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Field Crops: Sustainable Management by PGPR

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Preface

The sustainable management of field crops is a concern to cultivate them economically and eco-safe ways so as to reduce the abusive use of harmful agrochemical not only creating a 'soil-security' but also posing several health-related issues in the human race. Although, much progress has been made in understanding a technology-oriented sustainable agro-ecosystem, it is essential to involve the frontiers of knowledge of PGPR's roles to fill the gap between ever increasing population and crop productivity.

In the recent scenario, field crops are geared up to feed the phenomenally increasing population has largely become chemical based and input intensive. The plateauing crop yields and falling inputs response have severely reduced the sustainability of the crop ecosystem. In addition, there is a growing awareness to shift from chemical to organic agriculture. This will partially reduce the pressure on the chemicals demand to increase the credibility and sustainability to raise field crops healthy.

The present book is an endeavor to provide voluminous information on the role of PGPR in sustainable management of field crop production and enhancement of productivity. The main focus lies on different portrayals meant to establish significance of PGPR in minerals, nutrition and their assimilation, alleviation of abiotic stress of drought and salinity, influence of info-chemicals, in sustainable management of field crops. This not only ends with these crops but also expands horizons to the other vegetable species such as tomato, pepper, melon, radish, lettuce, etc. The plant–microbes relationships in soil-ecological system and their accurate benefits in concern to raise the question on the safety of food production become imperative to adapt biological fertilization strategy that may minimize the use of chemical inputs.

Plant growth-promoting microbes (PGPM) becomes an effective solution to the problem of mercury toxicity from the contaminated agricultural lands. These beneficial PGPR impose drought tolerance by the production of exopolysaccharides, phytohormone, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, volatile compounds and by up- or downregulation of stress-responsive genes and by altering root morphology during water scarcity. PGPR have abilities to induce

defense against insect herbivore. Some beneficial microbes also induce systemic resistance (ISR) against microbial pathogenic viruses, parasites, and herbivorous insects and some display direct insect pathogenicity.

This book will be valuable not only for the scientific community but also to the teachers, researchers, and students studying graduation and postgraduation in various streams of Agriculture, Horticulture, Biotechnology, Microbiology, Phytopathology, Agronomy, and Environmental Sciences.

We desire to acknowledge all the subject specialists, contributors, who were quite cooperative to spare their cooperation and patience to make this book a successful endeavor. Thanks are due to our research team members, who generously assisted in the compilation and completion of this task. We extend our sincere thanks to Dr. (Mrs.) R. Valeria and her colleagues for their valuable support to facilitate completion of this project. Support from MHRD-UGC BSR fellowship (DKM) is duly acknowledged.

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Chapter 1
Plant Growth-Promoting Rhizobacteria (PGPR) as Protagonists of Ever-Sustained Agriculture: An Introduction

Dinesh Kumar Maheshwari, Meenu Saraf and Shrivardhan Dheeman

Abstract The rhizosphere is a zone of soil surrounding to the plant roots, where the biology and chemistry of the soil is influenced by root metabolites pumped into the soil, called root exudates. The rhizosphere of ample quorum of microorganisms, thus, regarded as an ecology. The beneficial bacteria in the rhizosphere are recognized as plant growth-promoting rhizobacteria (PGPR) that influence plant growth and health promotion by several means of mechanisms. These can influence plant traits under fluctuating environmental conditions and improve yield productivity in a sustainable way. The use of PGPR in field crops has attended by enormous researches to enhance crop production and productivity in a sustainable manner. The inoculation strategies such as co-inoculation of two or more beneficial bacteria as bioinoculant apparently provided greater phytostimulation perhaps because of the synergistic and multifarious effects due to co-occurrence and co-interaction with field crops. PGPR are emerging tools of sustainable agriculture; also providing strategic avenues to combat biotic and abiotic stresses of crops. Further, this chapter introduces PGPR as a central candidate with multifaceted mechanisms and influences on sustainable management of field crops.

Keywords Rhizosphere · PGPR · Biofilm · Bacterial diversity · Field crops

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1.1 Introduction

Environmental sustainability, specifically for sustainable agriculture must be free of abusive use of chemical fertilizers spoiling biological diversity and soil fertility simultaneously and had raised several concerns to find the alternatives, which are natural in origin. Plants comprise an excellent ecosystem with microorganisms that interact with different degrees under attraction towards secretions of diverse metabolites called root exudates. Since Hiltner in 1904 has understood about 'Rhizosphere', i.e. the layer of soil influenced by roots is much richer in bacteria than the surrounding bulk soil. The role of rhizosphere microbiology has been established as an arena of sustained agriculture and economy as well. In this quest, the search for desired beneficial microorganisms including bacteria, fungi, actinobacteria, protozoa and algae are by far the most common. Each gram of soil contains up to 10 billion bacterial counts, possibly due to their ability to grow rapidly. Such bacteria are bound with the surface of soil particles and soil aggregates; quite a good number of these interact with plant roots, hence rhizospheric in nature. The interaction between bacteria and plant may be harmful or neutral and sometimes proved beneficial to that of plants. Such benefits may occur either by symbiotic, associative and free-living relationship with the roots of plants (Weller and Thomashow 1994; Glick 1995; Maheshwari and Annapurna 2017) to provide them a healthy status.

In a healthy plant, all the biochemical reactions are in a state of equilibrium. If any deviation due to biotic or abiotic stresses comes in any way, it tends to disrupt the metabolic processes making the plant unhealthy. Such plants overcome this state of the affair by using various inputs in the form of biological ways either by adding organic compost or by crop-rotation. There is another alternative in the form of plant growth-promoting rhizobacteria, i.e. PGPR which outcompetes the stresses affecting plant growth and development. These free-living or endophyte bacteria are not only functional and diverse in habitat but also capable of supporting plant growth and development.

In the recent scenario, cultivation of field crops are geared up to feed the phenomenally increasing population which has largely become chemical based and input intensive. This has accelerated the process of resource depletion and environmental pollution. The plateau crop yields and falling input response have severely reduced the sustainability of the crop ecosystem.

Microbial inoculants, which are naturally occurring beneficial microorganisms, hold the promise because of self-replication, non-toxic inputs and increase the productivity and protection for the benefits of the crop production. They make important contributions to fertility and productivity both for plants and soil. Efforts made during the past decade have generated awareness about the cheap input amongst the growers. In addition, there is a growing concern to shift farming from chemical to organic which, partially reduce the pressure on the chemicals demand, increase the credibility and sustainability to raise healthy field crops.

1.2 Rhizosphere: A Home of PGPR

'Rhizosphere' denotes the area of intense microbiological activity that extends to several millimetres from the root system of growing plant. In other words, the rhizosphere is a hotspot of microbial interactions, as exudates released by plant roots are the main food source for microorganisms and contribute as a driving force to enhance their population density and activities (Raaijmakers et al. 2009). Rhizosphere encompasses the millimeters of soil surrounding a plant root, where complex biological and ecological processes occur (Bais et al. 2006). Soil which is not a part of the rhizosphere and does not penetrate by plant roots is known as bulk soil. Natural organic compounds and microbial populations are much lower in bulk soil than in the rhizosphere (Stotsky et al. 2000). The above facts illustrate the significance of plant growth-promoting rhizobacteria (PGPR) as a potential candidate to be used as beneficial bio-fertilizers having merit over conventional fertilizers (Maheshwari et al. 2015). But, before providing their beneficial impact on the plants living in rhizosphere, they must be colonized and should stay there for long term, which is understood as root colonization. In some cases, associative interactions between plant and bacteria are accomplished with the help of rhizodeposits, which also pose growth-stimulating effects for microbial survival. As symbiotic systems, associative interactions are of great interest because many crops show an increase in yield after inoculation (Höflich et al. 1994). On the other hand, rhizosphere is the infection court where soil-borne pathogens establish a parasitic relationship with the plant. To infect root tissue, pathogens have to compete with the member of the rhizosphere microbiome for available nutrients and micro-niche (Chapelle et al. 2016). Soil can be considered as a microbial seed bank (Lennon and Jones 2011). The carry-over effect on the assemblage of the 'rhizomicrobes', i.e. the proliferation of microbes in, on or around the roots has important implications for the co-evolution of plant–microorganism interactions in natural ecosystems. It includes dispersal of microorganisms from a source of inoculum to the actively growing root, multiplication or growth in the rhizosphere.

In fact, rhizosphere is responsible for the success of free-living bacteria which requires a proper process for root colonization. Nowadays, there is a possibility to manipulate these zones of root-colonization via 'rhizosphere engineering'. This process is quite important from different points of view in order to produce bacterial-mediated growth-promoting substance to support crop yield and productivity. A successful root/rhizosphere colonizer exclusively means the existence of features, which survive in fierce competition of the indigenous micro-flora in the growth enhancement processes and in improving homeostatic mechanisms upon stress challenges. The environmental homeostasis in the rhizosphere of crop plant protect it against a broader range of pathogens. Also, as a consequence, the plant switches on downstream signalling pathways and produces antimicrobial compounds to kill the pathogen and maintain homeostasis (Thormar and Hilmarsson 2007). This is a very precisely controlled and complex process involves a number of genes and signalling pathways (Zipfel 2009). It is this complexity of plant–

pathogen interactions, which makes it very difficult to discern, due to which anatomical features, metabolites and signalling pathways become activated. The traditional, biochemical and genetic experimental methods are inadequate tools for the task.

Rhizospheric competence is a pre-requisite for plant growth and development, PGPR play a major role in two different ways, indirectly or directly, both share support mechanisms to bring the sustainability for major crops. For this, the bacterial genera are used as inoculants for seed dressing and allow them to raise the plants resulting in growth promotion and increased yield. Rhizospheric competence affects positively on root and plant biology in relation to provisional nutrition, growth promotion, development and health (Aragno 2005). Hence, to advance the future of agriculture, in terms to find more precise bacteria, which can invade in the rhizosphere of other plants too can be found by studying free-living association in depth (Cook 2012).

1.3 PGPR and Rhizospheric Biofilm

The success of PGPR in agriculture has been sorted out if PGPR attributed effective root colonization with the traits and subsequently able to form biofilms in the rhizosphere, which assures their tenancy in a manner to establish a successful relationship with the plant (Saleh-Lakha and Glick 2006). Rhizospheric ecology comprised reciprocal influence of inter-alia plant–microbe interactions influenced by its biotic and abiotic factors. Among the community of beneficial as well as deleterious bacteria, PGPR plant growth-promoting bacteria were entirely well-thought-out as beneficial bacteria and play a multifarious role in the environment and agriculture and being an important germ-plasm. Plant-associated bacteria generally interact with host tissue surfaces during pathogenesis and symbiosis, due to and in commensal relationships. The bacteria associated with plants are aggressive to form increasingly revealing biofilm-type structures that vary from small clusters of cells to extensive biofilms in nature. This implies that PGPR competence strongly depends either on their abilities to take advantage of a specific environment or their abilities to adapt according to changing conditions. PGPR may be uniquely equipped to sense chemoattractants, e.g. rice exudates induce stronger chemotactic responses of endophytic bacteria as compared to non-PGPR present in the rice rhizosphere.

1.4 Rhizospheric Dynamics and Diversity

The rhizosphere harbours one of the most complex, diverse and active plant-associated microbial communities. Although, selection for the rhizosphere community is evident, the specific bacterial traits that make them able to colonize

this environment are still poorly understood (Lopes et al. 2016). But, there is a quest that, is PGPR diversity quantifiable? Actually, to study microbial diversity, taxonomic and functional diversity are major concerns where taxonomic diversity integrates different aspects of diversity and provides a more complete picture with a deeper understanding of microbial interactions in soil ecosystems (Torsvik et al. 2002). The use of molecular methods for the study of genetic diversity primarily, the sensitive and accurate PCR-based genotyping methods enable differentiation among closely related bacterial strains and the detection of higher bacterial diversity (Doignon-Bourcier et al. 1999; Tan et al. 2001). Jha et al. (2010) reported that a good diversity index should encompass both Dominance indices (Example, Simpson Index) and Information indices (Example, Shannon-Wiener Index). To comprehend such diversity, it is advantageous to investigate the combined uses of species richness and diversity as well as to estimate the combinatorial effect of species richness and diversity in order to understand their role and distribution in their habitat. In another study focused on bacterial diversity that explored the Himalayan region as well-known biodiversity hotspots and rich in ecological diversity. However, it suffers from low agricultural productivity due to several climatic and agricultural limits. The research reveals the diversity of *Bacillus* population associated with *Eleusine coracana* (ragi). The study was carried out using two universal primers derived from the highly conserved region of 16S rRNA gene fD1 and rD1 for species identification. Overall, the site-specific diversity of the bacterial strains using the Simpson and Shannon–Wiener Index had positive correlation with the altitude gradient. Ragi, *Eleusine coracana* L., is one of the main food grain crops now being commercially exploited (Dheeman et al. 2017).

Microbial diversity is puzzled with co-existence of species that remains functional in their ecology and their degree of functionality has been studied under the term of functional diversity (Torsvik and Øvreås 2002). The functional diversity of species influences ecosystem dynamics, stability, productivity, nutrient balance and other aspects of ecosystem functioning (Tilman 2001). Embedded microbial community belongings to rhizosphere possesses functional diversity, which ultimately enhance agricultural production (Maheshwari 2014). Functional diversity in the rhizosphere considered the mechanistic behaviour of microbial guilds, which ultimately promotes the plant growth. It has multidimensional cloud of species trait and each trait represents an individual or a species (Fig. 1.1), e.g. Phosphate-Solubilizing Bacteria (PSB), whereas phosphate solubilization is a function of rhizospheric microorganisms to alleviate the nutritional requirement in soil, and further aid in plant growth promotion. The functionality of PGPR in agriculture is increased with its diversity (Tilak et al. 2005). Such groups of selective individuals are also considered as functionally diverse and are utilized to improve agricultural production as cited by Maheshwari (2014).

The transfer of nutrients from plant roots in the rhizosphere controls plant–microbe interactions and populations of bacteria have a functional role within communities that permit their survival. The relationship between microorganisms and plants confers the availability of nitrogen along with other nutritional requirements, viz. phosphorus, zinc, potassium, etc. (Maheshwari 2011; Dhiman

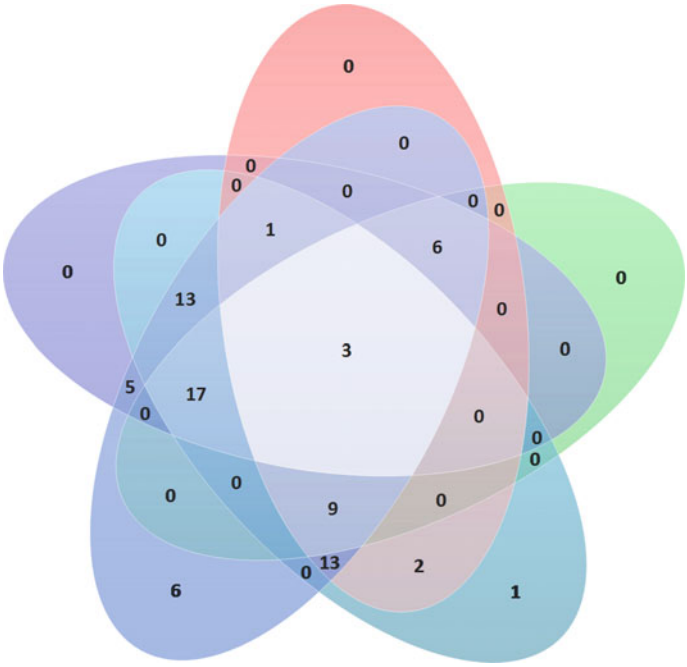

Fig. 1.1 A five-way Venn Set Diagram (VSD) showing multidimensional overlaps among 5 traits of PGPR and elucidating commonness in *Bacilli* on trait level (Author's Lab)

et al. 2019). Plant roots offer a niche to the proliferation of soil bacteria and sustain their life under the influence of root exudates and lysates (Lugtenberg et al. 2002). In the agro-ecosystem, several diverse genera of microorganisms are responsible for multifarious metabolic functions and interfere in soil fertility, plant health, growth, nutrient cycling, organic matter formation, decomposition and soil structure maintenance (Kennedy 1999). Plant growth is a multi-complex phenomenon and rhizobacteria acts as bio-stimulant, bio-fertilizer and plant-protective agent or sometimes in bioremediation of pollutants.

A large and ever-increasing number of genera in the community of PGPR have been discovered so far. These are different morphologically, however share nutritional and ecological preferences including ecology of rhizospheric niches. These were isolated from a varied range of habitats (from harsh to adaptive environments) such as rhizospheric soil, cow and buffalo dung, root nodules of various dicotyledonous plants and even from termitarium (Chauhan et al. 2016) and termite gut (Fröhlich et al. 2007)

Rhizospheric bacteria are communities heavily influenced by soil texture and rhizospheric ecosystem as illustrated in Fig. 1.2.

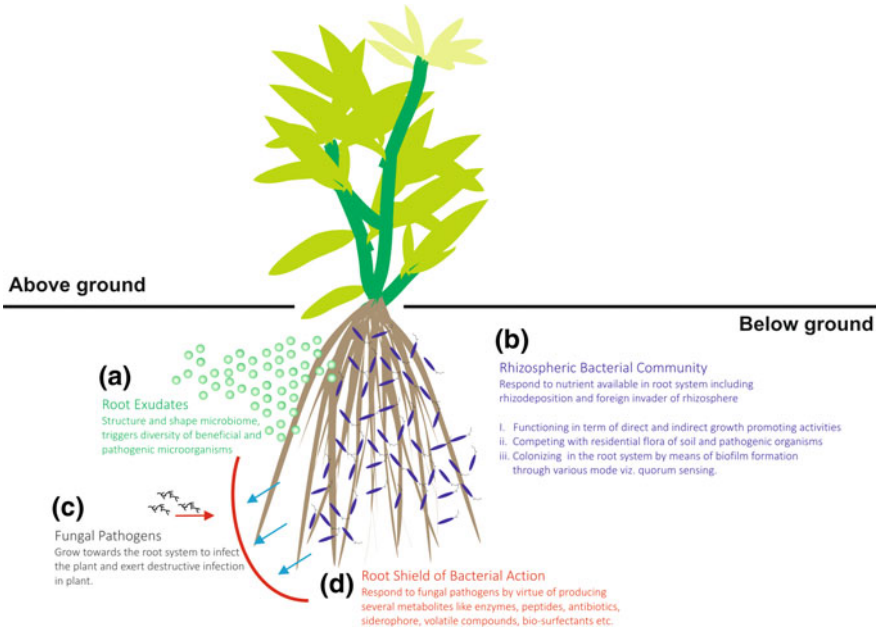

Fig. 1.2 Bacterial community in rhizosphere showing their sole importance from A to D

1.5 PGPR and Field Crops

Various countries spend tens of billions of dollars in importing food as outdated technologies, poor yields, shrinking farms and unreliable weather pattern inflict. However, the use of PGPR not only saves the biodiversity and is too cheap for farmers. Their wide contribution to growth and health promotion is now well established. PGPR enhance plant growth by a wide variety of mechanisms like biological nitrogen fixation, phytohormone production, phosphate solubilization, siderophore production, 1-aminocyclopropane-1-carboxylate deaminase production (ACC), exhibiting antifungal activity, production of volatile organic compounds (VOCs) promoting beneficial plant–microbe symbiosis, interference with pathogen toxin production, etc. (Ryu et al. 2003). Current advancements in the exploration of rhizosphere diversity along with PGPR and their functional ability and mechanism to facilitate plant growth promotion corroborated their application as a reliable phenomenon in the management of sustainable agricultural system. Use of PGPR strains have the potential to induce antioxidant enzymes, amino acids like proline under salinity stress and could serve as a useful tool for alleviating salinity stress in salt-sensitive plants (Patel and Saraf 2013).

Monitoring soil microbial life and their influence on the tripartite interaction of plant soil and microbes manage agricultural production. In understanding a technology-oriented sustainable agro-ecosystem, significant progress have been made, but it is essential to broaden the frontiers of knowledge of PGPR's roles in field crop and others to fulfill the gap between ever-increasing population and productivity. More recently, drone technology is proved to be beneficial for the spray of the plant protection agents, biostimulants, etc. In fact, precision monitoring of interaction of beneficial microbe with soil and plant proved to be instrumental for agriculture production (Baliyan et al. 2018). In addition, the chapters in the book expand the frontiers of PGPR in the arena of field crops cultivation and productivity enhancement of sustainable agriculture.

1.6 Conclusions

The plant growth-promoting rhizobacteria (PGPR) are emerging tool of sustainable agriculture and a central candidate with multifaceted mechanisms and influences on sustainable management of field crops. Further, a quantum and ample research is needed under the consideration of plant–microbe interaction to augment sustainable management of field crops.

Conflict of Interest The author(s) have no conflict of interest.

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Chapter 2
Bacterial Mixtures, the Future Generation of Inoculants for Sustainable Crop Production

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Abstract Plant growth-promoting bacteria (PGPB) have been extensively studied, because of different mechanisms to perform phytostimulation, as well as the abilities to colonize plants. The number of crop types and hectares of agricultural land, where PGPR are applied is low compared with the total crops or farming area.

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However, the PGPB application in crop fields is increasingly becoming more accepted due to the advantages to crops and environment such as the increment in productivity, the diminution in the use of chemical fertilizers and toxic compounds such as pesticides and herbicides. These traits make beneficial bacteria formulations the 'right choice' in healthy agriculture since they are highly compatible with sustainable crop production. The co-inoculation of plants with two or more beneficial bacteria apparently provides greater phytostimulation than mono-inoculation, perhaps because of the synergistic and multifarious effects occurring when two or more microorganisms are co-interacting. There is a consensus that bacterial mixtures provide greater benefits to the plants, the number of formulations containing more than three species of microorganisms in consortium is still limited. Therefore, we believe that more research and investment is needed to design and formulate multi-species inoculants containing compatible bacteria and other beneficial microorganisms in order to be capable of coexisting both in the designed formulation and associated with plants for sustainable benefits.

Keywords Bacterial inoculants · Bacterial desiccation · PGPB · Beneficial bacteria

2.1 Introduction

Bacteria were the first colonizers of the planet and it is believed that they sustain life on earth (Lin et al. 2014; Pace 1997; Strom 2008; Zavarzin 2008). Only around 1% of bacterial diversity have been isolated (Amann et al. 1995; Curtis et al. 2002; Prashar et al. 2014), and majority of them could be beneficial for agriculture (Lugtenberg and Kamilova 2009; Mitter et al. 2017; Philippot et al. 2013), biotechnology (Broadbent et al. 2003; Chemier et al. 2009; Zhang 2018), biomedicine (Morales-García et al. 2007), bioremediation (Böltner et al. 2008; Fernández et al. 2012; Liu et al. 2017b), and other benefits.

Bacteria have the capability to interact with plants and increase their health and growth. The plant growth-promoting bacteria (PGPB) have been isolated from diverse plant sources and geographical places as given in Table 2.1. The source of isolation could be from soils, rhizosphere, rhizoplane, root nodules, endophytic zones and the epiphytic region of the plants (Ahmad et al. 2018; Cazorla et al. 2007; Kumar et al. 2014; Molina-Romero et al. 2015; Morales-García et al. 2011; Vandamme et al. 2002; War Nongkhla and Joshi 2014). Bacteria associated with maize plants also have been isolated and some genera reported include *Azospirillum*, *Burkholderia*, *Bacillus*, *Rhizobium*, *Enterobacter*, *Klebsiella* and *Arthrobacter* (Table 2.2).

A heterogeneous group of bacteria may be associated with plants, but not all of them have the capability to improve their growth. Therefore, rigorous studies should be performed to test their beneficial traits and the mechanisms involved to

Table 2.1 Bacterial strains isolated from diverse environments and mechanisms involved in the plant growth promotion

Isolated strain	Mechanisms for plant growth promotion implicated	Place of isolation	Geographical place for isolation	References
Bacillus subtilis Q3 *Paenibacillus* sp. Q6	Phosphate solubilization	Cotton rhizosphere	Bahawalpur and Haroonabad Punjab—Pakistan	Ahmad et al. (2018)
Enterobacter sp. EP2a JN653461	Phosphate solubilization, BNF	Epiphytic from *Houttuynia cordata*	India	War Nongkhla and Joshi (2014)
Gluconacetobacter diazotrophicus UAP-Cf05	BNF, IAA	*Coffea Arabica* rhizosphere	Puebla—México	Jimenez-Salgado et al. (1997)
Azotobacter sp. NAT 13	BNF	Cotton rhizosphere	Tolima—Colombia	Guzmán et al. (2012)
Pseudomonas fluorescens ABE66285	ACC deaminase, Phosphate solubilization	*Larrea tridentata* rhizosphere	Chile	Jorquera et al. (2012)
Burrkholderia tuberum STM678^{T}	ACC deaminase	Legume nodules	France	Vandamme et al. (2002), Onofre-Lemus et al. (2009)
Bacillus subtilis PCL1605	Antifungal activity	Rhizoplane from avocado	Malaga—Spain	Cazorla et al. (2007)
Klebsiella variicola T29A	IAA	Sugarcane endophyte	Puebla-México	Rosenblueth et al. (2004)

Abbreviation meaning: BNF (Biological Nitrogen Fixation), IAA (Indol Acetic Acid), VOCs (Volatile compounds), ACC (1-aminocyclopropane-1-carboxylate) deaminase

unravel the hidden characters that how bacteria promote the plant growth (Lugtenberg and Kamilova 2009; Molina-Romero et al. 2015).

Adhesion and colonization to the root zone are the first critical steps that bacteria must overcome to the right integration on the plant–host so as to establish and develop their beneficial functions (Albareda et al. 2006; Muñoz-Rojas and Caballero-Mellado 2003). A number of reports have been published on the concept of cellular adherence to the surface of maize seeds and colonizing the rhizosphere (Table 2.3). Adhesion occurred in the range of 10^{5}–10^{6} CFU/seed while rhizosphere colonization was in the order of 10^{3}–10^{8} CFU/gV [Colony Forming Units/Vermiculite (g)], depending on different factors including bacterial species and experimental conditions. To demonstrate the PGPB capabilities, bacteria have to be bioprimed on seed surface or seed dressing and allow to grow them. The vegetative and reproductives such as seed germination index, length and diameter of stems,

Table 2.2 Bacterial strains isolated from maize and mechanisms involved in the plant growth promotion

Isolated strain	Mechanisms involved in the promotion of plant growth	Localization in the plant	Geographical place for isolation	References
A. brasilense UAP-154	IAA, siderophore production	Maize rhizosphere	Tlaxcala-México	Dobbelaere et al. (2001), Tapia-Hernández et al. (1990)
Arthrobacter sp. V54 *Bacillus* sp. V 39	Phosphate solubilization, BNF, Siderophore production	Maize rhizosphere	Ngaoundal, Adamawa, Cameroon	Tchakounté Tchuisseu et al. (2018)
Bacillus methylotrophicus M4-96	VOCs, Auxins	Maize rhizoplane	Morelia-Michoacán	Pérez-Flores et al. (2017)
Burkholderia tropica MTo 293	VOCs, BNF, Phosphate solubilization and siderophore production	Maize stem (Endophytic)	Oaxaca-México	Tenorio-Salgado et al. (2013)
Burkholderia tropica MCu-831	FBN	Maize rhizoplane	Morelos-México	Reis et al. (2004)
Burkholderia unamae MTl-641^T	BNF, ACC deaminase	Maize rhizosphere	Morelos-México	Caballero-Mellado et al. (2004)
Enterobacter sp. UAPSO3001	Unknown	Maize rhizosphere	Tlaxcala-México	Morales-García et al. (2011)
Klebsiella spp. (Zea)	BNF	Maize stem (Endophytic)	USA	Palus et al. (1996)
Rhizobium etli	BNF	Maize stem (Endophytic)	Morelos-México	Gutiérrez-Zamora and Martínez-Romero (2001)

Abbreviation meaning: BNF (Biological Nitrogen Fixation), IAA (Indol Acetic Acid), VOCs (Volatile compounds), ACC (1-aminocyclopropane-1-carboxylate) deaminase

number of leaves, height of stems, root and shoot length, fresh and dry weight of plants along with important physico-chemical characters such as chlorophyll content, total nitrogen, percentage of nitrogen and others (Ahmad et al. 2018; Molina-Romero et al. 2017d; Morales-García et al. 2011; Muñoz-Rojas and Caballero-Mellado 2003). In one of the study, Bashan et al. (2017) stated that fresh weight is less precise than the dry weight. The fresh weight is affected by numerous environmental and other parameters including relative humidity, temperature, air, soil environment, etc,. of the excised plant parts to interfere with excess moisture present in washed roots and shoots, besides, the total time involved in collecting and washing samples until weighing (Bashan et al. 2017). Therefore, differences in appearance observed between inoculated plants and non-inoculated one represent a

Table 2.3 Bacteria quantity associated with seeds or rhizosphere of maize

Bacterial strain	Cells number adhered to seeds (Log CFU/seed)	Cells number colonizing the rhizosphere of plants Log CFU/gV	Variety of maize	References
Azospirillum brasilense Sp7	5.71 ± 0.41	6.10 ± 0.16	Blue maize CAP15-1 TLAX	Molina-Romero et al. (2017b)
Azospirillum brasilense Sp7	6.95 ± 0.11	5.12 ± 1.40	Rojo-Criollo	Morales-García et al. (2013)
Pseudomonas putida KT2440	7.50 ± 0.14	6.40 ± 0.2	Blue maize CAP15-1 TLAX	Molina-Romero et al. (2017b)
Pseudomonas putida KT2440	7.61 ± 0.03	8.10 ± 0.18	Girona	Ramos Martin and Muñoz-Rojas (2006)
Pseudomonas putida KT2440	7.02 ± 0.15	3.90 ± 0.81	Rojo-Criollo	Unpublished results
Sphingomonas sp. OF178	6.55 ± 0.33	6.18 ± 0.71	Blue maize CAP15-1 TLAX	Molina-Romero et al. (2017b)
Sphingomonas sp. OF178	6.87 ± 0.16	4.74 ± 0.40	Rojo-Criollo	Morales-García et al. (2013)
Acynetobacter sp. EMM02	7.87 ± 0.20	6.70 ± 0.14	Blue maize CAP15-1 TLAX	Molina-Romero et al. (2017b)
Enterobacter sp. UAPS03001	7.02 ± 0.30	9.26 ± 0.55	Rojo-Criollo	(Morales-García et al. 2011)
Enterobacter sp. UAPS03001	7.23 ± 0.18	7.74 ± 0.25	Blue maize CAP15-1 TLAX	Pazos-Rojas et al. (2018)
Klebsiella variicola T29A	6.69 ± 0.03	7.4 ± 0.35	Blue maize CAP15-1 TLAX	Pazos-Rojas et al. (2018)
Klebsiella variicola T29A	7.85 ± 0.25	8.75 ± 0.31	White autochthonous from Papalotla-Tlaxcala, México	Unpublished results

good indicator for the capability of bacteria to promote the growth of plants (Fig. 2.1) but decisive conclusion comes from data of dry weight increments (Bashan et al. 2017; Molina-Romero et al. 2017b; Morales-García et al. 2011; Muñoz-Rojas and Caballero-Mellado 2003).

Various workers have suggested the lab's data do not coincide with field conditions (Çakmakçi et al. 2006; Mehnaz et al. 2010; Shahzad et al. 2013). Even a few have suggested to carry out experiments first, under well-controlled conditions at the plant chamber, then under greenhouse conditions and later under field conditions. Several research steps are involved to carry out in the three phases of experiments prior to developing a commercial formulation delivered to the market (Bashan et al. 2014). Numerous molecular mechanisms involved to participate and to demonstrate the capability or ability of one strain to promote the plant growth and health promotion (Lugtenberg and Kamilova 2009). The mechanisms could be classified in a general form as direct and indirect mechanisms (Goswami et al. 2016;

Fig. 2.1 Bacterial mixture (EMMIM-5) improving the growth of maize plants (Blue maize CAP15-1 TLAX) in comparison with non-inoculated plants (control), 45 days after the inoculation of germinated seeds

Jha and Saraf 2015; Molina-Romero et al. 2015; Paterson et al. 2017). Direct mechanisms involve the bacterial contribution to the assimilation of diverse nutrients or metabolites available for plants that have positive effects on their growth. The indirect mechanisms contribute to the health support to the plants that concomitantly enhance their growth and development. Among indirect mechanisms, induced systemic resistance by beneficial bacteria, antimicrobial production, etc., have been worked out.

2.2 Plant Growth Promotion by Direct Mechanisms

2.2.1 Biological Nitrogen Fixation

BNF refers to the ability of some bacteria to capture atmospheric nitrogen and transform it to combined nitrogen, usually in the form of ammonium (NH_4^+) (Annan et al. 2012; Dixon and Kahn 2004; Santi et al. 2013). Fixed nitrogen could be donated to the plants that in turn provide carbon source to bacteria. The interaction of different species of *Rhizobium* with legumes is one of the models more

widely studied. The interaction of *Rhizobium*–legumes is highly specific and both populations are favoured both for the plant and bacteria during relationships such as mutualistic symbiosis (Simms and Taylor 2002). Although BNF is highly effective in the interaction of rhizobia–legumes, this phenomenon has not been as significant in non-legume plants except very few such as sugarcane inoculated with the free-living bacterium *Gluconacetobacter diazotrophicus* (Muñoz-Rojas and Caballero-Mellado 2003; Sevilla et al. 2001). However, some grasses showed high levels of nitrogen obtained through the BNF process (Herridge et al. 2008). Further investigations are yet to be carried on the bacteria with highly effective BNF capability associated with non-legumes or performing genetic engineering of non-legume plants to introduce genes related to nitrogen fixation (Saikia and Jain 2007). The free-living bacteria with potential to perform the BNF process include *Pseudomonas fluorescens*, *Beijerinckia* sp., *Azoarcus* sp., *Azotobacter* sp., *Burkholderia unamae*, *Gluconacetobacter diazotrophicus*, *Herbaspirillum* sp., *Azospirillum brasilense*, *Nostoc* sp. and *Rhizobium* sp. (Caballero-Mellado et al. 2004; Defez et al. 2016; Fibach-Paldi et al. 2012; Gutiérrez-Zamora and Martínez-Romero 2001; Guzmán et al. 2012; Kaschuk and Hungria 2017; Sevilla et al. 2001).

2.2.2 Phytohormones Production

This is a widely distributed mechanism among plant-associated bacteria (Costacurta and Vanderleyden 1995). Various groups of PGPR secrete gibberellins, auxins and cytokinins, the known phytohormones that promote plant growth (Bottini et al. 2004; Costacurta and Vanderleyden 1995; Kang et al. 2014). Indole acetic acid (IAA), an auxin molecule, is the most studied phytohormone wherein biosynthetic pathway is well known in the genus *Azospirillum* (Cassán et al. 2014; Patten and Glick 1996). IAA induces the elongation and division of root cells, included root growth and has greater root surface enabling plants with higher nutrient absorption and growth (Patten and Glick 2002). *Gluconacetobacter diazotrophicus*, *Azospirillum brasilense*, *Pseudomonas* sp., *Enterobacter cloacae*, *Klebsiella variicola* and *Bacillus amyloliquefaciens* have been reported as producers both induced and constitutive IAA in vitro (Defez et al. 2016; Fuentes-Ramirez et al. 1993; Idris et al. 2007; Malik and Sindhu 2011; Patten and Glick 1996).

2.2.3 Phosphate Solubilization

A fundamental element of plant metabolism is phosphorus since it is an important structural element in DNA, RNA, phospholipids and communication signals. Although this component is abundant in the soil, but remains in unavailable form hence cannot be taken up by the plants in most soil conditions. Only monobasic or

dibasic form of P is soluble and hence bioavailable to the plants (Gyaneshwar et al. 2002). Certain bacterial and fungal genera have the capability to solubilize phosphate from soils and allow the phosphorus uptake by plants (Castagno et al. 2011; Gyaneshwar et al. 2002; Kang et al. 2002). The ability of phosphate solubilization in rhizobia has been previously reported (Pandey et al. 2005). However, various free-living aerobic bacteria were reported later for phosphate solubilization (Khan et al. 2007). Some PGPB solubilize phosphates from inorganic or organic compounds; involving the use of nonspecific phosphatases, C-P lyases, phosphatases and phytases (Lugtenberg and Kamilova 2009; Molina-Romero et al. 2015). On the other hand, releasing organic acids by different bacteria may chelate phosphorus, making it bioavailable to plants (Aeron et al. 2011; Vyas and Gulati 2009). Bacteria with the ability to solubilize phosphates include *Pseudomonas putida*, *Bradyrhizobium japonicum*, *Enterobacter agglomerans* and *Rhizobium leguminosarum* (Molina-Romero et al. 2015, 2017b; Rodríguez et al. 2006). Besides enzyme and organic acids of bacterial origin, other mechanisms of P solubilization include inorganic acids produced by chemoautotrophs and the H+ pump observed in *Penicillium rugulosum* (Khan et al. 2014).

2.2.4 ACC Deaminase Production

Under environmental conditions plants are exposed to adversities caused by abiotic and biotic factors influencing their growth (Morgan and Drew 2006); the climate, the amount of water available, solar radiation, attack by pathogens, pests and animals, and others. Changes in these biotic or abiotic factors represent intense stress on the plants which in turn trigger ethylene-mediated systemic defense response causing excessive energy expenditure to the plants. Some PGPB produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase and improve the growth of plants by decreasing ethylene levels (Bal et al. 2013; de Oliveira et al. 2006; Glick 2014; Glick et al. 2007). Following the discovery of the role of ACC deaminase in plant growth promotion (Glick et al. 1998), rhizobacteria able to synthesize ACC deaminase were reported by the pioneers in India (Aeron et al. 2017; Kumar et al. 2012; Maheshwari et al. 2015a). Kumar et al. (2012) reported the role of *Bacillus* sp. in ACC deaminase synthesis and other rhizobacteria were reported by Aeron et al. (2017). In the Indian research scenario, a beta class of Proteobacteria first reported as rhizobia, was identified as *Burkholderia* sp., having ACC deaminase activity (Pandey et al. 2005). The ACC deaminase enzyme breaks the ethylene precursor avoiding its synthesis and also releasing ammonium that can later be used by plants as a nitrogen source (Singh et al. 2015). Some PGPB with the capability to produce ACC deaminase are *Burkholderia unamae* MTl-641, *Azospirillum lipoferum*, *Pseudomonas fluorescens* TDK1, *Enterobacter cloacae, Bacillus* sp. AR-ACC1, and *Agromyces* ANR-ACC2 (Esquivel-Cote et al. 2013; Nadeem et al. 2007; Onofre-Lemus et al. 2009; Zahir et al. 2008). The ACC

deaminase system can also be considered an indirect mechanism of plant growth promotion since it blocks out an intensive defense response avoiding unnecessary energy expenditure by plants.

2.3 Indirect Growth Promotion Mechanisms

Today, this kind of mechanisms are increasing in knowledge, especially the elimination of microbial pathogens by ISR, which shows an interesting mechanism to protect plants from being attacked by phytopathogens.

2.3.1 Antagonistic Mechanisms

Phytopathogenic microorganisms are major causal organisms of plant diseases and crop losses. Various genera of PGPB are capable of eliminating those pathogens, hence, they can be used as biocontrol agents (Beneduzi et al. 2012; Compant et al. 2005; Liu et al. 2017a). Inhibitory substances produce by PGPB with biocontrol potential include siderophores, bacteriocins, broad-spectrum antibiotics, lytic enzymes, lipopeptides and antifungal metabolites (Mohamed et al. 2017; Molina-Romero et al. 2015; Morales-García et al. 2007; Sivasakthi et al. 2014). There are several PGPB able to prevent the deleterious effects of phytopathogenic organisms by producing inhibitory substances, e.g. *Gluconacetobacter diazotrophicus*, *Burkholderia tropica*, *Bacillus amyloliquefaciens*, *Pseudomonas fluorescens*, *Lysinibacillus sphaericus*, *Bacillus subtilis*, *Bacillus altitudinis*, *Azospirillum brasilense, Rhizobium etli, Rhizobium leguminosarum*, *Kosakonia radicincitans* (Bardin et al. 2004; Cawoy et al. 2015; Krishnan et al. 2007; Lambrese et al. 2018; Naureen et al. 2017; Príncipe et al. 2018; Russo et al. 2008; Saravanan et al. 2008; Sivasakthi et al. 2014; Tenorio-Salgado et al. 2013; Tortora et al. 2011).

2.3.2 Induced Systemic Response (ISR)

The interaction of plants with pathogens or beneficial microorganisms triggers the systemic response of plants (van Loon 2007). Systemic acquired resistance (SAR) is triggered by pathogens while induced systemic resistance (ISR) is triggered by non-pathogenic microorganisms (Pieterse et al. 2014; van Loon 2007). SAR is a phenomenon where plants acquire an enhanced defensive response against subsequent pathogen attack as a result of a primary, limited infection (van Loon et al. 2006), this response is mediated by salicylic acid and it is quite aggressive for plants causing necrosis in some cases (Pieterse et al. 2014; Ramamoorthy et al.

2001). ISR is triggered by beneficial bacteria, it is mediated by ethylene and jasmonate, and this response prevents the establishment of pathogens in the plant (Pieterse et al. 2014; Su et al. 2017; van Loon 2007). Induced systemic resistance (ISR) is the phenomenon to immunize the plants by PGPR against phytopathogens and confer substantially enhanced levels of peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), β−1, 3 glucanase and chitinase as a part of the systemic response (Sharma et al. 2018). Field application of PGPB with the ability to induce a systemic response in plants might prevent the attack of pathogens resulting in an increase of the yield in different crop plants (Gkizi et al. 2016; Su et al. 2017). Not only PGPB but some other bacterial components are also able to induce the ISR response, for example, flagella, lipopolysaccharides, siderophores and cyclic lipopeptides (Ramamoorthy et al. 2001). Some examples of PGPB capable to trigger ISR are *Pseudomonas fluorescens* FB11, *Bacillus altitudinis, B. cereus, B. subtilis*, *B. amyloliquefaciens, B. pasteuri, B. pumila, B. mycoide, B. sphaericus, Burkholderia phytofirmans, Rhizobium leguminosarum bv. viceae* FBG05, *Pseudomonas putida* 89B-27, *Serratia marcescens* and *Paenibacillus alvei* K165, *Rhodopseudomonas palustris* (Bhattacharyya and Jha 2012; Elbadry et al. 2006; Gkizi et al. 2016; Kloepper et al. 2004; Su et al. 2017).

2.3.3 Volatile Organic Compounds Production

Volatile organic compounds (VOCs) are small and gaseous molecules produced by bacteria, identified as proficient signal molecules functioning as chemical attractants or repellents (Hernández-Calderón et al. 2018; Ortíz-Castro et al. 2009). VOCs interact with plants in the soil and may promote plant growth by inducing the ISR, suppressing phytopathogens, stimulating of photosynthesis and modulating phytohormone signalling (Santoro et al. 2015; Sharifi and Ryu 2018). Some VOCs identified include aldehydes, alcohols, ketones, indoles, terpenes, fatty acids and jasmonate (Pieterse et al. 2014; van Loon 2007).

An alternative function of VOCs produced by the PGPB is to increase the resistance of plants to abiotic stresses such as salinity, drought and heavy metals (Farag et al. 2013). VOCs can act directly as (i) phytohormones, (ii) helping the acquisition of iron, (iii) regulating the growth and morphogenesis of the plant and (iv) exerting biocontrol of phytopathogens either by antibiosis or by triggering ISR (Farag et al. 2013; Park et al. 2013; Zhang et al. 2009). Examples of bacteria that produce VOCs are *Bacillus subtillis* SYST2, *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937a, *Erwinia carotovora*, *P. polimyxa* E681, *Pseudomonas fluorescens*, *Pseudomonas stutzeri* E25 and *Stenotrophomonas maltophilia* CR71 (Cheng et al. 2017; Ortíz-Castro et al. 2009; Park et al. 2013; Rojas-Solís et al. 2018; Santoro et al. 2015; Tahir et al. 2017; Zhang et al. 2007, 2009). VOCs can be exploited as an eco-friendly, cost-effective and sustainable strategy for agricultural practices (Kanchiswamy et al. 2015).

2.3.4 Elimination of Toxic Compounds for Plants

In modern agriculture, toxic compounds such as fungicides, pesticides and herbicides have been excessively used on crop fields. The indiscriminate and excessive applications of these compounds could have harmful effects for the development of plants, animals and human being (Benbrook 2016; Donham 2016; Igbedioh 1991; Park et al. 2015). These toxic compounds even modify the microbial diversity and microbial activity (Chen et al. 2001; Johnsen et al. 2001; Smith et al. 2000); which is fundamental for the proper development of plants (Berendsen et al. 2012). For this reason, it is necessary to eliminate these toxic compounds from the soil to allow the plants to grow in a sustainable manner an optimal growth of crop plants. There are several bacteria having the ability to eliminate toxic compounds from the soil while interacting with host plants. Among the most widely studied bacterial species are *Pseudomonas putida*, *Sphingomonas* sp. OF178, *Burkholderia unamae*, *Burkholderia tropica*, *Bacillus subtillis*, *Pseudomonas rhizophila* S211 etc. (Ahemad and Khan 2012; Böltner et al. 2008; Caballero-Mellado et al. 2004, 2007; Caballero et al. 2005; de Oliveira et al. 2006; Hassen et al. 2018). However, the ability of these bacteria to eliminate pesticides present in agricultural soils are yet to be elucidated.

Several published data related to PGPB stated that the actual mechanism comprising phytostimulation of PGPB neglected, and in some only the growth promotion characteristics have been reported. In fact, the transcription level of key genes involved in plant growth promotion or physiological characteristics such as ability to fix nitrogen, solubilize phosphates or produce phytohormones have been insignificantly tested in vitro (Ahmad et al. 2018; Caballero-Mellado et al. 2004; Fibach-Paldi et al. 2012; Fuentes-Ramirez et al. 1993; Molina-Romero et al. 2017b; Onofre-Lemus et al. 2009; Rosenblueth et al. 2004; Tenorio-Salgado et al. 2013). There is limited information about the actual genes involved in the plant growth promotion, making defective mutants and corroborating the lack of plant growth promotion characteristics in PGPB (Rajput et al. 2015; Schneider et al. 1991; Sevilla et al. 2001; Zhang et al. 2009). For example, the deletion of *nifH* gene in *Gluconacetobacter diazotrophicus* makes this bacterium no longer able to fix nitrogen both in vitro and in association with host plants, demonstrating that aforesaid mechanism has been involved in the promotion of growth (Sevilla et al. 2001).

2.4 The State of the Art of PGPB Publications and Patent Numbers

Literature on PGPB-type bacteria is broad, ranging from isolation, phenotypic, biochemical and molecular characterization, ability to colonize the rhizosphere of plants, plant growth promotion and studies of genes involved in plant–bacteria

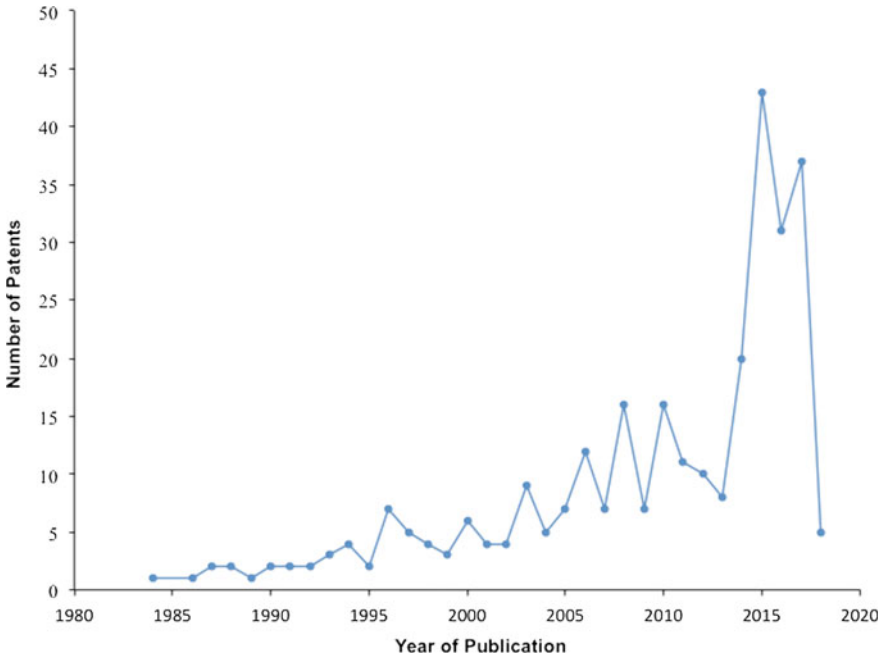

Fig. 2.2 Number of patents applied by year in the global world. All patents are related to the use of PGPB as crop plants inoculants. Source data were acquired from two prestigious platforms of patents search: Spacenet and Patent Inspiration

interaction (Huang et al. 2014; Lugtenberg and Kamilova 2009). Public databases such as NCBI or Google Scholar show an increasing trend in the number of articles published on issues related to the capacity of bacteria to promote plant growth. In fact, there are around 2742 published works in PubMed database related to this field up today (Table 2.3), but this data fluctuates according to the new publications that are stored in the system. Interestingly, the number of patents is approximately fivefold lower than that of published articles suggesting that very limited works have ended up in a potential application. Therefore the number of patents is lower than the number of publications and on the other hand, patent number continues to increase (Fig. 2.2). This could be due to the urgent need for the implementation of environmental-friendly technology provided to reduce the contamination of toxic compounds used in intensive agriculture (Baez-Rogelio et al. 2017). Countries with the major patent numbers related to the application of PGPB are USA, Germany, Canada, United Kingdom and Spain (Fig. 2.3).

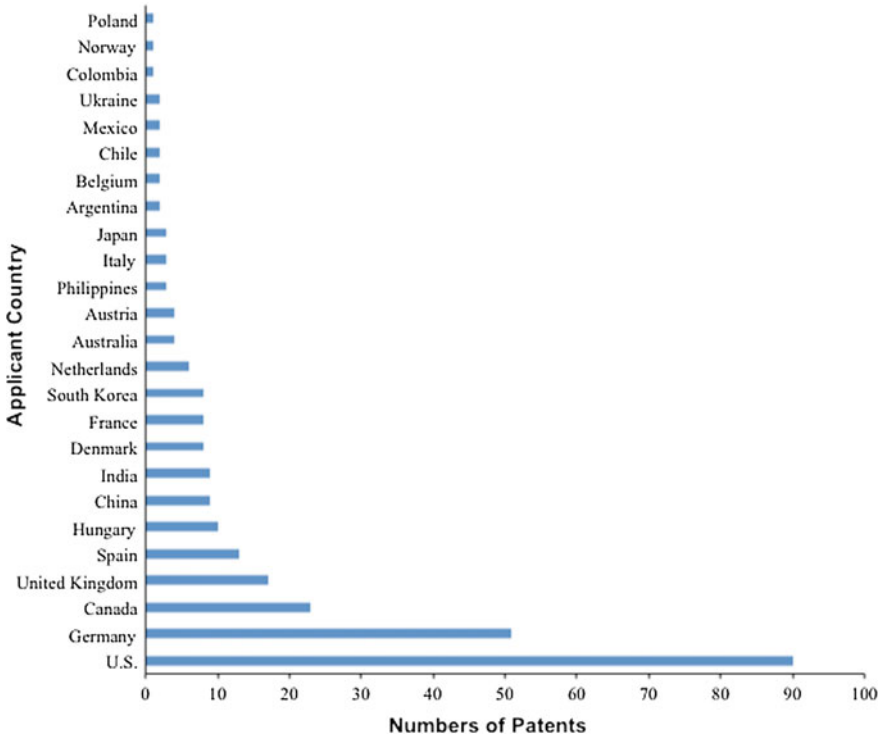

Fig. 2.3 Analysis of the number of patents carried out by applicant country. All patents are related to the use of PGPB as crop-plant inoculants. Source data were acquired from two prestigious platforms of patents search: Spacenet and Patent Inspiration

2.5 Bacterial Inoculants for Agriculture

Non-pathogenic bacteria with growth-promoting capacity whose mechanisms of phytostimulation are supported by molecular studies can be considered candidates to formulate bacterial inoculants. The number of crop types and hectares of agricultural land where PGPB are applied is quite low corresponded to that of the total crops or farming area. This is perhaps because of lack of a culture of adopting sustainable technologies, inconsistencies of yield production in yield and problems of technology associated to massive inoculation (Bashan et al. 2014; Carolan 2009; Cummings 2009). *Azospirillum brasilense* is one of the most studied bacteria applied in agricultural crops, it has been used in various crops around the world with successful results in more than 70% of cases in comparison to that obtained in less reported in other PGPB (Dobbelaere et al. 2001; Fuentes-Ramirez and Caballero-Mellado 2006; Okon and Labandera-Gonzalez 1994). Among the inoculants intended for sustainable crop production that are currently being marketed, we can find mono-inoculants formulated with a single bacterium such as

Azospirillum brasilense, *Azotobacter vinelandii*, *Rhizobium etli*, or *Bacillus* sp. (Baset Mia and Shamsuddin 2010; O'Callaghan 2016; Okon and Labandera-Gonzalez 1994). Countries that are adopting the use of these bacteria on crop fields are México, Argentina, USA, China, Belgium, Uruguay and to a certain extent in India (Bashan et al. 2014; Dobbelaere et al. 2001; Molina-Romero et al. 2015; Shen 1997).

In India, the first study on legume-*Rhizobium* symbiosis was initiated by N. V. Joshi in 1920, and commercial production began in 1956 (Barman et al. 2017; Ghosh 2004; Majumdar 2015; Mazid and Khan 2014). The development of technology for inoculants production in India evolved through the nineteenth century including some remarkable events: (A) the earliest documented production of *Rhizobium* inoculant by M. R. Madhok in 1934. (B) The discovery of nitrogen fixation by Blue-Green Algae (BGA) in a rice field and the report on the performance of *Azotobacter* in rice soil by B. N. Uppal, both events in 1939. (C) First commercial production of biofertilizer in 1956 by N. V. Joshi. (D) The study of microbial phosphate solubilization by Sen and Pal in 1957. (E) The first work for the quality standardization for legume inoculant in 1958. (F) Isolation of the first non-symbiotic N-fixing organism Derxiagummosa by P. K. Dey and R. Bhattacharyya in 1960. (G) Increment in the requirement of biofertilizers for soybean mainly in Madhya Pradesh in 1964. (H) Projects set up by the Indian Council of Agricultural Sciences (ICAR) in 1968, where *Rhizobium* study got priority. (I) Use of Indian peat as carrier reported by V. Iswaram in 1969. (J) Use of coal as an alternative carrier reported by J. N. Dube in 1975. (K) Indian standard specification for Rhizobium in 1976. (L) Use of ISI mark for *Rhizobium* in 1977. (M) In 1979, a coordinated project for BNF in all India took place and the ISI standardization was made for *Azotobacter* inoculant. (N) Setting up of National Project on Development and use of Biofertilizers by Ministry of Agriculture, Government of India, in 1983. (O) Five biofertilizers (containing: *Rhizobium*, *Azotobacter*, *Azospirillum*, Phosphate Solubilizing Bacteria and mycorrhiza) were incorporated in India's Fertilizer Control Order (FCO) in 1985, and the First National Productivity award on Biofertilizer was celebrated. (P) Setting up of National Facility Centre for BGA at IARI in 1988. (Q) The NIKU (National Input Complete and Utilization) Bio-Research Laboratory was established in 1997 at Pune. (R) The Tenth Plan document (2002–2007) that emphasize the use of biofertilizers, biocontrol agents, organic manures, etc. with infrastructure support (Barman et al. 2017; Majumdar 2015).

Through the history of biofertilizers in India, some adversities have limited the development of this important product (Ghosh 2004). Adoption of the technology has not consistently grown over time and has slowed down in the late 1990s. Although there have been more and more new entries in the market, the average capacity of bigger producers has come down, characterizing the industry by many small units. Lack or low diffusion of technology with the farmers and low participation of the private sector in the commercialization of inoculants (below 50%) such as problems in transportation and distribution represented the major problems in rural areas (Mazid and Khan 2014). Despite adversities, India is one of the most

important countries in biofertilizer production (Mahajan and Gupta 2009). The first biofertilizer modern unit was started by the Gujarat State Fertilizer Company (GSFC), Vadodara, in 1985 and many more followed thereafter. Today the number of microbial inoculants manufactured in India has increased and products include Rhizonick (*Rhizobium*), Azonik (*Azotobacter chroococcum*), Spironik (*Azospirillum brasilense*), Phosphonive (Phosphate solubilizing bacteria), Sulphonik (Sulphur-oxidizing bacteria and fungi), Niku-2000 (Decomposing culture), Trichonik (*Trichoderma viridi*), Vermiculture (mixed with N-fixing inoculant and P solubilizers), Blue-Green Algae (BGA) (containing photosynthetic nitrogen fixers), Vesicular arbuscular mycorrhiza (VAM), K-solubilizer (*Frauteria aurantia*), etc. (Barman et al. 2017; Majumdar 2015; Singh et al. 2014b). Agro Industries Corporation has the maximum capacity to produce biofertilizers in India, followed per State Agriculture Universities and the private sector (Singh et al. 2014b). Since 2016, Indian Government has been promoting biofertilizers development through various schemes of National Mission of Sustainable Development (NMSA)/ Paramparagat Krishi Vikas Yojana, Rashtriya Krishi Vikas Yojana (RKVY) and National Mission on Oilseeds and Oil Palm (NMOOP) and Indian Council of Agricultural Sciences (ICAR) (http://pib.nic.in/newsite/PrintRelease.aspx?relid=137762).

On the other hand, among the principal companies dedicated to produce and commercialize biofertilizers in México are Biofabrica Siglo XXI, Biosustenta, Fertilizantes Mexicanos, Biokrone. Biofabrica Siglo XXI developed products such as Azofer, an inoculant formulated with *Azospirillum brasilense*; Rhizofer, formulated with *Rhizobium etli,* etc. (http://www.biofabrica.com.mx/about.html). Another Mexican company is Biosustenta, which is developing and producing biological inputs of Ferbiliq inoculant, based on *Azospirillum brasilense* and *Glomus intraradices*; Endomaz biofertilizers made from *A. brasilense* (http://cosustenta.com/catalogo.html). Fertilizantes Mexicanos markets biofertilizers formulated with nitrogen-fixing bacteria (Azoton AA Plus); 'Biomatrix + powder' formulated with nitrogen-fixing bacteria and phosphate solubilizers, other of its products are Bioespiril L and Raizinn Biol (http://biofertilizantes.mx/index.html). Similarly, Bio Organica Mexicana provides biofertilizers such as Ultralite AZO (http://www.bio-organica.com.mx). All above-mentioned companies offer to the farmers an ecological alternative to increase the production of their crops, for impacting positively their economy, due to the investment of lower costs of these products compared to chemical fertilizers. In Argentina, agrobiotechnology has been developed for the past 50 years, using PGPR isolated from their soils for the formulation of bacterial inoculants (Molina-Romero et al. 2015). These formulations were developed to improve growth and increase the productivity of leguminous plants and cereals of agricultural importance. Among the companies with more experience in the production of microbial inoculants are NITRASOIL ARGENTINA S.A. Co., which has developed an inoculant that contains bacteria of the genus *Azospirillum* sp. strain AZ39, recommended by the INTA (National Institute of Agricultural Technology) for being considered the best microbial inoculant (http://www.nitrasoil.com.ar). The company Rizobacter Argentina S.A.

Co. (http://www.rizobacter.com/argentina/) also has a variety of products whose formulation is used in soybean, corn and wheat. The bacteria used for the formulation of these inoculants are *P. fluorescens*, *Bradyrhizobium* sp., *Mesorhizobium ciceri*, *Sinorhizobium meliloti*, *Rhizobium leguminosarum* biovar *trifoli* and *Bradyrhizobium japonicum*. The firm Nitrasoil S. A., FPC Argentina S.A. (http://www.fpcinoculantes.com.ar), Granaries and Elevadores Argentinos de Colon Soc. Coop. Ltda (GEA) (http://geadecolon.com.ar) and bionet (http://www.bionetsrl.com/inoculantes-bionet-soja-premium.php) are dedicated to the formulation and commercialization of fertilizers and biological inoculants for the agricultural sector (Molina-Romero et al. 2015).

Although the use of these formulations is still moderate today but, are increasingly accepted by farmers, due to the improved growth of cultivars inoculated with PGPB, their application have enhanced the crop productivity (Lugtenberg and Kamilova 2009) decrease in the use of chemical fertilizers (Dobbelaere et al. 2001) and potential to decrease in the use of toxic compounds such as pesticides and herbicides (Myresiotis et al. 2012). Such characteristics make these microorganisms the first choice for organic agriculture being highly compatible for sustainable practices.

2.6 Co-inoculation Versus Mono-inoculation

In fact, microbial co-inoculation is considered to be an innovative approach and had been applied worldwide (Wang et al. 2018). Compared with mono-inoculation, co-inoculation of microorganisms has apparently been more effective in stimulating plant growth because of the synergistic effect that occurs when more than one microorganisms are co-interacting with same or their diverse genera (Atieno et al. 2012; Barea et al. 2002; Zoppellari et al. 2014). For example, the co-inoculation of lettuce with *Bacillus* sp. and *Glomus intraradices* make the use of water more efficient under stress conditions (Vivas et al. 2003). Similarly, co-inoculation of pea with *Rhizobium* spp. and *Bacillus megaterium* increased the biomass of roots and aerial region, the percentage of nitrogen and productivity (Elkoca et al. 2007). The consortium of *P. aeruginosa* KRP1 and *B. licheniformis* KRB1 were reported suppressive for the fungal phytopathogens *F. oxysporum* and *S. sclerotiorum* causing disease in *Brassica campestris* (Maheshwari et al. 2015b). Although, there are promising results of co-inoculations,, formulations on the market containing three or more species of microorganisms are limited. Research papers have shown that the inoculation of sugar cane with a mixture of more than three bacteria enhanced the production of sugarcane in soil characteristically having low to medium-level and nitrogen fertilization (Table 2.4) (Molina-Romero et al. 2017b; Morales-García et al. 2013; Oliveira et al. 2009).

The design, formulation and optimization of an effective mixture of bacteria to be used as inoculants, is not so easy because, it requires microbe–microbe interaction, bacterial ability of adhesion to seeds and root colonization in plants

Table 2.4 Search of keywords related to plant growth-promoting bacteria and some beneficial bacterial species. The search was made on 13 August 2018

Keywords searched	Pub Med-NCBI	Scholar google	Patents searched in Spacenet
Plant growth-promoting bacteria	2742	1,070,000	560
Plant growth-promoting rhizobacteria	845	46,900	83
Bacterial plant inoculants	331	36,800	32
Azospirillum brasilense	777	29,800	53
Gluconacetobacter diazotrophicus	107	4270	7
Rhizobium etli	472	11,700	4
Herbaspirillum seropedicae	136	4450	5
Burkholderia unamae	16	454	1
Burkholderia tropica	24	2400	1
Pseudomonas fluorescens	5733	160,000	877

(Baez-Rogelio et al. 2017; Singh et al. 2014a; Sundaramoorthy et al. 2012). In addition, studies on the antagonistic relationships among the strains involved in a mixture of bacteria should be conducted before design and application of a multi-species inoculant. Some antagonistic effects also occur among bacteria when associated with plants (Baez-Rogelio et al. 2017; Molina-Romero et al. 2017b; Oliveira et al. 2009).

2.7 Steps in the Design of Mixed Inoculants and Some Experiences of Inoculation

The design and formulation of multi-species inoculants represent furthered challenges since it requires additional assays to guarantee the coexisting of bacterial strains when they are in the formulation and associated with the plants, to raise their growth promotion (Baez-Rogelio et al. 2017; Molina-Romero et al. 2017b; Morales-García et al. 2013; Wang et al. 2018). Due to the characteristics and advantages of multi-inoculant preparations in comparison with conventional mono-inoculants, the term second-generation inoculants has been assigned and some multi-species formulations have been patented (Alatorre-Cruz et al. 2015; Morales-García et al. 2013; Olovaldo et al. 2017).

There are different strategies to design a multi-species inoculant, but all of them should overcome some general challenges in order to obtain the desired results. Besides all experiments and challenges faced during the development of mono-inoculants, five additional challenges should be sorted out during the design of polymicrobial inoculants.

Table 2.5 Hypothetical antagonism assays using the double agar layer method

	Bacterial strains explored as sensitive of inhibitory substances								
BSEPIS	A	B	C	D	E	F	G	H	I
A		+	+	+		+	+	+	+
B					+				
C		+		+				+	
D		+			+		+		
E		+		+					
F		+	+						+
G		+							
H		+							+
I		+					+		

BSEPIS means bacterial strains explored as a producer of inhibitory substances. In this hypothetical example, strain A eliminates to almost all tested strains and strain B is sensitive to all strain tested. Therefore, these strains cannot be used to design a bacterial mixture, because the first could eliminate the others in a natural environment and the second could be eliminated by the other strains. Examples of compatible strains to formulate a mixture could be E, G, H, F or I, C, E, G

(1) Carry out antagonism assays. Several articles about bacterial antagonism have been published with the purpose to identify producer bacteria of inhibitory substances (Beneduzi et al. 2012; Muñoz-Rojas et al. 2005; Tenorio-Salgado et al. 2013). However, for the formulation of polymicrobial inoculants, antagonism assays should be carried out with the purpose of identifying compatible strains (Molina-Romero et al. 2017b). In this sense, the development of a matrix of bacterial interaction is highly important (Table 2.5). The methods used to perform the antagonism test for building the interaction matrix are the double-layer agar and simultaneous inhibition methods (Molina-Romero et al. 2017a). Both the methods provide complementary information. In the agar double-layer assay, the first bacterium is grown alone on the first agar-media layer, after this, the colony is removed and the remaining bacteria are killed with chloroform vapours leaving all metabolites produced by the bacteria on the first agar layer. The second bacterium is then incorporated into the second layer of agar media before gelling point of agar, if the growth of second bacterium is inhibited by metabolites produced by the first one, which means that antagonistic metabolites were produced without the influence of the second bacterium. In counterpart, during simultaneous inhibition method, both bacteria are grown simultaneously on the same agar media competing for the same space and nutrients. An observed inhibition could be the result of the bacterial interaction. The major challenge is to find compatible strains, able to coexist not only in the antagonism assays but also in other environmental conditions like growing in liquid media, during the formulation, in adherence to seeds and plant rhizosphere (Molina-Romero et al. 2017b). But, we recommend to test the interaction at other environmental conditions until the definitive members of a

multispecies inoculant have been selected, because it will be necessary to develop selective culture media for each member of the multi-species inoculant before to be able to identify and quantify each bacteria interacting in the consortium. All inoculants of second generation contain strains capable of coexisting without antagonizing each other and inclusive with the ability to inhibit the plant pathogens causing diseases (Alatorre-Cruz et al. 2015; Baez-Rogelio et al. 2017; Molina-Romero et al. 2017b; Morales-García et al. 2013; Oliveira et al. 2009; Olovaldo et al. 2017).

(2) Bacterial tolerance to desiccation. Desiccation of organisms is defined as the loss of intracellular water until the equilibrium with water is present in the environment, extreme desiccation occurs at 30 °C and 50% of relative humidity, during several days (Molina-Romero et al. 2017c; Pazos-Rojas et al. 2018). PGPB with the capability to tolerate extreme desiccation could be used to formulate more stable inoculants and such bacteria once associated to seeds can remain dormant but ready to colonize plant roots and rhizosphere when favourable conditions of rehydration occur (Molina-Romero et al. 2017b; Pazos-Rojas et al. 2018; Streeter 2003). Based on data of bacterial survival ratio to air desiccation (BSRad), five levels of bacterial tolerance have been proposed (Pazos-Rojas et al. 2018): highly tolerant bacteria (BSRad > 80), tolerant ($60 < \text{BSRad} \leq 80$), middle tolerant ($40 < \text{BSRad} \leq 60$), low tolerant ($20 < \text{BSRad} \leq 40$) and very-low-tolerant ($\text{BSRad} \leq 20$). Highly tolerant bacteria are desired for the formulation of bacterial inoculants of second generation, because they maintain their ability to promote plant growth even when they experienced desiccation stress (Molina-Romero et al. 2017b; Pazos-Rojas et al. 2018). Second-generation inoculants containing desiccation-tolerant bacteria were observed more efficient in environments with low water availability (Alatorre-Cruz et al. 2015; Molina-Romero et al. 2017b; Pazos-Rojas et al. 2018; Vilchez and Manzanera 2011).

(3) Choosing bacterial species for the mixture. Using the interaction matrix of PGPB (Table 2.5) and the results of tolerance to desiccation, we can select the appropriate compatible bacteria to formulate the inoculants of the second generation. Bacterial mixture formulations theoretically could be more successful than mono-inoculants (Baez-Rogelio et al. 2017). But even a careful selection of compatible bacteria for the hypothetical formulation do not warranty that selected bacteria will be compatible in association to plants or that mixed bacteria will promote the plant growth. In fact, some bacterial mixtures selected at this step could be ineffective to promote plant growth. Experiments of population dynamics of bacteria associated to plants and effectivity studies of these formulations should be carried out to verify the effectiveness of the designed formulations.

(4) Looking for selective media for members of the consortia. A very critical step for the design of bacterial inoculants of second generation is to confirm that bacteria really coexist associated with plants. For this, we require effective selective media to capture every single strain from a mixture discriminating the growth of the other strains sampled from the same environment. Bacterial

capability to growth on different conditions has been explored for each bacterial strain from the mixture (Alatorre-Cruz et al. 2015; Molina-Romero et al. 2017b; Morales-García et al. 2013), for example, use of different carbon and nitrogen sources, tolerance to heavy metals, abilities to grow in microaerophilic semi-solid media without nitrogen source (nitrogen fixation), resistance to different antibiotics, tolerance to salinity, peculiar growth colonies on media, etc. Culture media allow the monitoring of different inoculated strains both for seed adhesion and for bacterial colonization studies (Molina-Romero et al. 2017b; Rodríguez-Andrade et al. 2015). However, the identity of isolated bacteria should be corroborated using molecular tools, for example, by 16S rDNA sequence or by the characteristic restriction pattern of the gene 16S rDNA.

(5) Exploring multi-inoculation in different scenarios. In our experience, all bacteria selected for multispecies inoculants have shown the capability to adhere to seeds and colonize the rhizosphere of plants suggesting its compatibility in association to seeds or rhizosphere (Alatorre-Cruz et al. 2015; Molina-Romero et al. 2017b; Morales-García et al. 2013). However, levels of colonization could be different depending on plant species. For example, the formulation EMMIM-1 which contains 6 bacterial species (Table 2.6), all of them are capable to colonize maize in high numbers (Morales-García et al. 2013). Seed inoculation of tomato and bean with EMMIM-1 formulation resulted in a different *B. unamae* MTl-641, a bacterium part of EMMIM-1 formulation was able to colonize in high numbers the rhizosphere of tomato (Log CFU/gV around 6.8 (± 0.35)) but the numbers observed for colonization of bean rhizosphere (Log CFU/gV around 3.83 (± 0.33)) were lower than those for tomato. Despite these differences, the inoculant multispecies EMMIM-1 was able to increase the plant growth of both plant species suggesting that other strains rather than *B. unamae* MTl-641 promote the growth in bean plants (non-published results).

2.8 Comparing Plant Growth Promotion of Mono and Multi-inoculation

Effects of the bacterial–mixture inoculation on the plant growth promotion should be tested and compared against mono-inoculation. Inoculation of bacterial mixtures had resulted in higher increments of the plant growth than mono-inoculants maybe because there are synergic effects of bacteria.

In our laboratory, better growth-promoting effects were observed on plants inoculated with the multi-species formulations compared with mono-inoculated or non-inoculated plants (Figs. 2.1, 2.4, 2.5, 2.6, and 2.7) (Alatorre-Cruz et al. 2015; Morales-García et al. 2013; Molina-Romero et al. 2017b). An additional feature of multi-strain formulations compared to mono-species formulations is the higher

Table 2.6 Mixed bacterial formulations for enhancement of plant growth

Bacterial species in the formulation	Name of the formulation	Plant model explored	References
Gluconacetobacter diazotrophicus, *Herbaspirillum seropedicae, H. rubrisubalbicans, A. Amazonense, Burkholderia tropica*	No name	Sugarcane	Oliveira et al. (2009)
Acinetobacter sp. EMMS02, *Azospirillum brasilense* Sp7, *Pseudomonas putid*a KT2440, *Sphingomonas* sp. OF178	EMMIM-5	Blue maize	Molina-Romero et al. (2017b)
Ensifer sp. NYM3, *Acinetobacter* sp. P16 *Flavobacterium* sp. KYM3	No name	Cucumber	Wang et al. (2018)
Gluconacetobacter diazotrophicus PAl 5, *Burkholderia unamae* MTl-641, *Sphingomonas* sp. OF178, *Pseudomonas putida* KT2440, *Brdyrhizobium* sp. MS22, *Azospirillum brasilense* Sp7	EMMIM-1	Several maize varieties, potato, tomato, bean	Morales-García et al. (2013)
Microbacterium sp. UAPS01200, *Microbacterium* sp. UAPS01203, *Pseudomonas putida* KT2440	EMMIM-JMAC	*Echinocactus plathyacanthus*	Alatorre-Cruz et al. (2015)
Sphingomonas sp. OF178, *Pseudomonas putida* KT2440, *Gluconacetobacter diazotrophicus* PAl 5	EMMIM-2	Potato	Olovaldo et al. (2017)

Fig. 2.4 Comparison of plants of tomato inoculated with a multi-species formulation (EMMIM-1) versus non-inoculated plants

Fig. 2.5 Bacterial mixture (EMMIM-5) improving the growth of maize plants (Blue maize CAP15-1 TLAX) in comparison with mono-inoculated plants (*Azospirillum brasilense* Sp7), 45 days after the inoculation of germinated seeds

consistency of results obtained in the field crops. In fact, the bacteria of these polymicrobial formulations exert synergic effects on the inoculated plants. Similar results were obtained by a multi-species inoculant applied on corn and rice (Figs. 2.6 and 2.7). The multi-species inoculants containing plant growth-promoting bacteria have been summarized in Table 2.5. Inoculation of bacterial formulations of the second generation is in development, and we hope that in next few years an increased number of new multispecies formulations will appear in the market (Baez-Rogelio et al. 2017). The most advanced multispecies formulation in the context of technology transference in Mexico is the bacterial mixture named EMMIM-1, it is the closest to appear in the market and experiences of inoculation in fields have demonstrated its effectiveness and better positive results than mono-inoculants. Currently, around 5000 ha of maize have been inoculated with EMMIM-1 in the central region of Mexico, and other cultures also have been inoculated in minor proportion.

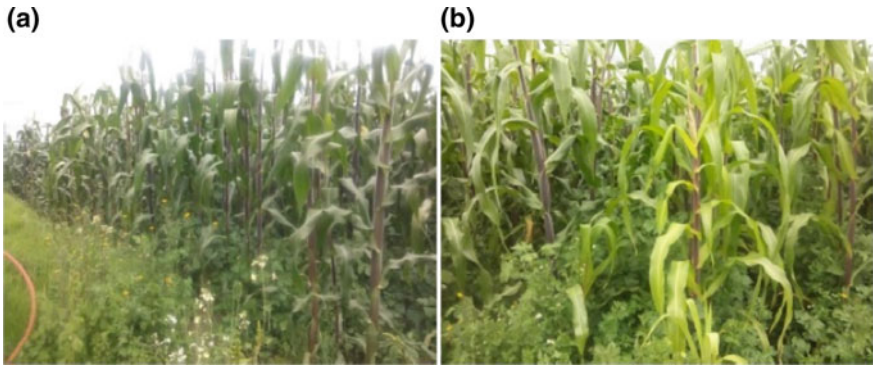

Fig. 2.6 Maize plants of Cacahuazintle, an autochthonous variety from Calpulalpan-Tlaxcala, México, at 90 days of growth. Maize inoculated with the multispecies formulation EMMIM-1 (**a**) and not inoculated (**b**). The inoculated maize is greener, with higher height, thicker stems, and larger adventitious roots and has less problem of herbs. Fertilization and form of tillage was the same for both treatments

Fig. 2.7 Rice plants inoculated with EMMIM-1 (right) compared to non-inoculated plants (left). Assays from Morelia, Michoacán, México

2.9 Conclusions

Plant growth-promoting bacteria have different mechanisms to perform phytostimulation. Although the use of PGPR-type bacteria for inoculation of crop plants has been moderated, their application is increasing over the time due to their proved benefits on productivity and reducing the chemical fertilizer, pesticides and herbicides inputs in soil. The co-inoculation of beneficial microorganisms on crop plant is apparently more effective in stimulating plant growth than mono-inoculation, perhaps because of the synergistic effect occurring when microorganisms are co-interacting. Despite promising results of co-inoculation, there are still few formulations containing more than three species of microorganisms in consortium. Therefore, a new challenge is the design and formulation of multi-species inoculants able to exercise a greater plant growth promotion in comparison with those of mono-species inoculants. In our laboratory, we have designed some polymicrobial formulations which are already patented. Due to the characteristics and advantages that they have in relation to conventional inoculants, they have been designated as the second-generation inoculants.

