mitochondria and hemocytes, which lead to the death of the insect within 3–14 days after infection. Fungi invade to insect organs after insect dying and consequently, fungal hyphae pierce the cuticle from the interior of the insect and appear at the surface, where spore formation is initiated in favorable environmental conditions (Diaz et al. 2006). In addition, some fungi kill insects via producing toxins like cycloheximide and novobiocin.

It has been shown that *Talaromyces flavus* SAY-Y-94-01 can act as a biopesticide on *Anthracnose*, which is caused by *Glomerella cingulata* and *Colletotrichum acutatum* (Ishikawa 2013). Entomopathogenic fungi can be used in the conidia or mycelia forms.

15.2.1.3 Viral Pesticides

Viral pesticides contain viruses with the ability to attack insects and other arthropods. A lot of viruses (>1000) have been isolated from insects (Srivastava and Dhaliwal 2010) (Table 15.6). These entomogenous viruses are divided into two categories, including inclusion body (IV)- and non-inclusion body (NIV)-producing viruses. Inclusion body-producing viruses are further subdivided into *polyhedrosis* and granulosis viruses, which produce polyhedral and granular bodies, respectively.

Table 15.6 Viral pesticides (Usta 2013)

Microorganisms	Trade name	Host range
Gypsy moth nuclear plyhedrosis (NPV)	Gypchek virus	Gypsy moth and caterpillars
Adoxophyes orana BV-0001 granulosis virus	Capex	Summer fruit tortrix (*Adoxophyesorana*)
Cydiapomonella granulosis virus	BioTepp, Cyd-X, Cyd-X Extra	Codling moth (*Cydia pomonella*)
Spodoptera exigua nucleopolyhedrosis virus	Spod-X GH	*Spodopteraexigua*
Zucchini Yellow Mosaic Virus, weak strain	Curbit	Yellow mosaic virus
Anticarsia gemmatalis nucleopolyhedrosis virus (AgNPV)	Baculo-Soja, Baculovirus, Nitral, Coopervirus PM, Protégé	*Anticarsiagemmatalis* and Lepidopterans
Tussock moth NPV	TM Biocontrol-1	Tussock moth and caterpillars
Pine sawfly NPV	Neochek-S	Pine sawfly larvae
Pseudomonas resinovorans bacteriophage	Agriphage	Insect pest control
Helicoverpa armigera nucleopolyhedrosis virus	Helicide, Virin-H, Helocide, Biovirus-H, Helicop, Heligard	*Helicover paarmigera*
Spodoptera litura nucleopolyhedrosis virus	Spodocide, Spodoterin, Spodi-cide Biovirus-S	*Spodoptera litura*

Source Usta (2013)

Polyhedrose viruses based on their inhabitance are categorized as nucleopolyhedrosis viruses (NPV) or cytoplasmic polyhedrosis virus (CPV) (GF. 2013). Thirteen NPV-based biopesticides are registered (Thakore 2006). It has been validated that *Spodoptera exempta* (Walker), nucleopolyhedrosis (SpexNPV) possess significant killing ability on armyworms (Mushobozi et al. 2005). Commercial viral pesticides are containing baculoviruses, nucleopolyhedrosis viruses, granuloviruses, acoviruses, iridoviruses, parvoviruses, polydnaviruses, reoviruses, cytoplasmic polyhedrosis viruses, nodaviruses, picrona-like viruses and tetraviruses. Elcar™ was first viral insecticide containing *Helicoverpa zea* NPV (HzSNPV), which is comparatively extent range baculovirus and control many pests which attacking to soybean, sorghum, maize, tomato beans and cotton species. These pests mostly belong to *Helicoverpa* and *Heliothis* genera (Rhodes et al. 1997; Usta 2013).

More than 10% of all viral insecticides contain baculovirus (Moore et al. 1987) which up to 100 insect species are sensitive to it (Usta 2013). These viruses are rod-shaped and have envelope and circular, supercoiled double-stranded DNA genomes (GF 2013). A lot of baculoviruses have been isolated from Lepidoptera (butterflies and moths), Hymenoptera (sawflies) and Diptera (mosquitoes) (Herniou et al. 2011). They are considerably selective and specifically kill insects and some arthropods and exhibit efficient horizontal transmission. Therefore, they are considered as safe for vertebrates and plants. There is no report on their pathogenicity in vertebrates and plants (Krieg et al. 1980). After viral infection, the expression of its protein can occur in three early (0–6 h), late (6–24 h) and very late (up to 72 h) phases. Produced proteins are assembled in late phase to form occlusion bodies. A lot of virions of NPVs are packaged within each occlusion body and form polyhedra while the granulovirus is packaged in one small occlusion body, to develop granules. Once consumption of occlusion bodies (OBs) by insects, their dissolution is triggered under the alkaline condition of insect mid-gut that is resulted in the disruption of covering proteins and release of virion in the midgut lumen (Adams 1991). Then, the released virions enter the midgut cell nucleus where viral proliferation occurs. Various tissues like the hemolymph, fat bodies, nerve cells and hemocytes may be infected by new virions. In this situation, viruses replicate in the nucleus of infected cells. New virions are occluded into polyhedral in the nucleus. Polyhedral containing virions are accumulated into the host and host become to a bag of viruses which with its liqueferation viruses are released and can infect other insects. Dead hosts are contained a high quantity of virions. It is possible that more than 100 occlusion bodies present in a single caterpillar. Negative geotropism is observed in infected larvae before their death which facilitates widespread dissemination of virions.

Environmental conditions affect the speed with that death occurs (3–7 days in optimum conditions and 3–4 weeks in unfavorable environmental conditions) (Kachhawa 2017). Some characteristics of baculovirus-based biopesticides like their killing speed, short stability in field conditions, and high production costs can limit the application of these biopesticides (C 2012; Mills 2010; WJ 2011). Some strategies can be applied to decline these limitations. For example, killing speed can be improved through applying genetic engineered baculoviruses instead of wild types. High cost, pest-specific activity of viral pesticides, which make control of several different pests difficult, low-speed action and instability of occlusion bodies under ultraviolet rays (280–320 nm) of the sun can limit their acceptance by farmers. In this regard, baculoviruses should be encapsulated with UV protectants to make certain a longer field life (Usta 2013). Transgenic baculoviruses have coding genes of hormones, enzymes or insect-specific toxins (El-Sheikh et al. 2011a, b). Engineered baculoviruses containing juvenile hormone esterase have shown promising results since this enzyme leads to a reduced level of juvenile hormone. In this condition, insect feeding and pupation are prevented. However, short half-life of juvenile hormone esterase in the hemolymph has restricted the application of these recombinant baculoviruses (El-Sheikh et al. 2011a, b).

Other influential viral-based pesticides are alphabaculovirus *Anticarsia gemmatalis* multiple nucleopolyhedrovirus (AgMNPV) and *Cydiapomonella* granulovirus (CpGV), which are applied to control *Anticarsia gemmatalis* (velvetbean caterpillar as a very important soybean insect pest in Brazil) and codling moth, *Cydiapomonella* (pest of fruits such as apple, pears and walnuts), which are causing agents of huge economic loss, annually (Arthurs et al.; Moscardi et al. 2011; Yang et al. 2012). It has been shown that viral-pesticide can augment the efficiency of chemical pesticides to control resistant pest e.g. combination of HaMNPV with endosulfan (organochlorine insecticide) has exhibited acceptable results in controlling Cotton Bollworm, *H. armigera*, which is resistant to a wide range of insecticides (Joußen et al. 2012; Mironidis et al. 2013) as well as transgenic Bt cotton (Luttrell 2012). These viral biopesticides have been commercialized in China. Large-scale production of baculovirus is conducted in an open field or laboratory through collecting infected larvae or feeding reared larvae with baculovirus contaminated food (Elvira and Caballero 2010) (Table 15.6).

15.2.1.4 Nematode Biopesticides

Entomopathogenic nematodes are other organisms that can be applied as biopesticides against weevils, gnats, white grubs and different species of the Sesiidae family (Koul 2011). They are soft-bodied, non-segmented roundworms that have an obligate facultative parasitism relationship with insects. These nematodes are frequently found in the terrestrial ecosystem. Species belonging to Heterorhabditidae and Steinernematidae families have been efficaciously applied as bioinsecticides in the management of pest population (Grewal and Shapiro-Ilan 2005). They are considered as a good biopesticide candidate for integrated pest management due to no toxicity effects on humans, their host-specific activity and low possibility of resistant insect emergence (Shapiro-Ilan et al. 2006).

Entomopathogenic nematodes have a free-living lifestyle in their infective juvenile stage. In this stage, they penetrate into the host insect via spiracles, mouth, anus or intersegmental membranes of the cuticle, and subsequently enter into the hemocoel (Bedding 1982). Species belong to Heterorhabditidae and Steinernematidae families are associated with bacteria of *Photorhabdus* and *Xenorhabdus* genera, respectively (Ferreira 2014). In this step, they release their symbiotic microbial cells into the hemocoel of insects. Released microbial cells reproduce in the hemolymph of insect and lead to insect death within 24–48 h. Nematodes continue to feed on the tissue of died host then mature, and consequently multiply. It is possible that one or more generations have emerged within the host cadaver. Released infective juveniles can infect other hosts and consequently resume their life cycle (Bedding 1982). Entomopathogenic nematodes like *Steinernema carpocapsae*, *Steinernema riobrave*, *Steinernema glaseri*, *Steinernema scapterisci*, *Heterorhabditis bacteriophora* and *Heterorhabditis megidis* have been produced in large scale using solid state or liquid fermentation (Lacey and Georgis 2012). Optimization of the application parameters and development of effective strains in order to attain acceptable control of pests via nematodes should be conducted with extensive research (Table 15.7) (Usta 2013).

15.2.1.5 Protozoan Biopesticides

Protozoa are microscopical single-celled organisms and are scarcely applied as biopesticides against an extent spectrum of pests. Entomopathogenic protozoans are a

Table 15.7 Biopesticides containing entomogenous nematodes

Microorganisms	Trade name	Host range
Steinernema feltiae (*Neoaplectana carpocapsae*) *S. riobravis, S. carpocapsae* and other Steinernema species	Biosafe, Ecomask, Scanmask, also sold generically (wholesale and retail), Vector	Larvae of a wide variety of solid welling and boring insects
Heterorhabditis heliothidis	Currently available on a wholesale basis for large-scale operations	Larvae of a wide variety of solid welling and boring insects
Ampelomyces quisqualis AQ10	Bio-Dewcon, AQ10	Powdery mildew and leaf diseases
Paecilomyces lilacinus PL 251	BioActWG	Common plant parasitic nematodes

diverse group of organisms that include more than 1000 species, which attack invertebrates like insects and also are known as microsporidians (WM 1988). Microsporidia are omnipresent, obligatory intracellular parasites that are responsible for diseases in diverse species of insects. *Nosema* and *Vairimorpha* genera are capable of attack lepidopteran and orthopteran insects (Solter et al. 2012). Their act is slow and specific. They produce spores. Germination of spores has occurred in the midgut, and their released sporoplasm invades to the target cells then a chronic infection is triggered by which debilitates their host via reducing their nourishment, vigor, fertility and length of life. A lot of investigations have been conducted on microsporan protozoans as possible constituents of integrated pest management programs. *Nosemapyrausta* is a useful microsporidian that declines fertility and length of life of the adults and also kills the larvae of European corn borer (Siegel and Ruesink 1986). It is sold under the trade names of NOLO Bait, Grasshopper and Attack against European corn borer caterpillars, grasshoppers and Mormon crickets. In sum, germinated spores in the inset midgut develop a polar filament and their sporaplasm is injected into a midgut cell. Then, more spores are generated and infect other tissues. These spores are eliminated along with feces and preserve their viability. They are ingested during larval nourishment; therefore, the infection cycle is repeated in midgut cells of the new host.

15.2.2 Biochemical Biopesticides

Biochemical pesticides are biological compounds that biologically control pests through non-toxic strategies. Sex-pheromones of insect which can interfere with their mating and population build-up, diverse scented extracts which can attract insect pests to traps and also various vegetable oils or extract or their synthesized analogs are some examples of biochemical pesticides (Ritter 2009).

15.2.2.1 Semiochemicals

Semiochemicals are message-bearing substances that can be derived from plants or animals in nature, which can cause a behavioral response like attraction to others or nutrients, locating a mate and sending an alarm in individuals of the same or other species (Chandler et al. 2011; Nerio et al. 2009). Jasmonic acid and sodium alginate application can lead to crop protection through inducing the production of a natural mixture of herbivore-induced plant volatiles and attracting natural enemies. One group of biochemical pesticides is insect pheromones. These chemicals are naturally used by an insect to inter-species communication. Identified sex pheromones can biologically control more than 30 target species pheromones. These chemicals themselves do not kill a target pest. They spread through the air and via attracting insects to traps, which contain a lethal pesticide or disruption mating impose their biopesticide activities. Many pheromones with biopesticide activities have been known and successfully applied in pest management programs (Dhaliwal et al. 2012; Witzgall and Cork 2010). Better pest management can be achieved via conducting a comprehensive study on mechanisms of the communication systems, behavior, mating systems and physicochemical characteristics of target insects as well as their substantial difference with non-target ones.

15.2.2.2 Insect Growth Regulators

As the name denotes, these biochemical pesticides can alter the growth and development of insects. Juvenile hormone-based insecticides are one group of the insect growth regulators, by using them, the developing process is disrupted. For example, precocene through interfering with the action of juvenile hormone-producing glands prevents the emergence of a reproductive adult (Yankanchi and Gadache 2010). The compounds with inhibitory effects on chitin synthesis can restrict the production of a new exoskeleton by insects after their molting. Therefore, they cause insect death through unprotecting the elements and from prey (O'Brien et al. 2009; Yankanchi and Gadache 2010). Cayenne has deterrent activity, others via suffocation or enhancement of the natural immune system of crop control pests (Kawalekar 2013; O'Brien et al. 2009).

15.2.3 Botanical Biopesticides

These compounds are derived from whole plants neem, custard apple, tobacco, pyrethrum or some parts of them like leaves, barks, seeds, flowers, roots, oil or extract with the ability to control pests (Byrappa and Divya 2012; Kovach et al. 1992). Botanical-based pesticides have diverse composition, target pest and mode of action and were used to control pest in the field or protect the crop and stored products from pests, especially insects for a long time. A large number of plants (>6000) with insecticidal characteristics are known, and some of them are commercialized (O 2012). Nicotine (*Nicotianata bacum* Linnaeus); Rotenone (*Lonchocarpus derris* Benth and *Tephrosia vogelii* Hook f.) and Pyrethrum (*Tanacetum cinerariifolium* Trevir) are the first known botanical pesticides (Khater 2012). Botanical pesticides can be regarded as safer pesticides compared to synthetic pesticides because of their volatile property, low environmental risk, and a minimum residue that minimizes their adverse effects on non-target organisms like predation and pollination insects.

One group of commercialized botanical pesticides is Azadirachtin compounds, which are derived from the neem tree and can be applied on several food and crops in order to control whitefly, thrips, scale and other pests (Sarwar and Tofique 2012). The extraction method and extracted compounds profoundly influence the pesticide activity of neem-based biopesticides. Extracted compounds can be a repellent, regulator of growth, inhibitor of ovipostion or toxin for pests of interest (Isman 2006). Neem leaves (against wide range of pests) (Immaraju 1998), leaf extracts of *Clerodendrum serratum* L. and powdered leaves and leaf extracts of *Olax zeylanica* Wall (against *Sitophilus oryzae* (L.)) (Fernando and Karunaratne 2012), *Cichorium intybus* L., *Melilotus parviflora* L., *Chenopodium album* L. (on *Trogoderma granarium* Everts) (Sarwar and Sattar 2012), methanolic extracts of medicinal plants (against wheat pest), *Tribolium castaneum* Herbst (Padin et al. 2013), *Phthorimaea operculella* Zeller against the potato tuber moth (Thakur and Chandla 2013), extract of the species *Clitoria ternatea* (butterfly pea) (against *Helicoverpa* spp.) (Mensah et al. 2014), stilbenes derived from grapevine extracts (against *Spodoptera littoralis*) (Pavela et al. 2017) and olive mill waste (against various pests) are some examples of botanical pesticides (El-Abbassi et al. 2017).

However, quality control, product standardization and phytotoxicity are the problems in the commercialization of botanical pesticides. For example, tomato, brinjal and ornamental plants are sensitive to a high concentration of neem oil. Also, all plant extracts with pesticide activities are not safe for humans and animals, e.g. *Aconitum spp.* and *Ricinus communis*, possess considerable toxicity for humans and *Tephrosia vogelii*, and impose adverse effects on fish (Stevenson et al. 2012).

15.2.3.1 Genetically Engineered Plants

One eco-friendly strategy to decline the yield loss of crops due to phytophagous arthropod pests is genetically engineering plants to possess genes encoding insecticidal toxins and successfully produce their corresponding products. Plant-incorporated protectants are transgenic plants in whose genome a coding gene of a pesticide is incorporated e.g., insertion of *Bt* gene, protease inhibitor, lectins, chitinase into the plant genome has been conducted. Therefore, these transgenic plants themselves can synthesize pesticide substances. These transgenic plants generate biodegradable pesticides with no detrimental effect on animal and human health and, therefore, can decline the application of chemical pesticides. For example, the lethality of *Bt* endotoxins is significantly related to the alkaline condition of the insect gut. This characteristic assures inactivity of these toxins in vertebrates, mostly in humans (Zhang et al. 2006). Plants incorporated protectants can profoundly enhance food, feed and forage production.

15.3 Improvement of Biocontrol Agents

Once the introduction of biocontrol agents, they should be survived, establish and colonize in the environment (rhizospheric region or phyllosphere) where they are applied. But their survival, establishment and colonization are affected by fluctuations of biotic (host species, nutritional status and competition with indigenous microbiota and pathogens) and abiotic (temperature, wetness and relative humidity) factors. These factors can lead to variability in efficacy or even lack of performance of biological agents and consequently their limited acceptance by farmers (Lugtenberg and Leveau 2007; Sundin et al. 2009). Colonization of biocontrol agents can be augmented by enhancing nutrients or inhibiting the growth of the competing microorganisms. This purpose can be achieved through applying nutrients or inhibitors along with biocontrol agents in their formulation to increase multiplication, survival rate and adaptation of biocontrol agents or suppress competing or antagonistic indigenous microbiota (Druvefors et al. 2005; Guetsky et al. 2002). The inhibitory effect of *P. fluorescens* 62e on *Erwinia amylovora* (causing agents of fire blight infections) was augmented by applying glycine and Tween 80 (Cabrefiga et al. 2011). Applying chemical compounds with stimulatory effects on beneficial characteristics of rhizobacteria like proline synthesis by *P. fluorescens* is another example of this strategy (van Veen et al. 1997).

Improving the efficiency of biocontrol agents via increasing their adaptation to environmental conditions is another approach. These conditions include unfavorable conditions like drought, salinity, freezing and high temperature. Adaptation of biological agents can be enhanced through their cultivation under suboptimal conditions to induce their tolerance mechanisms such as osmoadaptation via accumulating compatible solutes (sugars, polyols, heterosides, amino acids and amino acid derivatives) in their cells (Csonka and Hanson 1991; Miller and Wood 1996). This strategy has been applied to adapt *Pantoea agglomerans* EPS125, *Pseudomonas fluorescens* EPS62e (Bonaterra et al. 2005) and *Candida sake* CPA-1 (Teixidó et al. 1998) to saline, water and osmotic stresses. It is possible that the combination of the above strategies is applied through culturing biocontrol agents in a fermenter by supplementing the salts and osmolytes or adding specific nutrient to the harvested cells to prepare a liquid or dried formulation (Montesinos and Bonaterra 1996). Also, applying a mixture of compatible biocontrol agents can give better efficiency through controlling pathogens via various activities under an extended spectrum of environmental conditions (Stockwell et al. 2011). Finally, the efficiency of biocontrol agents can be improved through genetic engineering to enhance the expression of antibiotic compounds, which has been represented for *T. harzianum* or *P. fluorescens* (Flores et al. 1997; Girlanda et al. 2001) or produce new compounds (Walsh et al. 2001).

15.4 Safety, Detectability and Fate in the Applied Ecosystem

It is critical to determine survival rate, dispersal, genetic stability and horizontal gene transfer as well as effects of biofertilizers and biopesticides on the resident microbiota and fauna, and environmental impact of biocontrol agents including natural or genetically modified organisms before their commercialization and extensive use in agricultural environments. These characteristics should be monitored and validated after the release of biocontrol agents in field conditions via well-designed ecological monitoring programs (Van Elsas et al. 1998). This is while lack of a suitable method to analyze all populations of autochthonous microbiota to estimate which one is essential for qualitatively and quantitatively evaluation of the microbial community structure after the released biocontrol agents makes the monitoring difficult. Toxicity tests are crucial to assure the safety of biocontrol agents toward humans and animals. In this regard, microbial agents should not be phenotypically and genotypically similar to opportunistic microorganisms e.g., strains of *Burkholderia cepacia* (Parke and Gurian-Sherman 2001), *Pseudomonas putida* (Aumeran et al. 2007), *Pantoea agglomerans* (Rezzonico et al. 2009) and *Aureobasidium pullulans* (Gostinčar et al. 2011) that there is not considerable differences between their environmental and clinical isolates, may cause opportunistic infections. Interestingly, some of these microbial cells are frequent in nature and are inhabitants on the surface of many plants (C 1965).

Fate and behavior of released microorganisms as biocontrol agents in the environment should necessarily be monitored to evaluate risk assessment, investigation on traceability, residue analysis and environmental impact, which are perquisites for registration and subsequent commercialization of microbial pesticides (De Clercq et al. 2003). In this regard, various monitoring methods should be applied for accurate identification of biocontrol agents and their population dynamics over time. These methods should be capable of distinguishing biocontrol agents from the native inhabitants into the microbial community.

Culture-based methods, immunological assays, microsatellite markers examining (Doube et al. 1995; Plimmer 1999), the methods based on fluorescent antibodies or fluorescently labeled oligonucleotide probes, or transforming biological control agents via fluorescence (gfp) or bioluminescence (lux) reporter genes, PCR-based methods including 16S or 18S rDNA sequencing, real-time PCR (qPCR), BIO-PCR method, combined qPCR and plate-counting methods, reverse transcription (RT) coupled to qPCR, nucleic acid sequence-based amplification (NASBA), loop-mediated isothermal amplification (LAMP) are several strategies to monitor microorganisms of interests in soil, rhizospheric region, the phyllosphere and post-harvest of fruit. Although, some of them have limitations like being time-consuming (culture-based methods) and expensive (immunological assays, microsatellite markers examining), possibility of genetically modified microorganism persistence in the environment (methods based on transforming biological control agents via fluorescence or bioluminescence (lux) reporter genes), failure to do quantitative analysis (simple

PCR-based methods), lack of distinction between dead and live cells (conventional qPCR) and inability to estimate population (BIO-PCR method) constrain their application (Malusà et al. 2016).

15.5 Commercialization of Microorganisms as Biocontrol Agents

Large-scale production and formulation are influential steps in biopesticides biotechnology, which can preserve its pesticide activity for a long period (Burges 1998; Powell and Jutsum 1993). To industrially produce biocontrol agents, a suitable submerged or solid-state fermentation, and appropriate formulation, e.g. liquid, dried, peat, encapsulated types should be selected. In addition to microbial cells, a formulated microbial pesticide contains other ingredients called inerts. Therefore, these compounds should possess no hazard for human and animal health, ecosystems, and be free from allergens (Nerio et al. 2009).

Solid-state fermentation (SSF) is generally identified as the most effective and environmentally safe biotechnological strategy for mass production of high-quality biocontrol products like *Bacillus thuringiensis* in a cost-effective manner through employing agro-industrial wastes like wheat bran, rice bran, rice husks, soybean powder, fish wastes, molasses and protein hydrolysates (Morris et al. 1997; Vassilev et al. 2015). Seeds can be coated using fermentation products containing spores. Naturally occurring polysaccharide gels can be used to encapsulate spores. In addition, these spores can be introduced into compost. It has been revealed that the spores produced in SSF have higher efficiency to reduce phytopathogens and significantly preserve survival under unfavorable environmental conditions than that of produced spores in submerged cultivation (Pascual et al. 2000). SSF was used for multiplication of *Coniothyrium minitans*, a biofungicide against the soil-borne plant pathogen e.g. *Sclerotinia* spp. and production of it urin, an antifungal compound (Balakrishnan and Pandey 1996).

Microbial pesticides can be presented as liquid formulated products containing microbial suspensions in water oils or emulsions, which retained viability and efficacy for several months. Microbial pesticides in the liquid formulation should be preserved under refrigerated conditions (Abadias et al. 2003). Microbial pesticides can also be presented as wettable powders, dust or granules (Schisler et al. 2004). Storage and transportation conditions of microbial pesticides in the dry formulation are easier than liquid ones. Dehydration is a perquisite to obtain stable microbial pesticides in the dry formulation. The dehydration can be performed through freeze-drying, spray-drying and fluidized bed-drying.

To prevent cell damages during dehydration process, the compounds like sulfoxides, alcohols, monosaccharides and polysaccharides, amino acids, peptides and glycoproteins with protective activity must be added to preserve cell survival during dehydration (DJ 1993). Among these dehydration techniques, freeze-drying is less damaging but expensive method while, spray-drying is most damaging due to great water loss and temperature gradients, which creates a stressful condition for cells, but it is a cost-effective method. The third technique, the fluidized-bed drying, has been successfully used for desiccation-tolerant yeast. This method is cost-effective and less stressful in comparison with spray-drying (Larena and Cal 2003). In encapsulation formulation, microbial strains are surrounded by a protective inert layer such as alginate, carrageenan or cellulose (Bashan et al. 2002). Via encapsulating, the microbial cells can be protected from abiotic stress and released gradually.

Biopesticides should be introduced in the plant ecosystem, where they should be survived and colonized near or within entry sites of the pathogen in the host plant. Formulated biopesticides can be introduced through helper insects, coating the seeds or root microbial colonization of seedlings before transplanting, spraying or drenching plants with formulated biopesticides. To control post-harvest disease, treatment of products with microbial pesticide can be conducted before and after harvesting. Biocontrol agents can be applied with either low initial population (inoculative and augmentative strategies) or high population (inundative strategy). The success rate of applied biopesticides is directly dependent on the frequency of pathogen and introduced biological agents as well as pathogen aggressiveness (Francés et al. 2006).

In general, the determination of several characteristics including biological characteristics, efficiency, particular analytical strategies, residues, traceability and potential unfavorable effects on human health, non-target organisms and ecosystems is an essential perquisite for registration and commercialization of microorganisms as biocontrol agents. These measurements are pivotal to decline the number of registered biocontrol agents to ones with more selectivity, no toxicity for consumer health, animals and any non-target organisms, and no adverse effect on the environment (Gullino and Kuijpers 1994).

It was estimated that many commercial microbial biopesticides (90%) are derived from *Bacillus thuringiensis*, an entomopathogenic bacterium (Kumar and Singh 2015). It possesses a small portion (5%, $3 billion) of the global market of pesticides (Marrone 2014; Olson 2015). There are 200 and 60 commercial pesticides in the USA and European Union market, respectively. The annual increase in global usage of biopesticide is 10% (Kumar and Singh 2015). The universal market of biopesticides will be increased over time, and dependence on chemical pesticides will be decreased by their substitution with biopesticides with equal efficiency. The global acceptance of biopesticides is increased due to their less detrimental effects on human and animal health as well as environment, their specific activities on target pests, their effectiveness in small amounts and their quick decomposition without leaving hazardous residues. It has been predicted that global market size of biopesticides will be equalized with chemical ones between the late 2040s and the early 2050s (Marrone 2014; Olson 2015). Therefore, annual growth rates of biopesticides must outpace chemical pesticides. In this regard, comprehensive and systematic studies should be conducted to find and introduce new biological agents as biopesticides. Therefore, the collaboration of enterprises and research institutes is necessitated.

In addition, new guidelines should be considered to facilitate registration (from the aspect of time and cost) of biopesticide products (Czaja et al. 2015).

15.6 Conclusion and Future Prospects

Biopesticides compared to their chemical counterparts are more suitable to preserve quality and quantity of agricultural yield. Since they have no harmful residue and do not contaminate terrestrial and aquatic ecosystems. By using these ecofriendly pesticides, resistant weed, insects, mites, pathogenic fungi, bacteria and nematodes do not appear. Due to biopesticide-specific activity, non-target organisms remain healthy and biodiversity as well as beneficial microbial activities can be preserved. Despite having many considerable advantages, biopesticides have some limitations which can be alleviated through comprehensive studies on screening novel and efficient biological agents, determining their pesticide mode action, creating high-performance technologies to produce these biological agents or their derived compounds with high efficiency and without contamination, finding most efficient formulation. Also, appropriate strategies should be intended in order to biological agents (or their derived compounds) can be adapted, survived, established and colonized in the presence of biotic and abiotic stress conditions like chemical pesticides, heat, desiccation or exposure to ultraviolet radiation. Adapted biological agents can be applied in various ecosystems or along with chemical counterparts, which can augment their pest controlling efficiency. These adaptations to environmental conditions also can be achieved by applying suitable fermentation process, their cultivation under suboptimal conditions, their formulation or even genetic engineering of biological agents. Comprehensive investigations of these fields can lead to a constant and acceptable performance of biological agents and consequently their acceptance by farmers. Finally, accurate monitoring methods are extremely needed to detect population dynamics of biological agents over time, their dispersal, genetic stability as well as effects of biopesticides on the resident microbiota and fauna.

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Chapter 16
Mycorrhiza: Plant Growth-Promoting and Biocontrol Agent Ability Under the Abiotic Stress Conditions

Tayyaba Hussain, Muhammad Usmaan, Muhammad Numan, Aamir Abdullah Khan, Faiza Abbas, and Alvina Gul

Abstract Agriculture is the fundamental element among humans which leads to crop productivity and stability of the environment. Cutting edge techniques open doors to new dimensions of the research into soil microbiomes to find new ways to explore worthy resources. Microbiome explicitly has an uplifting role in host interaction. Mycorrhizal associations in particular have a remarkable innovation toward agricultural sustainability. Among them, arbuscular mycorrhizal fungi are surged above all other associations of host–microbiome interaction. Although it primarily depends upon gene manipulation and its expression of both host and associated microbe, AMF has an imperative role in controlling the pathogenic stress and plant growth advancement, viz., synthesis of essential secondary metabolites along with vital antioxidants that have a splendid impact on promoting plant growth and making a nutrient-rich rhizosphere. AMF symbiosis ameliorates myriad biotic and abiotic stresses ranging from salinity, drought (which leads to ROS stress), nutrient scarcity and heavy metal toxification which are highly lethal to plant's health and productivity. However, there is a need to unravel the function of arbuscular mycorrhizal fungi and peculiarities to overcome combine stresses. An eco-friendly approach is the need of time, such as the use of arbuscular mycorrhizal fungi, for better yield and

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production. However, future studies are being focused on arbuscular mycorrhizal fungi-mediated preferment of crop quality.

Keywords Mycorrhiza · AMF · Symbiosis · Plant health · Biotic stress

16.1 Introduction

Food security is the top priority of all nations in the world. Before "Green Revolution" crop yield was too low to meet the market demand and a number of acres were used to produce food merchandise. After the "Green Revolution" agriculture division heightened across the globe and crop yield also increased (Garibaldi et al. 2017). Inorganic chemicals gained more importance due to their high impact on crop productivity which leads to major health hazards in humans. Organic farming is the best considering human health but not preferable in developing countries due to its low yield per unit area of production. However, inorganic farming destroys nature continuously because of the extensive practices of chemical pesticides, insecticides, and non-organic fertilizers. Modern farming approaches and the use of genetically modified crops along with good agronomic practices enable us to ensure food security in the future. Precision agriculture with sustainability is the need of the hour to enhance crop productivity (Stevenson et al. 2013; Hesham et al. 2021; Sharma et al. 2021). During growth and development, plant faces different stresses and interacts with various micro and macro-organisms. Some of them are harmful which may collapse the overall plant's health quality and have an antagonistic effect of nutrients availability. Beneficial microbiomes live with plants by making different associations. Soil-dwelling microbes have a great influence on plant growth and lead to yield improvement, when they act as a biocontrol agent as well as a growth stimulant reported by Berendsen et al. (2012), Mendes et al. (2013), Yadav et al. (2020, 2021).

However, it is not being fully exploited yet, but modern techniques such as NGS and other molecular techniques have started a new generation of research that enables us to explore their potential within the context of the agriculture sector (Fig. 16.1).