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Chapter 3
Does PGPR and Mycorrhizae Enhance Nutrient Use Efficiency and Efficacy in Relation to Crop Productivity?

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Abstract With the increasing world's population, higher demand for sustainable food production so as to meet the requirement. It has increased tremendously due to excessive use of agrochemicals. Since, the imbalanced application of agrochemicals in agricultural field leads to soil and environmental degradation. Nowadays, the

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scientific community has shifted their focus on alternative eco-friendly management approach. The plant growth-promoting rhizobacteria (PGPR) and mycorrhizae has huge potential to substitute agrochemicals. These efficient eco-friendly microbes have different plant growth-promoting (PGP) activities; hence PGPR and mycorrhizae are gaining importance for restoring soil sustainability and agricultural productivity. Application of these efficient microbes in the soil–plant–environment system will be suitable strategies for improving the soil and crop productivity.

Keywords PGPR · Biological nitrogen fixation · Siderophore · Agronomic efficiency

3.1 Introduction

Nowadays, the sustainable crop production along with enhanced crop productivity relics a key global challenge for different communities (i.e., policy makers, business, and researchers) (Wezel et al. 2014). It is undoubtedly hard to believe that food demand is going to be double in 2050 with the rapid population explosion (Henry et al. 2018). It is also that, being fully dependent on artificial as well as traditional inputs (Kumar et al. 2017). Application of efficient microbes for multi-nutrient solubilization enhances the environmental sustainability (Choudhary et al. 2018c). Among these microbes, the rhizobacteria and arbuscular mycorrhiza (AM) has tremendous capabilities to be colonized in the rhizosphere and to enhance plant growth, development. Apart from this, they could improve nutrient use efficiency (NUE) by access to various nutrients from soil system (Meena et al. 2017). The AM plays a role in nutrient supply and uptake in between fungi and roots and is ubiquitous in nature (Smith and Read 2008). The sustainable crop productions required need-based crop yield that can be achieved prepared via multi-resistance and improve water use efficiency (WUE) in plants. AM is most heterogonous group of soil microbes, ubiquitously form plant–fungal association with 80% of higher plants (Giovannetti et al. 2006). Other than penetrating plant roots, AM fungal hyphae also grow in soil as extraradical hyphae with higher absorptive surface

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increases nutrient acquisition. Besides better nutrient availability, AM fungi provides multi-resistance (Parihar and Rakshit 2016), soil nutrient loss reduction (Parihar et al. 2019), improved soil aggregation (Borie et al. 2008), greater soil carbon storage (Wang et al. 2016), and enhanced overall plant productivity.

Judicious application of organic and inorganic minerals improve soil sustainability and crop productivity (Choudhary et al. 2018a), while the sole use of minerals have an adverse effect on the crop growth and development as compared to integrated manner. Imbalanced application of synthetic agrochemicals (mainly fertilizers, pesticides, fungicide, and weedicides) leads to soil and environmental degradation. In this article, the current status of NUE, mode of action of PGPRs and AM fungi, their potential use and benefits for farmer community where they are facing lots of problems related to the high cost of chemical fertilizer, pesticides, and other growth substances highlighted. These factors adversely affected the soil and environment, enhanced NUE through PGPRs and AM fungi, hence needed to encourage farmers for adoption of such cost-effective, efficient, and sustainable technologies for better crop growth and healthy environment.

3.2 Nutrient Use Efficiency (NUE)

It is a measure of nutrient uptake by crop/plants from the soil system as growth and development per unit input (Ramesh et al. 2014). NUE is dynamic and complex term and different scientific fraternities (agronomists, soil scientists, plant physiologists, and agricultural economists) are measured in various ways depending upon the perspective in which it is computed and considered. Conceptually, the word "efficiency" implies the achievement of an envisioned outcome with a lowest possible use of precious input (Fixen 2005). Therefore, NUW is considered an intended output (economic crop yield) as the numerator and input (applied nutrient) as the denominator. Thus, NUE is a simple measure of how beneficially plants use the mineral nutrients available in the soil environment. The determination of NUE is of great importance to differentiate plant species and their genotypes based on their ability to utilize the applied nutrients for maximum production of economic yield with minimum use of nutrient (Barbieri et al. 2008). Improved NUE can be helpful for spreading out of crop production over marginal and degraded lands which are potentially low with respect to nutrient availability so as to reduce mineral fertilization (Dobermann and Cassman 2005). NUE of any crop plant is product of (a) uptake efficiency (depends on ability of plant roots to acquire the nutrient present in soil, their inflow–outflow rate into plant roots, nutrient influx kinetics, and also related to the quantity of the subjected nutrient applied or present in soil), (b) incorporation efficiency (largely depends on ability of plant to transports the acquired nutrient to shoot and leaves, functions of shoot parameters), and (c) utilization efficiency (remobilization of nutrient from different plant parts, functions of whole plant (Wang et al. (2010). Fageria et al. (2008) outlined that nutrient efficient plant are those which can produce more biomass with a defined

Table 3.1 Commonly used NUE indices and their application

NUE index	Questions addressed	Typical use
PFP_N	How productive is the given cropping system in comparison to its nutrient input?	Using as a long-term indicator of NUE trends at various scales
PNB	How much of applied nutrient is being taken out (Uptake efficiency) by the crops in the system?	Also used as a long-term indicator of trends of NUE and provides more practical information when combined with soil fertility dataset
ARE_N	How much of the nutrient applied did the plant take up (the ability of plants to take up the applied nutrient from soil)?	Mostly used as an index of the potential for nutrient loss from the cropping system and to access the efficiency of management practices towards NUE
IUE	How the crop plants are able to transform the acquired nutrients into economic products?	Used to evaluate nutrient efficient and inefficient genotypes in breeding Programs
PE_N	What is the ability of the plant to transform nutrients acquired from the source into economic yield?	Research evaluating NUE among cultivars and other cultural practices

Accepted and modified from Dobermann (2007) and Dobermann et al. (2005)

amount of applied or absorbed nutrient over other similar growing environments. Therefore, it is very clear from the above findings that NUE can be defined in many ways depending on the perspective and is easily misunderstood and misrepresented. The commonly used measure of NUE is discussed below as well as in Table 3.1.

Partial factor productivity (PFPN): It is the simplest measure to depict nutrient use efficiency described as units of output (crop yield) per unit of input (nutrient applied) (Mosier et al. 2004).

$$\mathrm{PFPN(kg\,kg)} = \frac{\text{Crop Yield (kg)}}{\text{Amount of Nutrient plant tissuse (kg)}}$$

Agronomic efficiency (AE_N): AE_N is the most commonly used index, defined as units increase in economic yield per unit inputs (Fageria et al. 2008). To calculate AEN, one essentially needs data on yield from unfertilized plot (without nutrient input). It is critically required to establish a plot with zero nutrient input on the farm (Tilman et al. 2002).

$$\mathrm{AEN(kg\,kg)} = \frac{\text{Yield of fertillized plot (kg)} - \text{Yield of unfertillized plot (kg)}}{\text{Amount of nutrient applied (kg)}}$$

Physiological Efficiency (PEN): Physiological growth in relation to the increase in nutrient uptake by the crop. Like AEN and AREN, it requires knowledge of without application of the nutrient.

$$\text{PEN}(\text{kg kg}) = \frac{\text{BYf (kg)} - \text{BYuf (kg)}}{\text{NUf (kg)} - \text{NUuf (kg)}}$$

where BYf = Biomass yield (grain + straw) in fertilized plot, BYuf = Biomass yield (grain + straw) in unfertilized plot, NUf = Nutrient uptake in fertilized plot and NUuf = Nutrient uptake in unfertilized plot.

Apparent Recovery Efficiency (AREN)-: It is one of the more complex forms of NUE expressions, described by the difference in nutrient uptake (above-ground biomass of crops) between the fertilized plot and that of unfertilized plot relative to the quantity of input applied.

$$\text{AREN}(\%) = \frac{\text{NUf (kg)} - \text{NUuf (kg)}}{\text{Amount applied (kg)}} \times 100$$

where NUf = nutrient uptake in grain plus straw of fertilized plot and NUuf = nutrient uptake in grain plus straw of unfertilized plot.

Internal Utilization Efficiency (IEU): It is a simple indexing measure of quantifying nutrient use efficiency based on crop yield and nutrient uptake. The value of this index is depending upon agro-climatic conditions, crop cultivar, and level of soil–plant management (Witt et al. 2005). Nutrient utilization efficiency is the cross product of physiological efficiency and apparent recovery efficiency of nutrient which is calculated by using the following equation:

$$\text{IUE}\left(\text{kgkg}^{-1}\right) = \text{PE}_\text{N} \times \text{ARE}_\text{N}$$

where PEN is physiological efficiency and AREN is apparent recovery efficiency as defined above.

Partial nutrient balance (PNB): It is the simplest form to characterize NUE of crop production system. It is described as nutrient output in relation to nutrient input (Lopez-Bellido and Lopez-Bellido 2001). Over the short term and on individual farms, PNB can show substantial fluctuations due to cash flow and market conditions, especially for P and K. Long-term assessment of PNB over several years is, therefore, more useful (Table 3.2).

3.3 Current Scenario of NUE

Nowadays, an increase in global food demand ~110% is expected by 2050 compared to 2005, requiring a tremendous increase in production (Tilman et al. 2011). Approaches considered economic, social, and environmental dimensions are essential to sustainable agricultural systems and therefore provide an appropriate context for specific NUE indicators. Global phosphorus consumption continuously has been increased since 1960 (Fig. 3.1). Phosphorus is the second important

Table 3.2 Components of NUE and processes that influence genotypic differences in NUE in plants

A. Nutrient acquisition
• 1. Nutrient availability from soil system to roots through diffusion and/or mass flow: soil buffering power, nutrient density, bio–physico–chemical properties of element, tortuosity, soil moisture content, bulk density, and soil temperature
• 2. Root morphological factors: number and length of roots, root hair density and its efficiency, root forage area, and root density
• 3. Rhizosphere engineering
• 4. Physiological: root: shoot ratio, rhizosphere microorganisms dynamics (rhizobia, azotobacter, mycorrhizal fungi), concentration of acquired nutrient, transpiration rate (water Uptake), internal and outflow nutrient rates, nutrient movement within roots and shoots, affinity to uptake (Km), threshold concentration (Cmin)
• 5. Biochemical: secretion of various enzymes (phosphatase), chelating compounds, phytosiderophores, proton exudates, organic acid exudates
B. Nutrient movement in root
• 1. Transfer of acquired nutrient through endodermis and transport within the root
• 2. Compartmentalization/binding of absorbed nutrient within roots
• 3. Rate of nutrient release to root and shoot xylem
C. Nutrient accumulation and remobilization in shoot
• 1. Demand for given nutrient at the cellular level and their storage in vacuoles
• 2. Remobilization of stored nutrient from older to younger leaves and from vegetative to reproductive tissues as and when needed
• 3. Dynamics of chelates during transportation of nutrient through the xylem
D. Nutrient utilization and growth
• 1. Nutrient metabolism at cellular level
• 2. Concentration of nutrient in supporting structure, particularly stem
• 3. Elemental substitution (such as Na for K, Fe for Mn etc.)
• 4. Biochemical processes and factors involved in metabolism (nitrate reductase for N-use efficiency, glutamate dehydrogenase for N metabolism, peroxidase for Fe efficiency, pyruvate kinase for K deficiency, metallothionein for metal toxicities, ascorbic acid oxidase for Cu, carbonic anhydrase for Zn)

Modified from Baligar et al. (2001); Fageria and Baligar (2005)

primary nutrient element after nitrogen. Low P use efficiency (PUE) is a significant challenge for agricultural production on P-deficient soil as well as in acidic and calcareous soils (Shenoy and Kalagudi 2005). Acquisition of soil and fertilizer P by crops depends on soil and plant properties.

On the other hand, K use efficiency is more limited than either N or P. This is partly due to the environmentally benign nature of K where interest in efficiency is driven primarily by agronomic or economic factors. In general, NUE of sulfur is only 8–10% due to immobilization and leaching with water whereas in case of micronutrients NUE is only 2–5% due to fixation in soil.

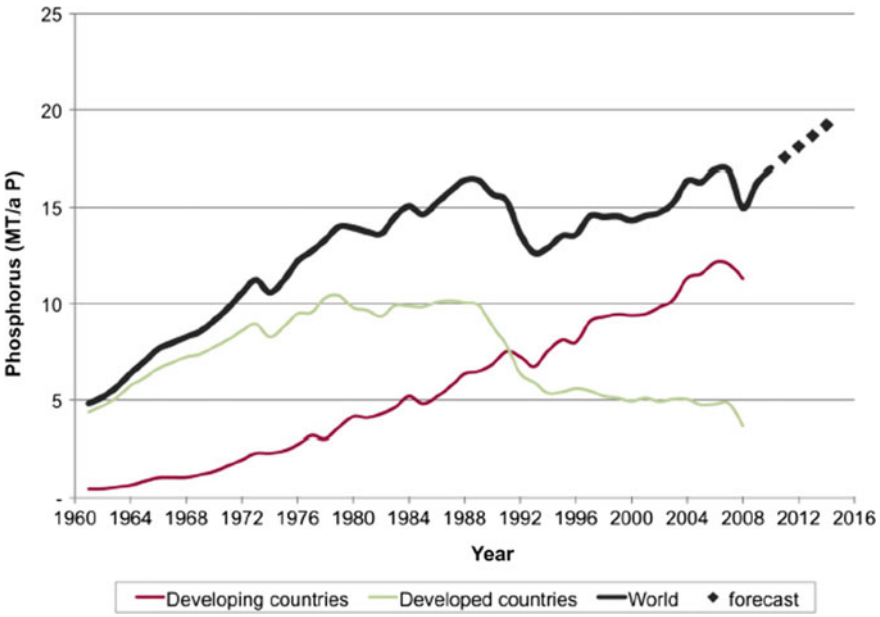

Fig. 3.1 Global phosphorus fertilizer consumption (International fertilizer industry association)

3.4 Why NUE Is Important for Agricultural System?

Nutrient deficiency is critically important and most yield-limiting constraints to crop production in the agro-ecological (Fan et al. 2004). The adoption of intensive chemical fertilizer led nutrient management during the past four to five decades undoubtedly reported to increase global food production around four times but has also increased chemical fertilizer consumption by fourfold which created implications for the environmental safety (Tilman et al. 2001). Overall, the contribution of chemical fertilizers in raising crop yields is ~40% in poor fertile soils when other productions factors (genotypes, irrigation and plant protection measures) are at an adequate level (Rahimizadeh et al. 2010). However, it is estimated that chemical fertilizer inputs in modern agriculture share about 30% of the total cost of production system (Richardson et al. 2011).

Ensuring food and fodder for human and livestock on sustainable systems approach has significant challenges and is highly critical especially in thhhe developing region of the world. Therefore, to combat this challenge, farmers are forced to overuse agrochemicals that leads in the deteriorating soil and environment (Foley et al. 2011). Long-term adoption of nutrient management practices dominated by chemical fertilizers led to declining NUE making fertilizer consumption uneconomical, imparting adverse effects on environment and groundwater quality (Hungate et al. 2003). Furthermore, the ANR of inputs is quite low such as global

cereals N recovery efficiency is ~33%. Likewise, the global recovery efficiency of PK is estimated less than 20% and 40%, respectively (Syers et al. 2008). Thus, it is very clear that usually a large quantum of applied nutrient through the precious inorganic fertilizers is lost from the soil–plant system or unavailable to crops. The lower efficiency of applied fertilizer is attributed to leaching and runoff, gaseous losses, fixation by soil, and use of inefficient nutrient absorbing/utilizing plant species or cultivars (Yadav et al. 2017).

Eutrophication, a process of water enrichment with chemicals (NP) can cause excessive algal growth of aquatic algal communities is another consequence associated with lower NUE (Garnett et al. 2009). This can cause a shortage of oxygen, and may produce substances, which are directly toxic to aquatic communities and indirectly to livestock and humans, is now big threat throughout the world (Baligar et al. 2001). Further, ammonia emitted to the atmosphere through volatilization losses from agricultural fields and other anthropogenic activities can return back to earth surface as co-deposition with sulfur dioxide gas (Buresh et al. 2004). Aquatic and forests ecosystems of the world are more prone to N deposition and excess enrichment of N can cause disruption in ecosystem functions and services. Larger N deposition in ecosystems can also lead to global warming due to larger emissions of nitrogen-based greenhouse gases, soil acidification due to excessive aluminum dissolution and reduced carbon stocks in the soil (Galloway et al. 2008). Nitrous oxide (N_2O) generated as a product of denitrification process considered as an important N based GHG gas which is responsible for around five percent of the total global climate change (Shoji et al. 2001).

Inefficient and excessive use of N-based fertilizers leads in environmental problems related due to associated large scale emission of NH_3, N_2, and N_2O to the atmosphere (Rockstorm et al. 2009). Further, improved NUE can play a great role in extending the crop production over marginal and degraded lands, which potentially low with respect to nutrient availability (Fig. 3.2).

3.5 What Are PGPR and Mycorrhizae?

PGPR is a group of rhizobacteria that inhabited in the rhizosphere, the term PGPR refers to rhizobacteria that colonize in the rhizosphere (Vejan et al. 2016). Under the PGPR, wide range of genera of bacterial species (*Pseudomonas*, *Alcaligens*, *Azospirillum*, *Arthrobacter*, *Burkholderia*, *Azotobacter*, *Bacillus*, *Klebsiella*, *Serratia*, *Enterobacter*) reported to improving growth and development (Saharan and Nehra 2011). The example of various mechanisms involved in growth and development by rhizobacteria has been reported by different researchers (Table 3.3).

Mycorrhizae define a mutualistic symbiotic beneficial relationship between the root of a plant (mainly woody plants) and a fungus that colonizes the plant root. In many plants, mycorrhizae are fungi that grow inside the plant's roots, or on the surfaces of the roots (Smith and Read 2008).

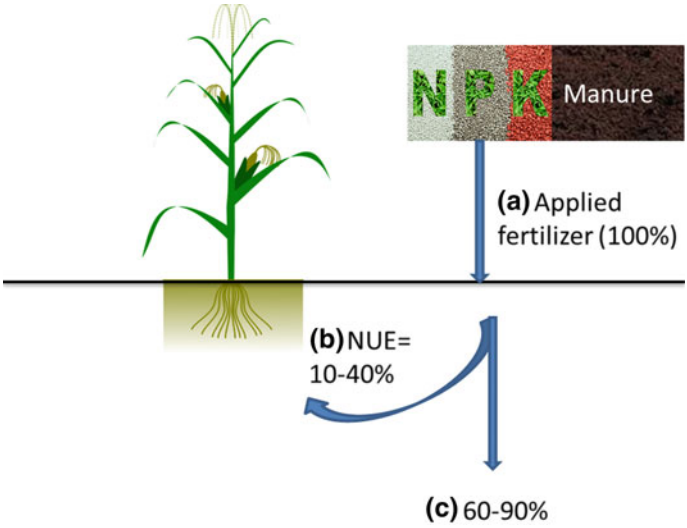

Fig. 3.2 Model for improved plant NUE with inoculants **a** total amount of fertilizer or manure applied to plants, **b** 10–40% of the applied fertilizer or manure is taken up by plants, and **c** 60–90% of the applied fertilizer or manure is lost

3.6 Mode of Action of Plant Growth-Promoting Rhizobacteria (PGPR)

3.6.1 Direct Mechanism

The direct mechanism of efficient PGPR strain entails either providing the plant with PGP traits that are synthesized by the bacterium. Biofertilizers contribute to plant nutrition both by facilitating nutrient uptake and by enhancing mineral availability by direct mechanisms, as fixing atmospheric nitrogen, solubilizing mineral nutrients like phosphorus, potassium, etc., mineralizing organic compounds, producing phytohormones and production of siderophores which sequestering micronutrient (Kaur et al. 2016).

3.6.2 Indirect Mechanism

The indirect mechanism of plant growth occurs has an insignificant role in plant nutrient management practices. Infect, the PGPR prevent deleterious effects of one or more phytopathogenic microbes (Kundan et al. 2015).

Table 3.3 Different plant growth-promoting rhizobacteria (PGPR) tested for various crop types

PGPRs	Host crop	Results of the addition of bacteria to crops	References
Achromobacter xylosoxidans	*Vigna radiata*	Influence plant homeostasis	Ma et al. (2009)
Azorhizobium		Nitrogen fixation	Sabry et al. (1997)
Azospirillum	–	Nitrogen fixation	Sahoo et al. (2014)
Acinetobacter spp.	–	IAA, phosphate solubilization, siderophores	Rokhbakhsh-Zamin et al. (2011)
Bacillus sp. *PSB10*	–	IAA, siderophores, HCN, ammonia	Wani and Khan (2010)
Bacillus	–	Potassium solubilization	Han et al. (2006)
Enterobacter sakazaki 8MR5	–	Inoculation increased growth parameters	Babalola et al. (2003)
Rhizobium Pseudomonas	*Medicago sativa, Trigonella foenum-graecum, Trigonella* sp., *Trifolium* sp., *Vigna radiata*	Biological nitrogen fixation	Maheshwari et al. (2010), Choudhary et al. (2017a)
P. fluorescens C7	*Arabidopsis thaliana* plants	The ironpyoverdin synthesized, it increased the iron level inside the plants and improved their growth	Vansuyt et al. (2007)
Xanthomonas sp. *RJ3, Pseudomonas* sp. *RJ10, Bacillus RJ31, Azomonas* sp. *RJ4*	*Brassica napus*	Stimulated plant growth and increased cadmium accumulation	Sheng and Xia (2006)
Rahnella aquatilis	–	Phosphate solubilization, IAA, ACC Deaminase	Mehnaz et al. (2010)
Bradyrhizobium MRM6	*Vigna radiate* Soybean, wheat	When herbicide-tolerant *Rhizobium* strain MRP1 was used with herbicide, it increased the growth parameters at all tested concentrations of herbicides (quizalafop-p-ethyl and clodinafop)	Ahemad and Khan (2012a)

(continued)

Table 3.3 (continued)

PGPRs	Host crop	Results of the addition of bacteria to crops	References
Pseudomonas sp. PS1	*Vigna radiate*	Significantly increased plant dry weight, nodule numbers, total chlorophyll content, leghaemoglobin, root N, shoot N, root P, shoot P, seed yield, and seed protein	Ahemad and Khan (2012b)
Pseudomonas aeruginosa	*Cicer arietinum*	Positively stimulate potassium and phosphorus uptake	Ahemad and Kibret (2014)
Pseudomonas cepacia	*Cucumis sativus*	Prevent pathogens in *Pythium ultimum*	Montano et al. (2014)
	Gossypium hirsutum	Help fight the *Rhizoctonia solani* virus	
Pseudomonas fluorescens	*Triticum aestivum Hordeum vulgare*	Help prevent *Fusarium culmorum*	Santoro et al. (2016)
	Pennisetum glaucum	Significant increase in plant height, ear length, yield	Arora (2003)
	Camellia sinensis	Increased NUE (+7%); nitrogen (+52%); phosphorus (+67%); potassium (+18%)	Thomas et al. (2010)
Pseudomonas sp.	–	Phosphate solubilization, IAA, siderophore, HCN, biocontrol potentials	Tank and Saraf (2009)
Bradyrhizobium sp. *750 Pseudomonas* sp., *Ochrobactrum cytisi*	*Lupinus luteus*	Increased both biomass and nitrogen content, accumulation of metals (phytostabilization potential)	Dary et al. (2010)
AM Fungi (*Coccus* DIM7, *streptococcus* PIM6) and PSB (*Bacillus* sp. PIS7)	*Zea mays*	Rock phosphate mineralization in soil and improved all growth parameters including shoot (56%), root yield (52%), height (41%), N (80%), and P (91%) uptake by the maize plants as compared to control	Wahid et al. (2016)

(continued)

Table 3.3 (continued)

PGPRs	Host crop	Results of the addition of bacteria to crops	References
Pseudomonas sp. *Paenibacillus Polymyxa*	*Piper nigrum Zea mays*	Significantly increased soil enzyme activities, total productivity, and nutrient uptake. Significantly increased the biomass of plants and elicited induced systemic resistance against bacterial spot pathogen *Xanthomonas axonopodis* pv. *Vesicatoria* untreated plants.	Sharma et al. (2011)
Pseudomonas and *Azospirillum*	*Piper nigrum*	Phosphate solubilization and increases the availability of phosphorus	Ramachandran et al. (2007)
Azotobacter chroococcum	*Brassica juncia*	Stimulated plant growth	Orlandini et al. (2014)
	Triticuma estivum	Phosphate solubilization	Bhattacharyya and Jha (2012)
	Fagopyrum esculentum	Biological nitrogen fixation	
Azospirillum brasilense	*Festuca arundinacea*	Increases biomass and increase plant tolerance to polycyclic aromatic hydrocarbons	Orlandini et al. (2014)
	Saccharum officinarum	Alter plant root architecture by increasing the formation of lateral and adventitious roots and root hairs	
	Camellia sinensis	Increased NUE (+13%); nitrogen (+65%); phosphorus (+25%); potassium (+14%)	Thomas et al. (2010)
AM fungi, *Azospirillum, Pseudomomas* sp.	*Pinus sabiniana, Solanum lycopersicum, Lactuca sativa, Triticum aestivum, Zea mays*	Roots stimulate root colonization, limits soil salinity stress, and affects plant yield,	Kohler et al. (2010),

(continued)

Table 3.3 (continued)

PGPRs	Host crop	Results of the addition of bacteria to crops	References
Acinetobacter sp.	*Oryza sativa*	Significantly increased the growth and yield parameters of rice as well as also increases the solubility of Zn from source of zinc such as ZnO and $ZnCO_3$ with inoculation	Gandhi and Muralidharan (2016)
Bacillus sp.	*Glycine max*	Phosphate solubilization and increases the availability of phosphorus	Wahyudi et al. (2011)
Bacillus polymyxa	*Lycopersicon esculentum*	Proline accumulation improved the physiological and biochemical parameters of plants	Shintu and Jayaram (2015)
Bacillus subtilis	*Brassica juncia*	Facilitate Nickel accumulation,	Prathap and Ranjitha (2015), Oyedele et al. (2014)
	Hordeum vulgare	Prevent powdery mildew	
	Gossypium hirsutum	Prevent from *Meloidogyne incognita* and *M. arenaria*	
Bacillus subtilis Pseudomonas aeruginosa	*Solanum lycopersicum, Abelmoschus esculentus, Amaranthus*	Dry biomass increased 31% for tomato, 36% for okra 83% for African spinach	Adesemoye et al. (2008)
PSB *(P. fluorescens* BAM-4 and *B. cepacia* BAM-12 and AM fungus *(G. etunicatum)*	*Triticum aestivum*	Significantly improved the plant growth and nutrient uptake and showed a significant increase in grain yield of wheat with the increases the availability of P from insoluble P sources.	Minaxi et al. (2013)
Azotobacter and *Bacillus*		Wheat inoculation increased its seeds yield of 30 and 43%, respectively. This increase due to the production of certain	Kloepper et al. (1991)

(continued)

Table 3.3 (continued)

PGPRs	Host crop	Results of the addition of bacteria to crops	References
		growth hormones such as IAA	
Enterobacter strain CIK-521R and *Klebsiella* strain CIK-518	*Zea mays*	Higher tolerance to Cd and thus could be deployed to manage Cd-contaminated soil. Both of the strains could be effective inoculants to get higher maize production in normal as well as in Cd-contaminated soils.	Ahmad et al. (2016)

3.7 Mode of Action by Mycorrhizae

AM fungi are obligate biotrophs depends on the plant for their carbon nutrition with the exchange of different nutrients (Ortas and Rafique 2017), have the ability to improve the availability of nutrients for plants growth and development (Teotia et al. 2017). The greater nutrient acquisitions by mycorrhizae inoculated plants are possibly due to (i) AM fungi-mediated nutrient mobilization and acquisition and (ii) transfer of nutrients from fungal hyphae to plant roots. Mycorrhizal pathways of nutrient uptake in plants root are rapid transit and well-regulated system. AM fungi form a large web of extraradical mycelium (ERM) which can explore a huge volume of soil beyond the nutrient depletion zone and facilitate uptake of inaccessible and mineral bound nutrients. Several studies revealed that mycorrhiza could be engaged in organic matter decomposition and relocate nutrients to host plants (Reynolds et al. 2005). Other than organic matter, AM fungi as alone or in alliance with other microbes are also take part in nutrient mobilization by mineral weathering. Some reports suggest that mycorrhizae produces low molecular organic compounds which solubilize rock bounds nutrients and enhance their absorption (Smith and Read 2008) as well as fungal ability to reduce different nutrient losses (runoff, leaching and volatilization) from the soil system (Parihar et al. 2019).

3.8 Mechanism of PGPR for Increasing Bioavailability of Nutrients and Crop Productivity

3.8.1 Nitrogen Fixation

Nitrogen (N) is one of the most important nutrients from plant nutrition and productivity point of view. Despite large reservoir of nitrogen in atmosphere, plants are unable to take it directly due to the high energy requirement to break the triple bond

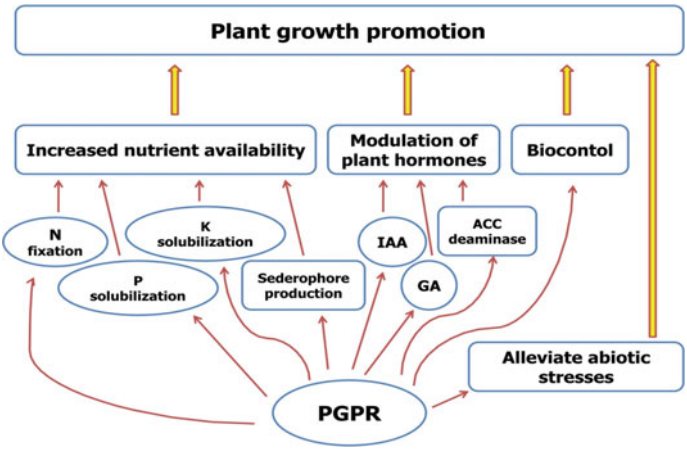

Fig. 3.3 Schematic representation of various mechanisms involved in plant promotion by PGPR

of nitrogen. Plants avail it through biological N_2 fixation (BNF) by changing nitrogen to ammonia by the help of N-fixing microbes with involvement of nitrogenase (Kim and Rees 1994). Two types of BNF are found in nature depending on types of microorganism involved, first, symbiotic nitrogen fixation, in which plant and microbes in symbiotic relationship and fix nitrogen (Ahemad and Khan 2012a), second, associative and nonassociative, non-symbiotic nitrogen fixation, which involves free-living microbes (Choudhary et al. 2017b). Hence, symbiotic N-fixation plays a major role in N nutrition of plant (Fig. 3.3). At the beginning of the process legume plant secret a specific flavonoid compound and rhizobium specific to that compound attracted towards the plant root. The bacteria attach firmly themselves to the root hair that involves lectin fibrils of the host plant. The host plant then senses the nod factor secreted by rhizobium leading to colonized root hairs to curl.

3.8.2 Phosphorus Solubilization and Mineralization

Phosphorus (P) is next to nitrogen among the essential nutrients that limit crop growth (Tak et al. 2012) and is present in huge amount in the soil in form of both inorganic and organic P. Besides its abundance in soil, it remains in insoluble form, thus its availability to plant is limited. The plant can absorb P in two of its soluble forms {monobasic ($H_2PO_4^-$) and diabasic ($H_2PO_4^{2-}$) ions}. The insoluble P remains in form of inorganic mineral, e.g., apatite and organic P, largely as inositol phosphate (Glick 2012). In the soil environment a considerable number of beneficial microbes are capable of releasing unavailable soil through P-solubilization (Bhattacharyya and Jha 2012). These groups of microbes are termed as

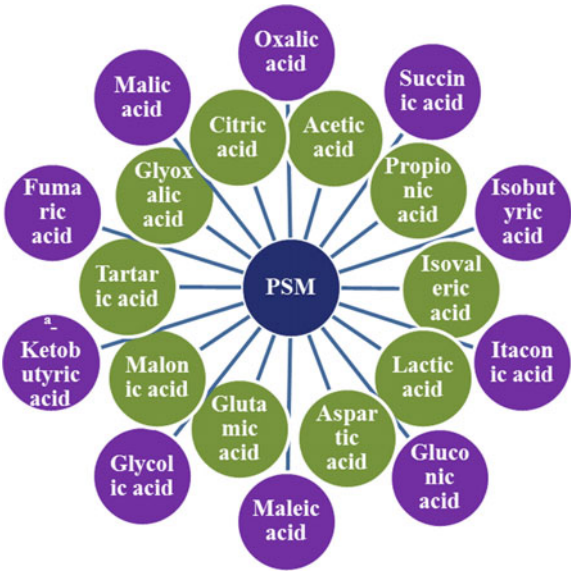

Fig. 3.4 Schematic representation of numerous organic acids released by PSM

P-solubilizing microbes (PSM). Many efficient bacteria (*Azotobacter*, *Bacillus*, *Enterobacter, Beijerinckia, Burkholderia, Erwinia, Microbacterium, Pseudomonas, Flavobacterium, Rhizobium and Serratia*), fungi, Actinobacteria, and algae show P-solubilization (Fig. 3.4). The major soluble form of inorganic phosphate is $H_2PO_4^-$, which found its existence at lower pH.

The existence of each category of the enzyme depends upon soil pH condition. Acid phosphatases are prevalent in acid soils, whereas, alkaline phosphatases are abundantly found in neutral and alkaline soils (Renella et al. 2006). Another enzyme involved in the process of organic P mineralization that is produced by PSM is phytase.

3.8.3 Potassium Solubilization

Potassium (K) is the third major essential plant nutrient affecting plant growth. Soil contains a large amount of K than any other nutrient, but its phytoavailability is limited. Potassium is present in four different forms in the soil such as mineral K, non-exchangeable K, exchangeable K, and solution K. In general, 90–98% of soil K remains in form of mineral K, hence, remains unavailable to plant (Sparks and Huang 1985). Among these microbes, the frequently studied by the researcher are K solubilizing bacteria (KSB), namely, *B. mucilaginosus, B. edaphicus* and *B.circulanscan* are effective in K solubilization (Meena et al. 2014, 2016). The major mechanisms involved are (i) lowering of pH; (ii) chelation of the cations bound to K; (iii) acidolysis (Meena et al. 2014; Maurya et al. 2014).

3.8.4 Siderophore Production

Iron (Fe) is an important essential micronutrient as it acts as a cofactor of many enzymes and is required in many physiological processes of plants such as N_2 fixation, photosynthesis, respiration. However, in aerobic environment, it occurs principally in the form of Fe^{3+} and is very likely to form insoluble hydroxides and oxyhydroxides, thus making it unavailable to both plants and microbes (Rajkumar et al. 2010). Microbes and plants acquire Fe through production of low molecular mass chelators termed as siderophore. In bacteria, synthesis of siderophores is induced by the low level of Fe^{3+}. Siderophore released by microbes form complex with iron (Fe^{3+}), further this complex is reduced to Fe^{2+} on bacterial membrane.

3.8.5 Plant Hormone Production

Plant growth is strongly influenced by the phytohormones through their various activities. Microbes also produce plant hormones; thus, affect plant growth through modulating the phytohormone level. Plant growth promotion by PGPR occurs through bacterial synthesis of hormones like indole-3-acetic acid (IAA), cytokinin, and gibberellins (GA) and breakdown of plant produced. Auxins in plant promote plant growth through their function such as cell division, extension, and differentiation. Microbial produced IAA change plant auxin pool, thus promote plant growth by interfering with above physiological processes.

3.8.6 Alleviate Abiotic Stress

Abiotic stresses are major sources of crop yield reduction. Extensive study has been done regarding the mechanisms of alleviating abiotic stresses in plants by PGPR Moreover, PGPR also promote plant growth when it is used as biofertilizers (Vessey 2003).

3.9 Mechanism of Mycorrhizae for Increasing Bioavailability of Nutrients and Crop Productivity

Like PGPR, mycorrhiza also enhances plan growth through various mechanisms. Between the two common types of mycorrhizae (AM and ECM) found in nature, AM are probably the dominant fungi that are commonly found in agricultural soils (Willis et al. 2013). These fungi form haustoria-like structure called arbuscule by penetrating into root cortical cells; the arbuscular function as a mediator for the

Table 3.4 Function of mycorrhizae in promotion of plant growth under stress conditions

Mycorrhizae	Type of stress	Stress alleviation and plant growth promotion trait	References
Glomus fasciculatum and *G. macrocarpum*	Semi-arid wasteland	Mycorrhizae decreased the alkalinity of rhizosphere and high concentration of P, K, Cu, and Zn was observed in inoculated plants	Giri et al. (2005)
Glomus spp.	Heavy metal	Plant height, basal diameter, seedling biomass, and superoxide-dismutase activity was more in mycorrhizal plants. Significant high lead concentration was observed in mycorrhizal plants roots	Zhang et al. (2010)
Glomus mosseae, Glomus intraradices	Heavy metal	AM fungus increased the infection of sunflower root and also increased the pollution tolerance and yield of sunflower in a degraded soil	Adewole et al. (2010)
Glomus intraradices	Water stress	Mycorrhizae protected the plant from drought. Higher leaf water potential was recorded in inoculated plants and kept the plant protected against oxidative stress	Porcel and Ruiz-Lozano (2004)
Glumos intraradices	Water stress	Drought caused a negative impact on sorghum length, shoot dry matter, 1000 kernel weight and yield. Mycorrhizae inoculation dilutes the negative impact of stress and enhanced yield. Grain yield increased 17.5% due to inoculation compared to drought	Alizadeh et al. (2011)
Glomus mosseae	*Salinity stress*	Plant salt tolerance increased in mycorrhizal plants mainly due to elevated levels of superoxide-dismutase, catalase, ascorbate peroxidase, and peroxidase which degraded reactive oxygen species and alleviated membrane damage	He et al. (2007)
Glomus etunicatum	Salinity Stress	Mycorrhizal inoculated plants grow better in saline conditions than uninoculated plants. Fresh and dry weight, root colonization, and proline contents were more in salt pretreated fungus that than non-salt-pretreated fungus	Sharifi et al. (2007)

interchange of metabolites in between fungus and host cytoplasm. The proliferated hypae of mycorrhizal increases the access of roots to a greater soil volume that facilitates host plant to acquire more nutrients than by non-mycorrhizal plants (Guo et al. 2010). Mycorrhizae can enhance the phytoavailability of slowly diffusing ions like phosphate (McArther and Knowles 1993). In addition to improving P nutrition, AM fungi are also capable of increasing availability of nutrients like N, K, Mg, Cu, and Zn, specifically where they exist in less soluble forms in soil (Meding and Zasoski 2008). The mycorrhizal mycelium also contributes to forms stable soil aggregates (Singh 2012) (Table 3.4).

3.10 Future Perspective

In the current scenario, due to abundant use of synthetic chemicals on crops, the sustainability of agriculture systems has distorted; the cost of cultivation has increased at a high rate; the income of farmers stagnated; and the provision of food security and safety has become a frightening challenge (Panday et al. 2018). Imbalanced application of agrochemicals leads to soil degradation (Choudhary et al. 2018b). For these reasons, PGPR that make use of microbes to improve soil sustainability has been recognized (Suhag 2016). PGPR add nutrients through the natural processes of N-fixation, nutrient solubilization, and PGP traits.

3.11 Conclusions

To know about the role of NUE by efficient PGPR aims to increase food security, and sustainable plant productivity, while maintaining environmental quality. However, to achieve this, basic and strategic studies must be undertaken to improve our knowledge of microbial interactions in the rhizosphere. Considering the good impact of PGPR exerts a positive influence on crop productivity and ecosystem functioning, encouragement should be given to its implementation in sustainable agriculture.

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Chapter 4
In Sustainable Agriculture: Assessment of Plant Growth Promoting Rhizobacteria in Cucurbitaceous Vegetable Crops

Musa Seymen, Ertan Sait Kurtar, Atilla Dursun and Önder Türkmen

Abstract One of the most important vegetable families commonly grown in around of the world is Cucurbitaceae for economic value, nutrition, consumer's preference, general adaptability and extent of cultivation. Plant growth promoting rhizobacteria (PGPR) mostly associated with the plant rhizosphere have been established as beneficial for plant growth, yield and crop quality. They are important to promote the circulation of plant nutrients and reduce the need for chemical fertilizers and interest in eco-friendly, sustainable and organic agricultural practices as well. Use of PGPR's containing beneficial microorganisms in lieu of inorganic chemicals are positively known to affect plant growth and may help to sustain environmental health and soil productivity, even in biotic and abiotic stress conditions. PGPR's also have potential bio-control agents against to a wide range of bacterial and fungal pathogens in agriculture. The effects of PGPR's on physiological mechanisms, plant growth, yield and yield components, uptake of mineral elements and contents, biotic and abiotic stress conditions in Cucurbits vegetables and future perspectives have been discussed in the review.

Keywords PGPR · Cucurbits · Growth · Yield · Biotic · Abiotic · Minerals

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4.1 Introduction

Cucurbitaceae is the largest family of summer vegetable group with about 125 genera and 960 species (Rahmatullah 2012). Cucurbitaceae family has economically important species grown all over the world such as watermelon (*Citrullus lanatus*), melon (*Cucumis melo*), cucumber (*Cucumis sativus*), summer squash (*Cucurbita pepo* L.), winter squash (*Cucurbita maxima* Duch.) and pumpkin (*Cucurbita moschata* Duch.), besides, bitter gourd (*Momordica charantia* L.), ridge gourd (*Luffa actangua* L. Roxb), and snake gourd (*Trichosanthes anguina*) are the members of family as a minor group. Watermelons, melons, cucumber, and squashes are used either fresh or cooked for consumption, while mature seeds of some species are used directly or indirectly in human nutrition. Cucurbitaceae family has an important share (about 25%) in world vegetable production with a total 255 million tons (117 million tons of watermelon, 80 million tons of cucumber, 31 million tons of melon and 26 million tons of pumpkin) production value (FAO 2016). 1.1 billion tons of vegetables are nearly produced in the world.

The cultivation techniques of vegetable species are more difficult than many herbal products due to higher water content, sensitive root, and morphological structure. Thus, vegetables are more affected by biotic and abiotic stress conditions. For these reasons, it is known that chemical pesticide and fertilizers are widely used in vegetable production at a high rate. Chemical fertilization, which has been unconsciously made in agriculture for many years, causes the accumulation of toxic substances, the depletion of organic carbon, the degradation of microflora and fauna, and consequently the reduction of soil fertility (Sairam and Reddy 2013). On the other hand, pesticides used for plant disease and pest control have negative effects on human health and ecology, along with, enhanced the systematic resistance of pest.

In countries with low-income levels, the use of pesticides is limited due to high pesticide prices it is, therefore, control of pest and diseases is a big problem (Dardanelli et al. 2010). Otherwise, it has become a necessity to increase the productivity in the unit area to meet the nutritional needs of the growing world population. To increase efficiency 1- better agricultural land management, 2- use of more chemicals, including fertilizers, 3- use of pesticides and herbicides with safely and effectively, 4- more agricultural mechanization, 5- widespread use of transgenic crops, and 6- use of plant growth promoting rhizobacteria (PGPR) (Glick 2014) have been examined by various workers.

PGPRs are important microorganisms to increase productivity in the sense of sustainability and ecological practices in agriculture and to reduce the use of chemical fertilizers and pesticides. Rhizobacteria positively interacts with plant roots and play an important role in the growth of the plants (Agrawal et al. 2014). Bacteria enhance the circulation of nutrients and provide limited use of chemical nutrients (Dursun et al. 2010; Seymen et al. 2013a, b). PGPRs greatly affect soil properties and play an important role in crop production in inefficient and poor-quality soils (Gouda et al. 2018). The use of PGPR has become an important

application for an increase in soil quality and yield in many parts of the world (Gabriela et al. 2015).

Beneficial, bacteria are also used as symbiotic (*Rhizobium, Bradyrhizobium, Mesorhizobium*) and non-symbiotic (*Pseudomonas*, *Bacillus*, *Klebsiella*, *Azotobacter*, *Acotobacter*, *Azospirillum*, *Azomonas*) agents to increase in plant growth (Saharan and Nehra 2011) in biotic stress conditions such as herbicides (Ahemad and Khan 2010), insecticides (Ahemad and Khan 2011), fungicides (El-Sharkawy et al. 2015; García-Gutiérrez et al. 2012; Salman et al. 2017) as well as abiotic stress conditions such as drought (El-Meihy 2016; Kang et al. 2014; Wang et al. 2012), salinity (Yıldırım et al. 2006), heavy metal (Tóth et al. 2013), soil alkalinity (Esitken et al. 2016; Ipek et al. 2014, 2017), low temperature (Selvakumar et al. 2008) and groundwater.

In this review, the effects of PGPR applications as plant growth regulators were evaluated in order to the agricultural sustainability and eco-friendly production in the Cucurbitaceae family, which contains the most cultivated vegetable species in the world. Likewise, the recent studies have been collected and future perspectives have also been discussed.

4.2 What Are the PGPR's?

The plants have been in constant cross-talk with the microorganisms (bacteria and fungi) found in the soil during development and growth periods. The microorganisms the plant species, provides important benefits to plant development through different mechanisms. PGPR's are able to colonize root surface, survive, reproducible and compete with other organisms throughout the development process in the plant besides, having positive effects on plant growth (Kloepper 1994). If the bacteria show a positive effect on plant development about 2–5% when inoculated into another soil flora, it is evaluated as PGPR (Kloepper and Schroth 1978). PGPR's can penetrate different parts of the plant such as stomata, lenticels, nodules, wounds, and cracks (Fig. 4.1).

The most important features of PGPR's are the fixation of free N in the atmosphere, solubilize organic phosphorus, production of some secondary metabolites (plant hormone, siderophore and antibiotics etc.), increase in the systemic resistance, competition of nutrient and colonization and suppress disease factor (İmriz et al. 2014). PGPR's are evaluated into two groups as directly and indirectly, according to their action mechanism (Gouda et al. 2018; Gupta et al. 2015) (Fig. 4.2).

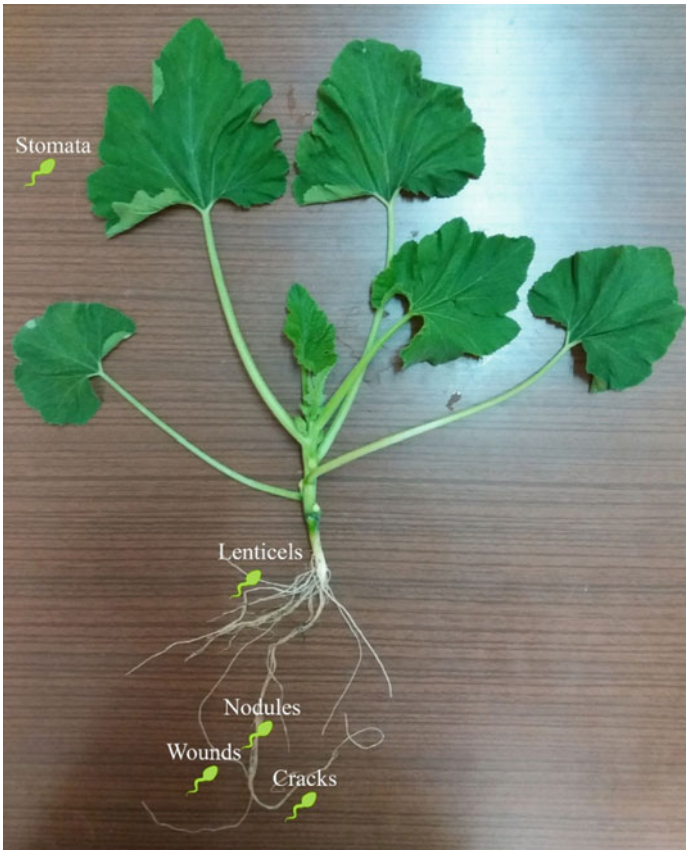

Fig. 4.1 The penetration ways of PGPR's in pumpkin plant (*Cucurbita pepo* L.)

4.2.1 Direct Mechanisms

PGPR's promote plant growth directly by providing nutrients to plants, N fixation, mineralization of organic compounds, resolution of mineral nutrients, and phytohormone production (Bhardwaj et al. 2014). These mechanisms vary according to the plant species, but different bacteria may show different effects in the rhizosphere. In this case, determination of PGPR strains is one of the most important issues in terms of plant species.

4.2.1.1 Nitrogen Fixation

Nitrogen (N_2) is one of the essential nutrients for plant growth and yield (Gupta et al. 2015; İmriz et al. 2014). It is the basic component of nitrogen nucleotides,

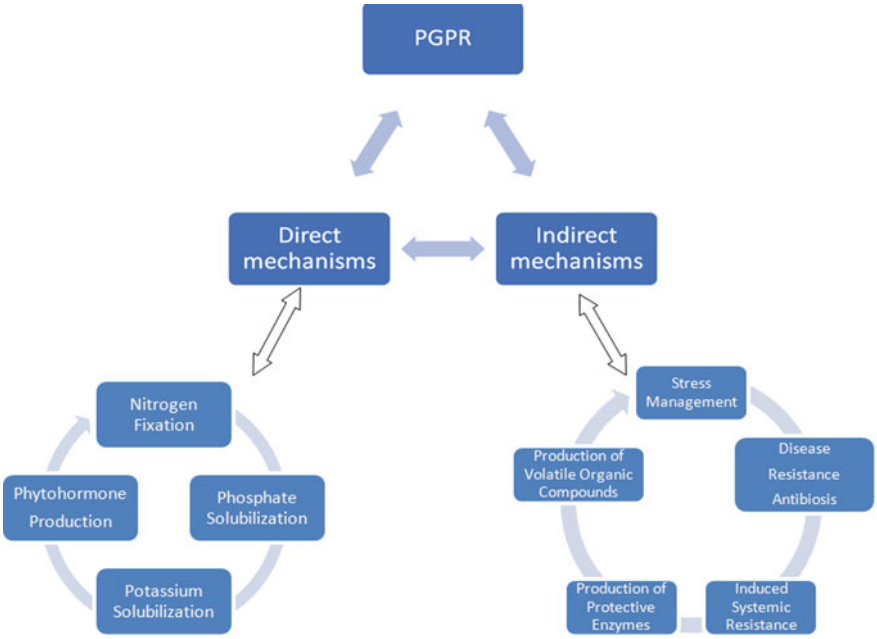

Fig. 4.2 The action mechanisms of PGPR's

membrane lipids and amino acids (Marschner 1995). Biological nitrogen fixation is the use of fixed nitrogen, which accounts for about two-thirds of the world's atmosphere (Shridhar 2012). The most studied N fixative PGPR's are *Rhizobium* sp., *Azoarcus* sp., *Pantoea agglomerans, Beijerinckia* sp. and *Klebsiella pneumoniae* (Ahemad and Kibret 2014). Rhizobacteria have positive effects on nodule production when they are applied as a mixture. Inoculation of PGPRs to plants or growing areas provides the nitrogen requirement of the soil and plant, as well as to prevent disease and to promote plant development (Damam et al. 2016).

4.2.1.2 Phosphate Solubilization

Phosphorus plays an important role in plant development for almost all metabolic processes such as energy transfer, signaling between plant receptors, respiration, macromolecular biosynthesis, and photosynthesis (Anand et al. 2016). However, 95–99% of the phosphorus is immobilized or precipitated, and is difficult to be taken up by plants. Plants can only utilize phosphorus from the soil as monobasic (H_2PO_4) and dibasic (HPO_{4-2}) forms (Bhattacharyya and Jha 2012; Gouda et al. 2018). One of the most important features of PGPRs is to solubilize insoluble phosphorus through the low molecular weight organic acids they synthesize (Bahadır et al. 2018; Sharma et al. 2013) of bacterial origin.

The most common of these organic acids which can solubilize the phosphorus produced by PGPR's, which contribute to the formation of organic acids in the soil, are lactic acid, gluconic acid, acetic acid, formic acid, oxalic acid, tartaric acid, fumaric acid, and succinic acid. Most common genera such as *Bacillus polymyxa*, *B. megatarium*, *B. circulans*, *B. subtilis*, *B. firmus*, *Pseudomonas striata*, *P. rathonia*, *Rhizobium leguminosarum* and *R. meliloti* are PGPR bacteria that can phosphorylate by producing organic acid (İmriz et al. 2014). Studies have shown that such bacteria increase phosphorus solubility when applied alone or as a mixture (consortia) (Zaidi et al. 2009).

4.2.1.3 Potassium Solubilization

Potassium is the third important plant nutrient element require for plant growth. The soluble potassium concentration in the soil is usually very low, and more than about 90% of potassium is in the silicates and rock form (Parmar and Sindhu 2013). In addition, irregular and unbalanced potassium fertilization has negative effect on plant development. Potassium deficiency causes slow root development of the plant, negatively affecting on plant growth, and causes small seed formation and loss of yield.

To ensure healthy plant development, it is necessary to find an alternative endemic source of potassium that provides potassium source from the soil (Kumar and Dubey 2012). Rhizobacterium which promotes plant development helps to dissolve potassium rocks by organic acid production and release and transform them into a useful form for plants (Han and Lee 2006).

Bacterium species such as *Acidothiobacillus* sp., *Ferrooxidans* sp., *B. edaphicus, Pseudomonas* sp., *B. mucilaginosus, Burkholderia* sp. and *Paenibacillus* sp. showed significant effects on potassium solubility (Liu et al. 2012). Therefore, the use of PGPRs in integrated nutrient management has an important role in the restriction of chemicals (Gupta et al. 2015; Setiawati and Mutmainnah 2016) led to sustainable agricultural production.

4.2.1.4 Phytohormone Production

In plant growth, some phytohormones such as indole-3-acetic acid (IAA), cytokinin and gibberellins have important role in the root development, expansion of root surface area, seed germination, chlorophyll accumulation, leaf growth, seed germination, dormancy, initiation of enzyme function, senescence of leaves and fruits etc. (İmriz et al. 2014; Sureshbabu et al. 2016). It is well known that PGPR's have important role in the synthesis of these phytohormones (Gouda et al. 2018). It was determined that 80% of the microorganisms isolated from the soil could synthesize IAA (Patten and Glick 2002). Indole-pyruvic acid and indole-3-acetic aldehyde mediated IAA synthesis were determined in *Erwinia herbicola*, in some saprophytic *Pseudomonas* and *Agrobacterium* species, *Bardyrhizobium*, *Rhizobium*,

Azospirillum, *Klebsiella, and Enterobacter*. In addition, tryptophan-derived IAA was found in Cyanobacterium, while tryptophan-independent IAA production demonstrated in Azospirila and cyanobacteria (Ahemad and Kibret 2014).

4.2.2 Indirect Mechanisms

PGPRs produce repressive substances to prevent or mitigate the harmful effects of phytopathogens on plants and increase in natural resistance (Singh and Jha 2015). This mechanism can also be described as a process that helps plants to actively grow under environmental stress (abiotic stress) or to protect plants from infections (biotic stress) (Akhgar et al. 2014).

4.2.2.1 Stress Management

Stress is one of the most important factors that imparts negative effects on plant growth (Foyer et al. 2016). In all stress conditions, reactive oxygen species (ROS) such as H_2O_2, O_2- and OH- are increased. Producing excessive ROS in plants causes oxidative damage to plants by oxidizing photosynthetic pigments, membrane lipids, proteins, and nucleic acids (Gouda et al. 2018). Plants accumulate metabolites to avoid stress such as poly-sugars, proline, glycine-betaine, abscisic acid, and upregulation in the synthesis of enzymatic and non-enzymatic antioxidants, as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase, ascorbic acid, ɑ- tocopherol, and glutathione (Agami et al. 2016). Under abiotic stress conditions that occur in different environmental conditions, PGPR applications provide positive effects on plant growth by providing metabolite balance in plants. Beneficial effects of PGPR's have also been observed in abiotic stress conditions, as for drought (El-Meihy 2016; Kang et al. 2014; Wang et al. 2012), salinity (Yıldırım et al. 2006), heavy metal (Tóth et al. 2013), soil alkalinity (Esitken et al. 2016; Ipek et al. 2014, 2017), low temperature, etc. (Selvakumar et al. 2008).

Different pathogens such as bacteria, viruses, nematodes, fungi, insects, and viroids are important biotic factors agricultural production and adversely affected on plant growth (Haggag et al. 2015). Various genera of PGPR such as *B. amyloliquefaciens* strain HYD-B17, *P. polymyxa* strain B2, B3, B4, *B. licheniformis* strain HYTAPB18, *P. favisporus* strain BKB30, *B. thuringiensis* strain HYDGRFB19 and *B. subtilis* strain RMPB44 gave positive response against to biotic agents (Gouda et al. 2018).

4.2.2.2 Disease Resistance Antibiosis

The use of PGPRs against plant pathogens in agriculture means the application and restriction of the use of agricultural chemicals. *Bacillus* spp. and *Pseudomonas* sp. microorganisms prevent pathogen damage by releasing antibiotics (Gouda et al. 2018).

The effects of microorganisms that produce antibiotics are the most studied topics in recent years. Some antifungal antibiotics (phenazines, phenazine-1-carboxylic acid, phenazine-1-carboxamide, pyrrolnitrin, pyoluteorin, 2,4 diacetyl phloroglucinol, rhamnolipids, oomycin A, cepaciamide A, ecomycins, viscosinamide, butyrolactones, N-butylbenzene sulfonamide, pyocyanin) and bacterial antibiotics (pseudomonic acid andazomycin), antitumor antibiotics (FR901463 and cepafungins) and antiviral antibiotics (Karalicine) are mostly produced by *Pseudomonas* species (Ramadan et al. 2016). Alcohols, aldehydes, ketones, sulfides and hydrogen cyanide are called volatile antibiotics, whereas, polyketides, cyclic lipopeptides, amino polyols, phenylpyrrole, and heterocyclic nitrogenous compounds are non-volatile antibiotics in nature (Fouzia et al. 2015).

4.2.2.3 Induced Systemic Resistance

When the plants are exposed to attack by pathogens, PGPRs are used to stimulate their defense mechanisms (Pieterse et al. 2009). This mechanism called Induced Systemic Resistance (ISR) provides resistance to pathogens the plant is exposed in future (Van Loon 2007). Gram-positive (*B. pumilus)*, Gram-negative (*P. fluorescens, P. putida*, *P. aeruginosa*), and enterobacteria (*Serratia marcesens*, *S. plymuthica*) provide resistance in ISR mechanism (Jourdan et al. 2009).

4.2.2.4 Production of Protective Enzymes

Ethylene is a very important plant signal hormone that shows a rapid increase in abiotic and biotic stress conditions, which play a regulatory role in seed germination, root growth, root nodulation, flowering and fruit ripening (İmriz et al. 2014). 1-aminocyclopropane-1-carboxylate (ACC) deaminase, also produced by PGPRs, promotes plant growth and development by regulating ethylene production in the plant (Yang et al. 2009). After the ethylene signal ACC is synthesized in the plant, it is taken up by the bacteria from the plant roots and hydrolyzed to the enzyme and 2-oxobutanoate. Thus, the level of ACC concentration in the plant is reduced and excessive ethylene formation is prevented and finally plant growth is promoted (Ahemad and Kibret 2014). In recent studies, ACC-deaminase activity has been determined in many bacterial strains belonging to the genus *Acinetobacter, Achromobacter, Agrobacterium, Alcalienes, Azospirillum*, *Bacillus, Burkholderia, Enterobacter, Pseudomonas, Ralstonia* and *Rhizobium* (Shaharoona et al. 2006; Zahir et al. 2009).

4.2.2.5 Production of Volatile Organic Compounds (VOCs)

VOCs increase in plant growth, providing systemic resistance to plants against phytopathogens by reducing the effects of fungal pathogens, bacteria and nematodes (Reza et al. 2016). Some bacterial species such as in *Pseudomonas*, *Bacillus, Arthrobacter, Stenotrophomonas* and *Serratia* induce plant growth promoting VOCs. 2, 3-Butanediol and acetone produced by *Bacillus* spp. stimulate plant growth by suppressing fungal development (Santoro et al. 2016). VOCs obtained directly or indirectly from PGPRs have positive effects on disease resistance, abiotic stress tolerance and plant biomass (Gouda et al. 2018).

However, the quantity and identity of the VOCs emitted vary among species, some soil microorganisms produced benzene, cyclohexane, methyl, 2,6,10-trimethyl, 2-(benzyloxy) ethanamine, dodecane, decane, 1-(N-phenylcarbamyl)- 2- morpholinocyclohexene, 1-chlorooctadecane, benzene (1-methylnonadecyl), tetradecane, 11-decyldocosane and dotriacontane having common characteristics of VOCs (Kanchiswamy et al. 2015).

4.3 The Effects of PGPR's on Growth and Yield in Cucurbits

Although the functions of PGPRs have not yet been fully described, but have lots of unique advantages on plant production and agricultural systems. Many studies have been conducted on the effects of PGPR's in cucurbit crops and it has been exactly revealed that PGPRs have positive effects on seed and seedling quality, plant growth, yield components, etc. But, a majority of field research examined under controlled conditions is scarce. Besides, the effectiveness of PGPR's depends on plant genotype, rhizobacteria strain, inoculation doses and ecology in relation to the plant growth and yield components.

4.3.1 Seed and Seedling Quality

As in all plants, a healthy seed germinates to produce seedling of plant production in cucurbit crops. It is well known that some soil-borne fungal diseases caused by *Fusarium* spp., *Didymella* spp. and *Phytophthora* spp. caused poor seedling growth and seedling loss at the beginning, thus, yield and quality are significantly reduced in Cucurbits. Seed and seedling applications of root-colonizing rhizobacteria are used for both controlling plant disease and also promote seedling growth without using any chemical preparation in watermelon, melon, cucumber, and squash. In this regard, PGPRs are known as eco-friendly practices in today's agriculture.

PGPR's can be applied to the seeds by seed soaking, alginate-encapsulation and seed coating (Bashan 1998; Reed and Glick 2005). The rhizobacteria are applied to seedlings by "roots dipped" or foliar spraying methods. Seeds were inoculated some PGPR strains and the symptoms of *Fusarium* spp., *Didymella bryoniae* and *Myrothecium* were significantly reduced, thus the seed germination and seedling vigor reported to increase in watermelon (Lokesh et al. 2007). The plants raised by seed treatments of some isolates (GBO3 and INR7) were effective on *Colletotrichum orbiculare*, *P. syringae* pv. *lachrymans* and *Erwinia tracheiphila* in *C. sativus* L. under greenhouse conditions (Raupach and Kloepper 1998). PGPR treatments provide considerable growth of seedling, stem diameter, leaf number, cotyledon diameter, shoot and root weight were significantly increased with treatments of *B. pumilus* and *Alcaligenes piechaudii* in cucumber (Kidoglu et al. 2007; Yıldırım et al. 2015). Similarly, Kokalis-Burelle et al. (2003) reported that PGPR's increased seedling quality (shoot weight, shoot length, and stem diameter) in muskmelon and watermelon. *Azotobacter chroococcum*, *B. megaterium,* and *B. mucilaginosus* generated germination and growth rate, the biomass of shoots, the number of lateral roots, and the hair root area in cucumber seedlings (Sokolova et al. 2011).

Root length was significantly increased in cucumber seedlings by bacterial inoculation under in vitro conditions (Utkhede and Koch 1999). *Gigaspora margarita, B. subtilis*, *Thermomonospora* sp. and *Thermoactinomyces* sp. considerably interrupted damping-off in 2–3 weeks old cucumber seedlings (Kabayashi 1989).

Coinoculation of seeds with soaking methods *A. brasilense* strains enhanced germination value, vigor index and the endogenous IAA content in cucumber seed and seedlings (Mangmang et al. 2015). The high germination vigor and emergence rate have been associated with phytohormones, (IAA and GA) synthesized by PGPR's (Kang et al. 2015).

4.3.2 Plant Growth and Yield

PGPR's promote plant growth and yield by involvement of different mechanism such as biological nitrogen fixation, phosphate solubilization, siderophores and exopolysaccharides production, phyto stimulation by IAA and GA production, bio-control for plant diseases, supply of some mineral elements and production of antibiotic in Cucurbit crops (Noumavo et al. 2016; Vikram et al. 2007). Phytohormones produced by some PGPR's are recognized as unique signaling substances for plant growth and strongly enhance to root growth, root surface area, and branching and plant habitus (Cassán et al. 2009; Levanony and Bashan 1989; Vessey 2003). In addition, recent studies stated that few proteins responsible for growth and photosynthesis activated by root inoculation of some PGPR's (Yaoyao et al. 2017).

In watermelon, continuous cropping system resulted to low yield and poor quality due to high incidence of soil-borne diseases (especially *Fusarium*

oxysporum f. sp. *niveum*) and limited plant growth (Adhikari et al. 2017; Ling et al. 2014). These handicaps were effectively eliminated by application of bio-organic fertilizers and functional microbes' combination (Zhao et al. 2018). Likewise, *Fusarium* wilt was considerably reduced by using organic fertilizer *Paenibacillus polymyxa* SQR-21 based (Ling et al. 2012). In a greenhouse experiment, P. *polymyxa* and *Sinomonas atrocyanea* enhanced total chlorophyll content, plant height, fresh weight and dry weight of three watermelon varieties (Adhikari et al. 2017). Earlier, the positive effects of PGPR treatments on shoot weight, shoot length and stem diameter were reported in muskmelon and watermelon transplant (Kokalis-Burelle et al. 2003).

The beneficial effects of rhizobacteria on cucumber growth and yield have been also observed by various researchers (Kang et al. 2014; Sturz et al. 2000). The application of *Pantoea agglomerans* FF increased in fruit number and fruit weight per plant, plant length, fruit width, fruit length and dry matter. The highest average fruit weight was obtained from *Bacillus megatorium*-GC subgroup A. MFD-2 in cucumber (Dursun et al. 2010). The combination of biogas slurry and *P. fluorescens* resulted in higher shoot fresh weight, shoot dry weight, root fresh weight, root dry weight and total yield (Ahamd et al. 2015). When the PGPR or compost tea was used as a bio-fertilizer, yield and quality were significantly increased under the sandy soil (Abou-El-Hassan et al. 2014). Farrag et al. (2015) reported that the inoculation of *Azospirillum* and *Trichoderma* promote vegetative growth, leaves dry matter percentage, early emergence and number of female flowers, and total yield (cv. hybrid Prince). Diverse genera such as *Rhodobacter sphaeroides, Lactobacillus plantarum,* and *Saccharomyces cerevisiae* have substantial increase in the shoot length, root length, shoot fresh weight, shoot dry weight, and chlorophyll content, via secretion of optimum IAA and/or organic acids and low ABA level in cucumber (Kang et al. 2015). *Pseudomonas putida* strain P13 and *Pantoea agglomerans* strain P5 have positive effects on cucumber yield and yield components (Isfahani and Besharati 2012). *R. sphaeroides*, *L. plantarum*, and *S. cerevisiae* increased in the quantities of amino acids perhaps responsible for photosynthesis and nitrogen fixation in cucumber (Kang et al. 2010; Kang et al. 2014; Kang et al. 2015). Earlier, Rhizobacteria strain FE-43 and N-17/3 inoculations had shown the positive effects on yield and yield components (Seymen et al. 2010). In soilless culture, Utkhede and Koch (1999) reported that the strains BACT-0 of *B. subtilis* and *P. aphanidermatum* promote growth affected by fruit yield, and fruit number in commercial greenhouse conditions. Furthermore, root volume and plant growth increased in by using AMF and charcoal compost (Kabayashi 1989).

In *Cucumis melo* L., *G. mossae* and *B. cepacia* either separately or in combination enhance the growth and yield (Zulkarami et al. 2012). As an eco-friendly application, the bio-fertilizers were found to be effective on growth and yield in soilless squash production (Dasgan et al. 2010). The application of *G. intraradices* improved growth and yield in Zucchini squash (*C. pepo* L.) (Colla et al. 2008). The combination of *Azotobacter chroococum* and mineral N-fertilizer was found to be a profitable practice in sandy soil (Refai et al. 2010). Bio-fertilizer Halex-2 significantly enhanced fruit yield due to female flower formation at a higher rate

(Abd-El-Fattah and Sorial 2000). Root and shoot dry weight, number of leaves, shoot length, stem diameter and number of ramifications significantly increased by application of three nitrogen (N) sources and PGPR in squash (Tchiaze et al. 2016).

4.3.3 *Fruit Quality*

The majority of the researches on PGPR application concentrated on plant growth and yield, but the knowledge about fruit quality parameters is still not sufficient and need to investigate in Cucurbit crops.

According to the findings of Dursun et al. (2010), PGPR's (*Pantoea agglomerans*, *Acinetobacter baumannii,* and *B. megaterium*) increased mineral contents (N, P, Mg, Ca, Na, K, Cu, Mn, Fe, and Zn) and dry matter in fruits, but TSSC (Total Soluble Solid Content) were not changed in cucumber. Likewise, FE-43 and N-17/3 PGPR strains had positive effects on water-soluble dry matter and pH content in cucumber fruit (Seymen et al. 2010). Soluble sugar, amino acids, and soluble proteins were considerably enhanced by the inoculation of *G. versiforme*, *G. mosseae,* and *G. intraradices* (Lu et al. 2006). Biogas slurry + *P. fluorescens* and some PGPR treatments produced high-quality cucumber fruits (Ahamd et al. 2015; Elwan and Abd 2015). Several other studies of plant growth and productivity have been sumarised-up in the Table 4.1 which illustrate the significanc of PGPRs in enahncement of yield and yield components of cucurbit crops.

4.4 The Role of PGPR's on the Uptake of Mineral Elements in Cucurbits

Rhizobacteria promotes plant growth by increasing the supply or availability of primary nutrients to the host plant (Isfahani and Besharati 2012: Seymen et al. 2014, 2015a). PGPR's, chemical or organic substances fertilizers either separately or combination with different doses are used for mineral resources in Cucurbit crops. The efficiency of PGPR's on mineral elements uptake and availability depended on many factors such as bacterial strains, application doses, plant species and soil fertility status.

In *C. sativus* L., the rock materials (K and P) and bacterial strains (*B. megaterium* var. *phosphaticum* and *B. mucilaginosus)* consistently increased in availability and uptake of minerals (Han and Lee 2006). Foliar spraying of rhizobacteria had positive effects on N, P and K percentages in cucumber leaves (Farrag et al 2015). *R. sphaeroides*, *L. plantarum*, and *S. cerevisiae* reported IAA-producing microorganisms and enhanced mineral nutrient uptake by plant roots such as potassium, magnesium, phosphate, and calcium (Kang et al. 2015; Nimnoi et al. 2014). Furthermore, some bacteria (*L. plantarum* and *S. cerevisiae*) produce

Table 4.1 The effects of PGPR's on plant growth, yield and yield components of cucurbit crops

Species	PGPR's	Comments	References
	G. versiforme, *G. mosseae* and *G. intraradices*	Soluble sugar, Amino acids, Soluble proteins	Lu et al. (2006)
	N-52/1, N-17/3, FE-43, F-21/3, 637 Ca, MfdCa1	Yield, Fruit per plant, Fruit weights, Dry matter pH content	Seymen et al. (2010)
	Burkholderia sp. KCTC11096BP	Shoot length, Shoot fresh weight, Shoot dry weight, Root fresh weight, Root dry weight, Chlorophyll (SPAD)	Kang et al. (2010)
	P. putida strain P1 3, *Pantoea agglomerans* strain P5	Yield, Length of plant, Chlorophyll content Shoots dry weight, Fresh weight, Dry weight, Fresh weight	Isfahani and Besharati (2012)
	B.s subtilis BA-142, *B. megaeorium-GC subgroup A.* MFD-2, *A. baumannii* CD-1 *P. agglomerans* FF	Fruit number, Fruit weight, Plant length, Fruit width, Fruit length, Dry matter pH	Dursun et al. (2010)
Cucumber	*B. pumilis, Alcaligenes piechaudii*	Seedling growth and quality	Yıldırım et al. (2015)
	P. fluorescens	Growth, Yield, Fruit quality, Shoot fresh weight, Shoot dry weight, Root fresh weight, Root dry weight	Ahamd et al. (2015)
	Azospirillum Trichoderma	Growth, Leaves dry matter	Farrag et al. (2015)
		Number of female, Fruit length, Fruit diameter, Early and total yield	
	B. megaterium var. *phosphaticum B. mucilaginosus*	Plant growth, Dry weight	Han and Lee (2006)
	Rhodobacter sphaeroides, Lactobacillus plantarum, Saccharomyces cerevisiae	Amino acids, Shoot length, Root length, Fresh weight, Dry weight, Chlorophyll (SPAD)	Kang et al. (2015)
	P. fluorescens DF57	Root dry weight, Root length	Ravnskov and Jakobsen (1999)
Watermelon	*Paenibacillus polymyxa* (SN-22), *Sinomonas atrocyanea* (NSB-27)	Total chlorophyll content, Plant height, Total fresh weight, Total dry weight	Adhikari et al. (2017)
Watermelon and Melon	*B. subtilis amyloliquefaciens B. subtilis B. pumilus*	Shoot weight, Shoot length Stem diameter	Kokalis-Burelle et al. (2003)
	A. chroococum strains (5 mutants and wild-type strain)	Stem length, Flowering, Fruits, Early and total yield	Refai et al. (2010)

(continued)

Table 4.1 (continued)

Species	PGPR's	Comments	References
Squash	*B. subtilis, B. amyloliquefaciens, B. pumilus, B. licheniformis, S. cerevisiae*	Root dry weight, Shoot dry weight, Total plant dry weight, Number of leaves, Shoot length, Stem diameter, Number of ramifications	Tchiaze et al. (2016)
	Paenibacillus polymyxa B. megaterium	Early fruit yield, Total yield, Good quality of fruits	Moussa (2006)
	A. brasilense AC1 *B. subtilis* AC2	Fruit yield Fruit weight Growth	Elwan and Abd (2015)

organic acids and increase in the availability of mineral elements, mainly phosphorus (Wang et al. 2014).

In *Cucurbita pepo* L., the treatments of rhizobacteria significantly reduced P- and N-fertilizer without any reduction in squash yield (Moussa 2006; Elwan and Abd 2015), importantly for sustainable plant production. The combinations of PGPR and different N sources (NO_3^-, NH_4^+, and NO_3NH_4) reported as efficient bio-fertilizers to significantly improve the minerals uptake in squash (Tchiaze et al. 2016). G. intraradices caused higher K and lower Na concentration in leaf tissue in squash (Colla et al. 2008).

4.5 Abiotic Stress Conditions and PGPR's in Cucurbits

The soil has a complex and dynamic system that promote plant growth. Some stress factors should be carefully examined in order to maintain plant growth in soil, regularly (Nadeem et al. 2014). While the most important abiotic factors affecting on plant growth are drought, salinity, and heavy metal stresses, some stress elements such as high temperature, soil alkalinity, high groundwater and low temperature also have negative effects on plant growth. In sustainable agriculture, abiotic stress factors are considered to be the main causes of yield loss. On the other hand, the effect of stress factors leads to yield losses of up to 50–82%, varying with soil structure, plant species and varieties (Christensen et al. 2007).

These stresses include plant growth hormone and nutritional imbalance among general effects, physiological disorders such as epinasty, abscess and aging, and predisposition to diseases (El-Iklil et al. 2000; Zhu et al. 1997). Drought and salinity stress directly affect plant growth, leading to increase in ethylene release in the plant and limitation of root and shoot development (Glick et al. 2007). Drought and salinity are typically encountered in arid and semi-arid regions of the world and effective about 7.6 million km^2 areas.

Agricultural areas used in the world are affected by drought stress (26%), mineral material stress (20%), cold and frost stress (15%) and other stress factors (29%) (Kalefetoğlu and Ekmekçi 2005). Unfortunately, it is also estimated that this area will be doubled and water resources will decrease by 30% up to 2050 (Falkenmark 2013). For this reason, some solutions are being searched to increase in plant development and productivity in stress conditions for sustainability of agriculture. It is known that rhizobacteria (PGPR), which support plant growth under stress conditions, play an important role in the growth and metabolism of plants (Kang et al. 2014). PGPR's produce induced systemic tolerance for the development of plants under abiotic stress conditions via generating physical and chemical changes in plants (Yang et al. 2009). It has also been reported that PGPR's are more effective against to abiotic stress when applied in combination with mycorrhiza (Mayak et al. 2004).

4.5.1 Drought Stress

Drought is examined under four main headings; meteorological, agricultural, hydrological and socioeconomic drought. Droughts begin as meteorological, develop as agricultural and hydrological and become visible as socio-economical (Örs and Ekinci 2015). In particular, drought stress is an important factor that negatively effects on agricultural productivity in arid and semi-arid regions and limited plant growth (Seymen et al. 2016; Yavuz et al. 2015a; Yavuz et al. 2015b). Ethylene, which released in arid conditions from plant tissue, has the property of restricting plant growth, inhibiting photosynthesis and changing chlorophyll content. Some chemicals such as amino ethoxy vinyl glycine (AVG), cobalt ion (Co^{2+}) and silver ion (Ag^{+}) can be applied to decrease the ethylene level and to protect against stress. However, these chemicals are not preferred because they are both expensive and adversely affect human health (Mckeon et al. 1995).