16.2 Evolutionary History: Fossil Evidence

Evolutionary history showed that microbial activity has a crucial impact on plant growth promotion and it also helps to adopt the ecological niche (Yuan et al. 2010). History of research reported that symbiotic associations, like *Rhizobium*, actinorhizal, and mycorrhizal associations, are considered as primary and beneficial mutualistic microbial and plant root associations (Diouf et al. 2003). Historically, (Pirozynski and Malloch 1975) stated that plant and fungus associations are responsible for plant movement onto land and these associations were also observed in fossil records to be

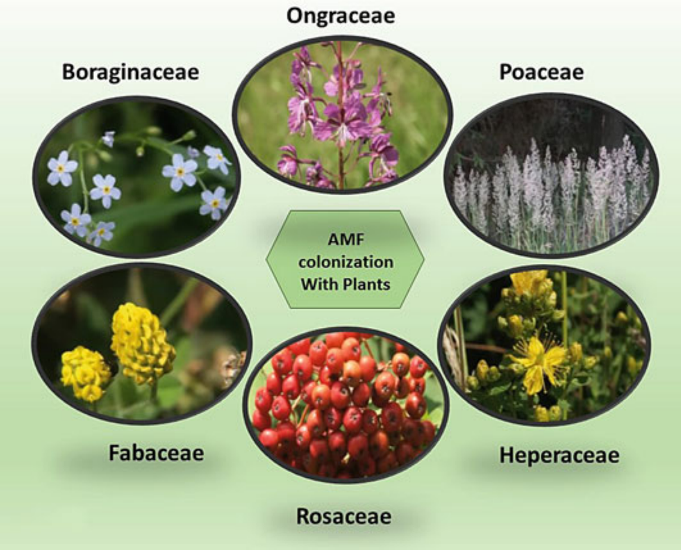

Fig. 16.1 AMF colonization with plant

400 million years old. Moreover, Sapp (2004) clarified that in the meantime, symbiotic relationships are declared as a fundamental association for the plant's health and developmental growth. It is illustrated from recent findings that most flora in the ecosystem is in correlation with microbial community (bacteria, yeast) as it interacts through leaves surfaces in the atmosphere or through roots surfaces in the rhizosphere, directly influencing the plant growth (Van Der Heijden et al. 2006). Modern studies reveal that eukaryotic cell evolution is also a result of primitive microbe interaction. In 1800 A.D. with the help of DNA-based technology, researchers observed that cell organelles such as plastids and mitochondria were derived from the association of primitive microbe (Nozaki 2005). The endurance of microbial interaction with plant tissues suggested that plant machinery in not working autonomously. Plant tissues act as a host for diverse communities of microbes that enhance their adaptability to different ecological zones (Brachmann and Parniske 2006).

16.3 Fungal Symbionts

Mycorrhiza means fungal interaction with any part of the plant, especially with roots. Different types of symbiotic relationships were observed among fungi and plants including mutualism, commensalism, and parasitism (Lewis 1985). Among all these associations mutualistic approach is more beneficial since it results in wider host adaptation to various environments and also strengthens their health to cope with different stresses such as heat, drought and disease tolerance, and enhanced nutrient acquisition (Read 1999; Devi et al. 2020). Plant vegetative growth is enhanced by arbuscular mycorrhiza fungi symbiosis as reported by Paszkowski and Gutjahr (2013). Particularly, root morphology showed a quick response toward arbuscular mycorrhiza fungal association-colonization. The tap root system is well adapted toward AMF symbiosis as compared to the fibrous root system. However, explicitly, it largely hinges on the plant's adaptability and its particular traits (Yang et al. 2015); whereas, enhanced root growth in mycorrhizal plants has greater hindrance toward pathogenic infections (Vos et al. 2014), making the host plant more resistant and compensate for the loss caused by soil-borne pathogens. Nematode also plays an indirect role in biocontrol strategy through the root conservation system via mycorrhizal arbuscules formation (Elsen et al. 2003).

16.4 Mycorrhiza

Fungal association with roots of higher plants by the mutualistic approach extended in rhizosphere zone and surrounding soil, and this particular symbiotic interaction is termed as mycorrhiza. A scientist named Frank in 1885 named this association as "mycorrhiza". All fungi in an arbuscular mycorrhizal association that produce mutualistic interaction with 80% of vascular plants belong to the phylum Glomeromycotan (Simon et al. 1993). After contact with host root tissues, fungi penetrate and establish its mycelial network through the epidermis of the cell in cortical of parenchyma (Powell 1984). Fungus penetration inside root tissues takes place via three different modalities: through intracellular hyphae originate, penetration through radical hair, or it enters through external layers of cells that are usually dead or flake off as represented in Fig. 16.2 and reported by Bonfante et al. (1982). After this, a mycelial network develops and starts penetrating in the root's cells and in this way arbuscular structure is formed within 7–12 days of infection (Gadkar et al. 2001). So, this site is responsible for the exchange of metabolites and acts as a reservoir of nutrient accumulation.

Being more abundant and common in agriculture than any other, AMF plays a paramount role in maintaining the sustainability of the environment via recycling of organic matter and make nutrients available by biodegradability of complex organic compounds. Collectively, all such properties of microorganisms enhance plant growth promotion to cope with the devastating conditions of environment. So by using techniques like microbes and PGPM improves crop health and reduces the health hazard of its consumers. These two are the best substitute for inorganic pesticides and fertilizers. Therefore, to ensure food security and sustainable agriculture in future, plant–microbe interactions are an important concern of the hour (Govindasamy et al. 2011). Food quality and crop yield can be improved by using microorganisms and stress-tolerant plant growth-promoting mycorrhiza (PGPM) in the changing climatic conditions. Also, through sustainable agriculture practices and

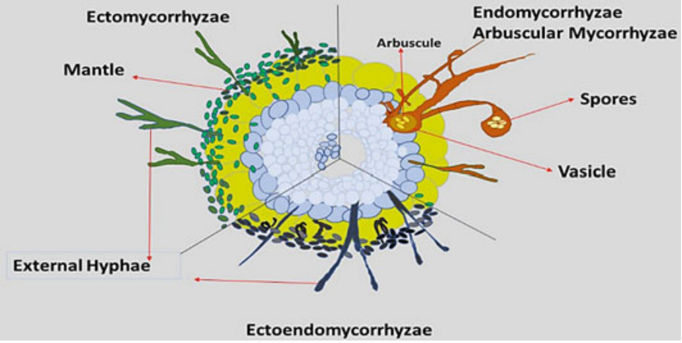

Fig. 16.2 This figure elaborates associations of AMF with the roots of the plant. AMF is shown on the right side developing arbuscules inside of the plant's root. While the other side of the figure is depicting the association of ectomycorrhizal fungi which fully covered the plant root tissue with a new tissue of fungus called the mantle (on the left), and hyphae seems to be surrounding the plant's cell in the cortical region of the root. At the bottom fungus-forming mantle with the bunch of hyphae piercing into the plant cells can be seen

using PGPM, we can save 20–25% cost of production by limiting inorganic pesticides and fertilizers. These practices of crop production can enhance the income of farmers and ensure organic agriculture.

16.5 Virtual Soil Diorama

Generally, three types of propagules are involved in colonization of AMF with plant's root; these are spores, fragments of mycorrhizal hyphae, and arbuscules (Fig. 16.2). These propagules extended in the soil with an extensive network of mycelium. In the first phase of colonization of AMF, hyphae formation is initiated through soil-borne propagules, i.e., mycorrhizal root segments or resting spores or from AM plant in the vicinity. Under the application of AMF and the use of plant growth-promoting microbes (PGPM), plant growth is significantly boosted. Moreover, these approaches paved the way for the best survival of plants and AMF in a changing environment. AMF is capable of altering the root exudates in rhizospheric soil from the perspective of its composition and distribution (Hage-Ahmed et al. 2013). But its specificity doesn't depend only upon AMF (Kobra et al. 2009). However, it contributes to the automatic regulation of symbiotic interaction among both plant and fungal partners reported by Schaarschmidt et al. (2013). This evidence is supported by Lioussanne et al. (2008) that it significantly depends on the level of maturity of AMF, i.e., colonizing the lure of *Phytophthora nicotianae* zoospores to root exudates of *R. irregularis* colonized diverted to repellence.

16.6 Abiotic Stresses

Abiotic stresses significantly impart changes in physiological, biochemical, morphological, and molecular properties of the plants, which critically damage the plant's health as reported by Zhao et al. (2001), Kour et al. (2019), Dikilitas et al. (2021), Tiwari et al. (2021). Myriad of stresses, likewise saline stress along with water scarcity, oxidative and high-temperature stress results in the induction of many lethal cellular changes (Wang et al. 2003). Homeostatic equilibrium in the plant body is primarily affected by drought and salinity stress that leads to osmotic stress eventually (Zhu 2001). Denaturation and accumulation of cellular protein is the effect of high-temperature stress mainly and if ignored, it leads to unrecoverable narcosis. Usually heat effects by causing mutation lead toward abnormal transcription and translation, resulting in the induction of heat shock proteins and its expression toward thermotolerance intimation (Hirt and Shinozaki 2003). Metabolic processes are largely pretentious by low-temperature stress which alters the structure as well as the function of proteins by changing the properties of membranes and particularly affecting the signaling mechanism among secondary metabolites along with halting enzymatic functions (Heino and Palva 2004). Unique transport mechanism is adopted by plants to uptake Cu—a heavy metal. Furthermore, chaperones act as a medium of intracellular transport of Cu to storage vesicle, where it specifically targets the enzymes.

Likewise, Cu/Zn_SOD and receptors of ethylene. Besides this, the copper radicle is highly lethal as it paved the path to programmed cell death (PCD), and this hype is seen in many oxides, e.g., hyperoxide, H_2O_2 accompanied by the composition of OH^- ion (Polle and Schützendübel 2004). Overall, all stresses converge into an "oxidative stress" which ultimately results in denaturation of proteins, structurally and morphologically (Smirnoff 1998). Production of ROS and its accumulation clearly indicates the warning sign of stress, either biotic or abiotic. Hence its accumulation is the root of all fundamental stresses associated with all biochemical processes. ROS causes severe damages to biological molecules such as DNA, proteins, and lipids. On the other hand, ROS is imperative to regulate signals under stress. Therefore releasing of ROS is the initial response of the plants toward any stress (Rodriguez et al. 2005). But symbiotic relationship with plants assists in combating variety of abiotic stresses, few of them are enlisted in Table 16.1.

16.7 Mycorrhizal Fungi as Biocontrol Agent

Increased application of chemical pesticides on crop plants resulted in increased environmental pollution. So we must use alternative ways to combat biotic stresses such as biocontrol measures, which are more prominent among all strategies. In this context soil microbiota is gaining more importance. In agriculture, different strategies are used to control the soil-borne diseases, such as soil fumigation, chemical

Table 16.1 Elaborates on the diversity of symbiotic association of fungi to mitigate environmental stresses subjected to higher plants

S. no.	Fungal endophytes	Environmental stress	Host plant species	References
1	*Neotyphodium* sp.	Drought	*Fest perennial*	Morse et al. (2002)
			Ryegrassuca pratensis	
			F. arizonica	
2	*Neotyphodium lolii*	Water scarcity	*P. ryegrass*	Ravel et al. (1997)
3	*Neotyphodium coenophialum*	Drought stress	*T. fescue*	De Battista et al. (1990)
4	*Neotyphodium uncinatum*	Water stress	*M. fescue*	Malinowski (1995)
5	*Curvularia* sp.	High temperature and water scarcity	*L. esculentum*	Rodriguez et al. (2008)
8	*C. protuberate*	Famine stress	*T. aestivum*	Rodriguez et al. (2008)
			Citrullus lanatus	
9	*C. protuberata*	High temperature	*L. esculentum*	Rodriguez et al. (2008)
10	*Rhizophagus intraradices*	Famine stress	*Zea Mays*	Zhao et al. (2015)

fungicides, seeds certification, resistant cultivars, and crop rotation. A lot of problems are associated with this strategy to control the pathogens on a persistent basis, due to lack of resistant cultivars (Azcón-Aguilar and Barea 1997). Therefore, to eradicate the soil-borne pathogens, botanists are working to use substituted approaches by adding microbiota to the soil medium to surge the healthy plant's yield potential (Grosch et al. 2005). Adding beneficial microorganisms in the soil increases the competition of space, water, and nutrients, with soil-borne plant pathogens. Some of the antibiotics attack the pathogens and some increases the immunity of the host plant to combat arduous situation.

Meanwhile, different microorganisms are used as biocontrol measurement of pathogens (Berg et al. 2007). Researchers have reported different mechanisms of biocontrol by arbuscular mycorrhiza fungi. These mechanisms include chemical and physical changes in plants such as nutrient exchanges, morphological changes in roots and biochemical changes in the rhizosphere (Hooker et al. 1994). Concerning biocontrol, AMF is well adapted to induce a systemic-induced system, particularly in plants (Cordier et al. 1998). Furthermore, system-induced resistance is well-defined as the inexorable induction of resistance or tolerance to infectious plants by a pathogen inoculation. Moreover, MAMPs are responsible for disease resistance by AMF elaborated by Zamioudis and Pieterse (2012).

16.8 Plant Growth-Promoting Mycorrhiza Impact on Plant's Health

Abiotic stresses are scientifically controllable by the application of PGPM and AM concerning plant growth (Nadeem et al. 2014). To promote healthy plant growth microbes use diverse molecular and biochemical mechanistic approaches; for example, through inoculation of PGPM, hormonal and nutritional balance of plants is regulated that enchants their growth and also induces resistance against pathogenic organism in plants (Spence and Bais 2015). Like metabolic reactions produced by PGPM in plants suppress the population of pathogens in plant vicinity, for example, siderophores secreted in the rhizosphere by soil microbes suppress the growth of the pathogens by reducing the iron availability to certain pathogens (Złoch et al. 2016). Moreover, they also strengthen the plant's growth development, readily available phosphates, fixing atmospheric nitrogen and by generating hormones (Ahmad et al. 2011). Other approaches like mobilization of nutrients and synthesis of exopolysaccharide and rhizobitoxine enable the plant to survive in harsh environments. Ethylene production inhibited under stress conditions by rhizobitoxine also promotes plant growth and development (Kumar et al. 2009). Besides hormones, enzymes are also produced by plants microbes to boost their mechanism to fight with stresses; for example, glucanase, chitinase, and ACC-deaminase are produced under stress conditions (Farooq et al. 2009).

16.9 Characteristics of Arbuscular Mycorrhizal Symbiosis

AMF symbiotic association with the plants is confirmed about 400 million years ago (Selosse et al. 2015). Such associations are customary like series of biological processes, which resulted in worthwhile effects in agriculture biota and natural ecosystem (Van Der Heijden et al. 2015). Among all associations, AMF is the oldest mutualistic interaction that helps to maintain plant health and survival. Nutrition uptake of fungi from the host cell takes place through the mycelium network that extends in the root system of plants. Mycelium network of fungi interacts with numerous plants that are from different species, and this type of association is recognized as a common mycorrhizal network (CMN). Hyphae networks make CNN the prime module of the ecosystem due to its splendid effects on flora, especially the invasive plants (Pringle et al. 2009), thus resulting in relocation of nutrients between fungi and the plants (Fig. 16.3).

This is how AMF has a paramount impact to establish tolerance for plants against environmental and biotic stresses (Navarro et al. 2014). They can restore the fertility of the soil and flourish the soil features along with improved plant health (Alqarawi et al. 2014). Furthermore, Hashem et al. (2015) reported that changes in the physiological traits of the plant are brought by AMF colonization that enhances the plant's ability to combat stress conditions. Barrow (2012) findings elaborated that

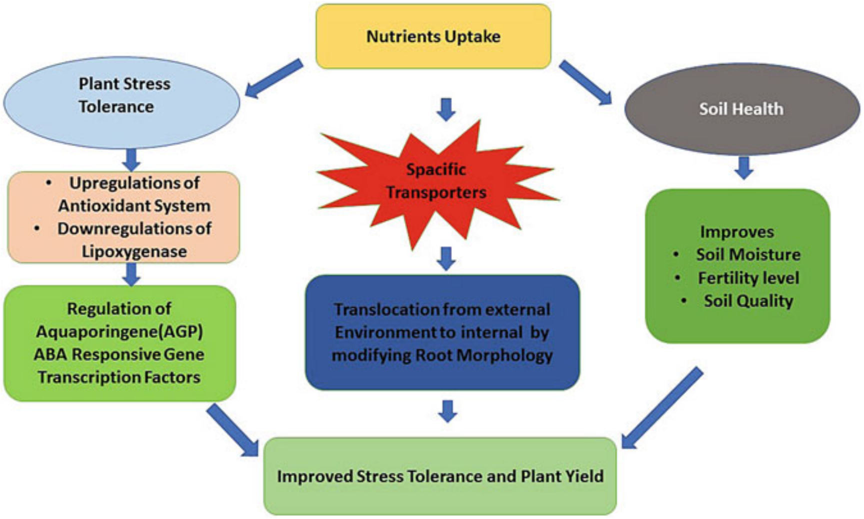

Fig. 16.3 AMF and its impact on plant and soil health

AMF is deliberated as a normal growth promoter of the bulk of global vegetation. Researchers suggested AMF inoculation, due to its constructive role in sustainable production acts as a biofertilizer. Moreover, it has been analyzed that soil containing infectious threads of AMF forms exhibit more persistent masses and prolonged extra radical hyphal threads in contrast to the soil with the non-AMF association (Syamsiyah and Herawati 2018). It has been presumed that glomalin soil protein (GSP) has great water-holding capacity in the soil that is subjected to various abiotic stress, which afterward stimulates the growth of plant immediately by controlling the water level (Wu et al. 2014). Moreover, Sharma et al. (2017) compromises 30–40% carbon content and its associated compounds that shield soils from erosion and desiccation due to upgrading soil water-holding capability.

Development-related functions such as stomatal conductivity, leaf water capacity, relative water content (RWC), (PSII) performance, and assimilation of carbon dioxide are influenced by the inoculation of AMF (He et al. 2017; Chandrasekaran et al. 2019). The objective of AMF is to increase the resistance to water tension through biochemical modification of the aerial parts of plants (Bárzana et al. 2012). AMF association also assists in reducing the retention of dry matter and boosts the uptake of water content, thus uplifting the plants resistance to stress, such as drought and saline stress. Application of AMF for the betterment of plant growth in different environmental conditions will make a major difference to organic agriculture to encourage production and optimize yield (Fig. 16.4) flowcharts. Castellanos-Morales et al. (2010) reported that rhizospheric beneficial microorganisms not only boosts the crop nutrients availability but also improves the crop quality with the same pace.

In exemplification, AMF association in strawberries explicitly increases the concentration of secondary metabolites which led to the improvement of antioxidant

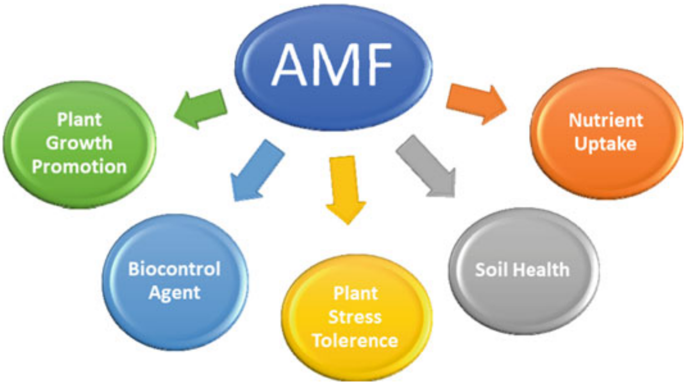

Fig. 16.4 AMF association has a direct positive approach toward better productivity of the plant, as plant growth promotion, biocontrol agent, plant stress tolerance, soil health, and uptake of nutrients

properties. By influencing and developing carotenoids and other volatile compounds, AMF contributes in enhancing the nutritional value of the crop yield that have been identified as beneficial effects of AMF on tomato production as cited by Bona et al. (2017). Improved content of vitamin C organic acids, sugar flavonoids, and minerals results in enhanced plant's yield (Zeng et al. 2014). Mycorrhizal symbiosis causes decreased anthocyanin aggregation, along with photosynthetic pigment, i.e., chlorophyll, and other mineral nutrients like carotenoids, absolute solvable phenolics, tocopherols as reported by Baslam et al. (2011). Later findings of Lu et al. (2015) illustrated that arbuscular mycorrhiza has been used in large-scale field maize, yam and potato production. Hijri (2016) confirmed that AMF has significant potential to increase crop yields. For edible plants, AMF has a pivotal role to boost the synthesis of useful organic compounds that are quite essential for a balanced food production chain. Furthermore, they stated that AMF's abiotic stress mitigation may occur by soil pH conservation, thereby preserving its horticultural interest.

16.10 Mycorrhiza Cope with Abiotic Stresses

Mycorrhizal hyphae assist the host plant by protecting it from water scarcity via higher water uptake mechanism established by the hyphae that remarkably extends into the soil as well (Abdel Latef and Miransari 2014). It is of paramount importance in sustaining the greater proportion of K/Na (Porcel et al. 2012), especially in osmotic stress. Besides, sodium ion concentration in soil is substantially high, hindering directly with myriad of other transporters, particularly in root plasma like potassium selective ion channels (Evelin et al. 2012). In summation, the uptake of essential mineral elements, e.g., iron, sulfur, copper, and zinc get reduced in numerous enzymatic processes, including protein synthesis (Maathuis and Amtmann 1999). Plants respond effectively with AMF association, especially by increasing the surface area of mineral absorption. It ultimately leads to high accumulation of potassium ion which assists in balancing the low Na^+/K^+ ratio. This is how mycorrhizal association with plants protect its biological functioning from damage (Kapoor et al. 2019). Numerous organic solutes (glycine, soluble sugars, proline, and betaine) play a pivotal role in the establishment of fungi–plant colonization (Kapoor et al. 2019). Production of such metabolites not only provides assistance to maintain the osmotic level but also plays a key role in detoxification of ROS, and maintains integral membrane functionality and stability of the enzyme and other proteins (Sanchez et al. 2008). Table 16.2 explicitly explains how symbiosis is conducive for plants in combating abiotic stress.

16.11 Arbuscular Mycorrhiza as Biocontrol Agent

Phyto-pathogenic microorganisms play a key role in the substantial loss of crop productivity. Numerous applications were applied at discrete levels of plant growth to control the phyto pathogenicity (Thakur et al. 2020). However, continuous use of such practices contributes significantly to the deterioration of the ecosystem (Bødker et al. 2002). Meanwhile, over time plant pathogenic microorganisms develop immunity in contradiction of these agrochemicals which are arduous to overcome. Subsequently, biological approaches as part of integral management considered as an impeccable substitute for the excessive use of agrochemicals. Moreover, the use of arbuscular mycorrhiza is accepted worldwide as a biocontrol tool for pathogenic microorganism (Harrier and Watson 2004). This concept was also assisted by Feldmann and Boyle (1998) when they analyzed the converse relationship among colonization of roots of *G. etunicatum* (that belongs to begonia species) and vulnerability specifically to the powdery mildew fungus named *Erysiphe cichoracearum.* On the other hand, Filion et al. (1999) findings elaborated that the growth rate of F. *oxysporum f.* sp. *chrysanthemi* is limited by extraradical mycelium of *G. intraradices*. Similarly, in one more research, Slezack et al. (2000) reported *Aphanomyces euteiches* to have AMF as a mutualistic approach with *Pisum sativum* declaring best defense against pathogens. In ramification, Trotta et al. (1996) reported that most common fungi used as model organism, i.e., *Phytophthora* spp., plays a pivotal impact in analyzing and demonstrating the control measures for plant diseases.

Moreover, Caron and co-workers (1985) depicted that AMF is responsible to reduce the risk of disease in plants supported by experiments conducted on tomato when they interact *G. intraradices* as an AMF and *F. oxysporum* as a pathogenic fungus. Another evidence provided by Torres-Barragan et al. (1996) elaborates that it is a healthy approach to delay the inception of the onion by the pathogen, i.e., *Sclerotium cepivorum* by two weeks. This pathogen is responsible to infect onion with white rot disease. Their conclusion is supported by Newsham et al. (1995) as they experimented *Vulpia ciliate* by pre-inoculating with the AMF *Glomus* sp. before subjecting it into the natural grass ecosystem. Later, it was indicated that this approach leads to the significant reduction of infection with *F. oxysporum.*

Table 16.2 Depicts the protagonistic response of plants in myriad stresses in association with fungal symbionts

S. no.	Type of stress	Host species	Fungi species	Pragmatic responses	References
1	High temperature	*Triticum aestivum* L.	*Funneliformis mosseae, Rhizophagus irregularis*	Increased grain production	Cabral et al. (2016)
			Claroideoglomus claroideum	Nutrients availability to roots	
			Funneliformis geosporum		
2	Heat stress	*Zea mays*	*Rhizophagus intraradices*	Leaf size and number increased along with plant height	Mathur et al. (2018)
			Funneliformis mosseae	Enhance the production of chlorophyll a, rate of photosynthesis, stomatal conductance, and the rate of transpiration	
			F. geosporum		
4	Saline stress	*Aeluropus littoralis*	*Claroideoglomus etunicatum*	Improved shoot and root dry mass, stomatal conductance, solvable sugars, free α-amino acids, and Na^+ and K^+ uptake	Hajiboland et al. (2015)
5	Heat	*Solanum lycopersicum*	*Rhizophagus irregularis*	Enhanced photosynthetic capacity	Calvo-Polanco et al. (2016)
				Root capability of water conductance	
				Aquaporin abundance and phosphorylation status	

(continued)

Table 16.2 (continued)

S. no.	Type of stress	Host species	Fungi species	Pragmatic responses	References
6	Saline stress	*Solanum lycopersicum* L.	*Rhizophagus irregularis*	Improved shoot, leaf zone, leaf number, and growth hormones levels	Khalloufi et al. (2017)
7	Metal	*Sesbania rostrate*	*Glomus mosseae*	Stimulate the formation of root nodules development, and boosted nitrogen and phosphorous contents	Lin et al. (2017)
8	Metals-Cadmium	*Trigonella foenum-graecum* L.	*G. clarum* *Gigaspora nigra* *Acaulospora laevis* *Glomus* *monosporum*	Increased antioxidant enzymes activities and malondialdehyde content	(Abdelhameed and Metwall 2019)
9	Saline stress	*Oryza sativa* L.	*Claroideoglomus etunicatum*	Efficient PSII photochemistry hence increased net rate of photosynthesis and ultimately stomatal conductance	Porcel et al. (2015)
10	Salinity-alkalinity	*Leymus chinensis*	*Glomus mosseae*	Increased rate of colonization Along with its seedling weight, water contents, efficient phosphorous, and nitrogen uptake	Lin et al. (2017)
11	Cadmium and zinc	*Cajanus cajan L.*	*Rhizophagus irregularis*	Better-quality root biomass, availability of nutrient like (P, N, Mg, Fe) and biosynthesis of proline	Garg and Singh (2018)

(continued)

Table 16.2 (continued)

S. no.	Type of stress	Host species	Fungi species	Pragmatic responses	References
12	Salinity stress	*Cucumis sativus* L.	*Glomus etunicatum* *Glomus intraradices* *Glomus mosseae*	Improved biomass production, synthesis antioxidant enzymes along with photosynthetic pigments, and	Hashem et al. (2018)
13	Salinity stress	*Solanum lycopersicum* L.	*Glomus intraradices*	Improved biomass, increased chlorophyll content Improved ion uptake	Hajiboland et al. (2010)

16.12 Mycorrhizae-Mediated Biocontrol Mechanisms

16.12.1 High Nutrient Uptake

AMF association assists in developing the immune system against various diseases. It also accounts for the advancement of nutrition uptake, especially phosphorus and nitrogen (Baum et al. 2015). Myriad endophytes have been acknowledged to enhance plant growth promotion when they act synergistically with arbuscular mycorrhiza (Puppi et al. 1994). Plant's residues decaying and recycling nitrogen from leaf litter in (15 N–13C) labeled *Lolium perenne* leaves significantly surged due to AM symbiont glomus (Hodge et al. 2001).

Phosphorous is chiefly consumed by plants in the form orthophosphate (Pi) but unfortunately it is merely available in the soil, approximately 10 mM (Bieleski 1973; Kour et al. 2020). This is because solubility and mobility of this compound is low, and the rhizosphere has greater chances of phosphorous depletion. Arbuscular mycorrhizal fungi play a pivotal role to overcome phosphorous deficiency by mutual interaction with plants. This improvement has been upgraded by using isotope dilution approaches specifically 32P/33P-based isotopes (Barea 2010). In summation, fungal partners are assisted by plants in the maximum uptake of phosphorous (Barea et al. 2014). It has been reported that high phosphorus content has a crucial role to establish AMF symbiosis (Bever et al. 1996).

Moreover, along with phosphorous uptake, arbuscular mycorrhizal fungal partner also assists plants to overcome nitrogen deficiency via both organic and inorganic nitrogen sources (Mohanta and Bae 2015). Peptidases and proteases enzymes are released by fungal partners into the soil that catalyze and freed the bounded nitrogen organically and make nitrogen available to plants (Behie and Bidochka 2014). Furthermore, nitrogen transporters are upregulated in plants that accompany fungal translocation of nitrogen. In the case of *Sorghum bi color*, ammonium ion transporters are reported to be unregulated in cortical cells containing arbuscules and the expression of ammonium ion transporters in plants SbAMT3; and SbAMT4 is confined only in cells containing arbuscules (Koegel et al. 2013). Likewise, NO_3^- transporters expression was also reported in arbusculated cells in *M. truncatula* (Gaude et al. 2012; Behie and Bidochka 2014). Respective corresponding and specific expression by plants and fungal NH_4^+ and $NO_3^{\overline{}}$ transporters in mycorrhizal infectious cortical cells are highly conducive in bringing fungal nitrogen transmission to plants (Behie and Bidochka 2014).

16.12.2 Competition for Nutrients and Space

The main factor associated with pathogenic clampdown in mycorrhizal plants is competition among the nutrients like carbon, which is essential for both mycorrhiza and rhizosphere soil microorganisms (Vos et al. 2014). Furthermore, it is estimated that 4–20% of the carbon content is transferred from the host plant to AMF from total assimilated carbon, reported by Hammer et al. (2011). Various studies reported different aspects of AMF in association with plants and the way it guards the host plant against deleterious pathogens. As aforementioned, it all depends upon the characteristics of the host plant and AM species. Similarly, Lerat et al. (2003) support this view by reporting results of AMF which adopt different measures of biocontrol due to differences in the carbon sink among various AMF species. It has been concluded that *Phytophthora* is unable to penetrate into tomato plant which has an association with AMF (Cordier et al. 1998). On the contrary, it is testified by Vos (2012) that arbuscular mycorrhizal fungus-*rhizophagus irregularis* is unable to build a strong biocontrol effect on pathogenic nematode *Rhadopholus similis* and *Pratylenchus coffeae* in banana.

16.12.3 Phytoalexins and Phytoanticipins

Under defense mechanism plants produce various natural hormones like "phytoalexins" which do not possess the protagonist approach toward any symbiotic mutualistic association. Formally, it was known that in response to microbial infection phytoalexins are produced by plants (Wyss et al. 1991). They exhibit lipophilic nature which helps them cross the plasma membrane and carry out their activity inside the cell (Braga et al. 1991). Interestingly, secondary metabolites, i.e., coumaric acids, lignin, ferulic, syringic phenolics, viz., iso-flavonoids, or flavonoids surged up to the mark by mycorrhizal colonization with roots of the host plant (Morandi 1996). As compared to control, plants show great defense against *F. oxysporum* which leads to high beta-glucosidase and phenylalanine activity with entire phenol content in their roots, reported by Dehne and Schönbeck (1979). Moreover, phytoalexins are imperative to neutralize the counter effect of pathogens in plants having arbuscular mycorrhizal association in contrast to the control ones (Caron et al. 1986).

16.12.4 Hydrolases, Antibiosis, and Antioxidant Enzymes

AMF assists in exploring the genes that are associated with the defense mechanism in plants having mycorrhizal association (Lambais and Mehdy 1995). Mycorrhiza contributes to the induced assembly of hydrolytic enzymes such as superoxide dismutase chitinase, b-glucanase, and chitosanase in tomato roots against the *Pseudomonas parasitica* in host defense mechanism, reported by Pozo et al. (2002). The productive relationship among the level of glucanase action and fighting against phytopathogens in host tissues was analyzed by Graham and Graham (1991). Formally, it is being reported by Filion et al. (1999) that anonymous antimicrobial substances synthesized by *G. intraradices* are conducive to rheostat conidial germination of *F. oxysporum f.* sp. *chrysanthemi* under the non-influential effect of pH.

On the other hand, it is a cosmopolitan belief that antioxidants have salient role in building the symbiotic associations among plants and fungi, particularly in abiotic stress defense mechanisms (Rouhier and Jacquot 2008). There are many antioxidants, enzymes such as superoxide dismutase ascorbate or thiol reliant on peroxidase, catalases dehydroascorbate reductase, glutathione reductases, monodehydroascorbate reductases. Low molecular weight antioxidants involve ascorbate glutathione and tocopherol compounds (Rouhier et al. 2008). The enzymes such as thiol-dependent peroxidases, catalases, and ascorbate- or superoxide dismutases have specificity to eradicate ROS via renaissance of the two main redox molecules in the cell, glutathione and ascorbate dehydroascorbate reductases, and monodehydroascorbate reductases and glutathione reductases (Rouhier and Jacquot 2008). A thought-provoking feature of the chemistry among antioxidants and oxidants is that it befalls in all subcellular partitions together with plastids and mitochondria, two spots of catholic ROS production (Navrot et al. 2007).

16.13 Conclusion

The genotype of the host plant and fungi species has a paramount role in AMF association and their potential toward plant growth promotion and its productivity. Bioactive compounds are largely produced by fungal symbionts which have the protagonist effect on humans, as well as on other living creatures. Henceforth, environment has a profound effect on AMF and its associated host, likewise availability of nutrients, water supply, and fluctuation of temperature. It has been observed that instead of unfavorable growth conditions, plants having minor ratio of AMF association, especially vegetable crops, show significant growth rate. This is because this mutualistic symbiosis is conducive to promote plant growth and enhance tolerance under abiotic stress conditions and, meanwhile, increase immunity against pathogenic organisms. Mycorrhiza plays a significant role in plant growth promotion, both individually or mutualistically. It could be used on commercial scale as bioinoculants and biocontrol agents for crop production under normal and stressed environments. Furthermore, bioactive compounds as a by-product of symbionts are potentially useful for bioremediation.

16.13.1 Prospective Research

It has been observed that AMF has a high potential against phytopathogens but on the same ground, there are restrictions to AMF as a biological tool for this purpose. Bever et al. (1996) demonstrated that the abundance of diverse communities of arbuscular mycorrhizal fungi surely has a great potential of biocontrol against phytopathogens. Meanwhile, the versatility of AMF in the rhizosphere has been largely influenced by the genotype of the host plant and crop rotation level. Myco-trophic host is most suitable for AMF colonization and imitation as compared to plants that are not adapted to myco-friendly environment. Endophytic symbionts are biological tools that have great potential to be used as genetic markers, vectors. It can be used wisely to overcome the scarcity of food—the global challenge. Moreover, they can be used commercially as a source of natural antioxidants and secondary metabolites. There is a need to explore its hidden treasure in antiviral compounds, anti-carcinogenic compounds, and antibiotics. AMF can also aid in producing immune-suppressants. Its all-rounder ability to combat future challenges should be traced and launched. It's a need of time to dive deep in nature and explore proficient endophytic fungi to mitigate abiotic stress and develop tolerance against it. Plethora of endophytes is presumed to exist in nature in distinct extreme environmental conditions that have not been discovered yet, and ecological perspective to such myco-organisms is not well understood. Bioengineering is an interesting feature to be adopted to enhance biological competences of plants. This strategy will have an impeccable impact on the plant-fungal association and might be conducive to the betterment of the agriculture industry.

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Chapter 17
Entomopathogenic Soil Microbes for Sustainable Crop Protection

Neelam Thakur, Preety Tomar, Simranjeet Kaur, Samiksha Jhamta, Rajesh Thakur, and Ajar Nath Yadav

Abstract The insect pest nuisances in the agricultural industry are most likely as old as the agriculture itself. Insects are the most ubiquitous and versatile among all living organisms and are responsible to develop successful survival mechanisms as compared with other living fauna that also share the same planet. The main reason for insect's dominance in the world is their huge adaptability. A large number of agrochemical insecticides, pesticides and herbicides are used against these insect pests, which are neurotoxicants and affect all living organisms with soil fertility. Food security, energy renewability, rural livelihood and agricultural sustainability depend mainly on soil richness or fertility. Global increase in the population and degradation of environment possess a challenge in crop production and it is a need to find solutions for abiotic stress, pests and pathogens. These demands for food cannot prevail until the fertility of the soil is restored. In addition, today's prime public worry is about environmental pollution, mostly caused by the use of chemical synthetic pesticides, herbicides and fertilizers. Hence, a cleaner and greener approach against crop production and protection is essential by the use of microbial biopesticides. Microbes are a vital part of soil not only involve in transforming nutrients within the soil but also influence the multiple functions and are among the commonly used eco-friendly means of pest management. There are some specific microbes that help the plants in rhizospheric soil to grow healthy in that environment by performing various mechanisms. The direct mechanism consists of fixation of nitrogen, production of different enzymes and phytohormones and solubilization of some minerals in the rhizospheric soil, whereas indirect mechanism comprises inhibiting phytopathogens. Originated from a variety of naturally occurring microbes such as viruses, bacteria, fungi, nematodes, rickettsia and protozoan etc. microbial biopesticides protect our crops from

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diseases and pests thus enhance crop productivity and soil fertility. They make it possible to increase yield as well as the productivity in a sustainable way. Ultimately, results in more production give food to our ever-growing world population with a novel opportunity to protect this planet. The significance of rhizospheric microorganisms may be huge as they are capable of managing the pest population, nutrient acquisition and nutrient transformation, thus results in crop sustainability.

Keywords Biological control · Commercialization · Entomopathogenic · Microbial pesticides · Rhizospheric microbes · Sustainable agriculture

17.1 Introduction

Insects are the most ubiquitous and versatile among all living organisms and are responsible to develop successful survival mechanisms as compared with other living fauna that also share the same planet. Insect's biological success in nature is quite obvious. Now, more than 1 million insect species are identified, which is the highest in number as compared to the total vertebrate population 62,000 species, including fishes, amphibians, reptiles, birds and mammals. The main reason for insect's dominance in the world is their huge adaptability, which enables them to inhabit every imaginable environment where existence can be present and stay alive under adverse ecological conditions. The appliance of extremely toxic insecticides to eradicate harmful insects is termed as 'insect pests' or 'pest insects' and exerted a large selection force on insects (Kumar and Shivaraju 2009). In results the insects developed the adaptability for survival against these toxicants and that phenomenon is well known as insecticide resistance within insects. Almost 30–50% of crop yields be vanished due to the damage caused by insect pests and also some insects have the possibility to cause approximately 50–100% loss in outbreaks (Oerke et al. 1994). Reductions in the agricultural losses caused by pests are the potential vicinity for rising food production, and in these circumstances, we take advantage of the rhizospheric entomopathogenic microbes to decrease the level of losses due to the insect pests. It is difficult to reduce the losses caused by the pest due to less resources and limited area (Pandey and Seto 2015). Over the next four decades, the world's population will reach to a predictable increase of 10 billion. So the instant and the main concern of the agriculturist is to attain high production in such a way that it is ecologically sustainable and worthwhile.

There are large numbers of agrochemical insecticides, pesticides and herbicides introduced in the world market for the management of these insect pests. But there are many factors that are found at risk for the use of these agrochemicals. Some of the factors include resistance among the insects against conventional insecticides, adverse effects on human health, environmental issues and less awareness among the people towards the use of synthetic chemical insecticides, which results in deregistration and cancelation of certain insecticide formulations (Nicholson 2007; Thakur et al. 2020). Therefore, an alternate and eco-friendly method is required to improve the quality and quantity of agricultural goods, which leads to sustainable crop protection (Yadav et al. 2020; Hesham et al. 2021; Kumar et al. 2021). Keeping in mind the ill effects of insecticides, there is a need to develop biopesticides, which are environment friendly, highly effective and easily decomposable. The use of natural enemies against arthropod pests is a successful biocontrol method under the integrated pest management (IPM) technique (Pilkington et al. 2010). Biopesticides are obtained from natural resources and living organisms such as plants and animals. These biopesticides manage the insect pest population through non-toxic mechanism as they are produced from the microbiomes. Microbial biocontrol agent (MBCA) is an alternative method against chemical pesticides. The presence of epizootics through microbiomes controls the population of pest species. Nowadays, entomopathogenic microbiome is also employed as an effective method of pest control under integrated pest management (IPM). Bacteria, fungi, protozoa, nematodes and viruses are widely used to manage the population of insect pests (Evans 1986; McCoy et al. 1988; Rastegari et al. 2020a, b).

Microbial biopesticides include a live organism which is natural enemies or their by-products are used for the control insect pests, whereas the microbial biofertilizers of living microbes which are used to enhanced crop productivity (Kour et al. 2020a,2020b; Mondal et al. 2020; Rai et al. 2020; Yadav et al. 2021). Host specificity of these biopesticides provides an effective solution, which is an eco-friendly approach to pest management. Presently, microbial biopesticides are used, which include bacteria, viruses, fungi, protozoan and nematodes (Islam and Omar 2012; Verma et al. 2017, 2018; Yadav et al. 2017). There are about more than 100 pathogenic species of bacteria that have a potential to manage the population of insect pest among which entomopathogenic bacteria *Bacillus thuringiensis* acquire the top position (Abtew et al. 2015). Although *B. thuringiensis* have been identified for its entomopathogenic properties but there is a requirement of industrial efforts too for the detection of new strains and specific toxins. Entomopathogenic bacteria consist of *Serratia, Burkholderia*, *Chromobacterium*, *Streptomyces, Saccharopolyspora*, *Yersinia* and *Pseudomonas* species. Groups of entomopathogenic fungi (EPF) mainly include *Beauveria* (Vuillemin), *Trichoderma, Metarhizium* (Metschnikoff)*, Isaria* (Wize), *Hirsutella, Verticillium* (Zimm.)*, Lecanicillium* and *Paecilomyces.* EPF acquire an important place as a biocontrol agent under IPM because of their large host range, path of pathogenicity and capability to manage both insect pests having a chewing type of mouth parts as well as sucking type of mouth parts (Khan et al. 2012). Among viruses, baculoviruses have the insect-killing properties. Two genera of entomopathogenic nematodes (EPNs) were also reported to have insecticidal properties. These are genus *Heterorhabditis* and *Steinernema.* Both of these genera have a symbiotic association with bacteria *Photorhabdus* and *Xenorhabdus* (Koul 2011; Ruiu 2018). Entomopathogenic microbiomes in general are eco-friendly, more suitable, specific, cheaper and do not show any harmful effect on the non-targeted organisms and human health as well (Rekha et al. 2020; Yadav et al. 2018). The reason behind their use is that they are capable of living in the natural environment. So they are much better adapted than conventional insecticides. Development of new effective biopesticides will lead to reduced trust on chemical synthetic pesticides in

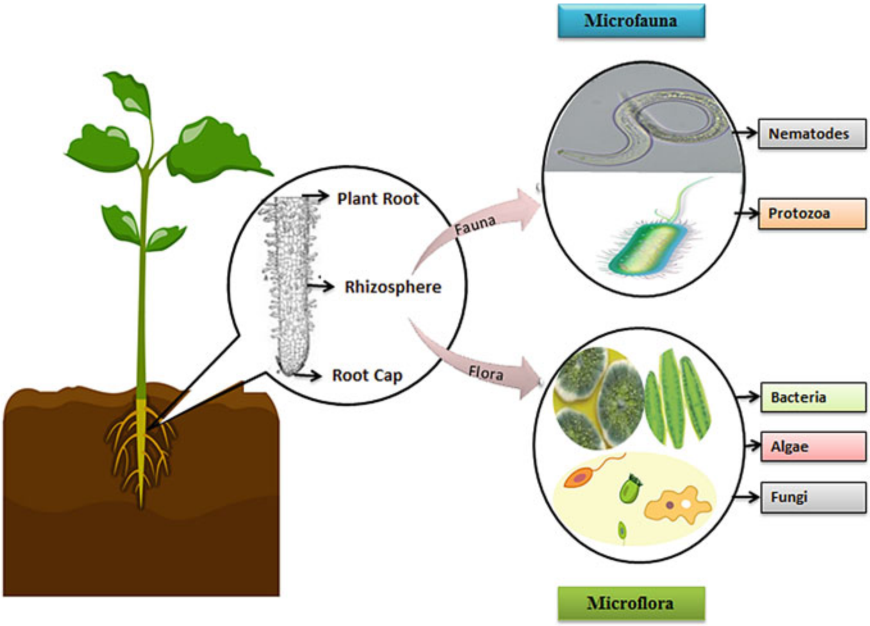


Fig. 17.1 Rhizospheric microbiome present in the soil, Mendes et al. (2013)

this manner decrease crop protection cost by farmers, at the same time as benefiting the public health and environment.

Rhizosphere is the portion of soil, which is directly in touch with plant roots. Lorentz Hiltner in 1904 gave the term rhizosphere (rhiza: root and sphere: area of influence). This region of soil is concentrated with diverse groups of microorganisms (Hartmann et al. 2009; Kour et al. 2019) (Biswas et al. 2018; Singh et al. 2020; Yadav 2021). Flora and fauna are the two important groups of organisms having macro and micro soil-inhabiting organisms (Fig. 17.1). Nearly 10^{11} microbial cells along with more than 30,000 prokaryotic organisms have been found near the marginal area of the soil (Mendes et al. 2013).

17.2 Background of Entomopathogenic Microbes

Entomopathogenic microbes are the organisms that are pathogenic to insect pests. These organisms have the capability of killing the insect pests and are now used as biocontrol agents in IPM. Entomopathogenic microbes include bacteria, fungi, viruses, nematodes and protozoa. Entomopathogenic bacterial use for the killing of insects starts in the 1960s. Goldberg and Margalit (1977) discovered the pathogenic effect of *B. thuringiensis* against the larvae of dipterans (De and Barjac 1978). In 1800s, the existence of EPF has been studied in silkworm industries of France.

Agostino Bassi (1773–1856) reported that in silkworms, muscardine disease is caused by *Botrytis bassiana* (*Beauveria bassiana*). The idea of using fungus for the management of insects strikes from the study of diseases in silkworm industry. During this study, it was observed that fungus is not only killing silkworms but also virulent to other insects (Ainsworth 1956; Audoin 1837). Elie Metchnikoff (1845–1916) reported *Entomopthora anisopliae* (*Metarhizium anisopliae*) as disease-causing agent in wheat cockchafers in Russia. This fungus is also used for the control of weevils in sugarbeet (Krassilstschik 1888). Pasteur (1874) and LeConte (1874) also proposed the insecticidal properties of fungus. Steiner found the first insect-killing nematode *Aplectana kraussei* in 1923, which is now regarded as *Steinernema kraussei*. *Neoaplectana glaseri* Steiner (1929) isolated as the second entomopathogenic nematode by Glaser and Fox (1930). These discoveries are not gaining people's attention toward the pathogenicity in insects until *Neoaplectana carpocapsae* and DD-136 strain were isolated from the larvae of codling moth (Dutky and Hough 1955; Weiser 1955). Nematodes have a symbiotic association with bacteria, families Steinernematidae are symbiotically associated with *Xenorhabdus* genus of bacteria and bacterial genus *Photorhabdus* is symbiotically associated with family Heterorhabditidae (Akhurst and Boemare 1990; Boemare 2002). Due to this mutualistic association, nematodes are regarded as effective biocontrol agents.

17.3 Entomopathogenic Microbes

17.3.1 Entomopathogenic Bacteria

Bacteria are prokaryotic (without nucleus), single-celled organism, neither animal nor plant, few micrometers in their length and exist in communities of millions. One gram of soil contains approximately 40 million and one milliliter sample of freshwater also holds about 1 million bacterial cells. Dormant survival cells (spores) are produced by few bacterial cells as mentioned below (Fig. 17.2).

Bacterial populations pathogenic to insect pests can cause major damage to the target insect population (Lacey et al. 2001) and are known as entomopathogenic bacteria. These single-celled bacteria are very minute, primitive creatures of approximately 1 μm to several μm in size. These rod, spiral and cocci-shaped bacteria possess inelastic cell wall. Some bacteria lack cell walls and showing variability in their morphology. There are more than 100 species of bacteria, found to be pathogenic to insect pests. Among the entomopathogenic groups of bacteria *Bacillus thuringiensis* (Abtew et al.), *B. popilliae*, *B. Sphaericus* and *B. cereus* are used as biocontrol agents nowadays. Families of bacteria having the properties of pathogenesis comprise Bacillaceae, Enterobacteriaceae, Micrococcaceae, Pseudomonadaceae and Streptococcaceae (Fig. 17.3).

Some of these bacterial families are highly lethal to the various insect pests. Among these virulent families, Bacillaceae contain the genus *Bacillus* having *B.*

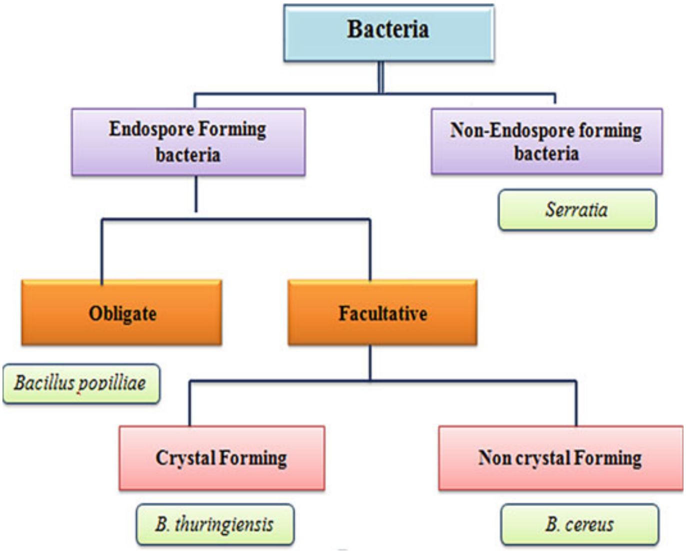


Fig. 17.2 Classification of entomopathogenic bacteria

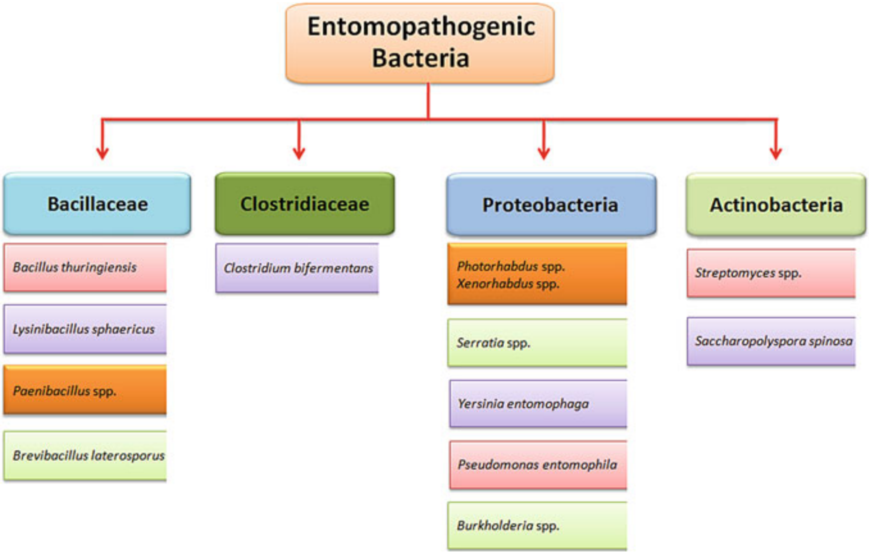


Fig. 17.3 Different species responsible for causing pathogenicity in various insects

popilliae species, which is responsible for causing the milky spore disease in the scarab beetles. Even one more species *B. sphaericus* is highly infectious to mosquitoes. Pathogenicity of *B. thuringiensis* is also well known. They are virulent against a wide range of insect pests mainly lepidopterans and are world widely distributed as biocontrol agents. Even there are more than 40 commercial formulations of *Bt* are available in the market accounting for 1% of total global insecticide productions (Evans 2008). As the bacterium enters inside the host body through spore consumption, it produces cry proteins having δ-endotoxins, which are responsible for the death of the insect. These δ-endotoxins communicate with the receptor in the epithelium cells of insect midgut and form crystal-like inclusions (Pigott and Ellar 2007). *Lysinibacillus sphaericus* cause injury to the epithelial microvilli in the midgut of the insect (Charles et al. 2000). *Paenibacillus larvae* causing pathogenicity in honey bee colony and are responsible for causing American Foulbrood (AFB), a destructive disease (Davidson 1973). Ruiu (2013) reported the pathogenic effect of the *Brevibacillus laterosporus* on a wide range of antimicrobial communities as well as on some invertebrate species. They show their pathogenic effect against different insect orders namely Lepidoptera, Diptera and Coleoptera. They are also injurious against bacteria, fungi, nematodes and molluscs. *Clostridium bifermentans* is highly pathogenic against black flies and mosquitoes as it has Cbm71 protein showing a similar effect like delta endotoxins of *B. thuringiensis* (Barloy et al. 1996; Nicolas et al. 1990).

Endosymbionts *Xenorhabdus* and *Photorhabdus* bacteria also live in mutual symbiotic association with nematodes of genera *Steinernema* and *Heterorhabditis*. As the nematode gets entered into the insect body, it releases the bacteria inside hemocoel. The bacteria then release insect-killing toxin as well as antimicrobial substances that have high efficacy against insect pests and other developing microorganisms (Waterfield et al. 2001).

Serratia species also produce enzymes such as lipases, chitinases and proteases that show insecticidal properties (Kwak et al. 2015). Serious damage to the cells of the gut has been caused by *Pseudomonas entomophila* that infects the insect larvae through oral path. Post ingestion responses of immune system have been observed in an experiment over *Drosophila melanogaster* (Vodovar et al. 2005). *Burkholderia* spp. lives in mutual association with some insects in their gut region and their effect on the egg-laying capacity has been observed in bean bugs (Kil et al. 2014; Kim et al. 2013; Martinson et al. 2011). Cordova-Kreylos et al. (2013) discovered a new species *B. rinojensis* and reported their insecticidal properties. Insecticidal effect of a strain of *Chromobacterium* spp. has been reported on different insects including *Aethina tumida, Bemisia tabaci, Diabroticaundecim punctata, Plutella xylostella, Leptinotarsa decemlineata* and *Nezara viridula* (Martin et al. 2007a,b). *Streptomyces* spp. produces substances like antimycin A, flavensomycin, macrotetralides, piericidins and prasinons, which are toxic against insect pests (Box et al. 1973; Craveri and Giolitti 1957; Kido and Spyhalski 1950; Oishi et al. 1970; Takahashi et al. 1968).

Avermectins produced by *Streptomyces avermitilis* shows its effect on the gamma-amino butyric acid (GABA) receptor present on the peripheral nervous system of insect, which inhibits the neurotransmission and results in neuromuscular paralysis

Table 17.1 List of some biopesticides produced by entomopathogenic bacteria

Bacterial species	Commercial formulations	Target species
Bacillus thuringiensis subsp. *israelensis*	Tacibio Technar	Lepidopteran pests Fungus gnats
Bacillus thuringiensis subsp. *kurstaki*	Bio-Dart Biolep Halt Taciobio-Btk	Lepidopteran pests
Bacillus subtilis		Soil-borne pathogens
Bacillus firmus	Bacillus firmus I-1582 WP5	Nematodes
Pseudomonas fluorescens	ABTEC Pseudo Biomonas Esvin Pseudo Sudo Phalada 104PF Sun Agro Monus Bio-cure-B	Plant soil-borne diseases

(Bloomquist 1996; Turner and Schaeffer 1989). Insecticidal spinosyn-A derived from *Saccharopolyspora spinosa* is highly effective against dipterans and lepidopteran insect pests (Kirst 2010; Mertz and Yao 1990) (Table 17.1).

17.3.2 Entomopathogenic Fungi

A fungus is a eukaryotic organism that absorbs nutrients directly and digests food externally via cell wall. Among the biocontrol agents, entomopathogenic fungi (EPF) were the earliest known for pest control (Fig. 17.4). About 90 genera of EPF contain more than 700 species having insect-killing properties (Khachatourians and Sohail 2008). Samson et al. (1988) reported that the Zygomycota, Ascomycota and Deuteromycota contain the fungal pathogens having insecticidal properties. Roy et al. (2006) classified the EPF into two divisions.

It is reported from the earlier studies that more than 500 fungal species are responsible for insect pathogenicity. Some of them are *Beauveria, Entomophthora, Metarhizium, Neozygites, Nomuraea* and *Verticillium* (Deshpande 1999). EPF attain a greater position amongst the biocontrol agents due to its lethal nature against various pests in field conditions. They are used against both insect pests those having chewing type of mouth parts as well as against sap-sucking insects. The route of infection by EPF completely differs from the other microbial biocontrol agents. After breaking the host cuticle, they entered into the hemocoel and causing pathogenic effects. Chitin, proteins and fatty acids are the three major components of insect cuticle. Degradation starts with the secretion of cuticle degrading enzymes mainly chitinase, lipase and protease (Khan et al. 2012). The severity of pathogenesis by EPF depends upon several factors discussed below (Fig. 17.5) (Boucias et al. 1998).

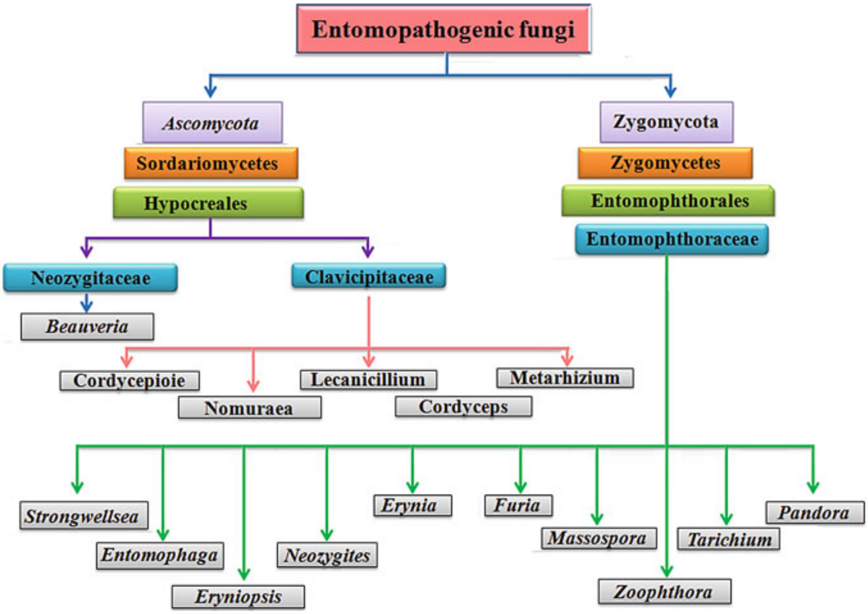
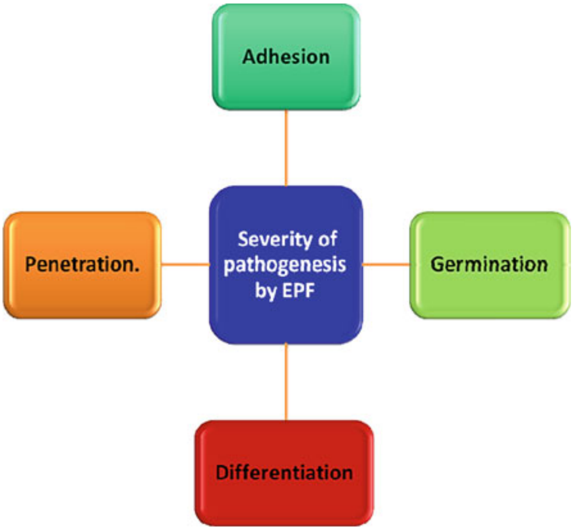


Fig. 17.4 Classification of entomopathogenic fungi

Fig. 17.5 Extremity of pathogenesis by entomopathogenic fungi



Inside the host integument, adherence and penetration power are the primary steps of a successful infection (Shahid et al. 2012). The major fungal biocontrol agents include *Metarhiziuma nisopliae, Beauveria bassiana, Isaria fumosorosea* and *Lecanicillium. M. anisopliae* was reported to be the most effective biological control agent and is applied against beetles, termites, spittlebugs and locusts (Bischoff et al. 2009). A naturally occurring entomopathogen is *B. bassiana*, which has been used against many arthropod pests. This microbial biopesticide shows a significant effect against the orthopterans and lepidopterans (Charnley and Collins 2007; Faria and Wraight 2007). Among fungus as an insecticide (mycoinsecticides), *B. bassiana* and *M. anisopliae* contribute 33.9% and *Isaria fumosorose* contributes 5.8% while *B. brongniartii* contributes 4.1%, respectively (Faria and Wraight 2007) (Table 17.2).

17.3.3 Entomopathogenic Viruses

A biological agent that has an extraordinary capacity to reproduce inside the living cell is known as virus (Dimmock et al. 2016). Genes having DNAand RNAare the core elements of virion particle, which are enclosed in protein coat called capsid. Insect-specific viruses are mainly responsible for causing high pathogenicity in the caterpillar's stage of several insects. Insects acquire infection by the consumption of virus particle whereas infection from one insect to other is transmitted during mating and ovipositioning. A number of plant pests have been destroyed by rod like target-specific baculoviruses. They are also responsible for causing mortality in the lepidopteran insect pests of cotton, rice and vegetables (Nawaz et al. 2016). Baculoviruses as a successful pest controlling agent were accidentally introduced before World War II. Among 73 known families of viruses, 13 Baculoviridae families belong to entomopathogenic viruses (Murphy et al. 1995). These 13 families show high pathogenicity against Diptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera and Orthoptera. *Nucleopolyhedrovirus* (NPV) and *Granulovirus* (GV) are the two genera of family Baculoviridae (Murphy et al. 1995). In India, the population of *Helicoverpa* spp. and *Spodoptera* spp. was controlled using *Nucleopolyhedroviruses* (NPV) in citrus, cotton, cocoa, maize, groundnut, legumes, sorghum potato, tobacco, tomato and other vegetables.

Bioinsecticide developed from the NPV is a substitute in place of chemical pesticide and is the best option for the control of insects that become resistant to chemical pesticides. Resistant insect populations of *Helicoverpa zea* and *Helicoverpa armigera* were destroyed using NPV-based bioinsecticides (Kranthi et al. 2002). Bioinsecticides developed from 26 baculoviruses are being employed for the management of Hymenopteran as well as Lepidopteran insect pest population worldwide (Lacey et al. 2015). Production of NPVs for commercialization is done under small cottage industries and under commercial units of medium size in India (Rao et al. 2015). In Hyderabad at International Crop Research Institute for Semi-Arid Tropics (ICRISAT), training has been provided to the farmers for the production of *Helicoverpa armigera* nucleopolyhedrosis virus (HaNPV). The crude extract than filtered

Table 17.2 List of some commercially available biopesticides derived from entomopathogenic fungi

Fungal Strain	Brand	Country	Target organism
Aschersonia aleyroides			Whitefly
Beauvaria brongniartii	Betel	France	Scarab beetle larvae
B. bassiana	Mycotrol WP, Naturalis L, Myco-Jaal, Conidia	USA, India, Germany	Whiteflies/thrips/aphids/white grub, Diamonback moth, Coffeeberry borer
Conidiobolus thromboides	Vektor 25SL	South Africa	Aphids/Thrips/ Whiteflies
Hirsutella thompsonii	Mycohit	India	Acari
Isaria fumosoroseus	Pae-Sin, PFR-97	Mexico USA	Whiteflies
Lecanicillium longisporum	Vertalec	Netherlands	Aphids
L. muscarium	Mycotal	Netherlands	Whiteflies/Thrips
Lagenidium giganteum	Laginex	USA	Mosquitoes
Metarhizium anisopliae	Metaquino, Bioblast, DeepGreen	Brazil, USA, Colombia	Spittle bugs, Termites, White grub
M. anisopliae var. acridum	Green Muscle	South Africa	Locust, Grasshoppers
M. flavoviride	Biogreen	Australia	Scarab larvae
M. anisopliae + *B. bassiana* + *I. fumosoroseus*	Tri-Sin	Mexico	Psyllid
Nomuraea rileyi	Numoraea 50	Colombia	Lepidoptera

(Copping (2004); Kabaluk and Gazdik (2005); Khachatourians (1986); RL (2014); Zimmermann (2007)).

out and is applied over the field. In India and Nepal, NPV production units were established in 96 villages so that rural farmers get benefits from them (Ranga Rao et al. 2007). Although GV is not available for marketing in India but still during research, it was found that they are very effective for the management of *Chilo infuscatellus* in sugarcane (Rao and Babu 2005). Jayanth (2002) also demonstrated that they are effective for the management of diamondback moth larvae (Table 17.3).