Besides, these types of chemicals are not recommended because they have a permanent effect on the soil and they will cause environmental pollution and other stress factors in the future. As an alternative method, eco-friendly production techniques and practices should be developed to ensure sustainability in agriculture. While plants have developed some specific mechanisms to combat such stress conditions, it is known that some useful microorganisms in root regions play an important role in reducing stress intensity (Nadeem et al. 2014). It is possible to explain the mechanisms by which PGPRs develop against abiotic stress factors; 1- produces some phytohormones such as ABA, GA and IAA, 2- reduce the level of ethylene in the roots with ACC deaminase, 3- creates systemic resistance with bacterial compounds, 4- enhance bacterial exopolysaccharides (Kim et al. 2013; Timmusk et al. 2014; Yang et al. 2009). In sustainable agriculture, PGPR's, an environmentally friendly practice, have been realized to promote plant development with nodules formed in the root zone of the plant in case of drought stress (El-Meihy 2016; Wang et al. 2012).

Cucumber, melon, watermelon, and squash need a lot of water in economic cultivation for both open field and protected cultivation. The drought stress during the cultivation season causes great yield loss in an economic sense. In particular, melon, watermelon, and squash are grown in open field conditions. These species have medium root structure and they are moderate resistant vegetable species to drought stress. In fact, some species and varieties are grown by limited irrigation in arid and semi-arid regions with their deep root structure (Sensoy et al. 2007; Yavuz et al. 2015a; Yavuz et al. 2015b). However, PGPR applications have an important role in the cultivation of Cucurbit species due to increasing in the agricultural land affected by drought and correspondingly more economical use of irrigation water to improve plant development and productivity.

In a study, the effects of *B. cereus* AR 156, *B. subtilis* Sin 21 and *Serratia* sp. XY 21 bacterial strains were investigated in cucumber. As a result of the study, the bacterial strains increased the electrical conductivity and the root ratio by 40% and 50%, respectively. In addition, PGPR inoculations decreased the effects of drought stress by increased MDA, SOD, proline, and ascorbate peroxidase contents (Wang et al. 2012). Likewise, the effectiveness of *Burkholdera cepacia* SE4, *Promicromonospora* sp. SE188 and *A. colcoaceticus* SE370 were examined and used for reducing the effects of drought and salinity stress, consequently, bacteria strains increased in biomass and chlorophyll contents in drought stress conditions. PGPR practices have led to increases in water potential by reducing the electrolytic exudation. In addition to reducing oxidative stress, PGPR applications have also affected on phosphorus and potassium uptake, positively. It has also been reported that PGPR practices increase productivity in stress conditions and PGPR's are an important application for sustainable agriculture (Kang et al. 2014). In squash (*C. pepo* L.), *A. chroococcum* ML1, *B. circulans* ML2, *B. megaterium* ML3 and *P. fluorescence* ML4 enhance the plant growth and produce a higher yield in drought stress. Bacteria have reduced the effect of drought stress by causing enzyme activities, IAA, and GA3 increases. It is clarified that the abscisic acid secreted under stress conditions was found to be less in bacterial applications. Researchers have reported that PGPR inoculations constitute better results on plant growth and yield than that of humic acid and chemical fertilizer applications (El-Meihy 2016) (Table 4.2).

4.5.2 Salinity Stress

There are about 1.5 billion hectares of agricultural land in the world, and 77 million hectares (5%) of this area are considered as inefficient agricultural land due to the high salt content (Abdel Latef and Chaoxing 2011). Besides, 20% of world agricultural land is negatively affected by salinity due to the using salty irrigation water (Wu et al. 2010). The salinity problem is increasing in regularly all over the world. When soil salinity increases, osmotic stress is triggered in the plant. Thus, the high

Table 4.2 The effects of PGPRs on the mineral elements uptake of cucurbit crops

Species	PGPR's	Comments	References
	N-52/1, N-17/3, FE-43, F-21/3, 637 Ca, MfdCa1	N, P, K, Mg, Ca, Na, Cu, Fe, S and B	Seymen et al. (2015b)
	B.subtilis BA-142, *B. megaeorium-GC subgroup A.* MFD-2, *A. baumannii* CD-1 *Pantoea agglomerans* FF	N, P, Mg, Ca, Na, K, Cu, Mn, Fe, and Zn	Dursun et al. (2010)
	P. fluorescens	N, P, and K	Ahamd et al. (2015)
Cucumber	*Azospirillum* *Trichoderma*	N, P, and K	Farrag et al. (2015)
	B. megaterium var. *phosphaticum* *B. mucilaginosus*	N, P, and K	Han and Lee (2006)
	Rhodobacter sphaeroides, Lactobacillus plantarum, Saccharomyces cerevisiae	Ca, Mg, P, and K	Kang et al. (2015)
	A. brasilense	Fe	Pii et al. (2015), (2016)
	P. fluorescens DF57	P	Ravnskov and Jakobsen (1999)
	B. subtilis, B. amyloliquefaciens, B. pumilus, *B. licheniformis, Saccharomyces cerevisiae*	N, P, K and Mn	Tchiaze et al. (2016)
Squash	*Paenibacillus polymyxa* *B. megaterium*	N, P, and K	Moussa (2006)
	A. brasilense AC1 *B. subtilis* AC2	N and P	Elwan and Abd (2015)

concentration of Na^+ and Cl^- in the soil causes nutrient imbalance, which reduces nutrient uptake and ion toxicity (Daei et al. 2009).

Soil salinity induces drought stress, ion toxicity, ion imbalance and degradation of soil structure and pH, hereby, inhibit plant growth (Gopal et al. 2012). While some plants try to counter the stress with the mechanisms of genetic structure in order to sustain its development in saline soil, some sensitive species are adversely affected. Some of the plant growth promoting rhizobacteria and fungi in the rhizosphere are reducing plant pathogens or affecting the production of phytohormones, increasing in plant nutrient uptake from the soil and increasing in plant growth, indirectly (Grichko and Glick 2001). Many studies have reported that PGPR's have positive effects on plant growth under salt stress conditions (Kang et al. 2014; Palacio-Rodríguez et al. 2017; Yıldırım et al. 2006).

Cucumber, melon, watermelon, and squash are economically important species of the Cucurbitaceae family and known as sensitive or moderately susceptible species to salinity (Francois 1985). Today, cucumber, melon, watermelon, and

pumpkin irrigated with drip irrigation system for both open field and protected areas. The results of salinity of the irrigation waters, salinity increases in agricultural areas day by day and the cultivation of cucumber, melon, watermelon, and squash is negatively affected. For this reason, PGPR practices have been important in the cultivation of cucumber, melon, watermelon, and pumpkin in salty soils.

Some PGPR inoculation *(Burkholdera cepacia* SE4, *Promicromonospora* sp. SE188 and *Acinetobacter colcoaceticus* SE370) produced the higher yield under drought and salty soil conditions in cucumber (Kang et al. 2014). In squash, AgBlend, SoilBuilder, Yield Shield, Plant Shield, Inoculoid, and Equity bacterial strains considerably increased in plant fresh weight under salt stress compared to control lots. On the other hand, bacterial applications showed positive effects on potassium uptake. In 100 mM salt application, SoilBuilder, Yield Shield, and Equity bacteria inoculations increased in sodium concentration while other applications reduced. The most important effect of the bacteria is to increase in the K^+/Na^+ ratio which is an important parameter for plant development. Researchers have reported that bacterial applications have positive effects on plant growth and are feasible under salt stress conditions (Yıldırım et al. 2006). In another study conducted in watermelon and cucumber under salt stress conditions, from the 38 isolates, *Bacillus* sp. (LBEndo1) and *Pseudomonas lini* (KBEcto4) strains have shown important results on stimulation of root and shoot growth. It was determined that the bacteria increased in IAA and phosphorus uptake. Palacio-Rodríguez et al. (2017) demonstrated that the bacteria provide tolerance to salt stress and promote plant growth (Table 4.3).

4.5.3 Heavy Metals Stress

Some nutrient sources are needed for plant development at microelement level. However, when it is above the desired levels, it causes a toxic effect on the plant and limited the plant growth. Besides, mineral toxicity like the other stress factors has a negative effect on growth and economic yield of plants economically by accelerating the synthesis of ethylene (Safronova et al. 2006).

Fields contaminated with mineral toxicity is increasing in as a result of misapplications on fertilization made by human beings or in naturally. Agriculture is restricted in such areas and the consumption of crops yielded these areas also negatively affects human health. Accumulation of heavy metals such as Cd, Cr, and Pb in the human body leads to serious systemic health problems (Oliver 1997). One of the most important factors of heavy metal accumulation in the soil is the irrigation with dirty waste city or industrial water, because of these reasons, Cd, Zn, Cr, Ni, Pb, and Mn accumulate in the surface soil (Sharma et al. 2007). Many strategies have been conducted to counteract toxic substances in the soil in order to make the reclamation of agricultural areas. The use of microorganisms to increase in plant productivity and resistance to heavy metal pollution in the soil is one of these strategies (Gopal et al. 2012). Although heavy metal stress is not a very

Table 4.3 Effect of different PGPR's on cucurbit species in abiotic stress conditions

Plant species	PGPR	Comments (enhancements)	References
Cucumber (in drought stress)	*B. cereus* AR 156 *B. subtilis* Sin 21 *Serratia* sp. XY 21	40% electrical conductivity 50% root Prolin content Ascorbate peroksidaz MDA SOD	Wang et al. (2012)
Cucumber (in Al stress)	*A. chroococcum* *B. megaterium*	Shoot dry weight Root dry weight Root/shoot ratio Chlorophyll content Fe, Mn, Zn and Mg uptake	Tóth et al. (2013)
Cucumber (in drought and salinity stress)	*Burkholdera cepacia* SE4 *Promicromonospora* sp. SE188 *A. colcoaceticus* SE370	Shoot dry weigh Chlorophyll content K and P uptake Salicylic acid Gibberellin	Kang et al. (2014)
Squash (in salinity stress)	AgBlend SoilBuilder Yield Shield Plant Shield Inoculoid Equity	Biomas K uptake K^+/Na^+	Yıldırım et al. (2006)
Squash (in drought stress)	*A. chroococcum* ML1 *B. circulans* ML2 *B. megaterium* ML3 *P. fluorescence* ML4	Plant growth Enzyme activity IAA GA_3 Higher yield Low Abscisic acid	El-Meihy (2016)
Cucumber and Watermelon (in salinity stress)	*Bacillus* sp. (LBEndo1) *P. lini.* (KBEcto4)	Plant growth IAA P uptake	Palacio-Rodríguez et al. (2017)
Squash (in cold stress)	*S. marcescens* SRM	Shoot and root length Shoot and root dry weight N, P, K uptake	Selvakumar et al. (2008)

common problem in today's vegetable industry (Savvas et al. 2010), approximately 7% of cadmium was determined in eggplant fruits in Japan (Arao et al. 2008). This level is highly over the limits established by the international health organization

(Savvas et al. 2010). It is inevitable that these kinds of problems increase with the use of non-agricultural wastewater for plant production areas where water-scarce. Cucurbitaceae family vegetables are not so much affected by heavy metal toxicity by reason of the rootstocks used with some grafting techniques (Savvas et al. 2010). Although the grafting technique is widely used in watermelon cultivation, it is not preferred much in cucumber, melon and zucchini species; therefore, cucurbit production areas are in danger of being faced with heavy metal toxicity. To overcome this problem, it is important to develop PGPRs that reduce the efficacy of heavy metal toxicity and promote plant growth in such soil.

A. chroococcum and *B. megaterium* bacteria used against aluminum (Al) stress decreased Al contents in cucumber leaves. It has also been reported that bacteria inoculations reduced the negative effects of Al on the roots and caused to higher chlorophyll content in shoots. Al applications have been shown to reduce the root/shoot rate while bacterial applications have removed this negative effect. The use of biological fertilizers instead of chemical fertilizers has emerged as an alternative way. Biological fertilizers also positively affected on plant growth in the case of heavy metal stress. However, researchers think that the interaction of these bacteria with other bacteria and their effects may be different in the main growing sites of the plant under heavy metal stress conditions (Tóth et al. 2013) (Table 4.3).

4.6 Biotic Stress Conditions and PGPR's in Cucurbits

Since the beginning of agriculture, synthetic pesticides have been widely used for plant diseases and pests. The pesticides have caused adverse effects on human health and the environment as well as the systemic resistance of the pests. In addition, countries with low-income levels have limited use due to high pesticide prices (Dardanelli et al. 2010). PGPR's have been used as an alternative to chemicals against soil-borne diseases through human health and environmentalist approaches in sustainable agriculture (Kloepper et al. 1993). When PGPR's were started to be used in agriculture, they decreased in plant growth and productivity as well as the effect of diseases and pests (Gerhardson 2002; Reddy 2016).

In general, bacteria used as biopesticides belong to the *Agrobacterium*, *Bacillus* and *Pseudomonas* (Fravel 2005). In insect control, *Bacillus thuringiensis* constitute 70% of the used bacteria (Sanchis and Bourguet 2008). *Bacillus* such as *B. subtilis*, *B. licheniformis,* and *B. pumilus* represent approximately half of the bacterial biocontrol agents present in the market (Ongena and Jacques 2007).

Many soil pathogens are one of the most important factors limiting productivity. Soil pathogens are more dangerous than other diseases and pests, and their control is more difficult. These pathogens can cause serious damage in different parts of the world. For example, fungal and bacterial pathogens caused yield losses of 7–15% in products such as wheat, soybean, corn, which are the most cultivated in the world between 2001 and 2003 (Oerke 2005). It is very difficult to predict the yield losses because of the difficulty of diagnosing the pathogen (Dardanelli et al. 2010).

PGPR's penetrate the rhizosphere of plants, and they destroy the negative effects of nematodes. PGPR-nematode interactions have been studied to control nematodes. It is important to select bacteria that reduce or eliminate the effect of nematodes in plants (Reddy 2016). Beneficial bacteria are reduced to nematode populations by colonizing the plant's rhizosphere.

Agrobacterium, Alcaligenes, *Bacillus, Clostridium, Desulfovibrio, Pseudomonas, Serratia* and *Streptomyces* are the important bacteria that reduce or eliminate the population of nematode (Reddy 2016). PGPR's also provide systemic resistance to nematode pests. Although the use of PGPR against nematodes is limited, successful results have been obtained from studies on the patato cystic nematode (Sikora 1992).

The use of PGPR against to insects has been a subject of limited study. Bacterial pathogens of insects and the majority of related taxa are found in the Bacillaceae, Pseudomonadaceae, Enterobacteriaceae, Streptococcaceae and Micrococcaceae families (Reddy 2016). Most of these bacteria are toxic and very few have a lethal effect, and often expose insects to environmental stress and slow their growth and development.

Cucurbitaceae is a large family that is consumed as vegetables and has economic importance in the world. Ecological and biotic factors caused the biggest yield losses in cucurbit crops. In cucurbit production, pests and diseases are the preliminary important factors which have negative effects on productivity. In squash *Didymella bryoniae* (Black Rot), *Meloidogyne javanica*, and Root Rot/Wilt, *Macrophomina phaseolina*, *Fusarium oxysporum*, *F. solani* (Root-Knot Nematode), in cucumber, *Pythium* sp. (Damping-Off), *Colletotrichum orbiculare*, *C. lagenarium (*Anthracnose*), F. oxysporum* f. sp. *cucumerinum (*Fusarium Wilt*), Erwinia Tracheiphila (*Bacterial Wilt*), P. syringae* pv. *Lachrymans (*Angular Leaf Spot*),* Cucumber Mosaic Virus (CMV), *Meloidogyne* spp. (Root-Knot Nematodes), *Acalymma vittatum*; Spotted Cucumber Beetle, *Diabrotica undecimpunctata (*Striped Cucumber Beetle*),* in watermelon *F. oxysporum* f. sp. *niveum (*Fusarium Wilt*),* Watermelon Mosaic Virus, *Meloidogyne javanica* and Wilt, *Fusarium solani* Disease Complex (Root-Knot Nematode), in melon *Fusarium oxysporum* f. sp. *melonis (*Fusarium Wilt*)* are the important pests and diseases (Reddy 2016). The successful reports have been reported in cucumber (*Pseudomonas* spp., *Bacillus* spp., *Flavomonas oryzihabitans, S. marcescens, Klebsiella pneumonia, Stenotrophomonas maltophilia, Flavomonas oryzihabitans*), in watermelon (*Pseudomonas* spp., *P. polymyxa,* and *Trichoderma harzianum*), in melon (*Pseudomonas* spp. and *Bacillus* spp.) and in squash (*Bacillus* spp.) (Table 4.4).

4.7 The Future Perspectives of PGPR's in Cucurbits

In today's agricultural perspective, increasing the productivity of the unit area as well as cultivating healthy crop is one of the most important issues. For this reason, PGPR's applications are a current and important issue and are the priority areas in

Table 4.4 Effect of different PGPRs on cucurbit species in biotic stress conditions

Plant species	PGPR	Diseases	References
Cucumber	*P.* WB1, Wb15, Wb52	*Pythium ultinum* *Rhizoctonia solani*	Arndt et al. (1998)
Cucumber	*B. subtilis,* *P. fluorescens,* *A. chroococcum* sp.	*Cucumber mosaic cucumovirus*	El-Borollosy and Oraby (2012)
Cucumber	*B. pumilus* INR-7 *Flavomonas oryzihabitans* INR-5	*Diabrotica undecimpunctata howardi* Barber	Zehnder et al. (1997)
Cucumber	*B. subtilis,* *B. amyloliquefaciens,* *P. aeruginosa,*	*Pythium aphanidermatum*	Elazzazy et al. (2012)
Cucumber	*B. polymixa,* *P. fluorescens*,	Squash mosaic virus	Firmansyah (2017)
Cucumber	*P. putida* BTP1, M3	*P. aphanidermatum*	Ongena et al. (2000)
Cucumber	*P. putida* strain 18/1 K, *S. marcescens* strain 62	*F. oxysporum f.* sp. *cucumerinum*	Gül et al. (2013)
Cucumber	*A. brasilense SBR,* *A. chroococcum ZCR,* *Klebsiella pneumoneae KPR,*	*F. oxysporum f.* sp. *lycopersici,* *R. solani,* *Pythium* sp.,	Hassouna et al. (1998)
Cucumber	New strains of *P. stutzeri*, *B. subtilis*, *Stenotrophomonas maltophilia,* *B. amyloliquefaciens*.	*P. crown*	Islam et al. (2016)
Cucumber	*S. marcescens* (90-166), *P. fluorescens* (89B61)	*Colletotrichum orbiculare*	Jeun et al. (2004)
Cucumber	*P. fluorescens* (isolate 9A-14), *Pseudomonas* sp. (isolate 8D-45), *B. subtilis* (isolate 8B-1).	*P. ultimum*	Khabbaz and Abbasi (2013)
Cucumber	*P. putida* strain 89B-61, *S. marcesens* strain 90-166, *F. oryzihabitans* strain INR-5, *B. pumilis* strain INR-7.	*Erwinia tracheiphila*	Zehnder et al. (2001)
Cucumber	*P. putida* 89B-27 *S. marcescens* 90-166	*F. oxysporum f.* sp. *cucumerinum*	Liu et al. (1995)
Cucumber	*P. fluorescens* *P. corrugata* *S. plymuthica*	*P. aphanidermatum*	McCullagh et al. (1996)
Cucumber	*P. fluorescens*, *B. subtilis*, *Rhizobium* sp., *Trichoderma harzianum* *T. viride*	*F. oxysporum f.* sp. *cucumerinum*	El-Sharkawy et al. (2015)

(continued)

Table 4.4 (continued)

Plant species	PGPR	Diseases	References
Cucumber	*B. pumilus* INR7, *B. subtilis* GB03, *Curtobacterium flaccumfaciens* ME1	*Colletotrichum orbiculare, P. syringae pv. lachrymans, Erwinia tracheiphila*	Raupach and Kloepper (1998)
Cucumber	*B. subtilis* B4	*Colletotrichum orbiculare*	Park et al. (2013)
Watermelon	*P. aeruginosa* 231-1	*Didymella bryoniae*	Nga et al. (2010)
Watermelon	*P. aeruginosa* 231-1	*F. oxysporum f.* sp. *niveum Didymella bryoniae*	Nga et al. (2013)
Watermelon	*P. fluorescens*	*F. oxysporum f.* sp. *niveum*	Salman et al. (2017)
Watermelon	*P. polymyxa Trichoderma harzianum*	*F. oxysporum f.* sp. *niveum.*	Wu et al. (2009)
Watermelon	*P. fluorescens* WR8-3, WR9-11 *P. putida* WR9-16	*Didymella byroniae*	Lee et al. (2001)
Melon	*P. fluorescens*	C. mosaic virus	Al-ani and Adhab (2012)
Melon	*Pseudomonas* spp. *Bacillus* spp.	Powdery mildew	García-Gutiérrez et al. (2009)
Melon	*B. subtilis* UMAF6614, UMAF6639 *B. cereus* UMAF8564, *P. fluorescens* strains, UMAF6031, UMAF6033	Powdery mildew	García-Gutiérrez et al. (2012)
Melon	*Bacillus* sp. RAB9	*Acidovorax citrulli*	Medeiros et al. (2009)
Squash	*B. macauensis* (SE52, SE76, INR7, IN937a, and IN937b)	*P. capsici*	Zhang et al. (2010)
Squash	*B.* IN937b	*P. capsici*	Mo (2013)
Pumpkin	*B. subtilis, B. pumilus,*	Watermelon mosaic potyvirus	Elbeshehy et al. (2015)
Watermelon and Melon	*C. flaccumfaciens, Microbacterium oxydans, P. oryzihabitans*, *P. fluorescens*	*A. citrulli*	Horuz and Aysan (2016)

new agricultural research which are increasing our knowledge of plant-bacterial interactions that take place in the root zone of the plant will allow us to develop molecular and biotechnological approaches to achieve integrated management of microorganisms in the soil (Gouda et al. 2018). PGPR's are also utilized as an important key factor for agricultural sustainability and eco-friendly vegetable production, worldwide. In this sense, PGPR's, PGPR strains and their combinations (multi-strain or combined inoculants) with or without commercial fertilizers have shown great advantages for both farmers and researchers. In spite of PGPR's have

multi-way advantages, their performances are not clear under open field conditions. Because of numerous researches about PGPR's were examined under laboratory or controlled greenhouse. Hence, PGPR's should be experienced in large areas with multiple effects to determine the compatibility and interaction among the PGPR's, plants and the other microbial organisms. Thus, appropriate combinations and multiple applications of PGPR's will be clarified and recommended for local production in larger areas. Because of, appropriate PGPR strain for each different production area and extreme conditions should be determined due to complex environmental interaction. Additionally, it will become more important in the context of global climate change.

The cost of PGPR's in larger areas is the other important point for widespread applications. Within sustainable agriculture and eco-friendly production, PGPR's should be available easily and cheaply. Molecular biology and biotechnology may be a solution to generating low-priced and specialized PGPR strains with a different formulation. Nevertheless, in environmentalist approach, transgenic technology has a series problem such as bio-safety and phytotoxicity.

In respect to Cucurbit crops, application methods of PGPRs (such as seeds, roots, leaves), application periods (such as seedlings, flowering) and put on the market are important issues. PGPRs, which give positive results in many studies, have not been actualized on as bio-fertilizer. A number of studies have been conducted on the effects of PGPRs on plant growth, flowering, and fruit quality. When the studies are examined, most of the works about yield and quality are concentrated on cucumber and squash in cucurbit crops. Limited works have been realized on the other important cucurbits such as melon and watermelon. It is important to conduct PGPR studies on these species which are widely cultivated on open field conditions in the world.

A number of studies have been conducted on the effects of PGPRs on nitrogen and phosphorus uptake from soil. However, there is not much work on potassium uptake and mechanisms in the soil. It is obviously sad that this nutrient element which is important for plant development will be subject to the future-day's research. Investigation of the effects of PGPRs on nutrient uptake in watermelon and melon is one of the important issues.

Understanding the mechanisms of abiotic stresses expressed by multiple genes and causing adverse effects on plants is an important issue. Molecular and biotechnological approaches have been included in current work in order to reveal the genetic structure of these mechanisms. It will be possible to develop more effective PGPR's for abiotic stress conditions in future studies by the introduction of genetic expressions of bacteria. Limited works have been conducted on PGPR application in cucumber, watermelon, and squash, on the other hand, there is not any study in melon. Moreover, determination of bacteria that increase in plant growth against salt stress is an important topic for cucurbit species grown under protected areas. In addition, studies on other abiotic stress conditions are very limited, and it is thought that working with other stresses will be increased in day by day. When PGPR's were started to be used in agriculture, they increased in plant growth and productivity while decreased in the effect of diseases and pests

(Gerhardson 2002; Reddy 2016). In cucurbits, there has been a lot of work on this subject, especially in the cucumber.

Cucurbits are more susceptible to phytopathogens than many plant species due to having more sensitive root structure and grown under optimal conditions where diseases and pests develop. Apart from fungal pathogens, insect damage is one of the other important points should be worked on.

4.8 Conclusion

The most important factors affecting on agricultural cultivation is ecological conditions. To feed the population of the world, the effects of bacteria on increasing in plant growth and yield, and also the relationship between bacteria and plants should be examined. The yield of the plants should be increased in the feeding of the population. Biotic and abiotic agricultural areas are getting an increase in the world and chemical fertilizers applied the area may cause economically important problems in agriculture area and health problems in the world. Because of the reason, uses of PGPR's containing beneficial microorganisms instead of inorganic chemicals are positively known to effect on plant growth in terms of supplying of plant nutrients and may help to sustain human and environmental health and soil productivity. A number of inoculated bacterial species mostly associated with the plant rhizosphere in laboratory conditions have been tested and determined to be beneficial for plant growth, yield and crop quality so far. But, it is necessary to know PGPR's effects on field conditions.

The effects of PGPR's on yield, plant growth, quality, uptake of mineral elements, biotic and abiotic stresses in Cucurbits especially cucumber and squash have been studied so far. However, not much is known about promoting effects of PGPR's on yield, growth and nutrient contents of melon and watermelon vegetable species. The species should be evaluated in terms of effecting of PGPR's.

Nowadays, biotic and abiotic stress conditions in agricultural area have restricted the agricultural management. While there are adequate studies on biotic stress conditions, there is limited study on abiotic stress conditions in cucurbits. Especially, it is very important to know the effects of PGPR's on arid and salinity soil conditions.

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Chapter 5
Harnessing Beneficial *Bacillus* in Productivity Improvement of Food Security Crops of Himalayan Agro-Climatic Zones

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Abstract Food security is a burning problem before scientists, which mainly concern with the scarcity and accessible food for all. Scientists are ever-involved to find-out the solutions to overcome on these hurdles, majorly by boosting soil fertility. Over the last 20 to 30 years, the role of soil microbiome in the improvement of soil fertility and crop productivity by involving role of the microbial life has been emerged sustain and facilitated soil nutrients availability to the plants. The microbial life as the great engines enriching soil and helping to facilitate the breakdown of organic matter, that can be recycled into new life, if only they could be unlocked from that organic matter and also, from the mineral matter. The microbes, especially endospore forming *Bacilli* are incredibly important in the

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rhizosphere. *Bacillus* is a versatile candidate providing its services in plant growth and health promotion tirelessly. This aerobic microorganism is powered with super abilities to produce endospore resting fruiting bodies, whenever it feels unhappy under adversity. *Bacillus* is also known for its several characteristics, to help crop plants by virtue of producing metabolites similar to plant in the form of phyto-hormones. Besides, it is able to mineralize rocks and minerals into bio-available form and can metabolize organic matter into much simpler forms. Plant pumps huge amount of sugar and other organic matter in the soil through roots, which attract bacteria to fasten their growth on spent of these supplements. In addition, *Bacillus* is known to produce sort of secretions of which assist in root colonization due to rhizo-competence on root surface and sometimes invade in root cells. In this chapter, we have reviewed the benefits of *Bacillus* species to the food security crops in term of raising productivity and yield.

Keywords *Bacillus* · Food security · *Eleusine coracona* · *Amaranth* · Buckwheat

5.1 Introduction

Mankind is practicing agriculture since time immemorial for their survival and proliferation on earth. However, due to ever increasing population and depleting amount of food raised an alarming situation. This situation can be revised looking in thorough history of agricultural revolutions. Presently, the agricultural fields being fertilized abundantly with pesticides and agrochemicals that were began in nineteenth and twentieth centuries. Initially, the application of agrochemical had shown quantum jump in crop productivity but later, with the rapid technological evolution and un-precedent application of increased dose of fertilizers declined in fertility indices of soil. This not only increased the soil toxicity, but also increased the financial un-sustainability of farmers especially in Asia. Hence, application of chemicals is no more a solution for sustainable crop production. It is accounted that around 870 million populations are under hunger-stricken slab due to severe scarcities of accessible food and FAO in 2012 putted several reports addressed the need to increase the agriculture production by 60% to plateauing food production corresponding to population blast, which is roughly estimated to reach about 9 billion by 2050.

In the present scenario, farmers have blind reliance on the use of chemical fertilizers and pesticides, which not only depleting nutrition index in crops but also affecting microscopic life of soil. Across the globe, governments are now discouraging farmers for the use the chemical fertilizers and pesticides in agriculture production. To sort this matter, farmers have to raise trend of organic crop production and their alternatives specifically, the use of beneficial microorganisms. Actually, earlier, it was not believed that microbial lives in the soil can naturally regulates the ecology of soil and provide plenty and sustained nutrients for crop health and growth. But, now at this diaspora, to obviate these problems, it has

become an indispensable need to administer such methods of farming which are ecologically compatible, holistic and organic in nature. Sustainable approaches in agricultural sector are of utmost importance to improve the food security and nutrition problem around the globe (Arora 2018).

Looking to the history, the very first microbe as the fertilizer was symbiotic nitrogen fixing strain of rhizobia that was patented in the year 1896 under the brand name "Nitragin" for 17 different leguminous plants. Evolution in the knowledge about the role of microbes in agriculture resulted over 2000 tons of rhizobia based inoculants production in the recent scenario which is increasing exponentially and regressed in market size to be reached around 13.25% (annual growth rate) by the year 2020. On the other hand, the microbe-based inoculants are lower in cost, protect indigenous flora and fauna and other natural resources, have less or no harmful byproducts, improve soil organic matter and above all, maintain sustainability of ecosystems (Arora 2018). At present we know that biological alternatives are the only ways to save planet Earth from the abusive chemical fertilizers entering in our food chain and causing serious health hazards to mankind.

Food security and climate change are emerging issues all over the world and consequently resulting serious influence on crop production in general and pressure for higher production of major cereal crops in particular (Asseng et al. 2013; Springmann et al. 2016). The major crops such as rice, wheat, and maize are cultivating to mitigate food demand since a decade besides, over-looked cultivation of other crops such as millets bearing rich amount of nutrients, i.e. essential amino acids, vitamins, minerals etc. is an another cause of nutrient deficiency and malnutrition especially in children (Gundersen and Ziliak 2015).

Cultivation of major crops due to their high demand (domestic as well as industrial) and good economic value, the other nutritional crops has attracted less attention after evergreen revolution (Swaminathan et al. 1998). The marginalized and poor farmers of India, particularly in remote area(s) of hill districts lies in the provinces of Kumaun and Garhwal of Indian Himalaya are deprived of procuring better seeds and practices for raising the crop yield.

In the geographical point of view, the mighty Himalaya is a scenic beauty of diverse ecosystems and eco-regions, including different forest types and eco-agriculture regions at distinct elevation bands. Majorly, the Himalayan subtropical covers approximately 3,000 km pine forests. Moreover, it expenses into broadleaf forests covering an area of 38,000 km^2. It is also coincide with Western Himalaya covering subalpine conifer forests and appear as temperate forests. The temperate forests in the eastern Himalayas also include broadleaf forests, subalpine conifer forests, Northern Triangle temperate forests, and Northeastern Himalayan subalpine conifer forests. Thus, Himalaya itself enunciates its wealth in biodiversity to emerge as hotspots on the world's chart and offer a haven for endemic plants and animals. On the other hand, The Himalayan terrains also have significant agro-climatic zone suitable for the cultivation of range of crops and cultivars in relatively less area available for the cultivation of agricultural crops.

Biogeography of Uttarakhand Hills in India differs from plain especially to the concern of topography, elevation, geographical features, diversity of habitats for flora and fauna, ethnic diversity, land use system and socio-economic conditions. Mehta et al. (2010) stated the productivity of cereals, oilseed crop, millets and vegetables is major hindrance in the food security of the region. Bungla et al. (2012) stated, among the diverse food and staple crops grown in Uttarakhand region *Mandua* (local name) or *Ragi* (commercial name) may act as an alternative of wheat. Mehta et al. (2010) underpin several non-conventional but ethnic crops in food security. According to National Food Security Mission (NFSM 2012) and clause of Food Security Bill (NFSB 2013), several native crops of Himalayan provinces comes under food security and, therefore, essential to be considered for increase their production and productivity using microbial life back into course of fertilization and plant growth improvement.

To mitigate the hurdles of productivity with the benign use of microbes in general and aerobic endospore forming *Bacillus* in particular improvements in soil nutritional indices and soil fertility is needed, thereby stated that there are certain crops which are nutritionally rich but neglected by the farmers. Such crops are defined as "Underutilized crops" which include grain amaranth, barley, ragi, sorghum, buckwheat, barnyard millet, etc., growing in agricultural belts of mighty Himalaya covering the Garhwal ranges of Himalaya. This review is focused to assign the introduction to inoculants of crops, economic importance, productivity status, and current advancement of use of *Bacillus* for raising these valuable crops in a package. These further extend the horizons to address the hurdles of cultivating "Food Security" on higher altitude of agricultural lands. The review is outlined to explore the current prospects and scenario of using beneficial soil inhabiting "*Bacilli*" to the food security crops for enhancement of production enhancement.

5.2 Need of Crop Productivity Improvement

As earlier, the sound problems of agriculture in the means yet to meet the challenges of food requirements of the burgeoning population and plateauing productivity of agricultural lands persuade via adopting "Ever-sustained Green Revolution". The major crop such as rice and wheat were largely and adaptively cultivated on the call of green revolution (Swaminathan 2006) but now, found no more sustainable to mitigate food demand and affordable agriculture, besides hitting back the fertility of soil. Since, these crops are staple food, scientists coming across the world have paid ultimate attention to enhance the production of rice and wheat. Magkos et al. (2003) stated that most of these crops possess less amounts of essential nutrients such as amino acids, vitamins, minerals, etc., thus do not meet out the complete nutrition requirement for a healthy life.

On the other hand, Blum and Bartha (1980) mentioned that the chemicals such as pesticides and fertilizers got accumulated in the ecosystem and consequently enter in the food chain, when used in high doses in order to raise disease free crops.

The pesticides once escaped in the environment influence soil and climatic factors according to their half-life, amounts applied and physicochemical reactions with the existing minerals of the soil (Navarro et al. 2007). Pesticide residues have been detected from various leafy vegetables including spinach, fenugreek, mustard and cabbage ($\sim$21.5 ppm), tomato ($\sim$17.5 ppm), cauliflower ($\sim$1.70 ppm), etc., which unfortunately are above the maximum acceptable daily intake (ADI) as prescribed by WHO in India (Bakore et al. 2002). The subsequent investigation revealed the presence of significant amounts of pesticide residues in the ground water resources and trophic levels at a magnitude (Maloney 2001). Chauhan and Singhal (2006) examined these residual chemicals and reported mutations in chromosomes of humans, animals and thereby inducing carcinoma of lung and liver. The harmful effect of such chemicals in ground water, and agricultural products have been discussed in various studies elaborating agriculture-environment relationship (Eser and Geçit 2010; Meena et al. 2016a, b; Chandra et al. 2018). Majorly, under-utilized crops including amaranth (*Amaranthus hypochondriacus*), barley (*Hordeum vulgare*), buckwheat (*Fagopyrum esculentum*), finger millet (*Eleusine coracana*), and barnyard millet (*Echinochloa frumentacea*) enriched with plenty essential nutrients so as to complete a balanced food and can be used to accomplish the escalating food requirement (Mayes et al. 2011).

5.2.1 Solution(s) for Enhancement of Crop Productivity

The harmful effect of agrochemicals as a concern among the scientific community and also provoked to search other avenue so as to earn better productivity. One of the eco-friendly and cost effective approaches is the use of beneficial group of bacteria such as plant growth promoting rhizobacteria (PGPR) as a bio-fertilizer and biocontrol agents to reduce crop losses and enhance crop productivity and soil fertility. Along with plant growth promotion they reforest eroded areas, restored the contaminated sites and thereby cause positive effect on degraded ecosystem (Gupta et al. 2015). These PGPR seemed as successful bacteria in getting established in soil ecosystem due to their high adaptability in a wide variety of environments, faster growth rate and biochemical versatility to metabolize a wide range of natural and xenobiotic compounds. Several worker have earlier studied that in the rhizosphere ecology, plant growth promoting rhizobacteria (PGPR) enhance plant growth by a wide variety of functions like biological nitrogen fixation, phytohormone production, phosphate solubilization, siderophore production, 1-Aminocyclopropane-1-carboxylate deaminase production (ACC), exhibiting antifungal activity due to the secretion of chitinolytic enzymes and production of volatile organic compounds (VOCs), promoting beneficial plant-microbe symbiosis, interference with pathogen toxin production, etc. (Nelson 2004; Babalola 2010; Bhattacharya and Jha 2012; Kundan et al. 2015; Prasad et al. 2015; Maheshwari 2010, 2011a, b, c, 2015; Goswami et al. 2016). Successful studies using PGPR on the growth enhancement of various crops have been achieved in laboratory and field conditions (Gray and

Smith. 2005; Agarwal et al. 2017). In the recent scenario, harnessing the benefits of PGPR exhibited quite interesting to unlock new horizons of sustainable agriculture (Maheshwari et al. 2013).

To overcome these situations, there is a need to develop eco-friendly and cost-effective microbial inoculants which may be withstand in the extreme environmental conditions of Himalayas. In Himalayan hills, soil temperature remains low (6–25 °C), during different cropping seasons. Few other stresses such as water-deficit and salinity stress also impose serious impact on morphology and physiology of plants in the mighty Himalaya. PGPB are known to improve crop health even at low soil temperature (Mishra et al. 2012) and the survival of the endospore forming *Bacilli* at different temperatures makes them suitable candidates for enhancement of vegetative and reproductive plant growth even in adverse conditions of Himalayan hills. Various workers across the globe stated that these bacteria are well known for their beneficial effect on different host plant (Schroth and Kloepper 1978; Glick 1995; Gray and Smith 2005; Yadav et al. 2014; Maheshwari et al. 2015a, b; Agarwal et al. 2017; Gouda et al. 2017).

As stated, PGPR ameliorate plant health and productivity by enhancing the nutrient status of soil and host plants subsequently (Dey et al. 2004). The bioavailability of nutrients, their increased uptake may significantly enhance the nutrient use efficiency of plants. Increased solubilization of nutrients (macro and micro) by PGPBs enhanced their uptake and accumulation in grain amaranth (Parmar and Patel 2009). Nutrient availability has been influenced by solubilization, chelation and oxidation–reduction reaction in soil (de Santiago et al. 2011).

The plant growth significantly influenced by the micronutrients along with the macronutrients supported metabolic and enzymatic activities in plant. Application of PGPR has been reported as an effective approach under field conditions in the management of plant diseases (Siddiqui and Akhtar 2009; Beneduzi et al. 2012; Kumar et al. 2012a, b). PGPR such as *Bacillus*, has been reported for crop production of few food security crops such as *Eleusine coracana*, *Fagopyrum esculentum* Moench. (Agarwal et al. 2017), *Amaranthus hypocondriacus* (Pandey et al. 2018).

5.3 Food Security Crops

Cultivation of food security crops offering a solution to maintain a sustainable production of indigenous crops that are overlooked in recent scenario or suffering with productivity loss. Most of the nutritional crop varieties are not been cultivated widely in entire globe and thus, meets shortage of access to the consumers, and hence been considering under food security. It is an urgency to mitigate the health problems of human race with organic crop production and improve financial state of farmers especially in developing countries of Asia to revitalize agricultural sustainability. Few of them are below:

5.3.1 *Buckwheat (*Fagopyrum esculemtum *Moench)*

Buckwheat belongs to the dicot family Polygonaceae also known as 'Japanese buckwheat' and 'silverhull buckwheat'. It is widely cultivated in the Himalayas as staple grain crop. Buckwheat is not related to wheat, despite of its name. The name 'buckwheat' or 'beech wheat' understands its triangular seeds shape. It is a translation of Middle Dutch boecweite. Beside this, buckwheat is also related to knotweed, sorrel, and rhubarb. The seeds of buckwheat and its floor are consumed due to its richness with carbohydrates, protein and fiber, therefore, it is also referred to as a pseudocereal.

Buckwheat contains 9–13% crude fat and 2–2.7% ash (Thakur et al. 2016), 57.9–103.4 mg/g N methionine content, 62.2–79.2 mg/g tryptophan etc. (Dogra 2010). It can be cultivated in moist soil to semi-dry soil as its branching root system has profused penetration power to reaches deeply into the soil (Stone 1906). It produces white and pink flowers as per plant variety (Li and Zhang 2001). Buckwheat plant has more complete adaptations of environment due to their ability of producing suckers (vegetative growth) but, sometimes reduce productivity (Stone 1906). The seed hull density is less than that of water, making the hull easy to remove (Li and Zhang 2001).

5.3.1.1 Economic and Nutritional Importance

The buckwheat is a short-term crop having importance due to nutritional profile that contains high amount of protein, amino acids vitamins, starch, minerals, dietary fiber and a plenty source of gluten-free diet for celiac disease patients, Sedej et al. (2011), Wronkowska et al. (2010). It is sometimes also used as silage or manure..

Buckwheat is a trustworthy cover crop during summer as it quickly establishes defence mechanisms to cope temperature changes (Björk et al. 2008). The harvesting period is observed from 10–12 weeks especially at high latitude to grow it up to 30–50 inches (75–125 cm) tall.

Being an important functional food, cultivated various polyphenols (Luthar 1992), proteins with high biological value and balanced amino acid composition (Eggum et al. 1980, Ikeda et al. 1986, Kayashita et al. 1999, Liu et al. 2001 and Tomotake et al. 2000), relatively high fiber content (Bonafaccia et al. 2003 and Steadman et al. 2001), retrograded starch in groat products (Skrabanja and Kreft 1998; Skrabanja et al. 2001; Kreft and Skrabanja 2002), high contents of available zinc, copper, and manganese (Ikeda et al. 1990, Ikeda and Yamaguchi 1993 and Ikeda and Yamashita 1994) and dietary selenium (Stibilj et al. 2004) proved its significance in modern world.

On the other hand, it also contains some anti-nutritional factors. Allergenic reactions occurred due to ingesting buckwheat and its products or by exposure to buckwheat dust. The hypersensitive symptoms involve asthma and asthmatic attacks, urticaria, and gastrointestinal disorders (Li and Zhang 2001 and Wieslander

and Norback 2001). As buckwheat does not contain gluten, it is a common supplement for patients with coeliac disease. Buckwheat intolerance is rare among patients with gluten intolerance alone, but more common in those with coeliac disease combined with other food allergies. Allergic reactions are caused by ingestion of allergenic buckwheat proteins (Wieslander and Norback 2001). Ingestion of the entire plant can cause serious photosensitization. Phototoxity of fagopyrin is connected with sensitivity to ultraviolet rays (Li & Zhang 2001). Polyphenols in buckwheat may also inhibit the action of certain enzymes (Eggum et al. 1980).

Basically, flour and groats dishes are generally used to prepare from buckwheat seeds. The buckwheat noodles are more often popular in Asian countries like China and Japan. The buckwheat is rich with plenty amount of rutin as one of the important cause for the desired production. The tartary buckwheat (*Fagopyrum tataricum* Gaertn.) is another variety which has higher amount of rutin than other variety of buckwheat (Suzuki et al. 2002). Few other commercially important products are prepared by buckwheat includes floral honey (Nagai et al. 2011), green tea (Paradkar and Irudayaraj 2002), buckwheat sprouts, vinegar, beer, and spirit irrespective to use as vegetable in some Asian countries such as India, Pakistan, China, and Japan.

In summarizing as nutritious crop, it consists of 25% starch, 75% amylose and amylopectin. It is riched with crude proteins of 18% and the high concentration of all essential amino acids especially lysine, threonine, tryptophan, and the sulfur-containing amino acids. Minerals like iron, zinc, selenium are importantly found in seeds additionally it has antioxidants properties with due to rutin average 10–200 ppm and fagopyrin range 0.4–0.6 mg/g of flour. Aromatic compound like salicylaldehyde has also identified as a characteristic component of buckwheat aroma.

On Hindu fasting days in northern states of India people eat items made of buckwheat flour except eating cereals such as wheat or rice being prohibited. Since, buckwheat is not a cereal, it is considered acceptable for consumption. Buckwheat (Kuttu/Ugal) is an important crop and is commonly cultivated for international trade. Alike, consumption increase the economic value in India and requisite the increase production and productivity. This crop is extensively grown in hilly region of Uttarakhand, especially in province of Garhwal in India. Taking into consideration of such properties present research has foremost emphasizes to develop some bioinoculant, could be used organically grown buckwheat crop having significant in productivity and production.

5.3.1.2 Productivity Enhancement: Status of Use of PGPR

Buckwheat is widely cultivated in several Asian countries in certain European countries. Therefore, buckwheat emerged as important food crop but, productivity observed declined sharply in the twentieth century especially in hilly regions of India beside, its popularity as vegetable and pseudocereals. It is also noted that

Table 5.1 Effect of PGPR and fungal pathogens on plant growth promoting parameters of *Fagopyrum esculentum* (60 DAS) (Adopted from Agarwal et al. 2017)

Treatment	Seed Germination (%)	Length (cm)		Fresh wt. (mg)		Dry wt. (mg)		Disease Index (DI)
		Root	Shoot	Root	Shoot	Root	Shoot	
B. pumilus MSUA3	93.5	4.550**	13.480**	0.258**	2.087**	0.034**	0.212**	0
R. solani + *B. pumilus* MSUA3	72.0	3.897**	11.206**	0.216**	1.947**	0.028**	0.182**	20.0
F. oxysporum + *B. pumilus* MSUA3	61.7	2.583**	7.917**	0.194**	1.413**	0.019**	0.136**	20.0
F. oxysporum	10	1.140**	3.820**	0.044**	0.867**	0.003**	0.017**	90.0
R. solani	12	1.118**	3.112**	0.054**	0.756**	0.004**	0.014**	90.0
Control	65.0	2.613	10.153	0.192	1.890	0.023	0.165	

Values are mean of ten replicates; Analysis of Variance (ANOVA): [a] = significant at 0.01 level of lowest standard deviation (LSD) as compared to control; [**] = Significant at 0.01 level of LSD as compared to control; [*] = Significant at 0.05 level of LSD as compared to control; [ns] = Not Significant at 0.05 level of LSD as compared to control. None of the value in ANOVA were observed significant at 0.01 level (a), at 0.05 level (*) and not significant (ns)

people colonized in hilly regions with the adoption of fertilizer in farming experienced decreased in net productivity of other staples also. Irrespective to this, when this is compared with the other cereals, seed yield of *F. esculentum* is often relatively low without adding fertilizers (Dogra 2010). Low productivity is mainly due to abortive fertilization and several other physiological factors such as self-incompatibility based dimorphic heterostylism, underdeveloped female reproductive organs, and kernel development in the early stage of embryo development (Kumar et al. 2002). The fungal diseases in the buckwheat are also observed as detrimental factor for productivity loss beside, buckwheat itself has significant metabolite with the ability of biocontrol of fungal pathogens. However, not reviewed extensively after Sidorova (1963).

If the crop becomes susceptible, the standing crop suffers from 50% loss due to infection of fungal pathogens, *Fusarium oxysporum* and *Rhizoctonia solani* causing wilting and root rot diseases respectively (Nyvall 1989; Huang et al. 2015). To combat these pathogens in an eco-friendly manner beneficial *Bacillus* spp. of native soil was devised to mitigate the harmful effect of both the pathogens (Agarwal et al. 2017). Biocontrol agents in carrier-based inoculant (vermiculite) were observed suitable in enhancing the yield (Table 5.1; Fig. 5.1).

*5.3.2 Ragi (*Eleusine coracana)

Eleusine coracana L. (Moench.) (Commercial name: Ragi; Common/local name: Mandua) belongs to family Poaceae. Ragi is a significant food crop and world-wide known with several names (Table 5.2). Ragi (Finger millet) is important as food grain and source of straw. It is very nutritious abundant protein, minerals, fibers,

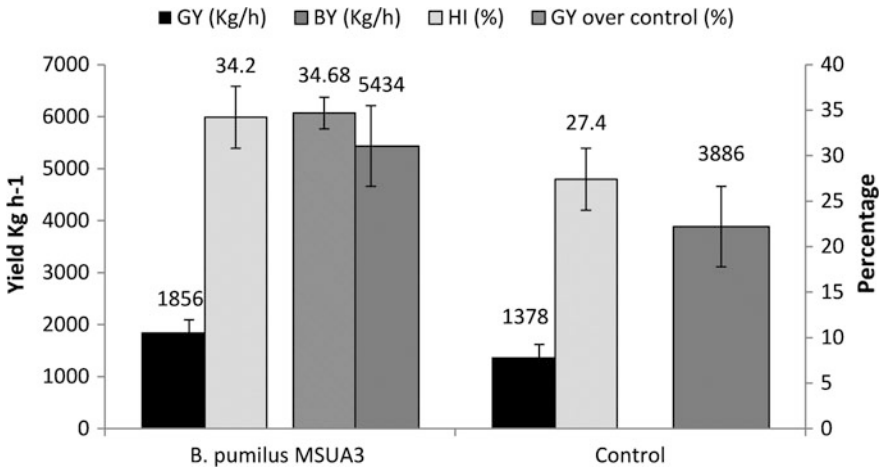

Fig. 5.1 Yield and biocontrol parameters of *Fagopyrum esculetnum* at harvesting (Abbreviation: GY = Grain yield, BY = Biological yield, HI = Harvest Index; error bar on column represented standard deviation at 0.5%) (Adopted from Agarwal et al. 2017)

Table 5.2 Common name of Ragi in different of the globe

Countries/Languages	Common name
UK	Finger millet, African millet, Ragi, Koracan
France	Eleusine cultivee, Coracan, Koracan
Germany	Fingerhirshe
India	Ragi (Kannada, Telugu), Manduva (North India), Nachani (Marathi)
Kenya	Wimbi, Ugimbi
Nepal	Koddo
Sri Lanka	Kurakkan
Zimbabwe	Rapoko, Zviyo, Njera, Poho

and vitamins along with 8–10 time more carbohydrate than in rice and wheat. Finger millet's has slower digestibility and regarded as storage food. It has unique malting properties so why it is used in variety of food processing like brewing porridge, bread, biscuits, and pudding production.

Among the diverse food and staple crops in Uttarakhand, Himalayan region, the crop is grown for alternative of wheat, locally called Mandua or Ragi (commercial name) and is widely grown in Himalayan region to south coastal region of India. It is invariably adaptable to costal land and higher elevations of Himalaya up to 2,300 m above mean sea level (MSL).

5.3.2.1 Economic and Nutritional Importance

Finger millet (*Eleusine coracana* L.) is an important millet crop cultivated extensively in Asia and Africa and produced as low as ranked sixth after wheat, rice, maize, sorghum, and bajra in India. Anatomically small round-shaped seed are coated with hull. The naked seed has brick red-colored seed coat. It is used as complete meal for chapati and biscuits preparation. As stated earlier it is rich in nutrition with high calcium (344 mg/100 g), phytates (0.48%), polyphenols (0.61%), trypsin and dietary fibers (Brajdes and Vizireanu 2012). The entire seed is edible with its seed coat as rich source of phytochemicals, dietary fiber and polyphenols (0.2–3.0%) (Hadimani and Malleshi 1993; Ramachandra et al. 1977). Earlier Bravo (1998) has reported that phytates, polyphenols, and tannins provides antioxidant activity as a factor to affect health, aging, and metabolism of consumers (Bravo 1998). As per above, it is submitted as same that it is beneficial as antidiabetic, antioxidant and hypocholesterolaemic (Devi et al. 2014). The mixture of benzoic acid and cinnamic acid derivatives as millet polyphenols exhibit enzymatic activities and anti-cataractogenic properties. Finger millet consumption as regular in snacks helps to control diabetes (Devi et al. 2014).

Probably tradition of ragi's cultivation first reached in the south coastal regions of India and subsequently in Himalayan regions which is a hotspot of diversity and distribution (Hilu and Wet De 1976). It (Chandra et al. 2016).

Among the food grain (Maize, Jower, Ragi, Bajra, Small Millets and Barley) its cultivation decreased from 45.9 million hectares in 1970–71 to 24.1 million hectares in 2014–15 and ranked among food security crop as millet crops in the world. Food grain production is increased from 50.83 million tonnes in 2015–16. It is expected to attain higher by 1.14 million tonnes over the production of 252.02 million tonnes during 2018–19 (Economic Survey 2018–19).

5.3.2.2 Productivity Enhancement: Status of Use of PGPR

This crop has low productivity in Himalayan range for fulfillment of food demand in sub-terrain of mountains and Indo-Gangetic population. Thus, it is essential to elicit this hurdle and boost up the production of *E. coracana* using *Bacillus* as beneficial PGPR and enhance the productivity in term of grain yield, biological yield, and harvest index.

Accordingly, soil and climatic condition of Himalayan region as well as in south India, Ragi is season bound crop and the best season for sowing is December–January and June–July. Ragi is adapted to a wide range of environmental adversities, tolerance to a significant level of salinity, relatively resistant to water (Dida et al. 2007). It is a stable diet in many villages across south India, especially in north Karnataka besides Maharashtra and North West zones of Tamil Nadu, India.

Several workers have reported use of diverse *Bacillus* for productivity enhancement of other millet crop belong to family Poeacae such as, *Pennisetum glaucum* (Pearl millet) (Raj et al. 2003) and *Setaria italica* (foxtail millet)

Table 5.3 Yield parameters of *E. coracana* at harvesting (120 DAS). (Unpublished data)

Treatment	1000 seeds weight (gm.)	Shelling percentage	Grain yield (Kg/ hectare)	Biological yield (Kg/ hectare)	Harvest Index (%)	% Grain yield rise over control
T1	1.520 ^{ns}	34.36 ^{ns}	1074 ^{ns}	8430 ^{ns}	12.74 ^{ns}	8.19 ^{ns}
T2	2.056**	49.55**	1481**	10740**	13.78**	33.42**
T3	2.096*	50.22*	1511*	9510*	15.88*	34.74*
T4	1.710*	35.22*	1083*	8540*	12.68*	8.95*
T5	2.124**	51.14**	1522**	10870**	14.00**	35.21**
T6	2.187*	52.35*	1587*	9646*	16.45*	37.87*
Control	1.300	37.82	986	7972	12.36	

Abbreviations: T1 = MSTA8 bacterized seed; T2 = MSTD26 bacterized seed; T3 = MSTA8 + MSTD26 bacterized seed; T4 = bioinoculant of MSTA8; T5 = bioinoculant of MSTD26; T6 = bioinoculant of consortia of MSTA8 and MSTD26; C = Control (non-bacterized seed). Values are mean of ten replicates; Analysis of Variance (ANOVA): ^{a} = significant at 0.01 level of lowest standard deviation (LSD) as compared to control; ** = Significant at 0.01 level of LSD as compared to control; * = Significant at 0.05 level of LSD as compared to control; ^{ns} = Not Significant at 0.05 level of LSD as compared to control

(Khatri et al. 2016). Veer and Goel (2015) have reported increase in plant growth parameters including fresh/dry weight and length of root/shoot but, available literature exhibited the limited information on its cultivation during this era of food security to raise crop productivity using microbial inoculant. However, few publications reported yield improvement using chemical fertilizers as an alternative way to raise crop productivity (Raman et al. 2004; Rangaraj et al. 2007; Bama and Ramakrishnan 2010).

From the author's lab *Bacillus pumilus* MSTA8, *Bacillus amyloliquefaciens* MSTD26 and their consortia (MSTA8 + MSTD26) increased vegetative parameters such as plant length, fresh weight and dry weight with respect to controls. Effects of bioinoculant formulation on harvesting parameters and yield of ragi were recorded higher to that of non-bacterized seeds. During our investigations, an increase in seed yield by 37.87% with 16.45 harvest index over control at 120 DAS was reported (Table 5.3).

*5.3.3 Amaranth (*Amaranthus hypochondriacus)

Among the different underutilized crops grain amaranth (*Amaranthus hypochondriacus*) is one of the important nutritionally rich pseudocereals crop which belongs to the order Caryophillales, Sub-family Amaranthoideae, family Amaranthaceae, Amicarelli and Camaggio (2012), Østerberg et al. (2017), Niranjana and Kumar (2017). The genus *Amaranthus* embraces approximately 60 species and most of them are weeds. Among all, widespread species are *A. hypochondriacus, A.*

cruentus, A. spinosus, A. hybridus, A. tricolor, etc. Amaranth plant has an outward appearance which is having branched inflorescence bearing thousands of minute flowers to set seeds with variable colors for instance cream, golden, pink, and black. Different species of amaranth are used either as leafy vegetable, grain, animal feed, or as ornamentals in different countries. The seeds of amaranth are lenticular and relatively small (Pandey et al. 2013). Grain amaranth is grown worldwide in many countries including Africa, Argentina, China, India, Pakistan, Peru, and USA. However, much variation in the productivity is recorded among the major countries growing amaranth (Chan et al. 2016).

5.3.3.1 Economic Importance

Amaranthus hypochondriacus has gained maximum attention due to its high nutritive value as reported by Raina and Dutta (1992). A very high content of carbohydrates (62–67.9%), fiber (4.9–5%), fat (6.1–7.3%), and protein (15–16.6%) was observed in this crop. Dodok et al. (1997) observed higher (5.95 g/16 gN) lysine content in the amaranth grain in comparison to wheat flour (2.9 g/16 gN). Gorinstein et al. (2002) acquainted grain amaranth as a substitute of conventional cereals due to the presence of high essential and other nutrients. Amino acids (Lysine 5.95%, Histidine 2.5–3%, Tryptophan 0.9–1.8% etc.) in the seeds of amaranth were reported by Písaříková et al. (2005) and Mlakar et al. (2009). Thus, the protein and high essential amino acid contents found in this crop proved to be useful to lessen the scarcity of nutritionally rich food to human beings (De La Rosa et al. 2009; Barrio and Añón 2010). Due to the high nutritive value, nurturing of this nutritive crop suggested to improve food security and to augment farm incomes (Mburu et al. 2012). Sanz-Penella et al. (2013) noted the nutritive value of amaranth seeds as prosperous resource of macro and micronutrients such as iron, calcium, magnesium, zinc, as well as vitamins including riboflavin, ascorbic acid, niacin and thiamine. The amaranth is rich in protein, essential amino acids, vitamins, micronutrients and useful as a medicinal plant to cure various diseases. Recently, Perales-Sánchez et al. (2014) reviewed the antioxidant, anti-allergic properties, plasma cholesterol level decreasing and immunomodulatory abilities of grain amaranth. Several studies have put forward to advocate the quality of amaranth proteins comparable to the optimum protein reference pattern in human diet, and almost reaching the requirements according to the norms given by FAO/WHO (Rastogi and Shukla 2013; Shevkani et al. 2014a, b). Amaranth has high medicinal value, provides vitamin C, purifies blood, soothes cough, and improves general health (Miraj 2016; Shirani et al. 2017). Additionally, being a gluten-free grain, it is suitable for diets of celiac disease patients (Lamacchia et al. 2014; Taylor and Awika 2017). Different compounds such as alkaloids, triterpanoids, anthocyanins, and amaranthine (Castrillón-Arbeláez and Frier 2016; Shirani et al. 2017) are responsible for its beneficial effects. Globulins, albumins, and glutelins are the proteins present in the amaranth seeds with essential amino acids which are deficient in traditional cereals and legumes (Awasthi et al. 2011; Jimenez-Aguilar and

Grusak 2017). Lysine-Methionine richness dwelling gene (*AmA*1) was reported from *Amaranthus* which was successfully used in the development of genetically modified sweet potatoes for enhanced protein quality with balanced amino acid composition.

5.3.3.2 Productivity Enhancement: Status of Use of PGPR

In India, it is cultivated in different regions of Uttarakhand, Himachal Pradesh, and southern parts of Kerala and Tamil Nadu. In most of the areas it is grown as traditional crop but has gained recognition among the farmers in past few decades. Its low cultivation cost, short growth cycle and good adaptability to varied agro-climatic conditions proved its suitability among the farmers. Amaranth seeds are recommended as a health food for feeding children to increase their immunity (Kanensi et al. 2013; Dhangrah et al. 2015). It has significant influence to overcome various ailments/diseases including malnutrition. Amaranth has been called as poor farmer's crop but now attracted attention worldwide due to its high protein and amino acid contents in comparison to maize and wheat (Das 2015).

In India, amaranth is used as an important ingredient in the meal of the people from the entire Himalayan region, and to some extent in the states of Gujarat, Maharashtra, Karnataka, and Eastern parts of Uttar Pradesh. In northern parts, it is regarded as "Holy food" and consumed during ritual fasts where the other cereals and pulses are restricted.

In Uttarakhand, the crop is mostly cultivated in hilly areas. However, its cultivation area (6072 ha) is much lower in comparison to rice (2,73,686 ha), wheat (3,79,196 ha) and maize (28,283 ha) (https://www.agriculture.uk.gov.in). Other than the less market value and low consumption, frequent attack of fungal diseases, pests and insects are responsible for its lower productivity (Kagali et al. 2013; Awurum and Uchegbu. 2013). Since, organic farming in agriculture policy recommends not to use harmful chemicals for raising crop productivity further, due to their toxicity besides deleterious to beneficial microorganisms, undesirable to soil and environment (Glenn et al. 2013; Meena et al. 2016a, b; Mallick et al. 2018). Hence, disease containment through an eco-friendly biocontrol approach, using natural antagonistic microflora, is becoming an inevitable component in the management strategy of plant diseases.

Among the major insects, *Spodoptera litura, Helicoverpa armigera, Hymenia recurvalis, Sylepta derogate, Hypoxilus nubilosus, Epilachnae laterii,* etc., were found most harmful (Sharma 2009; Aderolu et al. 2013). Prior to this study, the lepidopteran insects were reported to cause significant damage in amaranth crop and further two groups of lepidopterans reported to affect and reduce maximum productivity in several countries (Clarke-Harris et al. 2004). The first group of the lepidopteran includes the leafwebbers or webworms which folds their larvae in order to produce web or glue on amaranth leaves and feed within the leaves (Storer et al. 2010) whereas, *Udea ferrugalis, Pterolophia basalis, Herpetogrammabi punctalis* and *Achyrarantalis* considered the second lepidopteran group, belongs to

the family Crambidae reported as the infrequent pests of amaranth (Othim et al. 2018). Their larvae feed on amaranth but unlike webworms they do not glue or fold amaranth leaves. Aderolu et al. (2013) and Mureithi et al. (2017) reported *Spodoptera litura* and *Spodoptera furgiperda* as the major representative of the lepidopteran's group. On the other hand, the great loss in the crop productivity was observed by James et al. (2010) due the frequent attack of other insects. García et al. (2011) reported 92% damage to the *A. hypochondriacus* due to attack of borers and 45% decline was due to white grubs thus; the overall yield was reduced by the other general insects of foliage and soil.

In the accompaniment with insects, different microorganisms, for instance, various fungi have been reported to influence amaranth productivity by causing extensive damage to the crop through tissue discoloration, decay of stems and branches of mature plants. Since decades, *Rhizoctonia solani* has been reported as an eminent causal agent of amaranth (Kamala et al. 1996) and exhibited huge number of symptoms such as light and dark brown spots in stem, necrotic lesions, blister like lesions on the leaves and sheaths. Smitha (2000) observed leaf blight symptoms on the foliage of amaranth with small irregular whitish cream spots on leaves, which enlarged under high humidity. Several other fungi such as *F. oxysporum, F. subglutinans, F. sambucinum, Alternaria solani, Alternaria tenuissima,* etc., were reported as the major pathogens of amaranth (Blodgett et al. 2004). Recently, various workers observed foliar blight disease in amaranth caused by *R. solani* owing to diminished productivity of amaranth in our country (Nair and Anith. 2009).

On the other hand, some other fungi were described as a factor behind the diminished productivity of amaranth. For instance, *Pythium myrlotylum* accounted for causing damping off in different amaranth species including *A. hypochondriacus* (Sealy et al. 1988). Mihail and Champaco (1993) observed death and decay of *A. hypochondriacus* and *A. hybridus* due to the infection of *M. phaseolina* causing green black spots on stems. It was stated that severe pre and post emergence of damping off caused by *P. aphanidermatum* in *A. hypochondriacus* and *A. hybridus* were most common and prevalent diseases affects seed germination and seedling survival. Discoloration of branches, stems, and root collars due to *Fusarium oxysporum, Fusarium subqlultinans, A. tenuissima* were observed antecedently by Blodgett et al. (1998). Further, Blodgett and Swart (2002) noticed dark brown to black, necrotic lesions on the leaves of *A. hybridus* accounted *Alternaria tenuissima* as causative agent. Subsequently, Mandal and Das (2002) observed severe damage as a result of leaf spot disease caused by *A. amaranthi*. It was noted that phytotoxin produced by the *F. oxysporum,* toxic to the seedling and callus growth and thereby caused stem decay and root rot of amaranth (Chen and Swart 2001). Further, Priyadarsini (2003) stated that the symptoms of leaf blight disease of amaranth began as small irregular whitish cream spots on the foliage that enlarged under high humidity. In the later stage, the spots became translucent with irregular brown margins and shot hole was observed in severely infected leaves which finally led to defoliation. On the other hand, Talukder et al. (2012) described defoliation and withering of whole plant of red amaranth due to white rust caused by *Albugo*

occidenta. The agrochemicals were used to restrain these pests and fungi with instant effect, however, their arbitrary use has caused a lot of side effects on human beings (Lawrence et al. 2004, Chaturvedi et al. 2013), soil and environment (Aktar et al. 2009; Tiryaki and Temur 2010) and animals (Odukkathil and Vasudevan. 2013).

5.4 *Bacillus*: The Protagonist of Crop Productivity

Specially aerobic endospore-forming bacteria *Bacillus* (AEFB'B) remain viable in drastic environmental conditions due to dormant body (endospore) which, in favorable condition become viable and showed their finest rhizospheric competence rhizosphere (Kadyan et al. 2013). There are several free-living, associative and symbiotic bacterial genera effectively involved in plant growth promotion. The other important and widely accepted genera are *Acetobacter, Acidovorax, Azorhizobium, Azotobacter, Azospirillum, Beijrenckia, Bradyrhizobium, Burkholderia, Ensifer, Enterobacter, Erwinia, Mesorhizobium, Paenibacillus, Pseudomonas, Rhizobium, Serratia,* etc., have been exploited for growth promotion and suppression of crop diseases (Maheshwari 2016). *Bacillus* such as *Bacillus subtilis*, *B. licheniformis*, *B. polymyxa*, *B. pumilus, B. amyloliquifaciens,* etc., are closely related species having biocontrol potential against different fungal pathogens including *Fusarium oxysporum, Rhizoctonia solani, Sclerotium rolfsii, Macrophomina phaseolina* (Dubey and Gupta 2012; Agarwal et al. 2017). *Bacillus* spp. aggressively colonizes the root system, and exhibited biocontrol and plant growth promoting properties.

Among the PGPR, *Bacillus* genera has predictably immense potential application in term of functionality to raise productivity of crop under field trials (Maheshwari et al. 2013). On the other hand, many regions of Uttarakhand state in India are becoming food insecure today with net sown area, per capita food availability and across to food especially in the hilly districts have been declined. The availability of pulses and cereals has significantly narrowed (Chopra and Pasi 2002). A large number of crops have been introduced in this region by early settlers or civilians those who created a huge diversity of crop for human consumption. In Garhwal Himalaya, average 78–85% population solely depends upon agriculture for their livelihood and 80% of area consists of hills, whereas, remain plain is maximum urban. So, the cereals, pulses, oil-seeds crops and millets grown have low productivity (NFSM 2012). In fact, agricultural production is also affected with climatic and seasonal changes, as in monsoon, flood and landslide are common in Himalaya and in winter snow fall proved deleterious one for various crops (Sharma and Ambili 2009).

Among all endospore-forming *Bacillus* spp. offer several advantages in comparison to that of other beneficial bacteria. These *Bacilli* tolerate adverse conditions including cold temperature and low pH and other abiotic stresses exist in of the high-altitude regions. Diversified populations of aerobic endospore forming species

of *Bacillus* occur in soil, and agricultural fields contributed to crop productivity (Dheeman et al. 2017; Agarwal et al. 2017). Physiological traits, such as multi-layered cell wall, stress resistant endospores formation, secretion of peptide or non-peptide secondary metabolites and extracellular enzymes are ubiquitous to these *Bacilli* make them most suitable to restore benefits to the plants in adverse environmental conditions for extended periods of time. Exploiting these abilities, the bacteria exert and inhabit diverse niches in agro-ecosystems and compete with other microorganisms during plant-microbe interactions. The colonization niches for the bacteria being reproducibly stable are also likely to be used in precision management of agro-ecosystems (Timmusk et al. 2014).

Numerous *Bacillus* species express in promotion of plant growth and suppress soil-borne plant pathogens by three ecological pathways viz., providing nutrients for plant growth promotion (Chauhan et al. 2017), antagonism against fungi, and bacteria, and stimulation of host defence mechanisms (Sharma et al. 2018). Recently, a number of *Bacillus* species have been developed commercially as plant growth promoters and biocontrol agents for their use in agriculture (Muis and Quimio 2016).

Drastic changes in Himalayan region are a problem to sustain crop productivity. The more frequent and intensity of climate cannot be ruled out. Hence, there is always a necessity to overcome these abiotic factors using a technology that address issues of farmers in general and seed industry in particular. One of the possibilities is by using the cold tolerant microbes endowed with the ability to synthesize several cryoprotectant compounds for instance, glycine betaine, glycerol, mannitol, sorbitol, glucose, and fructose to overcome the ill effects of cold temperature induced stress (Angelidis and Smith. 2003). Cold tolerant PGPB were suggested as growth promoter because of their ability to solubilize nutrients which enhanced their bioavailability to the plants (Katiyar and Goel. 2003; Trivedi and Sa. 2008). Rinu and Pandey (2009) conducted field based experiment to evaluate the growth promotion abilities of *Bacillus* for cultivars, i.e., lentil at Himalayan terrain under cold conditions. An increase in protein concentration and yield improvement was reported due to the effect posed by combination of PGPB. Plant growth promoting abilities of *Bacillus megaterium* isolated from the cold region of Himalayan terrains was found pragmatic in the form of bioformulation (Trivedi and Pandey. 2008). Kumar et al. (2013) conducted green-house experiment at 20–25 °C by inoculating phytase producing psychrotolerant *Bacillus* sp. in solubilization of phosphorus in the soil. A significant enhancement in biomass of *Brassica juncea* was reported in such condition. Sati et al. (2013) advocated the use of psychrotolerant PGPBs for the growth promotion and productivity enhancement of crops especially in the low temperature environments. Growth promotion of *Cicer arietinum* (L.), *Vigna mungo* (L.) Hepper, *Vigna radiata* (L.) Wilczek, *Cajanus cajan* (L.) Mill sp. and *Eleusine coracona* (L.) Gaertn. at 28 °C was due to the increased uptake of N and P by psychrotolerant *Pseudomonas jesenii* strain MP1 (Kumar et al. 2014). Kaur et al. (2015) observed increased seedling parameters of i.e. lentil with increase in productivity by the inoculation of psychrotolerant *Rhizobium* and other PGPRs

Several other workers have also observed biocontrol activities of *Bacillus* spp. against many common fungal phytopathogens (Kadaikunnan et al. 2015; Zohora et al. 2016; Abdallah et al. 2018). Diverse populations provide better resources for the improvement of plant growth promotion and biocontrol abilities, as different strains possess varied mode of action and survival in extreme environmental conditions. Since, climatic conditions may affect their potential, it is imperative to isolate native *Bacilli* strains from the soils having PGP activity that could influence the crop.

Bacillus spp. considered as the safe microorganisms that hold remarkable abilities for synthesizing a vast array of beneficial substances for the suppression of pathogens (Stein 2005). Majority of antifungal metabolites produced by *Bacillus* spp. could be peptides (Bacillomycin, Iturins, Mycosubtilin, Fengycin, Surfactins, etc.) or non-peptides (Zwittermicin A, Kanosamine, etc.) (Fernando et al. 2005). Largely these are secretary compounds released by PGPBs in soil or any other habitant (Podile and Kishore 2007).

Bacillus species such as *B. amyloliquifaciens, B. subtilis, B. cereus, B. pumilus, B. mycoides* and *B. sphaericus* have been reported to elicit significant reduction in the severity of various diseases of diversified host (Kloepper et al. 2004; Choudhary et al. 2008). Shanmugam et al. (2013) evaluated chitinase producing *B. subtilis* for disease management of ginger because of reduction in the incidence of rhizome rot caused by *F. oxysporum* and *F. solani.* Tan et al. (2013) observed *B. amyloliquifaciens* as antagonist toward *Ralstonia solanacearum*. Consortium of *P. aeruginosa* KRP1 and *B. licheniformis* KRB1 were reported suppressive for the fungal phytopathogens *F. oxysporum* and *S. sclerotiorum* causing disease in *Brassica campestris* (Maheshwari et al. 2015a, b). Pane and Zaccardelli (2015) reported suppression of early blight disease of *Solanum lycopersicum* L. caused by *Alternaria alternata* by *Bacillus* spp. *Bacillus subtilis* treated seeds of *Solanum lycopersicum* showed suppression of *R. solani* with 80% reduction in disease incidence (Zohora et al. 2016). Recently, Rais et al. (2018) evaluated *Bacillus* spp. for blast disease suppression on rice crop. *Bacillus subtilis* XF-1 also reported to inhibit the growth of *Plasmodiophora brassicae* causing infection in cruciferous crops (Liu et al. 2018).

This implies that PGPBs competence strongly enhanced quality enhancement and crop growth. Supanjani et al. (2006) applied *Bacillus megaterium* var. *phosphaticum* and *Bacillus mucilaginosus* in nutrient limited stressed soil where the strains increased bioavailability of minerals, their uptake and subsequently enhanced growth of pepper and cucumber. Hafeez et al. (2006) suggested *Bacillus pumilus* as a bioinoculant to promote the crop yield in wheat. Beneduzi et al. (2008) reported *Bacillus* isolate SVPR30 as an efficient bioinoculant for growth enhancement of the rice. Furthermore, Singh et al. (2008) reported increase in the dry weight of root with the *Bacillus* bacterization of seeds of *Pinus roxburghii* in Himalayan terrains. On the other hand, Zongzheng et al. (2010) evaluated growth promoter effect of *Bacillus subtilis* SY1. A significant increase in seedling parameters such as sprout tendency, germination percentage, sprout index and vigor index were observed. *Bacillus* isolates exhibited seedling length, fresh weight and

dry weight in cow pea (Thomas et al. 2010). Agrawal and Agrawal (2013) reported growth promotion of tomato by PGP *Bacillus* sp. Mehta et al. (2015) supported the fact of planting value parameter enhancement by the treatment of P-solubilizing *Bacillus circulans* CB7 on the growth enhancement of tomato. Significant increase in early vegetative plant growth parameters along with increase in nitrogen, potassium, and phosphorus was observed.

5.5 *Bacillus*: In Action as PGPR

5.5.1 Bacillus *as Mineral Solubilizers*

Evidences of phosphorus solubilizing microorganism (PSM) were dates back to 1903 (Wani et al. 2008). Khan et al. (2010) stated that efficiency of P fertilizer throughout the world is around 10–25% and bio-available P in soil reaching the level of 1.0 mg kg–1 soil (Goldstein 1994). Further, several contributions were made to establish the concept of phosphorus (P) solubilization as major growth-limiting factor for the plants (Richardson 2001; Ezawa et al. 2002; Saharan and Nehra 2011; Pingale and Virkar 2013). He et al. (2004) observed heterotrophic microorganisms secreted organic acids responsible for inorganic P solubilization into phosphatic minerals and/or chelate cationic partners. An advance finding in the same manner on the metabolic processes that diverse group from autotrophs to heterotrophs and diazotrophs to phototrophs have been reported to secrete enzyme phosphatases (Gupta et al. 2007). The production of microbial metabolites resulted in decrease in soil pH, probably played a major role in P solubilization (Chen et al. 2010). Yadav and Verma (2012) applied P as fertilizer which become immobile pools via precipitation in soils. It has also been noted that PGPR as PSB inoculants enhances the nutritional uptake of plant and influence growth factors under stressed conditions (Nadeem et al. 2014a, b). In addition, Nenwani et al. (2010) proposed proton extrusion and organic acid production as a microbial processes/mechanisms for phosphate solubilization.

In between lot of concept notes were postulated on P-solubilizing microorganisms. Dubey et al. (2014) reported that the *Bacillus subtilis* BSK17 solubilized inorganic phosphate in soil resulting its easy uptake and enhanced yield of the *Cicer arietinum.* Inoculation of the *Bacilli* compensated the nutrient deficiency and improved the overall plant growth and development (Schoebitz et al. 2013; Sandilya et al. 2018). Due to the treatment of *B. thuringiensis,* an 11% increase in phosphorus availability in soil and 34% in wheat plant occurred (Delfim et al. 2018).

Organic phosphate being another form of phosphate in soil constitutes 30–50% of total phosphorus available amounts in soil. It was stated that organic phosphorus is largely in the form of inositol phosphate (soil phytate), the most stable form of organic phosphate synthesised by microorganisms and plants (Dalai 1977).

Myo-, scyllo-, chiro- and neo-inositol phosphates were widely spread phytases, of which most myo-inositol has been reported as most common and distributed in various plant tissues. Phytase produced by microorganisms able to change-over soil phytate into phosphate for the plant's uptake (Patel and Kanungo 2010). Earlier, Idriss et al. (2002) reported *B. amyloliquefaciens* in the degradation of extracellular phytate (myo-inositol hexaklsphosphate). Inoculation of the culture filtrate of these *Bacilli* containing phytase at enhanced root weight, shoot weight and root length of maize. Various studies on enhancement of plant growth by the phytase producing *Bacillus* strains have been described by researchers (Kumar et al. 2012a, b; Balaban et al. 2016).

5.5.2 Bacillus *as Iron Scavengers*

Iron is the fourth most essential element of the earth's crust (Pasek and Lauretta 2005). dates back in 1952, "Neilands" isolating and purifying siderophores in crystalline form and honored as the "Father of ferruginous facts". The term siderophore stands for "iron carriers" or "iron bearers" in Greek.

Iron has been proved essential nutrient for virtually all microorganisms to control enzymatic reactions as necessary cofactor. More than 500 siderophores have been reported (Boukhalfa and Crumbliss 2002; Hider and Kong 2010). Kraemer (2004) stated most, but not all, siderophores are hexadentate ligands forming 1:1 complexes with Fe^{3+}. Miethke and Marahiel (2007) observed carboxylate siderophore produced by fungi in acidic environment has low capacity to form stable Fe^{2+} complexes. Also, Miethke and Marahiel (2007) examined siderophore complexes varies based on their structure and ligand type varies their stability of Fe^{3+} influence pH and affect chelation efficiency thereby. On the other hand, Raymond et al. (2003) observed higher affinity for Fe^{3+} in catecholates siderophore.

Earlier, Liles et al. (2000) discovered *Legionella pneumophila* produced a non-classical siderophore, legiobactin, conserved among the members of legionellae. Like other PGPR, rhizobia utilize a large spectrum of these molecule to overcome iron starvation (Plessner et al.1993) and produce strain specific siderophores (Arora et al.2001; Deshwal et al. 2003). Sharma and Johri (2003) characterized bacterial siderophores of low-molecular-weight with high Fe^{3+} chelating affinities meant for easy transport across the membrane. Further, their role to inhibit the growth of plant pathogens was also reported by siderophore producing microorganism. Siderophore production has been reported in *Pseudomonads* spp. (Haas and Défago 2005), *Bradyrhizobium* (Deshwal et al. 2003), *Rhizobia* (Arora et al. 2001). Pandey et al. (2005) have been reported bacteria produce hydroxamate-type and catecholate-types siderophores invariably and observed that *Pseudomonas aeruginosa* GRC_1, excel in PGP traits and also have prolific production ability of hydroxamate siderophore in iron-deficient conditions. The purified siderophore appeared to be of pyoverdin type with typical amino acid composition. On the other hand, siderophore production by root nodulating rhizobia

(Carson et al. 1992; Arora et al. 2001). Various strains of PGPR have been reported to produce a wide range of siderophores such as rhizobactin, citrate, hydroxymate, catechol, anthranalate under low iron (deficient) conditions (Guerinot et al.1990; Sridevi and Mallaiah 2008).

5.5.3 Bacillus *as Plant Growth Regulators*

Several decades before, the term "Auxin" was introduced into the identification of scientific community (Went and Thimann 1937). IAA significantly influenced plant growth and development (Went and Thimann 1937). Several workers observed mechanism of plant hormones secreted by PGPR in plant growth and development (Kumar et al. 2009; Maheshwari et al. 2012; Reetha et al. 2014). The indole acetic acid (IAA) enhance root proliferation and increase nutrient uptake by involvement of most common IAA biosynthesis by Indole-3-Acetamide (IAM) and Indole-3-Pyruvate (IPyA) (Barazani and Friedman 1999). Representatives of *B. subtilis* and *B. amyloliquefaciens* group secreted IAA-like substance in reasonable amount when fed with tryptophan (Idris et al. 2007). Lambrecht et al. (2000) studied the involvement of IAM pathway in plant gall size, whereas the IPyA pathway determined epiphytic fitness in plants. On the other hand, Ali et al. (2009) reported auxin-producing rhizobacteria exert positive effect in *Triticum aestivum.* Whereas, Grunewald et al. (2009) explained auxin responses during microbe-induced de novo organ formation which modify their host's auxin transport. Hussain and Hasnain (2009) examined rhizobacterial extract of *B. subtilis* BC1 and *P. aeruginosa* E2 strain in enhancement of cell division, fresh weight and cotyledons size in cucumber. Morrone et al. (2009) demonstrated that *B. japonicum* encodes separate diterpenoid from plant and fungi *ent*-copalyl diphosphate and *ent*-kaurene involved in biosynthesis of gibberellin. Earlier, Bottini et al. (2004) reviewed the involvement of gibberellins-mediated symbiotic and soil-endophytic microorganisms in PGP activities. Cytokinin is dominantly produced by rhizobacteria (Arkhipova et al. 2007). On the other hand, Liu et al. (2013) observed cytokinin producing PGPR inoculation in seedlings alleviated drought stress in arid environments.

5.5.4 Bacillus *in Stress Management*

Certain enzyme containing microbes have dual role to be played in plant–bacteria interactional studies. The mechanism of PGP involve 1-aminocyclopropane-1-carboxylate deaminase (ACCD) production. PGPRs played significant role in the regulation of the plant hormone, ethylene, thus influence the growth and development of plants (Davies 2010). Belimov et al. (2009) demonstrated bacteria-mediated ACCD in alleviation of stress-induced ethylene-mediated adverse

impact in plants, abiotic and biotic factors. Accelerated ethylene production under high and chilling temperatures has been reported by researchers in both plants and rhizospheric microbial species (Wright and Osborne 1974). Penrose and Glick (2003) proposed the standard methodology to characterize rhizospheric bacteria for the production of ACC-deaminase in vitro. Thereafter, several advancement were made in of rhizosphere microbiology, especially to establish the characteristically ACCD active in PGPRs. A psychrotolerant ACCD producing bacterium *P. putida* UW4 reported to promote plant growth at low temperature under salt stress conditions in canola (Cheng et al. 2007). PGPR containing ACCD boost plant growth particularly under stressed conditions due to regulation of accelerated ethylene production in response to a multitude of stresses such as salinity, temperature, and drought (Marshall et al. 2012), water logging, pathogenicity (Lulai and Suttle 2004), and contamination (Arteca and Arteca 2007). Various workers observed PGPR having ACCD caused marked improvement in root growth and biomass production under stressed conditions (Belimov et al. 2001, 2005; Safronova et al. 2006; Zahir et al. 2009; Nadeem et al. 2014a, b). The decreased ACC level resulted in low endogenous ethylene concentration reduced the harmful effects of stress-induced ethylene so as to allow plants to develop a better root system. PGPR containing ACCD mitigates the ACC-imposed effect in the similar way as did the chemical inhibitor such as carbon-di-oxide (Shaharoona et al. 2007; Nadeem et al. 2010).

5.5.5 Bacillus *in Biocontrol of Phytopathogens*

Among diverse group of microorganisms, about 350 bacterial species studied to date, are important producers of volatile substances (Wenke et al. 2010). Beauchamp and Drury (1991) reported that rhizobia are relatively less efficient in HCN production than that of other rhizosphere bacteria but its production is common by fluorescent group of pseudomonads (Sacherer et al. 1994; Bagnasco et al. 1998; Rodríguez and Fraga 1999; Siddiqui et al. 2006; Ahmad et al. 2008). Cyanide as one among secondary metabolite produced from glycine by HCN synthase reported by Castric and Deal (1994). Secondary volatile metabolite produced by majority of gram-negative bacteria have deleterious effect on growth of phytopathogens (Knowles and Bunch 1986). Cyanides play important role in the suppression of root rot in tobacco caused by *Thilaviopsis basicola* (Ahl et al. 1986). HCN inhibits the enzyme Cytochrome C oxidase and other metalloenzymes (Voisard et al. 1989) of the pathogens thus helps plants against the attack soil-borne diseases (Blumer and Haas 2000). Long back, Glick et al. (1998) observed that certain bacteria along with fungi were also reported that inhibits by the action of HCN because HCN negative microorganisms do not resist the HCN activity. The volatile cyanogens production in liquid cultures proved inhibitory to various fungal genera (O'Sullivan and O'Gara 1992; Dowling and O'Gara 1994). Haas and Défago (2005) elaborated understanding of action of HCN in plant disease control.

Kremer and Souissi (2001) demonstrated that the production of HCN by rhizobacteria was similar to its exogenous concentrations, inhibiting the seedling growth, suggesting that HCN produced in rhizosphere of proved potential and environmentally compatible mechanism for biocontrol. Dubey et al. (2014) found plant growth-spromoting *Bacillus subtilis* BSK17 strain able to produce HCN and other inhibitory metabolites to act against *Fusarium oxysporum*.

5.6 Biofilm Formation by *Bacilli*

The root exudation process includes the secretion of ions, free oxygen and water, enzymes, mucilage, and a universal array of carbon-containing primary and secondary metabolites helps in maintaining rhizospheric ecology. In rhizosphere microbes in root-association forms biofilms, basically depends on the availability of root exudates nutritional factor to favor cell aggregation (Seneviratne et al. 2011). Biofilm formation is central factor triggering root colonization (Ortíz-Castro et al. 2009; Bais et al. 2006). Chemotaxis behaviors of rhizobacteria (in particular flagellated bacteria) for root exudates have also been observed (Tan et al. 2013; Yuan et al. 2015;). Root exudates are less diverse but often compose a larger proportion of the exudates by mass. They include low-molecular weight compounds such as amino acids, organic acids, sugars, phenolics secretion of low- and high-molecular weight root exudates into the soil changes its environment. The polysaccharides, mucilage, and proteins are comes under the category of high-molecular root exudates. Mucilages are released from the root cap, these are primary cell between epidermal and sloughed root cap (including root hairs). Few rhizobacteria also produce microbial mucilages. Further, autolysis of root cells is another reason for the production of lysates as root exudates in the soil. Collectively, lysate, plant and microbial mucilages associate organic and mineral matter (Rovira 1969).

A marked concept about root exudates was put forwarded by Bais et al. (2004) that plant root cells has functional way to secrete chemicals which also includes activity and turnover of microbes and thus, influence nutrient availability (Leff et al. 2015) in the rhizosphere (Magiorakos et al. 2012). On the other hand, chemicals and polysaccharides secretions of root cells are responsible for initial attachment of other low-molecular organic compounds such as ethylene, sugars, amino acids, vitamins, polysaccharides, and enzymes present in soil. Hence, these nutritional resources influence microbial population structure and play a vital role in niche stabilization and rhizospheric homeostasis. During microbial interactions, the root cells release exudates either passively (diffusates) and actively (secretions). Whereas, the low-molecular weight organic compounds released in a passive process along with their own steep concentration-gradient that usually exists between the cytoplasm of intact cells and the external solution (Kuzyakov 2002).

Exopolysaccharide (EPS) of bacterial origin modulate the chemical and physical properties of biofilms on abiotic surfaces (Friedman and Kolter 2004). The bacterial EPS production merit as important factor for effective colonization on root surfaces.

More than 90% of the EPS volume consists of water (Schmitt & Flemming 1999) and proteins and polysaccharides which enhance bacterial adhesion (Sutherland 2001) while lipopolysaccharides (Prakash et al. 2003), uronic acids (Kavita et al. 2014) and biosurfactants (Banat et al. 2010) depress bacterial adhesion. Sutherland (2001) noted that structure of the EPS has a marked effect on the biofilm formation. Biofilm EPS is not generally uniform but vary spatially and temporally. Honma et al. (2007) described the inhibitory role of glycosylated surface-glycoprotein in *Tannerella forsythia* biofilms. Li et al. (2008) stated that EPS play vital role in the biofilm formation and structure of membrane-aerated biofilms (MABs). Production of a novel glucose, galactose, and mannose-rich polymer that contributes to cell–cell interactions necessary for pellicle and biofilm formation and its stability (Armitano et al. 2014).

Several workers have studied the role of biofilms in various systems of industrial, ecological and environmental backgrounds. However, two major tools in the past few decades have emerged to enhance our understanding of biofilm and its accomplishment. Foremost is the use of scanning electron microscopy (SEM) to elucidate ultrastructure of biofilm (West et al. 2014), and second, exploration of the genes governs metabolite production that involve in cell adhesion and biofilm formation (Mielich-Süss and Lopez 2015).

Although, *Bacillus* and *Paenibacillus* species among *Bacilli* showed pragmatic biofilm formation (Branda et al. 2006; Bais et al. 2004). But, *B. subtilis* forms adhering biofilms on inert surfaces under the control of a variety of transcription factors (Cho et al. 2003; Kinsinger et al. 2003; Bais et al. 2004). Zeriouh et al. (2014) reported that the surfactin production by *Bacillus subtilis* not only necessary for biofilm formation but also exhibits antimicrobial activities. The antimicrobial activity of surfactin seems to be responsible for the inhibition of several phytopathogens. The role of biofilm in biocontrol initiation has also been highlighted by Haggag and Timmusk (2008) who observed the biofilm-forming *P. polymyxa* in controlling crown root rot disease caused by *Aspergillus niger* and suggested that the superior biofilm former offers significantly better disease protection.

Biofilms hold tremendous practical significance, exhibiting both beneficial and detrimental activities (Zhang et al. 2003; Ribeiro et al. 2015). The *in vitro* production of biofilm formation of PGPR gave better crop yields through a range of plant growth mechanisms bio fertilizers through improved N_2 fixation and by solubilization of micro- and macronutrient and their uptake. Further, enhanced growth observed due to the production of beneficial metabolites. Their performance during host-plant bacteria relationship exhibited significant and sustainable enhancement of productivity and yield both in green houses and field practices.

5.7 Conclusion

Scientists in general and biologists in particular focus their attention for sustainable crop production because, food security as a challenge of now cope food security problems. Different species of *Bacillus* are really versatile with that rendered enhancement of plant growth and health promotion powered with super abilities to produce resting fruiting bodies in the form of endospores. During adverse situations, several characteristics these organisms and because of provide all benefits to the productivity enhancement in field crops. Thus, assistance of such group of bacteria is fitted for luxuriant growth and food production enhancement. However, a proper evaluation be made about their pathogenicity before releasing for commercial practices.

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Chapter 6
Utilization of Endophytic Bacteria Isolated from Legume Root Nodules for Plant Growth Promotion

Winston Franz Ríos-Ruiz, Renzo Alfredo Valdez-Nuñez, Eulogio J. Bedmar and Antonio Castellano-Hinojosa

Abstract For decades, rhizobia were described as the single inhabitant of legume nodules. However, other bacteria, which are not typical rhizobia, are often found within nodules and suggested to affect the behaviour and fitness of the host plant. Here, we highlight their diversity, role in the promotion of legumes growth and in the recuperation of degraded soils. Studies have shown the capacity of Non-Nodular Endophytic Bacteria (NNEB) to stimulate plant growth by direct mechanisms including production of phytohormones such as auxins, facilitation of acquisition of plant resources/nutrients that plants lack such as fixed nitrogen, iron, phosphorous, besides, production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC deaminase) involved in reduction of plant ethylene, etc. Among the indirect mechanisms, those associated to the enhancement of plant growth are production of siderophores, antibiotics and lytic enzymes. Finally, we described greenhouse and field experiments that successfully used NNEB to both increase the growth and yield of legumes and to recover degraded soils.

Keywords Legume · Plant-growth promotion · Nodule · Endophytic bacteria · Soil

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6.1 The Bacteria Inside the Legume Root Nodules

Legumes (family Fabaceae or Leguminosae) constitute the third largest family of angiosperms plants with a critical importance in human and animal feeding as well as for benefits of agricultural systems. Leguminous and actinorhizal plants are unique among the living beings because they have the characteristic to establish N_2-fixing symbiosis with soil bacteria, collectively known as rhizobia; as a consequence of the plant-bacteria interaction, roots, and occasionally stems, nodules are formed where N_2-fixation occurs (Gresshoff and Ferguson 2017; Lace and Ott 2018). Briefly, nodulation is a complex and specific molecular 'conversation' between the host legume and the rhizobia where the former produce flavonoids in their radical exudates which are detected by rhizobia (Hayashi et al. 2014). Then, flavonoids induce a cascade of nodulation genes in the rhizobia that start the synthesis of nodulation factors, the formation of an infection thread to deliver rhizobia within the epidermal cells of the plant host and, finally the transformation of vegetative rhizobial cells into specialized, N_2-fixing bacteroids (Oldroyd and Downie 2008; Downie 2014).

6.2 The Diversity of Nodule-Forming Rhizobial Bacteria

The rhizobia are a polyphyletic group of bacteria which, in addition to their symbiotic N_2-fixing lifestyle with legumes, are also able to colonize plant roots and even to maintain an endophytic role in non-legume plants (Bhattacharjee et al. 2008; Poole et al. 2018; Schneijderberg et al. 2018). Classical nodule-forming, N_2-fixing, symbiotic rhizobia belong to the Alphaproteobacteria and Betaproteobacteria classes, albeit members of the Gammaproteobacteria and Actinobacteria have been also reported as symbiotic bacteria (Martínez-Hidalgo and Hirsch 2017 and references therein). Currently, classical rhizobia include the genera *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Neorhizobium*, *Pararhizobium* and *Allorhizobium* within the family Rhizobiaceae, and genera *Mesorhizobium*, *Bradyrhizobium* and *Azorhizobium* of the Phyllobacteriaceae, Nitrobacteriaceae (Bradyrhizobiaceae) and Hyphomicrobiaceae families, respectively. Comprehensive reviews on the current classification of bacteria able to establish N_2-fixing legume symbioses, including both classical and non-classical rhizobia, have been published (Mousavi et al. 2015; Peix et al. 2015; Shamsheldin et al. 2017; Martínez-Hidalgo and Hirsch 2017; Velázquez et al. 2017).

The ability for nodulation of non-classical rhizobia, those which do not belong to the above-mentioned genera, has been related to their coexistence with classical symbiotic rhizobia leading to horizontal transfer of nodulation genes (Martínez-Hidalgo and Hirsch 2017). This attribute constitutes the main driver of evolution for the acquisition of new symbiotic abilities for bacteria residing within

the nodule (Estrela et al. 2016; Zgadzaj et al. 2016). A list of valid species of rhizobia is constantly updated and recorded in the list of Prokaryotic names with standing in nomenclature (https://www.bacterio.cict.fr).

6.3 Non-nodulating Bacteria from Legume Root Nodules

In the interior of the legume nodules, in addition to the symbiotic rhizobia, the presence of a vast diversity of bacteria unable to form nodules by themselves has been reported (Peix et al. 2015; Aeron et al. 2015; Martínez-Hidalgo and Hirsch 2017; Velázquez et al. 2017). There are several denominations for bacteria that co-exist with symbiotic rhizobia; they have been called non-rhizobial bacteria (Tariq et al. 2012; Dhole et al. 2016), non-rhizobial endophytes (De Meyer et al. 2015), nodule endophytes (Velázquez et al. 2013), bacteria associated with the nodule (Rajendran et al. 2012), and non-symbiotic bacteria with disinfected nodules (Da Costa et al. 2013). In this review, we will refer to them as Non-Nodular Endophytic Bacteria (NNEB).

The first report published on the presence of bacteria different from the classic rhizobia recovered from the interior of healthy nodules is more than 100 years old (Beijerinck and Van Delden 1902) and was associated to *Agrobacterium radiobacter* isolated from root nodules of *Trifolium* plants. These results did not go unnoticed by Philipson and Blair (1957) who, in addition to *Rhizobium*, reported the presence of *Aerobacter, Bacillus* and *Flavobacterium* from the interior of *Trifolium* plant nodules. For a long time, based on the morphocolonial characteristics and biochemical tests as well as on the absence of nodulation traits after reinfection tests with the original host, many authors underestimated the presence of endophytic bacteria different to those of classical rhizobia (Fred et al. 1932; Vincent 1970; Somasegaran and Hoben 1994). Even, they were catalogued as 'contaminants' by Somasegaran and Hoben (1994). For many years, endophytic bacteria were discarded based mainly on two tests: the absorption capacity of Congo Red when they grow in Petri plates containing yeast extract mannitol medium, and the colour change of bromocresol purple indicator on Petri plates containing peptone glucose agar (Martínez-Hidalgo and Hirsch 2017). Nowadays it is well stablished that nodule disinfection is required for the correct isolation of NNEB. There are several methodologies to confirm the efficiency of surface-sterilized nodules: (a) incubation of disinfected nodules on plates containing YEM medium (Tariq et al. 2012); (b) plating aliquots of the rinsing water after the disinfection process in growth media (Bai et al. 2002; Leite et al. 2017); (c) rolling the surface-sterilized nodules on plates containing growth media (De Meyer et al. 2015).

In any case, the appearance of bacterial growth invalidates the experiment and bacteria grown in the planes can be associated to external contamination coming from the outer surface of the nodule (Bai et al. 2002). About a hundred of different genera considered NNEB have been isolated from root legumes worldwide, of which 29.7% belong to the Alfaproteobacteria, 20.8% to the Actinobacteria, 18.8% to the

Gammaproteobacteria, 14.9% to the Betaproteobacteria, 9.9% to the Bacilli and 5.9% to other classes Table 6.1. The greatest presence of some groups inside the nodule is unknown, though believed to be associated with the genotype of the host plant (De Meyer et al. 2015; Leite et al. 2017; Trabelsi et al. 2017). Soil physicochemical characteristics also influence structure and composition of NNEB; De Meyer et al. (2015) showed that genera *Paenibacillus*, *Kocuria* and *Leifsonia* were dominant in legumes grown in extensive moors, tracts of sandy heath and wetlands, *Bosea*, *Moraxella* and *Microbacterium* were in dune ecoregions and *Brevibacterium*, *Mycobacterium* and *Micromonospora* were more abundant in sandy soils. Moreover, the diversity of NNEB within nodules from *Vigna unguiculata* growing in different types of soil was dependent on the soil pH (Leite et al. 2017).

6.4 Role of Non-nodulating Endophytic Bacteria in the Promotion of Legumes Growth

More than 30% of the NNEB and symbiotic bacteria present in leguminous nodules are potential Plant Growth Promoting Bacteria (PGPB) (Trabelsi et al. 2017 and references therein). It is also known that the endophytic microbiome promotes plant growth and health and that this beneficial effect is mediated by secondary metabolites (Brader et al. 2014). NNEB aids in plant-growth promotion by several mechanisms such as N_2-fixation, inorganic phosphate solubilization, release of siderophores, production of phytohormones, biocontrol activity, etc. A list of NNEB with PGPB properties is presented in Table 6.2.

Many NNEB are N_2-fixers capable of converting atmospheric dinitrogen (N_2) into ammonium (NH_4^+) without causing morphological changes in roots but increasing the growth and yield of the plants (Hayat et al. 2010) Table 6.2. NNEB also improves the availability of P, with the concomitant increase in the yield and nutritional efficiency of the plants, even under effective biological N_2-fixation conditions (Santoyo et al. 2016) Table 6.2. Siderophores act as iron scavenging molecules and create nutrient-limiting conditions for phytopathogenic microorganisms (Berg et al. 2005) Table 6.2. Iron is considered an important cofactor for enzymes involved in many biochemical pathways such as photosynthesis in plants and nitrogen fixation in bacteria. In this sense, Khandelwal et al. (2002) reported that the production of siderophores by NNEB improve the symbiosis through the increase of ferric ion necessary for an efficient nitrogenase activity. Microbial production of phytohormones such as auxins, and auxin-like compounds, is known to trigger cell elongation, division and differentiation in plants (Santoyo et al. 2016). They also play an important role in the ontogeny of the nodules in the legume-rhizobium symbiosis and many studies indicate that changes in the content of indole acetic acid (IAA), or in its balance with cytokinins, are a prerequisite for the organogenesis of the nodule (Downie 2014).

The hormone ethylene produced within the plant endosphere has a major consequence on the bacterial microbiota residing within. NNEB with

Table 6.1 Non-nodular endophytic bacteria (NNEB) isolated from the interior of worldwide grown legume nodules

Host legume		NNEB—Origin (Reference)
Caesalpinioideae	*Acacia salicina*, *A. stenophylla*, *A. ehrenbergiana*, *A. nilotica*, *A. seyal*, *A. tortilis*, *A. laeta*.	*Acinetobacter haemolyticus*, *Ancylobacter* sp., *Arthrobacter* sp., *Bacillus fusiformis*, *B. senegalensis*, *Brevibacillus brevis*, *Caulobacter vibriodes*, *Chitinophaga sancti*, *Comamonas testosteroni*, *Enterobacter* sp., *Herbaspirillum frisingense*, *Kaistia* sp., *Microbacterium flavescens*, *Mycobacterium frederiksbergensis*, *Paenibacillus agarexedens*, *P. amylolyticus*, *P. glycanilyticus*, *P. pabuli*, *Pseudomonas fluorescens*, *P. putida*, *Rhizobium radiobacter*, *Roseateles depolymerans*, *Stenotrophomonas maltophilia*, *Variovorax paradoxus*—Australia (Hoque et al. 2011); *Advenella kashmirensis*, *Agrobacterium tumefasciens*, *Brevibacillus nitrificans*, *Microbacterium oxydans*, *Ochrobactrum anthropi*, *O. intermedium*, *Paenibacillus glycanilyticus*, *P. humicus*, *Pseudomonas aeruginosa*, *Rhizobium* sp., *Stenotrophomonas maltophila*—Algeria (Boukhatem et al. 2016)
	Enterolobium saman	*Shinella* sp.—Philippines (Bautista et al. 2017)
	Leucaena leucocephala	*Ensifer morelense*-México (Wang et al. 2002)
	Mimosa pudica	*Pantoea agglomerans*—Phillipines (Bautista et al. 2017)
	Neptunia natans	*Labrys neptuniae*—Taiwan (Chou et al. 2007)
	Prosopis farcta	*Paenibacillus prosopidis*—Tunisia (Valverde et al. 2010)
Papilionioideae	*Adesmia emarginata*	*Labrys methylaminiphilus* sp.—Chile (Gerding et al. 2017)
	Aeschynomene sensitiva	*Pseudomonas moselli*, *Rhizobium rhizogenes*—Phillipines (Bautista et al. 2017)
	Alysicarpus spp.	*Stenotrophomonas* sp.—Phillipines (Bautista et al. 2017)
	Arachis duranensis	*Agrobacterium* sp., *Burkholderia cepacea*, *Herbaspirillum frisingense, Rhizobium mesosinicum*, *R. multihospitium*—China (Chen et al. 2014)
	Arachis hypogaea	*Enterobacter* spp., *Klebsiella* spp., *Pseudomonas* spp.—Argentina (Ibáñez et al. 2009); *Chryseobacterium indologenes*, *Enterobacter cloacae*, *E. ludwiigii*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*—India (Dhole et al. 2016)
	Argyrolobium uniflorum	*Agromyces* sp., *Phyllobacterium* sp.—Tunisia (Zakhia et al. 2006)
	Aspalathus abietina	*Burkholderia aspalathi*—South Africa (Mavengere et al. 2014)
	Astragalus gombiformis, *As. algerianus*, *As. armatus*, *As. chrysopterus*.	*Bosea* sp., *Inquilinus* sp., *Mycobacterium frederiksbergense, Phyllobacterium* sp., *Sphyngomonas* sp.—Tunisia (Zakhia et al. 2006); *Nocardioides astragali*—China (Xu et al. 2018)
	Calicotome villosa	*Bacillus circulans*, *Inquilinus* sp., *Phyllobacterium* sp., *Sphingomonas* sp.—Tunisia (Zakhia et al. 2006)
	Calopogonium mucunoides	*Enterobacter cloacae*, *Herbaspirillum putei*—Phillipine (Bautista et al. 2017)
	Cicer arietinum	*Ochrobactrum ciceri*—Pakistan (Imran et al. 2010); *Agrobacterium tumefasciens*—Tunisia (Säidī et al. 2011); *Paenibacillus endophyticus*—Spain (Carro et al. 2013); *Bacillus subtilis*—India (Saini et al. 2015); *Enterobacter* sp.—India (Koli and Swarnalakshmi 2017)

(continued)

Table 6.1 (continued)

Host legume		NNEB—Origin (Reference)
	Colutea arborescens L.	*Buttiauxella* sp.—Belgium (De Meyer et al. 2015)
	Crotalaria incana, *C. spinosa*	*Agrobacterium radiobacter*, *Bacillus simplex*, *Burkholderia* sp., *Cronobacter dublinensi Enterobacter cancerogenus*, *E. cloacae*, *Pantoea agglomerans*, *Rhizobium lusitanum*—Ethiopia (Aserse et al. 2013)
	Cytisus scoparius (L.) Link	*Bacillus* sp., *Caulobacter* sp., *Kocuria* sp., *Leifsonia* sp., *Microbacterium* sp., *Paenibacillus* sp., *Paracoccus* sp., *Phyllobacterium* sp., *Rhodococcus* sp., *Sphingomonas* sp., *Streptomyces* sp.—Belgium (De Meyer et al. 2015)
Papilionioideae	*Dalbergia* spp.	*Burkholderia caribensis*, *Phyllobacterium* sp., *Ralstonia picketti*—Madagascar (Rasolomampianina et al. 2005)
	Dipogon lignosus	*Burkholderia dipogonis*—New Zealand and Western Australia (Sheu et al. 2015)
	Erythrina brucei	*Agrobacterium radiobacter, Rahnella aquatilis, Rhizobium* sp., *Variovorax paradoxus*—Ethiopia (Aserse et al. 2013)
	Glycine max	*Bacillus subtilis*—Canada (Bai et al. 2002); *Acinetobacter* sp., *Agrobacterium* sp., *Bacillus* sp., *Burkholderia* sp., *Pantoea* sp., *Serratia* sp.—China (Li et al. 2008); *Diaphorobacter ruginosibacter*—China (Wei et al. 2015); *Acinetobacter* sp., *Bacillus* sp., *Enterobacter* sp., *Ochrobactrum* sp., *Pseudomonas* sp.—China (Zhao et al. 2017); *Acinetobacter calcoaceticus*, *Burkholderia cepacia*, *Enterobacter cloacae*, *Ochrobactrum anthropi*, *Pantoea agglomerans*, *Proteus mirabilis*, *Pseudomonas* spp.—United States of America (Tokgöz 2018)
	Hedysarum carnosum	*Pseudomonas* sp.—Tunisia (Zakhia et al. 2006)
	Indigofera amorphoide, I. arrecta	*Enterobacter* sp., *Paenibacillus sonchi*, *Planomicrobium glaciei, Rhizobium leguminosarum*—Ethiopia (Aserse et al. 2013)
	Lathyrus latifolius L., *L. numidicus*, *L. pratensis* L., *L. silvestris* L.	*Phyllobacterium* sp.—Tunisia (Zakhia et al. 2006); *Bosea lathyri*—Belgium (De Meyer et al. 2012); *Bacillus* sp., *Enterobacter* sp., *Erwinia* sp., *Microbacterium* sp., *Paenibacillus* sp., *Pantoea* sp., *Promicromonospora* sp., *Pseudomonas* sp., *Staphylococcus* sp., *Streptomyces* sp.—Belgium (De Meyer et al. 2015)
	Lespedeza sp.	*Arthrobacter nitroguaiacolicus*, *Bacillus megaterium*, *Burkholderia phenazinium*, *B. phytofirmans*, *B. caledonica*, *B. semidinicola*, *B. glathei*, *B. sordidicola*, *Dyella koreensis*, *D. marensis*, *D. japonica*, *Methylobacterium fujisawaense, Microbacterium ginsengisoli*, *Staphylococcus warneri*—Korea (Palaniappan et al. 2010; Subramanian et al. 2015)
	Lotus argenteus	*Paenibacillus* sp., *Sphingomonas* sp.—Tunisia (Zakhia et al. 2006)
	Lotus corniculatus	*Phyllobacterium loti*—Uruguay (Sánchez et al. 2014); *Actinoplanes* sp., *Ancylobacter* sp., *Arthrobacter* sp., *Bacillus* sp., *Corynebacterium* sp., *Inquilinus* sp., *Mycobacterium* sp., *Oerskovia* sp., *Phyllobacterium* sp., *Staphylococcus* sp., *Xanthomonas* sp.—Belgium (De Meyer et al. 2015)
	Lotus pedunculatus	*Acinetobacter* sp., *Aeromicrobium* sp., *Bacillus* sp., *Chryseobacterium* sp., *Curtobacterium* sp., *Paenibacillus* sp., *Pantoea* sp., *Plantibacter* sp., *Pseudomonas* sp., *Sphingomonas* sp., *Staphylococcus* sp.—Belgium (De Meyer et al. 2015)
	Lupinus albus	*Cohnella lupini*—Spain (Flores-Félix et al. 2014); *Paenibacillus lupini*—Spain (Carro et al. 2014)
	Lupinus angustifolius	*Micromonospora lupini*, *M. saelisecensis*—Spain (Trujillo et al. 2007)

(continued)

Table 6.1 (continued)

Host legume		NNEB—Origin (Reference)
	Lupinus polyphyllus	*Bosea lupini*—Belgium (De Meyer et al. 2012a); *Arthrobacter* sp., *Bacillus* sp., *Brevibacillus* sp., *Cohnella* sp., *Enhydrobacter* sp., *Kocuria* sp., *Lysinibacillus* sp., *Microbacterium* sp., *Microbispora* sp., *Roseateles* sp., *Staphylococcus* sp.—Belgium (De Meyer et al. 2015).
	Macroptilium lathyroides	*Pleomorphomonas oryzae*, *Rhizobium rizogenes*—Phillipines (Bautista et al. 2017)
Papilionioideae	*Medicago falcata* L., *M. lupulina* L., *M. polymorpha*.	*Bacillus* sp., *Corynebacterium* sp., *Massilia* sp., *Microbacterium* sp., *Moraxella* sp., *Pantoea* sp., *Paracoccus* sp., *Pseudomonas* sp., *Staphylococcus* sp.—Belgium (De Meyer et al. 2015); *Pseudomonas brassicacearum*—China (Kong et al. 2017); *Bacillus megaterium*—Spain (Chinnaswamy et al. 2018)
	Medicago hispida	*Kaistia* sp., *Pseudomonas* sp, *Achromobacter* sp., *Stenotrophomonas* sp., *Xanthomonas* sp., *Duganella* sp, *Rheinheimera* sp.—Peru (Arone et al. 2014)
	Medicago sativa	*Endobacter medicaginis*- Spain (Ramírez-Bahena et al. 2013); *Micromonospora* spp. (Martínez-Hidalgo et al. 2014); *Paenibacillus medicaginis*—Taiwan (Lai et al. 2015); *Streptomyces* sp., *Variovorax* sp.—Belgium (De Meyer et al. 2015); *Pseudomonas* sp., *Variovorax* sp.—New Zealand (Wigley et al. 2015); *Bacillus* sp., *Novosphingobium* sp., *Methylibium* sp., *Mycobacterium* sp., *Shinella* sp.—New Zealand (Wigley et al. 2017).
	Medicago truncatula	*Ornithinicoccus* sp., *Pseudomonas* sp.—Tunisia (Zakhia et al. 2006)
	Melilotus albus Medicus., *M. altissimus* Thuillier., *M. indicus* (L.) Allioni; *Melilotus officinalis* (L.) Pallas	*Agrobacterium* sp.—China (Kan et al. 2007); *Bacillus* sp., *Brevibacterium*., *Lysinibacillus* sp., *Microbacterium* sp., *Moraxella* sp., *Paenibacillus* sp., *Pantoea* sp., *Phyllobacterium* sp., *Pseudomonas* sp., *Sphaerisporangium* sp., *Streptomyces* sp.—Belgium (De Meyer et al. 2015).
	Ononis vaginalis, O. natrix, O. repens L.	*Bosea* sp., *Microbacterium* sp., *Rhodopseudomonas* sp.—Tunisia (Zakhia et al. 2006); *Bacillus* sp., *Promicromonospora* sp., *Streptomyces* sp.—Belgium (De Meyer et al. 2015)
	Ornithopus perpusillus L.	*Bacilllus* sp., *Herbaspirillum* sp., *Leifsonia* sp., *Microbacterium* sp., *Micromonospora* sp., *Paenibacillus* sp., *Sphingomonas* sp.—Belgium (De Meyer et al. 2015)
	Oxytropis ochrocephala	*Acinetobacter bouvetti*., *A. junii*., *Bacillus amyloliquefasciens*., *B. aryabhattai*., *B. litoralis*., *B. infantis*., *B. psychrosaccharolyticus*., *B.safensis*., *B. simplex*., *B. subtilis*., *Brevibacterium frigoritolerans*., *Cohnella ferri*., *Erwinia piriflorinigrans*., *Leclercia adecarboxilata*., *Microvirga aerophila*., *Mycobacterium monacense*., *Paenibacillus sepulcri*., *P. costaneae*., *Paracoccus chinensis*., *Phyllobacterium trifolii*., *P. bourgognense*., *Pseudomonas baetica*., *P. salomonii*., *P. frederiksbergensis*., *Sphingomonas astaxanthinifaciens*., *Sporosarcina termotolerans*., *Staphylococcus epidermidis*—China (Xu et al. 2014); *Bacillus radicibacter*—China (Wei et al. 2015)
	Oxytropis triphylla	*Bosea vestrisii*—Russian federation (Safronova et al. 2017); *Phyllobacterium zundukense* (Safronova et al. 2018b)
	Oxytropis popoviana	*Bradyrhizobium* sp.—Russian federation (Safronova et al. 2018a)
	Phaseolus coccineus	*Cohnella phaseoli*—Spain (García-Fraile et al. 2008)

(continued)

Table 6.1 (continued)

Host legume		NNEB—Origin (Reference)
	Phaseolus vulgaris	*Agrobacterium* sp.—Tunisia (Mhamdi et al. 2005); *Agrobacterium tumefasciens*—Tunisia (Säidī et al. 2011); *Achromobacter* sp., *Enterobacter* sp., *Serratia proteamaculans, S. liquefaciens, Pseudomonas* sp., *Pantoea* sp.—Ethiopia (Aserse et al. 2013); *Herbaspirillum lusitanum*—Spain (Valverde et al. 2013); *Phyllobacterium endophyticum*—Spain (Flores-Félix et al. 2013); *Fontibacillus phaseoli*—Spain (Flores-Félix et al. 2014); *Acinetobacter* sp., *Enterobacter* sp., *Delftia* sp., *Klebsiella* sp., *Pseudomonas* sp., *Providencia* sp., *Rhizobium* sp.—Kenya (Wekesa et al. 2017); *Rhizobium hidalgonense*—México (Yan et al. 2017b); *Bacillus megaterium*, *Paenibacillus polimixa*—Kenya (Korir et al. 2017)
Papilionioideae	*Periandra mediterranea*	*Paenibacillus periandrae*—Brazil (Menéndez et al. 2016)
	Pisum sativum	*Micromonospora pisi*—Spain (García et al. 2010); *Ochrobactrum* sp., *Enterobacter* sp.—Pakistan (Tariq et al. 2014); *Micromonospora aurantiaca*., *M. carbonacea*., *M. chalcea*., *M. chokoriensis*., *M. coxiensis*., *M. halophytica*., *M. humi*., *M. krabiensis*., *M. lupini*., *M. marina*., *M. matsumotoense*., *M. mirobrigensis.*, *M. purpureochromogenes*., *M. rifamycinica*., *M. saelicesensis*, *M. siamensis*—Spain (Carro et al. 2012); *Micromonospora noduli*, *M. ureilytica*, *M. vinacea*—Spain (Carro et al. 2016); *Micromonospora luteifusca*—Spain (Carro et al. 2016); *Micromonospora phytophila*, *M. luteiviridis*—Spain (Carro et al. 2018).
	Pterocarpus indicus	*Labrys neptuniae*, *Rhizobium rhizogenes*—Phillipines (Bautista et al. 2017)
	Pueraria candollei	*Rhizobium puerariae*—Taiwan (Boonsnongcheep et al. 2016)
	Pueraria lobata	*Devosia yakushimensis*—Japan (Bautista et al. 2010)
	Pueraria thunbergiana	*Bacillus thuringiensis*, *Enterobacter asburiae*, *Serratia marcesens*—India (Selvakumar et al. 2008)
	Retama raetam	*Bosea* sp., *Microbacterium flavescens*, *M. barkeri*, *Ochrobactrum* sp., *Paracraurococcus* sp., *Starkeya novella*—Tunisia (Zakhia et al. 2006)
	Robinia pseudoacacia	*Bosea robiniae*- Belgium (De Meyer et al. 2012a), *Tardiphaga robiniae*—Belgium (De Meyer et al. 2012b); *Paenibacillus enshidis*—China (Yin et al. 2015); *Arthrobacter* sp., *Chryseobacterium* sp., *Leifsonia* sp., *Pantoea* sp., *Rahnella* sp., *Stenotrophomonas* sp., *Xanthomonas* sp.—Belgium (De Meyer et al. 2015); *Mitsuaria noduli*—China (Fan et al. 2017); *Herbaspirillum robiniae*—China (Fan et al. 2018).
	Scorpiurus muricatus	*Phyllobacterium endophyticum*, *P. ifriqiyense*; *Pseudomona* sp., *Rhizobium vignae*, *R. radiobacter*, *R. leguminosarum*, *Starkeya* sp.—Algeria (Bouchiba et al. 2017)
	Sesbania cannabina	*Agrobacterium deltaense*—China (Yan et al. 2017a)
	Sphaerophysa salsula	*Paracoccus sphaerophysae*—China (Deng et al. 2011)
	Sophora alopecuroides	*Bacillus cereus*—China (Zhao et al. 2011)
	Sulla capitata, S.pallida	*Arthrobacter* sp., *Neorhizobium galegae*, *Phyllobacterium* sp., *Pseudomona fluorescens*, *Rhizobium nepotum*, *Sinorhizobium* sp., *Variovorax* sp.—Tunisia-Algeria (Beghalem et al. 2017)
	Trifolium pratense	*Agrobacterium rhizogenes*, *Bacillus brevis*, *B. insolitus*, *B. megaterium*, *B. subtilis, Bordetella avium*, *Curtobacterium luteum, C. citreum, C, flaccumfaciens*, *Mesorhizobium loti*, *Phyllobacterium myrsinacearum*, *Pseudomonas corrugata*, *P. fragi*, *Rhizobium leguminosarum*—Canada (Sturz et al. 1997); *Xanthomonas* sp.—Belgium (De Meyer et al. 2015)

(continued)

Table 6.1 (continued)

Host legume		NNEB—Origin (Reference)
	Trifolium arvense L., *T. dubium* Sihthorp., T. *hybridum* L., *T. repens* L.	*Arthrobacter* sp., *Bacillus* sp., *Corynebacterium* sp., *Dyadobacter* sp., *Microbacterium* sp., *Novosphingobium* sp., *Paenibacillus* sp., *Pantoea* sp., *Pseudomonas* sp., *Streptomyces* sp.—Belgium (De Meyer et al. 2015)
	Trigonella foenum-graecum	*Exiguobacterium* sp.—India (Rajendran et al. 2012).
	Vavilovia formosa	*Bosea vaviloviae*—Russian Federation (Safronova et al. 2015a); *Tardiphaga* sp.—Armenia (Safronova et al. 2015b)
	Vicia faba	*Agrobacterium* sp.—China (Kan et al. 2007); *Agrobacterium tumefasciens*, *Shinella* sp.—Tunisia (Säidï et al. 2011); *Bacillus* sp., *Clostridium* sp., *Desulfovibrio* sp., *Desulfatimicrobium* sp., *Methylobacter* sp., *Phyllobacterium* sp., *Rhizobium* sp., *Sphingomonas* sp., *Streptomyces* sp.—Tunisisa (Trabelsi et al. 2017); *Pseudomonas brenneri*, *Ps. fluorescens, Ps. frederikbergensis*, *Ps. fragi*., *Ps. putida*, *Ps. rhodesiae, Ps. yamanorum*—Tunisia (Bahroun et al. 2018)
	Vicia alpestris	*Microvirga ossetica*—Russian federation (Safronova et al. 2017)
	Vicia cracca (L.)., *V. hirsuta* (L.) S.F. Gray., *V. Lathyroides., V. sativa* (L.)., *V. sepium* (L.)., *V. tetrasperma* (L.) Schereber	*Agrobacterium sp.*—China (Kan et al. 2007); *Arthrobacter* sp., *Bacillus* sp., *Curtobacterium* sp., *Exigobacterium* sp., *Kocuria* sp., *Leifsonia* sp., *Lysinibacillus* sp., *Paenibacillus* sp., *Pantoea* sp., *Pseudomonas* sp., *Staphylococcus* sp., *Stenotrophomonas* sp.—Belgium (De Meyer et al. 2015)
	Vigna radiata	*Agrobacterium tumefasciens*, *Bacillus subtilis*, *B. simplex* —Pakistan (Tariq et al. 2012); *Paenibacillus* spp., *Klebsiella* spp., *Ensifer* spp., *Agrobacterium* spp., *Blastobacter* spp., *Dyadobacter* spp., *Chitinophaga* spp. —India (Pandya et al. 2015); *Pseudomonas* sp.—Pakistan (Noreen et al. 2015); *Chryseobacterium indologenes*— India (Dhole et al. 2017)
	Vigna unguiculata	*Bacillus* sp., *Brevibacillus* sp., *Paenibacillus* sp., *Enterobacter* sp.—Brazil (Da Costa et al. 2013); *Acinetobacter* sp., *Chitinophaga* sp., *Dyella* sp., *Herbaspirillum* sp., *Novosphingobium* sp., *Pseudomonas* sp., *Stenotrophomonas* sp.—Brazil (Castro et al. 2017); *Enterobacter* sp., *Chryseobacterium* sp., *Sphingobacterium* sp.—Brazil (Leite et al. 2017)
	Wisteria sinensis (Sims) Sweet	*Bacillus* sp.—Belgium (De Meyer et al. 2015)

1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) Table 6.2 are involved in reduction of ethylene levels by cleaving ACC into alpha-ketobutyrate and ammonium (Shah et al. 1998). This activity is also related with the tolerance to various types of stress such as flooding, drought, salinity, wilting and organic contamination (Glick 2014). It is likely that NNEB with ACC deaminase activity plays an important role in the microaerophilic metabolism of the nodule by reducing the level of ethylene and thus leading to a better ontogeny and organogenesis (Murset et al. 2012). Biocontrol is the process of suppressing pathogenic living organisms by using other living organisms. Antagonism and antibiosis, and production of hydrogen cyanide, exopolysaccharides and lytic enzymes (cellulase, pectinase and chitinase) are main mechanisms involved in biocontrol activity (Hayat et al. 2010; Bhattacharyya and Jha 2012; Bulgarelli et al. 2013; Santoyo et al. 2016). Methodologies to evaluate PGPB traits have been reported by Arora et al. (2001) and Castellano-Hinojosa and Bedmar (2017).

Table 6.2 Direct and indirect mechanisms of plant growth promotion in non-nodular endophytic bacteria (NNEB)

PGPB trait	NNEB strain	References
Direct mechanism		
N_2 fixation	*Burkholderia* sp. CCBAU 15508, *Pantoea* sp. CCBAU 15488, *Serratia* sp. CCBAU 15465	Li et al. (2008)
	Bacillus cereus MQ23	Zhao et al. (2011)
	Enterobacter sp. MSP10	Tariq et al. (2014)
	Bacillus megaterium LNL6	Subramanian et al. (2015)
	Enterobacter sp. A3CK	Ghosh et al. (2015)
	Enterobacter ludwigii ABG6	Dhole et al. (2016)
	Acinetobacter calcoaceticus DD161, *Bacillus cereus* DD176, *Bacillus amyloliquefasciens* DD222, *Enterobacter cloacae* DD198, *Pseudomonas putida* DD201	Zhao et al. (2017)
Phosphate solubilization	*Serratia* sp. CCBAU 15465	Li et al. (2008)
	Serratia marcesens KR-4	Selvakumar et al. 2008
	Microbacterium ginsengisoli BLN6	Palaniappan et al. (2010)
	Exiguobacterium sp. M2N2c	Rajendran et al. (2012)
	Bacillus subtilis M6	Tariq et al. (2012)
	Bacillus UFPI CB1-8	Da Costa et al. (2013)
	Burkholderia sp. CSR2, *Enterobacter cancerogenus* CIR17C, *Paenibacillus sonchi* IAR22, *Pantoea* sp. HBR8, *Rahnella aquatilis* ERR5, *Rhizobium leguminosarum* IAR30, *R. phaseoli* ERR17, *R. lusitanum* CPSR4B,	Aserse et al. (2013)

(continued)

Table 6.2 (continued)

PGPB trait	NNEB strain	References
	Serratia proteamaculans HBR15	
	Pseudomonas sp. NCHA35	Ibáñez et al. (2014)
	Ochrobactrum sp. MSP9	Tariq et al. (2014)
	Enterobacter sp. A3CK	Ghosh et al. (2015)
	Bacillus megaterium LNL6	Subramanian et al. (2015)
	Paenibacillus sp. M15	Pandya et al. (2015)
	Bacillus subtilis CNE215	Saini et al. (2015)
	Klebsiella pneumoniae AG4	Dhole et al. (2016)
	Enterobacter sp. NAB69	Koli and Swarnalakshmi (2017)
	Bacillus megaterium NMp082	Chinnaswamy et al. (2018)
ACC deaminase activity	*Burkholderia* sp. CCBAU 15508, *Pantoea* sp. CCBAU 15488;	Li et al. (2008)
	Bacillus thuringiensis KR-1, *Serratia marcesens* KR-4	Selvakumar et al. (2008)
	Microbacterium ginsengisoli BLN6	Palaniappan et al. (2010)
	Bacillus cereus MQ23	Zhao et al. (2011)
	Exiguobacterium sp. M2N2c	Rajendran et al. (2012)
	Bacillus subtilis M2	Tariq et al. (2012)
	Enterobacter sp. CIR19	Aserse et al. (2013)
	Paenibacillus UFPI CB7-8	Da Costa et al. (2013)
	Micromonospora saelicesensis AL16	Martínez-Hidalgo et al. (2014)
	Ochrobactrum sp. MSP9	Tariq et al. (2014)
	Enterobacter sp. A3CK	Ghosh et al. (2015)
	Paenibacillus sp. M10	Pandya et al. (2015)
	Bacillus megaterium LNL6	Subramanian et al. (2015)

(continued)

Table 6.2 (continued)

PGPB trait	NNEB strain	References
	Enterobacter ludwigii ABG6	Dhole et al. (2016)
	*Bacillus subtilis*EB10	Egamberdieva et al. (2017)
	Pseudomonas brassicacearum Zy-2-1	Kong et al. (2017)
	Pseudomonas putida DD201.	Zhao et al. (2017)
Ammonia Production	*Enterobacter asburiae* KR-3	Selvakumar et al. (2008)
	Bacillus subtilis CNE215	Saini et al. (2015)
Siderophore production	*Microbacterium ginsengisoli* BLN6	Palaniappan et al. (2010)
	Bacillus megaterium LNL6	Subramanian et al. (2015)
	Enterobacter sp. A3CK	Ghosh et al. (2015)
	Chryseobacterium indologenes AM2, *Enterobacter cloacae* ACP3, *Pseudomonas aeruginosa* ABG5	Dhole et al. (2016)
	Pseudomonas brassicacearum Zy-2-1	Kong et al. (2017)
	Bacillus megaterium NMp082	Chinnaswamy et al. (2018)
	Microbacterium ginsengisoli BLN6	Palaniappan et al. (2010)
	Bacillus cereus MQ23	Zhao et al. (2011)
	Exiguobacterium sp. M2N2c	Rajendran et al. (2012)
	Burkholderia sp. CIR1, *Cronobacter dublinensis* CIR9B, *Enterobacter cancerogenus* CIR17C, *Panteoa agglomerans* CSR8A, *Pseudomonas* sp. HBR44, *Serratia proteamaculans* HBR15	Aserse et al. (2013)
	Pseudomonas sp. NCHA35, NVAM24, *Klebsiella* sp. TT001	Ibáñez et al. (2014)
	Enterobacter sp. A3CK	Ghosh et al. (2015)
	Bacillus anthracis M1	Pandya et al. (2015)

(continued)

Table 6.2 (continued)

PGPB trait		NNEB strain	References
		Pseudomonas aeruginosa ABG5	Dhole et al. (2016)
		Pseudomonas brassicacearum Zy-2-1	Kong et al. (2017)
		Acinetobacter calcoaceticus DD161	Zhao et al. (2017)
		Pseudomonas yamanorum B12, *Ps. fluorescens* B8P, *Rahnella aquatilis* B16C,	Bahroun et al. (2018)
		Bacillus megaterium NMp082	Chinnaswamy et al. (2018)
Root colonization and biofilm production		*Agrobacterium tumefasciens* M5, *Bacillus simplex*, *B. subtilis* M2, M6	Tariq et al. (2012)
		Ochrobactrum sp. MSP9	Tariq et al. (2014)
Indirect mecanisms			
Extracellular enzymatic activity	Protease, lipase y celulase	*Paenibacillus sonchi* IAR22; *Rahnella aquatilis* ERR5; *Pseudomonas* sp. HBR44; *Serratia* sp. HBR25; *Burkholderia* sp. CSR2; *Serratia liquefaciens* HBR16B; *Variovorax paradoxus* CIR11Bs.	Aserse et al. (2013)
	Pectinase, celulase, xilanase, caseinase, gelatinase, amilase y lipase, alkaline phosphatase	*Micromonospora saelicesensis* AL16, ALFb1, ALF7, *M. chokoriensis*AL20, *M. echinospora* ALFb4, *M. aurantica* ALFb5, *M. lupini* ALFpr18C	Martínez-Hidalgo et al. (2014)
	Pectinase, quitinase	*Bacillus* sp. M11, M17, *Paenibacillus* sp. M15	Pandya et al. (2015)
	Lipase, protease, celulase y quitinase	*Bacillus cereus* EB2, *B. subtilis* EB10	Egamberdieva et al. (2017)
Antifungic activity	HCN production	*Bacillus thuringiensis* KR-1	Selvakumar et al. (2008)
		Rahnella aquatilis B16C	Bahroun et al. (2018)

(continued)

Table 6.2 (continued)

PGPB trait		NNEB strain	References
	Fusarium oxysporum, *Magnaporthe grisea*, *Botrytis cinerea*, *Alternaria alternata*	*Bacillus cereus* MQ23	Zhao et al. (2011)
	Alternaria burnsii	*Exiguobacterium* sp. M2N2c	Rajendran et al. (2012)
	Macrophomina phaseolina	*Bacillus* sp. M11, M17 y *Paenibacillus* sp. M15	Pandya et al. (2015)
	Macrophomina phaseolina, *Rhizoctonia solanii*, *Fusarium solanii*, *F. oxysporum*	*Pseudomonas* sp. NAFP-4, NAFP-7, NAFP-27	Noreen et al. (2015)
	Phytophthora sojae	*Acinetobacter calcoaceticus* DD161	Zhao et al. (2017)
	Fusarium solanii	*Bacillus subtilis* EB10	Egamberdieva et al. (2017)
		Rahnella aquatilis B16C	Bahroun et al. (2018)
	Sclerotinia sp., *Botrytis* sp.	*Bacillus megaterium* NMp082	Chinnaswamy et al. (2018)
Nematicidal activity	*Meloydogine javanica*	*Pseudomonas* sp. NAFP-12 to NAFP-32	Noreen et al. (2015)

6.5 Utilization of Non-nodulating Endophytic Bacteria for Plant Inoculation

Although agricultural production heavily depends on the use of synthetic fertilizers to provide essential plant nutrients (e.g. as nitrogen, phosphorus and potassium), the overuse of fertilizers is causing unexpected environmental problems (Erisman et al. 2015). In this sense, the use of efficient inoculants based on PGPB, by decreasing the use of chemical fertilizers, is a vital strategy for sustainable agricultural management and mitigation of environmental impacts (Bulgarelli et al. 2013; Santoyo et al. 2016; Erisman et al. 2015). The success of NNEB as inoculants for agricultural crops is dependent of various factors such as their ability to: colonize plant roots where co-exist microbial competition and survival in the soil (Alquéres et al. 2013; Beauregard et al. 2013); increase the production of plant exudates which interfere with the plant-bacteria interaction (Carvalhais et al. 2013); improve soil health which is highly dependent of management practices, etc. (Hayat et al. 2010).

Examples of NNEB used as inoculants for different plant species, including cereal and legumes, under greenhouse and field experiments have been reported (Lugtenberg and Kamilova 2009; Compant et al. 2010; Hayat et al. 2010; Bhattacharyya and Jha 2012; Gamalero and Glick 2011; Souza et al. 2015; Santoyo

et al. 2016 and references therein). The effect of NNEB on growth promotion has been widely demonstrated in oilseed legumes, such as soybean (Li et al. 2008; Bisht and Mishra 2013; Zhao et al. 2017) and peanut (Ibáñez et al. 2009; Dhole et al. 2016), as well as grain legumes such as lentil (Bisht and Mishra 2013), chickpea (Egamberdieva et al. 2017; Koli and Swarnalakshmi 2017), cowpea (Da Costa et al. 2013) and mung bean (Noreen et al. 2015) Table 6.3. Forage legumes such as clover (Sturz et al. 1997) and alfalfa (Martínez-Hidalgo et al. 2014; Chinnaswamy et al. 2018) showed a grow-positive effect after inoculation with NNEB Table 6.3. A list of NNEB and their effects of plant growth promotion after single inoculation is shown in Table 6.3.

Nevertheless, utilization of NNEB in plant inoculation experiments has been mostly confined to greenhouse assays and in vitro screenings. Assessment of the feasibility of beneficial bacteria under field conditions is difficult since the response of microorganisms differs from laboratory to greenhouse and field conditions (Glick 2012). Inoculation methods are essential for the success of NNEB as biofertilizers and several studies show the differences found in relation with the method used (Herrmann and Lesueur 2013; Schoebitz et al. 2013; Bashan et al. 2014). A study aimed to test the NNEB revealed that genera *Azospirillum*, *Bacillus*, *Pseudomonas*, *Azotobacter*, *Serratia*, *Rhanella* and *Herbaspirillum* are associated with yield promotion in cereal and other crops (Szilagyi-Zecchin et al. 2014).

Because the ancestral relationship between legumes and rhizobia, it is assumed that the bacterial partners are not pathogenic for their cognate plants, and legumes are used without any prejudice for human and animal feeding. In this sense, co-inoculation of NNEB with rhizobial species is a common practice aimed to increase crops productivity due to their positive effect related with the increase in root development and nodule biomass (Korir et al. 2017). *Bacillus* and *Paenibacillus* promoted plant growth when used together with *Rhizobium* in chickpea plants and co-inoculation of P-solubilizing NNEB and *Rhizobium* stimulated plant growth more than their separate inoculation (Souza et al. 2015). Bai et al. (2002) also reported that co-inoculation of soybeans with *Bacillus* and *Bradyrhizobium* increased nodulation, plant growth, nitrogen content and the yield of the grain harvest. Results by Tariq et al. (2012) showed that co-inoculation of crop specific rhizobia together with NNEB improve nodulation and grain yield of *Vigna radiata* plants using strains of *Bacillus subtilis*, *Bacillus simplex* and *Agrobacterium tumefaciens*.

Nevertheless, NNEB strains do not necessarily increase the efficiency of the rhizobia among different leguminous plants (Camacho et al. 2001). Thus, the different responses to co-inoculation underscore the need to describe appropriate rhizobia-NNEB combinations to enhance growth of legumes under particular environmental conditions and soil types, but co-inoculation, frequently, increases growth and yield, compared to single plant inoculation (Araújo et al. 2009). In some cases, however, inoculation with NNEB had a negative effect on growth and yield parameters. Whereas inoculation with many *Agrobacterium* strains reduced the nodulation of *Rhizobium gallicum* in common beans, nodulation of alfalfa plants by *Ensifer meliloti* was not affected (Mrabet et al. 2006). Table 6.4 shows the effects of co-inoculation with NNEB and rhizobia under greenhouse conditions.

Table 6.3 Growth promotion effects of single inoculation of non-nodular endophytic bacteria (NNEB) under greenhouse conditions

Host	Type of effect	NNEB	References
Trifolium pratense, Red trebol	Increase plant height (1.6%), Shoot length (45.8%), Plant dry weight (57.6%), Shoot dry weight (35.3%), and Root dry weight (112%).	*Curtobacterium luteum*	Sturz et al. (1997)
Glycine max, Soybean	Increase shoot lenght (11.2%)	*Serratia* sp. CCBAU 15460	Li et al. (2008)
	Shoot fresh weight (4.3%)	*Bacillus* sp. CCBAU 15518	
Arachys hypogaea, peanut	Increase shoot fresh weight (52.9%)	*Klebsiella* sp. (NTI31, TT001)	Ibáñez et al. (2009)
	Increase shoot dry weight (58.6%)	*Pseudomonas* sp. (NCHA33, NCHA35, NVAM24)	
	Increase shoot dry weight (48.6%)	*Enterobacter* sp. (*NMAN11, NONC13*)	
Sophora alopecuroides	Shoot lenght (34.8%), Root lenght (8.9%), shoot Fresh Weight (53.6%), Shoot Dry Weight (116.7%) and Root Dry Weight (73.4%)	*Bacillus cereus* MQ23	Zhao et al. (2011)
Trigonella foenum-graecum	Increase in shoot and root lenght, chlorophyll content, Nodule number per plant and Nodule Dry Weight.	*Exiguobacterium* sp. M2N2c	Rajendran et al. (2012)
Vigna unguiculata, cowpea	Shoot dry weight (166.7%), Root dry weight (109.2%), plant dry weight (149.4%) and accumulation nitrogen in the shoot (350%)	*Paenibacillus* UFPI B3-9	Da Costa et al. (2013)
Glycine max, Soybean	Increase root dry weight (7.5%), Shoot dry weight (32.5%); Increase root lenght (11.6%), shoot lenght (13.9%) and root fresh weight (7.8%)	*B. thuringiensis* VL572.1, VL4C	Bisht and Mishra (2013)
Lens culinaris, Lentil	Increase root lenght (8.1%), shoot lenght (25.4%), root dry weight (46.5%) and shoot dry weight (42.1%)	*B. thuringiensis* VLG15	
Macrotyloma uniflorum	Increase root lenght (20.0%), shoot lenght (40.6%), root dry weight (53.0%) and shoot dry weight (85.0%)	*B. thuringiensis* VL4C	
Vigna umbellata, Ricebean	Increase root lenght (9.7%), shoot lenght (13.9%) and shoot dry weight (35.8%)	*B. thuringiensis* VL4C	

(continued)

Table 6.3 (continued)

Host	Type of effect	NNEB	References
Medicago sativa, Lucerne	Shoot to root ratio (75.7%)	*Micromonospora saelicesensis*ALF7	Martínez-Hidalgo et al. (2014)
	Shoot Dry Weight (30.0%), Shoot Carbon (26.2%), Shoot Nitrogen (101%), shoot P (37.7%) and shoot K (41.9%)	*Micromonospora aurantiaca* ALFr5	
	Root Dry Weight (22.5%)	*Micromonospora aurantiaca* ALFb5	
Vigna radiata, mung bean	Increase in seddling Vigour Index and Plant Lenght	*Bacillus safensis* M11	Pandya et al. (2015)
Vigna radiata, mung bean	Increase Shoot length (14.0%), Shoot weight (51.3%)	*Pseudomonas* sp. NAFP-19	Noreen et al. (2015)
	Increase root lenght (24.2%), Root weight (65.4%)	*Pseudomonas* sp. NAFP-32	
Arachis hypogaea, peanut	Increase germination (38.5%), Shoot fresh weight (45.8%), dry biomass (68.54%)	*Chryseobacterium indologenes* AM2	Dhole et al. (2016)
	Increase germination (38.5%), Root lenght (116.6%), nodules per plant (87.4%)	*Enterobacter cloacae* ACP3	
	Shoot lenght (48.1%)	*Klebsiella pneumoniae* AG4	
	Increase chlorophyll content (16.1%)	*Pseudomonas aeruginosa* ABG5	
Adesmia emarginata	Increase plant height (28.1%)	*Labrys* sp. AG-45	Gerding et al. (2017)
	Increase root dry weight (9.8%), shoot dry weight (38.1%)	*Labrys* sp. AG-49	
Adesmia tenella	Increase root dry weight (171.4%), shoot dry weight (62.5%)		
Cicer arietinum, Chickpea	Increase in shoot lenght (3.6%), root dry weight (40.0%), shoot dry weight (20.0%)	*B. subtilis* NUU4	Egamberdieva et al. (2017)
Cicer arietinum, Chickpea	Increase in shoot dry weight (40.63%), root dry weight (45.09%)	*Enterobacter* sp. NAB69	Koli and Swarnalakshmi (2017)
Glycine max, Soybean	Increase Shoot lenght (19.2%), root lenght (38.3%), Fresh weight per plant (36.5%) and chlorophyll content (36.7%)	*Bacillus cereus* DD176	Zhao et al. (2017)
Vicia faba, fababean	Increase shoot/root lenght and weight	*Rahnella aquatilis* B16C	Bahroun et al. (2018)
Medicago sativa, Lucerne	Increase shoot weight (68.3%), root weight (62.2%)	*Bacillus megaterium* NMp082	Chinnaswamy et al. (2018)
M. polymorpha	Increase shoot weight (100.0%), root weight (89.2%)		
M. lupulina	Increase shoot weight (89.2%), root weight (60.0%)		
M. truncatula	Increase shoot weight (125.0%), root weight (66.7%)		

Table 6.4 Growth promotion effect of co-inoculation with non-nodular endophytic bacteria (NNEB) and rhizobia under greenhouse conditions

NNEB	rhizobia	Host legume	Growth promotion effect	References
Curtobacterium luteum	*Rhizobium leguminosarum* bv. trifolii	*Trifolium pratense,* red trebol	Increase shoot height (cm) (60.7%) and root lenght (cm) (97.8%),	Sturz et al. (1997)
Bordetella avium			Root dry weight (g/plant) (442.9%)	
Phyllobacterium myrsinacearum			Increase shoot dry weight (cm) (47.9%), total plant weight (g/plant) (118.7%), shoot dry weight (g/plant) (107.7%).	
Bacillus insolitus			Increase Number nodule (442.9%)	
Streptomyces lydicus	*Rhizobium* sp.	*Pisum sativum*, pea	Increase shoot lenght (83.85), root lenght (78.4%), shoot dry weight (61.0%) and number nodules (297.5%)	Tokala et al. (2002)
Bacillus thuringiensis NEB17	*Bradyrhizobium japonicum* 532C	*Glycine max,* soybean	Increase nodule numbers and nodule dry weight	Bai et al. (2002)
Bacillus sp. CCBAU 15518	*Bradyrhizobium japonicum* B15	*Glycine max,* soybean	Increase shoot lenght (cm) (11.0%), Fresh weight (g/plant) (18.3%) and nodule numbers (15.2%)	Li et al. (2008)
Klebsiella sp. (NTI31, TT001)	*Bradyrhizobium* sp. SEMIA6144	*Arachys hypogaea,* peanut	Increase number nodules (43.9%) Shoot dry weight (17.1%)	Ibáñez et al. (2009)
Pseudomonas sp. (NCHA33, NCHA35, NVAM24)			Increase number nodules (10.3%), Shoot dry weight (14.3%)	
Enterobacter (NMAN11, NONC13)			Increase number nodules (79.9%), shoot dry weight (12.4%)	
Bacillus thuringiensis KR1	*Bradyrhizobium japonicum* SB1	*Glycine max, soybean*	Increase in root fresh weight (22.2%), root dry weight (40%), root lenght (35.9%), nodule number (73.3%), shoot fresh weight (12.5%) and shoot dry weight (12%)	Mishra et al. (2009)

(continued)

Table 6.4 (continued)

NNEB	rhizobia	Host legume	Growth promotion effect	References
Bacillus cereus MQ23	*Mesorhizobium* sp. MQ23II	*Sophora alopecuroides*	Increase in shoot lenght (21.3%), root lenght (19.5%), shoot fresh weight (84.9%), shoot dry weight (33.7%), root dry weight (21.4%), number nodules (85.8%)	Zhao et al. (2011)
Exiguobacterium sp. M2N2c	*Sinorhizobium meliloti*	*Trigonella foenum-graecum*	Increase in shoot and root lenght, chlorophyll content, nodule number per plant and nodule dry weight	Rajendran et al. (2012)
Bacillus subtilis M6	*Bradyrhizobium* sp. MN-S	*Vigna radiata,* mung bean	Increase nodule number per plant (78.5%), Nodule dry weight per plant (127.4%) and total plant dry weight (35.6%)	Tariq et al. (2012)
Micromonospora aurantiaca (ALFb5)	*Ensifer meliloti* 1021	*Medicago sativa*, Lucerne	Shoot to root ratio (54.2%), shoot dry weight (26.0%), shoot carbon (23.7%), shoot nitrogen (24.9%), shoot K (35.0%). increase nodulation (107.1%)	Martínez-Hidalgo et al. (2014)
Klebsiella sp. TT001	*Bradyrhizobium* sp. SEMIA6144	*Arachys hypogaea*, peanut	Increase Root dry weight (38.2%), Nodule number per plant (23.2%)	Ibáñez et al. (2014)
Enterobacter sp. NMAN11			Increase dry weight (4.7%)	
Bacillus megaterium LNL6	*Bradyrhizobium japonicum* MN110	*Glycine max*, soybean	Shoot lenght (43.9%), Root lenght (33.8%), Dry Weight (51.0%)	Subramanian et al. (2015)
Bacillus safensis M11	*Ensifer adhaerens* M8	*Vigna radiata*, mung bean	Increase in seddling Vigor Index and Plant Lenght	Pandya et al. (2015)
Pseudomonas sp. NAFP-32	*Rhizobium* sp. NFB109		Increase shoot lenght (5.3%), shoot weight (24.4%), root weight (22.5%), number nodules per plant (8.3%)	Noreen et al. (2015)

(continued)

Table 6.4 (continued)

NNEB	rhizobia	Host legume	Growth promotion effect	References
B. subtilis NUU4	*Mesorhizobium ciceri* IC53	*Cicer arietinum*	Increase in shoot Lenght (35.0%), nodule number (141.7%), Root Dry Weight (20.8%), Shoot Dry Weight (24.3%)	Egamberdieva et al. (2017)
B. megaterium HK6	*Rhizobium* sp. IITA-PAU 987	*Phaseolus vulgaris*	Increase in nodule fresh weight (25.0%), Fixation Biological nitrogen (42.1%), N derived from atmosphere (31.1%)	Korir et al. (2017)
Paenibacillus polimixa HK1	*Rhizobium* sp. IITA-PAU 983		Increase in Shoot dry weight (39.1%), root dry weight (52.3%)	
Bacillus megaterium NMp082	*Ensifer medicae*	*Medicago sativa*, Lucerne	Increase shoot weight (28.2%), root weight (66.1%), number nodules (53.4%)	Chinnaswamy et al. (2018)
		M. polymorpha	Increase shoot weight (71.1%), root weight (196.7%), number nodules (71.1%)	
		M. lupulina	Increase shoot weight (45.1%), root weight (76.5%), number nodule (81.3%)	
		M. truncatula	Increase shoot weight (43.9%), root weight (37.9%), number nodule (81.5%)	

Despite the potential to improve plant growth, the use of NNEB as biofertilizers is not widespread, with the exception of *Azospirillum* which is used for a variety of crops in Europe, South America and Africa (Dobbelaere et al. 1999). The most challenging aspect that limits commercialization of NNEB is the inconsistency in the response to inoculation depending of the plant variety and field location (Bulgarelli et al. 2013; Souza et al. 2015; Santoyo et al. 2016).

6.6 Utilization of Endophytic Bacteria in the Recuperation of Degraded Soils

The increase of the global human population demands greater extensions of arable land to cover the production of food, fodder, fibre and biomass which, in turn, is causing biotic and abiotic stresses to the soil (Dubey et al. 2017). About 30% of the global soil area is degraded or contaminated due to anthropogenic activities (Abhilash et al. 2013). Soil degradation implies reduction and even loss of its physicochemical and biological characteristics, poor agricultural practices and the use of xenobiotic contaminants being the most common cause of the loss of soil quality (Schloter et al. 2018). Among the cultural practices that generate soil degradation are the burning of the vegetation cover, deforestation and monoculture farming, leading to a loss of organic matter by reducing the soil microbial activity and biomass (Kaschuk et al. 2010). Many soils are contaminated with heavy metals and chemical organic compounds that prevent soil utilization for agricultural practices (Dubey et al. 2017 and references therein). NNEB is being used as a biotechnological tool for the recovery of degraded soils and of those contaminated with xenobiotic compounds (Barac et al. 2004; Brader et al. 2014; Bao et al. 2015; Fernández-González et al. 2017; Kong et al. 2017; Pawlik et al. 2017; Dubey et al. 2017; Imran et al. 2017).

In association with NNEB, legumes manage to tolerate high concentrations of heavy metals, improving the phytoremediation process, preventing the entry of heavy metal into the food chain (Kong et al. 2017) and restoring soil fertility by increasing the nitrogen content of the soil (Dary et al. 2010). In legumes inoculated with NNEB, a hyperaccumulation of heavy metals has been observed due to the production of siderophores, biosurfactants and acid phosphatases produced by NNEB (Ray et al. 2017). Excessive use of xenobiotics in agriculture, such as pesticides and chemical fertilizers, results in severe soil contamination (Dubey et al. 2017). Phytoremediation using NNEB is a low-cost technology that can be applied to the restoration of contaminated soils (Ahemad and Khan 2011; Tétard-Jones and Edwards 2016). The recovery of degraded soils can be facilitated by using microorganisms that increase the vegetation cover. Several studies have shown that NNEB has a critical role in the restoration of marginal, degraded and contaminated soils in the prevention of soil erosion and in the afterwards reforestation events (Bashan and de-Bashan 2010). In this sense, soils contaminated with hydrocarbons were successfully recovered using *Lotus corniculatus* and *Oenothera biennis* plants inoculated with *Rhizobium*-, *Pseudomonas*-, *Stenotrophomonas*- and *Rhodococcus*-NNEB (Pawlik et al. 2017). Germaine et al. (2006) showed that the inoculation of *Pisum sativum* with *Pseudomonas putida* VM1450 diminished the content of the herbicide 2, 4-D in the soil and prevented its accumulation in the aerial part of the plant. Similarly, Wani and Khan (2010) showed that treatment with *Bacillus* sp. PSB10 of *Cicer arietinum* seeds mitigated the toxic effects of the hexavalent chromium present in contaminated soils. Moreover, inoculation of *Cytisus striatus* with *Rhodococcus erythropolis* ET54b and *Sphingomonas* sp. D4 resulted in a

better dissipation of hexachlorocyclohexane contaminated soils as compared to the control treatment (Becerra-Castro et al. 2013). Inoculation of legumes with their specific microsymbiont together with an NNEB is also a common practice. Kong et al. (2017) showed that the co-inoculation of *Sinorhizobium meliloti* and *Pseudomonas brassicacearum* Zy-2-1 improved the growth of *Medicago lupulina* in the presence of toxic Cu^{2+} concentrations, and Chinnaswamy et al. (2018) reported that the co-inoculation of *Medicago polymorpha*, *M. lupulina*, *M. truncatula* and *M. sativa* with *Ensifer medicae* and *Bacillus megaterium* NMp082 increased nodulation and plant growth in salty soils. Based on the influence on the physical, chemical and microbiological properties of a soil contaminated with heavy metals, inoculation with NNEB resulted in the improvement of the ecosystem services such as nutrient cycling, microbial biomass and basal soil respiration (Burges 2017). There are still few greenhouse studies, and even less field experiments, directed to demonstrate the ability of NNEB isolated from root nodules of legumes in the recovery of degraded soils; the aforementioned background, however, allows us to infer they have an excellent potential to improve soil health.