Table 17.3 List of some commercially used entomopathogenic viruses along with their target organism

Types of virus	Target organism
Cytoplasmic polyhedrosis virus	*Helicoverpa armigera*
Nuclear polyhedrosis virus	*Amsacta albistriga, Antheraea mylitta, Corcyra cephalonica, Dasychira mendosa, Helicoverpa armigera, Plusia peponis, Pericallia ricini, Pseudaletia separate, Plusia chalcites, Spodoptera litura, Spilosoma obliqua,* *Spodoptera mauritia*
Pox virus	*Amsacta moorei*
Granulosis virus	*Achaea janata, Cnaphalocrocis medinalis*, *Chilo infuscatellus* *Pericallia ricini* and *Phthorimaea operculella*

17.3.4 Entomopathogenic Nematodes

Nematodes are worm-like unsegmented invertebrate organisms that are distributed worldwide. They exhibit a huge range of habitats like soil, water (fresh as well as marine), plants and animals. Hugot et al. (2001) illustrated that nematodes exhibit more than 25,000 spp. among which terrestrial and free-living forms possess 10,000 spp., vertebrate parasitic forms include 12,000 spp. and about 3,500 spp. are parasitic to the non-chordates. Entomopathogenic nematodes (EPNs) are the microscopic worms that have the ability to kill insects. Entomopathogenic nematodes belong to order Rhabditida and families Heterorhabditidae and Steinernematidae present naturally in soil habitat and find their host via signal responses (chemical and physical) (Shapiro-Ilan et al. 2012). Both of these families have species, which have been successfully used as bioinsecticides in pest management programs (Ehlers and Shapiro-Ilan 2005) as they are known to be non-pathogenic to humans and are highly specific to their host (Shapiro-Ilan et al. 2006). Rao and Manjunath (1966) first demonstrated DD-136 strain of *Steinernema carpocapsae* in India for the management of lepidopteran insect pests of apple, rice and sugarcane. Exotic strains of *Heterorhabditis bacteriophora* and *S. carpocapsae* were sold in the market with the trade names ‘Soil Commandos’ and ‘Green Commandos’. These exotic strains were applied for the management of root pests as well as against several foliar insect pests. Survey on indigenous EPN species was done and the EPN strains of mainly *H. bacteriophora, H. indica* and *S. carpocapsae* were found to be effective against various soil-dwelling insects pest under field conditions at ICAR-NBAIR, Bengaluru (Sankaranarayanan and Askary 2017). Kalia et al. (2014) first reported the pathogenicity of *S. thermophilum* towards the eggs of lepidopteran insects at IARI, New Delhi (Table 17.4).

Table 17.4 List of some entomopathogenic nematodes used as biological control agents

EPNs species	Target insects
H. bacteriophora	Cutworms, flea beetles, black vine weevil, citrus root weevils, white grubs, corn rootworm,
H. indica	Grubs, fungus gnats, root mealybug
H. zealandica	Scarab grubs
H. megidis	Weevils
H. marelatus	Black vine weevil, cutworms, white grub
S. kraussei	Peach tree borer, black vine weevil, shore flies
S. scapterisci	Mole crickets (*Scapteriscus* spp.)
S. glaseri	Black vine weevil, banana root borer, white grubs
S. feltiae	Shore flies, fungus gnats (*Bradysia* spp.), western flower thrips
S. riobrave	Mole crickets, citrus root weevils
S. carpocapsae	Armyworms, billbugs, banana moth, cutworms, chinch bugs, codling moth, crane flies, cranberry girdler sod webworms, dogwood borer

17.3.5 Entomopathogenic Protozoan

Single cellular, eukaryotic organisms having nucleus is protozoan. They show variability in their size and shape. Very little interest has been given to the entomopathogenic group of protozoans. A highly diverse group of entomopathogenic protozoans contain about 1000 protozoan species called microsporidians, which attacks arthropods and other invertebrates (Brooks 1988). There are some protozoa that cause pathogenicity in several arthropods include *Nosema*, *Theileria*, *Haemogregarina* and *Babesia*. *Nosema locustae* cause mortality in cricket and grasshopper, European corn borer was managed by *Nosema pyrausta*. Population of fall webworm, armyworm, cabbage looper and corn earworm were killed by *Vairimorpha necatrix* (Hoffmann and Frodsham 1993; Tanada and Kaya 1993; Weinzierl and Henn 1989). *Nosema fumiferana* is the only species of microsporidium that is responsible for causing up to 70% of infection in spruce budworm (Wilson 1982).

17.4 Entomopathogenic Microbes and Their Modes of Action

The entomopathogenic microbes are insecticidal in nature and have specific foraging strategies as well as mode of action. The mode of action of different entomopathogenic microbes viz entomopathogenic bacteria, fungi, nematode and virus is explained with the help of the following figures (Figs. 17.6, 17.7, 17.8, 17.9).

The process of pathogenesis initiates with the attachment of pore to the larval body and is a series of developmental changes within the body of host. The fungus

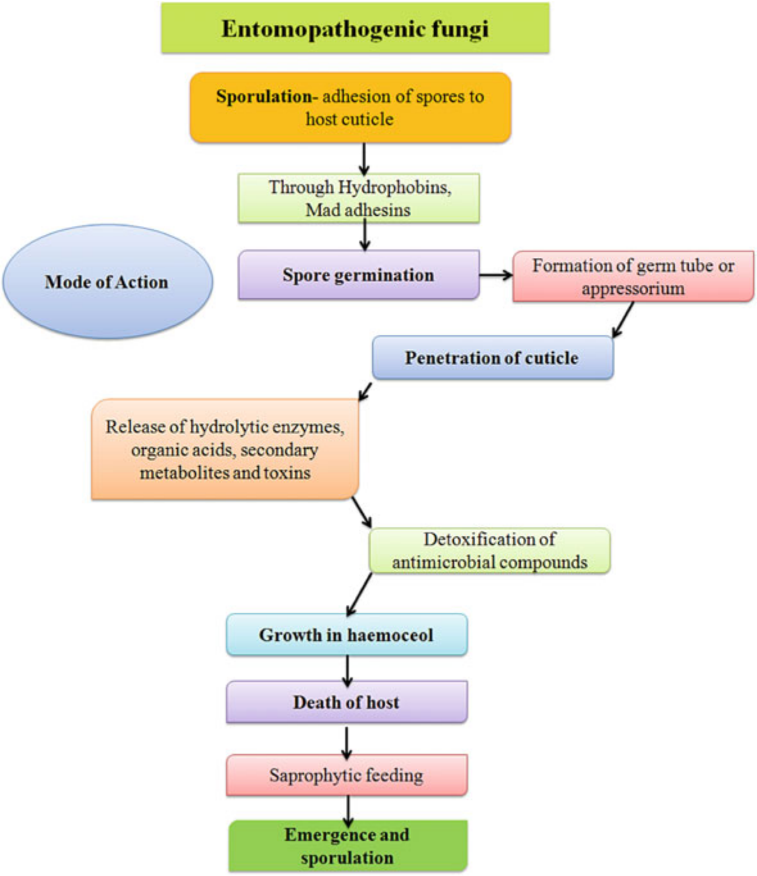


Fig. 17.6 Mechanism of action by entomopathogenic fungi

exhibits the cuticle degradation and formation of appressorium hydrophobins. The death of host insect is caused by toxins production by fungus and the host tissue destruction (Hasan 2014).

The δ-endotoxins are produced throughout sporulation by the bacteria and their ingestion by the larval stage results in toxicity. The toxins cause severe damage to the tissues and end in gut paralysis. The lepidopteran larva dies in the end due to starvation (Zhu et al. 2000).

The first-generation juveniles of *Heterorhabditis* are hermaphrodites (Smart 1995), whereas in Steinernematids, they are amphimitic in nature. In case of hermaphrodite of *Heterorhabditis*, the eggs hatch inside the uterus and feed on maternal tissue leading to intrauterine birth with the death of mother. This phenomenon is usually triggered by the presence of less number of adults in the internal environment and is called endotokia matricida.

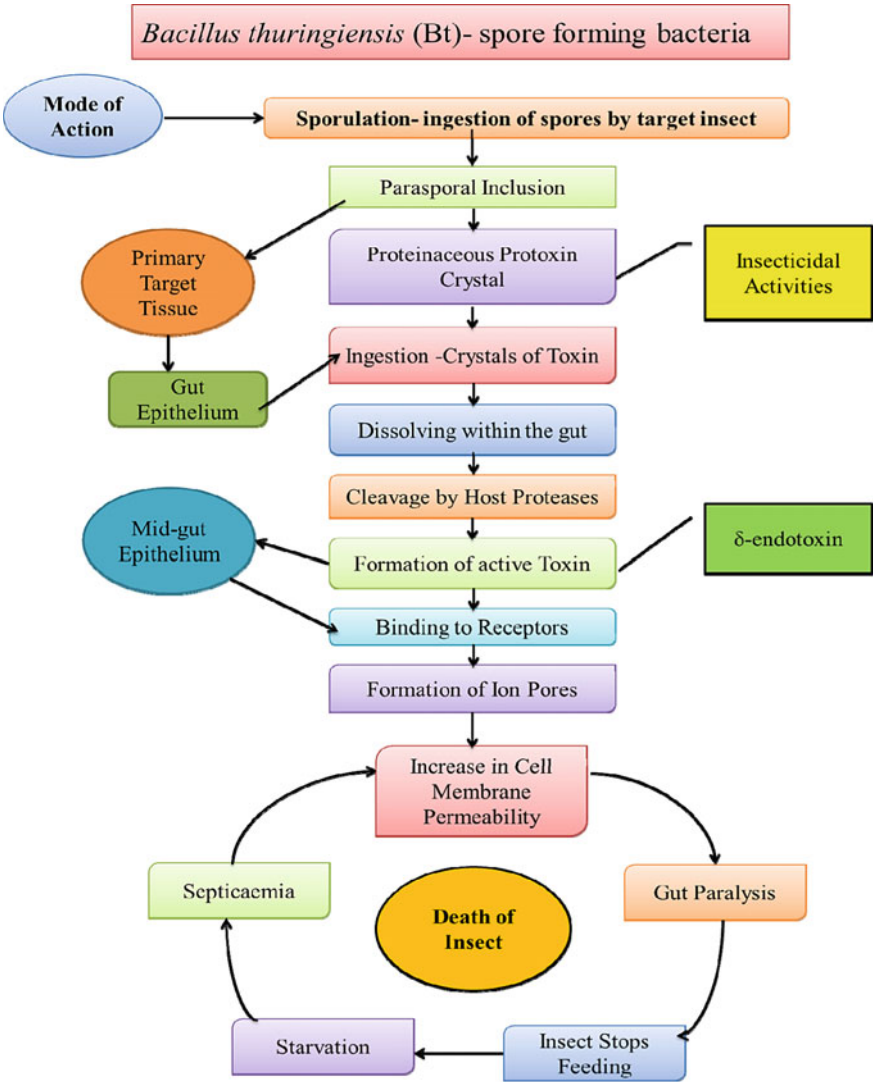


Fig. 17.7 Mechanism of action by entomopathogenic bacteria

17.5 Mass Production of Entomopathogenic Microbes

17.5.1 Mass Production of Bacteria

Different types of methods have been used for mass production of sufficient bacteria, which are given below:

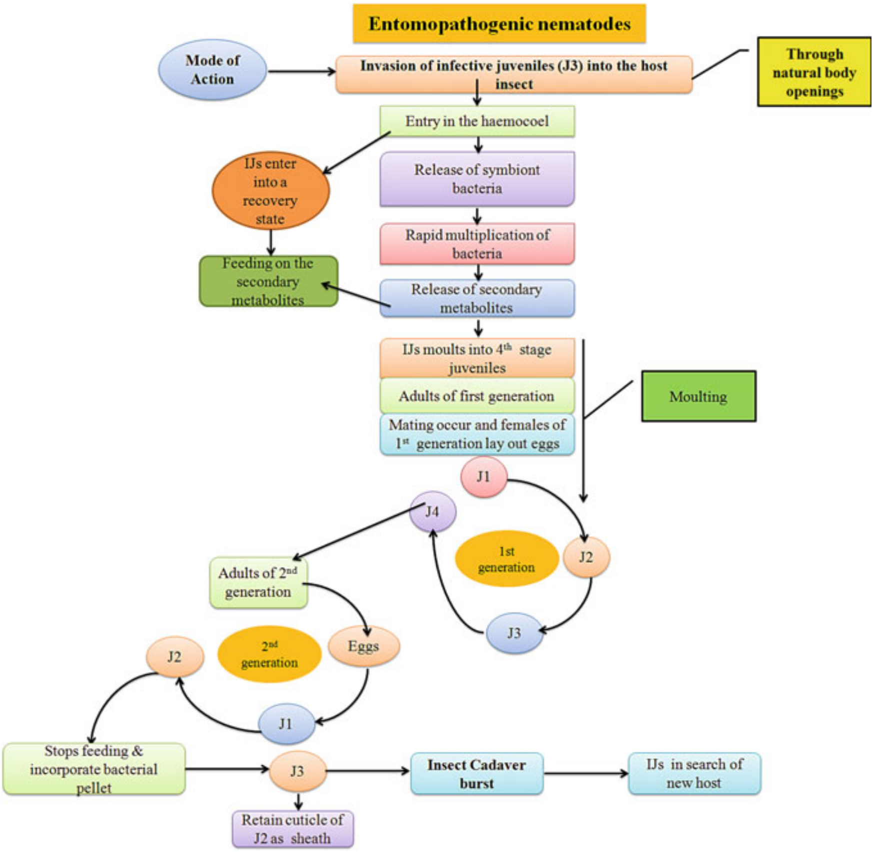


Fig. 17.8 Mechanism of action by entomopathogenic nematodes

- In vivo production
- Solid substrate fermentation
- Liquid fermentation
- Objectives of fermentation for spore-forming and non-spore-forming bacteria.

17.5.1.1 In Vivo Production

To control the population of Japanese beetle, *Popillia japonica* for the first time bacterium *Paenibacillus* (*Bacillus*) *popilliae* was registered in the USA (Klein 1992). This bacterium caused milky disease in the larvae of the beetle and the in vivo method of production was elaborated by Fleming (1968) and defined by the hands of Koppenhöfer et al. (2012). Till today, this in vivo production of milky spore powder is in use for control of insects in the home lawn and organic markets (Stahly and Klein 1992).

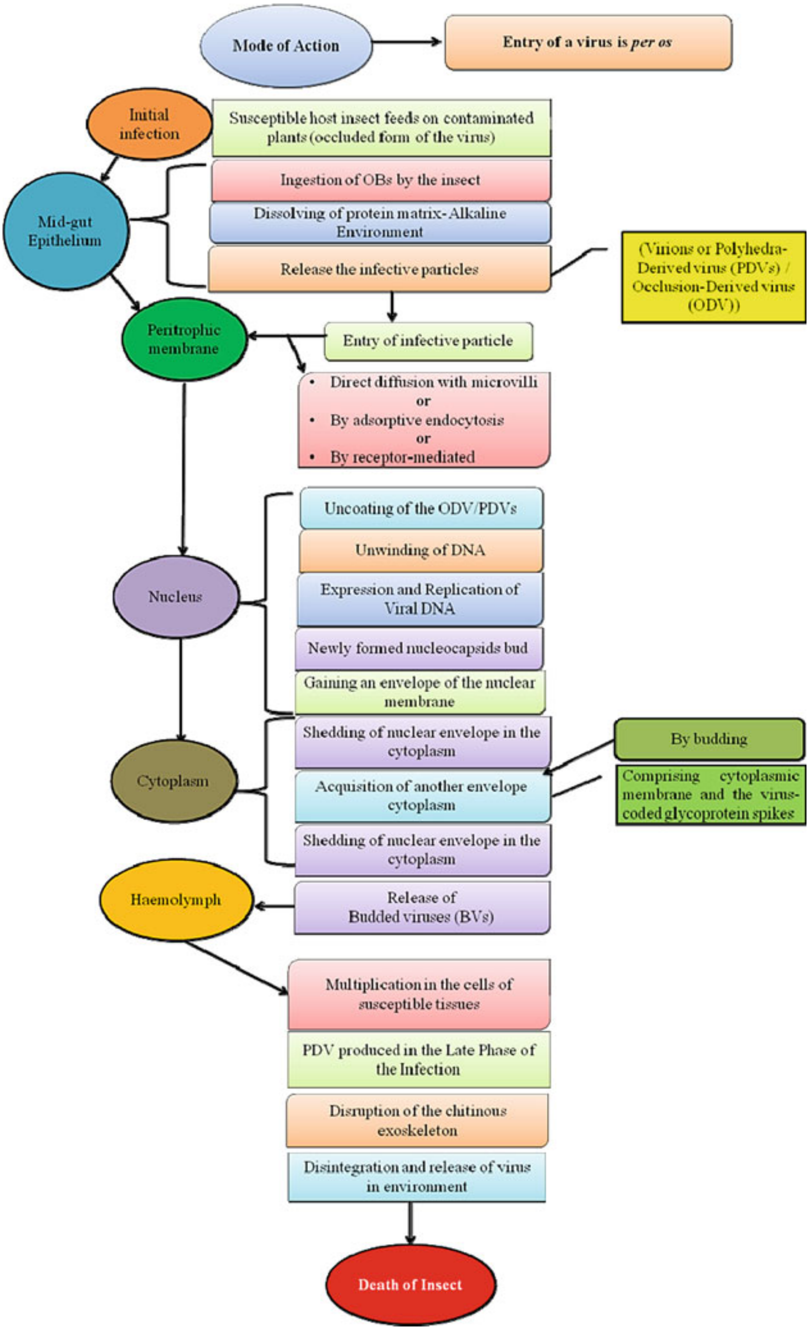


Fig. 17.9 Mechanism of action by entomopathogenic viruses

Solid substrate fermentation (SFF)

In the production of microorganisms, the solid substrate generally contains porous material amended with nutrient and moistened grains. For solid substrate fermentation, mainly grains are used as a fine medium for the production of microorganisms in the F & B industries. When there is no water, the process of SFF involves moist solid substrate for the production of mycoinsecticides, fermented enzymes and food (Mitchell et al. 2009).

Liquid fermentation

Liquid fermentation is the most common method used for the mass production of bacteria. This method can be modified for its use in the laboratory to large-scale commercial massive production according to the requirement. In this biomass of cells, some other secondary products from the soluble nutrients are produced. For the growth of bacteria—carbon, nitrogen, other trace elements are suspended in water and desired strain is obtained after undergoing the process of sterilization and inoculation. Bacterial cell growth can be described in four stages later inoculation. These stages are—lag, log, stationary and death stage.

In **Lag stage—**the adaption of cell to physiochemical environment with slight replication occurs. In **Log stage—**the development and splitting of cell in exponential manner occur. In **Stationary stage—**the cell growth is halted or dawdles due to the accumulation of toxic metabolites on substratum. In **Death stage—**due to exhaustion of energy reserves the cell or the culture dies.

Liquid fermentation of Non-spore-Forming Bacteria and Spore Forming

The aim of fermentation is to produce an active ingredient for biopesticide production. The method of fermentation is different for non-spore and spore-forming bacterial production. In the case of spore-forming bacteria e.g. *Bacillus thuringiensis*—the most important step is the yield of toxin, for non-spore-forming bacteria e.g. *S. entomophila*—the development of a maximum of living cell in the fermenter. Visnovsky et al. (2008) first introduced the liquid fermentation of non-spore-forming bacterium, *S. entomophila.* The bacterium develops on carbohydrates rather than proteins. For the improvement of fed batch method, yeast extract can be used for enhancement of cell yield. Classical batch fermentation for *S. entomophila* is carried out at 30 °C, aerated to sustain dissolved oxygen levels less than 20%, and completed in 26–28 h as soon as the fermentation is well developed in the stationary growth stage. A fully developed fermentation will generate a cell yield of less than 5×10^{10} CFU/mL corresponding to less than 30 g/L dry weight of cell (Jackson 2017). The development of Bt occurs through batch fermentation with a sir feed of less than one volume of air per volume of liquid per minute and primary concentration of glucose of 18 g/L (Couch and Jurat-Fuentes 2013). A kind of variance is shown by different strains of Bt on media in terms of toxin production and sporulation. This helps in the selection of strain from wild or cultured strain (Monnerat et al. 2004, 2007).

17.5.2 Mass Production of Fungi

The mass production of fungus regulates on a strategy that delivers stabilized, viable and virulent propagules in large numbers (Jackson et al. 2010). Certain parameters that need to be retained in mind while the mass production of the fungus. These parameters are:

1. Selection of fungal propagule development
2. Maintenance of culture
3. Sterility of the process
4. Nutrients composition and quality
5. Selection of strain.

17.5.2.1 Solid-State Fermentation

Production of aerial conidia by the method of solid-state or substrate fermentation is the primary method of current times. This method is used by the pilot scale to large industries. In this method, aerial conidia are the end product of down-streaming process. This process is known by other names such as solid-substrate fermentation and solid-state fermentation. This type of fermentation is simple but labor intensive in nature (Feng et al. 1994).

17.5.2.2 Liquid Fermentation

In most of the cases of entomopathogenic hypocrealean fungi, a pattern of dimorphic growth is observed in liquid media. This growth pattern resembles the developmental stages of fungus inside the insect hemocoel.

Types of liquid fermentation:

1. Submerged liquid fermentation (SLF)
   a. Blastospores
   b. Submerged (Microcycle) Conidia
   c. Microsclerotia
2. Aerial conidia by liquid surface fermentation (Jaronski and Mascarin 2017).

In SLF, the fungus is immersed in an aerated liquid medium, which is disturbed constantly. This disturbance leads to the formation of blastospores, microsclerotia or microcycle conidia. For the case of stationary liquid fermentation, the sporulation process occurs on a tranquil liquid. This produces aerial conidia and mycelium (Jaronski 2014). Submerged liquid fermentation scales up the production manifolds in terms of commercial availability and is less time-consuming than solid-state fermentation.

17.5.3 Mass Production of Nematodes

In the literature, the first record on mass culture of EPNs dates back to 1931 by Glaseri after discovery of nematodes infected Japanese beetles from the golf course, New Jersey (Glaser and Fox 1930). He also succeeded in the EPNs production on agar plates for the biological control of the Japanese beetle (Gaugler et al. 1992). In Australia, Commonwealth Scientific and Industrial Research Organization (CSIRO) was the first to control an insect pest using the EPN species S. *carpocapsae* (Divya and Sankar 2009). It was earlier commercially used to control few other species as the black vine weevil, *Otiorhynchus sulcatus* (Fabricius), the currant borer moth, *Synanthedon tipuliformis* (Clerk), in ornamentals and in black currants (Bedding and Miller 1981).

Bedding and Miller (1981) revealed that in the last 20 years, EPN production has seen a progressive upliftment. From commercial point of view, in vitro technology was utilized but in case of small-scale cottage setups, in vivo production has played an eminent role.

Smart (1995) and Ehlers and Shapiro-Ilan (2005) utilized the technique of in vivo and in vitro technology for culturing of EPNs. They attained the desired result by innoculatin, a suitable host with specific virulent strain. EPNs can be easily reared for field trials and laboratory culture using as bait insect. This work is a bit labor intensive but serves the purpose well in research laboratory. Georgis et al. (2006) compared the two mass-production technologies and concluded that in vitro production as far more programmed, less labor oriented, with advanced technology as well as capital, therefore most suitable for commercial production. A number of commercial EPN products are available in the American, European and Asian markets nowadays for environmentally favored suppression of insect pests.

For culturing of EPNs, certain factors may be kept in mind to avoid any hindrance. These factors are temperature, humidity, applied concentration, host density and method of inoculation (Woodring and Kaya 1988). It is estimated that the EPNs obtained from inoculation in insects are of greater quality and virulence (Grewal et al. 1994; Shapiro-Ilan et al. 2002).

In vivo mass production optimizes the White trap method given by White (1927) and was later on reconstructed by Dutky et al. (1964). The redescription of the method was given by Poinar (1975) and a modification in it by Kaya and Gaugler (1993). In this method, IJs emerge out from insect cadaver in the water after bursting. This water containing the IJs is harvested and IJs are recovered from it (Gokte-Narkhedkar et al. 2008). The most favorable host for EPN mass production is the greater wax moth and rice moth. Other susceptible hosts are silkworm, root grub, cotton bollworm and armyworms (Flanders et al. 1996) (Ali et al. 2008). Georgis and Kaya (1998) for the first time formulated EPN product in 1979 with a shelf life of 30 days.

17.6 Genetic Improvement in Entomopathogenic Microorganisms

Genetic perfection of entomopathogenic microbiomes can conquer the delimitations of easily available microbial pesticides. Biotechnology gifted us unique gene resources and tools to integrate them with genetically improved variety. The concept of cross-species genetics (genetic variation among the species that are going to be extinction results in a superior population) has unwrapped new gates for boundless opportunity (HS 2018). In order to grow and keep feasible bioprocesses, microbial stains are required that can be able to tolerate different hassles for maintaining high productivity and yield. Microbial strains require constant genetic fortification for keeping or achieving high production. As we are aware that the wild strains have very a low production rate but contain desirable characteristics that are required in biotechnological applications. Thus, different strategies have been applied to genetically improve microorganisms to solve problems and directly or indirectly to increase productivity and consequently the profitability of the bioprocess (Paes and Almeida 2014). The improvement of product formed by microorganisms requires four key factors, which are: (i) enhance tolerance against toxic compound, (ii) driving carbon flux, (iii) raise in substrate uptake and (iv) generation of novel products.

In this era, integrated approach and synthetic chemical pesticide-free farming are in trends to deal with agricultural crop pests. The use of entomopathogenic microbes such as fungi (*Beauveria* and *Metarhizium*), bacteria (*Bacillus thuringiensis* Bt), viruses (Nuclear polyhedrosis virus) and nematodes (*Steinernema* spp. and *Heterorhabditis* spp.) is gaining the prominent position in biocontrol methods. We can say that the above-mentioned microbes provide a better alternative against chemical pesticides (Vurro and Gressel 2007). Now a day in agriculture, various tools are engaged for the genetic enhancement of entomopathogenic microbes using protoplast fusion, vector-mediated transformation, electroporation, biotransformation etc. (Fig. 17.10).

17.6.1 Protoplast Fusion

The word protoplast mainly refers to the algal, fungal and bacterial whose outer cell wall removed, either mechanically or enzymatically and may be accomplished by definite lytic enzymes (Verma et al. 2000). This fusion has occurred as a result of physical phenomenon in which two or more protoplasts come together either in the presence of fusion agents or spontaneously. In plant cells, spontaneous protoplast fusion has also been recorded (Usui et al. 1974). This fusion is a flexible method to induce or to support genetic recombination among various eukaryotic and prokaryotic cells (Bhojwani et al. 1977). It is a significant tool used in gene manipulation, as it breaks down the barriers to genetic swap forced by traditional mating systems results in the production of even intergeneric or inter-specific hybrids. This technique has

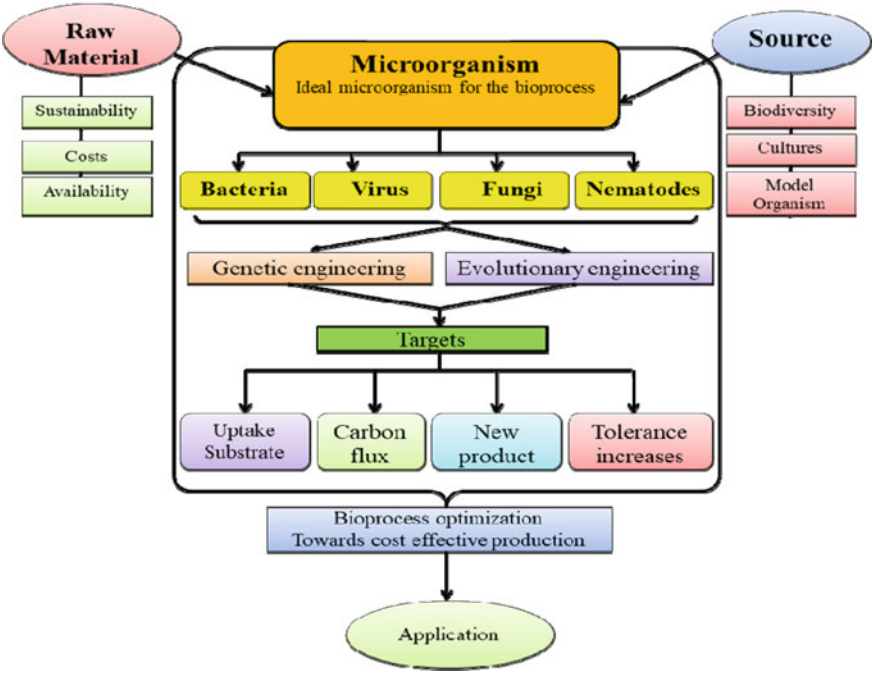


Fig. 17.10 Genetic improvements in entomopathogenic microorganisms Kotnik et al. (2015)

huge potential for genetic study in stain enhancement and is mostly used against microorganisms (Muralidhar and Panda 2000). It is feasible to transfer few valuable genes viz; nitrogen fixation, disease resistance, high product formation, herbicide resistance, frost hardness, drought resistance, rapid growth rate, protein quality, cold and heat resistance from one particular species to another through protoplast fusion. Genetic recombination technique has been prepared by joining the genes extracted from different strains of living beings (organisms) to get ideal possessions of the organisms (Fowke et al. 1979; Lee and Tan 1988).

17.6.1.1 Methods of Protoplast Fusion

Protoplast fusion is classified into two main categories:

- Spontaneous fusion
- Induced fusion.

Spontaneous fusion:

Protoplast at some point in isolation commonly fuses spontaneously and this naturally occurring phenomenon is known as spontaneous fusion. At the time of enzymatic treatment, protoplasts from adjacent or nearby cells combine together by their plasmodesmata and result in multinucleate protoplasts.

Induced fusion

Fusion of freely inaccessible protoplasts obtained from dissimilar sources by using fusion inducing agents (chemicals) is generally called as induced fusion. Typically protoplast is not able to fuse with one another due to the presence of negative charge in the region of outer plasma membrane (-10 to -30 mV). Due to these same charges, protoplast has the affinity to resist each other. Thus, this particular type of fusion also needs chemicals that really overcome the presence of electronegativity in the inaccessible protoplast and permit them to mingle or fuse (Narayanswamy 1994). Isolated protoplast may be encouraged to fuse in three different ways:

- Mechanical fusion
- Chemo fusion
- Electrofusion.

Mechanical fusion

In this process, isolated protoplast is brought together mechanically into an intimate physical contact under the microscope by using perfusion micropipette or micromanipulator.

Chemo fusion

Several chemicals have been used for the induction of protoplast fusion viz; polyethylene glycol, sodium nitrate and calcium ions (Ca++). Chemical fusogens are responsible for isolated protoplast to stay with each other, which leads to rigid agglutination followed by the fusion of protoplast (Jogdand 2001). In the presence of fusogen mediators, it is essential to soak the cells in an alkaline (pH 09.0–10.4) solution to stimulate the chemical protoplast blend into two or more viable protoplasts (Muralidhar and Panda 2000; Navrátilová 2004). Microbiological polyethylene glycol (PEG) is used as a fusogen agent, mainly due to its fabulous binding property and stability action. Calcium ($Ca^{2+)}$) is one of the common divalent ions and is used in combination with PEG. After the fusion, hybrids obtained are studied on the basis of their genotypic and phenotypic characteristics (Navrátilová 2004). Gene expression can also differentiate the protoplast fusion after identification. The finding of unique genotype specifies the incidence of gene recombination through cell fusion and also distinguishes the individual organization of the hybrids in terms of metabolite construction of parental strains or enzymatic activity to estimate the recombination profitability (Muralidhar and Panda 2000). Chemofusion is very cheap with non-specific fusion that may cause giant fusion products, which can be cytotoxic and non-selective.