6.7 Conclusions and Perspectives

The presence of symbiosis specific N_2-fixing nodule bacteria in legume roots is known since the seventeenth century, albeit it was at the end of the 19th century when Hellriegel and Wilfarth showed that the legume nodules were responsible for nitrogen fixation. In 1888, Beijerinck isolated bacterial cells from nodules of *Vicia faba* that were called *Bacillus redicicola* and later renamed *Rhizobium leguminosarum* by Frank in 1889 (revised in Leigh 2004). Since then, the bacteria nodulating legumes, best known as rhizobia, were studied, and all other morphologically different cells were discarded as contaminants. In the last 20 years, however, evidence accumulated to demonstrate the existence in the nodule interior of other non-nodulating bacteria which are recognized as nodule endophytes. Using confocal microscopy, NNEB have been shown to reach the inner of nodules together with the rhizobia (Pandya et al. 2015) and that accession and accommodation within the nodule is regulated genetically by the host plant (Zgadzaj et al. 2016). Thus, the legume nodule is a complex ecological niche whose microbiome is made up of rhizobia, responsible for nodule formation, and by other bacterial endophytes, named here as NNEB, whose function is poorly known.

The NNEB inside the nodules are analyzed using culture-dependent (culturomic) methods aimed to the obtaining of bacterial species whose plant growth promotion abilities and biocontrol activities could be studied to allow selection of rhizobia and NNEB for the formulation of biofertilizers. The metagenomic techniques, on the other hand, are of valuable interest not only in the sequencing of the 16S rRNA core genes, but also in that of the nodulation genes which will make it possible to define which bacterium was involved in nodule formation and what are the NNEB. Like rhizospheric bacteria, NNEB have direct and indirect mechanisms of plant growth

promotion, and their utilization, whether alone or in co-inoculation with rhizobia, could constitute an ecological and healthy alternative to synthetic fertilizers for legume and non-legume plants.

Most of the research on the mechanisms of plant growth promotion has been done in rhizosphere bacteria, and it is generally assumed that similar mechanisms occur in NNEB. However, the environment in the rhizosphere is quite different to that in the nodule interior, so that differences in the biotic and abiotic stresses outside and outside the nodule (soil type, temperature, pH, oxygen concentration, nutrient availability, etc.) could affect the survival and lifestyle of NNEB. Thus, it is likely that new mechanism of plant growth promotion could be found in NNEB that are unknown in rhizobacteria. Despite several genes have been sequenced that provide some clues on the endophytic lifestyle, the question about what turns a rhizobacteria into a bacterial endophyte is not answered yet, and identification of undiscovered genes involved in endophytism has not been pursued systematically. All this designed to engineer NNEB with improved plant-probiotic capabilities and their use as biofertilizers to increase plant growth and development and to recover degraded soils.

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Chapter 7
Plant–Microbes Relationships in Soil Ecological System and Benefits Accruable to Food Health

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Abstract The excessive use of chemicals in agricultural production gives rise to various issues such as unanticipated environmental impacts, soil biological degradation as well as water contamination. This in many instances has led to eutrophication as well as human health hazards. The concern has raised the question on the safety of food products obtained from this conventional method. It has, therefore, become imperative to adopt biological fertilization strategy that may minimize the use of these inputs. Exploiting the relationships among plants and rhizospheric soil microbes is a rational option. Such interactions are the major factors that determine the health of a plant, plants' yield, and fertility of the soil. The Plant Growth Promoting Rhizobacteria (PGPR) are being used as bio-inoculants for the provision of nutrients, plant growth promotion and to combat plant diseases. The PGPR includes 72 bacterial genera including *Agrobacterium*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, *Serratia*, etc. With the use of these genera, the chemical inputs, and agrochemicals are bound to be reduced in order to sustain benefits to human health. The application of effective PGPR in inoculant technology, therefore, is considered as a vital approach for sustainable soil management and solving environmental issues.

Keywords Plant growth promoting rhizobacteria · Plant-microbe interrelationship · Soil ecology · Food health

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7.1 Introduction

Globally, the significance of sustainable agricultural production cannot be overemphasized, in order to achieve food security for a growing populace. Chemical fertilizers which have become an integral part of present-day agriculture are being used extensively to supply essential plants nutrients in agricultural production. Indiscriminate application of these fertilizers used in the bid to improve crop production has led to soil ecological disturbances such as a reduction in soil biota, nutrient imbalances in plants, increased plants' vulnerability to pests and diseases, reduced nodulation in leguminous plants, plant–mycorrhizal relationships as well as constituting environmental hazards. In addition, the gradual decrease in the population of soil microbes that are beneficial has been linked to the indiscriminate use of chemical fertilizers. The overdependence on chemical fertilizers and its excessive use have also brought about other environmental related issues including degradation of soil and its components, eutrophication caused by excessive runoff of the nutrients into water bodies and also several health issues in humans arising from the consumption of plants having residual chemicals.

7.2 Biological Degradation of Soil

This has been defined as the impairment or elimination of soil microbial population which brings about alterations in biogeochemical processing within the associated ecosystem (Sims 2018). One of the sources of pollutants is the agrochemicals which have shown an imbalance in some of the ecological processes disruption due to the introduction of these chemicals. Aside from polluting the soil environment, it also leads to a reduction in soil fertility. Annual bush fire especially within the savanna ecology for game hunting in the zone also destroyed the ecological biodiversity, depletes the accumulating soil organic matter that has seriously affected the soil macro and microflora and fauna. Soil degradation also manifests by a decrease in the organic matter, as well as the total and available nitrogen and phosphorus forms.

More sustainable alternatives are being exploited in the form of use of plant growth promoting bacteria (PGPR) to boost crop production, maintaining the fertility of soils, as well as decreasing the overdependence on chemical fertilizers. Thus, PGPRs are seen as promising alternatives because of their unique characteristics. Due to the distinctive characteristics of microbes to be able to display several spontaneous biosynthetic activities in response to particular environmental and growth conditions, they have been considered suitable for providing solutions to challenging issues related to life sciences and other aspects. Some soil microbes especially in the rhizosphere, have been shown to secrete plant beneficial substances that enhance crop production such as growth promoters, siderophores, antibiotics, and assisting in the uptake of essential plant nutrients such as phosphorus, potassium and zinc among several others. Plant-microbe interrelationship

within the rhizosphere is the basis for plant well-being, production, as well as the fertility of soils.

In cropping systems, the continuous application of chemical fertilizers decreases the fertility status of soils and also has health implications in humans. Therefore, the integration of PGPR inoculants with chemical fertilizers is a necessity in cropping systems so as to reduce the use of chemicals but at the same time increase productivity. Several authors have proposed an integrated approach in fertilizer technology, which will involve the use of PGPR-based inoculation alongside the right and required levels of chemical fertilizer, this will not only reduce the high usage and overdependence on chemical fertilizers but will also contribute to improved plant growth. Kumar et al. (2009) reported a research carried out using effective plant growth promoting bacteria with a reduction in the amount of chemical fertilizer applied, as an approach for reducing the environmental issues that arise as a result of excessive input of chemical fertilizers while at the same time improving crop production.

7.3 Plant Growth Promoting Rhizobacteria (PGPR)

Different authors have provided various but similar definitions of PGPR. Maheshwari et al. (2010) defined PGPR as the bacteria which through diverse mechanisms can enhance plant growth, reduce plants' susceptibility to disease as well as confer on the plants, a form of defense from abiotic stresses. Grover et al. (2011) noted that PGPRs belong to a beneficial and diverse group of microbes domiciled within the root environment including the rhizosphere and rhizoplane. Ahemad and Kibret (2014) described PGPR as the soil bacteria present within or associated with root surfaces, which synthesize a wide range of regulatory chemicals within the rhizosphere environment thereby directly or indirectly enhancing the growth and development of plants.

The PGPR includes the extracellular PGPR and the intracellular PGPR. The extracellular PGPR could inhabit the rhizosphere surrounding including the rhizosphere itself, root surfaces and even within cellular spaces of root tissues, examples of extracellular PGPR includes *Arthrobacter*, *Azospirillum*, *Bacillus*, *Burkholderia* and, *Pseudomonas* (Gray and Smith 2005). *Frankia* species and the endophytes which include rhizospheric bacteria belonging to the Rhizobiaceae family are examples of intracellular PGPR (Aeron et al. 2014).

7.4 Mechanisms of Action of PGPR

A key attribute of PGPR is the possession of some traits and the mechanisms for influencing plant growth. These traits include nitrogen fixation, nutrient solubilization, phytohormone, and antibiotics production among several others. These

bacterial species enhance plant growth via various systematic ways which include the production of plant hormones (e.g., Indole acetic acid (IAA) and Gibberellin), solubilization of major nutrients (e.g., phosphorus and potassium) and micronutrients such as zinc and also siderophore synthesis. Rocheli de Souza et al. (2015) also stated that PGPR has several mechanisms through which they incite plant growth, these involve genomic processes to make nutrients available for plant use, such as biological nitrogen fixation and solubilization of complex forms of phosphorus, regulation of ACC deaminase to reduce plant stress, as well as production of beneficial compounds that contribute to plant growth, and these include siderophores and phytohormones and several other plant stimulating mechanisms. In addition, Kumar et al. (2012), also listed some ways through which this set of microbes stimulates the growth of plants; these include nutrient availability through biological nitrogen fixation and phosphate solubilization, release of plant beneficial metabolites such as phytohormone, siderophore, 1-Aminocyclopropane-1- carboxylate deaminase and volatile organic compounds (VOCs), bio-control activity such as antifungal activity, defense mechanisms such as disrupting the production of toxic substances disease-causing organisms, stimulation of systemic resistance, rhizosphere engineering, intrusion of sensing signals and prevention of the establishment of biofilm as well as enhancing beneficial plant-microbe symbioses.

Although various researchers have proposed some of the mechanisms of action of PGPR for plant growth promotion, the exact mechanisms are complex and not entirely unraveled. Different species and different strains of bacteria enhance the growth of plants through any of the mechanisms and some strains have also been seen to show multiple mechanisms of plant growth. Earlier researchers have also reported some of the mechanisms to include cytokinins and ethylene production (Glick 1995), non-symbiotic biological nitrogen fixation by free-living bacteria (Boddey and Dobereiner 1995), as well as cyanide production (Flaishman et al. 1996).

Biological nitrogen fixation, solubilization of minerals, resource acquisition, regulation of plant hormone levels, phytohormone productions, synthesis of vitamins, siderophores, enzymes and stimulation of systemic resistance are categorized as direct mechanisms of plant growth promoting activities. These plant growth promoting bacteria reduce plant development impeding impacts caused by various disease-causing organisms through bio-control activities such as antibiotic secretion, chelation of Fe, production of extracellular enzymes which break down the cell walls of fungi and competition for niches within the rhizosphere, these activities are however categorized as indirect methods.

7.4.1 Biological Nitrogen Fixation

A major plant beneficial mechanism that can occur either through symbiotic or asymbiotic association with rhizospheric soil bacteria is through biological nitrogen fixation (BNF). The process of BNF usually occurs through the conversion of

unreactive atmospheric nitrogen through the action of nitrogenase enzyme by bacteria to ammonium (NH_3) which is a form that can be utilized by plants (Bhattacharjee et al. 2008).

7.4.2 Nutrient Solubilization/Availability

The soil is a sink of nutrients from which plants acquire nutrients needed for their growth. A wide range of soil microbes including the major groups plays major roles in the solubilization process depending on the soil environment. Therefore, PGPR is a major source of these microorganisms that accelerate the solubilization process. Solubilization of calcium phosphate is an example, which leads to the release of phosphorus, a vital nutrient required for plant growth but exists in insoluble and inaccessible forms in the soil; as a result, it is the second major chemical fertilizer being applied for crop production. Available P exists in the soil majorly as insoluble organic and inorganic compounds in complex forms.

Plant Growth Promoting Rhizobacteria can solubilize complex soil nutrients by secreting organic acids, sugar acids and carbon dioxide, resulting in a reduced soil pH making it a suitable condition for the solubilization of inorganic compounds. Several phosphate solubilizing soil bacteria including both aerobic and anaerobic strains have been isolated and identified around the rhizosphere and its vicinity. Earlier reports have shown the ability of some isolated and characterized rhizospheric bacteria such as *Agrobacterium*, *Bacillus*, *Burkholderia*, *Erwinia Pseudomonas* and *Rhizobium*, to solubilize complex forms of phosphate such as tricalcium phosphate, dicalcium phosphate, hydroxyapatite and rock phosphate (Hayat et al. 2010). PGPR/plant–root relationship is fundamental in the availability and uptake of phosphorus, especially in low phosphorus soils.

A large percentage of soil potassium which is the third major essential macronutrient is present as complex insoluble forms such as silicate minerals, hence the amount of potassium accessible to plant are usually inadequate. Therefore, the discovery of other easily accessible and/or readily available sources of soil potassium is crucial for sustainable cropping. Potassium solubilizing bacteria can solubilize complex potassium compounds by the synthesis of organic acids. Several rhizospheric bacteria such as *Acidothiobacillus* sp., *Bacillus* sp., *Pseudomonas* sp., *Burkholderia* sp. and *Paenibacillus* sp. are effective soil Potassium solubilizers (Liu et al. 2012).

Other essential soil minerals are the micronutrients, required for plant nutrition although, in very small quantities. While the requirement of these micronutrients is usually in minute quantities, the absence or shortage of one or more of these in the soil may lead to critical issues that may hamper the totality of plant growth in addition to making the macronutrients available as well as accessible for plant use, PGPRs also enhance the availability of soil micronutrients, thereby making them available for plant use. Abaid-Ullah et al. (2011) reported the effectiveness of PGPR in enhancing the availability of soil macronutrients (phosphorus and potassium), as

well as some micronutrients Fe, Zn, and silicate) for plant uptake. Biological plant promoting technology provides a cheaper and eco-friendly alternative, coupled with its ability to carry out soil nutrient bioavailability can, therefore, be a valuable tool in solving micronutrient deficiency-related issues. Aside from the macro- and micronutrients, Plant growth promoting regulators and hormones play crucial roles in plant development. Plant hormones also referred to as phytohormones have been defined as a class of organic substances that are produced during plant metabolism (Shi et al. 2017). Quite a large amount of plant metabolic processes such as nutrient uptake, spatial differences in cellular processes, cell elongation, embryo formation and development and many more biological cellular processes necessary for plant growth are modulated by these phytohormones (Sauer et al. 2013). Phytohormones are classified into five main groups which are: auxins (e.g. indole acetic (IAA) acid), cytokinins, ethylene, gibberellic acid and abscisic acid which reportedly have evident physiological impacts on plant growth when present even at very little concentrations (Shi et al. 2017). Generally, plant hormones are produced by microorganisms as secondary metabolites, which though are not the basis for plant survival but are an integral part of a number of plant metabolic processes which includes competition and defense mechanisms vital for proper plant growth and development. Several rhizosphere bacteria are able to synthesize the five classes of phytohormones, and this has been validated through various laboratory studies, while majority of soil microorganisms can synthesize auxin as well as ethylene, the production of gibberellic acid has however been noted to be limited to a minute category of bacterial and fungal strains (Hedden and Thomas 2012).

Several beneficial bacteria secrete the auxin phytohormone, i.e., IAA which is of great physiological importance in the interrelationship between plant and bacteria. Rhizospheric bacteria have been reported to secrete more auxin-related compounds compared to bulk soil-associated bacteria. In a study carried out by Taiwo et al. (2017), different Plant growth promoting microorganisms isolated from rhizosphere of *Zea mays* were reported to be positive for the production of some plant growth promoting hormones such as IAA, gibberellin and cytokinin and the most promising among the isolates were identified as *Pseudomonas putida, Klebsiella varricola,* and *Bacillus thuringiensis* which produced 2.693, 19.697, and 15.091 mg/l of gibberellic acid; 0.152, 0.348, and 0.132 mg/l of IAA and 5.066, 1.804, and 2.410 mg/l of cytokinin, respectively.

Other studies have shown the production of these phytohormones by different rhizosphere associated bacterial strains of different crops in different countries dating back to several decades and up till now. Among other plant enhancement traits possessed by PGPR, their capability to secrete plant growth hormones in addition to their nutrient solubilizing ability as well as other plant enhancement beneficial substances synthesis such as siderophores and, cyanogens makes them the most suitable group of microorganisms to be considered in crop production.

Another important metabolite produced by PGPR is siderophore, which are extracellular iron transport agents that solubilize and sequester iron which availability to plant is inhibited by its chemical oxidation to highly insoluble ferric salts (Buyer and Sikora 1990). These siderophores play critical roles in the composition

and structure of soil microbiota, in bio-control of soil-borne plant disease-causing organisms and in enhancing growth and grain yield (Sahu and Sindhu 2011).

Ethylene which is a stress hormone is an important growth hormone that can be produced aggressively by plants under stress conditions, however, its uncontrolled production can affect plant root and hence the plant aging process. Plant Growth Promoting Rhizobacteria modulates ethylene production in plants by secreting a deaminase enzyme known as 1-aminocyclopropane-1-carboxylate (ACC).

7.4.3 Induced Systemic Resistance (ISR)

This is a mechanism by which some PGPR enhance the protection of plants against pests and diseases. Prathab and Ranjitha (2015) defined ISR as a physiological state by which the defensive ability induced as a reaction to a specific environmental stimulus is enhanced, The authors further stated that PGPRs through this mechanism bring about resistance against several environmental stressors. Induced System Resistance is not targeted against specific pathogens and a diverse range of soil microbes are able to help plants to be defensive against a broad range of pathogens (Kamal and Yogendra 2014).

As stated earlier, the plant growth promoting bacteria protects plants against pathogens through direct or indirect mechanism. Induced systemic resistance is an indirect method of plant protection mechanisms as against secretion of several antagonistic metabolites like siderophores, bacteriocins, and antibiotics which are direct methods of plant protection (Amar et al. 2013).

7.4.4 Production of Disease Resistance Antibiotics

Bio-control activities through the production of various antibiotic substances are an indirect way by which PGPR promotes plant growth. Many of these rhizobacteria, like *Bacillus* spp. and *Pseudomonas* sp. inhibit pathogens by producing antibiotics which are extracellular metabolites capable of inhibiting plant pathogens even at low concentrations. A large percentage of *Pseudomonas* species and *Bacillus* sp. secretes a wide range of both antifungal and antibacterial metabolites (Chauhan et al. 2016). Antimicrobial metabolites produced by *Pseudomonas* include phenazines, sulfonamide, pyocyanin and pseudomonic acid and azomycin (Ramadan et al. 2016) while *Bacillus* sp. produce metabolites such as polymyxin, circulin and colistin (Maksimov et al. 2011). In addition to siderophore and antibiotics secretion, the majority of bacteria also produce at least one bactericidal activity with some having a broad inhibition spectrum.

7.4.5 Production of Protective Enzymes

As indicated earlier, one of the mechanisms by which Plant Growth Promoting Rhizobacteria promote plant growth is by the secretion of bio-control compounds that acts against plant pathogens. The ability of the majority of PGPR to release cell wall lysing enzymes is one of the devices employed by this set of microbes to control soil-borne pathogens. Chitinase, cellulase, and protease are examples of the cell wall degrading enzymes secreted by PGPR, which through their actions suppress the growth of pathogenic fungi by degrading their cell wall. For instance, chitinase degrades chitin, the major component of the fungal cell wall (Goswami et al. 2016). Their cell wall degrading ability are highly effective such that they can inhibit a wide spectrum of fungi pathogens even *Phytophthora capsici* and *Rhizoctonia solani*, which are considered to be the utmost disastrous plant pathogens worldwide e (Islam et al. 2016). A range of microorganisms including both Gram-positive and Gram-negative bacteria such as *Bacillus* species (e.g., *B. licheniformis, B. cereus, B. subtilis and B. thuringiensis), Serratia marcescens, Enterobacter agglomerans, Pseudomonas aeruginosa,* and *P. fluorescens* have chitinolytic activities which makes them to be considered as potential bio-control agents (Sadfi et al. 2001).

7.4.6 Exopolysaccharide Production

Exopolysaccharides (EPSs) are produced by a diverse group of bacteria as well as algae and plants. They have been defined as high molecular weight, biodegradable polymers formed of monosaccharide residues and their derivatives (Sanlibaba and Çakmak 2016). Exopolysaccharides play several major roles that are directly involved in plant development, these include the maintenance of water potential, soil particles aggregation, facilitating plant root-rhizobacteria interrelationship, sustenance of plants when exposed to pathogens or under stress conditions (salinity, drought, or waterlogging) (Pawar et al. 2013).

7.5 Factors Affecting the Efficiency of PGPR

The success and efficiency of PGPR as effective inoculants is determined by a number of factors and these range from the soil environment, including the soil status, interactions with plant roots and effects of root secretions as well as the capability of the PGPR itself to colonize and establish itself in the rhizosphere. In determining the suitability of bacterial strains to be classified as PGPR, the bacterial strains should have the ability to exhibit at least two of three key traits which are the ability to establish and colonize the soil ecosystem in aggressive manner, enhance

plant growth and exhibition of biological control activities (Vessey 2003). It is, however, noteworthy to state that though inoculating plants with PGPR may temporarily promote the rhizosphere microbial population, sustaining a dense population of the microbes in the rhizosphere for a long time is fundamental in achieving the effectiveness of PGPR in the rhizosphere. Various biotic and abiotic factors including the soil type, pH and microflora have a large impact on PGPR efficiency. Soil health is also an important factor affecting the inoculation efficiency and is determined by several characteristics such as the type of soil, nutrient reservoir, concentrations of toxic metals, soil moisture, microbial composition, and soil perturbations resulting from management activities (Rocheli de Souza et al. 2015). Zahir et al. (2004) noted that the modification of the rhizosphere increases the production and health of the plant by supplementing/replacing the resident microflora with beneficial microorganisms. Roots exudates have also been stated to play a central role in the success and effectiveness of PGPR as inoculants. The plant roots produce quite a limitless variety of compounds in reaction to the prevailing factors in their habitat which includes both the biotic and abiotic factors; this action consequently affects the plant-bacteria interaction.

7.6 Effect of PGPR on Major Crops

Maheshwari et al. (2012) highlighted some ways PGPR technology can contribute to the achievement of agricultural sustainability and these include reducing the dose of chemical fertilizers usage, hence a reduction in production cost and environmental hazards, improved soil fertility through growth enhancement activities that promote sustainable crop production and soil ecology management. Several reports have documented that most of the PGPR strains isolated from rhizospheric soils of several crops in different locations significantly increased plant growth parameters and biomass of various agricultural crops like maize (Gholami et al. 2009), wheat (Cakmakci et al. 2014) and legumes such as common beans, runner beans and beans and soybean (Stefan et al. 2013; Korir et al. 2017). Ashrafuzzaman et al. (2009) reported that most of the PGPR isolates have a significant effect on the emergence, growth parameters and biomass production of rice seedlings. Çakmakçia et al. (2014) showed the effect of PGPR on yield of two cereal crops (spring wheat and barley) under both greenhouse conditions and field studies and noted that they significantly affected their yield, yield components and quality parameters and concluded that this satisfied the nitrogen requirements of the crops under greenhouse and field conditions even irrespective of land elevation above sea levels.

Under field conditions, Zahir et al. (1998) carried out biological growth promoting studies on maize seeds with a combination of four isolates (two *Azotobacter* spp. and two *Pseudomonas* spp.) after NPK fertilizer application and observed that collective inoculation of the isolates considerably increased grain yield by 19.8%, cob weight, cob length, 1000 grain weight, plant height, nitrogen content in the

straw and grain by 21.3%, 20.6%, 9.6%, 8.5%, 18% and 19.8% respectively compared to the un-inoculated control plants. Other reports on maize inoculation were documented by Vedder-Weiss et al. (1999) who showed that maize seed inoculated with *Azospirillum* spp. at a concentration of 10^6 cfu/ml enhanced fresh root and shoot weight of seedlings while Stancheva et al. (1992) showed that maize seeds inoculated with *Azospirillum brasilense* strain 1774 in a blend with 100 kg N/ha fertilizer gave the same result as 200 kg N/ha of non-inoculated plants.

7.7 Influence of PGPR on Soil Respiration

Plant Growth Promoting Rhizobacteria (PGPR) influence some soil microbial activities which include soil respiration. Findings indicate that soil inoculation using some PGPR increased soil respiration by (18%) when compared to the control (Taiwo et al. 2018) as shown in Fig. 7.1. Increasing microbial numbers through inoculation with appropriate and N_2 fixing microbes that are infective and effective in nodulation might lead to an increase in nodulation activities on the rhizoplane. The production of exudates, infection threads arising from plant-microbe interaction and presence of molybdenum (Mo) nitrogenase enzymes could be responsible for the increase in activities of nodulating bacteria and hence improvement in nodulation of cowpea by about 70% as shown in Table 7.1.

7.8 Safety Regulation Considerations

The usage of a wide range of synthetic products including chemical fertilizers, pesticides and growth regulators which are currently being employed for agricultural production calls for public health concerns as they have been implicated to

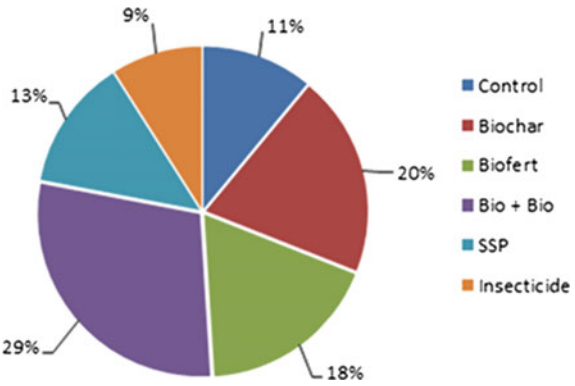

Fig. 7.1 CO_2 efflux evaluation (million/g) in the screenhouse soil (Post-Harvest Analysis) (Taiwo et al. 2018)

Table 7.1 Effect of treatments on the number of nodules of cowpea on the field (Taiwo et al. 2018)

Treatments	Number of nodules
Control	6.0[e]
Biofertilizer	8.0[d]
Biofertilizer + Biochar	10.0[a]
Biochar	9.3[b]
SSP	8.7[c]
Insecticide	9.0[b]

Values followed by different letters are significantly different from each other ($p \leq 0.05$)
SSP = Single Super Phosphate applied at a rate of 60 kg P_2O_5/ha

pose threats to human health and the environment. Owing to the volatile nature of the composition of these products, they cause contamination of groundwater, are taken up by plants and subsequently transferred to the food chain thereby causing public health hazards.

In the search for a more viable biotechnological approach to overcoming the challenges mentioned above, the use of biological growth promoting technique has been explored. These are known to be exogenous bacteria employed in agricultural production to generate a positive impact on the agrobiology of plants. Compared to chemical products, Plant Growth Promoting Rhizobacteria are also effective, but environmentally safe and non-toxic to naturally occurring microorganisms. Up till recently, the focus of inoculant technology was more on the use of nitrogen-fixing bacteria such as *Rhizobium*, *Azospirillum*, *Azotobacter*, however with the recent advances in inoculant technology, there has been a remarkable expansion in the range of microorganisms that are used and this includes a wider range of rhizosphere associated bacteria and fungi. The use of a wide variety of bacteria in inoculant technology has brought about safety concerns thereby necessitating the need for biosafety considerations in the formulation of microbial inoculants. Quite a number of common microbes associated with the environment are opportunistic pathogens, therefore having a knowledge that most PGPR used for inoculant technology originates from the environment, detailed screening and analysis should be carried out in the selection of novel bacterial for their eventual usage as microbial inoculants (Selvakumar et al. 2014).

Plant and human pathogenic rhizobacteria and the likes cannot be considered for application in the field; therefore, safe PGPR should be given utmost priority. In earlier research carried out by Taiwo et al. (2017), some PGPR such as *Chryseobacterium* spp., *K. pneumonia, P. vulgaris, B. cereus, P. monteilli, E. asburiae,* and *Myroides odoratimimus* isolated were eliminated from further study due to their known human pathogenic characteristics. Safety consideration in the formulation and use of PGPR is of paramount importance, not only for human safety and not to impart toxicity to mammals but also to protect the environment. As earlier stated, some of the microbial strains may be opportunistic pathogens with the possibility of causing health hazards to humans, animals or plants, therefore, urgent attention should be given to the establishment of holistic procedures that take

into consideration the predictability, effectiveness, consistency, and especially the biosafety of PGPR for human and animal health and the environment (Vílchez et al. 2015). Important and imperative efforts are required in the field of microbial technology. The scientists are to be aware of the advances in biosafety, to enable them to make up-to-date decisions in their work routine.

7.9 Conclusion

All the beneficial traits of PGPR such as nitrogen fixation, phosphorus and potassium solubilization, micronutrient availability and bio-control activities through various defense mechanisms are key important traits in the formulation of effective bio-fertilizers. Plant Growth Promoting Rhizobacteria when exploited as bio-fertilizers can enhance plant growth, increase grain yield, lower malnutrition rates, ameliorate degraded land, improve soil fertility and reduce over-dependence on chemical fertilizers. The characteristics of PGPR besides economical and eco-friendly attributes can also represent a natural and inexpensive alternative that can mitigate the hazards related to the continuous use of chemical fertilizers. Current practices in agriculture are tilting toward focusing on the reduction of chemical fertilizers and pesticides input; therefore, the exploitation of PGPR inoculants as bio-inoculants offers a promising alternative for more sustainable agriculture.

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Chapter 8
The Role of Rhizobacterial Volatile Organic Compounds in a Second Green Revolution—The Story so Far

Darren Heenan-Daly, Siva L. S. Velivelli and Barbara Doyle Prestwich

Abstract The role of microbial-emitted volatiles (mVOCs) also termed 'info-chemicals' in agriculture is an emerging area of research with many perceived attributes including but not limited to the alleviation of abiotic and biotic stress factors. Several reports in the literature to date have demonstrated the potential of these mVOCs in plant growth-promotion and disease-suppression, albeit mainly under artificial conditions. The mVOCs are low molecular mass compounds with a high vapour pressure and low boiling point and through diffusion can affect a response over a long distance both above and below ground. They belong to many different classes of chemicals that include terpenes, alcohols, alkenes and ketones amongst others. This review examines recent literature in this area and cites examples of mVOCs, or more particularly; bacterial-derived volatile compounds hereby referred to as 'BVCs', that have plant growth promoting and biocontrol effects. The multifaceted role of BVCs can be viewed as an integral part of a second green revolution in agriculture where alternative environmentally-friendly solutions are being sought for crop protection and bio-stimulation. Their ability to modulate plant photosynthetic and ISR pathways may provide the agricultural sector with more sustainable solutions for increased crop protection and production in the face of increasing climate and population changes.

Keywords PGPR · Volatile organic compounds · BVCs · Biocontrol

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8.1 Introduction

The plant rhizosphere is a highly competitive environment with plants releasing as much as 40% of their photosynthetic carbon through their roots with these secreted nutrients enabling the creation of a 'hot-spot' of microbial activity (including rhizobacterial activity) (Kai et al. 2016). Rhizobacteria enhance plant growth through a number of different mechanisms, some known, others as yet unknown (Velivelli et al. 2015). Over the past four decades these microbes have been commonly referred to as 'Plant Growth-Promoting Rhizobacteria' (PGPR) (Kloepper and Schroth 1978; Ryu et al. 2005a). Different mechanisms are involved in the enhancement of plant growth by rhizobacteria. Some of these mechanisms are termed direct, others indirect. Examples of direct mechanisms can include the biosynthesis of chemicals analogous to plant hormones involved in the plant growth process such as indole-3-acetic acid (Shao et al. 2015). The optimisation of plant nutrient-uptake is also facilitated through phosphorus solubilisation (Oteino et al. 2015), nitrogen fixation (Singh 2014) and/or by modulating the levels of ethylene in the plant through the activity of enzymes such as aminocyclopropane-1-carboxylic acid (ACC) deaminase (Glick 2014). Indirect mechanisms include the synthesis of non-volatile antibiotics such as pyoluterin, surfactin and fengycin (Dimkić et al. 2017); competition for nutrients mediated by siderophore production for enhanced iron-uptake from soil (Ahmed and Holmström 2014); the secretion of lytic enzymes (e.g. chitinase, β-1,3-glucanase) and the modulation of plant immunity via activation of the induced systemic resistance (ISR) pathway (Compant et al. 2005; Lugtenberg and Kamilova 2009; Velivelli et al. 2015; Tahir et al. 2017a) Fig. 8.1. In recent years, there has been increased interest in the effects of rhizobacterial volatiles on plants (Weisskopf et al. 2016). The metabolic activity of the soil microbiota involves the synthesis of a broad variety of infochemicals, of which volatile organic compounds (VOCs) comprise a large proportion (Kanchiswamy et al. 2015; Velivelli et al. 2015). VOCs are characterised as having a relatively low molecular weight (<300 Da), a low boiling point and high vapour pressure (Vespermann et al. 2007; Velivelli et al. 2014). Microbial-emitted volatiles (mVOCs) belong to a number of different chemical classes including, but not limited to; alcohols, ketones, alkenes and terpenes (Schulz-Bohm 2017) and to date bacteria have been found to produce over 1000 VOCs (Sharifi and Ryu 2018a). The profile of VOCs emitted depends to a large extent on the external environment, be that soil properties or media components (Fincheira and Quiroz 2018). Infochemicals are of great importance, because volatiles can facilitate both the intra and inter-kingdom interaction between many organisms including plants and microbes (Farag et al. 2017). Due to their capacity to disperse in the atmosphere and to circulate through permeable soil structures, volatiles can exert their effects on plants above and below ground (Sharifi and Ryu 2018a). There are two types of VOCs—organic (e.g. 2,3-butanediol) and inorganic (e.g. HCN, CO_2). The complex

blends of VOCs that rhizobacteria are capable of generating have been the focus of numerous studies over the past decade (Yuan et al. 2017; Song and Ryu 2018; Tahir et al. 2017b; Blom et al. 2011a) These VOC blends can have beneficial or detrimental effects on the growth of plants, fungi and other associated organisms within the environment of the respective VOC-emitter (Effmert et al. 2012) Table 8.1. Exposure to BVCs can enhance plant growth under certain conditions, but can induce phytotoxic effects in others (Rath et al. 2018). Different blends of volatiles have been implicated in seed germination, flowering time and number, and in fruit and seed production (Sharifi and Ryu 2018a). A variety of chemical signalling molecules are produced by both rhizobacteria and plants when grown together, demonstrating that active communication exists between these kingdoms during plant development (Leach et al. 2017; Farag et al. 2017). For example, microbe-derived compounds are detected by plants, which can then adapt their defence and growth responses to specific types of microorganism. Furthermore, for the exploitation of BVCs in agronomical contexts, we need to determine both their activity and validity-for-use in the field (Rosier et al. 2018). Therefore, it is essential to have a comprehensive understanding of the biocontrol mechanisms of these agents so as to facilitate efficient and effective agronomic application.

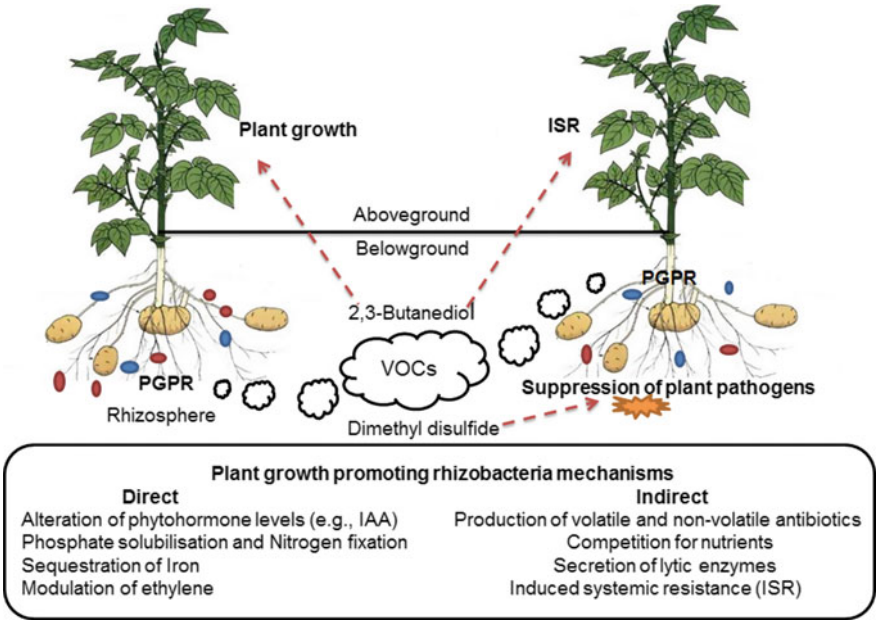

Fig. 8.1 Representation of interactions of bacterial volatile organic compounds (VOCs) on plants (reproduced with permission from Velivelli et al. 2014)

Table 8.1 List of some of volatile-mediated effects of bacteria on plants, fungi and nematodes

Bacteria	Volatile metabolites	Functions	References
B. subtilis GB03,	2,3-butanediol	Growth promotion and ISR	Ryu et al. (2003, 2004); Song et al. (2019)
B. amyloliquefaciens IN937a *P. chlororaphis* O6	2,3-butanediol	Protection against drought stress	Cho et al. (2008)
B. subtilis FB17	Acetoin	Induced systemic resistance (ISR)	Rudrappa et al. (2010)
B. megaterium XTBG34	2-pentylfuran	Growth promotion	Zou et al. (2010)
A. agilis UMCV2	Dimethylhexadecylamine	Growth Promotion	Velázquez-Becerra et al. (2011)
P. polymyxa E681	Tridecane	Induced systemic resistance (ISR)	Lee et al. (2012)
B. ambifaria	Dimethyl disulphide, Acetophenone, 3-hexanone and 2,5-dimethyl pyrazine	Growth promotion	Groenhagen et al. (2013)
P. vulgaris JBLS202	Indole	Growth promotion	Yu and Lee (2013)
S. plymuthica HRO-C48	Dimethyl disulphide	Fungal growth inhibition	Muller et al. (2009)
Bacillus sp.	Acetoin	Fungal pathogen inhibition	Arrebola et al. (2010)
Flavobacterium sp. GSE09 *Lysobacter enzymogenes* ISE13	2,4-di-tert-butylphenol	Fungal growth inhibition	Sang et al. (2011)
P. polymyxa BMP-11	1-octen-3-ol,benzothiazole and citronellol	Fungal growth inhibition	Zhao et al. (2011)
X. campestris pv. *vesicatoria* 85-10	Decan-2-one	Fungal growth inhibition	Weise et al. (2012)
B. ambifaria	Dimethyl disulphide, 2-nonanone, 1-phenyl-1,2-propanedione, 2-undecanone, dimethyl trisulfide, 4-octanone, S-methylmethanethiosulphonate and acetophenone	Fungal growth inhibition	Groenhagen et al. (2013)

(continued)

Table 8.1 (continued)

Bacteria	Volatile metabolites	Functions	References
A. agilis UMCV2	Dimethylhexadecylamine	Fungal growth inhibition	Velázquez-Becerra et al. (2013)
B. atrophaeus CAB-1	O-anisaldehyde	Fungal growth inhibition	Zhang et al. (2013)
B. megaterium YMF3.25	Benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone and dimethyl disulphide	Nematicidal activity	Huang et al. (2010)
Streptomyces spp.,	Caryolan-1-ol	Fungal growth inhibition	Cho et al. (2017)
P. flourescens SS101	13-Tetradecadien-1-ol	Plant growth promotion	Park et al. (2015)
B. subtilis SYST2	Albuterol 1,3-propanediol	Plant growth promotion and ISR	Tahir et al. (2017a, b)
B. amyloliquifaciens FZB42, *B. artrophaeus* LSSC22	1,2-Benzisothiazol-3(2 H)-one, Benzaldehyde, 1,3-butadiene	Bacterial growth/ motility inhibition and ISR	Tahir et al. (2017c)
S. odorifera 4Rx13	Carbon dioxide	Growth promotion	Kai and Piechulla (2009)

8.2 Rhizobacterial Volatiles and Plant Growth

The direct physical interaction between rhizobacteria and their respective plant host underpins most PGPR-plant interactions. However, an emerging field over the past number of years has examined the long-distance relationships which plants and rhizobacteria can achieve via the medium of VOCs (Velivelli et al. 2014). The first observation of this phenomenon was by Choong-Min Ryu and co-workers and this has led to the opening of many new avenues in the field of plant–microbe interactions. Where physical contact with the plant is not possible, certain rhizobacteria rely on the production of BVCs, a classic example being the volatile alcohol, 2,3-butanediol or more specifically its stereoisomer '2R, 3R- butanediol' to stimulate plant development or activate ISR (Ryu et al. 2003, 2004; Lee et al. 2012; Fincheira and Quiroz 2018) Fig. 8.1. The identification of various plant growth promoting infochemicals and the determination of their structures and their associated functions have been ground-breaking moments in the study of plant-microbe interactions and pinning down the roles of VOCs in the intricate signalling systems between plants and rhizobacteria has been the key area of interest among a number of research groups (Bailly and Weisskopf 2017; Sharifi and Ryu 2018a).

Nevertheless, the contribution of rhizobacterial VOCs to plant development and the importance of these compounds in agricultural systems are still topics of significant debate and speculation. In addition, only a handful of VOCs that are secreted by rhizobacteria have been identified to date. Therefore, a comprehensive understanding of the biological and ecological functions of BVCs—let alone a full understanding of their potential uses—has yet to be achieved.

However, according to Fincheira and Quiroz (2018), mVOCs can influence plant growth in at least four ways: 1. Modulation of nutrients; 2. Alteration of hormone levels; 3. Influencing plant metabolism and 4. Changing sugar concentrations.

Most importantly, future studies will need to address the types of responses and signalling cascades that are induced in plants by BVCs. Research focusing on the effects of plant exposure to different BVCs has uncovered a wide range of effects, including significant plant growth, the induction of ISR and even plant phytotoxicity. In particular, 2,3-butanediol (Ryu et al. 2003, 2004) dimethylhexadecylamine (Velázquez-Becerra et al. 2011), 2-pentylfuran (Zou et al. 2010), indole (Blom et al. 2011a; Yu and Lee 2013; Fincheira and Quiroz 2018) and dimethyl disulphide (DMDS) (Groenhagen et al. 2013), are amongst some of the infochemicals that have been shown to increase plant growth, whereas negative effects are at least in part due to the presence of high levels of hydrogen cyanide (HCN) (Blom et al. 2011b), DMDS and ammonia (Kai et al. 2010; Weise et al. 2013). To determine the extent to which BVCs stimulate plant growth, Choong-Min Ryu and co-workers used two-compartment Petri dishes, hereby by referred to as 'I-plates', to physically separate *Arabidopsis thaliana* from rhizobacteria under laboratory conditions. In this way, the dispersal of non-volatile metabolites through the medium was prevented, allowing for only the exchange of volatile organic compounds.

The researchers observed that plant growth was most strongly stimulated by the bacterial strains *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a. When the volatiles produced by these two strains were examined, it was found that these bacteria produced the compounds 3-hydroxy-2-butanone (acetoin) and 2, 3-butanediol, which were not detected in bacterial strains that were unable to induce volatile-mediated plant growth. The exogenous application of these two compounds in pure solutions induced similar effects in a dose-dependent manner, and *Bacillus* spp. mutants defective in 2,3-butanediol and acetoin synthesis showed no plant growth-promotion, which confirmed the role of these compounds in mediating plant growth. A set of hormonal mutant *A. thaliana* lines impaired in specific regulatory pathways was then tested to identify the signalling networks necessary for these growth-promoting activities. It was found that exposure to volatiles from the *B. subtilis* GB03 strain did not promote growth in cytokinin receptor-deficient (*cre1*) or cytokinin/ethylene-insensitive (*ein2*) mutants. On the other hand, the *B. subtilis* GB03 volatiles did promote growth in ethylene-insensitive (*etr1*), auxin-transporter-deficient/ethylene-insensitive (*eir1*), gibberellic acid-insensitive (*gai2*), and brassinosteroid-insensitive (*cbb1*) mutants, suggesting that the promotion of growth elicited by GB03 VOCs is mediated by the cytokinin-signalling pathway (Ryu et al. 2003). Further experiments demonstrated that disease severity caused by the necrotrophic bacterial pathogen *Erwinia carotovora*

subsp. *carotovora* was significantly decreased when *A. thaliana* seedlings were exposed to VOCs produced by *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a. This phenomenon, called 'induced systemic resistance' (ISR), occurred in as little as 4 days. The exogenous application of pure 2,3-butanediol induced similar effects in a dose-dependent manner. Seedlings exposed to *Bacillus* mutants defective in 2,3-butanediol synthesis showed no disease protection, which confirmed the priming activity of this compound in ISR-induction. A set of mutant *A. thaliana* lines impaired in specific regulatory pathways, including a jasmonic acid (JA)-insensitive (*coi1*), an ethylene-insensitive (*ein2*), a salicylic acid (SA)-degrading line (NahG), and a line that is SA-insensitive or non-expressor of pathogenesis-related (PR) genes (*npr*1), was then tested to identify the signalling networks necessary for ISR. Pre-exposure to VOCs from *B. subtilis* GB03 did not trigger ISR in the ethylene-insensitive line (*ein2*) and did not show pathogen resistance. In addition, to further test whether these VOCs induced known signalling pathways in *A. thaliana*, transgenic plants with β-glucuronidase (GUS) fusions to *Pr-1a* (a gene activated by SA), *Pdf1.2* (a gene activated by JA and ethylene), and *Jin14* (a gene activated by JA) were exposed to VOCs released by *B. subtilis* GB03 (Ryu et al. 2004). Of these lines, the JA/ethylene-activated *Pdf1.2*-GUS line showed increased GUS activity compared with untreated control plants.

The plants carrying an ectopic copy of the JA-activated *Jin14* gene were unaffected by *B. subtilis* GB03 VOCs; thus, ethylene signalling may be required for the activation of ISR in *A. thaliana,* independently of the SA and JA signalling pathways. Surprisingly, the VOCs of *B. amyloliquefaciens* IN937a functioned independently of all of the signaling pathways, indicating that some VOCs utilised alternative pathways to trigger ISR (Ryu et al. 2004), and are still not known. Meanwhile, a proteomics study revealed that ethylene biosynthetic enzymes were significantly up-regulated in *A. thaliana* plants exposed to *B. subtilis* GB03 VOCs, and a transcriptomic analysis showed the up-regulation of genes related to ethylene biosynthesis (*SAM-2*, *ACS4*, *ACS12* and *ACO2*) as well as ethylene response genes (*ERF1*, *CHIB* and *GST1*) following exposure to *B. subtilis* GB03 VOCs (Kwon et al. 2010; Velivelli et al. 2015). It was demonstrated that the long-chain volatiles produced by *Paenibacillus polymyxa* E681 stimulated plant growth in *A. thaliana* and induced systemic resistance against *Pseudomonas syringae* pv. *maculicola* ES4326 (Lee et al. 2012; Velivelli et al. 2014).

A set of hormonal mutant *A. thaliana* lines impaired in specific regulatory pathways was tested to identify the signalling networks necessary for plant growth promoting activities. Lee et al. (2012) found that exposure to volatiles from *P. polymyxa* E681 did not promote growth in cytokinin/ethylene-insensitive (*ein2*) mutants. On the other hand, the *P. polymyxa* E681 volatiles did promote growth in jasmonic acid-insensitive line (*coi1*), a salicyclic acid-degrading line (NahG), and gibberellic acid-insensitive line (*gai2*) mutants, indicating that cytokinin/ethylene signalling is essential for the promotion of plant growth in response to *P. polymyxa* E681 volatiles. Further experiments demonstrated that the severity of the disease caused by the hemibiotrophic bacterial pathogen *Pseudomonas syringae* pv. *maculicola* ES4326 was significantly decreased where *A. thaliana* seedlings were

pre-exposed to VOCs produced by *P. polymyxa* E681. In addition, to further test whether *P. polymyxa* E681 VOCs induced known signalling pathways in *A. thaliana*, transgenic plants with β-glucuronidase (GUS) fusions to *Pr-1a* (a gene activated by SA), and *Pdf1.2* (a gene activated by JA and ethylene), were exposed to VOCs released by *P. polymyxa* E681. Of these lines, the SA-activated *Pr-1a*-GUS line showed increased GUS activity compared with untreated control plants; thus indicating SA signalling may be required for the activation of ISR. A further transcriptomic study of *A. thaliana* exposed to VOCs from *P. polymyxa* E681 followed by pathogen challenge revealed the induction of salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) signalling marker genes, *PR1*, *ChiB*, and *VSP2*, respectively. When the volatiles produced by *P. polymyxa* E681 were examined, it was found that this rhizobacteria produced the long-chain volatile compound tridecane. The exogenous application of pure tridecane induced *PR1* and *VSP2* in a dose-dependent manner after pathogen challenge; thus indicating that SA/ET signalling is essential for the activation of ISR in response to tridecane. The researchers performed additional tests to demonstrate whether the observed growth promotion of *A. thaliana* when exposed to *P. polymyxa* E681 was correlated to carbon dioxide (CO_2). Plant growth was still enhanced when exposed to barium hydroxide ($Ba(OH)_2$) which traps CO_2, indicating that some other unknown VOCs are involved in the promotion of growth (Lee et al. 2012; Jeong et al. 2019).

In addition to the impact of BVCs, it has been speculated that increased plant growth could be due to the increase in CO_2 concentrations that is seen to rise when using the sealed petri dish method. Based on co-cultivation studies involving *Arabidopsis* and *Serratia odorifera* in a closed system, it was observed that growth promotion was closely linked to carbon dioxide enrichment. In particular, the growth of *A. thaliana* was stimulated in a closed system, where carbon dioxide was the dominant component of the volatile mixture (390–3000 ppm). By contrast, in an open system under ambient carbon dioxide concentrations, volatiles with negative effects on plant growth became dominant. It is possible that activation of the tricarboxylic acid cycle (TCA) triggers the emission of carbon dioxide, although this molecule does not accumulate to higher-than-ambient concentrations in an open system (Kai and Piechulla 2009). Similarly, the growth of *Physcomitrella patens* (moss) was stimulated in a closed system in which carbon dioxide was the dominant component of an *S. odorifera*-derived volatile mixture, growth of this moss was inhibited in an open system due to the negative influence of volatiles (Kai and Piechulla 2010). At most, high levels of carbon dioxide have been observed to increase plant biomass by as much as 25%, although this was primarily the result of increased starch accumulation rather than biomass expansion. However, it is likely that volatiles are present at much higher concentrations in closed systems than in any found under natural circumstances (Van der Kooij et al. 1999; Ward and Strain 1999; Blom et al. 2011a).

In another study, C16 hexadecane, a long-chain hydrocarbon emitted by *P. polymyxa* E681, also protected *Arabidopsis* plants from infection by the necrotrophic pathogen *Pectobacterium carotovorum* and the hemibiotrophic pathogen *Pseudomonas syringae* pv. *maculicola* ES4326 (Park et al. 2013). Certain

volatiles produced by rhizobacteria regulate plant auxin homeostasis, and can promote growth in *Arabidopsis*. Genes for auxin biosynthesis were up-regulated when aerial parts of the plant were exposed to *B. subtilis* GB03. As observed in a transgenic (DR5:auxin-responsive reporter) *Arabidopsis* line expressing a DR5:: GUS fusion, exposure to *B. subtilis* GB03 volatiles induced a decrease in auxin accumulation in leaves and an increase in roots, indicative of basipetal auxin transport activation. The decrease in auxin accumulation in leaves resulted in enhanced leaf cell elongation, whereas the increase in auxin accumulation in roots led to the development of lateral roots. Thus, despite the fact that auxin is not produced by *B. subtilis* GB03, auxin signalling must be present in the root architecture response elicited by one or more BVC produced by *B. subtilis* GB03. Auxin accumulation to the sites of synthesis was impeded by the application of the auxin transport inhibitor 1-napthylphthalamic acid (NPA), which prevented the *B. subtilis* GB03-induced reduction in shoot auxin levels and the associated growth promotion. Moreover, modifications in cell wall-loosening were observed during transcriptional analysis, which might explain the accelerated cell expansion and leaf growth associated with exposure to *B. subtilis* GB03 volatiles (Zhang et al. 2007). Further experiments revealed that exposure to *B. subtilis* GB03 volatiles caused *Arabidopsis* to increase both its photosynthetic activity and chlorophyll content.

Exposure to BVCs also enhanced endogenous sugar accumulation and also led to the partial suppression of sugar sensing in plants. In contrast to wild-type plants, enhanced photosynthetic capacity (that was not additionally increased by exposure to *B. subtilis* GB03) was observed in the two glucose-insensitive *Arabidopsis* mutants, *gin1* and *gin2*, which lack hexokinase-dependent sugar signalling. Photosynthesis is promoted by BVCs through repression of the hexokinase-dependent sugar signalling pathway. Exposure to *B. subtilis* GB03 causes an overlap in sugar/ABA sensing in plants, as ABA-synthetic transcripts, ABA-responsive genes and ABA levels in leaves become reduced. Furthermore, the increase in photosynthetic efficiency and chlorophyll content induced by *B. subtilis* GB03 can be abolished by exogenous ABA treatment. Therefore, to enhance photosynthesis, some modulate endogenous sugar/ABA signalling and use soil symbionts as regulators of energy procurement by plants (Zhang et al. 2008b). Common photosynthetic markers, which are enhanced by high carbon dioxide levels, include increase of photosynthetic efficiency, chlorophyll content, and sugar accumulation (Kai and Piechulla 2009). Indeed, *Arabidopsis* exhibited enhanced photosynthetic capacity (e.g. chlorophyll content) and iron accumulation following protracted exposure to *B. subtilis* GB03 (Xie et al. 2009). Under normal growth conditions, *B. subtilis* GB03 volatiles triggered a rise in the mRNA levels of Fe-deficiency-induced transcription factor 1 (FIT1), as well as two of its downstream targets, ferric reductase *FRO2* and the iron transporter gene *IRT1*. However, in *Arabidopsis fit1-2* knockout mutants, volatile-induced increases in iron assimilation and photosynthetic efficiency are impaired, suggesting that volatile-induced iron assimilation is mediated by FIT1 (Zhang et al. 2009). To stimulate iron assimilation, *Sinorhizobium meliloti* VOCs induced acidification of the *Medicago truncatula* rhizosphere, which triggers enhanced photosynthetic activity (e.g.

chlorophyll content), an indicator of nutritional Fe status in plants (Carmen Orozco-Mosqueda et al. 2013). *B. subtilis* GB03 volatiles enhance salt tolerance through the sodium transporter HKT1, which is down-regulated in roots and up-regulated in shoots, resulting in a plant-wide reduction in Na+ accumulation versus control plants not exposed to GB03 volatiles (Zhang et al. 2008a). It was demonstrated that tolerance to abiotic stress could be induced in *Arabidopsis* by *Pseudomonas chlororaphis* O6 and the results suggested that this phenomenon was largely due to production of the volatile compound 2,3-butanediol. A *P. chlororaphis* O6 mutant defective in 2,3-butanediol production showed no drought resistance upon bacterial colonisation, which confirmed the role of this compound in induction of drought tolerance.

Interestingly, it was shown that 2,3-butanediol produced by this rhizobacterium facilitated both stomatal closure and drought tolerance through an ABA-1- and OST-1 kinase-dependent manner. A set of mutant *A. thaliana* lines impaired in specific regulatory pathways, including a mutant with reduced ABA synthesis (*aba1*) and a mutant deficient in the protein kinase mediating stomatal regulation in response to drought (*ost-1*) showed no drought tolerance upon *P. chlororaphis* O6 root colonisation. When drought-stressed plants were exposed to 2,3-butanediol, the plants accumulated greater levels of SA than unexposed plants, indicating that the SA signalling pathways are involved in *P. chlororaphis* O6-induced drought tolerance (Cho et al. 2008). *Arbidopsis* plants treated with *Bacillus subtilis* FB17 significantly reduced the severity of the disease caused by the hemibiotrophic bacterial pathogen *Pseudomonas syringae* pv. tomato DC3000. This phenomenon, called 'induced systemic resistance' (ISR), also occurred when *Arabidopsis* plants were exposed to acetoin. *B. subtilis* FB17 mutants defective in acetoin biosynthesis showed reduced disease protection, and this result confirmed the priming activity of this compound in ISR. A set of mutant *A. thaliana* lines impaired in specific regulatory pathways, including a jasmonic acid (JA) mutant (*jar1-1*), an ethylene mutant (*etr1-3*), a salicylic acid (SA) deficient mutant (*NahG*), and a line that is SA-insensitive or non-expressor of pathogenesis-related (PR) genes (*npr1-1*), was then tested to identify the signalling networks necessary for ISR. Of these lines, treatment with *B. subtilis* FB17 and acetoin did not trigger ISR in the *etr1-3*, *NahG* and *npr1-1* lines and did not show the pathogen resistance against *Pseudomonas syringae* pv. tomato DC3000; thus indicating that ISR elicitation is mediated via NPR1 and SA/ET signalling pathways to activate ISR in *Arabidopsis* independently of JA signalling pathway (Rudrappa et al. 2010).

In species such as *B. subtilis,* 2,3-butanediol synthesis is mediated by the transformation of pyruvate into acetocholate by the enzyme 'acetocholate synthase'. Following this, acetocholate decarboxylase converts alpha-acetocholate into acetoin which is subsequently converted to 2,3-butanediol via catalysis mediated by the acetoin reductase/2,3-butanediol dehydrogenase (AR/BDH) (Nicholson 2008).

The conversion of glucose into 2,3-butanediol and acetoin occurs under hypoxic conditions and serves as an electron sink for the generation of NAD+ when aerobic respiration is restricted. Furthermore, low partial oxygen pressure (as generally exists in soil surrounding roots) induces the bacterial acetoin pathway that controls

the production of 2,3-butanediol. Consequently, it is likely that 2,3-butanediol and/or other biologically active molecules are produced by certain root-colonising rhizobacteria at concentrations appropriate to elicit plant reactions (Ryu et al. 2003, 2004). The Methyl Red Voges Proskauer (MR-VP) medium is generally used to determine the ability of bacteria to ferment 2,3-butanediol (Nicholson 2008). As a by-product of the fermentation pathway employed by some rhizobacteria to avoid acidification, the biosynthesis of 2,3-butanediol is often induced on low pH Murashige and Skoog (MS) medium containing sucrose (Ryu et al. 2003). The growth of *Penicillium* spp. was suppressed both in vitro and in vivo by volatiles released by *Bacillus* spp., and citrus fruit inoculated with *Penicillium crustosum* showed reduced disease incidence and severity due to the presence of acetoin. Furthermore, it was observed that longer exposure times led to stronger volatile-mediated antifungal effects; this was attributed to the extended incubation period within the closed system, leading to the restriction of oxygen over time (Arrebola et al. 2010).

On the other hand, it was also demonstrated that the acetoin pathway is optimal in the lifecycle of the necrotrophic bacterial pathogen *Pectobacterium carotovorum* subsp. *carotovorum* WPP14. Mutants defective in the 2,3-butanediol pathway were unable to alkalinise growth media and also showed reduced virulence on potato tubers (Marquez-Villavicencio et al. 2011). Furthermore, the capacity of *Bacillus megaterium* XTBG34 to promote growth in *A. thaliana* was validated by Zou and Co-workers. In particular, a number of compounds produced by this organism, including 2-pentylfuran, were identified by GC/MS analysis, and they showed that plant growth was significantly enhanced by 2-pentylfuran in a dose-dependent manner. The lowest dose at which this compound could enhance plant growth was 0.1 μg, and maximum growth was achieved with 10 μg; by contrast, doses greater than 10 μg inhibited growth (Zou et al. 2010). Santoro and Co-workers examined the effects of BVCs on growth promotion and the enhanced biosynthesis of essential oils (EO), such as pulegone and menthone in *Mentha piperita* (peppermint). The results of this study indicated that BVCs exhibit species-specific effects on plants. BVCs not only trigger secondary metabolite production but also impact pathway flux during certain stages of monoterpene metabolism (Santoro et al. 2011). It was demonstrated that volatiles released by *Proteus vulgaris* JBLS202 stimulate growth in Chinese cabbage and GC/MS analysis showed that indole was the primary headspace volatile compound produced by this bacteria. They showed that plant growth was significantly enhanced by indole in a dose-dependent manner. When plants were exposed to 0.63 μg of synthetic indole, growth was significantly enhanced. Indole and its derivatives are known to be involved in the auxin signalling pathway (Yu and Lee 2013).

Blom and colleagues analysed the effects of different bacterial strains cultured on four distinct media on the growth of *A. thaliana*. Of the bacterial strains tested, one strain promoted growth on all four media tested. GC/MS analysis revealed the presence of a range of compounds, including indole, 1-hexanol and pentadecane, and they showed that plant growth was affected in a concentration-dependent manner by these compounds. Indole promoted growth at low concentrations but showed lethal

effects when used at high concentrations. Furthermore, when 1-hexanol was applied in moderate amounts, it showed weak growth promotion, and pentadecane promoted growth when applied at high concentrations (Blom et al. 2011a).

In another study, rhizobacterial strains were isolated from the rhizosphere of lemon plants (*Citrus aurantifolia*) and then analysed to determine whether their VOCs had an effect on the development of *A. thaliana* roots. Using a simple experimental system involving I-plates, the authors observed several morphological changes in root architecture due to VOCs. It is interesting to note that some rhizobacterial strains stimulated primary root growth and lateral root development. Several compounds were detected by GC/MS, including aldehydes, ketones and alcohols. However, short-chain alcohols, such as 2,3-butanediol and acetoin were not identified in this study, indicating that other VOCs can also trigger plant growth (Gutiérrez-Luna et al. 2010). Exposure to *A. thaliana* plants with *Bacillus megaterium* UMCV1 modified the architecture of the root system in this plant. In particular, the authors observed an inhibition of primary root growth as well as increases in lateral root number, lateral root growth, and root hair length, and they found that reduced cell elongation and cell proliferation in the root meristem was the cause of the inhibition of primary root growth. The analysis of *Arabidopsis* mutant lines defective in either ethylene (*etr1 and ein2*) or auxin (*aux1-7*, *axr4*, *eir1*) signalling revealed that, modifications in root architecture caused by *B. megaterium* UMCV1 may involve either auxin- or ethylene-independent mechanisms. Furthermore, transgenic *Arabidopsis* line expressing a DR5:*uidA* (a reporter line for auxin and ethylene-inducible gene expression) GUS fusion showed reduced expression in root tips (López-Bucio et al. 2007).

Velázquez-Becerra and Co-workers tested the effects of *Arthrobacter agilis* UMCV2 volatiles on alfalfa (*Medicago sativa*), and they found that *A. agilis* volatiles decreased taproot growth and increased lateral root formation, indicating that the BVCs emitted by this bacterium play an important role in root development. Analysis of BVCs produced by this organism revealed a range of compounds, at least one of which, N-N-dimethyl-hexadecanamine, may act as a growth-promoting trigger, affecting root development in *Medicago sativa* in a dose-dependent manner (Velázquez-Becerra et al. 2011).

A study by Tahir and colleagues determined the effect of BVCs from *Bacillus subtilis* SYST2 on tomato was examined. Two compounds, albuterol and 1,3-propanediol were identified as having a positive effect on plant growth with observed increases in auxin and cytokinin in the plant tissues and noticeable increases in expansin gene transcripts. Variations in VOC concentrations and/or plant exposure times can dictate whether an inoculation has positive or negative effects on primary root growth and/or lateral root formation (Tahir et al. 2017b). *Arabidopsis* plants exposed to *Burkholderia ambifaria* volatiles show enhanced biomass, greater numbers of secondary roots and shorter main roots. Analysis of the VOCs produced by this bacterium revealed a range of compounds, including dimethyl disulphide (DMDS), acetophenone and 3-hexanone, 4-methyl-2-pentanone, 4-octanone, and 2,5-dimethyl pyrazine. These compounds were shown to affect plant growth in a concentration-dependent manner, and indeed, treatment with very high amounts could inhibit plant

growth. Plants showed greater biomass when exposed to some concentrations of dimethyl disulphide (DMDS), acetophenone and 3-hexanone. By contrast, high concentrations of 4-methyl-2-pentanone and 4-octanone were lethal to the plants. Finally, 2,5-dimethyl pyrazine promoted growth at lower concentrations, whereas higher concentrations were deleterious to *Arabidopsis* plants (Groenhagen et al. 2013).

Many studies have shown that BVC interact with the host root system and in addition to its role as a structural support for the plant, it is also crucial for the acquisition of water and nutrients from the soil. From an ecological perspective, BVC-mediated alterations in the root system proteome and root architecture may have beneficial effects through increasing bacterial root colonisation and optimising symbiotic interactions (Yaoyao et al. 2017). These symbiotic relationships mediate biochemical interactions which stimulate root growth and development which leads to enhanced levels of bioavailable nutrients for the plant (Velivelli et al. 2015; Hérnandez-Calderón et al. 2018). In reciprocation, PGPR gain access to richer sources of nutrition and carbon through root exudates produced by a healthy plant host (Gutiérrez-Luna et al. 2010; Velivelli et al. 2015).

8.3 Inhibitory Effects of Rhizobacterial Volatiles on Plants

In addition to promoting plant growth, it has been demonstrated that certain BVC have negative effects on plants such as *A. thaliana* (Vespermann et al. 2007). One of the most important sources of nitrogen is ammonia, although this compound has recently been shown to play a number of other biological roles. When *S. odorifera* 4Rx13 is grown on a peptone-rich medium, it produces high levels of ammonia, and when this plant was exposed to *A. thaliana* plants in an I-plate, the bacterium caused the neighbouring plant medium to become alkalinised, leading to reduced plant growth (Weise et al. 2013). Under conditions of low oxygen, such as in a closed system, the production of HCN by some *Pseudomonas* sp. is enhanced (Athukorala et al. 2010). Deleterious effects were observed when *A. thaliana* was exposed to HCN, with a four-fold reduction in growth following exposure to 1 μmol HCN (Blom et al. 2011b). In has also been shown that rhizobacterial volatile compounds such as ammonia and DMDS have negative effects in higher concentrations on *A. thaliana* growth (Kai et al. 2010).

8.4 Effect of Rhizobacterial Volatiles on Fungi and Other Organisms

For truly sustainable agriculture, the strategies we employ to combat plant diseases must become more environmentally-friendly with lower inputs of synthetic chemicals. The use of beneficial microbes as a biological input to sustainable agricultural systems offers an alternative, and potentially more environmentally

stable approach, to conventional agri-chemical-based solutions for the suppression of plant pathogens and the treatment of plant diseases in an integrated pest management system (Velivelli et al. 2015). Despite their powerful antifungal activities, non-volatile antibiotics are unable to spread over long distances, making them only effective at preventing infection by pathogenic microbes/fungi when applied directly to plant roots. The ability of BVC to suppress the growth and proliferation of plant pathogens has attracted ample attention with regard to biological applications and rhizobacterial VOCs have displayed antagonistic activity against pathogenic fungi, which may classify them as novel antibiotic compounds (Velivelli et al. 2015). The best known example of one such inorganic volatile metabolite is hydrogen cyanide (HCN).

Hydrogen cyanide (HCN) is a secondary metabolite produced by some gram-negative *Pseudomonas* spp. upon the hydrolysis of glycine by HCN synthase. *Pseudomonas fluorescens* CHA0 was shown to inhibit the development of *Thielaviopsis basicola*, which causes black root rot in tobacco plants, through the production of HCN (Bailly and Weisskopf 2017). The biocontrol potential of these antibiotics has been experimentally validated through the use of mutant rhizobacterial strains with altered antibiotic production. A hydrogen cyanide negative mutant (*hcn*), *P. fluorescens* CHA0 strain was no longer able to protect tobacco against black root rot (Voisard et al. 1989; Blumer and Haas 2000). A more recent study (Rijavec and Lapanje 2016) proposed that the main contribution of HCN to biocontrol is more indirect and is related to the sequestration of metals and the associated beneficial increase of nutrients to the plant and rhizobacteria.

The volatile inorganic compound ammonia, which is released by the rhizobacteria *Enterobacter cloacae*, suppressed the growth of *Pythium ultimum* in dual-culture assays, thus describing its possible role in the biological control of *Pythium* pre-emergence damping-off (Howell et al. 1988). In addition to HCN and ammonia, the antifungal nature of the organic volatiles has been demonstrated in several experiments. *Pseudomonas* spp. isolated from canola and soybean plants were reported to produce volatile antibiotics including; n-decanal, nonanal, 2-ethyl-1-hexanol, benzothiazole and dimethyl trisulfide, that inhibit the fungal pathogen *Sclerotinia sclerotiorum* in I-plate assays (Fernando et al. 2005). Furthermore, the growth of *S. sclerotiorum* was also suppressed in antifungal bioassays performed in sealed plates containing pure synthetic volatiles such as furfural, benzaldehyde, 1-octanol, 1-octen-3-ol, 3,7-dimethyl-1-ol, 6-octadien-3-ol, 2-ethyl-1-hexanol (Liu et al. 2009).

The growth of *Fusarium oxysporum* f. sp. *cubense* was suppressed in a divided plate assay by BVC produced by *Bacillus amyloliquefaciens* NJN-6. The volatile organic compounds emitted by this organism were diverse and included; benzothiazole, phenol, 2,3,6-trimethyl-phenol, 2-ethyl-1-hexanol, 2-undecanol, 2-nonanone, 2-decanone, nonanal, naphthalene, naphthalene, 2-methyl and naphthalene 1-methyl. The application of pure, synthetic volatiles in the same bioassay revealed strong antifungal activities against *F. oxysporum* f. sp. *cubense* (Yuan et al. 2012).

Jasmonic acid BVC produced by *B. subtilis* significantly inhibited the spore germination of *B. cinerea* in an I-plate assay. An analysis of VOCs revealed a range

of compounds, such 4-Hydroxybenzaldehyde, 2-nonanone, Ammonium acetate, 1,2,4,5-Tetramethyl-pyrazine, 9-Methyl-nonadecane, 2,6,11,15-Tetramethyl-hexadecane, 2,6,10,15-Trimethyl-tetradecane and 8-Hexyl-pentadecane; however, the authors did not evaluate the antagonistic potential of these compounds against *Botrytis cinerea* (Chen et al. 2008). The BVC 2-nonanone showed an inhibitory effect towards *B. cinerea* fungal decay of strawberries in closed containers, thus suggesting its potential role in reducing post-harvest diseases of agricultural products, an area in which there is a significant increase in research activity worldwide (Almenar et al. 2007; Sharifi and Ryu 2018b).

The growth of the soil-borne pathogenic fungi *Rhizoctonia solani* was strongly inhibited in an I plate assay by BVC emitted by a number of common soil bacterial genera such as *Bacillus* spp., *Pseudomonas* spp., *Serratia* spp., and *Stenotrophomonas* spp. Further molecular analysis revealed a wide array of compounds including: β-phenylethanol, trans-9-hexadecene-1-ol, undecene, undecadiene, dodecanal, benzylnitrile, benzyloxybenzonitrile, and dimethyl trisulfide (Kai et al. 2007). Dimethyl disulphide was shown to inhibit the growth of *Fusarium culmorum* in a dual-culture assay and this inhibitory effect on mycelial growth was observed to occur in a dose-dependent manner; less obvious effects were also observed with the use of pure 1-undecene (Kai et al. 2009). Antifungal volatile metabolites produced by *A. agilis* UMCV2 inhibited the growth of *B. cinerea* on sealed plates. The volatile organic compound, dimethylhexadecylamine (DMHDA), which is released by the rhizobacteria *A. agilis*, inhibited the growth of both *B. cinerea* and *P. cinnamomi* in dual-culture assays when provided to the culture medium at low concentrations (Velázquez-Becerra et al. 2013). It has been demonstrated that BVC produced by *Streptomyces plantesis* F-1 could inhibit the growth of *R. solani*, *B. cinerea* and *S. sclerotiorum*. Exposure to *S. plantesis* F-1 BVC significantly reduced the incidence and severity of leaf blight/seedling blight caused by *R. solani*, leaf blight of oilseed rape caused by *S. sclerotiorum* and fruit rot of strawberry caused by *B. cinerea*; thus indicating its possible role as a biofumigant in the biological control of fungal diseases. The analysis of volatile organic compounds from this organism revealed diverse compounds, including but not limited to phenylethyl alcohol, phenol, 2,5-bis(1,1-dimethylethyl)-, (+)-epi-bicyclesesquiphellandrene and cyclohexane carboxylic acid; however, the potential role of these compounds remains to be investigated. As suggested by the complex nature of BVC, significant growth inhibition may require the synergistic activity of multiple compounds or the activity of extremely potent infochemicals normally present at low concentrations (Wan et al. 2008). It has been demonstrated that the volatile metabolites produced by fungistatic soils suppress the growth of *Paecilomyces lilacinus*, *Pochonia chlamydosporia* and *Clonostachys rosea*. In particular, VOCs produced by fungistatic soils, including trimethylamine, benzaldehyde, and N,N-dimethyloctylamine elicit strong antifungal activity in a sealed petri plate assay containing known amounts of fungal spore suspension, autoclaved soil and/or pure synthetic compounds (Chuankun et al. 2004).

In an I plate assay, the volatile organic compound, O-anisaldehyde, which is released by *Bacillus atrophaeus* CAB-1 inhibited the growth of *B. cinerea*; thus

suggesting its possible role in soil fungistatis and the subject of further study (Zhang et al. 2013). The pathogenic activity of various fungal pathogens was suppressed by volatiles emitted by *P. polymyxa* strain BMP-11. The mycelial growth of various fungal pathogens, including *R. solani*, was suppressed in sealed Petri dish antifungal bioassays involving pure, synthetic volatiles such as 1-octen-3-ol, benzothiazole and citronellol; mycelial morphological deformities were also observed (Zhao et al. 2011). Antifungal metabolites produced by *B. subtilis* inhibited the growth of two strains of *R. solani* in sealed I plate assays. Interestingly, these two fungal strains reacted differently to exposure to the *B. subtilis* BVC mixtures, indicating that BVC-mediated interactions between bacteria and fungi can be species/genus specific. Therefore, it is possible that complex volatile mixtures may trigger significantly different responses in different fungi, which may for example be due to differentially conserved molecular activities of fungi for detoxifying metabolites.

Fungal growth modifications due to BVC exposure are not uncommon and indeed are closely linked to growth medium and inoculum dose, and in soil, volatile emissions have been linked to nutrient availability, pH, temperature and oxygen availability (Schulz-Bohm 2017). Rhizobacterial strains emit volatiles that can have distinct effects on fungi or inhibit different fungal types to varying degrees. This could be due to the fact that different BVC blends are released by various rhizobacteria, and inhibitory effects may be induced due to the synergistic effects of several compounds within those respective blends (Velivelli et al. 2015). For example, the fungistatic BVC emitted by *Bacillus cereus* were shown to more strongly repress a *Trichoderma viride* strain than a *Gelasinospora cerealis* strain. Similarly, the BVC released by a strain of *Aerobacter aerogenes* were not as effective against *F. oxysporum* f. sp. *conglutinans* as they were against *T. viride* and *Penicillium* sp. (Fiddaman and Rossall 1994).

Using an I plate assay, it was shown that exposure to *Burkholderia ambifaria* VOCs reduced the growth of fungi, and this inhibitory effect was observed to be stronger against *Alterneria alternata* than it was for *R. solani*. In particular, the growth of *A. alternata* and *R. solani* was decreased by higher doses of dimethyl trisulphide, 2-nonanone, 1-phenyl-1,2-propanedione, and 2-undecanone. Moreover, *R. solani* was also suppressed by acetophenone, phenylpropan-1-one, DMDS, 4-octanone and S-methyl methanthiosulphonate. The growth of *Fusarium solani* was not reduced by any of the volatiles tested, indicating that fungi react to BVCs differently (Groenhagen et al. 2013; Velivelli et al. 2015).

Bacterial volatile patterns can also be affected by growth media. For example, BVC emission profiles differed based on whether the media (nutrient broth) they were grown on contained glucose. The growth of *R. solani* on nutrient broth (NB) was more strongly suppressed by the volatiles produced from *Xanthomonas campestris* pv. *vesicatoria* 85-10 when the latter was grown on NB than when it was grown on nutrient broth with glucose (NBG). *A. nidulans* and *F. solani* exhibited similar growth patterns. The inhibition of *A. nidulans* was stronger when *X. campestris* pv. *vesicatoria* 85-10 was grown on NB than when it was grown on NBG. When *X. campestris* pv. *vesicatoria* 85-10 was grown on NB, the growth of

A. nidulans and *F. solani* was inhibited by 85% and 14%, respectively, whereas growth inhibition on NBG was only 11% and 3.5%, respectively. The BVCs of *X. campestris* pv. *vesicatoria* 85-10 showed only weak effects on *F. solani*, indicating species-specific activity. These results demonstrate that when grown on glucose-containing media, *X. campestris* pv. *vesicatoria* 85-10 BVCs have only a weak effect on fungi, indicating that nutrient levels influence growth inhibition. There are several potential explanations for the observed reduction in growth suppression by *X. campestris* pv. *vesicatoria* when grown on NBG: (1) growth on NB media stimulates the production of a larger amount of suppressive volatiles; (2) the production of suppressive volatiles relies on peptone-rich NB media; (3) the production of suppressive volatiles is restricted by glucose through a mechanism such as catabolite repression; or (4) there is a delay in the production of suppressive volatiles on NBG media (Weise et al. 2012). Fiddaman and Rossall (1994) observed that *B. subtilis* only produced suppressive BVCs in the presence of D-glucose, and not L-glucose (Fiddaman and Rossall 1994). Previously, Fiddaman and Rossall (1993) had assumed that agar containing high levels of glucose, i.e. PDA (potato dextrose agar) and SGA (Sabouraud's glucose agar) with *B. subtilis* would stimulate significant antifungal activity in vitro. By contrast, limited or no in vitro antifungal activity was produced by agar containing little or no glucose (VJA (V8 juice agar), NA (nutrient agar) or 10% TSA (tryptic soy agar) (Fiddaman and Rossall 1993).

Serratia plymuthica strains emitting DMDS as the primary headspace BVC, were seen to inhibit the growth of *Agrobacterium tumefaciens* and *Agrobacterium vitis* strains in dual-culture assays. When *Solanum lycopersicum* plants were inoculated with *S. plymuthica*, it inhibited the growth of *Agrobacterium*, and resulted in the emission of DMDS by the *S. lycopersicum* plants (Dandurishvili et al. 2011). It was demonstrated that *S. plymuthica* HRO-C48 inhibited the growth of *R. solani* using I plates (Kai et al. 2007). When oilseed rape cv. Talent was treated with *S. plymuthica* HRO-C48, disease severity of *Verticillium dahlia* was significantly reduced. This strain also produces DMDS and is registered and distributed by RhizoStar®, E-nema GmbH Raisdorf, Germany (Müller et al. 2009). This strain was shown to suppress *V. dahliae* in strawberry and *R. solani* in lettuce (Kurze et al. 2001; Grosch et al. 2005). The development of DMDS has been targeted as a possible alternative to the fumigant methyl bromide. DMDS was observed to supress phytopathogenic nematodes and fungi in the soil, offering strong evidence for the effect of DMDS against plant-pathogenic fungi (Fritsch 2005) and nematodes (Coosemans 2005). Based on these findings, rhizobacteria that produce DMDS can be classified as natural fumigants and this biocontrol capacity is closely associated with VOC production. Therefore, antifungal VOCs should be considered as significant tools for the control of plant pathogens, in addition to more conventional agrichemicals. At present, Paladin®, a new and effective soil fumigant based on DMDS, had already been registered in the USA, (http://www.arkema.com/en/media/news/news-details/Arkema-receives-U.S.-registration-for-Paladin-soil-fumigant-00001/) and the development of new soil fumigants based on dimethyl disulphide (DMDS) is progressing in Europe.

The growth of *F. oxysporum* was suppressed in an I-plate assay by the BVCs produced by endophytic bacteria. A range of compounds was observed during the analysis of these volatiles, such as 2-pentanone 3-methyl, methanethiol and 3-undecene. However, the authors did not evaluate the antifungal properties of the individual compounds on *F. oxysporum* (Ting et al. 2011). It has been demonstrated that the volatile metabolites produced by endophytic *Burkholderia tropics* strains inhibited the growth of four phytopathogenic fungi: *Colletotrichum gloeosporioides*, *Fusarium culmorum*, *F. oxysporum* and *Sclerotium rolfsii*. Further analysis revealed the existence of numerous compounds, including ∝-pinene, ocimene, limonene and fencona, indicating that these compounds may also play important antifungal roles (Tenorio-Salgado et al. 2013). Considering the effects of BVC on the development of fungi and plants, an obvious question is whether these effects extend to animals living within the soil as well.

In an I-plate assay, volatiles released by *Bacillus megaterium* YMF3.25 were shown to inhibit the hatching of nematode eggs and reduce nematode infections. GC-MS analysis revealed a variety of compounds, such as benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone and DMDS that exhibited strong nematicidal activities against both juveniles and eggs. Additional research will be required to create integrated management systems for lowering root-knot nematode inocula and enhancing crop yields in the field, perhaps by improving bacterial formulation. (Huang et al. 2010).

An analysis of *Lysinibacillus mangiferahumi* BVCs showed nematicidal activity against the root-knot nematode *Meloidogyne incognita*. Volatile analysis revealed the presence of numerous compounds, including 2-octanol, cyclohexene, 3-chloro-4-fluorobenzaldehyde, dibutyl phthalate, 2-nitro-2-chloropropane, dimethachlore, and DMDS. When nematodes were exposed to these pure volatiles in a three-compartment Petri dish assay, the compounds showed growth-inhibitory effects towards nematodes (Yang et al. 2012). Similarly, BVCs produced by soil bacteria showed nematicidal activity against *Panagrellus redivivus* and *Bursaphelenchus xylophilus* in three-compartment Petri dish bioassays. Further analysis revealed significant difference in the nematicidal activity of the VOCs, indicating that VOC-mediated interactions between bacteria and nematodes can be species-specific/isolate-specific. Numerous distinct volatiles were identified, including phenol, octanol, benzaldehyde, benzene, acetaldehyde, decanal, 2-nonanone, 2-decanone, cyclohexene, and dimethyl disulphide. Finally, exposure to pure synthetic VOCs using the same bioassay revealed growth-inhibitory activities against both *B. xylophilus* and *P. redivivus* (Gu et al. 2007).

In a recent study by Cho et al. (2017) it was observed that a novel antifungal volatile, caryolan-1-ol, produced by *Streptomyces* spp., was effective at inhibiting the growth of the fungal pathogen *B. cinerea*. By using a homozygous profiling (HOP) assay in *Saccharomyces cerevisiae,* in which both copies of non-essential genes are deleted, it was determined that caryolan-1-ol most likely inhibits fungal growth by targeting membrane lipid processes and intracellular transport systems in fungi (Cho et al. 2017)

For many bacterial phytopathogens an integral component of their ability to infect susceptible plant hosts is the capacity to be motile, in order to actively seek out sites of colonisation and subsequent infection. To this end, Tahir and colleagues investigated the potential of BVCs from six *Bacillus* spp., to inhibit the motility of the bacterial phytopathogen *Ralstonia solanacaerum (Rsc)* TBBS1, the causative agent of bacterial wilt disease in tobacco. They observed a particularly strong inhibitive effect of BVCs from two strains; *Bacillus amyloliquefaciens* FZB42 and *Bacillus artrophaeus* LSSC22. Three BVCs; 1,2-benzisothiazol-3(2 H)-one, Benzaldehyde and 1,3-butadiene all negatively influenced cell viability, colony size, motility and chemotaxis. Transcriptomic investigation of this activity identified alterations in the expression of pathogenesis-related genes such as *PhcA* which is a global regulator of virulence factors in *Rsc,* as well as genes involved in type III and IV secretion systems, production of extracellular polysaccharides and chemotaxis. Defence genes in tobacco were also up-regulated with over-expression of the proteins *EDS1* and *NPR1* suggesting the activation of the SA pathway in the ISR response to *Rsc*-challenge (Tahir et al. 2017c). Interestingly, in a separate study by Tahir and colleagues it was observed that the BVCs produced by *Rsc* could not elicit a significant plant growth promoting effect. However they did inhibit the growth-promoting potential of *B. subtilis* SYST2 BVCs when plants were exposed to BVCs emitted by both SYST2 and *Rsc.* Co-culture of both bacteria together revealed that they inhibited the growth of one another, but the effect of inhibition by *Rsc* of SYST2 was not as great as SYST2 versus *Rsc* (Tahir et al. 2017c)

8.5 Species-Specific Rhizobacterial Volatiles

The qualitative and quantitative complexity of the VOC profiles of various rhizobacteria can vary significantly. For example, common rhizobacterial strains such as *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a, release a mixture of volatile compounds (e.g. 2,3-butanediol and acetoin) that promote growth in *Arabidopsis thaliana*, whereas other rhizobacterial strains that do not promote growth via VOCs produce different mixtures of compounds, indicating that synthesis of VOCs is a strain-specific phenomenon. Studies have shown that whereas some compounds are isolate-specific, others are produced by more than one type of bacteria (Ryu et al. 2003; Kai et al. 2007). Furthermore, BVC profiles may be affected by growth phase and environmental conditions. For example, different qualitative and quantitative VOC profiles are generated by growth on nutrient broths with and without glucose in *Stenotrophomonas rhizophila* P69. In particular, the production of dimethyl pyrazine and beta-phenylethanol occurs under both growth conditions, whereas trimethyl pyrazine, tetramethyl-pyrazine and beta-phenylethyl acetate are produced when glucose is absent from the growth medium (Kai et al. 2009).

The effect of different bacterial strains cultured on four distinct types of media on the growth of *A. thaliana* were analysed by Blom and Co-workers. They found that more nutrient-rich media Luria-Bertani (LB) caused plant death, whereas all other

media tested—including two less nutrient-rich media, Murashige and Skoog (MS) and the soil mimicking Angle medium—promoted growth (Blom et al. 2011a). MS and LB have significantly different compositions; MS is a mineral medium that contains sugar as a carbon (C) source and has low pH and agar concentrations, whereas LB is a nutrient-rich medium containing hydrolysed proteins with relatively high pH and agar concentrations. Therefore, it is perhaps unsurprising that the same bacteria cultured on these two media types can emit different types of BVCs that elicit different plant responses. Furthermore, these two media types also affect the growth kinetics (maximal volatile production, which is assumed to take place during the stationary phase of bacterial growth) of bacterial strain on these two media, with LB supporting faster growth than MS (Bailly and Weisskopf 2012). The primary factors that determine the qualitative and quantitative distribution of compounds in highly complex mixtures are the metabolic abilities of the bacterial species, as well as the nutrients available in the specific growth conditions. Indeed, differences in the types of BVCs produced by pathogenic and non-pathogenic mycobacteria grown on different types of media have been observed; furthermore, variations were sometimes observed, not only between different media but also within individual analyses (Nawrath et al. 2012). However, it is important to note that results obtained under artificial conditions may not accurately reflect natural conditions and an in-depth understanding of this area of plant-microbe research cannot be acquired solely from in vitro experiments of VOC-mediated interactions between all organisms involved in these interactions. Results obtained in controlled, artificial environments may not, and indeed most likely do not, represent interactions which would be observed in the field (Velivelli et al. 2015).

This issue of the interpretation of results from field versus lab is relevant for metabolic experiments utilising artificial growth media and nutrient sources and also for interactions where BVCs are outside of a detectable range. Such concentrations of BVCs observed under in vitro conditions are unlikely to be naturally present in the soil. Nevertheless, in vitro experiments contribute greatly to our understanding of the molecular interplay between bacterial volatiles and other organisms. This can give an insight as to what may be observed within these complex relationships in the field (Ryu et al. 2003; Blom et al. 2011a; Effmert et al. 2012; Park et al. 2015; Besset-Manzoni et al. 2017; Brilli et al. 2019; Song et al. 2019). Furthermore, not all plant species respond similarly to the same group of volatiles produced by a given bacterial strain, which could be due to several reasons: (1) fundamental differences in the pathways used by plants to respond to BVCs (2) differences in reactive sites and (3) differences in the capacity to metabolise volatiles (Santoro et al. 2011). The volatiles produced by a given bacterial strain elicited different responses in different fungi; in other words, differences exist in the interactions between different fungi and bacteria. For example, although *Arabidopsis* growth was significantly promoted by DMDS; the responses of different fungal species to this compound varied considerably: the growth of *R. solani* was suppressed, whereas *A. alternata* and *F. solani* were unaffected (Groenhagen et al. 2013). Therefore, it is necessary to employ a number of different approaches

and to test bacteria under distinct growth conditions to determine comprehensive bacterial emission patterns (Farag et al. 2017).

8.6 Analytical Approaches to Identify VOCs

The capture of VOCs which are emitted as a result of microbial metabolic activity is the first and most crucial step in the analysis of biological VOCs, and research in this area of 'separation science' has advanced significantly in the last half a century (Velivelli et al. 2015). SPME-GC/MS and PTR-MS are just two of the numerous approaches designed for the capture and subsequent identification of volatiles. Although each approach has its own advantages, no single method is currently capable of completely surveying bacterial-produced volatile profiles, either in terms of quantity or quality. To successfully identify volatiles, a number of sampling techniques are generally employed, such as purge and trap, solid phase microextraction (SPME) followed by Gas chromatography/Mass spectrometry (GC/MS) identification. The purge-and-trap method involves passing a given volume of purified air over the sample, collecting it onto an absorbent filter and then either directly releasing it using an organic solvent to rinse the filter or transferring it straight to the GC/MS (Ryu et al. 2003, 2004; Yuan et al. 2012). Solid phase microextraction (SPME) has become the method of choice for the extraction of bacterial volatiles in recent years because it minimises preparation time and has greater sensitivity than other extraction techniques.

The process of SPME for the analysis of bacterial volatiles is relatively fast and can be conducted under low oxygen conditions. Although SPME has many advantages over other methods, it is necessary to carefully consider the particular fibre coatings used in each experiment, as they can either absorb or exclude specific analytes based on polarity or size, leading to reduced sensitivity. For instance, non-polar metabolites are absorbed by Polydimethylsiloxane (PDMS) fibre, whereas short-chain polar compounds are absorbed by divinylbenzene/carboxen/PDMS (DCP) fibre. With respect to rhizobacterial volatiles, the best recovery is offered by DCP fibre, as it absorbs polar low molecular weight volatiles (Farag et al. 2006). Yuan and Co-workers tested three different fibres from Supelco—PDMS, 7 μm, stable flex DCP, 50/30 μm, and polydimethylsiloxane/divinylbenzene (PDMS-DVB, 65 μm)—and they found that DCP fibre performed best (Yuan et al. 2012). The volatile extraction methods discussed above are often used in combination with other analytical techniques, such as GC/MS. Considering its effectiveness for both separation and identification, GC/MS is the foremost method for the detection of bacterial volatiles. GC-MS can be used to separate, identify and quantify the volatiles present in a given sample. However, this technique has one significant drawback; namely, it does not allow for the identification of new compounds. Furthermore it can be difficult to obtain quantitative results using SPME, as volatile compounds compete for binding sites within the SPME fibre. Small bacterial molecules are characterised by high polarity and a strong tendency

to co-elute. As a result, overlapping MS spectra can be produced, limiting the precision of volatile detection and adversely affecting the process of matching peak quality against database entries.

The identification of existing volatiles is carried out using software programs and libraries of different mass spectra such as NIST/or reference standards. Nevertheless, as similar mass spectra can be produced by related compounds, particular care must be taken in performing these analyses (Kai et al. 2009). A recently developed technique with the advantage of real-time analysis without requiring sample preparation is PTR-MS. In proton transfer reaction-mass spectrometry (PTR-MS), the headspace air is drawn directly into the instrument, where interactions occur between protonated water (H_3O^+) and any molecules with a proton affinity greater than that of water. Next, a quadruple mass spectrometer in mass-to-charge (m/z) ratio is used to mass analyse and identify the resulting protonated organic molecules. Although PTR-MS cannot accurately detect the individual volatiles produced, it is advantageous because it ensures real-time emission observation.

In addition, PTR-MS cannot be used to distinguish between analytes of the same mass because it employs single reagent ions (Spinelli et al. 2012). PTR-MS was used to determine the volatile profiles of various bacteria and infected plants, and it allowed for the observation of pathogenic emissions in real time (Spinelli et al. 2011). Several researchers have analysed the volatiles emitted by bacteria, and a comparison of these signature compounds indicates that GC/MS analysis can be used to distinguish between different bacterial species. Indeed, the VOC-profile data obtained from GC/MS could be harnessed to develop so-called 'electronic-nose' (e-nose) sensor technology for the detection of different bacterial species, or they may be useful for real-time disease monitoring in agricultural settings and post-harvest monitoring where e-nose technology could detect ring and brown rot in commercial potato storage with a detection efficiency of 90% of samples (Biondi et al. 2014). Currently, the identification of bacterial species, including phytopathogenic bacterial isolates, is achieved through 'classical' molecular techniques such as polymerase chain reaction followed by dideoxy sequencing of 16S rRNA and these methods, although reliable, are expensive (Velivelli et al. 2015). The efficacy of e-nose technology has been demonstrated for the detection of a single phytopathogen within a wider microbial community; using a metal-oxide-based semiconductor sensor the pathogen that causes fire blight (*E. amylovora*)—could be differentiated based on volatile mixes alone from other bacteria (Spinelli et al. 2012). However, this technique has one significant drawback; it does not identify and quantify each compound; rather, it uses metal-oxide semiconductor sensors to characterise an aroma based on the signature profile that is generated.

The e-nose distinguishes between *Botrytis*- and *Sclerotinia*-induced rots on both green and yellow kiwifruits. In addition, it was successfully used to detect asymptomatic apple and pear plants that had been infected with *Erwinia amylovora*. More research is needed before e-nose applications in open fields becomes standard practice (Spinelli et al. 2010). In 2015, Cernava et al. described a novel assay for the detection of bacterial volatiles from lichen-associated bacteria using headspace

analysis and indicator assays (for HCN production) followed by the determination of the effect of the VOCs on the growth of *E. coli* and *B. cinerea*. The initial test was combined with a qPCR-based quantification assay (Cernava et al. 2015).

8.7 Discussion and Conclusive Remarks

Research into volatile-mediated plant–bacteria interactions is relatively new, and this field has the potential to yield significant agricultural applications, particularly in the context of growth promotion and induced systemic resistance (ISR) (Liu and Brettell 2019; Romera et al. 2019). This niche of plant-bacteria research is still emerging and at present, the biological effects of BVCs have only been assessed in a relatively small cohort of plant species with *Arabidopsis thaliana* being one of the main candidates, along with more economically relevant plants such as *Capsicum annum* and *Nicotiana tabacum* (Choi et al. 2014; Kim et al. 2015). How these bacterial volatiles will affect the growth and disease-suppression in other major crops remains to be seen. In general, I plates are used to perform experiments on the effects of bacterial volatiles on plants and fungi. This setup allows for the exchange of volatile compounds while preventing non-volatile metabolites from dispersing throughout the respective growth media. However, following identification of the bio-active compounds, further in vitro laboratory tests should be conducted under conditions that are either in, or similar to, field conditions (e.g. nutrient media that closely resembles soil environment), as opposed to the highly artificial Petri dishes used in the majority of existing studies (Choi et al. 2014; Brilli et al. 2019; Song et al. 2019).

To gain a comprehensive understanding of the role of BVCs, it is necessary to study mutant strains that do not produce such compounds. Adverse effects from chemical treatments and difficulties in establishing optimal treatment concentrations restrict the use of chemicals for growth promotion and resistance induction in plants. Therefore, future research programs should focus on measuring VOC levels produced by rhizobacteria in soil ecosystems (Ryu et al. 2005b; Sharifi and Ryu 2018a). An understanding of the relevant signalling pathways and the extent to which they resemble plant responses to pathogens, and whether the physiological and molecular plant responses vary between bacterial species is crucial to aid our understanding and will determine future technology transfer in this area (Velivelli et al. 2015). In addition, genetically altering rhizobacterial strains to produce greater amounts of volatiles that promote plant growth or that induce systemic resistance may represent promising avenues of future research. However, the use of GM organisms is becoming increasingly controversial in terms of human health and the environment. Phytopathogenic fungi—which are responsible for the majority of economically important crop diseases—are inhibited by BVCs, indicating that BVCs have the potential for use in agriculture as biological control agents. However, research on the effects of bacterial volatiles is still in the early stages (Sharifi and Ryu 2016).

In particular, it has yet to be determined whether the effects of volatiles are limited to specific plant tissues or if they affect plant development in general. Also, an understanding (positive or negative) of the impact of bacterial volatiles on plant metabolism is essential. Furthermore, it will be necessary to address whether effects observed in the laboratory transfer to the field (Velivelli et al. 2015). An alternative strategy that may prove beneficial for agriculture is the application of bio-active but affordable compounds, such as 2,3-butanediol, to aerial plant components to stimulate growth and ISR. Additional limitations on the use of rhizobacteria volatiles such as 2,3-butanediol and acetoin include the fact that they evaporate very quickly following application in the open field, however solutions are being developed to tackle this problem such as the use of microcapsules to slowly release BVCs to the environment (Song and Ryu 2013; Sharifi and Ryu 2018b). Nevertheless, significant positive effects for BVCs have been comprehensively analysed under growth-chamber, greenhouse and open-field conditions (Velivelli et al. 2015; Choi et al. 2014). For example, pathogen growth in *A. thaliana* by *Pseudomonas syringae* was found to be considerably suppressed by the direct application of acetoin to roots under growth-chamber conditions (Rudrappa et al. 2010). Under greenhouse conditions, the soil-drench application of volatile metabolites, such as DMDS (released by *B. cereus* C1L), inhibited the activities of *Botrytis cinerea* and *Cochliobolus heterostrophus* against tobacco and corn plants, respectively (Huang et al. 2012). Pre-treatment of cucumber plants with 3-pentanol and 2-butanone showed protective benefits against the biotrophic bacterial pathogen *P. syringae* in open-field trials. (Song and Ryu 2013; Velivelli et al. 2015). Notwithstanding the challenges of transitioning from laboratory to field with respect to the application of mVOCs (Bailly and Weisskopf 2017) the studies conducted to date should lead to new discoveries regarding the use of VOCs to control microbial pathogens under open-field conditions and can be expected to act as big players in any second green revolution.

Conflict of Interest Author(s) have no conflict of interest

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Chapter 9
Potential of PGPR in Improvement of Environmental-Friendly Vegetable Production

Haluk Caglar Kaymak

Abstract Plant growth promoting rhizobacteria (PGPR) can directly cause enhanced plant growth, early seed emergence or improvement in crop yields by supplying biologically fixed nitrogen and increasing minerals uptake, producing and secreting plant growth regulators and other beneficial substances. Also, PGPR indirectly influences the plant growth promotion by suppressing of pest and diseases in vegetables. Hence, replacement of chemical fertilizers and pesticides is required because of the adverse effect of these chemicals and their residues seriously pollute the environment, impart and also threaten the health of human and animals. Thus, people are focused on healthy products not only for growing vegetables but also for all agricultural products. In recent years because of increasing food-borne illnesses, the importance and potential of PGPR is hereby discussed for improvement of sustainable environment-friendly vegetable production for healthy human nutrition with special reference selected vegetable species, such as tomato, pepper, melon, radish and lettuce.

Keywords Plant growth promoting rhizobacteria · Vegetables · Sustainable production

9.1 Introduction

Although at least 10,000 plant species are used as vegetables worldwide, only 50 or so are considered of great economic and commercial importance (Decoteau 2000). These 50 species are vital for healthy diets and essential for human health, hence are not a luxury (Palada et al. 2006). Also, the widely used definition of the term vegetable is: herbaceous edible plants, or edible, usually succulent part of a plant that is eaten whole or in part such as roots, leaves or fruits, raw or cooked. In fact,

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all over the world over 1150 million tons of vegetables are produced annually. China produces over 50% of the world vegetable production. The United States of America, India and Turkey are the other important vegetable producer countries in the world. The production of tomato, potato, garlic, onion and watermelon accounted for over 60% of the total world vegetable production. In addition, tomato is one of the major vegetable produced and consumed throughout the globe. With worldwide production reaching near 170 million tons, tomato is the seventh most important crop species after maize, rice, wheat, potatoes, soybeans and cassava (Bergougnoux 2014; FAOSTAT 2016).

When farmers began to produce or cultivate vegetables, soil fertility be taken into consideration for selected vegetable crops, disease prevention, precisely, "damping off" control and pest management. Although the global nitrogen cycle pollutes groundwater and increases the risk of chemicals, the excessive use of chemical fertilizers affects the soil health, soil physicochemical characteristics and also pollutes the ecosystem in addition to the degradation in natural resources and high cost. It is now an established fact that high-input farming practices achieving high yields have created environmental problems (Şahin et al. 2004; Nosheen and Bano 2014). Phosphorous (P), next to nitrogen, is one of the major and key nutrients limiting plant growth (Kumar and Narula 1999; Sundara et al. 2002; Podile and Kishore 2006). The sustainable, environmental-friendly and cost-effective measures, such as PGPR, can replace chemical fertilizers (Nosheen and Bano 2014) and pesticides that cause environmental pollution and degradation (Robacer, et al. 2016), resulting in contamination of the vegetables with toxic pesticides, fungicides, herbicides and insecticides residues. Eventually, the growers had to turn to new methods of alternative fertilization, especially biological new sources, so as to meet out the requirement of minerals besides, assisting in diseases suppression so as not to harm the environment and do not leave any toxin behind. Recently, consumers have focused on healthy products because of increasing food-borne illnesses. This pressure has led to these new quests mentioned by producers. Also, the excessive usage of chemical fertilizers and pesticides not only affect the soil properties and residues in vegetables such as nitrate accumulation but also pollute the environment in addition to the depleting resources and high cost. Therefore, efforts are being made to replace chemical fertilizers and pesticides with organically, environmental-friendly and cost-effective resources such as plant growth promoting rhizobacteria (PGPR). It is known that biological control of plant diseases has gained importance for healthy production of vegetables and other crops in recent years.

Rhizosphere, a hotspot of microbial diversity which houses a wide range of soil bacteria, belongs to the different group and with diverse properties influence the growth and health of plants directly or indirectly (Gowtham et al. 2017). Long back, pioneer work of Kloepper and Schroth (1978) stated that microbial communities exert beneficial for plant growth, yield, crop quality and plant health which have been called "plant growth promoting rhizobacteria (PGPR)" including numerous species of the genera *Acinetobacter*, *Aeromonas*, *Alcaligenes*, *Arthrobacter*, *Azospirillium*, *Azotobacter*, *Azoarcus*, *Bacillus*, *Beijerinckia*, *Burkholderia*,

Clostridium, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Gluconacetobacter*, *Klebsiella*, *Pseudomonas*, *Serratia*, *Rhizobium* and so on (Kaymak 2010). PGPR plays an important role in plant growth by one or more mechanisms in direct plant growth promotion such as nitrogen fixation, phosphate solubilization, early seedling emergence, secreting of plant growth regulators and indirect plant growth promotion such as suppression of pest and disease (Tailor and Joshi 2014). In other words, Tenuta (2004) reported that PGPR improves plant health that can occur through three ways, namely: (a) decrease development of pest/disease (bioprotectant), (b) by secreting phytohormones (biostimulant) and (c) due to increasing availability of nutrients for plants (biofertilizer). For example, phosphate solubilizing bacteria (PSB) secretes organic acids and enzyme phosphatases, and converts the insoluble phosphates into soluble inorganic phosphates through the process of acidification, chelation, exchange reactions and production of organic acids (Whitelaw 2000; Gyaneshwar et al. 2002; Rodriguez et al. 2004; Chung et al. 2005; Hameeda et al. 2008). Generally, rhizobacteria has positive effects in occupying the ecological niche in order to provide compounds beneficial to the plants.

The use of plant–PGPR interactions for various crops is important and is useful not only for the enhancement of crop production but also for restoration of environment (Vessey 2003). Most of the free-living rhizobacteria confer protection against plant diseases via induced systemic resistance and promote growth and yield of numerous agronomically and ecologically important plant species, including vegetables. Therefore, the importance and potential of PGPR is discussed for improvement of environment-friendly vegetable production for human nutrition with special references to utilization of vegetable species such as tomato, pepper, melon, radish and lettuce.

9.2 Potential of PGPR in Some Selected Vegetable Crops

The potential of PGPR for environment-friendly vegetable production and healthy human nutrition in some selected vegetable species is discussed below.

*9.2.1 Tomato (*Lycopersicon esculentum *Mill.)*

Tomato, *Lycopersicon esculentum* Mill., is an annual shrubby member of Solanaceae family but it is a herbaceous perennial in a protected environment. The tropical coastal areas of Ecuador, Peru or Bolivia and portions of Northern Chile are considered originating areas and also native to tropical America. It was introduced to Central America and Mexico and also used by the Aztec and Toltec people, and seeds of tomato were taken back to Italy by the returning explorers as early as in the year 1554, and the plant quickly found favor in the warm Mediterranean climate. From there, tomatoes moved to Northern Europe and throughout the world. It was

considered poisonous in early times because of the toxic alkaloid tomatine. After finding out its non-toxic nature, tomato cultivation was spread worldwide (Decoteau 2000; Peralta and Spooner 2007; Welbaum 2015). Today, tomato is not only produced for fresh market but also used widely in the food processing industry. Besides, a source of nutrients such as lycopene, β-carotene and vitamin C, its production and consumption are increasing in various countries (Bergougnoux 2014). It is an important crop for both the greenhouse and field vegetable growers throughout the world with a production area nearly 5 million ha and over 170 million metric tons of total production produced by China, India, USA and Turkey (FAOSTAT 2018).

Tomato is a warm season vegetable and injured by light frosts. The nitrogen is important for vegetative growth with a form of NH_3^+. Phosphorus is also important for plant development and flowering (Decoteau 2000; Welbaum 2015). On the other hand, numerous diseases adversely affect the crop production, and many bacterial, fungal and virus diseases attack tomato. Bacterial speck, bacterial soft rot, bacterial wilt, syringae leaf spot and so on are the most important bacterial diseases. In addition, some important fungal diseases of tomato are early blight, black leaf mold, powdery mildew, Fusarium wilt and Verticillium wilt. A large number of viruses such as cucumber mosaic, tobacco mosaic, tobacco leaf curl virus and tobacco ring spot also cause deleterious disease-causing entities.

The direct and indirect effects of PGPR have a great potential for improving growth and yield of tomato under different environmental conditions. Protection of vegetables against different plant diseases is quite important for environmental-friendly production. As mentioned before, Fusarium wilt caused by *Fusarium oxysporum* f. sp. *lycopersici* (Sacc.) W.C. Snyder & H.N. Hans, is common and important disease for tomato. Recently, Boukerma et al. (2017) reported that *Pseudomonas fluorescens* PF15 and *Pseudomonas putida* PP27 showed a significant protection against Fusarium wilt in tomato. Similarly, Fatima and Anjum (2017) observed that *Pseudomonas aeruginosa* PM12 has a great potential against Fusarium wilt in tomato, and act as a biocontrol agent that provides a complementary tactic for sustainable integrated pest management. Pastor et al. (2016) reported that inoculation of tomato seeds with *P. putida* strain PCI2 increases the resistance of plants to root rot caused by *F. oxysporum* and that *P. putida* PCI2 produces compounds such as 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, involved at different levels in increasing resistance. More recently, *Bacillus amyloliquefaciens* SN16-1 promotes plant growth and has great potential as a biocontrol of *F. oxysporum* f. sp. *lycopersici* in tomato (Wan et al. 2018). Another important disease of tomato is bacterial wilt caused by *Ralstonia solanacearum* that infects roots and multiplies in xylem vessels. Bacterial wilt results in huge economic losses each year in many tropical and subtropical areas because an effective control measures yet not been developed (Peng et al. 2017). According to Peng et al. (2017) report, the combination of saisentong (N, N-methylene-bis-(2-amino-5-sulfhydryl-1,3,4-thiadiazole) copper) and *Bacillus subtilis* B-001 effectively controls tomato bacterial wilt. On the other hand, *B. amyloliquefaciens* SQY 162 efficiently colonized the tomato rhizosphere, which

directly suppressed *R. solanacearum* by secreting antibiotic surfactin in the tomato rhizosphere soil. Li et al. (2017) reported that *B. amyloliquefaciens* strain SQRT3 reduced tomato bacterial wilt by 68% and its biocontrol efficiency suppressed *R. solanacearum* populations in the rhizosphere soil significantly.

PGPR is being explored to harness their traits against *Meloidogyne incognita* causing root-knot in tomato. Sharma and Sharma (2017) reported that *Pseudomonas jessenii* strain R62 and *Pseudomonas synxantha* strain R81 reduced nematode infection in tomato under glasshouse conditions. Also, *P. putida*, *P. fluorescens*, *Serratia marcescens*, *B. amyloliquefaciens*, *B. subtilis* and *Bacillus cereus* reduced galling and egg masses on the roots by root-knot nematodes in tomato crops and increased yield (Almaghrabi et al. 2013).

Most of the vegetables are exposed to many abiotic stresses such as salinity and drought. The high level of salinity limited the crop productivity by influencing seed germination, growth, flowering and fruit setting not only in tomatoes but also in most of the vegetables that change according to the developing stages. PGPR can mitigate the adverse effect of salinity in tomato. For example, *Bacillus megaterium* strain A12 and *P. putida* strain A20 increased shoot length of tomato plants and dry biomass grown under varying salinity stress (100 and 200 mM NaCl). Further, *B. megaterium* strain A12 reduced endogenous ethylene production and increased water use efficacy better than *P. putida* strain A20 under field conditions (Aslam et al. 2018). In addition, Shen et al. (2012) suggested that *Erwinia persicinus* RA2 and *Bacillus pumilus* WP8 proved promising PGPR strains which are suited for application in salt marsh planting. Calvo-Polanco et al. (2016) reported that inoculation of *Variovorax paradoxus* 5C-2 and arbuscular mycorrhizal fungus *Rhizophagus irregularis* has a great potential in order to improve plant yield under conditions of drought stress.

It is well known that PGPR improves plant growth and yield via producing phytohormones and increases the availability of nutrients. There are many researches about the direct effect of PGPR in vegetable crops. Esquivel-Cote and Ramírez-Gama (2015) observed that *Azospirillum lipoferum* AZm5 proved useful for increasing N uptake in N-deficient soil by production of cytokinins, increase in ACC deaminase activity in tomato. Similarly, *Azospirillum brasilense* Sp7-S and *A. brasilense* Sp245 strongly enhanced root and shoot growth, seed germination index and vigor of tomato (Mangmang et al. 2015) Also, *B. fortis* IAGS162 and *B. subtilis* IAGS174 increased shoot length, root length, total biomass, total chlorophyll, carotenoid and sugar concentrations in tested tomato varieties under greenhouse conditions (Akram et al 2015). *B. circulans* CB7 increased seed germination, shoot length, root length, shoot dry weight and root dry weight, nitrogen, potassium and phosphorus content of shoot biomass in tomato (Mehta et al. 2015). IAA producing *P. putida* FA-8, FA-56 and FA-60 also increased the plant height, stem diameter, dry biomass and fruit yield of tomato (Hernández-Montiel et al. 2017). Similarly, phosphate solubilizing *P. putida* PCI2 exhibited a clear growth-promoting effect on shoot growth of tomato in the presence of L-tryptophan (Pastor et al. 2014). On the other hand, a commercial product, Bioroot®, containing *B. subtilis*, *P. fluorescens*, *Trichoderma harzianum*, yeast, algae and *Nocardia*

improved the leaf area, shoot dry weight, root dry weight, volume of roots and root forks compared with the control, and also recommended as an alternative to tomato seedling growers' dependence on synthetic agrochemicals (Brutti et al. 2015). Earlier, Lee et al. (2008) have reported that *Rhodopseudomonas* sp. KL9 acts as an eco-friendly biofertilizer for cultivation of tomato and other lycopene-containing vegetable crops. *Burkholderia* sp. 7016 also enhanced the tomato yield and significantly promoted activities of soil urease, phosphatase, sucrase and catalase and can be used as a biofertilizer (Gao et al. 2015). Tripti et al. (2017) reported *Burkholderia* sp. L2 as inoculum which can tremendously enhance the productivity of tomato, soil fertility, and can also act as a sustainable substitute for chemical fertilizers. Various examples about the improving plant growth and yield of tomato by PGPR are given in Table 9.1.

Table 9.1 Examples of promoting effect of PGPR in tomato (*Lycopersicon esculentum* Mill.)

PGPR	Promoting effect	References
Rhodopseudomonas KL9	Seed germination, total length and dry mass of germinated seedling	Koh and Song (2007)
Mixture of Pseudomonas *putida* and *Trichoderma atroviride* (fungi)	Fresh weight, shoot and roots of seedlings	Gravel et al. (2007)
Bacillus subtilis BS13	Yield per plant, marketable yield, fruit weight, length and quality	Mena-Violante and Olalde-Portugal (2007)
Pseudomonas putida, Azotobacter chroococcum, Azosprillum lipoferum	Lycopene and antioxidant activity, shoot and fruit potassium content	Ordookhani et al. (2010)
Pseudomonas sp. RFNB3, *Serratia* sp. RFNB14	Early growth, root and shoot length, seedling vigor and dry biomass	Islam et al. (2013)
Pseudomonas putida UW4	Shoot length, shoot fresh and dry mass, and the chlorophyll concentration of tomato seedlings under salinity stress	Yan et al. (2014)
Bacillus amyloliquefaciens	Fruit yield suppression of *Fusarium oxysporum* f. sp *lycopersici*	Patakioutas et al. (2015)
Bacillus pumilus	Seedling growth	Anith et al. (2015)
Herbaspirillum seropedicae	Fruit biomass, nitrate uptake and nitrate reductase activity	Olivares et al. (2015)
Pseudomonas spp., *Bacillus* sp.	Seed germination, time of germination seedling growth	Widnyana and Javandira (2016)
Bacillus amyloliquefaciens IN937a *Bacillus pumilus* T4	N and P uptake	Fan et al. 2017 (2017)

9.2.2 *Pepper (*Capsicum annuum *L.)*

Pepper (*Capsicum annuum* L.) is an economically important genus of family Solanaceae It is a warm season, frost-sensitive crop that requires somewhat similar conditions as tomato and eggplant, that is, higher temperature requirement and commercially cultivated around the world due to its better adaptation to different agro-climatic regions. This crop is native to the Americas, and likely domesticated from central to southern Mexico. The other major species of pepper are *Capsicum frutescens*, *Capsicum chinense*, *Capsicum baccatum* and *Capsicum pubescens*. Although there are many commercial names of peppers, cultivars can be classified into two main types: mild or sweet fleshed fruit and hot or pungent fleshed fruit. It is a good source of vitamin A and C, in addition to potassium, phosphorus, calcium and iron, and can also be processed by canning or drying. It is an important crop for both the greenhouse and field vegetable growers worldwide. The total world production of fresh peppers including chillies was 34 million metric tons in 2 million ha production area (Decoteau 2000; Welbaum 2015; FAOSTAT 2018).

Fertilizer requirement of peppers is not as much as tomatoes. Fertilization is performed according to the soil and foliar testing results, and nitrogen is often applied prior to transplanting and again at first bloom. Phosphorus is often applied as fertigation because of limited solubility of phosphorus at transplanting to improve early growth (Welbaum 2015).

Peppers are also affected by serious phytopathogenic diseases. During pepper cultivation in greenhouses and fields, bacterial spot, bacterial soft rot, gray leaf spot, *Phytophthora* blight, wet rot and virus diseases such as tobacco mosaic virus are few examples among these diseases. Also, aphids make serious damages on pepper plants and reduced plant growth and yield (Herman et al. 2008; Mardani-Talaee et al. 2017).

Although chemical control method is common for disease control approaches to protect pepper plants from various diseases, but chemical control method accumulates residual pesticides in the ecosystem, pollutes the natural environment and causes human toxicity. Therefore, eco-friendly farming methods, such as crop rotation, and use of biological control agent are essential for sustainable agricultural development (Jung et al. 2015). Biological control agents in the form of PGPR can also be used to inhibit pathogens-causing diseases. Hahm et al. (2012) reported that *Ochrobactrum lupini* KUDC1013 and *Novosphingobium pentaromativorans* KUDC1065 are capable of eliciting induced systemic resistance (ISR) in pepper against bacterial spot disease. PGPR mixtures have a potential as biological control agent on pepper under greenhouse and field conditions. In addition, three bioproducts, *Bacillus vallismortis* EXTN-1, *Bacillus* sp. and *Paenibacillus* sp. (ESSC) and *B. subtilis* (MFMF) are examined in greenhouse to reduce bacterial wilt, Fusarium wilt and foot rot. Thus, ESSC and MFMF reduced disease severity under greenhouse conditions and EXTN-1 provided a mean level of disease reduction under field conditions (Thanh et al. 2009). Infection of pathogenic fungi *Rhizoctonia solani* causes disease and decree in the yield of pepper. *B. subtilis*

SL-44 elicited strong inhibitory effect on *R. solani* and enhanced the biomass and length of pepper seedlings (Huang et al. 2017). On the other hand, *Kluyvera cryocrescens* KUDC1771 and *Brevibacterium iodinum* KUDC1716 have the ability of phosphate solubilization and production of phytohormones; *B. iodinum* KUDC1716 significantly decreased gray leaf spot disease in pepper hence, used as a potential agent for biological control (Son et al. 2014). In addition, Sang and Kim (2012) reported that Phytophthora blight of pepper caused by *Phytophthora capsici* is the most destructive disease in the commercial production of pepper. The biocontrol agent *Pseudomonas corrugata* CCR80 and *Chryseobacterium indologenes* ISE14 played a significant role in the suppression of *Phytophthora* blight of pepper. Similarly, Xu and Kim (2016) reported that *Paenibacillus polymyxa* SC0921 induced a defensive response against Phytophthora blight and promotes growth in pepper plants (Xu and Kim 2016).

The green peach aphid, *Myzus persicae*, is a polyphagous aphid that caused chlorosis in several vegetable plants. In one of the studies, *B. subtilis* and *B. amyloliquefaciens* proven useful in *Myzus persicae* management for pepper plants grown in locations having consistently high aphid pressure (Herman et al. 2008). Mardani-Talaee et al. (2017) investigated that the effect of zinc sulfate and vermicompost (30%) along with *B. subtilis*, *P. fluorescens*, *Glomus intraradices*, and combined effect of *G. intraradices* with *B. subtilis*, and *P. fluorescens* against biological parameters of *Myzus persicae*, and concluded that the best plant growth was attained due to application of zinc sulfate and *B. subtilis*.

The PGPR can directly cause modifications on plant metabolism such as N fixation, phosphate (P) solubilization, Fe sequestration, and cytokinin, gibberellin, indoleacetic acid, ethylene production and so on (Lucas et al. 2014). For example, inoculation with *Bacillus* spp. M9 and *B. cereus* K46 positively affected the performance of the photosynthetic mechanism in pepper plants. However, plants inoculated with *Bacillus* spp. M9 showed better performance in all vegetative plant growth characteristics in sustainable agriculture programs (Samaniego-Gámez et al. (2016). Similarly, *Bacillus licheniformis* increased the height of plants, leaf area and had less disease that of non-treated plants, and hence, it could be used as a biofertilizer or biocontrol agent in greenhouses (Garcia et al. 2004). Reduction of inorganic fertilizer application up to 25% with *P. putida* increased the growth and productivity of King Pakal hybrid habanero pepper (Chiquito-Contreras et al. 2017; Pastor-Bueis et al. 2017). During a field experiment, it is observed that the *Bacillus siamensis* that fertilized with decreased mineral N (80%) produced significantly better pepper yields. In addition, Supanjani et al. (2006) reported that phosphate and potassium solubilizing bacteria *B. megaterium* var. *phosphaticum* provides a sustainable alternative to the use of synthetic fertilizers for hot pepper production in soil with low fertility.

PGPR has potential to alleviate some stress factors such as salt and drought stress in different crops including pepper. The inoculation of pepper plants with *Microbacterium oleivorans* KNUC7074, *B. iodinum* KNUC7183 and *Rhizobium massiliae* KNUC7586 can alleviate the destructive effects of salt stress on plant growth (Hahm et al. 2017). Drought stress is also one of the important affecting

Table 9.2 Examples of promoting effect of PGPR in pepper (*Capsicum annuum* L.)

PGPR	Promoting effect	References
Formulation LS255 (*Bacillus subtilis* GBO3 + *Bacillus subtilis* IN937b), Formulation LS256 (*Bacillus subtilis* GBO3 + *Bacillus pumilis* INR7)	Yield of extra-large tomato fruit and total yield	Kokalis–Burelle et al. (2002)
Bacillus subtilis	Suppressing of *Phytophthora* blight	Lee et al. (2008)
Bacillus aryabhattai RS341 *Brevibacterium epidermidis* RS15 *Micrococcus yunnanensis*	Growth promotion under salt stress	Siddikee et al. (2012)
Pseudomonas corrugata CCR80 *Chryseobacterium indologenes* ISE14	Suppressing of *Phytophthora* blight	Sang and Kim (2012)
Pseudomonas sp. RFNB3 *Serratia* sp. RFNB14 *Novosphingobium* sp. RFNB21	Solubilizing tri-calcium phosphate and zinc oxide, nitrogen fixation, chlorophyll content, macro- and micro-nutrient nutrient uptake	Islam et al. (2013)
Bacillus sp.	Root and fruit weights and total yield	Hernandez-Castillo et al. (2014)
Bacillus amyloliquefaciens, *Bacillus subtilis*	Suppressing of *Fusarium* wilt	Wu et al. (2015)
Chryseobacterium sp. ISE14	Phosphate-solubilizing suppressing of *Phytophthora* blight	Sang et al. (2018)

factors for pepper plant, and auxin and ACC deaminase producing *B. licheniformis* K11 reduces drought stress in pepper in drought-affected regions without the need for overusing agrochemicals and chemical fertilizer (Lim and Kim 2013). Similarly, *Burkholderia seminalis* and arbuscular mycorrhizal fungi, *Rhizophagus intraradices* and *Rhizophagus fasciculatum* increase biomass, root length, shoot length and chlorophyll content of pepper plants under drought stress conditions (Tallapragada et al. 2016). Examples about direct and indirect effect of PGPR on pepper are given in Table 9.2.

9.2.3 *Eggplant (*Solanum melongena *L.)*

There are more than 1000 species of eggplant (*Solanum melongena* L.); however, a few of them are produced commercially as vegetable for human nutrition. Total world production of eggplant is over 45 million metric tons with an average yield of 10 tons/acre (Welbaum 2015). Production of eggplant is limited in a few region of world because it is a traditional vegetable crop in tropical, subtropical and

Mediterranean countries (Abd El-Azeem et al. 2012) but is an important vegetable in China, India, Turkey and Egypt. Fertilization is important in production of eggplant because of its fairly high nutrient requirement. Eggplants have better drought tolerance than other crops of the family and generally quite sensitive to salinity (Welbaum 2015).

The effect of PGPR in raising high yielding eggplant is insufficient when compared to that of pepper and tomato. PGPRs are focused as suppressive agent to pathogens and tolerate salt stress. For example, *Xanthobacter autotrophicus* BM13, *Enterobacter aerogenes* BM10 and *Bacillus brevis* FK2 from the salt-affected maize kidney bean reduced the negative effects of salinity while *E. aerogenes* was capable of promoting eggplant growth and yield when compared to an uninoculated control (Abd El-Azeem et al. 2012). Similarly, inoculating with *Pseudomonas* sp. DW1 increased shoot Ca^{2+} of eggplant compared to the non-inoculating eggplant plants under salinity. It is interesting to note that the salinity decreased superoxide dismutase activities, and increased peroxidase activities. Numerous soil-borne organisms are harmful to the crop.

R. solanacearum (Smith) Yabuuchi is an important soil-borne bacterial plant pathogen causing bacterial wilt. The talc formulation of two species of *Pseudomonas* (RBh41 and RBh42) completely suppressed the disease incidence of eggplant wilt up to 36 days of inoculation under greenhouse conditions. Also, *Pseudomonas mallei* (RBG4, ET17) and one *Bacillus* spp. RCh6 reduced eggplant wilt incidence by 83% compared to control (Ramesh and Phadke 2012). Ramesh et al. (2009) reported that *Pseudomonas* EB9 and EB67; *Enterobacter* EB44 and EB89 and *Bacillus* EC4 and EC13 reduced the wilt incidence by more than 70%. Similarly, *F. oxysporum* f. sp. *melongenae (Fomg)* caused the most destructive disease in eggplant (*Solanum melongena* L.). Various strains of *Pseudomonas* and *B. cereus* significantly reduced disease and induced resistance to that of Fusarium wilt of eggplant (Altinok et al. 2013). Yıldız et al. (2012) reported that *Bacillus* and *Pseudomonas* species showing good performance were tested against *F. oxysporum* f. sp. *melongenae* for the antagonistic activities in eggplant.

*9.2.4 Melon (*Cucumis melo *L.)*

Melon (*Cucumis melo* L.), belongs to the family Cucurbitaceae and is an important vegetable, widely grown in the world with a production of about 27 million mt. The crop is mainly cultivated in China, Iran, Turkey, Egypt and United States (Welbaum 2015; Sharma et al. 2017). It is originated from Iran (Decoteau 2000) with rich genetic diversity (Balkaya and Karaağaç 2006). The economically important groups of melons are Cantaloupensis and Indorous. A number of disease such as Fusarium wilt, powdery mildew, downy mildew, bacterial wilt and bacterial blotch seriously affect melons in conventional production.

Fertilizer requirements of melons are moderate compared with other vegetable species due to development of extensive root systems to uptake need-based water

and available nutrients (Welbaum 2015). Nitrogen and phosphorus are essential key nutrients for adequate growth and yield for melon. Welbaum (2015) suggested that nitrogen applied in two side-dressing or through fertigation must be low during flowering to promote fruit set. The phosphorus must be banded lightly but producers should be careful for alkaline mineral soils because of chemically tie up phosphorus, unavailable to the plants.

Available literature revealed that PGPRs are inadequate for melons and more work is necessary to carry out eco-friendly melon production. The effects of PGPR on melons reveal their suppressive effect on some plant diseases and plant growth promotion. For example, *B. subtilis* UMAF6639 was able to induce systemic resistance (ISR) in melon and provide additional protection against powdery mildew because of producing lipopeptides by activation of jasmonate- and salicylic acid-dependent defense responses (García-Gutiérrez et al. 2013). Further, García-Gutiérrez et al. (2012) observed that *B. subtilis* UMAF6614, UMAF6639 and *cereus* UMAF8564, and *P. fluorescens* strains, UMAF6031 and UMAF6033 provide protection for melon against powdery mildew and angular leaf spot. *Bacillus* sp. RAB9 and *B. lentimorbus* MEN2 can be used as biocontrol agent for both melon seedlings and for preventing against bacterial blotch (Medeiros et al. 2009). Suppression of various soil-borne disease caused by *F. oxysporum* and *R. solani* also occurred due to appreciation of *B. subtilis* (Singh et al. 2017). Preventing plants against fungal and bacterial diseases yet to explore require new, safer and effective formula as an alternative to chemical pesticides for growing melon and other vegetable production.

The early vegetative and reproductive plant, parameters such as plant height, root dry weight, nitrogen and sodium concentrations in foliage and fruit weight of melons increased when *B. cereus* (N198) and *P. fluorescens* applied under greenhouse conditions (Rodriguez Mendoza et al. 2013). Strains of *B. subtilis* UMAF6614 and UMAF6639, *B. cereus* UMAF8564, and *P. fluorescens* strains, UMAF6031 and UMAF6033 promote plant growth and increase fresh weight up to 30% of melon seedlings as stated by García-Gutiérrez et al. (2012). Lee et al. (2015) suggested that *Enterococcus faecium* LKE12 promotes plant growth by producing GAs and IAA. Application of its cell-free culture extract proved to enhance plant growth. The root fresh/dry weight, shoot dry weight, plant height, foliar area, fruit yield and quality increased when *B. subtilis* LAL-36, BEB-23, BEB22 and BEB-13 applied and finally concluded that *B. subtilis* has potential to obtain high-quality melon fruits with increased profits (Abraham-Juárez et al. 2018). Researches clearly showed that PGPR has a great potential not only to improve yield and quality of melons but also suppressive to different diseases.

*9.2.5 Cucumber (*Cucumis sativus *L.)*

Cucumber (*Cucumis sativus* L.) belongs to the family Cucurbitaceae and is an important crop for both greenhouse and field growers throughout the world. It is

cultivated in a production area near 2 million ha with average 37–40 million mt. total production. The centre of origin of cucumber is believed to be India and also cultivated in the ancient Egypt. Cultivation of cucumber spread to China and Greece from India about 2000 years ago before Italy, France and other European countries and USA (Welbaum 2015).

Cucumber is a good source of vitamin A, vitamin C, potassium and poor source of protein, carbohydrates and fats; however, it is highly sensitive to environmental conditions (Radhakrishnan and Lee 2013; Welbaum 2015). Cucumbers are warm season, cold-sensitive crop and require warm soil temperatures both for germination, early harvest and high yield (Decoteau 2000). Cucumbers respond to high levels of fertilizer, and nitrogen is the key nutrient for successful cucumber production. In fact, from seedling to the maturity, the crop experiences several influences of bacterial and fungal community able to cause diseases like downy mildew, powdery mildew, damping-off, angular leaf spot, bacterial wilt, Fusarium wilt, and so on (Folman et al. 2003), and can be given as examples for important fungal and bacterial diseases of cucumber.

Pesticides are generally the first choice for the control of the diseases for growers in conventional cucumber production, and gained importance at suppressing of cucumber pathogens because of ISR by triggered preinoculating with PGPR (Van Loon et al. 1998). Jeun et al. (2004, 2007) inoculation with *S. marcescens* and *P. fluorescens* induced systemic protection of cucumber plants against the anthracnose pathogen, *Colletotrichum orbiculare*. The application of *B. subtilis* strain B4 combined with acibenzolar-S-methyl resulted in promotion of plant growth and systemic resistance against anthracnose infection (Park et al. 2013). Recently, Akköprü and Özaktan (2018) reported that *P. putida* AA11/1 significantly reduced average severity of angular leaf spot in disease-sensitive cultivar. The plant defense enzymes stimulated in cucumber roots colonized due to *P. corrugata* and *P. aureofaciens*, thus reduced *Pythium aphanidermatum* (Chen et al. 2000). Utkhede et al. (1999) reported that *B. subtilis* BACT-0 increased shoot growth and weight of cucumber plants in terms of fruit yield, and fruit number under greenhouse conditions. According to Ongena et al. (2000) positive effects of *P. putida* BTP1 and its sid^{-} mutant M3 inhibited *P. aphanidermatum* by eliciting phytoalexins systemically. Du et al. (2016) showed that *P. polymyxa* NSY50 influenced amino acid metabolism to increase biomass of the plant and regulate jasmonic acid pathway that trigger resistance against *F. oxysporum* f. sp. *cucumerinum*. The plant defense-related enzymes such as peroxidase and polyphenol oxidase were significantly increased in seed treated with *B. subtilis* B579 against *F. oxysporum* f. sp. *cucumerinum* in cucumber plants (Chen et al. 2010).

Organic farming is a technique designed to produce healthy food for human nutrition, therefore biofertilization with PGPR has attained importance. Kang et al. (2010) reported an environment-friendly alternative of chemical fertilizers in the agriculture industry as beneficial bacteria such as *Burkholderia* sp. KCTC 11096BP if applied. The growth attributes of cucumber such as shoot fresh weight and biomass, chlorophyll contents, soluble sugar contents and crude protein content were promoted. Similarly, other genera, namely *Rhodobacter sphaeroides*,

Lactobacillus plantarum and *Saccharomyces cerevisiae*, induced the shoot length, root length, shoot fresh weight, shoot dry weight, chlorophyll contents and total amino acids via secretion of IAA and/or organic acids. In addition, *R. sphaeroides* increased the calcium, potassium, magnesium and phosphate contents involved to regulate the mineral content in cucumber (Kang et al. 2015). The elemental nutrients were increased due to application of PGPR (Orhan et al. 2006; Kaymak et al. 2013). Pii et al. (2015) observed the presence of *A. brasilense* in soil, which facilitate a rapid and faster recovery of cucumber plants from iron deficiency symptoms by increasing chlorophyll content, biomass and iron content of cucumber leaves.

Almost majority of vegetables including cucumber are exposed to many stresses including both biotic and abiotic stresses such as attach of pathogens, low temperature and soil salinity. Diverse bacterial genera such as *B. cepacia* SE4, *Promicromonospora* sp. SE188 and *A. calcoaceticus* SE370 not only reduced sodium ion concentration but also increased potassium and phosphorus contents. In such cases, the increased biomass and chlorophyll contents of cucumber under salinity and drought stress have also been observed (Kang et al. 2014). It was reported that auxin-producing *K. planticola* strain TSKhA 91 exhibited protective effect on development of cucumber increased seed germination and root formation under conditions of low temperature (Blinkov et al. 2014).

9.2.6 *Watermelon [*Citrullus lanatus *(Thunb.) Matssumura and Nakai]*

Similar to melon, watermelon (*Citrullus lanatus* (Thunb.) Matsum & Nakai) belongs to the family Cucurbitaceae. The origin of watermelon is unclear but it was known that its cultivation started in Nile valley before 2000 BC. It is the most common cucurbit cultivated in many regions of the world. It has over 3,500,000 ha production area with approximately 117 million mt production. It is generally grown for the sweet juicy fruit pericarp tissue and used fresh as a dessert fruit and fruit salads. Watermelon consists mostly of water and contain rich source of vitamins, minerals lycopene and soluble sugars. The crop is of warm season, frost-sensitive that requires up to 4 months of frost-free weather. Fertilizer requirements are moderate because watermelons tend to develop extensive root systems in the upper profile of the soil for available nutrients. Cultivators prefer direct-seeded production in warm regions but transplanting is more useful in temperate regions (Decoteau 2000; Zohary et al. 2012; Welbaum 2015; FAOSTAT 2018).

The most common diseases of watermelon are bacterial wilt, Fusarium wilt, leaf spot, anthracnose, alternaria leaf blight, downy and powdery mildew. Bacterial fruit blotch is known as a serious disease to watermelon growers in the world. Both *P. polymyxa* (SN-22) and *Sinomonas atrocyanea* (NSB27) showed inhibitory effect

on bacterial fruit blotch resulting in increase in growth parameters of watermelon under greenhouse conditions (Adhikari et al. 2017). Strains of *B. subtilis* GBO3, *B. amyloliquefaciens* IN937, *B. pumilus* INR7 and SE34 reduced angular leaf spot lesions and gummy stem blight and exhibit an increased shoot weight seedlings growth and health (Kokalis-Burelle et al. 2003). Nga et al. (2010) reported that gummy stem blight, caused by *Didymella bryoniae* (Auersw.) Rehm., can be checked by *P. aeruginosa* 23_{1-1} by antibiosis and induced resistance under greenhouse and field conditions. Recently, Yaoyao et al. (2017) recommended that *P. polymyxa* (SQR-21) is not only PGPR but also an effective biocontrol agent against Fusarium wilt. Kokalis-Burelle (2004) examined few strains of PGPR reduced angular leaf spot lesions caused by *P. syringae* pv. *lachrymans*, and gummy stem blight, caused by *D. bryoniae* resulted in formulation of a product (Bio yield (TM)).

*9.2.7 Lettuce (*Lactuca sativa *L.)*

Lettuce (*Lactuca sativa* L.) has four morphological forms: crisphead, butterhead, romaine or cos, and loose leaf is a member of family Asteraceae. It is a major world salad crop (Jeffrey 2007; Welbaum 2015), and is a source of vitamins and nutrients required for human health (Chamangasht et al. 2012). The crop is best in cool growing environments and can be grown in temperate regions and requires a well fertilized soil for high yield because of a weak, shallow root system (Decoteau 2000). Lettuce's nutritional requirements are fulfilled during 3–4 weeks before harvest. Nitrogen is the most important fertilizer because of the plant's limited root system for rapid and continuous growth (Swaider et al. 1992). On the other hand, lettuce mosaic virus, turnip mosaic virus, bottom root, lettuce drop, downy mildew, bacterial leaf spot, varnish spot verticillium wilt and so on are some of the most important diseases that adversely affected the lettuce growth and quality.

There are a lot of agricultural practices applied for increasing yield components of lettuce. One of them is application of PGPR for promoting growth and environment-friendly and sustainable production of lettuce. In one of the first reports, phosphate-solubilizing *Rhizobium leguminosarum* bv. *phaseoli* strains P31 and R1, *Serratia* sp. strain 22b, *Pseudomonas* sp. strain 24 and *Rhizopus* sp. strain 68 showed their PGP potential on lettuce and *R. leguminosarum* bv. *phaseoli* induced the growth of lettuce maximally under field conditions (Chabot et al. 1996). According to Flores-Félix et al. (2013), microbial bioinoculants are an effective way for sustainable and environment-friendly agriculture due to their reduction of the use of chemical fertilizers and declared that *R. leguminosarum* PEPV16 actively colonizes the rhizosphere of lettuce resulting in increase in plant growth as well as N and P contents in lettuce. Similarly, Chamangasht et al. (2012) reported that species of *Azotobacter, Azospirillum* and *Pseudomonas* strain 187 proved effective on the enhancement of vegetative characters of lettuce. Among these genera, *Azospirillum* spp. was most effective in increasing plant height and

yield due to its salt stress management (Fasciglione et al. 2012). In fact, *Azospirillum*-inoculated lettuce seeds yield a higher number of superior quality lettuce than non-inoculated controls grown under NaCl stress. A field-trial was undertaken to compare the effect of inorganic fertilizer. A PGPR, *Pseudomonas mendocina*, alone or in combination with inorganic fertilizer, on plant growth and nutrient uptake in lettuce exhibited a significant effect of PGPR bacteria on the dehydrogenase and phosphatase activities (Kohler et al. 2006). Hoffmann-Hergarten et al. (1998) demonstrated that *Pseudomonas* sp. W34 and *B. cereus* S18 inhibited *M. incognita* on lettuce and seed treatment by significant reductions in root galling resulting in enhanced seedling biomass, besides having a suppressive effect on pathogen *Fusarium* sp. for biological control in lettuce (Sottero et al. 2006).

9.2.8 *Spinach (*Spinacia oleracea *L.)*

Similar to other foliage vegetable crops, spinach (*Spinacia oleracea* L.) belongs to the Chenopodiaceae family and the group of leafy vegetables contains important minerals and vitamins, has good cooking adaptability, and hence consumer demand increases annually (Nishihara et al. 2001). This vegetable is consumed steamed, fried or even raw at the early growth stages (Krężel and Kołota 2014). Spinach is produced in all regions of the world, and it has over 900,000 ha production area with approximately 26 million mt agricultural field. China alone produced over 90% of total world production (FAOSTAT 2018). It is produced by direct-seeded method. The optimum seed germination occurs at about 15–21 °C. Spinach plants are sensitive to acidity because of this reason: rainy regions are not suitable for spinach production because of low soil pH (Vural et al. 2000; Welbaum 2015).

Nitrogen is the key nutrient for spinach, and easily accumulates in the form of nitrate which is harmful for human health. N_2-fixing plant growth promoting rhizobacteria has a great potential for eco-friendly and healthy production of spinach. N_2-fixing, phytohormone producing and P-solubilizing bacterial species *B. cereus* RC18, *B. licheniformis* RC08, *B. megaterium* RC07, *B. subtilis* RC11, *Bacillus* OSU-142, *Bacillus* M-13, *P. putida* RC06, *P. polymyxa* RC05 and RC14 increased spinach shoot fresh weight, leaf area and plant height (Çakmakçı et al. 2007). Hou and Oluranti (2013) reported that *P. putida* NWU12, *P. fluorescence* NWU65, *P. fluvialis* NWU37 and *Ewingella americana* NWU59 are all positive for ammonia, catalase, hydrogen cyanide and phosphate solubilization, thus helpful in increasing plant heights. Although growth of spinach was not promoted when only the organic materials were applied, multiple applications with fluorescent *Pseudomonas* strains and organic materials proved better for promoting the growth because fluorescent *Pseudomonas* strains aggressively colonized the roots when the organic materials were applied (Urashima et al. 2005). Interestingly, Jiménez-Gómez et al. (2018) reported *Rhizobium laguerreae* as an excellent plant probiotic, in increasing yield and quality of spinach.

9.2.9 *Radish (*Raphanus sativus *L.)*

Radish, *Raphanus sativus* L., is cultivated in three distinct types: spring or summer, daikon and winter. It is a member of Brassicaceae family, known as a cool season vegetable because it does not grow well in hot and dry weather, and considered hardy in cold temperatures. An optimal fertilization with N (100 kg h^{-1}) and P (80 kg h^{-1}) is sufficient to promote growth and yield of this salt-sensitive crop. The plant suffers from various diseases, such as rhizoctonia root rot, Fusarial wilt, black spot, powdery mildew and downy mildew. However, the most important physiological factor limited radish growth and yields are day length and vernalization. Especially in long days, most of the radish cultivars bear flowers without forming a root. In other words, radish cultivars have a facultative vernalization response because cold exposure is not required for flowering, but flowering will occur more rapidly after cold treatment. In contrast, radish cultivars have an obligate requirement for cold treatment and do not flower without prior cold exposure (Kaymak and Güvenç 2010).

Nitrate accumulation and heavy metal toxicity are major problems in production of most of the vegetables including radish. Heavy metals such as cadmium, nickel and lead contamination are ubiquitous and cause toxicity to radish. According to Ahmad et al. (2018), application of compost and PGPR ameliorates Pb toxicity in radish. *Bacillus* sp. CIK-512 and compost synergy improved growth and physiology of radish in contaminated soil, possibly by antioxidant activities and reduction in lead accumulation in shoot. Similarly, use of both PGPR *Bacillus* sp. CIK-516 and *Stenotrophomonas* sp. CIK-517Y improved the growth of radish under four different levels of Ni contamination. The plant growth, dry biomass, chlorophyll and nitrogen contents were significantly reduced in the plant due to exposure of Ni, but *Bacillus* sp. CIK-516 and *Stenotrophomonas* sp. CIK-517Y overcame the negative effects of Ni stress on radish by improving the overall growth parameters (Akhtar et al. 2018).

Bio-priming with PGPR genera (*Agrobacterium rubi* strain A 16, *Burkholderia gladii* strain BA 7, *P. putida* strain BA 8, *B. subtilis* strain BA 142 and *B. megaterium* strain M 3) significantly improved the percentage of seed germination of radish under saline conditions (Kaymak et al. 2009). Hong and Lee (2017) reported that *Arthrobacter scleromae* SYE-3, an isolate from local plants grown in saline soil, evidenced in enhancing yield in salinized environments. On the other hand, the evidence of gibberellin (GA) production by PGPR is rare (Vessey 2003). The new isolate *Leifsonia soli* sp. SE134 significantly promoted the growth of cucumber, tomato and radish due to significant GA production capacity (Kang et al. 2014).

It is known that PGPR commonly use to suppress the plant diseases. In this crop, seed and pre-plant applications of cell suspension of *P. fluorescens* Pf 9A-14, *Pseudomonas* sp. Psp. 8D-45 and *B. subtilis* Bs 8B-1 suppressed rhizoctonia damping-off of radish (Khabbaz et al. 2015). Long back, De Boer et al. (2003)

observed that combination of *P. putida* strains WCS358 and RE8 leads to more effective and more reliable biocontrol of Fusarium wilt in radish.

9.2.10 *Cabbage (*Brassicae oleraceae *var.* capitata *L.,) and Chinese Cabbage (*Brassica campestris *L. subsp.* pekinensis*)*

Cruciferous crops, such as broccoli, cabbage, cauliflower, are important vegetable crops and widely grown in different regions of world with a production of cabbages and other brassicas including cauliflowers and broccoli 96 million mt. in 3,816,000 ha production area (FAOSTAT 2018). Different fungi, harmful bacteria, pest and pathogens cause various seed and soil-borne disease. *Xanthomonas campestris* pv. *campestris* (Xcc) causes black rot disease in cabbage. The most significant bacteria *Bacillus velezensis* AP218 significantly reduced disease incidence and disease severity and exhibited biocontrol of black rot of cabbage under field and greenhouse conditions (Liu et al 2016a). Application of the *P. fluorescens* as seed treatment significantly reduced black rot of cabbage under greenhouse conditions (Umesha and Roohie 2017). Different species of *Bacillus,* namely *B. cereus*, *B. subtilis* and *B. amyloliquefaciens* treatments efficiently suppressed the cabbage aphid (*Brevicoryne brassicae*) field populations in varying magnitudes (Gadhave et al. 2016). Samancioglu et al. (2016a) reported that *B. pumilus* TV-67C strains increase drought stress tolerance in cabbage seedlings by accelerating the accumulation of inherent levels of superoxide dismutase, catalase and peroxidase, amino acid and hormone production. In addition, combined effect of *B. megaterium* TV6D and *Pantoea agglomerans* RK-92 + *Brevibacillus choshiensis* TV-53D mitigates drought stress tolerance in cabbage plants by accumulating antioxidant enzymes, osmolytes, hormone production and decreased electrolyte leakage in treated plants under water-deficit conditions (Samancioglu et al. 2016b). Yildirim et al. (2015, 2016) observed that seed and seedling inoculation with *P. polymyxa* RC14 increased shoot fresh and dry weight, root fresh and dry weight, macro- and micro-nutrient content of leaf and root of cabbage seedlings, yield and yield parameters as well as chlorophyll reading value and stomatal conductance versus controls. Turan et al. (2014) showed that treatments with *B. megaterium* TV-91C, *Pantoea agglomerans* RK-92 and *B. subtilis* TV-17C improved seedling growth and quality in cabbages.

Different strains of *Bacillus velezensis* AP136, AP188, AP213, AP218, AP295 and AP305 reduced the number of foliar lesions of black rot; other bacilli such as *Bacillus safensis* AP7 and *Bacillus altitudinis AP18* increased shoot fresh and dry weight, root fresh and dry weight of Chinese cabbage (Liu et al 2016b). Shrestha et al. (2009) reported that *Lactobacillus*, *Lactococcus* and *Paenibacillus* spp. can be further developed as a stable biological control agent to manage soft rot caused by *Pectobacterium carotovorum* subsp. *carotovorum*, which greatly affect the Chinese cabbage production worldwide.

9.2.11 *Broccoli and Cauliflower (*Brassica oleracea *L. var.* italica *Plenck and* Brassica oleracea *var botrytis L.)*

Broccoli (*Brassica oleracea* L. var. *italica* Plenck) belongs to the Brassicaceae family member, and is spread in the Mediterranean region (Decoteau 2000). This crop is an important vegetable because of its high selling price and its vitamin-rich, high fibers and low calorie properties (El-Nemr et al. 2011). In other words, broccoli is a low sodium food and is fat and cholesterol free, high in vitamin C and a good source of folate (Decoteau 2000). USA is the world's largest producer of broccoli in 60,000 ha (Welbaum 2015). Heads of broccoli are sold fresh and boiled or steamed for eating, and also uncooked broccoli is eaten in salads without cooking. Broccoli is also processed by freezing and dried (Welbaum 2015). There are many diseases such as black rot, blackleg, downey mildew, bacterial leaf spot, Verticillium wilt, Fusarium wilt, which adversely affect broccoli (Decoteau 2000; Rimmer et al. 2007; Welbaum 2015).

Available literature revealed that different groups of PGPR have a great potential for improving growth and yield of broccoli under different environment conditions. More recently, Altuntaş (2018) reported that *B. subtilis* strain QST 713 increased the yield, plant growth parameters and nutrient uptake of broccoli and ascorbic acid contents. Both Gram-negative and Gram-positive bacteria such as *B. cereus*, *Brevibacillus reuszeri* and *Rhizobium rubi* inoculations with manure increased yield, plant weight, head diameter, chlorophyll content, nitrogen, potassium, calcium, phosphorus, magnesium and iron content of broccoli (Yildirim et al. 2011). Further, *P. fluorescens* have great potential in enhancing the growth, phosphatase activity, chlorophyll content, nutrient uptake and yield of broccoli when combined with 80 kg ha^{-1} superphosphate (Tanwar et al. 2014).

Among vegetable crops, cauliflower (*Brassica oleracea* var. *botrytis* L.) is one of the most important winter vegetable crops (Devi et al. 2017). It is a cool season, frost-tolerant crop widely adapted and grown in both temperate and subtropical regions. It is a low calorie crop but a good source of vitamin C (Decoteau 2000; Welbaum 2015). Sold fresh and boiled, baked or steamed and is also processed by freezing and drying. In Asian countries like China and India, it is produced on large scale and about 70% of its total world production occurs in Asia. Cauliflower shares most of the same insect pest and disease similar to that of broccoli. The crop suffered from black rot, black leg, alternaria leaf spot, bacterial leaf spot, soft rot verticillium wilt and Fusarium wilt at various stages of development (Decoteau 2000; Rimmer et al. 2007; Welbaum 2015).

Cauliflower requires high nitrogen as nutrient, and thus deficiency of nitrogen causes low yield, delayed maturation and low productivity. Its requirements are also high for boron and molybdenum (Swaider et al. 1992; Welbaum 2015). The N_2-fixing PGPR has a great importance for this reason in healthy crop production.

Khan et al. (2018) reported that nitrogen-fixing by rhizobacteria has a great potential to improve the yield of economic plants like cauliflower. Bhardwaj et al. (2017) observed that *Bacillus* sp. SB_{11} has tremendous potential to be used as a biofertilizer/bioprotectant for growth promotion and natural protection of cauliflower under low hill conditions of Himachal Pradesh in India. Further, *B. pumilus* with inorganic P-source have been used to enhance growth, yield and quality of cauliflower under mid hill conditions (Dipta et al. 2017). The use of PGPR isolates as biofertilizers proved beneficial for cauliflower cultivation because of the enhanced growth occurred mainly due to bacteria-mediated IAA production and phosphorus solubilization (Kushwaha et al. 2013). Similarly, the role of *Bacillus* spp. MK_5 with N and P as biofertilizer established their nature as beneficial bacteria for cauliflower cultivation as evidenced by induced IAA production and phosphorus solubilization (Kaushal et al. 2011). The application of *Bacillus* spp. MK_5 combined with recommended dose of 75% NP fertilizers significantly and increased the cauliflower yield (Kaushal et al. 2013). In addition, Ekinci et al. (2014) reported that *B. megaterium* TV-3D, TV-91C, TV-87A and KBA-10, *P. agglomerans* RK-92 and *B. subtilis* TV-17C increased fresh shoot weight, dry shoot weight, root diameter, root length, fresh root weight, dry root weight, plant height, stem diameter, leaf area and chlorophyll contents of cauliflower transplants. In addition, combined application of fertilizers, manures and PGPR is not only a cost-effective nutrient module but also helps in getting higher yield and quality with 25% net saving of fertilizers, as reported by Thakur et al. (2018).

*9.2.12 Mint (*Mentha sps*)*

Mentha sps (Mint) belong to the family Lamiaceae aromatic. It is one of the most important essential oils crops with a specific flavor, and the crop is perennial. Its leaves are picked, dried and used until needed (Abbas 2009). It is also cultivated worldwide for production of essential oils (Lawrence 2007). Besides its dry usage, fresh leaves are also utilized as a leafy vegetable in Turkey and in some Middle-East countries (Kaymak et al. 2013). Total world production of mint or peppermint (*Mentha* × *piperita*) was 106,252 mt. in 3390 ha production area (FAOSTAT 2018).

Various groups of PGPR induced growth and reproduction in medicinal and aromatic plants Kaymak et al. (2013) reported that *P. putida* biotype B C3/101, *P. polymyxa* RC105 and urea treatments induced growth, which resulted in significant increase in total fresh and dry yields of mint compared with the control. Although yield obtained due to treated plant by bacterial inoculation was lower than urea treatment, but it was more than that of control. Both *P. putida* biotype B C3/101 and *P. polymyxa* RC105 have the potential to increase the yield, growth and

mineral composition of leaves. In addition, *B. subtilis* GB03, *P. fluorescens* WCS417r and *P. putida* SJ04 increased shoot and root biomass, leaf area, node number, trichome and stomatal density. There were marked qualitative and quantitative changes in monoterpene content of *M. piperita* (Cappellari et al. 2015). Similarly, *P. fluorescens* WCS417r, *B. subtilis* GB03 and *P. putida* SJ04 enhanced synthesis of phenolic compounds in leaves of *M. piperita* and have the potential to improve the productivity (Cappellari et al. 2017). Santoro et al. (2011) reported that volatile organic compounds of *P. fluorescens*, *B. subtilis* and *A. brasilense*, besides inducing biosynthesis of secondary metabolites, affect pathway flux or specific steps of monoterpene metabolism in *M. piperita.* The bacterial volatile organic compounds are rich source for new natural compounds that may increase crop productivity and essential oils yield of this economically important plant species. Inoculated with the native *P. putida* strains showed increased shoot fresh weight and root dry weight of *M. piperita* (peppermint) because indigenous bacteria which are generally more effective in terms of their acclimitization and adaptation to the environment have a competitive advantage over non-native strains (Santoro et al. 2015; Aeron et al. 2010).

Wide range of PGPR group of bacteria *pumilus* STR, *Halomonas desiderata* STR8 and *Exiguobacterium oxidotolerans* STR36 reduced the negative effects of salinity while cultivating *M. arvensis*, and application of *Halomonas desiderata* STR8 in sodic soil increased herb yield and oil content of *M. arvensis* under salt stress (Bharti et al. 2014). Ebstam and Nadia (2013) reported that the maximum values of growth parameters of *M. viridis* L. (plant height, number of branches, plant fresh and dry weight) as well as volatile oil percentage occurred in plants treated with *B. subtilis* and *P. fluorescence* as individual and consortia as well, which also showed biocontrol phenomenon against *Rhizoctonia solani*.