Electrofusion

The electrofusion technique is based on the reversible electrical breakup of the cell membranes. In microseconds (small-time period), rupturing is observed approximately between 0.5 and 1.5voltages, when membranes are polarized in electric field (Zimmermann and Scheurich 1981). In this, fusion membrane-bound polarization is repealed by applying electric current to the medium having protoplasts and results in the unplanned reversal of polarity that facilitates induction in protoplast. This process is not applied against fungal transformation. Two capillaries of glass microelectrodes are used with protoplast along with gentle electric stimulation to blend the protoplast. Low strength electric field i.e. 10Kvm^{-1} is responsible for dielectrophoretic dipole production inside the protoplast suspension, which directs pearl chain activities of protoplast. The application of high strength electric field (100 Kvm^{-1}) results in electric collapse of successive fusion (Jogdand 2001; Ushijima et al. 1991). In cell viability, as compared to chemofusion, electrofusion showed advantageous characters as it is simpler, quicker and not involved in a large number of chemical agents (Navrátilová 2004).

17.6.2 Electroporation

Electroporation is one of the modern invasive methods, which uses microsecond length pulses to modify the permeability of cell membrane and forming pores or nanoscale defects (Bertacchini et al. 2007; Rubinsky 2007). The procedure of electroporation is either reversible or irreversible. In reversible procedure, the use of an electric field at definite parameter temporarily permeabilizes its membrane and allowing the cell to come back to its natural position. In irreversible process, stronger electric field can cause them to permanently permeabilize of cell membrane, which ultimately leads to cell death (Rubinsky 2007). Exposure in biological membrane towards high electric field induces regular and elevated permeability and conduction of electric charge (Stampfli 1958). Electroporation is often used for the transformation of microorganisms by establishing new coding DNA. Even though some microorganisms can spontaneously transform themselves to acquire foreign gene for replication and allow passing them for a division. There is the availability of sufficient stimulus for controlling the artificial transformation. Natural membrane polarity stops the entry of foreign DNA into a cell as a result of well-developed defense mechanism. In this technique, intermediate fact or sin membrane polarity caused the electric field, which results in uptake of recombinant DNA in the media cell. These transformed cells can be cultured or identified without any difficulty in electroporation technique. There are four applications that utilize and allow both endogenous and exogenous molecules to eradicate or penetrate the cell. (1) Genetic transformation, (2) Inactivation in microorganisms, (3) Biomolecule’s extraction and (4) Acceleration in the drying of biomass (Kotnik et al. 2015) (Fig. 17.11).

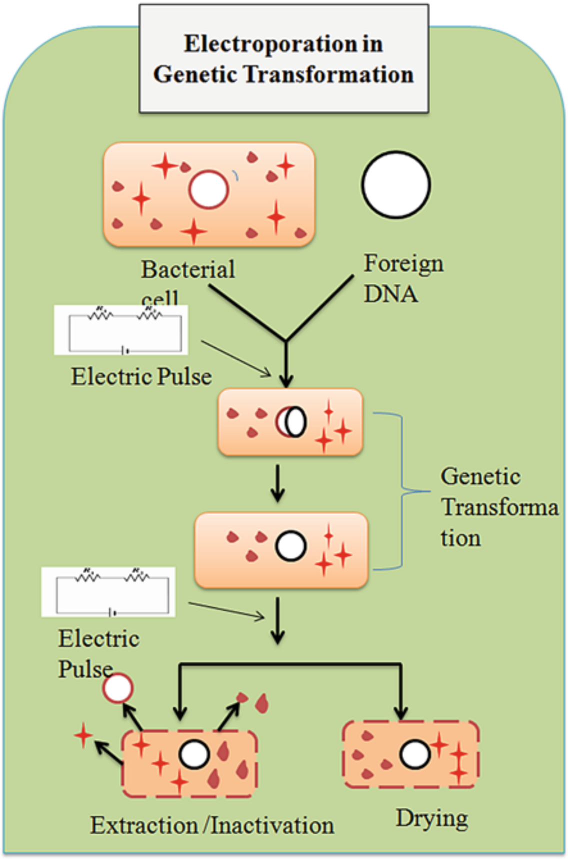


Fig. 17.11 Electroporation in genetic transformation. Kotnik et al. (2015)

17.6.2.1 Inactivation in Microorganism

In this application, microorganisms that are able to show strong pulses of electric field have extensive inhibition in their performances, which consist of their growth, division and synthesis of toxic substances. In this technique, the contamination is not recorded particularly in food preservation, where chemicals or radiation is avoided. Today, the wide application of processing food preservation is heating; due to which both taste and nutrients are affected, which results in deteriorating the value of food (Haberl et al. 2013). In electroporation-based inactivation, a mild heating takes place, nutrients and/or taste values are not affected (Haberl et al. 2013).

Genetic transformation

In genetic transformation, exogenous DNA is established on the basis of reversible electroporation, the foreign genes are expressed in their new host cells and they are inherited for cell division. This can turn the host microorganisms into "factories" of biomolecules, adapt them to a new environment or serve to study the role of individual genes (Kotnik et al. 2015).

Bimolecular electroextraction

In electroextraction, any multicellular tissues or microorganisms are electroporated to the extent, which are required for the releasing of biomolecules. On other hand, it is also viable with reversible electroporation. In the majority of cases, it is essential to limit electroporation to point that keeps away from quick breakdown of exposed cells and, in this way, there is the development of debris with contaminating extract Kotnik et al. 2015).

Genetic transformations in microorganisms produced spontaneously by taking foreign gene, leading them to division, duplicate and utter them. Many approaches have been attempted ranging from chemical and mechanical to thermal, but in view of the fact that, in mid-1980s, transformation is based upon electroporation and have prevail due to its high efficiency and relevant to the broadest range of bacterial microorganisms (Aune and Aachmann 2010). In tremendously diverse bacteria, in early 1990s, electro transformation was also confirmed and efficient against Archaea, unicellular fungi (yeasts) and unicellular algae (microalgae). In Archaea, generally, electroporation is not applicable. Halophilic Archaea may be unfeasible for electro transformation as it cannot tolerate NaCl concentration less than 1 M, but in suspensions of such salinity, the electric field is necessary for genetic transformation. In some other Archaea, despite attempts are at optimization, researchers are unable to detect transformants (Lucas et al. 2002). In yeast and microalgae, transformation efficiency is normally inferior then bacteria (Kilian et al. 2011). In recent time, successful electro transformation has been observed against recently documented taxonomic phyla of bacteria, Archaea, microalgae and yeasts (Kotnik et al. 2015) (Table 17.5).

17.6.3 Biolistic Transformation

In biolistic transformation, important microparticles like tungsten or gold are coded with DNA, and these particles are accelerated and collided with fungal cell or spores at very high velocity. At elevated pressure, these particles are inserted into host cells, and this transformation is also called bombardment. This bombardment can turn out to be cognizant for both short-lived and constant transformation. Different aspects involved in the efficiency of bombardment in multiple interaction prototypes (Sanford et al. 1995). Some important variables for biological parameters are growth condition, cell density and cell type. Whereas, the instrumental settings depend upon target distance, particle type and size, pressure level and vacuum (Gouka et al. 1997). Biolistic transformation is more powerful amongst all the genetic transformations. This technique takes very little time as compared to other transformation methods like protoplast. The particle bombardment is found to be an easy, efficient, convenient method among those organisms, which are not cultured easily and where the isolation

Table 17.5 List of successful electro transformation against recently documented taxonomic phyla of bacteria, Archaea, microalgae and yeasts Kotnik et al. (2015)

Phylum	Species
Bacteria	
Cyanobacteria	*Arthrospira platensis, Fremyella diplosiphon, Synechococcus elongatus*
Firmicutes	*Bacillus cereus, Clostridium perfringens, Enterococcus faecalis, Streptococcus pyogenes, Lactobacillus casei,*
Chlamydiae	*Chlamydia trachomatis, Chlamydia psittaci*
Thermotogae	*Thermotoga martima*
Actinobacteria	*Corynebacterium, Brevibacterium lactofermentum, Mycobacterium smegmatis, diphtheria*
Deinococcusthermus	*Thermus thermophilus, Deinococcus geothermalis*
Bacteroidetes	*Bacteroides uniformis, Prevotella Ruminicola, Bacteroides fragilis*
Fusobacteria	*Fusobacterium nucleatum*
Planctomycetes	*Planctomyces limnophilus*
Proteobacteria	*Campylobacter jejuni, Escherichia coli, Sinorhizobium meliloti, Salmonella enteric, Yersinia pestis*
Spirochaetes	*Serpulina hyodysenteriae, Borrelia burgdorferi*
Tenericutes	*Mycoplasma pneumonia*
Chlorobi	*Chlorobium vibrioforme*
Unicellular Fungi (yeasts)	
Basidiomycota	*Cryptococcus neoformans, Pseudozyma antarctica, Pseudozyma flocculosa*
Ascomycota	*Candida maltosa, Ogataea polymorpha, Pichia pastoris, Saccharomyces cerevisiae, Schizosaccharomyces pombe*
Archaea	
Euryarchaeota	*Methanococcus voltae, Pyrococcus furiosus*
Crenarchaeota	*Metallosphera sedula, Sulfolobus acidocaldarius, Sulfolobus islandicus, Sulfolobus solfataricus*
Unicellular Algae (microalgae)	
Rhodophyta	*Cyanidioschyzon merolae*
Chlorophyta	*Chlamydomonas reinhardtii, Chlorella ellipsoidea, Dunaliella salina, Chlorella vulgaris, Scenedesmus obliquus*
Heterokontophyta	*Phaeodactylum tricornutum, Nannochloropsis sp.* W2J3B

of protoplast is hard. Although these instruments are very expensive but can be used for easy transformation of fungi like *Aspergillus nidulans* and *Trichoderma reesei* (Barcellos et al. 1998; Hazell et al. 2000).

17.6.4 Vector-Mediated Transformation

In vector-mediated transformation, plasmids are used as gene carriers. In this, specific gene of interest is situating into the plasmid that allowed host cell infection, so that gene gets incorporated into its genome of all the types of vector-mediated transformations, mainly *Agrobacterium tunefaciens*-mediated transformation (ATMT) is frequently used. In this process, plasmids are used for the transformation of gene, which is considered to create gene cassettes. Further, these definite genes with nuclear cyclic DNAcoding against an array protein are concerned with host infection. A definite gene of interest is introduced into plasmids to allow infecting host cells; hence, the genes get integrated into its genome in a variety of vector-mediated transformation. *A. tumefaciens* is one of the soil-borne bacteria having Ti plasmid, which incorporate T-DNA to host plant genome that may be the reason of tumor in many plants. In *A. tumefaciens*, the T-DNA is replaced with the gene of interest mark with a suitable marker and assembles them to hit the host cells so that the target gene gets inserted into the host genome. Transformation is mostly used in plant cells but later on, this is used for transforming the fungi (De Groot et al. 1998). In this process, hygromycinis used as a resistance marker for transforming the *Aspergillus awamori,* in which *A. tumefaciens* is approximately 600 times more capable than the conservative protoplast fusion. At present, synthetic plasmids are used from different other sources apart from the various bacterial plasmid vectors like pAN52-1 N, pAN52-4, pAN52-1. An introduction to vector-mediated transformation has converted fungal transformation scenario by the addition of new gene sources that have enormous potential. Fungal adhesions facilitate the binding of spores to insect cuticle, as is done by the killing action of entomopathogenic fungi. Vector-mediated transformation and protoplast fusion equally popular in the provisos of their utility.

17.7 Effect of Entomopathogens in Combination with Other Microorganisms

In agricultural ecosystems, major challenges to yield and production are the damages caused by insect pests and pathogens that result in reduced soil fertility throughout the world. Under an optimum field condition, the application of a single biopesticide might be found effective but it can be further improved by combining multiple beneficial soil organisms (Imperiali et al. 2017). It was observed that insect pests get resistant by the continuous exposure to same biopesticides again and again. So there is a requirement of the addition of a new combination to manage the insect pest population. Steinhaus (1951) reported that the combinations of entomopathogenic bacteria *Bacillus thuringiensis* (Abtew et al.) and polyhedrosis virus can significantly manage the population of alfalfa caterpillar (*Colias philodice*) in California. Ansari et al. (2008) observed the interaction among EPNs (*Steinernema glaseri* and *Heterorhabditis megidis*) and EPF (*Metarhizium anisopliae* CLO 53) against the larvae of *Hoplia philanthus* (third instars). They found that combined application of these entomopathogens shows significantly increased larval death. Ansari et al. (2008) also reported 100% larval mortality in third-instar black vine weevil (*Otiorhynchus sulcatus*) when EPNs are applied at the same time or a week or 2 weeks after, along with *M. anisopliae.* Imperiali et al. (2017) studied the effect by combining of Arbuscular mycorrhizal fungi (AMF), *Pseudomonas* bacteria and entomopathogenic nematodes (EPNs) against *Oscinella frit* in wheat plants. Noskov et al. (2019) applied microbial metabolites along with pathogenic fungi for the control of the mosquito (*Aedes aegypti*) population. A synergistic influence has been observed in the killing of mosquitoes by combining these agents. Vega et al. (2012) also observed the effect of entomopathogens by combining the nematode *H. bacteriophora* along with fungi *B. bassiana* and *M. anisopliae* against the larvae of *Phyllophaga vetula.* A *s*ignificant increase in mortality has been observed. Wu et al. (2014) also reported the effect of combined dosage of entomopathogens against *Cyclocephala lurida* (third instar larvae). It was observed that the combination of these entomopathogens controls the pest population similarly as observed by using imidachloprid insecticide. The use of entomopathogens including bacteria fungi and nematodes in combination is an integrated approach to control the pest population for sustainable agriculture.

17.8 Role in Sustainable Crop Protection

Entomopathogenic biopesticides play a vital role in pest management strategy under Integrated Pest Management (IPM) system. Chemical or synthetic insecticides have been used for pest control since the nineteenth century and they have actually controlled the pest population undoubtly. But the continuous use of these chemical insecticides is toxic, not only to the human but also to the environment. Application of these insecticides leads to the emergence of new problems like resistance in insect spp. soil quality degradation and other environmental hazards. Due to the excessive use of chemical pesticides in agricultural land, yield of productive land is declined. According to the UN population depiction, the population will reach 9.1 billion in 2050. To fulfill the food demand of such an increasing population, sustainable agriculture is required. The use of biopesticides developed from entomopathogenic microorganism is an alternative to synthetic pesticides (Birech et al. 2006). Moreover, biopesticides developed from entomopathogens are non-toxic, environment friendly, easily degrade in the environment and do not cause resistance ((Leng et al. 2011; Tadele and Emana 2017). As people are more concerned about the health hazards caused by chemical pesticides so they prefer organic food products (Okunlola and Akinrinnola 2014). Application of these entomopathogens promotes sustainable agriculture through sustainable pest management (Nawaz et al. 2016; Singh and Yadav 2020). These biopesticides when sprayed over the field have no side effects on the consumer and applicant (Damalas and Koutroubas 2016). It is, therefore, concluded that in IPM, entomopathogenic biopesticides can successfully control the pest population and can replace the chemical insecticides for insect control (Şesan et al. 2015).

17.9 Limitations, Challenges and Opportunity

The incidence of disease due to insect pests has increased manifold in this era of modern agriculture. The natural ecosystems are now prone to instability with the out shinning fashion of the agroecosystems. In natural environments, there are certain checkpoints that help in regulating the potential pest species. To enhance the productivity and ease of application, the adaptation of certain ways of agriculture has now contributed to the degradation of the environment. The practice of monoculture has also resulted in the elevation of population densities of pest, which were restricted otherwise in the natural conditions. Irrigation techniques, warm temperature in the glasshouse, introduction of new cultivars and use of a broad spectrum of chemical pesticides are some of the practices that cause soil infertility, decrease in the number of certain natural predators and also develop new resistant pest strains. The pest population is naturally controlled by entomopathogenic microorganisms such as bacteria, viruses, nematodes and fungus. These are classified as classical biological control agents of insect pests and their efficiency can be multiplied by using habitat manipulation (Kalha et al. 2014).

17.9.1 Limitation

- Lack of awareness midst farmers
- Less knowledge about insecticidal activity
- Difficulty in mass production
- Cost and availability of commercial products
- Effects of biotic and abiotic constraints.

Due to the increasing awareness, farmers are acquainted with the use of parasitoids and predators as biological control agents against insect pests but there is a lack of knowledge regarding the use of microorganisms. The present knowledge of insecticidal activity in case of Bt is scarce. There is an enhancement in a number and diversity of Bt populations with the help of vegetable, crop and seasonal variation but still, their impact on the environment is unknown. Entomopathogenic microbes tend to take more effort for their mass production as they have a particular requirement of substrates like specific media, baits or even living tissues. This increases the level of difficulty in mass production and also multiplies the cost of production. With this, the cost of biopesticides is high in comparison to chemical pesticides. The inconspicuous use and popularity of biopesticides have also contributed to the less readily available of these microbial formulations in the market. Therefore, the amount of money and time consumed in attaining these bioformulations is also one of the limiting factors. Sometimes, the farmers with large upholdings or farm found it difficult to use biopesticides for a longer duration period.

The high specificity of these microbial organisms can be challenging in terms of application strategies as different types of combinations of formulations will be applied to control the array of insects. This can be problematic, time-consuming and stressing for farmers.

The environmental factors play a major role in the life cycle of microorganisms and also in the production of commercial formulations. The virulence and life span are dependent on the biotic and abiotic environmental factors. The efficacy of microbial pesticides against the target pests is prone to reduction or degradation in exposure to desiccation, heat, temperature and ultraviolet radiation. The time and scrutiny of procedure play a prominent role in the successful application case of certain biopesticides.

The evolutionary process of living organisms especially the target pest can face a big change in this scenario where it is in persistent exposure to toxins. The chemical or biological control can lead to the development of certain type of resistance in insects. The annihilation of target pest population can cause the acquisition of tolerance to exposed toxins in the surviving population; therefore, it results in the speeding of evolution.

In every niche, all the communities are interdependent, interference in one can cause disturbance in life process of others. So, the change in the insect population can cause long-lasting damage to higher trophic levels and functions of ecosystem. One of the results of this may be the advent of secondary pest, for example:

- Use of Bt cotton has increased the population of sucking pests like whiteflies
- In China, the problem of myriads
- In India, the prominence of mealy bugs (Kalha et al. 2014).

17.9.2 Challenges

- Registration and Regulation policies
- Effect on non-target organisms
- Proper technique of use
- Increase in shelf life
- Commercial availability
- Techniques to enhance mass production.

The introduction of exotic species and the disruption patterns caused by the use of microbial pesticides can be a serious issue of concern in future. In addition to this, the less knowledge regarding the long-term effects of biological control agents has raised certain doubts in the mind of conservationists. Therefore to save indigenous fauna and to keep a check on the activities of these biopesticides, it is important to develop some regulations and form regulatory bodies for its monitoring worldwide. There is a need to strictly implement regulatory policies for commercial biopesticides and biological control agents and their registration should opt for detailed study of their activities against insect pests, and also their impact on the environment should be analyzed thoroughly to avoid shortcomings in the future. Ecological models for the prediction of deleterious impact of the release of biological agents can be of great help.

The effect of microbial pesticides on non-target organisms such as parasites, predators and other invertebrates and vertebrates is less evident. The laboratory studies may result in some ill effects but in natural conditions, it is not prominently recorded. There could be a certain possibility of indirect or direct consumption of these biopesticides by the pollinators or other non-target organisms. Therefore, it is required to study the influence of usage of biopesticides on soil, plant, animals and other non-target organisms.

The population of biological control agents is required in large numbers for the production of commercial bioformulations. In order to increase the number, there is a need to develop better mass-production techniques. With time, the shelf life and virulence of biopesticides tend to decrease, and therefore, the production strategies also need to look into these aspects.

17.9.3 Opportunity

- Entomopathogenic microorganisms are ubiquitous in nature
- Ideal for Integrated Pest Management programs
- Efficiency can be improved
- Genetic improvement can play a big role.

Entomopathogenic microorganisms reside in a very diverse habitat and can be easily isolated from the most ecological niches of the world with few exceptions.

These entomopathogens can be formulated commercially in a way to lessen the usage spectrum of chemical pesticides. They are an excellent alternative to harmful chemical pesticides due to their beneficial characteristics. If selected carefully along with a planned application strategy, they can play an inevitable role in Integrated Pest Management. In this regard, there is a need to strengthen the research knowledge and overcome the drawbacks of production, efficiency and application in the field.

Genetic engineering can be operated as a tool for improving the efficacy and virulence of biological control organisms. The genetically improved strains of biological control agents with the amalgamation of traditional and newly developed genetic-engineered techniques can solve the problem like less shelf life and decrease in virulence with time. This opportunity can be utilized to develop better biopesticides and this may lead to a rise in their popularity commercially.

In recent years, a lot of attention is shifted toward the biological control agents, because of this worldwide, new subspecies/strains are being identified and registered, but their development in commercially available products is still lacking behind. So there is a lot of potential in the field of identification of toxic genes and the development of commercial products.

The advancement of molecular techniques upholds the opportunity to construct genetically improved strains with high virulence against a broad spectrum of insects. The discovery of new biological control agents will help in attaining the goal of sustainable agriculture and solves the problems of environmental degradation, pest resistance and deterioration of human health.

17.10 Conclusion and Future Prospects

The rapidly increasing human population needs an amplified quantity of fiber and food from the shrinking agricultural land. Today, current agriculture has mostly achieved these objectives, however; the strengthening of agriculture through the selection of high yielding variety, development of advanced irrigation facilities and the use of increased amount of agrochemicals throughout the last two to three decades have also increased crop losses due to the disease, insect pests and weeds. Interactions among soil microbial and crops' grown are a significant approach to raise food production in support of the ever-growing world's population at the least environmental costs or at the present scenario of global climate change. There are two main strategies for controlling the soil microorganism, which are based either on the progress made in the development of microbial inoculants or on the strategy for the naturally existing soil microbial populations. Particular importance is being waged in formulation, quality control and on the manners of application of soil rhizospheric microbiomes.

It again desires to be highlighted that insects are flexible and extremely successful living organisms. Whatever policies we may accept, they will move toward similarly successful responses. We have to constantly specialize the armory of missiles accessible at our command, thus we are capable to increase an upper hand in our struggle against a large number of insect pests. Sustainable crop production is one of the system that might be applied constantly for many years, that soundly depends on the potential within the limitation of a particular area, does not excessively drain its resources or humiliate/ degrade environment, best use of its materials and energy also ensure reliable and good yields and give profits the local residents at economical costs. This sustainable system characterizes a logical way between the extremes of ultra-intensive agrosystems and low productivity organic farming. Green revolution, which tackled the food–security calamity of the 1960–1970s, concerned with scientific novelty and energetic promotion of varies with high yielding that possibly will alter fertilizer inputs to grain production, however it does not involve the use of microbial biopesticides. The evergreen revolution is only possible to satisfy the feeding of population throughout the world by means of sustainable cropping systems, a determined and incorporated effort from farmers, scientist and policymakers required to generate awareness and regulatory environment where sustainable technologies like Integrated pest management (IPM) are required to meet the fiber and food needs of the twenty-first century. Computer-based systems might be installed at the Panchayat level that can help the local farmers in the pest identification, also forecasting the population of pests and series of choices available in pest management with their advantages and limitations. This technique will help the poor farmers in the pest identification and management option based on their resources and requirements.

The future aspects are mainly for the upgrading of microbial biopesticides through their high production with ecological stability. To enhance the efficacy of microbial pesticides in IPM, a systematic investigation must be carried out in diverse agroecological regions to categorize naturally occurring microorganisms. Thorough surveys are essential on the possessions, pathogenicity and mode of action of pests. Environmental studies are mainly required on the kind of infections in insects as the ecological factor plays a major role in expansion of diseases and eventually manages the population of insect pests. Proper pains must be prepared to reduce the loss of infectivity of pathogens due to the presence of photo-inactivation. Studies on the safety of insect pests to other animals, plants and beneficial insects have to be undertaken. The interaction of insect-associated microbes should be thoroughly studied for the development of better IPM approaches. The self-disseminate nature of the pathogens in time and space would certainly confirm to be a benefit in sustainable agriculture.

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Chapter 18
Global Scenario of Soil Microbiome Research: Current Trends and Future Prospects

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Abstract The current chapter is focused on the microbiome investigations that have been used to understand the linkages between soil microbiota and their environments. Advanced molecular "Omic techniques" such as metagenomics, metatranscriptomics, metaproteomics and metabolomics have been employed to understand in situ microbiomes and their interactions with soil-ecosystem services at micro-scales. The potential advances in "Omics approaches" are facilitated by high-throughput next-generation sequencing techniques and the current work discussed upon implementation of these technologies in soil microbiome research at global scale. In this chapter, we have summarized recent advancements and the current state of knowledge in soil microbial diversity and soil-ecosystem functioning. Different high-throughput sequencing technologies, molecular "Omic techniques" and their limitations in soil microbiome research have been addressed. Genome-centric metagenomic approach was highlighted over gene-centric approach to understand soil microbiomes and their functions hitherto. Impacts of different physical, chemical and biological factors on soil microbial communities were reviewed in the current chapter. It is suggested that soil microbiomes can be exploited to alleviate the negative impacts of environmental changes for increased crop production.

Keywords Climate change · Ecosystem function · High-throughput sequencing technologies · Omic techniques, metatranscriptomics · Soil ecological engineering · Soil microbiome

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18.1 Introduction

Soil is one of the most complex ecosystems that harbor billion of microbiota. Soil microbial communities perform crucial roles in the elemental cycling of micro and macronutrients which are vital for the functioning of the above-ground ecosystem (Prasad et al. 2021). Nevertheless, systemic understanding of the soil microbial ecology is difficult due to the high degree of spatial heterogeneity that is present at micro-scales (Raynaud and Nunan 2014). DNA-based microbial taxonomy using phylogenetic markers (ribosomal RNA gene, ITS, etc.) were enumerated around 10^6 different archaeal and bacterial species and approximately 1 billion microbial cells in 10 g of soil (Roesch et al. 2007; Schloss and Handelsman 2006). Further, Trevors 2010 estimated around 10^{-9} genomes and 10^{-12} prokaryotic genes in a gram of soil. Recent metatranscriptomics and subsequent taxonomic annotation of agricultural soils revealed complex microbiota from the diverse origin, in the following order: Viruses < Eukaryotes < Archaea < Bacteria (Sharma and Sharma 2018).

It is said that only 1% of soil bacteria are cultivable in the laboratory and is known as a great plate count anomaly. The major fraction (99%) of soil microbiomes is uncultivable in nature. Therefore, understanding the factors driving soil microbiome structure and their interactions (physical, chemical, biological, etc.) across a contrasting ecological gradient is difficult by using conventional microbiological tools. Recent advancements in high-throughput sequencing technologies enlightened the previously unknown soil microbiome compositions without the necessity for cultivation and enable us to study complex soil microbiomes in detail using metagenomics/transcriptomics (Thompson et al. 2017a, b). In this approach, genomic material DNA or RNA will be extracted from the microbiota of soil sample of interest followed by high-throughput sequencing of gene or transcript. Later the data will be accurately annotated and corresponding cellular or ecological functions will be precisely identified (Prosser 2015). The inferences drawn in these studies could be implemented in sustainable agriculture and other land-use management practices (Fig. 18.1).

According to Prosser (2015) “metagenomics and metatranscriptomics are defined as the characterization of all genes and RNA transcripts, respectively, in a given soil/environment sample”. Further, he has pointed that “single-gene/amplicon-specific high-throughput sequencing studies are sometimes described as “metagenomics” but include data for only one gene and, therefore, do not encompass the holistic element of the omics”. During the past decade, many “omics” studies have been conducted to elucidate the soil microbiomes in a wide variety of environments. In this chapter, we especially highlighted the importance of omic approaches to address the soil microbiomes and ecosystem function. Different high-throughput sequencing technologies and their characteristics have been well summarized in Table 18.1. Further rhizospheric microbiomes and the effect of different environmental perturbations on soil microbial diversity and activity have been discussed (Fig. 18.2 and Table 18.2). Potential opportunities available in soil microbiome research are highlighted at the end (Fig. 18.3).

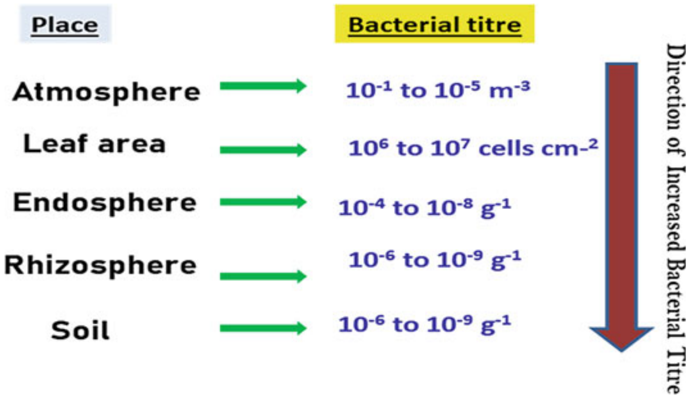


Fig. 18.1 Bacterial counts per unit in different habitats

18.2 Soil Microbiome Research in the "Omics" Era

Recent advancements in sequencing technologies along with increased computational power, including a significant reduction in sequencing costs have facilitated a substantial number of soil microbiome studies (Table 18.3, Jansson and Hofmockel 2018; Kang et al. 2019; Gans 2005; Wu et al. 2011; Prosser 2015; Fierer 2017). Further, high-throughput sequencing studies have succeeded in enlightening the previously unknown microbial diversity of soil microbial communities across a wide variety of soil habitats (Thompson et al. 2017a, b).

The global scenario of soil microbiome research commonly involves three different kinds of sequencing strategies: (1) high-throughput amplicon-based metataxonomic sequencing studies, which involves amplification of targeted regions of phylogenetic markers such as "intergenic spacer region" for Eukaryotes and 16S ribosomal RNA gene (16S rRNA) for archaea and bacteria (2) metagenomics/metatranscriptomics which involves high-throughput sequencing of the metagenome or transcriptome in a specific soil (3) metaproteomics which focuses on the detection of fragmented and separated proteins followed by sequencing with the combination of liquid chromatography-mass spectrometry (LC-MS), and (4) metabolomics wherein detection of metabolites through nuclear magnetic resonance spectroscopy (NMR) or mass spectrometry (LC-MS). Applications of different advanced technologies used in the soil microbiome research were comprehensively summarized in Table 18.3. These molecular approaches unraveled the physiological mechanisms behind unculturability and identified the factors suitable for growth promotion of previously uncultivable microorganisms in the laboratory (Stewart 2012; Biswas and Sarkar 2018; Yadav et al. 2015).