9.3 Conclusion and Future Prospects

Numerous plant growth promoting rhizobacteria (PGPR) have been examined under laboratory, greenhouse and field conditions for vegetable production. PGPR has a great potential for increasing yield, reducing of fertilizer requirement and synthetic pesticides. In the last few years, PGPR studies focused on the biocontrol of destructive diseases of vegetables such as Fusarium wilt and bacterial wilt in tomatoes, *Phytophthora* blight in peppers, Fusarium wilt in melons and angular leaf spot in cucumber. Similar to oil seed, pulses and maize, researches about the effects of PGPR on growth and yield of vegetables are also continuing.

PGPR replaces the chemical fertilizers and pesticides by reducing pollution, save the resources and cut down the high production cost. Evolvement of environment-friendly and cost-effective strategies with PGPR is still to be continued for the commercialization of PGPR for healthy production of vegetables. In other words, the chemical inputs are being used to increase yields, suppress

pathogens and pests but their excessive, uncontrolled and unconscious use over the years resulted in an accumulation of toxic chemical resides in the crop production areas. To overcome this adverse affects, an effective and sustainable alternative method is the application of PGPR in all stages of crop production.

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Chapter 10
Problem of Mercury Toxicity in Crop Plants: Can Plant Growth Promoting Microbes (PGPM) Be an Effective Solution?

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

Abstract Mercury is ranked as the most toxic heavy metals. It enters into the environment due to some natural processes and anthropogenic activities. It has a property of bioaccumulation into the food chain through uptake by crop plants from the contaminated agricultural lands, leading to detrimental impact on human health. Mercury has the toxic effect on plants as it disturbs many biological processes, including photosynthesis, respiration, transpiration, cell division and so on. Phytoremediation involves several plant species which have the ability to accumulate or degrade contaminants, including heavy metals. Another important strategy is the utilization of transgenic plants transformed with bacterial *mer* genes to increase phytoremediation of mercury. The mercury-resistant plant growth promoting microbes (PGPM) enhance plant growth under mercury stress as well as increase the mercury uptake by plants. This chapter summarizes the present understanding toward the mercury toxicity and their molecular responses in plants. It also illustrates the plethora of mechanism adapted by PGPM for plant growth promotion and detoxification of mercury. It also highlights the paradigms for synergistic use of PGPM for improved phytoremediation of mercury from agricultural lands.

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10.1 Introduction

The contamination of heavy metals in soil by various activities is a major environmental concern. The highly toxic heavy metals such as arsenic (As), lead (Pb), cadmium (Cd) and mercury (Hg) can enter the food chain through uptake by crop plants from the contaminated agricultural lands, leading to detrimental impact on human health (Puglisi et al. 2012). Among the heavy metals, mercury is ranked as the most toxic one and it is present in the environment due to some natural processes and anthropogenic activities. The anthropogenic activities which introduce mercury into the environment are production chemicals (paints, paper and pulp, disinfectants, microbicidal agents, agrochemicals, etc.), use of fossil-fuels in power plants and industrial waste incineration and disposal (Frossard et al. 2017). Mercury is mostly present in the environment in elemental form (Hg^0), which is readily oxidized to the ionic form, Hg^{2+} (Selin 2009). The ionic form of mercury (Hg^{2+}) makes complexes with many inorganic compounds to produce HgS, $ClHg_2$, Hg_2Cl_2 or other organomercurial compounds such as CH_3–Hg (Tiwari and Lata 2018). The agricultural soil has the ionic form (Hg^{2+}) in majority, through adsorption onto sulfides, clay particles and organic matters (Azevedo and Rodriguez 2012; Gontia-Mishra et al. 2016; Beckers and Rinklebe 2017). Interestingly, mercury is a bioaccumulative toxin as it remains in the environment for longer periods (Schroeder and Munthe 1998). Plants growing under mercury contamination are severely affected during all stages of their development. It is observed that plants exhibit poor germination, impaired photosynthesis, compromised biomass, and so on, under mercury stress (Patra and Sharma 2000). It is highly phytotoxic to plant cells, leading to various physiological abnormalities. At cellular level, mercury interferes with the proper water uptake (stomata closure), functioning of mitochondria and generates oxidative stress leading to lipid peroxidation, enzyme inactivation and DNA and membrane damage (Chen et al. 2014).

Hence, it is apparently the need of the hour to select an appropriate methodology for mercury remediation from the environment. There are physiochemical methods, including precipitation, conventional coagulation, adsorption, ion exchange, and so on, and biological methods (bioremediation and phytoremediation) for removal of this hazardous metal from the environment (Dash and Das 2012). The physiochemical methods have a very high operational cost, as well as are not suitable for large areas; therefore, the focus is rapidly shifting toward the cost-effective and eco-friendly biological alternatives for remediation of mercury (Oves et al. 2013). In this context, the use of plant growth promoting microbes (PGPM) for remediation of mercury contaminated site is an attractive and economical option. There are several reports which advocate the role of plant growth promoting rhizobacteria (PGPR) and fungi in enhancement of plant growth and endurance under heavy

metal stress condition (Arshad et al. 2007; Gontia-Mishra et al. 2016; Pietro-Souza et al. 2017). They also possess the ability to biotransform toxic ions to non-toxic forms. This chapter summarizes the present understanding toward the mercury toxicity and their molecular responses in plants. It also highlights the paradigms for synergistic use of PGPM for improved phytoremediation of mercury from agricultural lands.

10.2 Mercury Pollution in Agricultural Lands

There are various sources of mercury pollution to the environment. These sources are natural as well as due to human activities. The natural activities include ubiquitous breaking of mercury-containing rocks in the outer layer of the earth. The volcanic explosion and geothermal activity can contribute to the mercury pollution to some extent (AMAP/UNEP 2013). This kind of pollution depends on several factors, like presence of mercury containing rocks and period of geothermal activities (Ferrara 1998, 2000; Pirrone et al. 2001). Global mercury emissions are approximately 80–600 ton/year to the environment from such natural activities (Mason et al. 2012).

Since ancient times, mercury is being used for several purposes, like explosives, preservatives and treatments of various skin diseases (Azevedo and Rodriguez 2012). Anthropogenic activities are the major sources for mercury pollution in the soil and water. These activities include mining, coal burning, cement production, mercury containing pesticides and disposal of mercury containing waste in the environment (AMAP/UNEP 2013; Mason et al. 2012). Electricity generation by burning of coal and dependence of several industries on coal energy emit huge amounts of mercury to the atmosphere.

Some frequently used materials, like batteries, fluorescent lamps and medical instruments such as leftover thermometers and sphygmomanometer, also contribute to Hg emissions. Mercury is also used by dentists as dental amalgams and in various devices like barometers, manometers, float valves, mercury switches, mercury relays and various research activities. Although these devices are useful in weather stations, airports and air fields, wind tunnels and engine manufacturing, as well as in installations offshore or on ships, they also contribute to release of mercury in the atmosphere (Hutchison 2003). Mercury pollution also emerges from agricultural practices, like use of pesticides and fertilizers (Hseu et al. 2010). It was conventionally used in the form of fungicide or pesticide in agriculture. The amount of mercury present in the soil and its uptake by plants rely on various factors, like pH of soil, species of plant, presence of microorganisms, type of mercury ion and so on. It was observed that the mercury uptake can be minimized using high soil pH and/or high amount of lime and salts (Patra and Sharma 2000; Patra et al. 2004). It has been reported that mercury accumulation is much more persistent in soil as compared to aquatic and other biomes (Padmavathiamma and Li 2007; Tangahu et al. 2011).

10.3 Mercury Toxicity in Plants and Their Molecular Responses

The organic form of mercury severely affects plants as they are more toxic than inorganic (Hg^{2+}) counterparts (Patra and Sharma 2000). Mercury has its toxic effect on most of the crop species, beyond the tolerance limit. It tends to amass in the roots; hence the phytotoxic symptoms are also noticed in roots (Chen et al. 2014). The excess mercury in the soil is taken up by plants, causing disturbance and malfunction to many of the biological processes, including photosynthesis, respiration, transpiration and cell division (Fig. 10.1). The plausible mechanism of mercury toxicity is its ability to react with the sulfydryl (SH) groups of proteins and enzymes; similarly, it has high affinity for the phosphate groups of lipids, energy-rich molecules like ATPs and nucleotides. It is also noted that it also substitutes the essential ions such as Mg^{2+} ion in chlorophyll (Azevedo and Rodriguez 2012). Mercury also messes up with the aqua-porins (water channels), causing impaired transpiration and subsequent water uptake via vascular tissues (Zhou et al. 2008). It deliberately disrupts the plant antioxidant defense enzymes, especially glutathione reductase (GR), superoxide dismutase (SOD), catalase and ascorbate peroxidase (APX). Besides, it also affects the other antioxidant entities such as glutathione (GSH) and non-protein thiols (Israr et al. 2006; Zhou et al. 2008).

The plants can tolerate the effect of mercury toxicity to some extent by the interplay of various physiological and molecular mechanisms. First, when plants come into contact with mercury ions, they prohibit or reduce the uptake of mercury into the roots by either complexing them to cell wall or root exudates; if it enters the root cell, the metal ion is restricted to the apoplasts. But if still the mercury ions gain entry into the plant cell, they are countered by detoxification through compartmentalization into vacuoles or complexation with amino acids, organic acids, chelation by phytochelatins (PC) and metallothioneins (MT). Further, some non-enzyme antioxidants such as α-tocopherol and GSH also aid in combating mercury toxicity (Kalaivanan and Ganeshamurthy 2016). These processes mostly

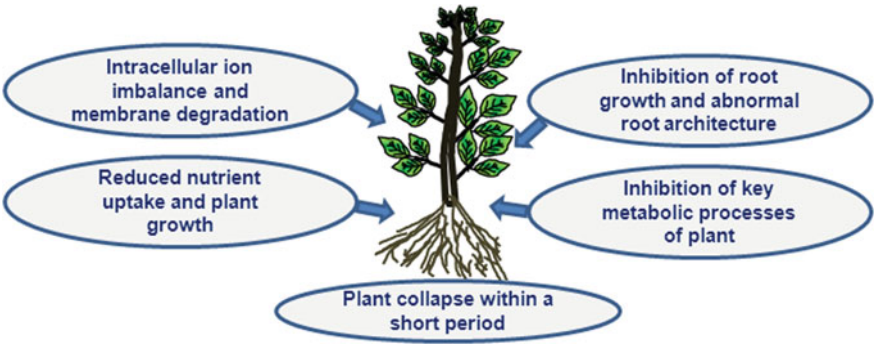

Fig. 10.1 Effects of mercury toxicity on plants

put a check on translocation of mercury ions to the leaf tissues and thereby shielding the photosynthesis from detrimental effect of mercury (Rascio and Navari-Izzo 2011). Finally, plants resort the mercury toxicity by induction of oxidative stress enzymes such as SOD, APX, catalase, glyoxalase and GR. They also trigger the stress-responsive proteins and hormones. Various signaling cascades are stimulated by encountering heavy metal ions, namely calcium-dependent signaling and mitogen-activated protein kinase (MAPK) signaling (Tiwari and Lata 2018). Recently, it was observed that mercury toxicity activates the biosynthesis of aromatic amino acids (tryptophan and phenylalanine), calcium accumulation and also stimulates MAPK in rice (Chen et al. 2014).

10.4 Phytoremediation

As already discussed, the physical and chemical methods of remediation of heavy metals are costly and time-consuming. The focus has shifted to phytoremediation. Phytoremediation is a process utilizing plants to eliminate, detoxify, volatilization or reduce the concentration of environmental contaminants, including heavy metals (Wood et al. 2016). In contrast, this technology is widely accepted as it is an economical, efficient and environment-friendly way to remove metals from contaminated soils. Phytoremediation, in general, involves several plant species with the ability to accumulate or degrade contaminants and in turn the biomass generated through this process can be used for other purposes. Phytoremediation occurs by the use of one or all the following mechanisms, such as phytoextraction, rhizofiltration, phytodegradation and phytovolatilization. In the context of mercury contamination, phytovolatilization is of great importance because Hg^{2+} ion is taken from soil and volatilizes it to non-toxic Hg^0 form from the foliage into the atmosphere (Kumar et al. 2017). Phytoremediation is adopted by using hyperaccumulator plants which have capacity to take up exceedingly enormous amounts of heavy metals from the soil in comparison to other plants (non-hyperaccumulators). Additionally, in hyperaccumulators the heavy metal ions are translocated to the shoots, and interestingly, no visible signs of phytotoxicity are observed in hyperaccumulators (Rascio and Navari-Izzo 2011).

In general, plants belonging to the family Brassicaceae (*Thlaspi* and *Alyssum*, *Brassica*, *Noccaea*), Crassulaceae (*Sedum alfredii*) and Pteridaceae (*Pteris vittata*) have been reported as proficient heavy metal hyperaccumulators (Reeves and Baker 2000). However, the reports for mercury hyperaccumulators are scanty and include plant species *Brassica juncea*, *Polypogon monospeliensis* and *Pteris vittata* (Su et al. 2007). Similarly, plants *Lindernia crustacea*, *Paspalum conjugatum* and *Cyperus kyllingia* have been used for potential phytoextraction of mercury for contaminated sites. It was also noted that these plant species efficiently take up and translocate mercury from roots to shoots (Muddarisna et al. 2013). In another study, *Medicago sativa* and *Dittrichia viscosa* were found suitable plants for phytoremediation of the site contaminated with mercury (Shehu et al. 2014). Hence, there is

an ever-increasing demand to search new mercury hyperaccumulators plant for their utilization in phytoremediation.

10.5 Plant Growth Promoting Rhizobacteria/Microbes (PGPR/PGPM)-Assisted Phytoremediation

PGPR are a dynamic group of bacteria which are associated with the roots or present in vicinity of roots, that is, in the rhizosphere and tend to benefit plants through plethora of mechanisms (Gontia-Mishra et al. 2017a). Microbes are well known to take part in the biogeochemical cycling of toxic metals and also in remediating heavy metals from the contaminated sites. The phytoremediation of heavy metals mostly relies on the availability of metal ions. The interference of heavy metal-resistant PGPR addresses this problem by increasing the bioavailability of metal ion by modifying the soil texture and properties (Mishra et al. 2017). PGPR play a major role in plant growth promotions as well as bestow with the ability to reduce the noxious effect of heavy metals on plants. PGPR are also equipped to detoxify the heavy metals. There are ample of reports which advocate that the use of PGPM proposes a better strategy by improving the phytoextraction and phytoremediation of heavy metals, particularly mercury from soil (Glick 2010; Quiñones et al. 2013; Gontia-Mishra et al. 2016; Ashraf et al. 2017; Etesami 2018). The comparative account of mercury detoxification via phytoremediation and PGPM-assisted phytoremediation is represented in Fig. 10.2.

10.5.1 Detoxification of Mercury via Mer *Operon*

With special context to bioremediation of mercury, PGPM can facilitate the process by direct interaction with the metal ion, through volatilization (reduction of Hg^{2+} to Hg^{0}), transformation and rhizodegradation (Gadd 2010). There are many studies which provide the details of mercury-resistant PGPR (Ruiz-Diez et al. 2012; Quiñones et al. 2013; Gontia-Mishra et al. 2016). These mercury-resistant bacteria have evolved numerous ways to combat the mercury toxicity, namely through volatilization, exopolysaccharide (EPS) sequestration, metal complexation and enzymatic detoxification (Dash and Das 2012). Mercury-resistant bacteria are also known to produce thiol compounds which have high affinity for Hg^{2+} ions, further lowering the metal toxicity. Another important mechanism adapted by bacteria to alleviate metal toxicity is bioaccumulation. Bioaccumulation is largely carried out by biosorption, which depends on various processes such as complexation (sulfur, phosphate and bicarbonate groups of cell wall), chelation (siderophore and PC), ion exchange and entrapment in intracellular spaces (Mishra et al. 2017).

Furthermore, many mercury-resistant bacteria also harbor mercury resistance genes, that is, the *mer* operon, either on plasmid or in the chromosome, transposons

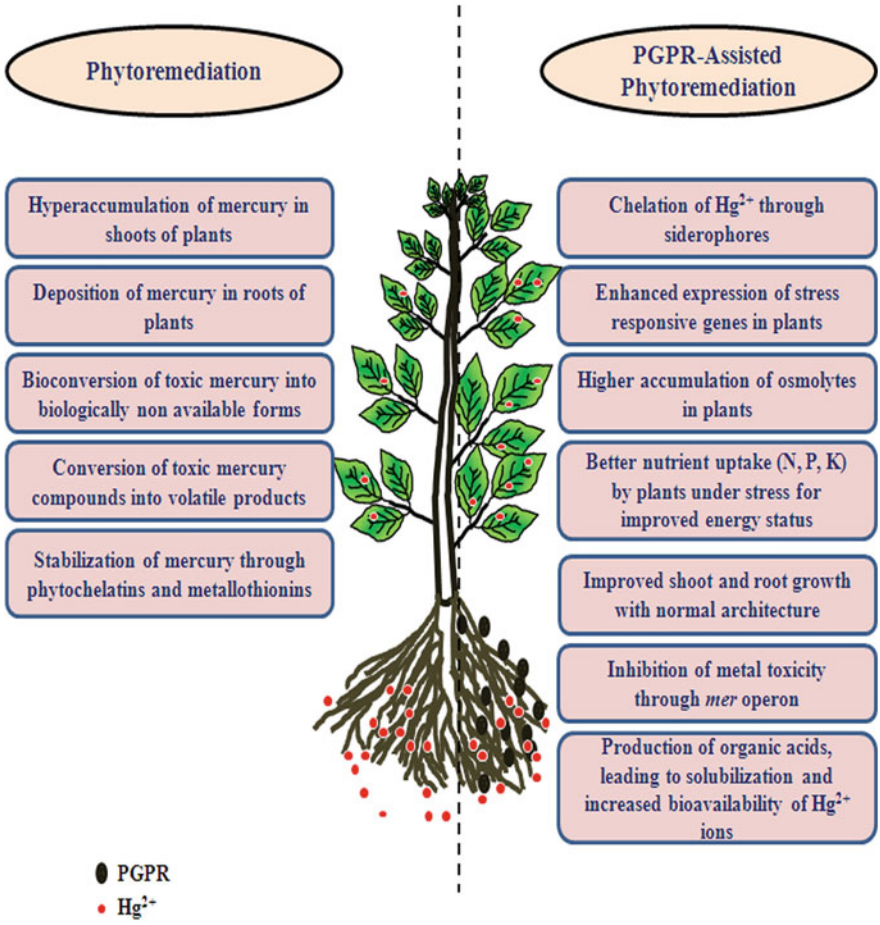

Fig. 10.2 The comparative account of mercury detoxification *via* phytoremediation and PGPM-assisted phytoremediation

or integrons for reduction from Hg^{2+} to Hg^0, the less reactive form (Mathema et al. 2011; Dash et al. 2017a). This is the most efficient mechanism of mercury detoxification widespread in the Gram-positive and Gram-negative bacteria (Chatziefthimiou et al. 2007). The *mer* operon consists of a series of operator, promoter, regulator genes and the functional genes. The functional genes comprise *merP*, *merT*, *merD*, *merA*, *merF*, *merC* and occasionally *merB*. Each gene codes for a functional protein participate in a specific way to detoxify mercury. The detoxification of mercury is generally achieved by the uptake and transport of Hg^{2+} by the periplasmic protein MerP, a mercuric ion transport protein MerF and the inner membrane protein MerT (Powlowski and Sahlman 1999; Mathew et al. 2015). Further, the final process of reduction of Hg^{2+} to volatile metallic mercury is carried out by mercuric ion reductase encoded by the most important *merA* gene

(Ní Chadhain et al. 2006; Dash et al. 2017a). Moreover, some bacteria also possess *merB* gene coding for organomercurial lyase (Reniero et al. 1995) which aid in cleavage of Hg^{2+} from organomercurial compounds. The *mer* operon is positively regulated by regulator protein merR in the presence of Hg^{2+} in the surroundings (Huang et al. 2002).

10.5.2 Bioremediation of Mercury by PGPR Using Different Strategies

PGPR which do not possess the mercury resistance via *mer* genes can also positively modulate plant growth under mercury stress by diverse mechanisms, which in turn aid in improved uptake and assimilation of mercury in roots and shoots. These mechanisms include: (a) better nutrient uptake by action of N_2 fixation, P, K, Zn solubilization; (b) by producing plant growth regulators, that is phytohormones [indole acetic acid (IAA), cytokinin and gibberellic acid]; (c) production of metal chelating compounds, for example, siderophores, PC, EPS; (d) production of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase; (e) production of organic acids; (f) protection of plants from deleterious plant pathogens (Jha et al. 2012). The use of various mercury-resistant PGPR for alleviating mercury stress and their positive impact on host plants is shown in Table 10.1.

10.5.2.1 Rhizobia–Legume Interaction in Mercury Bioremediation

The most important symbiotic interaction between rhizobia and legume which offer nutrients, especially nitrogen to plants, has been extensively exploited to improve the phytoremediation of mercury (Nonnoi et al. 2012; Lebrazi and Fikri-Benbrahim 2018). It is a well-known fact that rhizobia enter the roots of legumes to develop root nodules, where atmospheric N_2 is fixed to ammonia, which is assimilated by the plants. The nitrogen is the major nutrient element for plant growth, and legume–rhizobia interaction enhances plant productivity; hence rhizobia has been recognized as an important plant growth promoter (Teng et al. 2015). Recently, it is noted that many species of rhizobia have mercury resistance which promotes them to be used as excellent candidates for rehabilitating contaminated soils (Ruiz-Diez et al. 2012). Besides, the rhizobia–legume partnership also enhances soil fertility, promotes plant growth and provides ecological benefits. A recent study reports the isolation of mercury-resistant rhizobial strains *Ensifer medicae* and *Rhizobium leguminosarum* bv. *trifolii* from the root nodules of *Medicago* spp. and *Trifolium* spp. plants growing in Hg-contaminated soils. In addition to nitrogen fixation, these isolates also exhibited other plant growth promotion traits such as phosphate solubilization and siderophore production, which assists in increasing the bioavailability of metal ion in the soil through modulation of soil pH (Nonnoi et al. 2012). Similarly, mercury-resistant rhizobial strains *R. leguminosarum*, *Rhizobium*

Table 10.1 List of mercury-resistant PGPM used to enhance plant growth promotion and alleviation of mercury stress in plants

S. no.	Mercury-tolerant PGPRs	Isolation site	Interaction with plant	Level of Hg tolerance	Plant growth promoting traits	References
1	*Pseudomonas fluorescens*	Rhizosphere of soybean and pea	Soybean	147 µM	IAA, siderophore production and P solubilization	Gupta et al. (2005)
2	*Ensifer medicae* and *Rhizobium leguminosarum* bv. *trifolii*	Root nodules of *Medicago* spp. and *Trifolium* spp.	–	250 µM	P solubilization and siderophore production	Nonnoi et al. (2012)
3	*Rhizobium radiobacter*, *R. leguminosarum*, *R. gallicum*, *Bradyrhizobium canariense*, *Ensifer medicae* and *E. meliloti*	Nodules of legumes (*Medicago*, *Trifolium*, *Vicia*, *Lupinus*, *Phaseolus*, and *Retama*)	–	3–30 µM	N_2 fixation and ability to re-nodulate the host plants	Ruiz-Diez et al. (2012)
4	*Bradyrhizobium canariense*	Nodules of *Lupinus albus*	*Lupinus albus*	12.5 µM	N_2 fixation and nodulation at high concentration of Hg	Quiñones et al. (2013)
5	*Halobacillus* sp., *Halomonas* sp. and *Halobacillus* sp.	Mangrove rhizosphere	*Sesuvium portulacastrum*	0.04 mM	Salinity and other metal tolerance with IAA production and P solubilization.	Desale et al. (2014)
6	*Enterobacter, Cronobacter* and *Pseudomonas*	Nodules of different plants	–	–	N_2 fixation	Tariq and Latif (2014)
7	*Photobacterium* spp.	Rhizosphere soil of reed (*Phragmites australis*)	Long yard bean	33 $mg^{-1\ kg}$	IAA producing with multiple metal tolerance	Mathew et al. (2015)
8	*Cronobacter* sp., *Pseudomonas* sp. and *Bacillus* sp.	Root nodules of *Sesbania concolor*, *Trifolium alexandrinum*, *Iresine herbstii* and *Dahlia* sp.		50 µg of $HgCl_2$	N_2 fixation and H_2S producing	Rafique et al. (2015)

(continued)

Table 10.1 (continued)

S. no.	Mercury-tolerant PGPRs	Isolation site	Interaction with plant	Level of Hg tolerance	Plant growth promoting traits	References
9.	*Pseudomonas* sp.	Polluted water, rhizospheric soil and root nodules of different plant species	–	10–20 μg^{-1ml} $HgCl_2$	N_2 fixation and H_2S producing	Tariq et al. (2015)
10	*Enterobacter ludwigii*, *E. cloacae* and *Klebsiella pneumoniae*	Rhizosphere of the weeds *Alternanthera sessilis* and *Cyperus esculentus*	Wheat	500 µM	NH_3, siderophore, IAA, EPS production, ACC deaminase activity, Zn, P and K solubilization	Gontia-Mishra et al. (2016)
11	*Enterobacter* sp.	Rose (root section), Lemon (stem section) and Mosaami (stem section)	–	20–50 mg^{-1L}	N_2 fixation, HCN and H_2S production	Mobeen and Latif (2016)
12	*Bacillus* sp., *Bacillus cereus*, and *Enterobacter cloacae*	Rhizosphere soils near to districts Kasur and Sheikhupura, Pakistan	Chickpea	20 μg^{-1ml}	IAA production	Amin and Latif (2017)
13	*Pseudomonas* spp., *Bacillus* spp., *Paenibacillus sinopodophylli*, *Cupriavidus gilardii* and *Paenarthrobacter* sp.	Rhizosphere of *Lepidium meyenii*	*Trifolium pratense*	0.01 mM	IAA production and P solubilization	Ortiz-Ojeda et al. (2017)
14	*Azotobacter* sp.	Gold mining area at Buru Regency, Maluku	–	15–20 mg^{-1L}	EPS production	Hindersah et al. (2017)
15	*Azotobacter* sp. and *A. chroococcum*	Wild kale rhizosphere grown in tailings of Waekerta Village, Buru Regency, Maluku	Groundnut	0.64 $mg^{-1\ kg}$	EPS production	Hindersah et al. (2018)

radiobacter, *E. medicae* and *Bradyrhizobium canariense* were isolated from the root nodules of leguminous plants *Medicago*, *Trifolium*, *Vicia*, *Lupinus*, *Phaseolus* and *Retama* growing in the mercury-contaminated areas of Spain (Ruiz-Diez et al. 2012). The mercury-resistant *B. canariense* was used in interaction with *Lupinus albus* for phytoremediation of mercury from the contaminated soils (Quiñones et al. 2013). Another advantage with rhizobia–legume system is that it is a stable association over other free-living PGPR; hence it will definitely improve the performance of host plants under heavy metal stress (Li et al. 2012). Thus, it can be suggested that rhizobia-assisted phytoremediation is a feasible option to revitalize mercury-contaminated soils.

10.5.2.2 Production of Phytohormones

Phytohormones mainly comprise auxin, cytokinin (CK), gibberellic acid (GA), abscisic acid and ethylene. These phytohormones are the key players in metal stress mitigation (Bücker-Neto et al. 2017). Almost 80% of PGPR isolated from the rhizosphere are capable of producing IAA, which has selective impact of the root growth and development (Patten and Glick 2002). The phytohormone IAA is mostly associated with cell division and differentiation, formation of vascular bundles and also plays a vital role in nodule formation (Gopalakrishnan et al. 2015). Plants with better root system have greater access to the nutrient and heavy metal uptake further results in improved phytoremediation (Ma et al. 2016). PGPR bear the ability to produce IAA and, therefore, enhance the root surface area of plant for better adsorption of heavy metals from the soil (Etesami 2018). Additionally, IAA is also implicated with diverse metabolic processes in plants, namely, stimulation of plant defense system and function as a cell–cell signaling molecule (Spaepen et al. 2007; Ma et al. 2018). Krishnamurthy and Rathinasabapathi (2013) have revealed an affirmative role of auxin transport through *AUX1* on tolerance of plant to heavy metal stress via ROS-mediated signaling. In a study, *Halobacillus* sp. and *Halomonas* sp. produced IAA and indole butyric acid (IBA) and subsequently increased the root length and root dry weight of *Sesuvium portulacastrum* under mercury stress (Desale et al. 2014). In a similar study, consortium of mercury-resistant PGPR (IAA producing) *Bacillus* sp. and *Enterobacter cloacae* were inoculated with chickpea and showed improved growth of plant under mercury stress (Amin and Latif 2017). In a recent report, inoculation of mercury-resistant IAA producing fungi *Aspergillus* sp. and *Massariosphaeria* sp. was beneficial to host plants *Polygonum acuminatum* and *Aeschynomene fluminensis* in providing defense against the adverse effects of mercury (Pietro-Souza et al. 2017). These studies provide evidences that mercury-tolerant PGPR which produce IAA have capability to positively modulate plant growth under stressful conditions (Table 10.1). The role of other phytohormones such as CK, GA and salicylic acid (SA) is not known in mercury stress. In contrast, the involvement of CK, GA and SA is largely recognized in alleviating other heavy metals such as Mn, As and Cd (Gangwar et al. 2010; Zhu et al. 2012; Gondor et al. 2016).

10.5.2.3 Production of Organic Acids

The PGPR are extensively documented for increasing the bioavailability of essential nutrients such as P, K and Zn (Gontia-Mishra et al. 2017a). The chemical forms P and Zn applied as superphosphates and zinc sulfate, respectively, are readily converted into insoluble forms and are inaccessible for plant uptake (Richardson 2001; Gontia-Mishra et al. 2017b). The phosphate solubilizing bacteria (PSB) and zinc solubilizing bacteria (ZSB) render the insoluble phosphates and zinc into soluble form through the process of acidification (release of organic acids), chelation and exchange reactions (Kim et al. 1998; Kamran et al. 2017). The most important mechanism of P and Zn solubilization is through the action of organic acids. Several workers provided evidences that low molecular weight organic acids like gluconic acid, 2-ketogluconic acid, 5-ketogluconic acid pentanoic acids citric acid, lactic acid, succinic acid and propionic acid are produced during P and Zn solubilization (Chen et al. 2006; Saravanan et al. 2007). These organic acids lower the pH of soil and help in solubilization of P and Zn. The organic acids, such as citrate, malate, oxalate, malonate, tend to form strong bonds with heavy metal ions through metal chelation with carboxyl groups and these complexes are less toxic to plants than the free metal ions (Kavita et al. 2008; Osmolovskaya et al. 2018). Another important fact is that the organic acids produced by microbes have greater affinity for chelating heavy metals than essential nutrients (Gadd 2010). The organic acids also lower the pH of soil; hence they also help in solubilization of heavy metals and increase the mobilization of heavy metals in rhizosphere for uptake by the plants (Etesami 2018). There are reports on P and Zn solubilization by several mercury-resistant PGPR that can aid in alleviation of mercury stress (Gupta et al. 2005; Nonnoi et al. 2012; Desale et al. 2014; Gontia-Mishra et al. 2016). Consequently, organic acids producing PGPM can indirectly contribute to mitigation of heavy metal stress in plant.

10.5.2.4 Action of ACC Deaminase Enzyme

Ethylene is produced in plants subjected to variety of abiotic and biotic stresses encompassing exposure to salt, drought, flooding, heavy metals, organic and inorganic chemicals, attack of nematodes, phytopathogens and so on. (Gontia-Mishra et al. 2014). Hence the ethylene produced during such stress conditions is termed as "stress ethylene" (Glick 2014). Consequently, elevated levels of ethylene can impair root growth; overall plant growth is retarded and induction of senescence occurs in plants (Han et al. 2015). Interestingly, it is noted that 1-aminocyclopropane-1-carboxylic acid (ACC) works as precursor for ethylene biosynthesis. Moreover, several PGPR have potential to substantially lower the ethylene concentration in plants. This is attributed to the enzyme ACC deaminase (present in PGPR), which catalyzes the conversion of ACC to ammonia and α-ketobutyrate, and subsequently reduced ethylene concentration in stressed plants (Glick et al. 1999). Various researchers have documented the application of ACC deaminase producing PGPR

for improvement of plant growth under heavy metal stress (Ma et al. 2015; Han et al. 2015; Rizvi and Khan 2017). In context to mercury stress, Gontia-Mishra et al. (2016) have reported the application of mercury resistance PGPR with ACC deaminase activity for combating the effect on mercury in wheat plants.

10.5.2.5 Production of Siderophore, EPS, PC and MT

Iron is a vital nutrient for microorganisms. Fe^{3+} ion usually makes complex insoluble with hydroxide and oxyhydroxide under aerobic conditions and renders it unavailable to microbial uptake (Storey et al. 2006). Mostly, bacteria acquire iron by the secretion of low-molecular weight ferric-ion-specific chelating agents known as siderophores (Neilands 1995). Siderophores are produced by PGPR, both symbiotic and free-living bacteria and fungi, growing under low iron concentrations. Moreover, siderophore has registered a remarkable role in detoxification of various heavy metals (Nonnoi et al. 2012; Hesse et al. 2018). Nevertheless, the undeniable function of siderophore is iron acquisition, but they can bind with other heavy metals like Al, Cd, Cu, Pb, Hg and Zn (Neubauer et al. 2000; Braud et al. 2009). It is also noted that besides iron, other metals can stimulate siderophore production (Hesse et al. 2018). The siderophore–metal complex can increase the soluble metal concentration for uptake by plants (Schalk et al. 2011). The siderophore-producing PGPR provide dual benefit to plants under metal stress first, by improving iron availability, and secondly, by lowering the free metal ion concentration in the rhizosphere (as siderophore forms complex with heavy metals) (Dimkpa et al. 2008). Additionally, siderophores have also displayed an efficient role in biological control against phytopathogens (Kloepper et al. 1980). The siderophore-producing PGPM has canonical function to promote the plant growth via iron acquisition and for control of plant diseases but their use in PGPR-assisted phytoremediation has gained much attention (Rajkumar et al. 2010). A large number of mercury-resistant PGPR and endophytic fungi have been reported to increase the survival and growth of plants in mercury-contaminated soils by ameliorating the metal toxicity (Gupta et al. 2005; Nonnoi et al. 2012; Gontia-Mishra et al. 2016; Pietro-Souza et al. 2017).

Many PGPR have the unique ability to produce exopolysaccharide (EPS)/extracellular polymeric substances. The EPS has multifarious function in bacterial cells ranging from quorum-sensing signals, biofilm formation, development, survival and host colonization (Nocelli et al. 2016). The EPS largely constitutes high molecular weight macromolecules like polysaccharide along with smaller proportions of protein, lipids and uronic acid (Gupta and Diwan 2017). EPS shields the bacterial cells against various environmental stresses, such as heavy metal toxicity, drought and salinity. They have several anionic functional groups (e.g., sulfhydryl, carboxyl, hydroxyl, sulfonate, amine and amide), which binds with metal ions and decreases their mobility in the soils and their accessibility for plants (Rajkumar et al. 2012). In fact, *S. meliloti* produces two kinds of EPS: succinoglycan and galactoglucan that are associated with developing symbiotic relation with host plants. In a study, wild-type and mutant *S. meliloti* (deficient in EPS I and EPS II

synthesis) was treated with different concentrations of mercury. The mutant strains could not withstand mercury toxicity; hence it could be proposed that EPS production plays a pivotal role in combating mercury toxicity (Nocelli et al. 2016). EPS secretion is an extensively recognized phenomenon for plant growth promotion. The PGPR which are capable of EPS secretion has been widely known to decrease mercury toxicity during their interaction with host plants (Gontia-Mishra et al. 2016; Hindersah et al. 2018).

Recent studies investigating the role of PGPM in heavy metal uptake by plants have demonstrated that microbial PC and MT have the ability to chelate heavy metals. PC is produced by arbuscular mycorrhizal fungi as well as by plants in response to heavy metal stress (Miransari 2011). However, rhizobacteria do not produce PC; hence phytochelatein synthase gene from *Schizosaccharomyces pombe* (yeast) was transformed to *Pseudomonas putida*, which is induced by several heavy metals such as Cu, Cd, Pb and Hg and this recombinant bacteria improved germination and plant growth in wheat under multiple metal stress condition (Yong et al. 2014). These microbial PCs are cysteine-rich peptides which bind to heavy metals with great affinity and enhance phytoremediation of heavy metals by plants (Kang et al. 2007). In order to sequester, heavy metals such as Cd, Zn, Hg, Cu and Ag PGPR and mycorrhizal fungi produce MT and are also cysteine-rich polypeptides that bind to heavy metals (Ullah et al. 2015). A recent study reported the characterization of MT genes, from the ectomycorrhizal fungus *Laccaria bicolor* under heavy metal stress (Reddy et al. 2014). Thus, it could be predicted that PGPR and symbiotic fungi has capability to produce PC and MT, and can enhance metal tolerance in host plants. The role of different bacterial species as potential bioremediation candidates to control mercury pollution and their mode of action for detoxification of mercury are listed in Table 10.2.

10.6 Transgenic Plants Overexpressing *Mer* Genes

Phytoremediation through naturally occurring plants capable of alleviating heavy metal stress can be difficult to manage and achieve, except for hyperaccumulators. Usually, such plants fail to survive in diverse environment or even if they survive, they fail to alleviate the heavy metal stress, either due to change in soil type or due to excessively high concentration of phytotoxic compounds (Doty 2008). Therefore, development of transgenic has recently been employed in several important plant species, particularly those capable of growing in diverse climatic conditions. Transgenic technology for improving or inducing the phytoremediation uses the genes responsible for either metabolizing phytotoxic compounds or uptake or their translocation (Kawahigashi et al. 2002; Lee et al. 2003; Chowdhury et al. 2015). There have been three basic strategies used to develop transgenic plants for phytoremediation to extract genes, viz., from bacteria or non-plant sources, or transforming with genes derived from different plant species or overexpressing of detoxification genes in the same plant species (Maestri and Marmiroli 2011).

Table 10.2 Bioremediation of mercury using mercury resistant bacteria

Bacterial species	Genera	Mercury toxicity	Isolation site	Mode of action for detoxification of mercury	References
Sphingobium sp.	α-Proteobacteria	5.1 $mg.l^{-1}$	New South Wales, Australia	Volatilization of mercury by the action of mercuric reductase	Mahbub et al. (2016a)
Vibrio fluvialis, Serratia marcescens and *Bacillus megaterium*	γ-Proteobacteria Fermicutes		Tagus Estuary (Barreiro and Cala do Norte), Portugal	Biotransformation of mercury to methyl mercury in 48 h	Figueiredo et al. (2016)
Pseudarthrobacter oxydans and *Pseudomonas frederiksbergensis*	Actinobacteria γ-Proteobacteria	2.0 and 1.5 ppm, respectively	Tundra ecosystem of Ny-Ålesund, Svalbard	Biosorption of mercury in cell pellets	Balan et al. (2018)
Alcaligenes faecalis	β-Proteobacteria		Fatehgarh Sahib, Punjab, India	Biosorption of mercury followed by biotransformation of sequestered mercuric ions into monovalent mercury (Hg_2Cl_2).	Gupta and Nirwan (2015)
Bacillus tequilensis, *Bacillus pumilus*, *Bacillus subtilis* and *Achromobacter xylosoxidans*	Fermicutes β-Proteobacteria	0.3 mM mercuric chloride	Mysore, Karnataka, India,	–	Sunil et al. (2015)
Bacillus thuringiensis	Fermicutes γ-Proteobacteria	50 ppm of Hg as $HgCl_2$	Odisha, India	Volatilization of mercury at different environmental parameters, i.e. pH, temperature and salinity	Dash et al. (2014)
Vibrio fluvialis	γ-Proteobacteria	250 μg. ml^{-1}	Uppanar estuary, Tamil Nadu, India	Solubilization of mercury to non-toxic form	Saranya et al. (2017)
Afifella marina and *Rhodovulum sulfidophilum*	α-Proteobacteria	398.84 μg. l^{-1} $HgCl_2$	Thai Peninsular coastal areas (Andaman Sea and	Volatilization of mercury via mercuric reductase	Mukkata et al. (2015)

(continued)

Table 10.2 (continued)

Bacterial species	Genera	Mercury toxicity	Isolation site	Mode of action for detoxification of mercury	References
			Gulf of Thailand), Thailand		
Bacillus thuringiensis	Fermicutes	500 ppm of mercury	Mithi River, Mumbai, India	Solubilization of mercury to non-toxic form	Pushkar et al. (2018)
Pseudoxanthomonas sp.	γ-Proteobacteria	1.7 $mg.l^{-1}$ in low nutrition medium	New South Wales, Australia	Mercury volatilization potential via mercuric reductase and the presence of *merA* gene	Mahbub et al. (2016b)
Pseudomonas sp.	γ-Proteobacteria	250 μM	Brazil	Via action of mercuric reductase	Giovanella et al. (2016)
Bacillus cereus	Fermicutes	50 ppm	–	Through the action of biofilm and EPS trapping of mercury and finally volatilization	Dash et al. (2017b)

Phytoremediation of toxic metals like mercury offers an economic and non-accumulative mode of remediation. With increasing mercury pollutions, transgenics have been widely developed for phytoremediation of mercury toxicity. Most of the transgenics designed for mercurial phytoremediation introgress two major classes of bacteria-derived genes *merA* and *merB* (Rugh et al. 1996; Meagher and Heaton 2005). These transformants are achieved via nuclear or chloroplast genome transfer of *mer* genes. According to the latest reports, mercuric reductase is the only class of enzyme known to metabolize phytotoxic Hg^{2+} ions. The *merA* gene product, a chief enzyme of *mer* operon, codes for mercuric reductase enzyme responsible for conversion of Hg^{2+} to elemental Hg^{0}.

A similar activity has been initially reported to be associated with the plasmids of few bacteria (Clark et al. 1977; Schottel 1978). However, presence of *merA* genes is observed within the conjugative plasmids and their presence in diverse taxonomic subgroups indicate a possible horizontal transfer (Møller et al. 2014). The detoxification efficiency of *merA* genes varies between genera of bacteria which could probably be correlated with the wide sequence variations within the *merA* sequences (Dash et al. 2017a). Within different bacterial genomes, a 431 bp region is known to be conserved which can be effectively exploited to develop molecular markers (Sotero-Martins et al. 2008).

Volatilization of Hg^{2+} ions through *merA* genes essentially requires the formation of *merA*-NADPH-Flavo redox complex (Dash et al. 2017a), where the NADPH probably acts as an electron donor. The Hg poisoning is usually observed in chloroplast, due to which transformants with chloroplast genome transfer are favored. As the expression of *merA* requires NADPH, the gene is predicted to function efficiently in chloroplast as it has abundant NADPH (Ruiz and Daniell 2009).

To obtain higher volatilization efficiency, plants with higher biomass is usually preferred with intense root system for translocation or uptake of Hg^{2+} ions. Therefore, few forest tree species, capable of transformation, have been exploited to develop *merA* transgenics which can be utilized for large-scale in situ phytoremediation of mercury-polluted soils. The *merA* gene-transformed yellow poplar plantlets were capable of surviving in media containing normal toxic concentration of mercury (Rugh et al. 1998). Similarly, transgenic eastern cottonwood trees expressing *merA9* and *merA18* genes could metabolize 25 μM Hg^{2+} ions. However, wild-type plantlets were killed at this high mercury concentration (Che et al. 2003). Further transgenic studies have demonstrated a successful generation of tobacco transformants via nuclear genome, expressing *merA* gene derived from *E. coli*, metabolizing Hg^{2+} ions. These tobacco transgenics were tolerant to higher levels of mercury concentrations of 80–140 μM Hg^{2+} ions which are approximately five to seven times more than the normal levels (Haque et al. 2010). Such transformation has also been applied to rice, where transgenic rice produced through particle gun bombardment harboring *merA* gene resistant to 250 μM of $HgCl_2$ (Heaton et al. 2003).

Usually the broad-spectrum mercury tolerance is achieved through the compound integration of *merA* and *merB* gene products. Nonetheless, the reduction of

Hg^{2+} ions is accomplished by MerA enzyme, presence of additional *merB* facilitates the breakdown of organomercurial compounds like methylmercury chloride, ethylmercury chloride, and so on (Chien et al. 2010). The *merB* codes for organomercurial lyase, an enzyme that hydrolyzes the breakdown of C–Hg bond followed by reduction of Hg^{2+} ions with *merA* (Weiss et al. 1977; Nascimento and Chartone-Souza 2003; Lafrance-Vanasse et al. 2009). In addition to *merB* gene, *merG* gene is also associated with broad-spectrum mercury tolerance, located between *merA* and *merB* in a mer operon (Kiyono and Pan-Hou 1999). The model plant *A. thaliana* introgressed with *merB* could survive at varying concentrations of monomethylmercuric chloride and phenylmercuric acetate (PMA). The growth of control plants was severely hampered in the presence of Hg at same concentration (Bizily et al. 1999).

Improved detoxification of inorganic and organomercurial can be accomplished using an integrated *mer* gene complex, *merA* and *merB*. A nuclear genome integrated *merAB* complex was first introduced in *A. thaliana* which could survive at 5 μM PMA and 10 μM CH_3Hg. This resistance is a fivefold increase in tolerance to organic Hg in comparison to the plant expressing only *merB* genes (Bizily et al. 2000). The transgenic populus species have been successfully developed, expressing both the genes. The transformants could tolerate 50 and 2 μM of $HgCl_2$ and CH_3HgCl, respectively (Im Choi et al. 2007). A *merAB* complexed system when transformed to chloroplast genome in tobacco, demonstrated an enhanced uptake of inorganic and organomercurial compounds with simultaneous rapid Hg volatilization (Ruiz et al. 2003; Hussein et al. 2007).

Grasses have also been utilized to develop *mer* gene transgenics as they often act as natural pollutant remediators. Their transformation with *mer* genes can improve their phytoremediation capabilities (Czakó et al. 2005). *Spartina alterniflora* has been successfully transformed with *merAB* system which enhanced their resistance to PMA and $HgCl_2$ (Czako et al. 2006). These bacterial-derived *mer* genes functions sufficiently well in plants; however, they have to be modified with an additional requirement of plant promoters. Using genetic engineering to modify plant genome incorporating mercury-resistant genes can potentially help in reducing heavy metal pollution. However, such techniques may or may not offer complete and stable inheritance. Hence, few other alternative modes of phytoremediation should also be simultaneously employed.

10.7 Concluding Remarks and Future Strategy

The contamination of mercury in agriculture land is widespread. As stated, mercury can induce noxious effects on plant growth and development. Hence, it is the need of the hour to quest for the effectual solution to overcome the problem of mercury contamination Phytoremediation is one of the effective, environment-friendly and comparatively cheaper than the conventional strategies for remediation of mercury. The application of PGPM has attained ample attention to mitigate various

environmental stresses, especially heavy metals. The PGPM have been proficiently associated with plant growth promotion and simultaneously aid in combating mercury toxicity by varied mechanisms such as directly by utilization of mer operon and indirectly by production of siderphores, organic acids, PC, MT, phytohormones and ACC deaminase. Hence, in recent years, there is a profound upgradation in the role of PGPM from "nutrient provider" to "stress alleviator". In this respect, PGPM-assisted phytoremediation has been proved to be better solution and even stimulates the proficiency of mercury detoxification. In the parallel, several transgenic plants overexpressing *mer* genes from microbial origins have been developed. The transgenic plants overexpressing *mer* genes either individually or along with mercury-resistant PGPM could be used as integrative approach for phytoremediation of mercury-contaminated sites. In the present scenario, serious and constant efforts are to be made to increase the number and diversity of effective and competitive mercury resistance PGPM from the mercury-contaminated sites and investigating their role in phytoremediation of mercury with a suitable host plant. Despite several findings, studies are still needed to explore the underlying molecular aspects of interplay between plant-PGPM in soil, which can hasten the phytoremediation process of under mercury stress. In this context, researchers should investigate and develop an efficient technology using the consortia of mercury-resistant PGPM for preservation and protection of environment against mercury contamination.

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Chapter 11
Regulatory Role of Rhizobacteria to Induce Drought and Salt Stress Tolerance in Plants

Humaira Yasmin, Asia Nosheen, Rabia Naz, Rumana Keyani and Seemab Anjum

Abstract This chapter summarizes the role of rhizosphere dwelling beneficial bacteria for the induction of tolerance against drought and salt stresses in plants. A vast proportion of world's agricultural land is rendered less productive or completely unproductive due to different factors including water scarcity and salinity. Drought can be due to insufficient rainfall, dry spells or changes in rainfall patterns whereas salinity is because of excessive amount of salts in soil or water. This salinity can be primary (arise due to natural phenomena) or it can be secondary (anthropogenic in origin). Plants respond to drought and salinity via morphological, physiological and biochemical mechanisms. To overcome devastating effects of these stresses in plants, different strategies developed along with the traditional agricultural practices. An emerging strategy to overcome drought and salinity is the use of plant growth-promoting rhizobacteria (PGPR), which enable plants to combat these stresses by various direct and indirect mechanisms. Rhizobacteria are under extensive research for their beneficial effects, uncomplicated and cost-effective application methods and their environment-friendly behaviors. Now also serve as best alternatives to chemical and traditional methods so as to overcome to tolerate and ameliorate harmful effects in plants.

Keywords Drought · Salinity · PGPR · Induced systemic resistance · ACC deaminase · Phytohormone · Proline

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11.1 Introduction

Plants are the creatures of prime importance to Earth, as all other organisms are directly or indirectly dependent on them. Most plants are well adapted to their environment but there exists a huge range of biotic and abiotic stress factors that are strong enough to breach the protective barriers of plants to cause diseases and other adverse conditions in plants. The major biotic stresses for plants include bacteria, viruses, fungi, nematodes, insects, weeds, etc. whereas major abiotic stresses which are also equally or in some cases, more devastating for plants include drought, salinity, water logging, flooding, heat, cold, frost, heavy metal toxicity, etc. All these stress factors contribute to plant growth reduction and huge yield losses worldwide. When a plant faces abiotic stress, it also becomes vulnerable to other abiotic stresses. Abiotic stresses are a great threat to food security due to continuous climate changes and worsening of natural environment by human activities.

Abiotic stresses faced by the largest proportion of plants are drought and salinity. Drought refers to low water availability to plants to carry out their normal physiological processes. Drought is a result of change in rainfall patterns, less rainfalls, extreme high or low temperatures, faster evaporation rates than water replenishing to soils and saline conditions, etc. Salinity is a consequence of deposition of oceanic salts through rain and winds, inadequate agricultural practices, use of saline water for irrigation, insufficient rainfall, elevated evaporation rates, weathering of rocks. In a broader context, water stress is referred to both drought and salinity.

Plants respond to abiotic stresses by altering their functioning on different levels and also by exploiting mechanisms to avoid them. These responses are multiplexed and potent with the involvement of various changes on physiological, morphological, molecular and biochemical levels to ensure the maintenance of normal functions and survival. Plant responses can be reversible or irreversible. The type of plant responses to stress also depends on the intensity and time of exposure to stress.

Classical breeding methods helped to induce tolerance in plants against abiotic stresses, but the success rate is not satisfactory owing to various reasons such as inefficient criteria for selection, complex quantitative traits and less genetic variability in plants under stress. Genetic engineering has proved to be a valuable advancement in developing stress-tolerant plant varieties. An emerging research area to induce tolerance in plants against these stresses is the use of microorganisms specifically bacteria. Various bacterial strains are under extensive research for their potential to make plants resistant to stresses and to enable plants to survive and produce good yield if they encounter stress.

Bacteria are the most common microorganisms present in soil, the possible reason for their great numbers is their rapid growth rates and ability to exploit vast range of materials as carbon or nitrogen sources. Mostly bacteria remain bound to soil particles, a large number of bacteria are closely associated with plant roots. Plant rhizosphere dwelling bacteria that exert positive effects on plants are known

as plant growth-promoting rhizobacteria (PGPR). PGPR opened an infinitely broad new chapter about plant stress tolerance.

The criteria for soil bacteria to be called as PGPR are that they strictly colonize plants roots, they must be able to sustain themselves and reproduce in the microenvironment close to root surfaces and compete with the other soil-dwelling microbes for resources and they must promote plant growth either directly or indirectly.

PGPR are well studied for their abilities to increase seed viability and germination rates, enhancement of root proliferation, increased nutrient uptake and use of versatile mechanisms to help plants to survive abiotic and biotic stresses. PGPR have many advantages over classical methods for induction of stress tolerance such as they can be applied easily and by using a number of techniques at any stage of plant life, they are non-pollutants for the environment and do not accumulate in soil, water or on crops, etc. Implementation of PGPR on large scale of crops is an agreeable idea to make crops stress resistant.

11.2 Drought Stress: A Global Problem

Drought stress or water stress is defined as the condition in which the availability of water supply is short as compared to its demand (Wrathall et al. 2018). Recently, Nawrotzki and Bakhtsiyarava (2017) reported that the effects of drought stress which operate in the form of water scarcity change in rainfall dry spell, etc., on agricultural crops leads to the increased migration of communities. Various factors are responsible for an increase in water crisis problem, among those, climate change is the major water limiting factor which is produced due to increased level of atmospheric carbon dioxide, increase in temperature, decrease in rainfall, extreme environmental events, and population growth (Torres and Henry 2016).

According to estimation (United Nations FAO 2013), it was reported that about one-third of the world population is living in the water-scarce areas. The climate change will further increase the water shortage intensity in subtropical areas of Asia and Africa. Further it was reported that by 2035, the glaciers of the Himalayas which are feeding largest rivers of Asia such as Indus, Yangtze, Ganges, Salween, Brahmaputra, Mekong, Yellow, etc., may vanish due to increase in temperature and about 1.8 million people will live in the regions or countries which are suffering from water scarcity. Drought has severely affected the Central Asian countries and they are using the water resources by treaties or by bargaining (Athar and Ashraf 2009).

About 60% of the world is composed of arid and semi-arid regions. The water shortage severely affects the crops yield specifically in Asian countries (Swain et al. 2017). Drought is considered as a major global limiting factor of crop productivity, which hinders the growth of the plants and leads toward yield losses (Zhang et al. 2018). For example, wheat is considered as the major food in many countries of the world. It provides 20% of the daily calories and also acts as a source of protein for

4.5 billion peoples of the world (Shiferaw et al. 2013). It has been reported that the yield of wheat has been decreased by 4.1–6.4% for every 1 °C increase in temperature due to the global climate change (Liu et al. 2016). To meet the ever-increasing population needs the consumption of wheat is expected to rise in the next 40 years (Weigand 2011) and by 2050, the wheat production yet to increase 858 million tons to fulfil the predicted global food demand (Alexandratos and Bruinsma 2012).

11.3 Responses of Crops/Plants to Drought Stress

Drought stress may become worse if the control measures are not taken into consideration. It is one of the major environmental factors, which restrain the plant growth and yield (Butt et al. 2017). The water availability reduced to the plants, hence hindering the growth, development, efficiency, and water relations to several terrestrial plants. The maximum yield losses occur in the crops, which are prone to drought stress. In fact, under drought stress, plants tend to increase their immune response by osmoregulation in the tissues, activation of antioxidant defense system and modulation in hormonal balance (Butt et al. 2017).

The survival of the plants during the early growth stages is quite critical in drought stress areas. However, plants have adapted an array of physiological, morphological, and biochemical strategies to endure the drought stress condition (Basu et al. 2016). There are two major mechanisms by which plants survive under drought stress (i) either by escape from drought or (ii) they must avoid the stress. The prompt maturity and early completion of the life cycle is the phenological phenomenon, which is categorized under drought escape strategy. While to avoid the detrimental effects of drought by maintaining a higher level of water potential is the drought avoidance mechanism of the plants (Athar and Ashraf 2009). Peng and Ismail (2004) reported that dense and deep root system, increased stomatal conductance, increased root penetration ability, avoidance of rolling of leaves, increased water potential during pre-dawn, and greater cuticular resistance in order to reduce or prevent the water loss are some of the characteristics which plants adapt to avoid drought stress conditions.

Under natural dry conditions, a plant tends to mature early and produce seeds before the onset of the dry season. For example, *Escholtzia californica* (California poppy) completes its life cycle earlier before the start of the drought stress. Some xerophyte plants such as *Agave deserti* store water in their stem, leaves, and buds to survive in water stress conditions (Athar and Ashraf 2009). Some plants are characterized as having a deep root system (such as *Cicer arietinum* L., *Vigna aconitifolia, Brassica campestris,* etc.), which provides drought tolerance (Kumar 2005).

11.4 Plant Adaptations to Drought Stress

Plants have developed various mechanisms to maintain their vigor during different levels of water scarcity. Plants respond to drought stress of different intensities through a range of changes from morphological to molecular levels.

11.4.1 Root Morphology

Drought stress is firstly perceived by the roots wherein, shoot growth is significantly reduced. Primary roots are not affected but the lateral roots show a reduction in growth due to the suppression of lateral root meristems (Chen et al. 2012). It was reported that plant microRNA miR393 played a significant role in the root-mediated adaptations caused by reduction of auxin signaling under drought stress (Chen et al. 2012). The small roots in addition to lateral roots are also considered an adaptive response of the plants to absorb more water by increasing the surface area. Similarly, the presence of suberized exodermis, reduction in the number of cortical layers and rhizodermis are the adaptive strategies under drought stress conditions. On the other hand, drought stress, i.e., hydrotropism which is increased by the degradation of columella cells of roots and amyloplast. Hormonal cross-talk is another adaptive strategy to modify root architecture under drought stress condition. (Blilou et al. 2005).

11.4.2 Photosynthesis and Gaseous Exchange

Due to metabolic impairment, stomatal closure and leaf area reduction occur, the rate of photosynthesis decreased under drought stress (Basu et al. 2016). Photosynthesis is also reduced because the intercellular carbon dioxide concentration decreases resulting in the reduction of the components of electron transporter (ET). The reduction in ET leads toward the decreased concentration of molecular oxygen corresponded to the production of reactive oxygen species (ROS). Reactive oxygen species cause damage to photosynthetic apparatus and other macromolecules (Demmig-Adams and Adams 2006). Various photosynthetic pigment such as xanthophyll, light-harvesting complexes from the reaction centers and thermal dissipation of light energy causes some of the adaptive responses of the plants to drought stress. Further, the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity and regeneration of ribulose-1,5-bisphosphate adversely affect the photosynthetic biochemical efficacy. (Lawlor 2002; Chaves et al. 2009).

11.4.3 Transpiration and Stomatal Conductance

Due to drought, stomatal closure in the leaves is the prompt response which reduced the loss of water, uptake of nutrients, etc., which modulate the metabolic pathways (Xiong and Zhu 2002). The phenomena of leaf shedding, decrease in the number of leaves, leaf size, and branching as well as xeromorphic characteristics reduce the rate of transpiration under drought stress. Sclerophylly is among one of the adaptations of the plants under drought, where the plants do not suffer from wilting and permanent damage due to the formation of hard leaves and resume their activity under normal conditions (De Micco and Aronne 2009).

Reduction in the size and number of stomata is another adaptation of plants for survival under drought stress. Reduction in the surface of chloroplast and a decrease in stomatal conductance due to the reduced expression of *aquaporin* genes leads to stress avoidance (Tosens et al. 2012). Chloroplast differentiation and mesophyll modulation affect the light availability, developmental stage of leaf, and ultimately photosynthesis (Tosens et al. 2012). These adaptations reduce the damaging effects of drought stress on plants and improve water-use efficiency to ultimately increase yield (Blum 2005).

11.4.4 Regulation of Phytohormones

Plants contains ethylene (ET), abscisic acid (ABA), gibberellic acid (GA), cytokinin (CK), and auxin, which are meant for the regulation of physiology of plants. (Wilkinson et al. 2012). When plants face the harsh condition of drought stress, ABA is synthesized in the roots and its translocation is carried out to the leaves, where it causes stomatal closure and reduction in plant growth (Wilkinson and Davies 2010). The ABA signaling genes such as *DSM2*, *OsNAP,* and *OsNAC5* improved the yield of the crops under drought stress conditions (Du et al. 2010; Chen et al. 2014; Liang et al. 2014). If drought occurs at the reproductive stage of plant, ABA-induced senescence and stomatal closure due to the unintended reduction in carbon supply occur. Thus, it seems a great challenge towards the ABA-induced drought adaptation for better growth and yield (Ji et al. 2011). Similarly, another adaptive trait is the increased endogenous production of CK through the expression of CK biosynthetic gene *isopentenyltransferase (IPT)* which delays the senescence and death of premature leaves (Peleg et al. 2011).

Interestingly, auxins negatively regulate the drought adaptation in the plants. Upregulation of a gene that encodes late embryogenesis abundant (LEA) proteins resulted in a decrease of auxin contents under drought stress (Zhang et al. 2009). It has also been reported that auxins negatively regulate the *DRO1*gene (*DEEPER ROOTING 1*), which controls the root growth. Increased expression of *DRO1*gene

results in the phenomenon of drought avoidance in shallow rooting in rice cultivars resulting improved the yield under drought (Uga et al. 2013).

Ethylene has also been reported as a negative regulator of the response to drought stress. Ethylene responses under drought caused overall effect on root growth, leaf expansion, photosynthesis, grain development, and leaf senescence (Fukao et al. 2006; Perata and Voesenek 2007). Ethylene enhanced the abortion of embryo and grain and directly affects the crop yield, a rapid reduction in the level of GA occurred due to drought stress which acts as positive regulator of plants adaptation to stress (Wang et al. 2008). Along with these, other less explored hormones such as jasmonic acid (JA), brassinosteroids, strigolactone, and salicylic acid (SA) have also been reported to provide adaptation to the plants under drought stress. Thus, hormones interact with each other and modulate each other's biosynthesis and responses, therefore, the drought stress responses are regulated by a balance among the phytohormones which promote and those that inhibit the traits.

11.4.5 Osmotic Adjustment

The phenomenon of Osmotic adjustment (OA) is the mechanism, which helps in the maintaining of cell turgor during which the solutes are accumulated in the drying cell under reduced water potential (Chaves and Oliveira 2004). During drought stress conditions, the leaf water volume, stomatal conductance, photosynthesis, and plant growth are observed to be maintained by osmotic adjustment (Chaves and Oliveira 2004). The cell enlargement is believed to be inhibited due to osmotic adjustment during drought stress (Serraj and Sinclair 2002). Compatible solutes (i.e., proline, glycine betaine, etc.) are accumulated by OA and help the plant to cope with the detrimental effects of drought stress (Ashraf and Foolad 2007). Some enzymes like pyrroline-5-carboxylate reductase, betaine aldehyde dehydrogenase and ornithine δ-aminotransferase have been reported to play an important role in osmotic adjustment under drought stress.

11.5 Combat Drought Stress

Drought stress caused adverse impacts on the growth and output of the crops. Plants also have natural mechanisms to adapt under drought stress conditions, however, the tolerance mechanisms partially regulated by a variety of measures such as the use of plant mineral nutrients, plant growth regulators, genetic modifications, developing tolerant plant genotypes, compatible solutes, seed treatments, etc.

11.5.1 Role of Plant Growth-Promoting Rhizobacteria (PGPR)

Various authors have investigated the role of PGPR and other microorganisms in relation to drought tolerance. PGPR inoculation to crop plants is also an important strategy to enhance plant growth and yield under water scarcity conditions. The PGPR can increase plant growth by regulating the nutritional and hormonal balance to solubilizing nutrients and provide plant growth regulators under stress conditions. The plant–microbe interaction is very important to regulate plant growth and provide protection against drought stress (Dar et al. 2018). Application of plant growth-promoting rhizobacteria for plant growth and drought stress tolerance is an environment friendly, sustainable and cost-effective approach as compared to other measures.

PGPR are the group of bacteria that have the capability to colonize the root system of plants and improve the growth and yield of plants. A wide range of bacteria actinobacteria, fungi, etc., belong to this category. A total of 2–5% of soil microorganisms have PGPR properties (Saharan and Nehra 2011). Various genera play a significant role to improve drought stress tolerance of crop plants.

11.5.2 Engineering Plants for Drought Tolerance

Another strategy to combat with drought stress is the engineering of drought-tolerant crop plants, which involves the manipulation of functional and regulatory genes in plants which are not drought stress tolerant (Butt et al. 2017). Due to complete availability of the genome sequence, *Arabidopsis* is considered as a model plant to study the drought tolerance mechanism. For the identification of the target gene, the microarray gene expression technique is used. In alfalfa (*Medicago tranculata*), the engineered gene *APETALAL2* transcription factor induces drought tolerance through the process of wax production (Zhang et al. 2005). Insertion of *Mannitol dehydrogenase (MtlD)* gene in wheat improved the drought tolerance capability (Abebe et al. 2003). Similarly, in tobacco, the drought tolerance is enhanced by the overexpression of *inositol Methyl Transferase gene (IMTI)* gene isolated from the ice plants (Sheveleva et al. 1997).

11.5.3 Molecular and Functional Genomics Approaches

Though, conventional breeding methods have been used for a long time for drought tolerance. Recently, encroachments in genomics and molecular breeding techniques have a prominent role in the development of drought-tolerant cultivars (Kumar et al. 2014). Several genes that show response to the drought have been identified

(Yadav 2010; Todaka et al. 2015; Ali et al. 2017; Kaur and Asthir 2017). The drought tolerance mechanism at molecular level involves the regulation of gene expression and the identification of transcription factors. It has been reported that transcription factors (*DREB2A* and *DREB2B*) are involved in the expression of different genes that confer drought tolerance to plants (Ali et al. 2017). Aquaporins can be an important target for the development of plant genotypes, which are drought tolerant because aquaporins play an important role in the regulation of plant–water relations (Afzal et al. 2016). Kaur and Asthir (2017) observed that ABA-responsive elements-binding proteins respond at both levels, i.e., transcriptional level and posttranscriptional level and also important role in determining the capabilities of drought tolerance in plant.

11.5.4 Selection and Breeding Strategies

In order to develop plant genotypes tolerant to drought stress, different approaches such as conventional, omic-based, molecular proved to be successful (Maqbool et al. 2017). Conventional breeding techniques have been adopted to produce crop varieties with improved growth and yield under drought stress (Ahmad et al. 2014). In plant breeding techniques, drought tolerance is induced in crop plants by manipulating the genetic make of the crops to attain desired characteristics (Maqbool et al. 2017). However, in order to screen traits that are associated with drought tolerance, marker-assisted selection proved to be a better option rather than classical breeding technique (Ahmad et al. 2014). Segregation mapping and quantitative trait loci (QTL) analysis are the molecular basis of drought tolerance and QTL is important for the marker-assisted selection of plants with desired traits (Ali et al. 2017).

11.5.5 Application of Compatible Solutes

Compatible solutes such as proline, glycine betaine, organic acids, soluble sugars, trehalose, sugar, alcohols, etc., played important roles by providing protection against the detrimental consequences of osmotic stress on the macromolecules, membranes, and enzymes (Kiani et al. 2007). Proline, sugar alcohols and soluble sugars served as cryo-protectants and osmoregulators in plants and help in the scavenging of ROS under drought stress (Ruelland et al. 2009; Van den Ende and Valluru 2009). Application of glycine betaine exogenously played essential roles in modulating the osmotic adjustment, antioxidant activities, and detoxification of ROS (Farooq et al. 2008).

11.6 Growth Promotion Mechanisms of PGPR

Numerous studies have reported the mechanisms of growth promotion and drought tolerance of plants mediated by PGPR.

11.6.1 Direct Mechanisms

PGPR increase the drought tolerance ability of plants by directly enhancing the availability of nutrients to them in order to stabilize the structures of their biomolecules and to maintain their biomass production.

11.6.1.1 Nitrogen Fixation

Nitrogen is the most important nutrient, essential for plant growth, development, and productivity. It is a fundamental part of essential biomolecules such as nucleic acids and proteins. In the process of biological nitrogen fixation, the unavailable form of nitrogen is converted into ammonia or nitrate ions which can be readily taken up by the plants for growth promotion process. PGPR group of bacterial genera carry out the process of biological nitrogen fixation (Kim and Rees 1994). Both symbiotic and non-symbiotic or free-living microorganisms including few endophytes fix nitrogen that benefits both plant—soil microorganisms. (Bhattacharyya and Jha 2012).

11.6.1.2 Phosphorus Solubilization

Phosphorus (organic and inorganic forms) is among the main macronutrient necessary for plant growth and development. It is present in unavailable or insoluble form in soil but made available with the help of Phosphobacteria solubilized the soil inhibited P which produces phosphatase enzyme This enzyme efficiently hydrolyze the organic phosphate into a soluble form (Nosheen et al. 2018). Few low molecular weight organic acids also released by phosphate solubilizing bacteria. These compounds utilize their carboxyl and hydroxyl groups for the chelation of cations, which are bounded to the phosphate and convert the insoluble phosphorus into soluble form (Patel and Minocheherhomji 2018).

11.6.1.3 Potassium Solubilization

Potassium also is an important macronutrient, required for plant growth, development, and metabolic processes. It is usually absorbed as cationic form. The imbalanced use

of chemical fertilizers leads to the deficiency of potassium in the soil hence, hinders the plant growth and development (Sindhu et al. 2014). Therefore, it is pertinent to have alternative sources for the provision and uptake of potassium. The soil microorganisms have essential roles to recycle natural potassium resources. These microorganisms are called as *potassium solubilizing rhizobacteria* which provide potassium to the plants (Basak and Biswas 2010).

Recent investigations have shown that organic exudates of some bacteria play a key role in releasing otherwise unavailable K from K-bearing minerals. K-solubilization could be attributed to excreting organic acids, which either directly dissolves rock K or chelate silicon ions to bring K into solution (Prajapati et al. 2013).

Some bacteria produce organic exudates that exert central effects in the release of unavailable potassium from potassium-containing minerals. These organic acids may directly dissolve potassium in rocks or may cause chelation of silicon ions to cause release of potassium (Prajapati et al. 2013). Wheat inoculation with *Bacillus* sp. or *Pseudomonas* sp. cause a prominent elevation in the uptake of potassium, magnesium, and calcium from calcareous soil without supplementation with fertilizer (Öğüt et al. 2011).

11.6.1.4 Zinc Solubilization

Zinc is an imperious micronutrient, essential for the optimum growth of plants (Goteti et al. 2013). There are two types of zinc fertilizers based on their different solubilization properties, i.e., zinc sulfate and zinc oxide. Zinc sulfate is considered as highly soluble in water as compared to zinc oxide but it can go back to insoluble form (Hafeez et al. 2013). The application of zinc-solubilizing bacteria plays an important role and carries out conversion of insoluble form of zinc to soluble form using several mechanisms such as proton extrusion, excretion of organic acids, chelating agents, and gluconic acids production (Goteti et al. 2013).Different diverse genera, namely, *Pseudomonas* sp., *E. cloacae* and *Pantoea agglomerans* showed increased zinc contents in shoot and roots of inoculated plants (Kamran et al. 2017). A recent study indicated that *ZnSB2* strain increased the zinc solubilization in the soil and can serve as a potential zinc solubilizer to reduce the need of application of chemical zinc fertilizers (Dinesh et al. 2018).

11.6.1.5 Phytohormones Production

Phytohormones are molecules, which play an important role in plant growth and development. Various group of hormones, viz., gibberellins, auxins (Indole-3-Acetic Acid/IAA), abscisic acid, cytokinins, and ethylene are the major plant hormones (Egamberdieva 2013). Glick and Pasternak (2003) reported that PGPR play an important role in the growth and division of plant cells and provide tolerance against the environmental stresses through the biosynthesis of

phytohormones. Inoculation of PGPR to the plant species produce phytohormone, which increases the lateral roots and root hairs, thus increasing the water and nutrient uptake efficiency (Dimkpa et al. 2009) and provide tolerance to water-deficit conditions. Han et al. (2018) reported that bacterial strains such as *Streptomyces sundarbansensis* and *rochei* improved growth and development of plants through the production of IAA. Cytokinins, which are considered as purine derivative compounds, are involved in the cell division and differentiation process during growth and development. Recently, *Bacillus megaterium* has been reported to play an important role in the growth promotion by the production of cytokinin (Numan et al. 2018).

11.6.2 Indirect Mechanisms

PGPR exerts beneficial effects on plants against abiotic stresses by acting indirectly such as by enhancement of the activity of ROS-scavenging enzymes and water-use efficiency. PGPR are also known to produce enzymes and other molecules such as exopolysaccharides against phytopathogens. Role of PGPR in the induction of systemic resistance in plants is also well elaborated.

11.6.2.1 Stress Management

Any factor that causes a negative impact on plant growth and development is called as stress (Foyer et al. 2016). During stressed conditions many harmful molecules are formed which are called as reactive oxygen species (ROS), i.e., H_2O_2, OH, O^{2-} and free radicals which damage the photosynthetic machinery, proteins, membranes and nucleic acids (Ramegowda and Kumar 2015). The role of PGPR in stress management is imperative as reported by several authors. The mitigation of stress by the inoculation of plants with PGPR in leaf water potential under stress condition has been improved (Ahmad et al. 2013a; Naveed et al. 2014). Various studies suggested the role of PGPR to mitigate drought stress in soybean, wheat, chickpea etc. (Ngumbi and Kloepper 2016). Habib et al. (2016) reported the salt stress tolerance in *Abelmoschus esculentus* (okra) by inoculation of PGPR which improved the water-use efficiency and activity of ROS-scavenging enzymes.

11.6.2.2 Biocontrol Agents

Use of microorganisms as antagonists against the plant pathogens is called as biocontrol and it is considered safe as compared to synthetic chemical pesticides. Various genera including *Bacillus*, *Pseudomonas* sp. etc. produce antibiotics which play an important role in inhibiting the phytopathogens (Ulloa-Ogaz et al. 2015). A variety of antifungal and antiviral metabolites such as phenazines,

phenazine-1-carboxamide, pyoluteorin, cepaciamide A, 2,4 diacetylphloroglucinol, and azomycin, pseudomonic acid, karalicine, etc., have been produced by *Pseudomonas* species (Ramadan et al. 2016). *Bacillus* also reported to produce a large variety of antibiotics such as bacillomycin, iturins, and surfactin and can be used as biocontrol agents (Wang et al. 2015).

Bacillus pumilus and *Pseudomonas* sp. isolates from maize and rice rhizosphere respectively, growing in water-stressed areas increased the production of ABA in maize plants in combination with addition of l-tryptophan under drought stress (Yasmin et al. 2017). *Pseudomonas* sp. and *Proteus* sp. isolates from maize and rice rhizosphere, respectively, grown in water-deficient conditions elevated the concentrations of indole 3-acetic acid and gibberellic acid in maize plants under drought along with l-tryptophan addition. *B. pumilus* produced the most satisfactory results for helping maize plants against drought stress (Yasmin et al. 2017).

Glucanase-producing *Bacillus amyloliquefaciens* and *Bacillus subtilis* successfully inhibited important fungal pathogens of sugarcane including *Fusarium moniliforme* and *Colletotrichum falcatum* in addition to suppression of other damaging fungal plant pathogens such as *Fusarium oxysporum*, *Rhizoctonia solani* and *Macrophomina phaseolina*. These glucanase-producing plant growth-promoting bacteria also increased the activities of antioxidant enzymes (Zia et al. 2018).

Treatment of rice plants with *Bacillus* sp. strains *KFP-5*, *KFP-7*, *KFP-17* markedly elevated the activities of rice antioxidant enzymes against *Pyricularia oryzae* infection and reduced the incidence of blast disease (Rais et al. 2017).

11.6.2.3 Protective Enzymes

It has been reported that PGPR produce enzymes such as chitinase, β-1,3-glucanase, ACC-deaminase, etc., which induce lysis of the cell wall of pathogens (Goswami et al. 2016). The release of protective enzymes by the PGPR improve plant growth by controlling the phytopathogenic agents (Meena et al. 2016). The most catastrophic pathogens (*Rhizoctonia solani* and *Phytophthora capsice*) in the world can be controlled and their growth can be inhibited by PGPR (Islam et al. 2016). Fluorescent *Pseudomonas* isolate GRC_3 is reported to efficiently suppress the growth of fungal phytopathogens *Phytophthora capsici* and *Rhizoctonia solani* by producing antifungal enzymes, i.e., β-1,3-glucanase and chitinase along with antifungal metabolites of nonenzymatic nature (Arora et al. 2007).

PGPR strains *Sinorhizobium meliloti RMP1* and *Pseudomonas aeruginosa GRC2* successfully enhanced the yield from *Brassica juncea* plant. Both strains were tolerant to urea and diammonium phosphate (DAP) and colonized the plant rhizosphere successfully. Low concentrations of urea and DAP were beneficial for PGPR strains (Maheshwari et al. 2010). It was accessed that plant growth and yield parameters were increased when the strains were co-inoculated. Variants of *Sinorhizobium meliloti RMP1* and *Pseudomonas aeruginosa GRC2* that were not tolerant to urea and DAP showed less growth in presence of urea and DAP. Both strains exhibited urease activities (Maheshwari et al. 2010). Ramadan et al.