DNA-based high-throughput sequencing of 16S rRNA gene (V3–V4 region) demonstrated that dominant bacterial taxa in agriculture soils were found to be *Actinobacteria, Gemmatimonadetes, Proteobacteria, Acidobacteria* and *Chloroflexi*. pH

Table 18.1 Characteristics of different next-generation sequencing platforms used in soil microbiome research

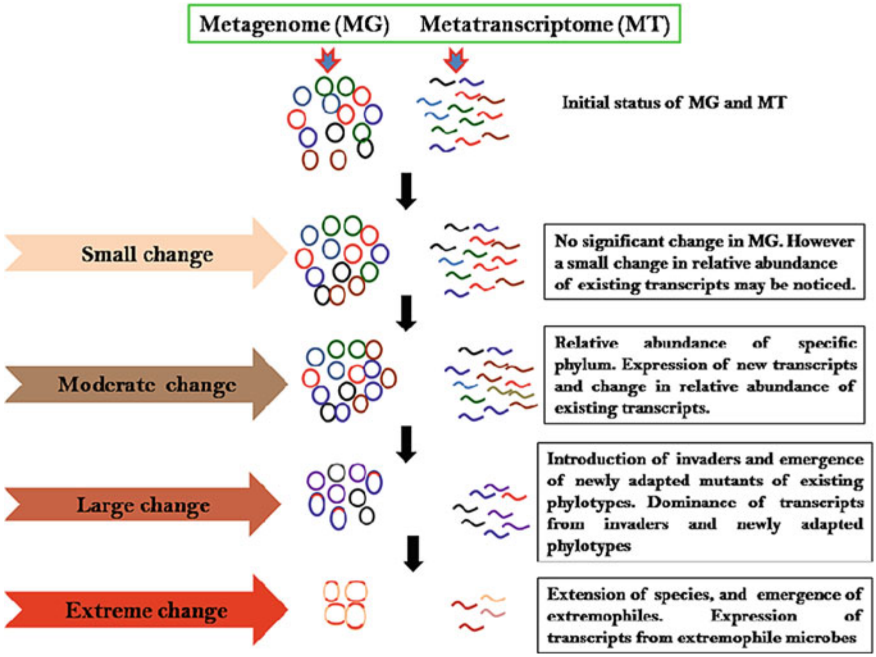
Platform	Year of establishment	Maximum Sequencing length/yield	Runtime	Specific feature	Technology	Error rate
Second-generation sequencing technologies						
Illumina	2006	150 bp/2–600 Gb	27–11 days	Highest throughput Signal interference among Long-/short-run times, low capital cost, low-cost per Mb	Cleavable dye terminators (Reversible terminators)	10^{-2} to 10^{-3}
Roche-454	2005	200–700 bp/700 Mb	24 h	Long read lengths	emPCR, pyrosequencing	10^{-3} to 10^{-4}
Ion torrent	2010	200 bp/200 Mb	2 h	Stable sequence quality, better sequencing GC depth distribution	emPCR, H+ detection	3×10^{-2}
SOLiD/ABI Life technologies	2006	35–50 bp/120 Gb	7–8 days	High-throughput, highest accuracy two-base encoding provides inherent error correction	emPCR, ligation with cleavable dye terminators	10^{-2} to 10^{-3}
Third generation sequencing technologies						
Pacific biosciences	2010	1500 bp/100 Mb	2 h	Single-Molecule Real-Time (SMRT) sequencing technologies	Adding hairpin adapters legated on each end of the linear DNA molecule, to create a “SMRTbell” template. Sequencing dyes are phospholinked to the nucleotide	1.5×10^{1}

(continued)

Table 18.1 (continued)

Platform	Year of establishment	Maximum Sequencing length/yield	Runtime	Specific feature	Technology	Error rate
Helicos™ biosciences Ω	2007	25–55 bp/35 Gb	3–6 days	Very small amounts of starting material. Overcoming the limitations of short read length. sequence the same segment of DNA multiple times for highly accurate sequences	Single-molecule specific Sequencing. Single base, reversible dye terminator extension reactions	0.2%
Nanopore/Oxford Nanopore Technologies/1 Gb	2007	>5000 bp/6 × 10^4	48–72 h	Strand sequencing wherein intact DNA is ratcheted through the nanopore base-by-base	Real-time Single-molecule sequencing	34%

Ω: Thompson and Steinmann (2010)



No significant change in MG. However a small change in relative abundance of existing transcripts may be noticed.

Relative abundance of specific phylum. Expression of new transcripts and change in relative abundance of existing transcripts.

Introduction of invaders and emergence of newly adapted mutants of existing phylotypes. Dominance of transcripts from invaders and newly adapted phylotypes

Extension of species, and emergence of extremophiles. Expression of transcripts from extremophile microbes

Fig. 18.2 Effect of a change in environmental condition on the response of soil microbiomes as revealed by metagenomics and metatranscriptomics. The concept illustrated in this figure was adopted, modified and redrawn from Prosser (2015)

was found to be one of the major soil characteristics that confer bacterial communities in agriculture soils. A significant positive correlation was found between soil pH, soil bacterial α-diversity and abundance of operational taxonomic units. Results demonstrated that soil pH is a relatively more important factor than nutrients in shaping soil bacterial communities in agricultural soils.

Metatranscriptomics revealed that the diversity of the rhizosphere microbiome has differed from bulk soil and in between plant species, for example, Pea had a stronger effect on the rhizosphere microbiome than wheat and oat resulted in a different rhizosphere community. A comprehensive understanding of the microbial communities of the paddy soils driving methane metabolism via the formation hydrogen and acetate has been established by RNA-based metatranscriptomics (Masuda et al. 2018). Deep metatranscriptomics analysis revealed that in the anoxic layer, *Deltaproteobacteria, Planctomycete, Acidobacteria* actively generated hydrogen; Further, *Acidobacteria, Betaproteobacteria, Alphaproteobacteria* and *Deltaproteobacteria* generated acetate; Utilizing both hydrogen and acetate as substrates for methanogenesis, the archaeal genera such as *Methanoregula, Methanocella* and *Methanosaeta* actively produced methane in anoxic layers. Subsequently, in the oxic layer, methanotrophs related to *Methylogaea* and *Methylocystis* readily oxidized methane (Masuda et al. 2018).

Table 18.2 Effect of various environmental changes or disturbances on soil microbiome

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Inorganic and organic contaminants into agriculture soils for 90 days	*16S rRNA* amplicon sequencing and shotgun metagenomics	Resilience and succession patterns of soil microbial diversity and community structure in response to chemical contamination	Jiao et al. (2019)
Land-use patterns and system restoration activities	High-throughput sequencing of V3–V4 region of bacterial *16S rRNA* as well as the ITS1 region	The alpha-diversities of bacteria, fungi and *Acidobacteria* were affected by land-use change. A higher abundance of bacteria, *Acidobacteria* and fungi were noticed in the arable land and lowest in the wetland soils. The composition of soil microbiomes was altered by changing land use. This study highlights that Once the soil microbial community is altered by human activity, it might be difficult to restore the same to its original state	Sui et al. (2019)
Diesel oil and unleaded petroleum polluted soils	High-throughput sequencing of bacterial 16S rRNA gene	The petroleum pollution disturbed the soil metabolic processes and the stability of the soil microbiome. The greater negative impact was noticed with diesel oil that unleaded petroleum	Borowik et al. (2019)
Hg pollution in soils across china	Shotgun metagenomic sequencing. The high-throughput V4 region of the bacterial *16S rRNA* sequencing	Hg pollution has significant negative impacts on multiple taxonomic and functional attributes such as bacterial diversity, abundance, ecological clusters, key soil processes and functional genes. An increase in soil Hg toxicity was linked to anthropogenic activities and will lead to predictable shifts in the taxonomic and functional attributes	Liu et al. (2018)
Agriculture practices and seasonal effects	Shotgun metagenomics approach	Soil microbial communities under seasonal changes were shaped principally by water deficit, with a strong increase of Proteobacteria and Actinobacteria members in the rainy and dry seasons, respectively. In contrast, nutrient availability played a significant role in driving the microbial community in agriculture-affected soils. Soil microbiomes of preserved and agriculture practices showed differences in the genetic potential for C acquisition and nutrient cycling	Lacerda Júnior et al. (2019)
Fungicides	Next-generation sequencing (NGS) method, liquid chromatography tandem-mass spectrometry (LC-MS/MS)	Obvious negative effect of fungicides on the composition of soil microbiota and in the biochemical properties of soil by inhibiting the activity of almost all tested extracellular enzymes	Baćmaga et al. (2018)

(continued)

Table 18.2 (continued)

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Soil pH and PAH contamination	High-throughput V4 region of the bacterial *16S rRNA* sequencing	pH was found to be the principal determinant of the bacterial community in arable soils, indicative of a more substantial influence of acidification than PAH pollution on bacteria-driven ecological processes. Bacterial community structure was strongly related to soil pH, with higher diversity in neutral samples and lower diversity in acidic soils	Wu et al. (2017)
Type of the ecosystem, various soil variables such as pH, OC, C/N ratio, latitude, potential evapotranspiration, temperature, etc.	DNA fingerprinting and sequencing (T-RFLP) analyses	The diversity and species richness of soil bacterial communities differed by type of the ecosystem. The differences in mcirobiome structure was largely explained by soil pH. Higher bacterial diversity was observed in neutral soils and lower diversity was noticed in acidic soils. Results suggested that microbial biogeography is primarily controlled by edaphic variables which is different from the biogeography of "macro" organisms	Fierer and Jackson (2006)
Different levels of N deposition and seasonal changes; Soil properties	High-throughput sequencing of V4 region of the bacterial *16S rRNA*; and ITS regions of Fungal 18S rRNA	Responses of soil microbial community to N addition are significantly varied in different seasons. The abundance and diversity of soil microbial communities were significantly affected by N addition and seasonal changes. Particular response of specific microorganisms to different N deposition was observed. Results indicate that specific microbial taxa could be used as biomarkers/biological indicators for microbial responses to the N addition and seasonal changes. pH, dissolved organic carbon, dissolved organic N and Total N was likely to be key variables for soil microbial community	Yan et al. (2017)
Heavy metals Cu and As	Metagenomics of *amoA* gene	Soil ammonia-oxidizing microbes were vulnerable to the stress of heavy metals Cu and As in acidic alfisols. The effect of As and Cu on the community structure of ammonia-oxidizing archaea (AOA) was not significantly different from unpolluted soil. Phylogenetic analysis of *amoA* gene revealed that the Thaumarchaeal-AOA group 1.1b plays an important role in nitrification in oligotrophic acidic soils and provide further importance of this group in ammonia oxidation in heavy metal polluted soils. Results suggested that soil contamination by Cu and As may have a significant negative impact on soil potential nitrification rates and soil fertility	Subrahmanyam et al. (2014a)

(continued)

Table 18.2 (continued)

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Industrial effluent pollution (IWE)	Molecular fingerprinting of soil microbiome by DGGE, cloning and sequencing analysis of phylogenetic and functional gene markers	The apparent deleterious effect of industrial waste effluent (IWE) on soil microbial activity, diversity and soil function was observed. Bacterial community shift in the IWE-affected soils were observed. Bacterial genera such as *Acidobacteria, Firmicutes* and *Actinobacteria* were predominant members in polluted soils indicating bacterial tolerance to pollutants. The study proposed specific bacterial phyla along with soil enzyme activities that can be used as relevant biological indicators for assessing long-term pollution of soils. Further, Ammonia-oxidizing bacteria (AOB) was more abundant than Ammonia-oxidizing archaea (AOA) in the highly contaminated soil. However, predominance of AOA was noticed in uncontaminated and moderately contaminated fields. Reduced diversity accompanied by apparent community shifts of both AOB and AOA populations was detected in highly polluted soils	Subrahmanyam et al. (2014c, 2016)
Soil pH	High-throughput sequencing of V4 region of the bacterial *16S rRNA*	pH was found to be the main soil parameter that determined microbial diversity, composition and biomass in the Park Grass experiment soil (PGE). This could be due to the mechanism of the pH for mediation of nutrient availability in the soil. Bacterial genera such as *Bradyrhizobium, Bacteroides*, *Clostridium*, *Mycobacterium*, *Paenibacillus*, *Rhodoplanes* and *Ruminococcus* were abundant in the soil. The addition of nitrogen decreased the soil pH through increased nitrification and soil C/N ratio	Zhalnina et al. (2015)

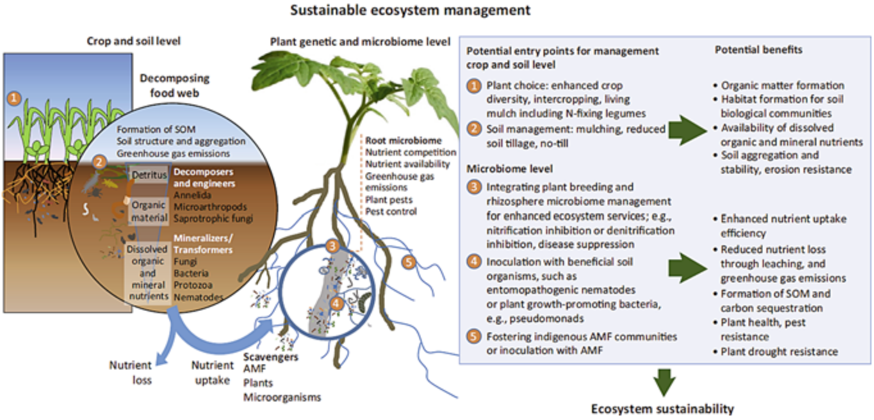


Fig. 18.3 Different soils ecological engineering approaches for local ecosystem management. The figure was adopted from Bender et al. (2016)

In a study, Sharma et al. (2019) demonstrated a high expression of microbial transcripts in agricultural and organic soils with diversified metabolic functions. This study provided insights about certain molecular markers which are indicative of metal and pesticide contamination in soil. It was observed that Archaea had relatively a greater role than bacteria in the soil nitrification process of polluted environments. Particularly, over-expression of aromatic hydrocarbon-degrading transcripts indicates the importance of soil microbiomes in the biodegradation of pollutants in agroecosystems (Sharma et al. 2019).

Community shifts in the structure and composition of the soil microbiomes are considered as biological indicators for assessing long-term pollution of soils (Subrahmanyam et al. 2011, 2014b, 2016; Ros et al. 2020; Liu et al. 2018; Kumar et al. 2020a, b, c, 2021). RNA-based metatranscriptomics of agriculture soils indicated that higher expression of transcripts related to heavy metals bioremediation (e.g., thioredoxin reductase, mercuric ion reductase, cobalt-zinc-cadmium resistance protein, etc.). Enhanced RNA transcripts in soils were related to soil C, N, P and S cycles (e.g., PstA, PstB SoxX, SoxD, SoxA, SoxB, etc.). Large quantity of the transcripts involved in soil denitrification suggesting its key role in the loss of nitrogen in agriculture soils. Transcripts of sulfur metabolic pathways demonstrated a higher expression of alkane sulfonate monooxygenase, arysulfatase and sulfonate monooxygenases. This is indicative of active sulfur metabolism wherein microbiomes in these ecosystems were able to acquire sulfur from organosulfur substances. Higher abundance of pesticides and heavy metal degrading bacteria such as *Pseudomonas*, *Streptomyces Achromobact*er, *Bacillus*, *Sphingobium*, *Serratia*, *Micrococcus*, *Desulfobulbus*, *Ralstonia*, *Acinetobacter*, *Desulfobacterium*, *Thiobacillus Rhodospirillum* and *Arthrobacter* were noticed in agricultural soils (Sharma and Sharma 2018; Yadav et al. 2020).

Table 18.3 Advanced molecular "omic techniques" used to establish soil microbiomes and ecosystem function

Soil	Source of sample	Technique/Tools	Observation	References
Agricultural soil, Norwich, UK pH 7.49	Rhizosphere of wheat, Oat, Pea and an Oat mutant	RNA-based metatranscriptomics	The diversity of rhizosphere microbiomes were differed from bulk soil and between plant species. Pea had a stronger effect on the rhizosphere microbiome than wheat and oat resulted in a different rhizospheric community. The relative abundance of eukaryotes in the Oat and Pea rhizospheres was fivefold higher than in the bulk soil or in the wheat rhizosphere. Cereals such as wheat and oat rhizospheres were enriched with cellulose degraders, whereas a legume rhizosphere was enriched for hydrogen oxidizing microbes	Turner et al. (2013)
Cd-contaminated soil, Sichuan province, China Soil pH 6.6 to 6.7	Soils were obtained from private land and Cd-contaminated site next to the sewage outlet of three phosphate rock chemical plants	DNA-based Metagenomics followed by COG and KEGG annotation	Cd pollution decreases both the diversity and function of soil microbial communities. It is observed that S*ulfuricella, Nitrosospira* and *Nitrososphaera* were abundant in Cd polluted soils where as *Candidatus Solibacte, Candidatus Koribacter* and *Bradyrhizobium* were the dominant genera in unpolluted soil. The relative abundance of dominant metabolic (KEGG) pathways increased in the Cd polluted soil. The enriched pathways cd polluted soils were biosynthesis and degradation of fatty acids, amino acids, and nucleotides	Feng et al. (2018)
Pristine soil, agriculture and Organic soils. Agriculture soil had pH of 7.5 to 8.0; soil was acidic and had pH of 6.5, Punjab, India	Agriculture field and a site free from agriculture	RNA-based metatranscriptomics	Proteobacteria are the dominant bacterial phyla in both pristine and agricultural soils. The top three abundant microbial phyla in agriculture soil was in the order of Proteobacteria > Ascomycota > Firmicutes, whereas in organic soils the order was Proteobacteria > Cyanobacteria > Actinobacteria Several soil microbial RNA transcripts which are related to ammonification, nitrification, stress response, and alternate carbon fixation pathways were overexpressed in agricultural soil. Further, transcripts of archaeal origin had high expression in agricultural soils than in organic soils. This indicates the active role of Archaea in metal- and pesticide-contaminated environment. It was observed that the nitrification process was dominated by Archaea as compared to bacteria in metal and pesticide polluted soils	Sharma et al. (2019)
Paddy field in Niigata Agricultural Research Institute, Japan	Paddy soil	RNA-based metatranscriptomics (Both rRNA seq and mRNA seq analysis)	Transcriptional profiles of genes encoding the enzymes that catalyze the formation of hydrogen, acetate and methane in paddy fields were comprehensively established. Deep metatranscriptomics analysis revealed that in the anoxic layer, *Deltaproteobacteria, Planctomycete, Acidobacteria* actively generate hydrogen; Further, *Acidobacteria, Deltaproteobacteria Betaproteobacteria*, and *Alphaproteobacteria* generate acetate; Utilizing both hydrogen and acetate as substrates for methanogenesis, the archaeal genera such as *Methanoregula, Methanocella* and *Methanosaeta* actively produce methane in anoxic layers. Subsequently, in the oxic layer, methanotrophs related to *Methylogaea* and *Methylocystis* oxidize methane	Masuda et al. (2018)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Soil samples from wheat fields treated with suppressive and non-suppressive (soilborne fungal pathogen *R. solani* AG8). Lithocalcic Calcarosol	Rhizosphere of Wheat	RNA-based metatranscriptomics followed by COG, KEGG, and SEED functions	In response to the infection of wheat roots by R. solani, both suppressive and non-suppersive soils had a different expression of functional genes. Suppressive samples had higher expression of a terpenoid biosynthesis gene i.e. polyketide cyclase and other cold shock proteins. Non-suppressive samples showed greater expression of antibiotic genes which is involve in pyrrolnitrin synthesis (e.g., Chloroperoxidase) and phenazine and its transcriptional activator proteins Further, genes involved in detoxifying superoxide radicals (ahp, cat, gpx1, bcp, trx, sod, etc.) and reactive oxygen species were expressed in the non-suppressive wheat rhizosphere samples	Hayden et al. (2018)
Soil from New Caledonia, a biodiversity hotspot located in the southwest Pacific	Surface serpentine soils (Depth 10 cm)	DNA-based metagenomics and high-throughput sequencing	Microbial species abundance, composition, and richness were linked to the surface vegetation type and the dominant plant species. Each plant possesses its own microbial community resulting from multiple interactions between abiotic and biotic factors. Soil fungal and bacterial communities are affected by diverse edaphic parameters and also site-specific	Gourmelon et al. (2016)
200 soil samples from Arctic region	Top soil (15 cm depth)	DNA-based metagenomics and high-throughput sequencing	Spatial and edaphic factors played an important role in the structure of Arctic soil bacterial communities. It was elucidated that pH as the key environmental driver shaping Arctic soil bacterial communities. The core microbiome of all the 200 samples composed of 13 OTUs, mainly affiliated to *Proteobacteria* and *Acidobacteria.* The *Alphaproteobacteria*, especially the *Bradyrhizobiaceae* family, was most abundant in acidic soils and decreased along with increasing pH, whereas *Betaproteobacteria,* especially the *Comamonadaceae* family decreased along with decreasing pH	Malard et al. (2019)
Soils collected from Arabidopsis, pine, corn and potato growing fields, USA		Metabolomics with GC-MS analysis; DNA-based pyrosequencing	Plant growth patterns, as well as leaf metabolome composition, have been differentially affected by soil microbiomes GC-MS analyses revealed that soil microbiomes applied in the rhizosphere of *Arabidopsis thaliana* were able to modulate leaf metabolome and plant growth	Badri et al. (2013)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Soils collected from agriculture field Punjab, India	Bulk soil (top 10 cm)	RNA-based metatranscriptomics	Studies indicated that higher expression of genes involved in the transformations of heavy metal (e.g., Thioredoxin reductase, mercuric ion reductase, Cobalt-zinc-cadmium resistance protein, etc.). Increased number of transcripts related to C, N, P and S cycles (e.g., PstA, PstB SoxX, SoxD, SoxA, SoxB, etc). Higher abundance of the transcripts linked to the denitrification process suggests its major role in process of nitrogen loss in the soils Transcripts of sulfur metabolic pathways demonstrated that higher expression of alkane sulfonate monooxygenase, arysulfatase, sulfonate monooxygenases, etc. This is an indication of active sulfur metabolism wherein microbes in this ecosystems acquiring sulfur from organosulfonated substances Higher abundance of pesticides and heavy metal degrading bacteria (e.g., *Pseudomonas*, *Streptomyces Achromobact*er, *Bacillus*, *Sphingobium*, *Serratia*, *Micrococcus*, *Desulfobulbus*, *Ralstonia*, *Acinetobacter*, *Desulfobacterium*, *Thiobacillus Rhodospirillum, Arthrobacter*) were noticed in agricultural soils	Sharma and Sharma (2018)
Soils collected from the Tea (*Camellia sinensis*) growing experimental station, Fujian China	Rhizosphere of *Camellia sinensis* fields treated with organic fertilizers	DNA-based high-throughput amplicon sequencing	The use of organic fertilizer (OF) positively increased beneficial bacteria such as *Nitrospirales*, *Streptomycetales*, *Burkholderiales*, *Gemmatimonadales*, *Ktedonobacterales*, *Myxococcales*, *Acidobacteriales* and *Solibacterales* in the rhizosphere of *Camellia sinensis* Results demonstrate that soil microbiome composition and recruitment of beneficial bacteria into the rhizosphere of tea were influenced by organic fertilizer amendment. Further, OF improved tea quality and substantially decreased heavy metals in the rhizosphere and in tea leaves	Lin et al. (2019)
Tropical forest, Yucatan Peninsula Mexico	Surface soil ata depth of 10 cm in the we	DNA-based high-throughput sequencing of 16S rRNA gene V3-to-V4 region	Soil heterogeneity and rainfall seasonality were the main factors that correlate well with soil bacterial community structure and function (e.g., potential nitrification and denitrification.) in this tropical forest	Pajares et al. (2018)
The experimental region, Jiangsu Province, China	Soil were collected from dry lands and paddy fields at a depth of 0–20 cm	DNA-based high-throughput sequencing of bacterial V3–V4 region and Fungal ITS region	Bacterial phyla *Firmicutes* and *Actinobacteria* and were dominant in paddy field and dry land and respectively. *Ascomycota* was a dominant member in fungal communities of both paddy field and dry land. Conversion of dry lands to paddy field showed an impact on diversity and molecular ecological networks in soil microbiomes. Interspecific relationships and molecular interaction networks among bacterial and fungal populations in paddy soils were relatively simpler and unstable than in dry lands. Results conclude that large-scale conversion of dry land-to-paddy fields may reduce the ecological stability of regional soil. A significant correlation ($p < 0.05$) between change in soil environmental factors, such as electrical conductivity, organic matter, pH, and available potassium directly affected the soil microbiome come community structure	Li et al. (2020)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Composts derived from different by-products and sludge from vegetable and fruit processing Industries rationing the Region of Murcia	Matured Compost	Metaproteomics and DNA-based high-throughput sequencing of bacterial V3–V4 region	Microbiomes of suppressive and non-suppressive compost vary at the phylogenetic levels. The proteins identified were assigned to the functions affiliated to the cell wall structure, carbohydrate and inorganic ion transport and metabolism. The study proposed a phyla Proteobacteria could be used as a bio-indicator for detection of *Phytophthora nicotianae* suppression in the compost	Ros et al. (2020)
sugarcane rhizospheric soil	Rhizospheeric soil	Metaproteomics	The comparative soil metaproteomics analysis deciphered that sugarcane ratooning induced changes in the expression patterns of soil proteins originated from microbes, plants, and fauna. A majority of upregulated plant proteins were affiliated to stress response, amino acid and carbohydrate metabolism whereas most of the upregulated microbial proteins were affiliated to signal transduction and membrane transport mechanisms. In conclusion, sugarcane ratooning practice negatively impacted soil enzyme activities involved in carbon, nitrogen and phosphorus cycles. Catabolic diversity of the microbial community and the expression level of metaproteome were significantly reduced by rationing of sugar cane in agriculture soil	Lin et al. (2013)
Agriculture soils from 206 locations at Jilin province, China	Topsoil at a depth of 0–30 cm	DNA-based high-throughput sequencing of V3–V4 of the 16S rRNA Gene	The dominant taxa in agriculture soils were found to be *Actinobacteria, Gemmatimonadetes, Proteobacteria. Acidobacteria* and *Chloroflexi*. pH was found to be the major soil characteristic that confers bacterial communities in agriculture soils. A significant positive correlation was found between soil pH, soil bacterial α-diversity and abundance of operational taxonomic units. Results demonstrate that soil pH is a relatively more important factor than nutrients in shaping soil bacterial communities in agricultural soils. Biogeographic distribution of microbes and soil ecological functions are directly influenced by soil pH	Wang et al. (2019)
Different rhizospheric soils, China	Rhizosphere of rice, sugar cane, and tobacco	Metaproteomics	Most of the proteins (1/3rd) could not be identified by existing MALDI-TOF/TOF/MS. Very complex interactions were observed between microbiomes and plants in a crop rhizosphere. Functional analysis proteins revealed various metabolic pathways and signal transductions involved in the soil biotic community	Wang et al. (2011)
Copper mine tailings, Upper Peninsula, Michigan, USA	Copper mine soil in the pot experiment	Metabolomics and metaproteomics	Maize metabolomic analysis revealed that plant growth-promoting bacteria inoculation upregulated hormone biosynthesis, photosynthesis and TCA cycle metabolites. The metaproteomic analysis identified the upregulation of several proteins related to plant development and stress response. The ability of plant growth-promoting bacteria to modulate and interconnected metabolic pathways could be exploited to enhance crop productivity in polluted soils	Li et al. (2014)

Metabolomics has the potential to characterize the plant–soil biochemical interactions in the soil ecosystem. Metabolomics has advantages over conventional "Omic technologies" by determining key metabolites which are utilized by both plants and microbes. However, only a few metabolomics studies were conducted in soil microbiome research (Li et al. 2014). Maize metabolomic analysis revealed that inoculation of plant growth-promoting bacteria upregulated the hormone biosynthesis, photosynthesis and TCA cycle metabolites. The ability of plant growth-promoting bacteria to transform soil metabolic pathways could be utilized to enhance production and productivity of agriculture crops in polluted soils (Li et al. 2014).

Metaproteomics indicated that proteins expressed in the agriculture crops rhizosphere are unique and are not identified by existing MS/MALDI-TOF. Very complex interactions were observed between microbiomes and plants in a crop rhizosphere. Functional analysis of proteins revealed several pathways and metabolic signal transductions involved in the soil biotic community (Wang et al. 2011). Metaproteomics of maize soils identified the upregulation of several proteins related to plant development and stress response (Li et al. 2014). Applications of omic techniques in soil microbiome research were comprehensively reviewed by many authors (Biswas and Sarkar 2018; Krishna et al. 2019).

18.3 Different Sequencing Technologies in Soil Microbiome Research

Although Sanger sequencing has been used for decades in soil microbial ecology, it has certain limitations such as time consuming, not economic and is not a high-throughput technology. Consequently, it is essential to develop economic high-throughput sequencing methodologies that will provide information on the soil microbiomes and their functions in different realms. In the recent past, new sequencing technologies were evolved and subsequently commercialized by different firm's viz. Applied Biosystems, Thermo Fisher Scientific, Roche Life Sciences and Illumina (Table 18.1). Generally, these methods were referred to as next-generation (NGS) or second-generation sequencing technologies which revolutionized soil microbiome research. Many sequencing platforms employing NGS have been developed, including Illumina/Solexa platform, Ion Torrent technology, SOLiD and pyrosequencing (Krishna et al. 2019), PacBio etc. Comprehensive details for different sequencing platforms were summarized in Table 18.1. Different sequencing technologies and their chemistry have been reviewed by previous authors (Ambardar et al. 2016; Thompson and Steinmann 2010; Krishna et al. 2019).

18.3.1 "Gene-centric" Versus "Genome-centric" Metagenomics

Molecular analysis and investigation of individual target genes obtained from metagenomes are known as "Gene-centric" metagenomics. Most of the soil microbiome research at the global scale involves a gene-centric approach. It mainly targets amplicon-specific sequencing of phylogenetic markers such as 16 rRNA, ITS, etc. So that it could not be possible to establish the origin of the genes like which genes originated from which genome. Therefore, it is difficult to establish a link between soil function and microbial phylogeny based on the taxonomic genes. Subsequently, it is difficult to reestablish interrelated metabolic pathways operating in complex soil microbiomes with the help of gene-centric metagenomics. The main technical limitation in the sequencing of single-cell genome is difficulty in annotating a full coverage of genome assembly. These limitations can be addressed with genome-centric metagenomics.

In contrast to gene-centric' metagenomics, "genome-centric" metagenomics is considered to be a holistic approach as it aims to obtain complete sequences of genomes in a given soil sample through single-cell genomics or the Denovo assembly of individual genes. Few disadvantages of genome-centric' metagenomics involve the risk of formation of chimeras during genome assembly, in which segments of other microbial genomes are assembled. These limitations can be minimized by bioinformatics and technological advancements. Kougias et al. (2018) employed a genome-centric metagenomics approach and reported a spatial distribution of lignocellulose degrading microbiota with diverse metabolic functions. Most recently "genome-centric metagnemics" were employed to resolve microbial diversity of denitrification pathways, coral reefs and the response of bacteria to operational disturbances in activated sludge (Gao et al. 2019; Pérez et al. 2019; Glasl et al. 2020). A detailed account of Gene-centric' versus "genome-centric" metagenomics was discussed by Prosser (2015).

Metatranscriptomics provide us to understand the functional roles of microorganisms in soil-ecosystem services. Nevertheless, the diversity and composition of microbiomes in diverse soils are rarely addressed owing to enormous habitat complexity and micro-scale heterogeneity. Furthermore, recent advancements in computational biology and the development of algorithms such as Check-M, MetaBAT and MaxBin, etc., facilitate us to reconstruct metabolic pathways of microbial genomes in complex soil microbiomes (Kang et al. 2019; Wu et al. 2011).

18.3.2 Functional Potential of Soil Microbiomes to Environmental Changes/Disturbances

Understanding soil microbiomes and their potential multifunctionality under contrasting environmental factors such as nutrient availability, pH, temperature, moisture, etc., is a complex subject in soil ecology (Yadav et al. 2020). It is essential to understand the dynamic responses of global soil microbiomes to physical, chemical, biological changes including soil-plant-microbe interactions for developing/predicting long-term soil-ecosystem models. However, small numbers of investigations have employed multi-omics technologies to decipher the impact of soil contamination/environmental changes at functional and taxonomic levels in the soil microbiome (Jiao et al. 2019). Identifying the factors for microbial community stability such as "resilience (the degree of rate of recovery after disturbance) and resistance (inherent capacity of insensitivity to disturbance)" is of paramount importance for forecasting microbiome response to environmental stress. Comprehensive details on concepts of microbiome resilience and resistance were reviewed by Shade et al. (2012). Measuring the soil microbiome response to a disturbance has been a subject of interest for many decades.

Agricultural ecosystems are currently facing various anthropogenic and environmental perturbations such as climate change, pollutants, heavy metals, antibiotics pesticides, fertilizers and organic residues (Trenberth et al. 2014; Callaway et al. 2011, Subrahmanyam et al. 2014a, c; Prasad et al. 2012; Singh et al. 2020) (Table 18.2). Soil microbes play significant roles in driving the global biogeochemical cycles (C, N, P, S, Fe, etc.) and recycling of organic and inorganic elements (Falkowski et al. 2008; Subrahmanyam et al. 2014b). Since microbes plays a crucible in soil-ecosystem functioning, it is imperative to elucidate spatio-temporal dynamics of soil microbiomes and their diversity under contrasting disturbances. This information is required to mitigate environmental pollution and mitigate agro-ecosystem contamination.

Metatranscriptomics is considered to be advanced technology to capture functional gene expression patterns in soil microbiomes and subsequently investigates their responses to environmental perturbations. The effect of a change in environmental condition/disturbance on the response of soil microbiomes as revealed by metagenomics and metatranscriptomics was comprehensively illustrated in Fig. 18.2. A small change in the soil environment (temperature, pH or any disturbance) is unlikely to change any significant soil microbiome community composition. This could be due to physiological plasticity and flexibility within the prevailing microbiome (Terzaghi and O'Hara 1990; Prosser 2015). However, a little environmental change in the soil-ecosystem could lead to a subtle change in both metabolic profiling and activity which can be reflected in metatranscriptomics. Such type of responses would not be traced in metagenomes as discussed earlier (Prosser 2015); A moderate environmental impact could lead to a change in the distribution of the different phylotypes at the metagenomics level. However, at the metatranscriptomics stage, one can notice a relative change in the expression of new genes which belong to phylotypes adapted to environmental disturbance. A change in the relative expression of existing transcripts was also noticed at the metatranscriptomics level. Large and extreme changes in the soil environment could possibly make either expression of new RNA transcripts (At metatranscriptomics level) or extinction of susceptible phylotype or the invasion of new species at metagenomics level. Extreme changes in the soil-ecosystem may also induce mutations/adaptations in existing phenotypes subsequently expression of new genes contributes to a different kind of metatranscriptome. Table 18.2 summarizes the important observations in microbiome research with response to soil physical, chemical and biological disturbances.

The diversity and species richness of soil bacterial communities differed by type of the ecosystem (Table 18.2; Fierer et al. 2009, Fierer and Jackson 2006). The differences in microbiome structure were largely explained by soil pH. Higher bacterial diversity was observed in neutral soils whereas lower bacterial diversity was noticed in acidic soils (Wu et al. 2017). Results suggested that microbial biogeography is primarily controlled by edaphic variables which are different from the biogeography of "macro" organisms (Fierer and Jackson 2006). The abundance and composition of soil microbiomes were greatly influenced by soil pH. This could be due to the mechanism of the pH for mediation of nutrient availability in the soil. Bacterial genera such as *Bradyrhizobium, Bacteroides*, *Clostridium*, *Mycobacterium*, *Paenibacillus*, *Rhodoplanes* and *Ruminococcus* were abundant in the soil (Zhalnina et al. 2015; Wu et al. 2017).

Land-use patterns and system restoration activities showed a greater effect on soil microbiomes (Sui et al. 2019). The diversities of fungi, bacteria, and *Acidobacteria* were influenced by the change in land-use patterns. A low abundance of bacteria, *Acidobacteria* and fungi were noticed in the wetlands and their abundance was substantially increased in arable land (Sui et al. 2019). The composition of soil microbiomes was altered by changing land use. The community structure of soil microbiomes was influenced by seasons and the diversity was shaped principally by water scarcity. A higher abundance of *Proteobacteria* and *Actinobacteria* were noticed in the rainy and dry seasons, respectively. In addition to this, the availability of nutrients also showed a significant role in shaping the microbiome assemblages in soils under agriculture management. Soil microbiomes were greatly influenced by agriculture practices and showed contrasting genetic potential for C acquisition and biogeochemical cycling (Lacerda Júnior et al. 2019).

18.4 Limitations of Soil Metagenomics/Metatranscriptomics

Soil metagenomics and metatranscriptomics have certain limitations and biases as like as in any other molecular techniques. These limitations are mainly confined to protocols that are related to lysis of microbial cells, genomic DNA/RNA extraction along with sequencing errors (Lombard et al. 2011). The stability of the extracted nucleic acids (DNA or RNA) has also posed a major problem in soil metagenomic studies. There are certain main limitations found in absolute quantification and accurate annotation of sequenced genes. Therefore, complete soil metagenome or metatranscriptome coverage is very difficult to achieve; for instance, Howe et al. (2014) in a study reported that deep coverage of the majority of a soil microbiomes was not accomplished, even after processing 398 billion base pairs of sequence data. It was highlighted that sixty percent of proteins predicted in sequencing data were not matched with existing databases indicating the limitations of the existing databases, for example, Genomes Orthology database and Kyoto Encyclopedia of Genes. Further, they suggested that more deep sequencing data are required to characterize the functional content of soil microbial communities. More importantly "Omic techniques" require substantial computational resources to annotate and predict the genes obtained through De novo metagenomic assembly.

Functional gene identification in a metagenomics library is not a substantiated proof of its expression at the RNA level or its activity at the protein level. The qualitative presence of functional gene may be cryptic in nature and the gene transcript could not be translated or the host organism may be inactive or dormant. One should be noted that the prevailing environmental conditions such as temperature, pH, water availability and substrate concentra-tion may likely inhibit the activity of the functional gene product. The amount of a particular enzyme in the soil may be accurately reflected by quantitative soil metagenomic data, but it would not deliver much information about the process rate/metabolic flux. It is a well-known phenomenon that the cellular flux of metabolites in a metabolic pathway relies on the available quantities of other co-enzymes and enzymes of the same metabolic pathway (Kacser 1983). Accordingly, the potential metabolic flux of the related pathway could not be sensitive to different quantities of the encoding gene. Prosser et al. (2015) opinioned that metagenomics may not provide complete information related to physiological characters, for example, susceptibility to predation, optimum pH and temperature for growth, minimum and maximum specific growth rates, saturation constants, etc. A small change in a soil environment (temperature, pH or any disturbance) is unlikely to induce any change in soil microbiome community composition. This could be due to plasticity and flexibility within the prevailing microbiome (Terzaghi and O'Hara 1990; Prosser 2015). However, it is noticed that a small change in soil environment may lead to subtle changes in metabolic profiling and activity. Such type of responses would not be traced in metagenomes (Prosser 2015).

Drawing correlations between soil physicochemical characteristics and metagenomic data for obtaining meaningful information is difficult. This could be due to temporal and spatial heterogeneity of soil matrix which will separate substrates physically from cells that contain a functional gene involved in the metabolism of those substrates (Prosser 2012; Schimel and Schaeffer 2012). The fundamental quest in soil microbiome research is how soil microbial diversity is produced and maintained. Conventionally, the fundamental processes that are responsible for inducing genetic diversity in species are defined as evolutionary processes which include genetic drift, gene flow, mutation, and selection (Hartl and Clark 2007). Conversely, the fundamental forces that are driving diversity among species are in general referred to as ecological processes which include ecological drift, selection, speciation and dispersal (Vellend 2010; Zhou and Ning 2017). Metagenomics, or metatranscriptomics may not deliver much information to understand these fundamental ecological mechanisms that are driving soil microbial communities.

Although metagenomic sequencing can provide certain information on great plate count anomaly, it is fundamentally difficult to understand the functionality of metabolic pathways of uncultivable microbes in soil (Stewart 2012). Cultivation of uncultivable soil microbiota in the laboratory is necessary to understand complete physiology and their functional roles in soil microbial ecology and host plant improvement. Stewart (2012) discussed advancements made in co-culture technique suitable for growing uncultivable microbes in the laboratory by providing in situ environment. Further, a novel “micro-cultivation technology” to increase more resolution and exploit rare microbial species from the complex environment was highlighted in the same study.

18.5 Future Prospects in Soil Microbiome Research

18.5.1 Biodiversity and Biogeography

Six distinct biogeographical regions are found on the Earth’s surface (Lomolino et al. 2006). The biogeographic regions are defined as land surface areas that harbor distinctive plants, animals and other biota. The distribution of specialized biotas is hypothesized to exist due to evolutionary events such as vicariance, separation and dispersal of species by various barriers (Womack et al. 2010). Much emphasis was given to the distribution of microbiota and the corresponding ecosystem processes that underlie species distribution. Gourmelon et al. (2016) inferred that microbial species distribution, abundance, richness were related to the type of surface vegetation and the prevailing plant species. Each plant possesses its specialized microbiome because of multifactorial linkages between abiotic and biotic factors in contrasting geographical regions (Gourmelon et al. 2016). Dispersal limitation in the context of the biogeographical-island theory proposed by MacArthur and Wilson (1963), can explain differences in microbiomes of various geographical locations (Gourmelon et al. 2016). Similar observations were reported by Malard et al. (2019) wherein spatial and edaphic factors played an important role in the structure of Arctic soil bacterial communities. It was elucidated that pH as the key environmental driver shaping Arctic soil bacterial communities. However, still, our understanding of the different processes of the biosphere is limited. Therefore, polyphasic studies should be carried out to understand the biosphere, one that links knowledge about biodiversity and biogeography in the atmosphere, hydrosphere and lithosphere (Hanson et al. 2012; Womack et al. 2010).

Gaston (2000) described that species richness is found to be higher in the tropics and gradually declines toward the poles. Molecular studies focused on the continental scale distribution and diversity of soil microbiomes revealed a lot of uncertainty in the global biogeography of soil biota due to a lack of data on patterns. Unraveling the factors that regulate soil microbiomes, biogeographical distribution, succession and functions are poorly understood in soil microbiology. Stochastic processes are thought to have minimal roles in driving soil microbiomes and their functions in the ecosystem process (Zhou and Ning 2017). It is believed that heterogeneous selection by different biotic and abiotic environmental conditions making for more dissimilar and more diversified microbial structures among microbiomes. This type of selection is known as variable selection (Zhou and Ning 2017) and we anticipate that variable selection is one of the major underlying forces in leading diversified microbiomes in soils at the global scale. It is demonstrated that biodiversity is of paramount importance for ecosystem functioning (Cardinale 2012; Knelman and Nemergut 2014; Bardgett and Van Der Putten 2014), but the underlying forces driving the relationships between microbial communities and ecosystem functioning are still not clear. A few studies indicate that stochastic processes are important for regulating both microbial community structure and corresponding ecosystem functions (Fukami et al. 2010; Zhou et al. 2013). Nevertheless, systematic studies across diverse ecosystems are necessary to understand whether stochastic community assembly processes affect ecosystem functioning or not.

18.5.2 Sustainable Soil-Ecosystem Management

Recent studies unraveled that soil biodiversity is crucial to support several ecosystem functions simultaneously (Delgado-Baquerizo et al. 2016; Wagg et al. 2014). It is observed that intensive management of agricultural practices, for example, indiscriminate use of pesticides, fertilizers, soil tillage and monocropping have adverse effects on soil biota consequently reduce overall soil microbial biomass and diversity (McDaniel et al. 2014). An apparent microbial community shift in soil microbiomes was observed because of intensive land-use management practices (Tardy et al. 2015). Similarly, Philippot et al. (2013) emphasized that the loss in microbial diversity affects nitrogen cycling and other terrestrial ecosystem process. Therefore, soil microbial diversity has to be enhanced and maintained for the proper functioning of agro-ecosystem. It is proposed that sustainability in agricultural soils can be maintained by regulating internal ecosystem processes (Hota et al. 2021; Bender et al. 2016; Kumar et al. 2019a, b; Kumari et al. 2020; Rai et al. 2020). Recently, soil ecological engineering has gained a lot of momentum and is considered to be an important concept to enhance sustainable productivity in human land-use systems (Bender et al. 2016).

Soil ecological engineering is a comprehensive approach wherein soil biological processes are maximized for sustainable ecosystem functioning. This is one of the holistic approaches to minimize negative environmental impacts in agro-ecosystems and provide global food security. Figure 18.3 illustrates different soil ecological engineering approaches for local ecosystem management. Bender et al. (2016) comprehensively reviewed soil ecological engineering and biodiversity for sustainable agriculture/human land-use systems.

Agro-ecosystems are generally characterized into extensive and intensive systems with a different rate of productivities. The extensive agro-system is accompanied by high biodiversity, low resource output and inputs, low level of productivity and enhanced internal soil regulatory processes. While the intensive agro-system is characterized by depleted biodiversity, high resource inputs-losses, high rate of productivity and decreased internal soil regulatory processes. Both of these systems have merits and demerits in terms of productivity and internal soil regulatory processes. Therefore, the ecological intensification approach needs to be implemented to bring sustainability in ecosystem multifunctionality. Bender et al. (2016) describe that the ecological intensification approach combines both traits (extensive and intensive agrosystems) and leads to an ideal sustainable agro-ecosystem that comprised rich biodiversity, moderate resource inputs/low nutrient losses, higher productivity and enhanced internal soil regulatory process. The ecological intensification approach further maximizes agro-ecosystem multifunctionality.

18.5.3 Rhizosphere Microbiome—Plant Health

Rhizosphere microbiomes that are assembled near roots can harbor up to 10^{-11} microbial cells and approximately 30,000 different microbial species per gram of root (Sharaff et al. 2020; Egamberdieva et al. 2008). Rhizosphere microbiomes are considered to be one of the complex-ecosystems on the Earth (Kour et al. 2019; Subrahmanyam et al. 2020; Weinert et al. 2011; Raaijmakers et al. 2009). Rhizosphere microbiomes utilize a diverse array of metabolites released by plant roots (Lu et al. 2018). Microbiomes of the rhizosphere are rich in diverse plant growth-promoting fungi and bacteria (Subrahmanyam et al. 2018, 2020; Sharaff et al. 2020; Kour et al. 2019). The density and distribution of microbial population in the root rhizosphere are much higher than in the bulk soil and this phenomenon is known as the “rhizosphere effect.” Increased plant growth is associated with enhanced plant defense mechanisms. Root microbiome plays important role in conferring host plant health (Berendsen et al. 2012). It is evidenced that the plant is able to recruit a wide variety of microbial populations as its microbiome by secreting root exudates (Ahemad and Kibret 2014; Rana et al. 2020; Subrahmanyam et al. 2020).

Several abiotic and biotic factors are found to be critical for rhizosphere microbiome diversity and species richness. Abiotic factors, such as seasonal variation, pH, soil temperature, root exudates/chemical substances and biotic factors such as developmental stages of host plants, root architecture, cultivars and host plant genotypes act as chemical messengers for heterogeneous soil microbiota and subsequently influence the microbiome structure and function (Lakshmanan et al. 2014; Kumar et al. 2019a, b; Verma et al. 2016; Verma et al. 2017; Yadav et al. 2019). The rhizospheric microbes can induce a series of plant defense mechanisms for host plant growth and health. Induced systemic resistance (ISR) is one of the defense mechanisms of plants induced by PGPR to increase vigor and the health of their host plant against invading pathogen (Pieterse et al. 2014). Recently, excellent reviews on rhizospheric microbiomes, plant growth-promoting characteristics and their potential agricultural applications are published (Berendsen et al. 2012; Subrahmanyam et al. 2020; Sharaff et al. 2020).

Rhizosphere microbiomes harbors both useful and harmful microbiota and can control host plant physiology, growth and development (Subrahmanyam et al. 2020; Subrahmanyam et al. 2018; Sharaff et al. 2020). Further, the healthy mcirobiomes can prevent plant infection by controlling the pathogen colonization by either competing or producing antimicrobial compounds such as siderophores, 2,4-diacetylphloroglucinol, polymyxin, colistin, etc. (Maksimov et al. 2011). The regulation of the plant defense system is generally involved by different phytohormones such as ethylene, jasmonic acid and salicylic acid (Pieterse et al. 2014). Beneficial rhizospheric microbes' triggers induced systemic resistance by modulating salicylic acid.

The key functions of rhizosphere microbiome include protection against plant pathogen infection, nutrient acquisition and abiotic stress tolerance in host plants. Therefore, it is essential to understand the molecular signaling mechanisms between host plant and microbiome assembly in the rhizosphere by using functional metagenomics and transcriptomics. This information can be exploited to develop soil management practices for increasing plant productivity, designing healthy rhizomicrobiomes and introduction of novel biocontrol and bio-fertilizer microbes in sustainable agricultural strategies. Unraveling the mechanisms such as how plants recruit their selective microbiome and how the rhizosphere microbiome controls host plant health will open new avenues to increase crop productivity.

18.5.4 Climate Change and Soil Microbiomes

Soil microbiomes perform crucial functions in the elemental cycling of micro and macronutrients which are vital for the functioning of the above-ground ecosystem. Nevertheless, still we do not have a general framework at a global scale for predicting microbiome responses and their ecosystem services to climate change. Recently, Jansson and Hofmockel (2020) comprehensively reviewed the effect of climate change on soil microbiomes in diverse soil ecosystems. Mekala and Polepongu (2019) highlighted the effects of climate change viz. elevated temperature, precipitation, drought and atmospheric CO_2 on beneficial plant–microorganism interactions. Further, they have emphasized that k-strategist or oligotrophic microbial groups and their abundance are increased under high temperature or drought and their abundance significantly decreased with elevated CO_2. In contrast, r-strategist or copiotrophic microbial groups shown potential resilience after the disturbance or stress has ended. Studies on climate change have shown both negative and positive impacts on soil microbial communities (Mekala and Polepongu 2019). In arid grasslands, Yu et al. (2018) observed increased expression of functional genes involved in carbon fixation, nitrogen fixation, CH_4 metabolism, decomposition, denitrification, and nitrogen mineralization under elevated atmospheric CO_2 levels.

It is observed that soil respiration, soil organic matter decomposition and microbial biomass content were increased with increased temperature (Bradford et al.

2008). Long-term experiments on the elevated temperature at Harvard Forest Ecological Research Station revealed microbial community reorganization, diversity shift toward oligotrophic communities, rapid loss of carbon through respiration in the heated plots than in control soils. A change in microbiome community structure followed by reduced recalcitrant carbon pools was observed in the same study (Melillo et al. 2017). Multiyear field experiments and Mesocosm studies revealed that draught had a more negative impact on bacteria than fungi in grasslands (Upton et al. 2018; de Vries et al. 2018).

The residential soil microbiomes can either adapt and or dormant or extinct in response to climate change. Depending on their physiological and genetic potential, soil microbiomes respond to environmental disturbances in contrasting ways (Schimel et al. 2007). For example, Hayden et al. (2012) reported community shifts of fungi, archaea and specific bacterial groups under elevated CO_2 in Australian grasslands. Mekala and Polepongu (2019) proposed that specific functional genes involved in the N and C cycles can be used to predict the consequences of climate changes on soil microbial community composition in soil functioning.

Around 30% of the land surface area is occupied by forests and forest soil ecosystems are the major potential sinks for atmospheric carbon as a stable soil organic matter (Llado et al. 2017). However, it is predicted that because of increasing global temperature and severity of drought, these forest ecosystems may get converted from net carbon sinks to net carbon sources globally in the coming future (Kirschbaum 2000). This could be due to increased soil organic matter degradation by microbial activity (Kirschbaum 2000). A similar kind of observations was made with grasslands which occupy approximately 26% of the earth surface land area and store around 20% of total soil carbon (Ramankutty et al. 2008; Malyan et al. 2019). Therefore, potential ways and strategies for predicting the response of soil microbial activity and diversity to climate change needed to be developed and accordingly soil microbiomes may be exploited to mitigate the negative impacts of climate change.

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Chapter 19
Functional Annotation and Biotechnological Applications of Soil Microbiomes: Current Research and Future Challenges

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Abstract The tiny organism of soil, known as soil microbes have several functional annotations like nutrients cycling and their fixation, mineralization and solubilization, alleviation of biotic caused by pest-insects, microbial pathogens as well as abiotic stresses by harsh environmental conditions, degradation of polluting elements in the environment. Their functional abilities can be utilized in the different fields of biotechnology i.e. environment and agriculture because these are one the best sustainable technique over others like conventional methods as already environment is heavily polluted by the activities of mankind. In agriculture, soil microbes can be used as a biofertilizer and biopesticides. Soil microbes as biofertilizers help in providing nutrients like nitrogen, phosphorus, potassium, zinc and iron. Along with nutrients, these microbes also help in releasing plant growth regulators that help in increasing plant development. These use various mechanisms like fixation, solubilization and scavenging (of iron) for providing nutrients. Soil microbes also help in alleviating biotic stress by releasing antibiotics, siderophores and hydrogen cyanide to kill unwanted or pathogenic pest and microbes. Such microbes can also be applied in the environment for various applications like alleviation stress, pollution which cannot be degraded naturally. The present chapter deals with the functional annotation and biotechnological applications of beneficial soil microbiomes for agricultural sustainability.

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19.1 Introduction

The micro-miracle, microbes are known to be present in each and every habitat of the planet earth including soil, air and water ecosytems. There they play some important hidden roles such as maintaining the environmental cycles like carbon, nitrogen, weathering of rocks, formation of fossil fuels and many more without which earth is are incomplete and can be destroyed (Gougoulias et al. 2014; Prasad et al. 2021; Yadav et al. 2021b). Microbes residing in the soil are diversified as bacteria, fungi, archaea and protozoa that plays such roles for the earth and have various functional abilities like mineralization of soil minerals like phosphorus, potassium, zinc, iron, selenium, calcium and sulfur, the release of various types of growth regulators like auxin, cytokinin, gibberellins, abscisic acid and ethylene (Alori et al. 2017; Egamberdieva et al. 2017; Kour et al. 2021a).

These soil microbes have also a have ability to alleviate various types of stresses of the environment i.e. biotic and abiotic. In biotic stress alleviation, soil microbes are used to control the different types of biological pathogens growth like insects, bacteria and fungi by releasing various types of antibiotics and hydrogen cyanide, competing with the nutrient's availability (Gómez Expósito et al. 2017; Dikilitas et al. 2021; Tiwari et al. 2021). Whereas, in abiotic stress, soil microbes undergo mechanisms like a release of ACC deaminase, reactive oxygen species by which various types of abiotic stress can be alleviated such as cold stress, temperature stress, water stress weather flooding conditions or rainfed conditions, salt stress in the soil and available heavy metals (Khan et al. 2020; Selvakumar et al. 2012; Suyal et al. 2021; Yadav et al. 2021a). Pollution remediation is also one of the functional abilities of the soil that helps in converting hazardous compounds into less toxic compounds that can be degradable in the soil (Kushwaha et al. 2018; Sharma et al. 2021).

All the functional abilities of the soil microbes can be used in various fields like agriculture and in the environment (Kour et al. 2020b). In agriculture, plant yield is one the most important criteria for the farmers to produces more crop products and earning more money. Over the past five decades, the required yield of the crop products was achieved by using various chemical products because of the depleted fertility and nutrients of the soil (Yadav et al. 2021c). Such chemical-based products are also used for controlling the different types of insect-pest, microbial pathogens. The use of such chemical-based products are ruining the soil structure by depleting fertility and increase of chemical pollution that effects not only the plant production or micro-lives living in soil but also effects the whole environment by causing environmental pollution. The soil microbes are one of the sustainable techniques to be used in the agriculture fields as their abilities can help in filling all the voids of farmers as well (Yadav et al. 2020d). These microbes present in the skin of the earth can also be used in solving environmental problems in a sustainable way (Kour et al. 2020c; Hesham et al. 2021; Yadav 2021a, b). As they help in degrading the pollution spreader by the mankind activities. All these above-mentioned functional annotation of soil microbiomes (archaea, bacteria and eukarya) and their potential biotechnological applications in agricultural and environmental sectors have been discussed in detail in this chapter.

19.2 Role of Soil Microbiomes in the Natural Ecosystem

Earth, the natural supplier of the various essential elements to every living organism like hydrogen, oxygen, carbon, sulfur, nitrogen, phosphorus, potassium, zinc and iron (Gougoulias et al. 2014). These all the elements essential minerals of a different organism, but they are present in a complex and stable form that cannot be utilized as such. These elements in this closed system are availed by the beneficial soil microbes (Viles 2012). Soil microbes are having the ability to break down the complex matter as they have several coding genes for enzymes that help in the fixation, solubilization and mineralization (Rastegari et al. 2020a, b; Patil et al. 2021). In the environment, microbes plays a role in breaking of dead organic matter which can be utilized by a different organism for various biological processes. Soil microbes are also involved in the cycling of various elements in the different habitats like carbon, nitrogen, oxygen-hydrogen, phosphorus, potassium, zinc and iron which are present in the ores and complex form (Akob and Küsel 2011). Apart from the biogeochemical cycles soil microbes are also help in the degradation of toxic elements and ultimately helps in the cleaning the earth's surface (Kushwaha et al. 2018).

19.3 Functional Annotation of Soil Microbiomes

19.3.1 Nutrients Acquisition

Soil microbiomes play a vital role in the circulation of plant nutrients. These microbes as bio-inoculants are being used across the world to improve the yield and nutrient status of agricultural ecosystems. The beneficial plant–microbe associations signify a promising sustainable solution to enhance productivity and reduce the diverse chemical fertilizers used.

19.3.1.1 Nitrogen

Nitrogen is the 7th abundant element of the universe and also the most common element in the atmosphere. Despite its abundance in the soil, it is still unavailable to the plants due to insoluble forms. Soil microbiomes are capable of fixing atmospheric N_2 and convert di-nitrogen into NH_3, which is then taken up by the plants (Singh et al. 2019). BNF is a significant process for determining nitrogen balance in the soil ecosystem. The inputs of the nitrogen through this process sustain environmentally sound agricultural production (Mohammadi and Sohrabi 2012). The bacteria possessing nitrogen-fixing ability belong to the genera *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium, Rhizobium,* and *Sinorhizobium* together termed as Rhizobia and the most remarkable relationship these have with plants is symbiosis. Free-living nitrogen fixers include *Acetobactor diazotrophicus, Azoarcus* sp., *Azospirillum amazonense, A. brasilense, A. lipoferum, Azotobactor* sp., *Burkholderia brasilensis, B. kururiensis, B. phynatum, B. tropicalis, B. tuberum, B. vietnamiensis, Herbaspirillum* sp. and *Pseudomonas* sp. i.e., they provide direct N nutrition to plants (Yadav et al. 2020d). Fixed nitrogen is then taken up through root uptake which contributes to the nitrogen account of the crop.

19.3.1.2 Phosphorus

Phosphorus (P) is the second vital nutrient for plants after nitrogen. An adequate supply of the P is important for diverse functions and metabolic activities of the plants (Khan et al. 2014). But the majority of the P is unavailable to the plants due to its fixation and insolubility (Kour et al. 2020c). Soil microbiomes possess the ability to transform insoluble form to soluble form which is then available to plants. Phosphorus solubilizing microbiomes use different mechanisms for this conversion such as they release organic acids such as citric, fumaric, gluconic, propionic and tartaric Yadav et al. (2015) which act as good chelators of divalent cations of Ca^{2+}, which releases phosphates from insoluble phosphatic compounds. In other way, the released organic acids sometimes form soluble complexes with metal ions in association with insoluble phosphorus and release phosphate (Jha and Saraf 2015). Phosphorus solubilizing capability has been observed in diverse soil microbial genera viz, *Acinetobacter, Arthrobacter, Aspergillus, Bacillus, Brevibacterium, Burkholderia, Leclercia, Pantoea, Pseudomonas, Raoultella, Serratia,* and *Trichoderma* (Pei-Xiang et al. 2012; Sharma 2011; Yasser et al. 2014). Thus, the use of P-solubilizing microbes is an environment-friendly approach for providing inexpensive P to plants.

19.3.1.3 Potassium

After phosphorus and nitrogen, potassium (K) is the third essential macronutrient necessary for the growth of plants (Kasana et al. 2017). In soil, the soluble K concentrations are normally very low and more than 90% of K exists in the form of insoluble rocks and silicate minerals. India entirely depends on the import of potassic fertilizers and farmers use either very little or no potassium in crop production. Thus it becomes very important to explore efficient microbial K-solubilizing strains for using them as bioinoculants and further reducing the use of agrochemicals. *Aspergillus, Bacillus, Exiguobacterium, Fomitopsis, Paenibacillus* and *Planococcus* have reported K-solubilizing genera (Gore and Navale 2017; Kasana et al. 2017; Verma et al. 2016).

19.3.1.4 Zinc

Zinc is a relatively soft, bluish-white metal essential for the proper functioning of enzymes. It occurs in distinct forms in the soil such as smithsonite, sphalerite, zincite, zinc silicates, zinc sulfide and willemite. Zn is unavailable to plants due to its poor mobility and hence supplied in the form of zinc chemical fertilizers (Kour et al. 2019b). Microbial zinc solubilization plays a versatile role in enhancing the bioavailability of zinc to plants. Microbes work by releasing Zn from its unavailable complexed form to plant accessible form (Saravanan et al. 2011). The reported zinc solubilizers include *Abisidia, Aspergillus, Phomopsis,* and *Penicillium* (Coles et al. 1999; Franz et al. 1993; Saravanan et al. 2011; Sutjaritvorakul et al. 2013).

19.3.2 Release of Plant Growth Regulators

Development and growth of the plants involve coordination of spatial and temporal organization of cell division, differentiation and expansion and the occurrence of such events actually requires the exchange of the signaling molecules between shoot and root (Jha and Saraf 2015). Plant growth regulators play a major role in the development and growth of the entire plant and are active in very minute quantities (Fuentes-Ramirez and Caballero-Mellado 2006). These growth regulators regulate many aspects of growth promotion through a range of biochemical and physiological means to ensure successful completion of the life cycle of plants (Singh et al. 2020; Tiwari et al. 2020). Plant–microbe interactions have been known for decades and are of great interest as these associations are highly beneficial for the development of new agricultural applications. Beneficial soil microbial communities are also known to produce different plant growth regulators including gibberellins, cytokinin, and auxin. Indole-3-acetic (IAA) acid is a major plant hormone involved in cell division and differentiation, vascular development, germination and root growth (Etesami and Beattie 2017). IAA production has been reported in archaea, cyanobacteria, methylobacteria, and streptomycetes. Additionally, it has been estimated that 80% of soil bacteria exhibit the ability to produce IAA (Khalid et al. 2004). IAA production has been also known in *Arthroderma cuniculi* (Karmakar et al. 2018), *Aspergillus niger* (Wang et al. 2018b), *Curvularia geniculata* (Priyadharsini and Muthukumar 2017) and *Penicillium menonorum* (Babu et al. 2015).

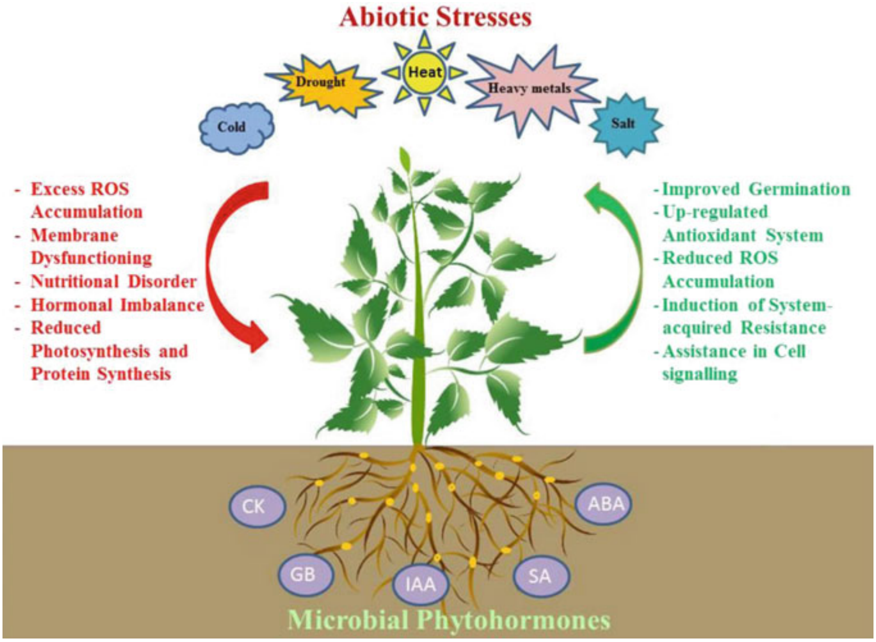

Fig. 19.1 Role of phytohormones in the alleviation of abiotic stresses in plant (Egamberdieva et al. 2017)

Gibberellins (GAs) are tetracyclic diterpenoid acids, *ent*-kaurene derivatives involved in increasing the rate of flower and fruit development, leaf growth, seed germination and stem elongation (Agafonova et al. 2018). Gibberellins production has been known in *Bacillus licheniformis* and *Bacillus pumilus* (Gutiérrez-Mañero et al. 2001). Fungal species including *Aspergillus niger, Neurospora crassa* and *Sporisorium reilianum* have been identified to either produce gibberellins during their growth or contain GAs biosynthesis gene clusters (Khan et al. 2015). Cytokinins increase cytokinesis in shoots and roots. It regulates stomatal opening, inhibits leaf senescence and plays a significant role in apical dominance. Cytokinin production has been demonstrated in *Arthrobacter, Azospirillium, Azotobacter, Bacillus, Rhizobium* and *Pseudomonas*. Different reports have also shown a positive impact of cytokinin-producing beneficial bacteria on plant growth during stress conditions (Fig. 19.1).

19.3.3 Amelioration of Biotic Stresses

Biotic stress is stress caused by micro and macro-pathogens such as bacteria, fungi, virus, nematodes, insects, and weeds on plants. This stress usually contributes to huge economic losses caused by cash crops, due to this it is considered as a major subject of agricultural research. It is estimated that the global loss due to these pathogens is 12% of potential crop productivity (Kumar et al. 2021a). Out of all pathogens, fungus is considered as the most divested pathogen which dramatically declines the crop yield (Yadav et al. 2020a). The major foliar diseases caused by fungi were reported as rusts, downy mildew and powdery mildews. Disease rust is caused by several species of genus *Puccini* including *Puccinia graminis* on the rust of wheat, *Puccinia sorghi* on forage legumes and maize (Ramteke et al. 2004).

Root rot caused through the *Fusarium solani*, *Rhizoctonia solani* and *Aphanomyces euteiches* in which the disease caused by *Fusarium solani* is the most critical soil-borne pathogen infecting the pea and chickpea (Infantino et al. 2006). The damping-off disease is another disease caused by fungi known as *Rhizoctonia solani* or *Pythium* spp., which can lead up to 80% plant death (Wang et al. 2003). Fusarium root rot caused through the species of *Fusarium* can also cause numerous seedling losses, especially in common tomato and lentils. In the most growing areas of the worlds, the disease affects seedlings and adult plants in which chlorosis of the skin, wilting and ultimately death occurs. Other major soil-borne diseases like southern stem rot (*Sclerotium rolfsii*) and white mold (*Sclerotinia sclerotiorum*) also affect the seedling and pod in cool and warm weather (Kolkman and Kelly 2003). Various studies support the promotional plant growth and improved disease ability such as *Pseudomonas* spp., *Trichoderma* spp. and *Bacillus* spp., on a variety of host plants including Arabidopsis, pepper, wheat, tomato, radish, okra, pigeon pea, pea and chickpea (Chauhan and Bagyaraj 2015).

19.3.4 Amelioration of Abiotic Stresses

Abiotic stress is the stress created by adverse climatic conditions that also restrict crop productivity. In nature, stress is a combined effect of multiple functioning unity rather than a single incident (Mahajan and Tuteja 2005). On earth, various types of stresses like drought, temperature extremes like cold and hot, salinity, heavy metals and water flooding exists, which result in reduction of plant growth and a substantial decrease in crop yield and productivity (Ramegowda and Senthil-Kumar 2015) (Table 19.1).

19.3.4.1 Temperature Stress

Low and high temperature are diverse abiotic stresses. Among these and other stresses low temperature is considered as a major limiting factor as 20% of the earth surface is filled with frozen soil, frozen soils (permafrost), glaciers and snow that adversely affects the productivity of agricultural products. In recent years, the diverse range of microbes inhabiting in low temperatures environments, which are known as psychrophilic microbes, has been thoroughly

Table 19.1 Soil microbiomes and thier potenatial biotechnological implications for alleviation of abiotic stress

Rhizobacteria inoculants	Stress condition	References
Acinetobacter pittii JD-14	Water stress	Daur et al. (2018)
Arthrobacter protophormiae (SA3)	Salinity stress	Barnawal et al. (2017)
Arthrobacter scleromae OB149	Cold stress	Subramanian et al. (2016)
Arthrobacter sp. SU18	Salinity	Upadhyay et al. (2012)
Arthrobacter sp.	Salinity, high pH	Banerjee et al. (2010)
Bacillus sp.	Salinity, high pH	Banerjee et al. (2010)
Aspergillus niger	Drought/salinity	Xiao et al. (2011)
Penicillium simplicissimum	Drought/salinity	Xiao et al. (2011)
Aspergillus japonicas	Drought/salinity	Xiao et al. (2011)
Aspergillus niger, F7	Salinity	Srividya et al. (2009)
Penicillium sp.	Salinity	Srividya et al. (2009)
Aspergillus usrus	Drought	Barrow and Osuna (2002)
Azospirillum brasilense Ab-V6	Salinity	Fukami et al. (2018)
Azospirillum spp.	Drought	Arzanesh et al. (2011)
Azotobacter chroococcum CAZ3	Heavy metal	Rizvi and Khan (2018)
B. amyloliquefaciens S-134	Drought	Raheem et al. (2018)
B. thuringiensis S-26	Drought	Raheem et al. (2018)
Bacillus amyloliquefaciens Bk7	Cold stress	Kakar et al. (2016)
Bacillus aquimaris DY-3	Salinity	Li and Jiang (2017)
Bacillus aryabhattai H26-2	High temperature	Yoo and Sang (2018)
Bacillus atrophaeus EY6	Salinity	Karlidag et al. (2013)
Bacillus cereus AR156	Cold stress	Wang et al. (2016)
Bacillus megaterium BOFC15	Water stress	Zhou et al. (2016)
Bacillus pumilus,	Salinity	Ali et al. (2017)
Bacillus siamensis H30-3	High temperature	Yoo and Sang (2018)
Bacillus sp. (MN54)	Salinity stress	Yang et al. (2016)
Bacillus sp. AZ-1	Heavy metal	Amin and Latif (2017)
Bacillus sp. CIK-516	Heavy metal	Akhtar et al. (2018)
Bacillus subtilis EY2	Drought	Karlidag et al. (2013)
Bacillus subtilis LDR2	Drought	Barnawal et al. (2017)
Bacillus subtilis RJ46	Drought	Saikia et al. (2018)
Bacillus subtilis SM21	Cold stress	Wang et al. (2016)
Bacillus subtilis SU47	Salinity	Upadhyay et al. (2012)
Brevibacillus laterosporus B4	Cold stress	Kakar et al. (2016)
Burkholderia phytofirmans PsJN	Temperature stress	Bensalim et al. (1998)
Burkholderia phytofirmans PsJN	Temperature stress	Su et al. (2015)

(continued)

Table 19.1 (continued)

Rhizobacteria inoculants	Stress condition	References
Citrobacter freundii J118	Water stress	Upadhyay et al. (2011)
Dietzia natronolimnaea (STR1)	Salinity stress	Barnawal et al. (2017)
Enterobacter aerogenes S-10	Drought	Raheem et al. (2018)
Enterobacter cloacae AZ-3	Heavy metal	Amin and Latif (2017)
Enterobacter cloacae HSNJ4	Salinity	Li and Jiang (2017)
Enterobacter cloacae ZNP-3	High temperature	Singh and Jha (2017)
Enterobacter sp. (MN17)	Salinity stress	Yang et al. (2016)
Enterobacter sp. P23	Salinity	Sarkar et al. (2018)
Enterobacter sp. S16–3	Osmotic stress	Oskuei et al. (2018)
Enterobacter sp.UPMR18	Salinity stress	Habib et al. (2016)
Eupenicillium parvum NRRL 2095	Salinity, acidity	Vyas et al. (2007)
Exiguobacterium sp. AM25	Salinity	Ali et al. (2017)
Flavobacterium phocarum, SE14T	Cold stress	Zhou et al. (2012)
Flavobacterium sp. OR306	Cold stress	Subramanian et al. (2015)
Flavobacterium sp.OS263	Cold stress	Subramanian et al. (2016)
Klebsiella sp. IG 3	Salinity	Sapre et al. (2018)
Klebsiella sp. SBP-8	Salinity	Verma et al. (2017)
Klebsiella variicola	Flooding	Kim et al. (2017)
Klebsiella variicola F2	Drought	Gou et al. (2015)
Kocuria erythromyxa EY43	Salinity	Karlidag et al. (2013)
Massilia sp. OS123	Cold stress	Subramanian et al. (2016)
Ochrobactrum pseudogrignonense RJ12	Drought	Saikia et al. (2018)
Pedobacter sp. OS312	Cold stress	Subramanian et al. (2016)
Penicillum citrinum	Salinity	Yadav et al. (2011)
Pseudomonas aeruginosa PRR1	Salinity	Kumar et al. (2017)
Pseudomonas aeruginosa strain OSG41	Metal stress	Oves et al. (2013)
Pseudomonas fluorescens FY37	Salinity	Bazyar et al. (2017)
Pseudomonas fluorescens MSP-393	Salinity stress	Paul and Nair (2008)
Pseudomonas fluorescens YX2	Drought	Gou et al. (2015)
Pseudomonas fragi CS11RH1	Cold stress	Selvakumar et al. (2009)
Pseudomonas frederiksbergensis OS210	Cold stress	Subramanian et al. (2016)
Pseudomonas frederiksbergensis OS211	Cold stress	Subramanian et al. (2015)
Pseudomonas jessani PGRs1	Cold stress	Mishra et al. (2011)
Pseudomonas lurida M2RH3	Cold stress	Selvakumar et al. (2011)
Pseudomonas lurida M2RH3	Cold stress	Mishra et al. (2012)
Pseudomonas lurida NARs9	Cold stress	Mishra et al. (2009)

(continued)

Table 19.1 (continued)

Rhizobacteria inoculants	Stress condition	References
Pseudomonas lurida NPRs3	Cold stress	Mishra et al. (2011)
Pseudomonas mohnii OS114	Cold stress	Subramanian et al. (2016)
Pseudomonas putida AKMP7	Heat stress	Ali et al. (2011)
Pseudomonas putida FBKV2	Salinity stress	Vurukonda et al. (2016)
Pseudomonas putida FBKV2	Drought	SkZ et al. (2018)
Pseudomonas putida GAP-P45	Drought	Sandhya et al. (2010)
Pseudomonas putida GAP-P45	Drought	Sandhya et al. (2009)
Pseudomonas putida N21	Salinity	Zahir et al. (2009)
Pseudomonas putida Rs-198	Salinity	Yao et al. (2010)
Pseudomonas sp. AKM-P6	High temperature	Ali et al. (2009)
Pseudomonas sp. NARs1	Cold stress	Mishra et al. (2011)
Pseudomonas sp. RJ15	Drought	Saikia et al. (2018)
Pseudomonas stutzeri A1501	Metal stress	Han et al. (2015)
Raoultella planticola YL2	Drought	Gou et al. (2015)
Rhizobium leguminosarum	Low temperature	Lee (2009)
Rhizobium tropici CIAT 899	Salinity	Fukami et al. (2018)
Rhodopseudomonas palustris G5	Salinity	Ge and Zhang (2019)
Rhodotorula sp. PS4	Salt-tolerant	Mundra et al. (2011)
Serratia marcescens CDP-13	Salinity	Verma et al. (2017)
Serratia nematodiphila PEJ1011	Low temperature	Kang et al. (2015)
Serratia sp. XY21	Cold stress	Wang et al. (2016)
Staphylococcus kloosii EY37	Salinity	Karlidag et al. (2013)
Stenotrophomonas maltophilia	Salinity	Singh and Jha (2017)
Stenotrophomonas sp. CIK-517Y	Heavy metal	Akhtar et al. (2018)
Streptococcus pluranimalium S-29	Drought	Raheem et al. (2018)

studied such as *Virgibacillus*, *Staphylococcus*, *Acinetobacter*, *Sporosarcina*, *Sphingobacterium*, *Planococcus*, *Paenibacillus*, *Planomicrobium*, *Rhodococcus*, *Pseudomonas*, *Arthrobacter*, *Psychrobacter*, *Pontibacillus*, *Bacillus*, *Desemzia*, *Jeotgalicoccus, Exiguobacterium*, *Janthinobacterium*, *Flavobacterium*, *Methylobacterium*, and *Micrococcus* (Yadav et al. 2016, 2020b, c).

These microbes, which resides in low-temperature area reported to fall in the phyla's like *Actinobacteria, Ascomycota*, *Firmicutes*, *Thaumarchaeota*, *Bacteroidetes*, *Cyanobacteria*, *Chloroflexi*, *Chlamydiae*, *Spirochaetes Mucoromycota*, *Nitrospirae*, *Planctomycetes*, *Proteobacteria*, *Gemmatimonadetes*, *Basidiomycota*, *Euryarchaeota*, and *Verrucomicrobia* (Yadav 2015). Many novel microbes have been isolated and characterized for beneficial applications in agriculture from cold environments. Several reports are available on whole-genome sequences of novel and potential cold adaptive microbes. Whereas high temperature also leads to low crop productivity as water losses very quickly. To alleviate high-temperature microbes such as *Pseudomonas* sp. (Ali et al. 2009), *Enterobacter cloacae* Kour et al. (2017), *Bacillus aryabhattai, B. siamensis* Yoo and Sang (2018) have been reported from the soil.

19.3.4.2 Drought Stress

In the agricultural sector, drought is one of the major problems (Malyan et al. 2016). In which crop productivity is greatly affected in the whole world of arid and semi-arid regions. Microbes are playing an important role in controlling this stress as well once they have been isolated and thoroughly studied about their functionalities, such as their ability to withstand extremities and their genetic diversity, and methods are created for their use in farming. Therefore, inoculating plants and microbes with multifarious PGP attributes also would help to resolve drought in arid regions. The incessant decline in rainfall year after year has resulted in a major drop in soil moisture content. Also, temperate regions are currently implementing new approaches to increase the efficiency of soil moisture content (Panwar et al. 2014). The photosynthesis of plants and the absorption of nutrients rely on the availability of water in soil on a large scale.

The plants basic requirements are seriously impaired by reduced moisture content in the soil or the drought conditions as they increase the solute concentration within the cell of the plant, and decrease the water potential, which in turn affected, which in turn affects plan shooting and root elongation. In addition, water deficiency reduces plant exposure to carbon dioxide, resulting in the formation of reactive oxygen species (ROS) like peroxide, superoxide, and radical hydroxyl in plant cells, which leads to cell apoptosis and plant death (Sgherri et al. 2000). Plant growth-promoting rhizosphere such as *Glomus intraradices, G. mosseae Pseudomonas mendocina*, and was reported. To release catalytic enzyme and quench ROS from lettuce plants produced under extreme drought conditions has been documented (Kohler et al. 2008).

The drought-tolerant microbes were collected from various sources and applied as a biofertilizer in the place of chemical-based fertilizers which is eco-friendly tools to encourage plant growth and alleviate drought stress. soil inhibiting microbes belong to different genera such as *Azotobacter*, *Aeromonas*, *Azospirillum*, *Achromobacter*, *Enterobacter*, *Bacillus*, *Pseudomonas*, *Variovorax* and *Klebsiella* these microbes have been shown to enhance plant growth under drought stress condition (Kumar et al. 2019; Rai et al. 2020). Pereira et al. (2019) suggested that microbial communities of *Arthrobacter*, *Pseudomonas*, *Microbacterium*, and *Bacillus* are associated with sugarcane of rhizosphere was strongly affected by under drought stress condition. *Acinetobacter calcoaceticus* EU- LRNA-72, *Penicillium* sp. EU-FTF-6 is phosphorus solubilizing microbes under drought stress conditions (Kour et al. 2020b). *Pseudomonas libanensis* EU-LWNA-33 plant growth-promoting bacteria under drought adaptive condition and also the *Streptomyces laurentii* EU—LWT 3–69 and *Penicillium* sp. strain EU—DSF—10 (Kour et al. 2020a), *Pseudomonas putida*

NBRIRA and *Bacillus amyloliquefaciens* NBRISN13 with the ability to tolerate drought stress (Kumar et al. 2016).

19.3.4.3 Water Flooding Stress

Water flooding stress is another abiotic stress which also an agricultural product destroyer factor. Generally, This stress mainly exists in rice-producing field areas, as every year one-fourth of the world's rice land are inundated with volatile flash floods that now a day's arise a few times a year (Mackill et al. 2012). To survive the plants need oxygen (O_2), but extreme flooding decreases the amount of O_2 in the soil. The lower level of O_2 can limit aerobic restoration. Water flooding also induced the accumulation of ethylene and, depending upon the light condition of submerged plant organs, raises the CO_2 concentration. Flooding agricultural land could suffer from the intensity of light and consequently decrease photosynthetic activity (Bailey-Serres and Voesenek 2008). Plant species showed some adaptive features to survive under low concentration of O_2 such as the petiole change: cellular modification, aerenchyma tissue formation, internode elongation ratio and leteral and root adventitious root developments. There are available water flooding microbes from the soil like *Pseudomonas* and *Enterobacter* (Grichko and Glick 2001), *Bacillus cereus* and *Bacillus* sp. (Bao et al. 2010), *Citrobacter freundii* J118 (Upadhyay et al. 2011), *Bacillus megaterium* BOFC15 (Zhou et al. 2016), *Acinetobacter pittii* JD-14 (Daur et al. 2018), *Aquabacterium*, *Clostridium*, *Flavobacterium*, *Ilumatobacter*, *Bacillus*, *Solirubrobacter*, *Arenimonas* and *Mycobacterium* (Furtak et al. 2020).

19.3.4.4 Salinity Stress

Salinity is the key cause of environmental stress that decreases agricultural, area yield and quality of the crops. Salinity has affected and depleted 20% of the earth's agricultural land, that is, ~45 million ha. The soil salinity rate is estimated to be 30% of the global agricultural lands (Shrivastava and Kumar 2015). Salinity is worst in the arid and semi-arid regions that cause osmotic stress, which also decreases the growth and productivity of crops. Stalinization usually occurs in two different ways i.e. natural causes and the second type is the result of human activity for agricultural production. In soils and waters, there are main salinity zones are salt lakes, ponds, marshes and flats. The presence of excess cations amounts such as Na^+, Mg^{2+} Ca^{2+} and K^+ with anion such as Cl^-, NO_3^-, SO_4^{2-}, HCO_3^-, and CO_3^{2-} has been characterized as saline stress in agriculture soils (Yadav et al. 2019).

According to the standard of the US department of agriculture (USDA), soil that has electrical conductivity (EC) of ds^{m-1} or higher can be classified as saline soil. Many studies have suggested that stress of salt as the main cause of the creation of drought-like condition due to water shortages, the creation of the payment of higher ionic content in plants, thereby disrupting the usual physiological pathways and the lack of the other nutrients of soil due to high concentration of salt (Vaishnav et al.

2016). Munns (2002) recorded decrease plant growth when it is exposed to salinity due to reduction in water content with simultaneous salt elevation. There are various studies are available for plant growth promotion in the condition of salinity stress such as *Achromobacter piechaudii* ARV8 from tomato (Mayak et al. 2004), *B. subtilis* and *Arthrobacter* sp. (Upadhyay et al. 2012), *Brachybacterium paraconglomeratum* SMR20 (Barnawal et al. 2016), *Curtobacterium albidum* SRV4 from paddy plants (Vimal et al. 2019), *Bacillus pumilus* strain FAB10 from wheat (Ansari et al. 2019), *Aneurinibacillus aneurinilyticus* ACC02, *Aenibacillus sp.* ACC06 from bean (Pandey and Gupta 2019), *Curtobacterium* sp. SAK1 (Khan et al. 2019).

19.3.4.5 Heavy Metals Stress

The industrial revolution and anthropogenic actions, has resulted in a drastic increase of heavy metals and radionuclide's in the soil. Few among these as chromium (Cr), mercury (Hg) and cadmium (Cd) are reported to non-essential elements while, and other important to the photosystem molybdenum (Mo), manganese (Mn) and iron (Fe). Significant accumulation of especially non-essential elements not only affects soil microflora (Wani and Khan 2010) but also translocates to various photo-organelles, causing membrane destruction and simultaneous cell organelles disintegration as well as a complete collapse of important physiological functions, such as photosynthesis and protein synthesis (Morsy et al. 2012; Subrahmanyam et al. 2020).

The poor formation of plant growth and root production in metal contaminated soil are major limiting factors for the metal phytoaccumulation. In addition to organic modification, enhancement of the microbial behavior in the rhizosphere is important to solve these problems. Under the condition of heavy metal contamination, plant growth was hypothesized primarily via IAA production and ACC deaminase activity also siderophore that can help plant accumulation Fe in the presence of the excessive amount of other metals. There are available several reports instance in which bacterial species mitigated heavy metal stress. Different studies have focused especially on plant growth-promoting rhizosphere as an efficient bioremediation, as well as plant growth enhancers (Madhaiyan et al. 2007) such as *Micrococcus* sp. and *Aspergillus* sp. are used for the elimination of chromium and nickel from wastewater of industries (Congeevaram et al. 2007), *Burkholderia* sp. J62 from paddy soil (Jiang et al. 2008), *Serratia* sp. SY5 (Koo and Cho 2009).

In this study (Dary et al. 2010) suggested that plants treated with a microbial consortium of *Bradyrhizobium* sp., *Pseudomonas* sp. and *Ochrobactrum cytisi* help to increase the biomass, yield as well as nitrogen content in plants. Similarly (Marques et al. 2013) reported the lower accumulation of metal within sunflower tissues when treated with the *Ralstonia eutropha* and *Chryseobacterium hispalense* when grown in Cd- and Zn-infected soil (Marques et al. 2013), *Bacillus, Pseudomonas, Streptomyces*, and *Methylobacterium* also have the capability to enhance growth and production of plant via reducing the heavy metals damaging effects (Sessitsch et al. 2013), *Pseudomonas* sp. enhanced of growth of plant of wheat under metal (cadmium) stress condition (Verma et al. 2015a), *Pseudomonas libanensis* TR1 and *Pseudomonas reactans* Ph3R3 (Ma et al. 2016), *Citrobacter freundii* JPG1 (Wang et al. 2018a), *Pseudomonas taiwanensis* (Satapute et al. 2019), *Microbacterium testaceum* B-HS2 (Elahi et al. 2019), *Bacillus* sp. S3 (Zeng et al. 2020).

19.3.5 Remediation of Environmental Pollutions

The environment is continuously threatened by the use of persistent organic pollutants. Bioremediation is the method by which microbes interact with pollutant and degrade it (Kour et al. 2021b; Mishra et al. 2020). Microbes are cosmopolitan in their distribution and play a very important role in xenobiotic bioremediation (Kumar et al. 2021b; Panigrahi et al. 2019). The compounds which do not occur naturally or synthesized in the laboratory are commonly known as xenobiotics (Bhatt et al. 2019). The pesticides which are continuously used in agriculture and non-agriculture areas for protecting crops itself causing environmental pollution and also showing ill-effects to both fauna and flora (Łozowicka 2009). Microbes secret some low molecular-weight organic metabolic acid that can dissolve heavy metal which is further processed by different methods such as biosorption, enzymatic degradation, and precipitation, thus converted into more stable, non-toxic or inert form (Kumar and Bharadvaja 2020). The microbial enzymes are used to degrade and metabolized the xenobiotic compounds. The enzymes involved in degradation or mineralizing metabolic pathways are of dehydrogenases, hydrolases, and oxygenases categories (Phale et al. 2019). The pathway used by the microbes for the biodegradation of xenobiotic compounds is mainly β-ketoadipate (Stainer and Ornston 1973).

The bioremediation of aromatic pollutants like phthalate isomers, naphthalene, phenanthrene, benzopyrene is done by microbes mainly *Acidovorax*, *Arthrobacter*, *Brevibacterium*, *Polaromonas*, *Mycobacterium*, *Rhodococcus*, and *Sphingomonas* (Phale et al. 2019; Seo et al. 2009). Teeraphatpornchai et al. (2003) isolated microbial strain named *Paenibacillus amylolyticus* from soil and found their enzymatic (esterase and protease) action in degrading plastic. Vamsee-Krishna et al. (2006) reported the biodegradation of phthalate, used in the plastic industry with the help of *Acinetobacter lwoffii*, and *Pseudomonas aeruginosa.* Auta et al. (2017) reported *Bacillus cereus* and *B. gottheilii* strain of bacteria and found their capability to degrade microplastic. *Alicycliphilus* is reported as favorable strain to degrade xenobiotics (Solís-González and Loza-Tavera 2019). Pacwa-Płociniczak et al. (2019) studied the degradation of hydrocarbons from the petroleum-contaminated soil by gram-negative bacteria called *Rhodococcus erythropolis*, *Pseudomonas aeruginosa* (Varjani et al. 2020), and *Bacillus vallismortis* (Basumatary et al. 2020). Heidarrezaei et al. (2020) reported the biodegradation of halogenated compound mainly Trichloroacetic acid by *Lysinibacillus boronitolerans.* Sukirtha (2020) reported the bioremediation of glyphosate herbicide by xenobiotic degrading bacteria *Nocardia mediterranie.* The dye degrading bacteria named *Pseudomonas flourescens* (Pandey et al. 2020), and *Streptomyces sviceus* (Chakravarthi et al. 2020) found its application in textile effluent degradation.

19.4 Biotechnological Application of Soil Microbiomes

On the basis of the soil microbes function abilities, they can be utilized in the field of biotechnology. Agriculture and the environment are the two major fields in which soil microbiomes can be utilized for various purposes.

19.4.1 Agriculture Applications

Agriculture is one of the widely practiced activities of mankind. It has been practiced in the different geographical location that has different soil types and conditions. The production of food way more long practice which was done in the past and also going to continue till life exist. Crop yield is one of the major criteria to feed the growing population of the earth. The drastic increase of the population is one of the biggest reasons to worry because, for the last 50 years, agriculture has been practiced by following the conventional agriculture methods that include the use of chemical-based products i.e. fertilizer and pesticides (Clark 2007). The use of such chemicals without a doubt increases the yield of the crop but on the other side, they have destroyed the structure by depleting the fertility of the soil (Mishra et al. 2016). The current soil has the least amount of nutrients present in soluble form and maximum is present in the insoluble form. These insoluble or complex forms of nutrients or minerals are not is utilized by the plant crops for their fulfillment. Moreover, overexploitation of chemicals in the fields also polluted the soil as of metals aggregation (Gadd 2010).

Soil microbes are one the best alternative and eco-friendly technique to such types of chemicals, which can also solve environmental-related problems. On the basis of various studies, soil microbes have been reported as the better fertilizer that provided various kinds of essential nutrients such as nitrogen, phosphorus, potassium, iron and zinc. Soil microbes are able to provide such nutrients as they help in the fixation, solubilizing and scavenging of these minerals from soil and the air. These microbes can undergo producers like lowering of pH i.e. acidification, release of extracellular-polysaccharides, organic acids and enzymes that helps in the breakdown of such complex and insoluble minerals (Schloter et al. 2018). Apart from the nutrients, plants also require various plant growth regulators like auxin, cytokinin and gibberellins (Wong et al. 2015). Although, these hormones are produced endogenously by the plants in stress conditions they are not able to produce them, so, for better yield soil microbes can be for secreting such hormones (Frankenberger Jr and Arshad 2020) (Fig. 19.2).

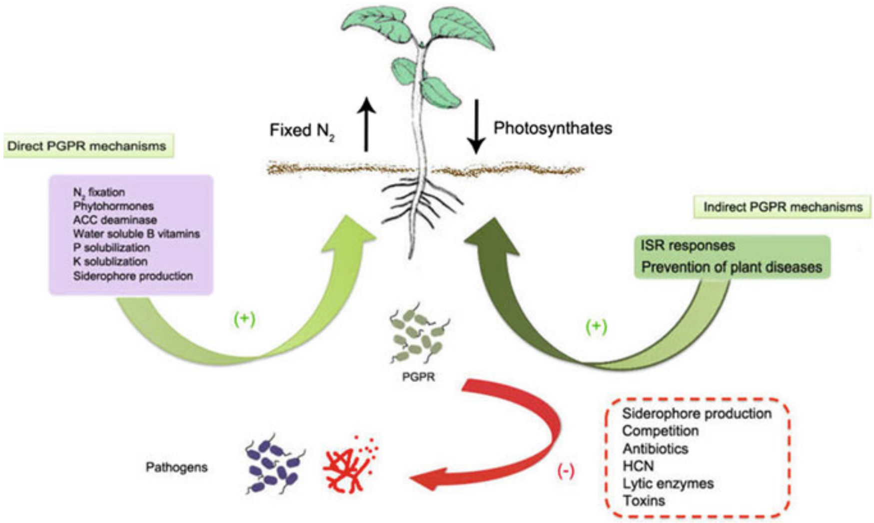

Fig. 19.2 Mechanism of plant growth promoting soil microbiomes in the enhancement of plant growth and development

Various types of microbes have been reported for playing solubilizing, scavenging and fixing of different minerals like *Azospirillum lipoferum*, *Bradyrhizobium japonicum*, *Paenibacillus durus*, *Klebsiella variicola* (Navarro-Noya et al. 2012), *Mesorhizobium atlanticum* (Helene et al. 2019) have reported for fixing nitrogen. Microbes like *Bacillus megaterium*, *B. subtilis*, *B. cereus*, *B. pumilus*, *Pseudomonas tolaasii*, *Staphylococcus sciur* (Kumar et al. 2011), *Enterobacter asburiae*, *Acinetobacter* sp., *Bacillus cereus* (Teng et al. 2019), *Streptomyces laurentii*, *Penicillium* sp. (Kour et al. 2020a) have been reported for solubilizing phosphorus. Whereas, *Paenibacillus glucanolyticus* (Sangeeth et al. 2012), *Rhizobium pusense* (Meena et al. 2015), *Pseudomonas azotoformans* (Saha et al. 2016), *Burkholderia cepacia* (Bagyalakshmi et al. 2017), *Pantoea agglomerans*, *Pseudomonas orientalis*, *Rahnella aquatilis* (Khanghahi et al. 2018) have been reported for solubilizing potassium. *Curtobacterium*, *Plantibacter*, *Pseudomonas*, *Stenotrophomonas* (Costerousse et al. 2018), *Pseudomonas* sp., *Bacillus* sp. (Zaheer et al. 2019), and *Bacillus megaterium* (Bhatt and Maheshwari 2020) are the few reported zinc solubilizing microbes that can be used for the zinc solubilization and mobilization and *Streptomyces laurentii* and *Penicillium* sp. (Kour et al. 2020a) reported strains that produce siderophores that are used for the biofortification of iron. *Enterobacter ludwigii* (Lee et al. 2019), *Penicillium* sp. (Kour et al. 2020a), *Citrococcus zhacaiensis,* and *Bacillus amyloliquefaciens* (Selvakumar et al. 2018), *Burkholderia cepacia* (Bagyalakshmi et al. 2017) have been reported for producing phytohormones.

19.4.2 Environment

Environmental stresses including cold, drought, flooding, heavy metals, heat and salinity negatively affect agricultural productivity (Gontia-Mishra et al. 2014). Stress conditions lead to various biochemicals, molecular and physiological changes in plants such as decreased photosynthesis, reactive oxygen species (ROS) production, denaturation of proteins, and lipid peroxidation rate which adversely affect the yield and quality of the crops. Beneficial soil microbiomes alleviate stress conditions by different mechanisms such as the production of osmolytes, ROS scavenging enzymes and decreased lipid peroxidation (Yadav 2020). ACC deaminase activity is another important mechanism important for stress alleviation. ACC deaminase enzyme reduces the increased levels of ethylene by cleaving ACC into ammonia and α-ketobutyrate (Kour et al. 2019a). Additionally, the microbes also increase the availability of the macro and micronutrients, produce different plant growth regulators, HCN and ammonia.

Many studies have reported mitigation of cold stress in wheat, tomato, pepper, and green gram by *Bacillus amyloliquefaciens* (Verma et al. 2015b), *Pseudomonas frederiksbergensis* and *Pseudomonas vancouverensis* (Subramanian et al. 2016), *Serratia nematodiphila* (Kang et al. 2015) and *Pseudomonas migulae* (Suyal et al. 2014) respectively. Mitigation of drought and heat stress has been reported in maize by *Alcaligenes faecalis, Proteus penneri and Pseudomonas aeruginosa* (Naseem and Bano 2014) and great millet by *Streptomyces laurentii* (Kour et al. 2020b), salinity and heavy metal stress in maize by *Pseudomonas fluorescens* (Zerrouk et al. 2016).

Another important role of microbes that have been focused on is in the area of decreasing pollution and greenhouse gas emissions. Fungi especially are known to play a significant role in addressing major global challenges. The utilization of either the fungal processes or the products can lead to enhanced sustainability. The wide range of applications includes upgrading bio-waste for value-added products to the use of renewable plant biomass as a substitute for oil-based products such as biochemicals, plastics, fertilizer, and fuel (Lange 2014).

Another major challenge is the disposal of sludge generated from the sewage treatment plant in an environmentally safe way. The wastewaters consist of a range of dyes, heavy metals, and phenolics which are harmful to living organisms. Filamentous fungi are known to be potent organisms for sludge treatment with their major functions including organic solids reduction, pathogens removal, detoxification, dewaterability, and bioflocculation (Lu et al. 2016). The efficiency of archaeal, bacterial and fungal communities in municipal solid waste has also been investigated in different studies (Voběrková et al. 2017). Thus, with the combination of beneficial microbiomes with other advanced genetic engineering techniques, a potentially transformative example in plant health, nutrition and sustainability could be achieved.

19.5 Conclusion and Future Propects

Looking up to the abilities and applications of soil microbes in the agriculture and environments, it can be concluded that these tiny miracles can be utilized in the environment and agriculture field. The microbes are ubiquitous in nature and have been reported all the habitats studies. The microbes are associated with plant systems in three-ways such as epiphytic, endophytic and rhizospheric. The microbes from soil and air are useful for different processes in plants and ecosystems. The soil microbiomes have the capability to nutrient acquisitions in plants. The microbes the multifunctional plant growth-promoting attributes could be utilized as biopesticides and biofertilizers for sustainable agriculture and environments. In future also, these microbes can also replace chemical-based products, which will be support the sustainability and make earth more clean and green i.e. pollution free environment.

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