(2016) reported that *Sinorhizobium fredii* and *P. fluorescens* release chitinase and β-glucanases which can inhibit *Fusarium oxysporum* and *Fusarium udum* wilt. *Fusarium oxysporum* responsible for wilt and *Rhizoctonia solani* causing root rot of *Fagopyrum esculentum* were antagonized by biocontrol agent *Bacillus pumilus MSUA3* by employing the activities of chitinolytic enzymes and surfactin which is a heat-stable antibiotic (Agarwal et al. 2017).

11.6.2.4 Exopolysaccharide Production

Exopolysaccharides (EPSs) are biosynthesized by plants, algae, and bacteria. These are high molecular weight biodegradable polymers which are formed by the residues of monosaccharides and their derivatives (Sanalibaba and Çakmak 2016). The EPSs play an important role in aggregating soil particles, maintaining water potential, sustaining the host under stress conditions, maintaining the contact between rhizobacteria and roots of host plant (Pawar et al. 2017).

EPS producing PGPR strains are well elaborated for their potential to reduce salinity stress in plants. EPS produced by PGPR can bind to the cations in soil including sodium ions, as a result, the amount of salts present in the soil becomes restricted for uptake by plant. In this way, the salt stress on a plant can be reduced. EPS-producing PGPR alleviated salt stress and promoted the growth of maize and soybean. The PGPR such as *Rhizobium* sp., *Azotobacter*, *Enterobacter cloacae, Bacillus, Agrobacterium* sp., *Xanthomonas* sp., etc., produce EPSs and play a substantial role in improving the soil fertility and taking part in sustainable agriculture (Mahmood et al. 2016).

11.6.2.5 Siderophore Production

Majority of siderophores are produced under iron-limiting conditions by microorganisms to enhance the capacity of iron uptake. These are small organic molecules, which extract the iron metal ions (Saha et al. 2016). *Pseudomonas putida* uses the siderophores which are produced by other microbes and augment the amount of iron available in the natural habitat (Rathore 2014). PGPR are increased iron uptake capacity of plants, where the availability of iron is low. Hence, production of siderophores is an important mechanism used by PGPR to enhance growth and development of plants and induce stress tolerance under nonavailability of iron in their soil environment.

11.6.2.6 Hydrogen Cyanide (HCN) Production

HCN is a secondary metabolite produced by PGPR and overpowers the harmful pathogens development. An enzyme called HCN synthase (associated with the rhizobacterial plasma membrane) is responsible for the synthesis of HCN from glycine.

Many bacteria are capable of producing HCN such as *Pseudomonas*, *Alcaligenes*, *Rhizobium*, *Bacillus*, and *Aeromonas* (Ahmad et al. 2008). HCN produced by PGPR is reported to increase the availability of phosphates to plants (Rijavec and Lapanje 2016). HCN-producing PGPR can be utilized as biopesticides/weedicides to eliminate weeds from vicinity of a crop (Kamei et al. 2014).

11.6.2.7 Induced Systemic Resistance (ISR)

Induced systemic resistance (ISR) is the state of enhanced defensive capacity of the plant under environmental stress. PGPR have the capability to induce systemic resistance in plants under stress conditions (Prathap and Kumari 2015). When pathogen invades a plant, specific signals are produced through vascular system, as a result of these signals, enzymes such as polyphenol oxidase (PPO), catalase (CAT), chitinase, β-1,3-glucanase, ascorbate peroxidase (APX), phenylalanine ammonia-lyase (PAL), superoxide dismutase (SOD), and peroxidase are produced which provide tolerance to the plants against the stress. The ISR helps the plant to combat various diseases and it is not specific against a particular pathogen (Kamal et al. 2014).

PGPR consortium consisting of *Pseudomonas putida CRN-09* and *Bacillus subtilis CRN-16* increased the seed germination rate of *Vigna radiata* and also boosted the levels of antioxidants, i.e., peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), β-1,3-glucanase, and chitinase for the induction of systemic resistance in *Vigna radiata* against pathogen *Macrophomina phaseolina* (Sharma et al. 2018). Majority of PGPR induces ISR in plants and revolutionized the research in agriculture sector (Gouda et al. 2017).

11.7 Improvements in Physiological and Morphological Processes

PGPR positively improves the physiology and morphology of plants to eliminate the deleterious effects of stresses such as changes in root and shoot growth patterns, modification of plant water contents and hormones concentrations and osmolytes production.

11.7.1 Enhanced Root Architecture for Stimulating Water Uptake

It has been seen through different studies that PGPR-treated plants exhibited improved root growth along with changes in root architecture (Kloepper et al. 2004; Ngumbi 2011; Yasmin et al. 2017). Further studies suggested that alterations in roots induced by bacteria lead to overall increase in root surface area that directly

improved nutrients and water uptake (Somers et al. 2004; Timmusk et al. 2014). For maize study, in growth chamber tests, the seeds were treated with strain *Alcaligenes faecalis (AF3)* (Naseem and Bano 2014). Planting after 3 weeks, an increase in root length by 10% was observed in PGPR-treated plants than non-inoculated control plants under drought stress (Table 11.1). PGPR-treated plants can tolerate drought stress, due to developed root system that allows increased water uptake. Significant increase in root biomass of in *Mazurka* and *Kaleo* cultivars appeared when maize plants were inoculated with *Burkholderia phytofirmans* strain *PsJN* (Naveed et al. 2014). Similarly, when inoculated by *Enterobacter* sp. strain, an increase in root length was observed in *Mazurka* and *Kaleo* cultivars, under drought stress.

Under drought stress, maize plants have enhanced root length, when inoculated with PGPR isolate *9K* (Yasmin et al. 2013). Similar effects were also observed in wheat under drought stress when treated with *thuringiensis AZP2*. Longer root hairs and intense growth of lateral roots were visible in wheat root inoculated with BT. The alteration in root architecture also helps the plants to tolerate drought stress (Timmusk et al. 2014) (Table 11.1) enhancement and alteration of root parameters. Yet, numerous studies are required for better understanding of the direct signaling between drought tolerance and bacterial-induced root architecture. More elaborated studies are required to trace the ideal root traits that could provide tolerance against drought stress.

11.7.2 Shoot Length

Shoot growth is one so as of the major responses to drought stress, that benefits plants by reducing the available leaf area to decrease the evaporative loss of limited water reserves (Sinclair and Muchow 2001; Wang and Yamauchi 2006; Neumann 2008; Skirycz and Inzé 2010). However, essential solutes are diverted from plant growth requirements to stress-related housekeeping functions such as osmotic adjustment as a result of resisted shoot growth. To tolerate drought stress, inhibition of shoot growth is considered a classical adaptive response (Neumann 1995, 2008; Achard et al. 2006). The limited yield potential of a plant declines severely because of drought tolerance but increase the chances of plants survival (Sinclair and Muchow 2001; Neumann 2008; Claeys and Inzé 2013). Therefore, when plants are exposed to moderate stress and inhibition of shoot growth appears as a counter-response, Hence, in such examples, plant survival is not a question but the main concern is about limited yield production of plants under drought stress paired with reduction in shoot growth.

This advantageous strategy could be in the improvement in crop varieties that sustain an ability to maintain near to normal shoot growth during drought stress (Neumann 2008). PGPR-treated plants showed prominently increased shoot growth. Because plants under drought stress are capable to maintain near to normal shoot growth, resulting in increasing crop productivity. A study demonstrated that corn plants had improved shoot growth when inoculated with *Bacillus*

Table 11.1 PGPR in Mitigation of Drought Stress

Plant	Means of applying drought	PGPR	References
Arabidopsis thaliana	Drought induction by removing the covers of culture dishes for 3 days	*Paenibacillus polymyxa*	Timmusk and Wagner (1999)
thaliana	Drought induction by terminating irrigation. Drought started with the emergence of first two true leaves	*Phyllobacterium brassicacearum*	Bresson et al. (2013)
thaliana	Drought-induced when plants were 30 days old by stopping irrigation until symptoms of temporary wilting were visually observed (ca. water was with held after 10 days)	*Azospirillum brasilense*	Cohen et al. (2015)
Capsicum annuum	Progressive drought by suppressing water supply for 15 d. Drought introduced after 5 d of transplantation	*Bacillus licheniformis*	Lim and Kim (2013)
Cucumis sativa	Drought applied by stopping irrigation for 13 days. Drought started after 15 days of transplanting 15 days old cucumber seedlings	*Bacillus cereus*, *B. subtilis*, *Serratia* sp.	Wang et al. (2012)
Helianthus annuus	Drought applied by watering with polyethylene glycol (PEG) 6000 at a concentration sufficient to produce ψ_a = 2.03 MPa	*Achromobacter xylosoxidans Bacillus pumilus*	Castillo et al. (2013)
Hyoscyamus niger	Continuous drought by restraining irrigation for 60 days. Drought introduced when plants were 45 days old	*Pseudomonas putida Pseudomonas fluorescens*	Ghorbanpour et al. (2013)
Pisum sativum	Drought induced by stopping watering when plants were at the stage of vegetative growth (ca. 3 weeks after germination) or at flowering stage (ca. 7 weeks after germination) or at the pod formation stage (ca.8 weeks after germination). Plants were re-watered when symptoms of wilting were visualized	*Pseudomonas* spp.	Arshad et al. (2008)

(continued)

Table 11.1 (continued)

Plant	Means of applying drought	PGPR	References
lycopersicum annuum	Induction of drought by stopping irrigation after 2 weeks of seeds transplantation. Plants were re-watered after 7 or 12 days	*Achromobacter piechaudii*	Mayak et al. (2004b)
tuberosum	Drought application by watering plants with 10% PEG. Drought started after 2 weeks of inoculation of plants with PGPR	*Bacillus pumilus Bacillus firmus*	Gururani et al. (2013)
Sorghum bicolor	Continuous drought by withholding irrigation for 5 days. Drought started when plants were 27 days	*Bacillus* sp.	Grover et al. (2014)
aestivum	Application of drought by stopping water supply for 6 days or 12, 18, and 24 days. Drought started after 50 days of planting. Drought had three intensities: control, moderate and high drought. After drought stress, irrigation was restored	*Azospirillum lipoferum A. lipoferum A. lipoferum*	Arzanesh et al. (2011)
aestivum	Continued drought by withholding irrigation for 4, 5, or 7 days. Drought was introduced when plants were 12 days	*Bacillus amyloliquefaciens*, *Azospirillum brasilense*	Kasim et al. (2013)
aestivum	Progressive drought by withholding irrigation for 10 days (growing plants in sand soil) or 14 days (growing plants in sand soil added with 10% greenhouse soil). Drought introduced after 10 days of seed germination	*Bacillus thuringiensis*, *Paenibacillus polymyxa B*	Timmusk et al. (2014)
Vigna radiata	Progressive drought by 6 d of withholding water. Drought was introduced when plants were 30 days old	*Pseudomonas fluorescens* strain *Bacillus subtilis*	Saravanakumar et al. (2011)
Vigna radiata	Drought applied by withholding watering 10 days after planting	*Pseudomonas aeruginosa* strain	Sarma and Saikia (2014)
Zea mays	Progressive drought by stopping irrigation for 6 days. Drought introduced after 21 days of seed germination	*Pseudomonas entomophila, P. stutzeri*, *P. putida*, *P. syringae, P. monteilli*	Sandhya et al. (2010)

(continued)

Table 11.1 (continued)

Plant	Means of applying drought	PGPR	References
Z. mays	Drought induced at the vegetative stage by conserving the moisture content of the soil at 15 ± 1%	*Azospirillum lipoferum* strain	Bano et al. (2013)
Z. mays	Drought introduced by withholding watering for 6 days after 7 days of germination	PGPR	Yasmin et al. (2013)
Z. mays	Progressive drought introduced after 1 week of seed germination by stopping irrigation for 10 days	*Proteus penneri* strain, *Pseudomonas aeruginosa*, *Alcaligenes faecalis*	Naseem and Bano, (2014)
Z. mays	Progressive drought introduced when plants were 45 days old by withholding watering and observing for wilting signs	*Burkholderia phytofirmans*, *Enterobacter* sp.	Naveed et al. (2014)
Z. mays	Introduction of continuous drought when plants were 21 d old by stopping irrigation for 6 days	*Bacillus amyloliquefaciens*, *B. licheniformis, B. thuringiensis*, *Paenibacillus favisporus*, *B. subtilis*	Vardharajula et al. (2011)
Z. mays	Drought introduced when plants reached the 4 leaves stage by withholding watering for 10 days	*Burkholderia* sp. strain	Fan et al. (2015)
Z. mays	Induction of drought by terminating watering for 7 days when plants reached the 4 leaves stage	*Pseudomonas* sp. *Bacillus pumilus Proteus* sp. *Pseudomonas* sp. *Bacillus cereus*	Yasmin et al. (2017)
C. arietinum	Plants were subjected to drought stress after well-watering till 1 month, and then by withholding water for 1, 3, and 7 days. Plants were re-watered for recovery for 3 days	*Pseudomonas putida*	Tiwari et al. (2016)
Oryza sativa	Drought stress applied by withholding water at the panicle initiation stage of reproduction for 15 days	*Pseudomonas fluorescens*	Saakre et al. (2017)
Z. mays	Drought stress introduced by stopping water after 14 days of planting	*Pseudomonas putida*	SkZ et al. (2018)

sp. (Vardharajula et al. 2011). All plants inoculated with *Bacillus* sp. under stress conditions showed relatively higher shoot growth and dry biomass as compared to non-inoculated plants. PGPR-treated wheat plants confirmed their potential in enhancement of plant performance by showing higher biomass (Timmusk et al. 2014). Likewise, under drought stress pepper plants were inoculated with *Bacillus licheniformis K11* increased shoot length biomass, etc. (Lim and Kim 2013).

Improved plant growth and increment in shoot growth during drought stress have been reported in several other crops treated with PGPR in sorghum (*Sorghum bicolor* L.) (Grover et al. 2014), mung bean (*Vigna radiata* L.) (Sarma and Saikia 2014), wheat (*Triticum aestivum*) (Arzanesh et al. 2011; Kasim et al. 2013), sunflower (*Helianthus annuus* L.) (Castillo et al. 2013), green gram (*Vigna radiata* L.) (Saravanakumar et al. 2011) and maize (*Zea mays*) (Sandhya et al. 2010; Naseem and Bano 2014; Naveed et al. 2014; Yasmin et al. 2017) Given in Table 11.1.

11.7.3 Relative Water Content (RWC)

One of the major criteria to measure plant water status called relative waste content (RWC) In such cases, leaf tissues exhibited limited cell expansion as a result of a decrease in RWC that occur due to loss of turgor, leading to a decline in plants growth (Ashraf 2010; Lu et al. 2010; Castillo et al. 2013). On the other hand, the high RWC was observed in species that were better adapted to dry environments (Jarvis and Jarvis 1963). Therefore, an important drought tolerance enhancement strategy could be the increment in RWC.

For instance, *Bacillus* sp. strain *129 KB*-treated sorghum, showed an increase in sorghum (Grover et al. 2014) and maize (Sandhya et al. 2010; Vardharajula et al. 2011; Bano et al. 2013; Naveed et al. 2014; Naseem and Bano 2014, Yasmin et al. 2017). In fact, oxidative and osmotic stresses caused by drought stress can be reverted back to higher RWC, contributing to greater productivity of. Maize plants treated with *brasilense BR11005* sp. showed high RWC as a result of bacterial mediated abscisic acid (ABA) that in return induced closing of stomata and mitigate drought stress (Casanovas et al. 2002). Alterations of the sensitivity of physiological processes such as stomatal closure may be the reason for increase in RWC. In light of contrasting views, it is yet to investigate the mechanism involved in bacterial-induced drought tolerance.

11.7.4 Role of Phytohormones

Another mechanism used by rhizobacteria to impart drought tolerance in plants is alteration in their phytohormones contents. Indole-3-acetic acid (IAA), Cytokinins (CK), abscisic acid (ABA), and ethylene (ET) have been reported to be involved in ensuring plant tolerance to drought stress.

11.7.4.1 Indole-3-Acetic Acid (IAA)

PGPR synthesizes indole-3-acetic acid (IAA), is adsorbed on the root surface or seeds. Some of the newly synthesized IAA is taken up by the plant from root exudates, which facilitate plant cell proliferation and elongation in combination with the endogenous nature of plant IAA. Meanwhile, IAA stimulates the activity of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) synthase to convert *S*-adenosyl methionine (SAM) into ACC (Naveed et al. 2014). A bacterial cell surviving under drought stress conditions also needs to cope up with the osmotic stress, bacteria help to tolerate osmotic stress generated by drought conditions in plants (Boiero et al. 2007).

Second most important function of bacterial IAA is its involvement in altering the root architecture in terms of root area and tips extension, which help associated host plants to assimilate nutrients from soil more efficiently underwater limiting conditions (Mantelin and Touraine 2004). Plants inoculated with IAA-producing bacteria showed more tolerance to drought stress (Yasmin et al. 2017, Marulanda et al. 2009). The volatile organic compounds were observed to enhance the production of IAA by upregulating IAA regulating transcripts (Zhang et al. 2007). Higher production of IAA was observed in *lipoferum* due to upregulation of indole-3-pyruvate decarboxylase gene. Re-inoculation studies showed that strain-induced morphological changes in coleoptile xylem of wheat seedlings grown under osmotic stress conditions (Pereyra et al. 2012).

11.7.4.2 Gibberellins

Several types of GAs secreted in diverse genera of PGPR *Pseudomonas putida H-2-3* induces physiological alterations and cause better growth of soybean under drought stress conditions by secretion of gibberellins (GAs) (Sang-Mo et al. 2014). Cohen et al. (2009) found that PGPR strains producing ABA and gibberellic acid (GA) remediated the consequences of drought stress in maize plants.

11.7.4.3 Abscisic Acid (ABA)

ABA has been considered as stress hormone as its secretion is stimulated by stress signals under drought stress conditions. Yamaguchi et al. (1994) found that ABA is involved in stomatal regulation to prevent water loss under drought stress conditions. *Azospirillum brasilense (Sp245)* treated *Arabidopsis* spp. accumulated higher levels of ABA as compared to non- treated plants (Cohen et al. 2008). Bresson et al. (2013) found that *Arabidopsis* plants inoculated with *Phyllobacterium brassicacearum* strain *STM196*. showed a reduction in transpiration and osmotic tolerance by producing higher contents of ABA. On the other hand, cytokinin-producing *Bacillus subtilis* ameliorate the growth retarding effects of drought stress on *Platycladus orientalis* seedlings (Liu et al. 2013).

11.7.4.4 Ethylene (ET)

Ethylene usually regulates the growth and functions of plants through various mechanisms. Physiological indicators induced by ethylene aid in shoot and root growth differentiation, release of dormancy, adventitious root formation, induction of flowering and increased femaleness in dioecious plants, leaf and fruit abscission, fruit ripening, and flower and leaf senescence (Davies 2013). It also helps in overabundance of ethylene which leads to abnormal growth of roots, imparting a visible dent on plant growth and development. Both biotic and abiotic stresses accelerated ethylene production in plant roots. The increase in ethylene concentrations has inhibitory effects on root growth crucial to regulate production in the vicinity of plant roots for normal growth and development (Naveed et al. 2014).

11.7.4.5 Influence of 1-Aminocyclopropane-1-Carboxylate (ACC) Deaminase

The enzyme ACC deaminase metabolizes ACC into ammonia and α-ketobutyrate and checks ethylene production, which inhibits plant growth (Glick 2007). The plants treated with bacteria having ACC deaminase may have comparatively increased root growth due to decreased ethylene production and can resist various stresses more effectively (Glick 2007).

The uptake and hydrolysis of ACC by microorganisms lessen the levels of ACC outside the plant. On the other side, the equilibrium between the external and internal ACC levels is continued through the diffusion of more ACC into the rhizosphere (Shaharoona et al. 2006a). Microbial communities of soil having ACC deaminase activity increased biosynthesis of ACC than the plant needs and stimulate exudation of ACC from roots provide microorganisms with a unique nitrogen source (ACC), and hence, the growth of ACC deaminase containing microbes is accelerated in the close vicinities of plant roots in comparison to the other soil microorganisms Not only the ACC levels decreased within the plant but also inhibits the biosynthesis of the stress hormone ethylene (Shaharoona et al. 2006b). A plant inoculated with ACC deaminase containing bacteria exhibited more root growth. In various studies, inoculation with ACC deaminase containing PGPR has been unequivocally shown to modify the endogenous levels of ethylene, which results in changes in plant growth (Shaharoona et al. 2006a, b; Madhaiyan et al. 2006; Shahzad et al. 2013)

A considerable increase in fresh and dry biomass of pepper and tomato was observed when treated with ACC producing *Achromobacter piechaudii (ARV8)* against water-deficit conditions (Mayak et al. 2004b). Lim and Kim (2013) observed that ACC deaminase-producing *licheniformis K11* impart significant increase in drought tolerance of pepper plant. Similarly, ACC deaminase producing *Pseudomonas* sp. treated P. pea showed significant root elongation which subsequently enhanced uptake of nutrients and water under water scarcity conditions (Zahir et al. 2008). A significant decrease in transcription of stress-responsive genes

and upregulation of genes related to cell division was observed in ACC deaminase producing strain *Enterobacter cloacae UW4* treated canola plants (Hontzeas et al. 2004)

11.7.5 Effect of Osmolytes and Secondary Metabolites

The great concern lies in of osmoregulation in plants under drought stress conditions by the production and accumulation of certain secondary metabolites. The most commonly acclimated osmolytes in water-stressed plants and bacteria includes proline, trehalose, and glycine betaine (Kaushal and Wani 2016; Chen et al. 2007; Rodriguez et al. 2009).

11.7.5.1 Amino Acids

Rhizobacteria induce drought tolerance to the plants. The quantity of amino acids sorghum, pepper and wheat have been observed to get increased underwater deficit conditions due to protein breakdown in response to fluctuation in osmotic pressure (Zhu 2002; Yadav et al. 2005; Kaushal and Wani 2016) as stated below.

11.7.5.2 Proline

Accumulation of proline is a common metabolic response of higher plants to drought and salinity stress (Rhodes et al. 1999; Yasmin et al. 2017). Drought-affected cellular machinery responds by proline accumulation via osmoregulation, ROS-scavenging mechanisms, and stabilization of cytoplasmic organelles. Generally, proline protects plants from stress through different means such as detoxification of reactive oxygen species, contribution toward osmotic adjustment, stabilization of native structures of enzymes, proteins, and membranes (Binzel et al. 1987; Kaushal and Wani 2016).

Under water-limiting conditions bacteria produce osmolytes in soil, which are readily taken up by the plants (Kaushal and Wani 2016; Yasmin et al. 2017). PGPR *Bacillus subtilis*, *Pseudomonas* sp. isolated from water-deficient habitats showed more proline production in inoculated maize plants as compared to un-inoculated plants (Yasmin et al. 2017). Long back, Yoshiba et al. (1997) showed significant upregulation in proline synthesis gene *P5CS* and downregulate the proline metabolism gene *ProDH*. Moreover, transgenic *thaliana* plants with *ProBA* genes from *Bacillus subtilis* produced higher amount of proline (Chen et al. 2007).

A significant higher accumulation of osmolytes proline, sugars, and free amino acids in *Bacillus* sp. treated maize plants produced higher biomass, improved relative water content, and overall plant health status under drought stress condition (Vardharajula et al. 2011). Ansary et al. (2012) observed significant increase in

accumulation of proline in *P. fluorescens* inoculated maize plants. On the other hand, *lipoferum* showed increase in soluble sugars and free amino acids during drought stress (Qudsaia et al. 2013).

11.7.5.3 Glycine Betaine (GlyBet)

Salt stress leads to water stress because of excess solute concentration. GlyBet amount elevates in both saline and drought conditions. It is a quaternary ammonium compound with osmoprotecting functions, protects the plants by stabilization of both the highly ordered quaternary structure of membranes and proteins. Excess ions may disturb the proper structures and functions of enzymes and other proteins, so GlyBet acts as molecular chaperons and helps in refolding of enzymes and in regaining of proteins functions. This metabolite is synthesized via two-step oxidation (Chen and Murata 2008). *Pseudomonas pseudoalcaligenes* inoculation in rice plants stimulated the synthesis and accumulation of GlyBet (Jha et al. 2011). According to Zhang et al. (2010) volatile organic compounds produced by *subtilis GB03* induced systemic drought tolerance in *Arabidopsis* plants. But, *xipotl* mutant of *Arabidopsis* showed less accumulation of choline with reduced drought tolerance when treated with *GB03*.

11.7.6 Antioxidants Defense

Reactive oxygen species (ROS) are generated at a low level in the organelles chloroplast, mitochondria, etc., under normal growth conditions. However, when the plants encounter any of the abiotic stresses, the dramatic acclimation of ROS level is observed (Sheteawi 2007). During the stress conditions, CO_2 uptake is reduced due to the stress-induced stomatal closure and reduction in leaf area. This indirectly favors the photorespiration in plants. Photorespiration is responsible for the overproduction of H_2O_2 in the peroxisomes. Moreover, the level of H_2O_2 or singlet oxygen is upregulated by over reduction in the photosynthetic electron transport chain (ETC) (Rejeb et al. 2014).

Fortunately, plants possess the defense mechanism that is activated upon the upregulation of ROS than the optimal level and scavenge the activated oxygen species (AOS) (Das and Roychoudhury 2014). The defense response is actually the generation of antioxidant enzymes. There are different antioxidant enzymes like catalase (CAT), superoxide dismutase (SOD), glutathione reductase (GR), glutathione peroxidase (GPX) and ascorbate peroxidase (APX) (Cho and Park 2000). The protective response also involves some other defense enzymes such as polyphenol oxidase (PPO), peroxidase (PO), phenylalanine ammonia-lyase (PAL), and tyrosine ammonia-lyase (TAL) (Valifard et al. 2015). These enzymes not only have antioxidant capacity but also have role in defense against pathogens attack in a

variety of crops. Apart from their other normal functions, these enzymes are also involved in the formation of defense barrier for reinforcement of cellular structures (Gao et al. 2008).

Plants have to regularize the production and scavenging of ROS to prevent themselves from cell injury and for normal functions under drought stress conditions. A visible decrease in antioxidant enzymes activity of plants has been observed under water-stressed condition (Yasmin et al. 2017). However, PGPR inoculation showed significant positive effects on ROS-scavenging enzyme machinery to mitigate the adverse effects of drought stress (Bindu et al. 2018). Vardharajula et al. (2011) and Yasmin et al. (2017) observed that *Bacillus* sp. treated maize plants showed obvious reduction in ROS accumulation and decrease in the activities of ROS-scavenging enzymes.

11.8 Salt Stress/Salinity

Soil salinity is a threat and is defined as excessive salt accumulation in the soil causing plant growth inhibition that ultimately leads to plant death. On a world scale, salt is the most toxic substance among other substances that restricts plant growth. that significantly reduces crop yield (Qadir et al. 2014). Salinity poses an increasing threat to agriculture (Gunes et al. 2007). Among multiple sources of salt stress, the combined effect of irrigation with poor drainage is a common and most serious threat, as it causes losses to the productivity of agricultural land.

In comparison to primary salt stress in the seashore, the reason for this secondary salinization is simple, i.e., salts remain in the soil after water evaporates and adversely affect crop growth and yield (Ghassemi et al. 1995). The stresses caused by excessive salt accumulation in the soil are twofold; First, most of the salt ions causing toxicity to plant cells when exposed to high salt concentrations internally or externally. Characteristically, NaCl comprises of majority of the salts. Na^+ ions are toxic to most of the plants, and growth of some plants is also inhibited by excessive Cl^- ion accumulations. Second, salt stress causes a decrease in osmotic potential of the soil leading to osmotic stress (Gilroy et al. 2014; Roy et al. 2014). The objectives are to understand the control of ion homeostasis and osmotic regulation, and to use the knowledge to engineer crop plants with enhanced salt tolerance.

Among various abiotic stresses, salt stress is one of the major limiting factors in crop productivity, particularly in arid and semiarid areas. It has been stated that about 7% of the total land and 20% of the total arable lands are affected by salt stress (Zhu 2001; Shrivastava and Kumar 2015). Soil reclamation is essential as the cultivable lands are being greatly affected by salinity (Gunes et al. 2005). Salt stress/salinity is a complex trait to study as it hinders designing and interpreting the experiments but current OMICS-driven research has made it comparatively easier to study (Negrão et al. 2017). Plant growth could be recovered when salt stress is relieved but the plants primarily respond to salinity by reducing the leaf surface area followed by cessation of expansion as the stress intensifies (Parida and Das 2005).

Salinity causes ionic and osmotic stress that ultimately leads to oxidative stress (secondary stress) affecting different metabolic processes that include protein synthesis, photosynthesis and lipid metabolisms (Jampeetong and Brix 2009).

Salt stress is one of the major issues affecting agricultural lands worldwide. *Food and Agriculture Organization (FAO)* states that about 397 million hectares (ha) of land has been salinized globally. It also stated that out of 230 million ha of irrigated land, 45 million ha (19.5%) have been affected by salinity and in 1500 million hectares of dryland cultivation, 32 million ha (2.1%) have been under salt stress.

Secondary salinization, which is the result of mismanaged irrigation, is also a vital issue with regards to the world's food production. Though irrigation accounts for 17% of the world's cultivable land, it provides over 30% of its agricultural yields (Pitman and Läuchli 2002). Salt stress is a pervasive issue in irrigated regions of dry and hot territories, especially in countries of Africa and Asia like India, Egypt, and Iran. According to estimates, 33% of irrigated land is salt-affected in which 20% is due to secondary salinization (Shrivastava and Kumar 2015). About 75% of secondary salinization in dry, subhumid, arid, and semiarid regions occurs in the Asian-Pacific region; during the mid-1980s, about 50% (30 million ha) of irrigated land damaged by salinization was found in Pakistan, India, and China (Pitman and Läuchli 2002).

11.9 Effects of Salinity in Pakistan

In Pakistan, salinity is among the most serious abiotic stresses. It is increasing day by day affecting both quality and quantity of crops. The major cause of salinity is due to imbalance of entrance and exit of salt in the soil. Every year, around 120 million tons of salt is added to the land from canal and brackish water and from this only one-fifth of this salt can go to the seawater. Remaining salt leaches in the soil and causes reduction in growth of plants (Elnaggar and Noller 2009). About 2.5 million hectares of irrigated land is being adversely affected by severe saline conditions in Pakistan. Out of this, 18% of this land is affected in Sindh while NWFP and Punjab contribute 2% and 3%, respectively. Areas affected by moderate saline conditions are 10%, 4%, and 2% in Sindh, Punjab, and NWFP, respectively (Ali et al. 2005).

Crop yield losses in Pakistan are estimated to reach to feared amount of Rs. 880 million ($ 28.5 million) this year due to water logging and salt stress, while total economic loss is around $ 300 million. As for as wheat is concerned, the yield losses in moderate saline areas are about 65% (El-Hendawy et al. 2005). Yield losses in important crops due to salt stress are given in Table 11.2.

Other than crop yields, salinity also affects photosynthesis, ion regulation, and water relations. It also affects plant physiology at adult plant stages as well as at cellular levels through ionic and osmotic stress (Parida et al. 2004). It has been observed that various physiological processes that are severely affected by salt stress include mineral distribution, plant growth inhibition, membrane instability

Table 11.2 Yield losses of different crops caused by salinity

Crop	Yield loss (%)	References
Wheat	60–65	El-Hendawy et al. (2005)
Rice	30–50	Joseph and Mohanan (2013)
Sugarcane	40–50	Rao and Shaw (1985)
Pepper	8–15	Navarro et al. (2002); Chartzoulakis and Klapaki 2000)

as a result of calcium displacement by sodium, membrane permeability, and drastic reduction in rate of photosynthesis and Na^+ and K^+ discrimination (Shafi et al. 2010).

11.10 Strategies Used to Overcome Salinity

Supply of sufficient water along with proper drainage and irrigation management are also good but comparatively expensive practices to control salinity problem (Cominelli et al. 2013; Mwadzingeni et al. 2016).

The most significant step to control salinity issue is developing salt-tolerant plant varieties. Improvements in the field of genetic engineering have greatly reduced the risk of salinity by the production of salt-tolerant plants. However, the progress in this field is still slow because of the contradiction in views among plant physiologists, plant breeders, and plant molecular biologists (Munns 2002; Blum 2014; Flowers 2004; Ashraf et al. 2008; Hasegawa et al. 2000; Mittler and Blumwald 2010; Hasegawa 2013; Munns and Gilliham 2015; Yeo 1998; Zhang et al. 2014). But still several salt-tolerant plants have been developed through genetic engineering technique (Zhang et al. 2001; Zhu 2001).

Forests are the environmental buffers which keep the soil in place, deforestation leads to soil erosion and ultimately increase the risk of salinity and water logging so planting more trees to renovate the custom of the green revolution is the need of the hour. Acid rain also causes leaching of important nutrients from the soil such as calcium and potassium. To reduce the risk of acid rain, use of biofilters in industries is emphasized so that soil could be protected from grave problem of salinity and soil erosion.

In irrigated soil, reclamation of soil involves the replacement of sodium ions with calcium ions. The released sodium ions are finally percolated out of the root zone by using excess water which is later carried out of the fields in the drainage water. Because of continuous process of evaporation, salt concentration increases in the top soil surface which is then scraped and transported out of the field. Pre sowing irrigation with good quality water is a good strategy to remove salt from the soil surface. This ensures better seed germination and establishment of seedling.

Mulching (a practice that uses crop residue, straw) reduces water loss from the top soil causing reduction in uptake of salts. Reduced evaporation also improves

water-use efficiency. As a result, lesser salts are accumulated. Mixing organic matter with crop residues or green-manure crops also improves soil surface, supply structure, and improves water infiltration which prevents adverse effects of salinity. Halophytes being native flora of saline environment complete their life in salinity which also plays a positive role in reduction of salt stress.

11.11 Concerns with Strategies

Currently, numerous crop improvement approaches are being used against salt stress. In the past, selection breeding using the mechanism of stress tolerance has led to smaller crop improvements. For example, salt stress causes 40–70% reduction in yield and crop yield improvement is only 5–20% through conventional or molecular breeding techniques (Ashraf et al. 2012; Ashraf and Foolad 2013; Munns et al. 2012; Negrão et al. 2011, 2017). There are several transgenic approaches available (more than three thousand reports of improved salt tolerance in wheat, rice, maize, sorghum, canola, etc.) but unfortunately none is being used by farmers.

Salinity has been reported as one of the major limiting factors in crop productivity in Pakistan. In the past, several agricultural regions have significantly lost their productivity due to soil stress. The saline conditions are found in various parts of the country but the most affected lands as mentioned earlier are found in Sindh, Punjab and few areas of Khyber Pakhtunkhwa. Farmers do not pay proper attention to salinity. It indicates that farmers did not adopt any consistent strategy to fight against this serious issue. No significant pattern in farmers' response toward salinity has been noticed. Farmers were just preferring to buy lands with minimal soil salinity and increasing production of existing agricultural lands. Instead of adopting strategies to get rid of salinity, farmers were demanding larger government actions to install a proper drainage system for successful reclamation. Suggestions of farmers for land reclamation (Tanwir et al. 2003) are included in Table 11.3.

The above table suggests that farmers were unable to form any opinion which is quite alarming. Salt stress has emerged as a serious issue that not only causes a loss in crop productivity but also puts far-reaching impacts on the livelihood strategies of small farmers. The problem has been intensified to such an extent that it has made it very difficult for the farmers to fight against the severity of the problem. A joint step by government, NGOs, and the farmers is promptly required to control the alarming situation (Tanwir et al. 2003).

Table 11.3 Farmers' suggestions for reclamation of land

Suggestions	Percentage, n = 150
Laying of tile drain	19.8
Installation of tube well	21.5
Cleaning of drainage	11.2
Tile drain, tube well and cleaning	9.1
No opinion	38.4

11.12 PGPR-Mediated Amelioration of Salt Stress

Over the past century, large volumes of publications have appeared on the beneficial interactions between microbes and plants. Microbial communities dwelling in the nutrient-enriched plant rhizosphere play an essential role in plant functioning by influencing their growth, physiology, and other developmental processes (Mendes et al. 2013). PGPRs residing as free-living in the rhizosphere and carry out useful activities for plants. Few bacteria are facultative endophytes invading the host plant tissues to mutually establish a beneficial interaction. Most of the PGPR inhabit the roots by colonization and proliferate in rhizodermal spaces and root hairs, while few species reside without any physical contact with roots (Gray and Smith 2005). Both rhizospheric, as well as endophytic bacteria, promote plant growth through various direct as well as indirect mechanisms. In such mechanisms, bacteria directly enhance the plant growth efficiently by improving plant nutrition through phytohormone production and solubilizing several important minerals (Chauhan et al. 2016; Vaishnav et al. 2016; Maheshwari et al. 2014).

For regulation and rhizospheric signal communication, root secretions play the most important role and are involved in the plant–microbe interaction. In the field of agriculture, the main focus is to remove the unadorned stress conditions and adverse outcomes, through exogenous application of inoculum of these microbial organisms (Shrivastava and Kumar 2015). Before introducing commercially, the PGPR that are isolated from the rhizospheric soil are screened in vitro for testing the characteristics of PGP and some other valuable effects in field trails and greenhouse experiments. Plant growth is promoted by PGPR through the vast chain of signaling and mechanisms like efficient uptake of nutrients by fixing nitrogen biologically, iron chelation and solubilization of phosphorus as well as pathogen control through competition for survival and antagonistic relationships (Compant et al. 2005; Steenhoudt and Vanderleyden 2000; Maheshwari 2010; Beneduzi et al. 2012; Sharma et al. 2013; Jin et al. 2013; Chowdhury et al. 2015; Kuan et al. 2016), soil decontamination by degrading several organic contaminants and reduction of heavy metals from the soil, and assistance in phytoremediation (Nie et al. 2011; Divya and Kumar 2011; Janssen et al. 2015).

PGPR inoculation is known to induce the abiotic stress regulatory mechanisms through direct and indirect systemic induced resistance pathways (Yang et al. 2009; Maheshwari 2010). The mechanism involved in the elevation of salt stress, maintenance of ion homeostasis, improvement of photosynthesis and water plant relations. A complex channel of plant–microbe interaction and cascade of signaling mechanism is implemented in the removal of salinity stress (Smith et al. 2017). The plant growth promotion by the application of different salt-resistant PGPR genera including *Bacillus*, *Serratia, Pseudomonas*, *Rhizobium*, *Azospirillum* and *Acetobacter* under salt stress conditions is given in Table 11.4.

Table 11.4 Plant growth-promoting rhizobacteria mediating salt tolerance in plants

Plant	PGPR specie	Effects	References
Glycine max	*Rhizobium*	Increased nodulation	Ma et al. (2002)
Zea mays	*Azospirillum*	Obstructed Na^+ uptake, increased uptake of K^+ and Ca^{2+}, and increased nitrogenase and nitrate reductase activity	Hamdia et al. (2004)
Lycopersicon esculentum	*Achromobacter piechaudii*	Reduced ethylene and improved plant growth	Mayak et al. (2004a)
Triticum aestivum	*Aeromonas hydrophila/ Caviae, Bacillus insolitus*, *Bacillus* sp.	Exopolysaccharide production	Ashraf et al. (2004)
Triticum aestivum	*Azospirillum*	Improved water relations and yield	Creus et al. (2004)
Vitis vinifera	*Burkholderia phytofirmans*	Increased chilling resistance	Barka et al. (2006)
Arachis hypogea	*Pseudomonas fluorescens*	Increased ACC deaminase activity	Saravanakumar and Samiyappan (2007)
Zea mays	*Pseudomonas syringae*, *Pseudomonas fluorescens*, *Enterobacter aerogenes*	ACC deaminase activity increased	Nadeem et al. (2007)
Arabidopsis thaliana	*Bacillus subtilis*	Regulation of tissue-specific sodium transporter HKT1	Zhang et al. (2008)
Zea mays	*Rhizobium*, *Pseudomonas*	Electrolyte leakage decreased, increase in proline, relative water content and K uptake	Bano and Fatima (2009)
Lactuca sativa cv. *Tafalla*	*Pseudomonas mendocina*	ACC deaminase activity, improved nutrient uptake	Kohler et al. (2009)
Gossypium hirsutum	*Pseudomonas putida* Rs-198	Increased K^+, Mg^{2+}, and Ca^{2+} absorption, decrease Na^{2+} uptake from soil	Yao et al. (2010)
Zea mays	*Bacillus megaterium*	Upregulated expression of *ZmPIP* two isoforms	Marulanda et al. (2010)
Oryza sativa	*Pseudomonas pseudoalcaligenes*, *Bacillus pumilus*	Increased glycine betaine concentration	Jha et al. (2011)
Zea mays	*Micrococcus luteus*	Increased IAA and HCN production	Raza and Faisal (2013)
Fragaria ananassa	*Kocuria erythromyxa (EY43)*, *Bacillus atrophaeus (EY6), Staphylococcus kloosii (EY37)*	Increased yield and nutrient uptake	Karlidag et al. (2013)

(continued)

Table 11.4 (continued)

Plant	PGPR specie	Effects	References
Triticum aestivum	*Pseudomonas putida*, *Pseudomonas fluorescens*, *Serratia ficaria*, *Enterobacter cloacae*	Increased germination percentage, rate and index, enhanced nutrient status	Nadeem et al. (2013)
Oryza sativa	*Pseudomonas pseudoalcaligenes, Bacillus Pumilus,*	Increased antioxidants, plant growth, and nutrient uptake	Jha and Subramanian (2013)
Vigna radiata	*Rhizobium* and *Pseudomonas*	IAA production and ACC deaminase activity	Ahmad et al. (2013b)
Solanum lycopersicum	*Pseudomonas putida (UW4)*	Increased shoot growth and expression of *Toc-GTPase*	Yan et al. (2014)
Hordeum vulgare and *Avena sativa*	*Acinetobacter* sp., *Pseudomonas* sp.	Improved IAA and ACC deaminase production	Chang et al. (2014)
Oryza sativa (GJ-17)	*Bacillus pumilus*, *Pseudomonas pseudoalcaligenes*	Decreased superoxide dismutase and lipid peroxidation activity	Jha and Subramanian (2014)
Solanum lycopersicum 'Micro tom'	*Streptomyces* sp. strain PGPA39	Enhanced IAA production, ACC deaminase activity, phosphate solubilization	Palaniyandi et al. (2014)
Glycine max	*Pseudomonas simiae (AU)*	Upregulating the expression of storage vegetative proteins, RuBisCO large unit proteins. Increased chlorophyll and proline contents and decreased root *NaCl* accumulation	Vaishnav et al. (2015)
Abelmoschus esculentus	Enterobacter sp. (*UPMR18)*	Improved antioxidant activities, upregulation of ROS specific pathway genes	Habib et al. (2016)
Triticum aestivum	*Dietzia natronolimnaea*	Protection by modulating the expression of stress-responsive genes	Bharti et al. (2016)
Zea mays	*Bacillus amyloliquefaciens (SQR9)*	Improved photosynthesis and nutrient uptake	Chen et al. (2016)
Glycine max	*Bacillus thuringiensis (NEB17)*	Upregulation of the expression of RuBisCo-oxygenase, PEP carboxylase, proteins and pyruvate kinase, antioxidants, photosystems I and II, Glutathione-S transferase and isocitrate lyase.	Subramanian et al. (2016)

(continued)

Table 11.4 (continued)

Plant	PGPR specie	Effects	References
Capsicum annum	*Microbacterium oleivorans* (*KNUC7074*), *Brevibacterium iodinum* (*KNUC7183*), *Rhizobium massiliae* (*KNUC7586*)	Greater plant height, fresh and dry weight, enhanced chlorophyll content	Hahm et al. (2017)
Triticum aestivum	*Arthrobacter protophormiae (SA3)*, *Dietzia natronolimnaea (STR1)*	Enhanced photosynthetic efficiency	Barnawal et al. (2017)
Panax ginseng	*Paenibacillus yonginensis (DCY84T)*	Induction of the defense-related systems, for instance, ROS-scavenging enzymes, ion transport, proline content, biosynthetic ABA genes, total sugars and induction of genes involved proliferation of root hairs	Sukweenadhi et al. (2018)
Lolium perenne	*M30-35* strain (novel bacterium)	Improved chlorophyll contents, shoot fresh and dry weights, root activity, root volume, soluble sugar, catalase activity, and proline content	He et al. (2018)

11.12.1 PGPR-Mediated Induced Systemic Tolerance

It is important to develop the knowledge about the vibrant functions of PGPR by using different standardized techniques and understanding the basic mechanisms and functions of PGPR regarding the conductance of stomata, transport of ions, phytohormonal status, antioxidant enzymes, carbohydrate metabolism, and proteins signal transduction. On improvement of salt stress different PGPR traits have been reported, e.g., ACC deaminase, phosphate, and potassium solubilization, exopolysaccharides, volatiles, and IAA production, etc. In this context, Dodd and Pérez-Alfocea (2012) reported that the hormonal root to shoot signaling in plants is altered by different rhizospheric microbes. Secretion of flavonoids by bean plants stimulated by IAA-producing PGPR regulates the nutrient uptake, nitrogen fixation and reduces unfavorable results of salt stress. The ACC-deaminase (ACC-D), is produced by PGPR that reduces the ethylene level under salt stress conditions through hydrolysis of ethylene precursor ACC (Choudhary et al. 2015).

Further, during saline conditions reduction of the chelation of excessive Na^+ and decrease in its bioavailability to the plants is maintained by the microbial secreted exopolysaccharides (EPSs) (Choudhary et al. 2015). PGPR increase the

bioavailability of nutrients like phosphorus, potassium, zinc, and iron through secretion of different enzymes in soil for enhanced nutrients uptake by plants. In the past few years, the volatile organic compounds produced by specific bacterial strains were proved as advanced way of communal signaling between plants and PGPR, enhancing the plant growth through regulation of different biological processes including nutrient uptake, osmoprotectant biosynthesis, ion balance and distribution of hormones (Liu and Zhang 2015).

11.13 Mechanisms of PGPR for Salinity Stress Tolerance

Mechanisms employed by microbes which help in the improvement of plant growth and reduction of negative effects of salt stress are given below:

11.13.1 Osmotic Balance

Osmotic stress affects the plant growth that is partially recovered by osmolytes accumulation during salt stress. Salt ions gathering around the root creates water stress which results in an osmotic imbalance in plants. Photosynthetic structures and osmotic balance are dire to the salt stress so their maintenance proved crucial for the removal of unsafe effects of salinity on plant growth (Iqbal et al. 2014). PGPR not only improve plant–water relations through accumulation of osmolytes in the plants but enhanced synthesis of proline in the under abiotic stress through application of *Burkholderia*, *Arthrobacter*and *Bacillus* (Choudhary 2012). Vardharajula et al. (2011) reported the higher proportion of proline in the salt-stressed plants inoculated with *Bacillus* sp. Kumari et al. (2015) further confirmed that roots maintain osmotic balance because of accumulation of higher proline content, resulting in enhanced water uptake into the roots. Increased proline, as well as water content, was observed in the *Z. mays* inoculated with *Rhizobium* and *Pseudomonas* strains (Bano and Fatima 2009). Osmotic potential, antioxidants, relative water content, proline and endogenous phytohormones ABA and salicylic acid (SA) were found to be increased in *H. annus* due to PGPR under salt stress (Naz and Bano 2013; Naz and Bano 2015). The relation between accumulated proline and *pyrroline-5-carboxylate synthase (P5CS)* gene expression has been determined by the PGPR applications. The bacterial applications resulted in free proline accumulation in plant roots by upregulating *P5CS* gene expression (Kumari et al. 2015). In addition to proline, total soluble sugars increased in PGPR inoculated salt-stressed plants (Shukla et al. 2012).

Under salinity, water conductance from soil to the plant through roots is maintained by the rhizobacteria (Marulanda et al. 2007). During salt stress, curtailment of the relative water content indicated water stress. Bacterial exopolysaccharides play a primary role in providing resistance to the plants against drought stress in addition to other activities (Vardharajula et al. 2009).

Inoculation with *Pseudomonas putida* sp. *GAP-P45* in sunflower increased the rate of survival as well as its biomass and root adherence to the soil under water scarcity (Sandhya, et al. 2009). Earlier, Mhadhbi et al. (2004) reported *Sinorhizobium medicae, Mesorhizobium mediterraneum,* and *Mesorhizobium ciceri* potential to cope with salt stress and provide tolerance to the plants in salinity through increasing POD enzyme activity. *Lactuca sativa* seedlings were exposed to drought stress at different levels after being inoculated with *P. mendocina,* showed an increase in photosynthetic activity, biomass content and relative water content occurred due to increase in peroxidase (POD) and catalase (CAT) activities (Kohler et al. 2008). Rice plants were inoculated with salt-resistant *B. amyloliquefaciens NBRISN13 (SN13)* reported increase in the chlorophyll content, plant–water relations, root shoot lengths, and biomass by upregulating the catalase activity and proline content as a defensive mechanism (Nautiyal et al. 2013).

PGPR helps in the maintenance of transpiration rate and water conductance so as to regulate plant stomatal openings and water potential. In saline conditions, maize plants inoculated with *B. megaterium* exhibited an increase root water conductance in relation to the upregulation of two isoforms of plasma membrane aquaporin protein *(ZmPIP)* (Marulanda et al. 2010). PGPR genera supported osmolytes and different phytohormones storage after salinization to cope with initial osmotic shock. Genetically engineered *proBA* genes that were derived from *B.subtilis* in *A. thaliana* provided salt stress tolerance by upregulating the synthesis of proline (Chen et al. 2007). When the rice plants inoculated with salt-tolerant *B.amyloliquefaciens (SN13)* exposed to the saline environment in hydroponic and saline soil, the plants tolerance against stress was increased due to the altered expression of 14 genes, among them four genes *(NADP-malic enzyme NADP-Me2*, *somatic embryogenesis receptor-like kinase SERK1*, *ethylene responsive element binding proteins EREBP* and *SOS1*) were upregulated and the expression of 2 genes *(glucose insensitive growth GIG* and *serinethreonine protein kinase SAPK4*) was downregulated in hydroponic setup, while in greenhouse experiment only *MAPK5* was upregulated. *SN13* inoculation enhanced the gene synthesis that is involved in the osmotic and salt stress tolerance (Nautiyal et al. 2013). Carbohydrate synthesis and transport is enhanced by the beneficial microbes directly associated with the relationship between source and sink, rate of photosynthesis, biomass accumulation, and plant growth rate. Wheat seeds inoculated with *B. aquimaris* have shown an increase in the total soluble sugar content and reducing sugars resulting in higher biomass, sodium reduction and NPK accumulation (Upadhyay and Singh 2015).

In another study, it was observed that the inoculation of pepper plants with *Pantoea dispersa* and *A. brasilense* following salt stress resulted in increased dry mass storage in relation to stomatal conductance and photosynthesis, but no change in the chlorophyll content and photosynthesis was observed (del Amor and Cuadra-Crespo 2012).

Large amount of osmoprotectants used to store in the cytosol of microbes exhibiting in osmolality fluctuating environment (Kempf and Bremer 1998). The osmolytes synthesis and accumulation by PGPR under such conditions became faster. Under oxidative stress, the absorbance of compatible solutes through roots

assisted them to impart resistance under salinity. Increased nodulation and better plant growth were observed in the bean (*Phaseolus vulgaris*) inoculated with *P. polymyxa* and *R. tropici* due to upregulation of *trehalose-6-phosphate* gene synthesis. Excessive trehalose synthesis acts as osmoprotectant and provide salt stress tolerance (Figueiredo et al. 2008).

11.13.2 Ion Homeostasis in Abiotic Stress

To control the ion uptake at the initial stages rather than spending a large amount of energy in damage repair and clearing excessive salts, plants cells have adaptive mechanisms to control the excessive salt by storing them in the large membrane-bound vacuoles. The most important factors limiting the plant growth and adolescence occurred due to the accumulation of excessive salts like Na^+ and Cl^- ions in the plant tissues. Glycophytes are known to have ion exclusion strategy as a tolerance mechanism in the salt stress. A group of rhizobacteria is known to remove the toxic ionic stress and improved development and growth under saline conditions (ref.). These microbes supported tolerance to salt stress by altering the ion transporters expression and by secretion of specialized biomacromolecules around roots, i.e., EPS that acts as a physical barrier between the roots and excessive salt. It was reported that the wheat plants inoculated with *Aeromonas hydrophila/caviae* and *Bacillus* sp. reduced uptake of Na^+ because of EPS secretion that clogs Na^+ by binding to the plant roots and preventing its transport to the leaves (Ashraf et al. 2004). In addition, the EPS producing *B. circulans* and *B. polymyxa* have potential in higher dry matter accumulation in wheat roots and shoots during the salt stress. Khodair et al. (2008) evide by due to the Bacterial volatile organic compounds (VOCs) also involved in Na^+ exchange pathways in PGPR-based ion mediated homeostasis. Bacterial VOCs are distant signaling low molecular weight compounds that help in signal transduction between two microorganisms. Exposure of *Arabidopsis* to *B. subtilis* volatile organic compounds (VOCs) exhibited salinity tolerance as compared to the unexposed plants by downregulating *AtHKT1* expression in roots and increasing expression in the shoots to facilitate root to root recirculation (Shkolnik-Inbar et al. 2013). The vegetative storage protein expression was increased through *P. simiae* AU-mediated VOCs expression in soybean leaves in relation to reduced Na^+ uptake under salinity stress by altering the sodium transport channels (Vaishnav et al. 2015).

Bacteria have ability to reduce the salt uptake by trapping cations with the help of rhizosheath in the EPS matrix and altering the ion exchange channels. Macro and micronutrients imbalance and mineral nutrients exchange caused by the sodium and chloride ions is controlled with the help of PGPR. Siderophore production by microbes, nutrients circulation and pH changes in the rhizospheric area facilitate bioavailability of minerals in the soil (Lugtenberg et al. 2013). In plant shoot, the Na/K ratio and ionic balance is maintained with the help of PGPR by decreasing the Na and Cl buildup in the leaves and increasing the Na removal from roots along

with increasing the affinity K transporter channels. In maize plants K uptake and Na exclusion enhanced by inoculating with *Azotobacter* strains *C5* (auxin producing) and *C9*. Plant stress response observed to enhance increase in proline, chlorophyll and polyphenol contents in leaves after PGPR inoculation (Rojas-Tapias et al. 2012). Similarly, *B. subtilis GB03* inoculation in *P. tenuiflora* (a halophyte grass) showed less Na salt accumulation because of increased expression of *PtHKT1* and *PtSOS1* genes in roots but under salt stress the gene *PtHKT2* in roots was down-regulated (Niu et al. 2016).

11.13.3 Phytohormone Signaling and Salt Tolerance

Many soil bacteria secreted, modulated and altered the status of endogenous phytohormones by releasing exogenous enzymes, metabolites and hormones, contributed to enhance salinity tolerance. Plant–microbe associations are known to initiate signaling events to enhance the endogenous production of phytohormones and several other metabolites under stress conditions (Dodd et al. 2010).

A number of studies elaborated the roles of abscisic acid (ABA), auxin (IAA), cytokinins (CK), ethylene and gibberellic acid (GA) under salinity stress. These hormones alter morphology, metabolism, water uptake, and nutrient acquisition efficiency of plants and consequently result in the larger, healthier and sturdy plants.

11.13.3.1 Abscisic Acid (ABA)

Abscisic acid (ABA) mainly cuts off the leaf and shoot growth of the plant, but recent research evidenced that the elevated concentrations of ABA in stressed plants suppress the excess production of ethylene. Mainly the raised ABA level generate an adaptive response that is fundamental for plant endurance (Pliego et al. 2011).

The aspects of exogenously applied ABA in plant–microbe associations under salinity stress and the role of the bacterial ABA. In salt-stressed plants, PGPR regulated the synthesis of ABA and its signaling pathways that resulted in the heightened plant growth. Halotolerant *Dietzia natronolimnaea* (*STR1)* persuaded the salt stress (150 *mM NaCl*) resistance system in wheat plants through regulation of ABA signaling course via upregulation of *ABA-reactive gene (TaABARE)* and *12-oxophytodienoate reductase 1 (TaOPR1)* activating *TaWRKY* and *TaMYB* input signal, resulting trailed due to expression of stress-sensitive genes including upregulation of *TaST* (a salt stress instigated gene). In PGPR-inoculated plants, the enhanced antioxidant enzyme gene expression and proline content provided maximum resistance against salt stress (Bharti et al. 2016). Under salinity *Cucumis sativus* plants inoculated with *Acinetobacter calcoaceticus* (*SE370)*, *Promicromonospora* sp. *SE188* and *Burkholderia cepacia* (*SE4)* resulted in greater biomass. PGPR reduced electrolyte leakage and increased water potential and, also caused ABA upregulation and decrease in salicylic acid and gibberellin *GA4* contents (Kang et al. 2014).

Decreased ABA accumulation and increased plant biomass in salinized soil were observed in cottonseed inoculated with *P. putida* (*Rs-198)*. However, the enhanced salt resistance likewise is credited to control ionic balance and enhanced endogenous IAA content (Yao et al. 2010). Under salinity stress conditions, wheat inoculation with *B. subtilis (LDR2)* and *Arthrobacter protophormiae* (*SA3*) resulted in enhanced IAA content and decreased ACC and ABA contents. The upregulation of *Serine/Threonine protein kinase–ethylene responsive* (*TaCTR1*) and *drought responsive element (TaDRE2)* genes exerted an improved impact and was additionally approved (Barnawal et al. 2017).

11.13.3.2 Auxin (Indole-3-Acetic Acid)

Biosynthesis of auxin occurs by means of complex pathways in rhizobacteria involved utilization of tryptophan secretion from root exudates and its into IAA (Spaepen et al. 2007). Upgraded plant cell growth occurred due to activated auxin signaling pathway and endogenous IAA pool in plants. In plant–microbe associations, the bacterial signaling molecule is IAA produced by PGPR. Under ideal conditions of growth, gaining of bacterial IAA in triggered, repressed or impartial plant growth (Dodd et al. 2010; Spaepen and Vanderleyden 2011). Salinity in soil influenced cell elongation due to the accumulation of IAA in roots. This accumulated IAA is likewise expected to hinder the synthesis and transport of cytokinin from root to shoot and brings in increased root lengthening under pressure conditions (Dodd et al. 2005). Enhanced salt stress tolerance was observed in maize when inoculated with *B. amyloliquefaciens* (*SQR9)*. It was supported by increased total soluble sugar and chlorophyll contents, enhanced catalase and peroxidase activity, improved KC/NaC ratio, and glutathione content. The negative impacts of 50 *mM NaCl* on *Phaseolus vulgaris* grown under hydroponic conditions were found to be alleviated by *Azospirillum brasilense* application because of higher accumulation of flavonoids as well as improved proliferation of roots (Dardanelli et al. 2008). Improved germination and development of corn and soybean was found when an IAA-producing co-inoculations of *Bradyrhizobium japonicum (E109*) and *Azospirillum brasilense (Az39*) were done (Cassán et al. 2009, 2014).

Research revealed that plants displayed higher root and leaf development inoculated with IAA-producing bacterial strains and considered as an adaptive response to salinity (Albacete et al. 2008). Under hydroponic conditions, PGPR strains producing IAA documented for enhanced efficiency of nutrient uptake (Shukla et al. 2012). Recent research avowed that GB03 activated the plant growth by cell wall releasing enzymes and auxin homeostasis as well (Zhang et al. 2007). Interestingly, the reduced effects of salt stress in the PGPR inoculated seedlings were affirmed by the upregulation of genes of *RuBisCo* encoding subunits *(RBCS, RBCL)*, *HC encoding pumping pyrophosphatase (H(C)-Ppase)*, *NHX2*, *NHX3*, *NHX1*, and *HKT1*, and downregulation of gene encoding *9-cisepoxycarotenoid dioxygenase* (NCED expression) (Chen et al. 2016).

11.13.3.3 Ethylene

In plants ethylene, a stress hormone synthesized under stress conditions. Rhizobial nodulation of legumes is also inhibited by ethylene. However, low production under normal condition soccurred due to adjustment of some physiological reactions, for instance, breaking of seed dormancy (Dodd et al. 2005). Yang cycle in plants is involved in ethylene synthesis. In this process ACC oxidase catalyze the conversion of ACC into ethylene. In stress conditions, transportation of ACC to a specific stressed organ resulted in ethylene production in that particular organ (Yoon and Kieber 2013). Under salt stress, growth of tomato is reduced due to the Na^+ build up and it is associated with elevated foliar ethylene (Mayak et al. 2004a). In another study, Albacete et al. (2008) reported that the application of salt, elevated the ACC levels along with the Na^+ accumulation in the leaf, xylem sap, and root. This phenomenon is associated with initiating the oxidative stress and decrease in photosynthetic capacity indicating ethylene's role in foliar senescence. In several studies, there is a decrease in ethylene quantity in stressed plants as numerous rhizobacteria contain ACC-deaminase enzyme, which splits ACC into ammonia and α-ketobutyrate. As stated in the reported model, plant roots are known to release and then hydrolyze ACC via ACC-D mechanism as ACC-D producing bacteria gets attached to the plant roots and absorb the released ACC (Glick et al. 1998). Consequently, more ACC is exuded from roots to keep the balanced ACC level inside the plant cell. Few reports revealed that PGPR containing ACC-D reduce salt stress (Wu et al. 2012). *Achromobacter piechaudii (ARV8)* inoculated strain under salt stress in tomato produce ACC-D which in turn has remarkably increased the efficacy of nutrient uptake and plant weights (Mayak et al. 2004a).

Researchers reported that improved nodulation in mung bean can be done by applying the ACC-D co-inoculated with *Bradyrhizobium* as it can bring down ethylene synthesis compared to the *Bradyrhizobium* alone (Shaharoona et al. 2006a). Red pepper under 150 *mM NaCl* stress increased the ethylene production that has been accounted for to decrease by ACC-D producing *B. iodinum (RS16)*, *Z. alba (RS111)* and *B. licheniformis (RS656)*. (Siddikee et al. 2011). Additionally, plants treated with PGPR strains those have capability to produce ACC-D showed even more root nodules, and improved plant growth and productivity under oxidative stress conditions (Zafar-ul-Hye et al. 2013).

Under saline conditions, up to 90 *mM NaCl* tomato seedlings inoculated with *P. putida (UW4)* exhibited enhanced shoot development in *Pisum sativum* cv. Alderman. Inoculation with *Variovorax paradoxus (5C-2)* reported to have positive effects under salt stress conditions. In saline soil, ACC-D producing *Enterobacter* sp. and *P. fluorescens* enhanced maize productivity. In inoculated plants under salinity stress elevated KC/NaCl proportion and NPK uptake were also recorded (Nadeem et al. 2009). *Pantoea dispersa (PSB3),* local bacterium remarkable improvement in pod number, biomass, seed weight, seed number and pod weight under salt stress. The enhanced salt resilience was related to critical decrease in electrolyte leakage and Na^+ uptake while increase in KC uptake, chlorophyll and relative water contents (Panwar et al. 2016).

11.13.3.4 Cytokinins

Cell division and differentiation are critically regulated by auxin and cytokinin proportion. Some PGP bacteria synthesize rhizobacteria is cytokinin generation (Dodd et al. 2010; García de Salamone et al. 2001; Aslantaş et al. 2007; Kudoyarova et al. 2014). The biomass content within the lettuce plant shoot was found to be raised by the application of CK-mediated *B. subtilis* under drought stress (Arkhipova et al. 2007). The role of CK signaling pathway in the plant development was anticipated by observing the increased CK levels in *A. thaliana* roots as a result of the application of cytokinin-producing bacterium *B. megaterium* (Ortíz-Castro et al. 2008). Giraud et al. (2007) reported that in the absence of nod factor in soybean plants the nodulation process occurred with the help of CKs after inoculating plants with PGPR strain *Bradyrhizobium*.

11.13.3.5 Gibberellins

Inoculation of wheat and soybean by GA-producing PGP strains of various genera involved in their growth and Gibberellins development under salt stress (Cassán et al. 2014). According to another study, tomato plant growth was enhanced by GA-producing *Promicromonospora* sp. *SE188,* revealed in the form of higher biomass and shoot length (Kang et al. 2012). Kang et al. (2014) also reported that GA-producing *P. putida H-2-3* essentially improved the plant weight, length, and chlorophyll substance in GA-deficient mutant soybean plants.

It is reported that PGPR isolates *B. cepacia*, *A. calcoaceticus,* and *Promicromonospora* sp. exerted positive effects on cucumber plants growth under salinity and drought conditions induced by sodium chloride and polyethylene glycol treatments (Kang et al. 2014). *Enterobacter cloacae*, P6 and *Bacillus drentensis*, P16 were used in combination with foliar application of silicon to maintain yield and growth of mung bean plants under saline conditions. The combination produced good results (Mahmood et al. 2016).

11.14 Impact of PGPR on Crop Growth Under Salinity

Researchers observed that PGPR enhance plant growth and have ability to promote their salinity tolerance levels, Besides the improvement in physiological responses and antioxidant potential. Ability of PGPR activated indole-3-acetic acid (IAA), gibberelins (GA), cytokinins (CK), abscisic acid (ABA), ethylene, and cofactor pyrroloquinoline quinone (PQQ), helpful in promoting the plant growth (Perrig et al. 2007). When spermidine introduced against saline stress as a new defender molecule produced by *S. rhizophile*, induced plant–microbe interaction process (Alavi et al. 2013). In soybean seedlings, IAA level decreases during stress conditions but by PGPR inoculation, major improvement was observed in the level of

hormones increased. The morphological changes in the roots improved the growth of shoots and ultimately increasing the yield (Asim et al. 2013). Isolation of halotolerant bacteria and their characterization by a high proline production with other plant hormones like trans-zeatin riboside, ABA, IAA and GA3 and the bacterial inoculation into the soybean plant improved length of roots shoots, and dry mass under salinity stress.

An osmotolerant PGPR named as *A. brasilense NH* isolated from the salt-affected soil in Algeria near Mediterranean coast, positively enhanced the growth of durum wheat in salinity effected soil (Nabti et al. 2007, 2010). To produce IAA at very high salt concentration, the strain was found effective. IAA played important role in providing resistance to plants against salt stress and in growth promotion of plant (Kang et al. 2014; Khalid et al. 2013; Kaya et al. 2010, 2013).

A variety of halophilic bacterial strains belong to the genus *Halomonas* isolated from the root zone of Salicornia plants, *Halomonas* spp. exhibited PGP characters under high salt concentration specifically due to IAA production(Mapelli et al. 2013). The effect of *B. cereus* and *Pseudomonas* sp., in wheat cultivation, revealed that osmotolerant bacteria have a direct and indirect effect on seed germination of paddy under saline conditions (Jha and Subramanian 2013). Thus may be due to important role of bacteria in upregulating IAA that helps in seed germination. PGPR through the enhancement of IAA under salinity stress cause reduction in toxin uptake results in the improved plant growth (Chakraborty et al. 2011; Zhang et al. 2008).

Hormones such as ABA, IAA, and GA3 ameliorated high concentration of salt stress after treatment with halotolerant strains like *P. extremorientalis* and *P. chlororaphis* resulted in improved growth of staple crops such as common bean (*Phaseolus vulgaris*) (Jha and Subramanian 2013).

11.15 Conclusions

Drought and salinity are major problems faced by the agricultural world. PGPR are the best alternatives to the chemical and traditional methods used against these problems. PGPR are proved to be efficient in increasing plant growth, yield and stress tolerance levels. They are non-pollutants and methods for their application are not costly, moreover, PGPR can be applied on plants at different life stages such as treatment of seeds with PGPR before planting or after emergence. Development of the bioinoculum is beneficial to promote economically important crops grown in arid and semiarid and salt-affected regions of the world. Extensive research on PGPR is needed to explore mechanisms of their beneficial effects on different cash and food crops along with searching for suitable methods of PGPR application according to crop types.

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Chapter 12
Growth and Yield of Field Crops Grown Under Drought Stress Condition Is Influenced by the Application of PGPR

Naeem Khan and Asghari Bano

Abstract Water stress causes significant losses to agriculture crops mostly grown in rainfed condition. Water stress affects the plant–water relation that causes specific and nonspecific damages to crop. Water stress is categorized as the dominant abiotic stress that is responsible for secondary stresses including oxidative stress that has hazardous effects on the biomolecules of cell. Plant growth-promoting rhizobacteria (PGPR) inoculated plants grow well under biotic and abiotic stresses. Plant survival in abiotic stresses defends on many adaptations and mitigation strategies. PGPR play dominant role in protecting plants from these stresses either directly or indirectly. PGPR colonize the rhizosphere and impose tolerance by producing different metabolites and other volatile compounds and by regulating gene expression and altering root morphology under water scarcity. PGPR influence physiology of plant in response to drought. Considerable growth in cereals has been noted in response to bacterial inoculation. PGPRs like *Azospirillum*, *Pseudomonas*, *Bacillus* and *Azotobacter* are associated with plant roots, improve shoot and root growth and drought tolerance; however, current works unveiled that PGPRs not have just stimulated the systemic tolerance to abiotic stresses but also improve nutrient uptake.

Keywords Drought · PGPR · EPS · Tolerance

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12.1 Introduction

Crop production is significantly reduced worldwide as a result of drought stress. Crop growth models calculation suggest that this matter will be harsher in the forthcoming days (Khan et al. 2018). Drought damages normal growth interrupts plant–water relation and decreases water-use efficiency. It had been reported that less precipitation and high evapotranspiration result moisture deficient condition (Mishra and Cherkauer 2010). Agriculture drought is the absence of sufficient wetness needed for growth of plants (Manivannan et al. 2008). Drought-induced reduction in growth causes significant decrease in plant biomass. The key effects of drought consist of a reduction in cell division, leaf size; stem growth and nutrient uptake (Li et al. 2009; Farooq et al. 2009). Plants need to adopt different mechanisms against drought (Khan et al. 2017). In plants, changes in response to unfriendly environmental conditions could be used while selecting drought-tolerant germplasms for better growth and productivity even under stressful unfriendly condition (Nam et al. 2001; Martínez et al. 2007). The response of the plant to various abiotic stresses fluctuates from species to species and at different organizational levels which depends on the age of the plant, the intensity of stress, and duration of stress (Chaves et al. 2002; Jaleel et al. 2008). Drought stress tolerance could be understood from plant reactions to lesser water condition (Reddy et al. 2004). Though the responses of plants to various stresses are well known, the performance of the plant under multiple stresses is scrappy. This is why it is important for plants to respond instantaneously to numerous stresses co-occurring at one time. These types of inquiries are typically not expectable from single factor study (Zhou et al. 2007). It is noted that water shortage, high rate of evapotranspiration, and intense sunlight reduces the yield 30–50% (Fathi and Tari 2016) (Fig. 12.1).

Soil inhabitant bacteria have some useful effects on soil properties and plant health. Kloepper and Schroth (1981) were the first to use the term PGPR for these

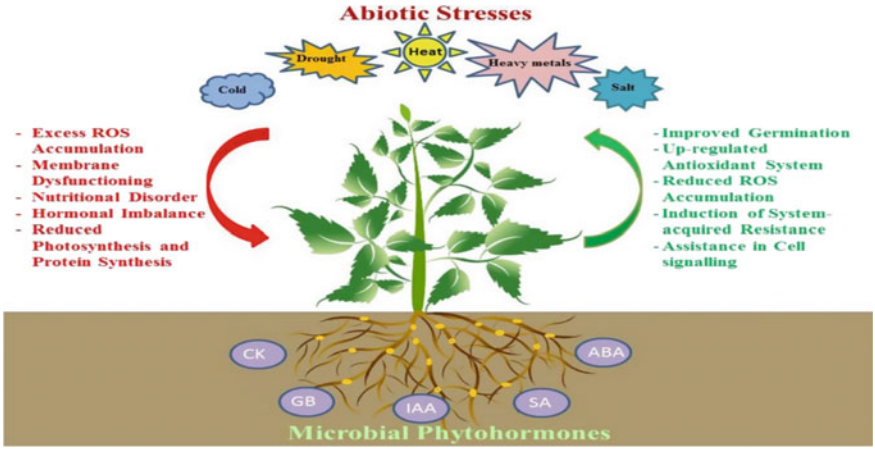

Fig. 12.1 An overview of mechanism in microbial phytohormone-mediated plant stress tolerance (Egamberdieva et al. 2008)

rhizobacteria. Whereas, the rhizosphere is the region in the vicinity of roots and an active zone for microbial activities and is of vital significance for plant health and nutrition (Nihorimbere et al. 2011). The number of rhizobacteria is relatively higher near roots than surrounding soil due to the presence of root exudates in this region (Khan and Bano 2016a). PGPR enhance plant growth and impart drought tolerance by a number of different mechanisms. PGPR improve plant growth by enhancing abiotic stress tolerance in plants, increase uptake of nutrients, production of phytohormones and ACC-deaminase activity that prevent diseases in plants (Saleem et al. 2007). PGPR have been utilized commercially (Dutta and Podile 2010) and hold great potential for sustainable agriculture. Growth-promoting potentials of PGPR have been examined in a large number of cereals (Gray and Smith 2005; Khan and Bano 2016b; Khan et al. 2017).

12.2 Effects of Drought Stress on Plant Growth and Development

Drought affects plants to the extent that impairs normal functions (Siddique et al. 2000) and brings significant changes in plant physiology and morphology (Rahdari et al. 2012). Drought stress induces a decline in growth have been examined in many crops (Samarah 2005; Kamara et al. 2003; Oh et al. 2005; Rampino et al. 2006). Drought stress adversely affects fresh weight and water content of the developing plant (Jaleel et al. 2009). Besides this it affects the accessibility and nutrient movement in soil. Therefore, drought reduces nutrient availability and diffusion (Barber et al. 2000). Free radicals like ROS are induced in plants as a result of water shortage, affecting plant growth by producing oxidative stress. The higher concentration of ROS is harmful to various plant tissues as it initiates lipid peroxidation, protein degradation, and destruction of lipids in the affected plants (Smirnoff 1993; Sgherri et al. 2000; Nair et al. 2008).

Drought coupled with high temperature reduces photosynthesis and is responsible for the continuous production of ROS that may cause plant death (Chaves et al. 2009). A surge in drought leads to the ionic condition in roots, resulting in osmotic stress and ion toxicity. In fact, with an increase in droughty period, cell-wall shriveled and gets loose, resulting poor turgor pressure which ultimately leads to decreased growth (Anjum et al. 2011; Farooq et al. 2012; Simões-Araújo et al. 2003). The continuous increase in the period of water stress, increase in the events of heat waves that enhance drought and heat stresses (Sekhon et al. 2011; Wahid et al. 2007). There are three main factors responsible for the decrease in yield by soil water deficit, i.e., reduce in plant canopy, decrease in radiation-use efficiency, and reduction in harvest index (Earl and Davis 2003). A slow pace in illuminating drought tolerance mechanism has weakened both traditional breeding efforts as well as modern genetics approaches for the development of drought-tolerant varieties (Xiong et al. 2006).

Water deficit has dominant effects on the incidence of kernel abortion in maize during pollination (Sangoi 2001). Water stress diminishes normal growth and productivity by affecting grain filling (Morgan et al. 1990; Ober et al. 1991). In cereals, filling of grains is an important step of starch biosynthesis and four enzymes, viz., sucrose synthase, adenosine diphosphate–glucose–pyrophosphorylase, starch synthase, and starch branching enzyme are known to play a key role during this process (Taiz and Zeiger 2006). It is believed that a decrease in sucrose synthetase results in a decrease in the rate of grain growth in water-stressed wheat (Ahmadi and Baker 2001). In pigeon pea and rice, drought stress concurring with the flowering stage causes a reduction by 40–55% in grain yield (Nam et al. 2001; Yang et al. 2009).

Lack of moisture results in a substantial decrease in dry matter of plant organs, though this varies from organ to organ (Asrar and Elhindi 2011). Similarly, drought greatly restricted the biomass of Asian red sage, though roots were more resistant in comparison to shoots (Liu et al. 2011; Farooq et al. 2010; Ge et al. 2006; Blum 2005). New plantation and ill-developed plants are very vulnerable to drought stress because of a limited number of developed roots and a huge mass of stems and leaves in contrast to roots. Different plant species respond differently to drought stress. For instance, maize plant responds by delaying flowering (McMaster et al. 2008), a similar response is also present in quinoa (Geerts et al. 2008) and rice (Fukai et al. 1999), whereas in other crops (soybean, wheat, etc.) drought accelerated flowering and physiological maturity (Desclaux and Roumet 1996). Under drought stress, plants modify their functions in order to curtail adverse effects and enhance existence (Thapa et al. 2011). In reaction to drying soils, plants adjust the expression of entire genome that intricate in drought tolerance, thus impart tolerance to plants experiencing stress condition (Clement et al. 2008).

12.3 PGPR and Their Mode of Action

PGPR have the ability to inhabit the rhizosphere and improve the tolerance of plants to various stresses. This is because of their ability to solubilize inorganic phosphate, produces plant hormones, siderophore, exopolysaccharides (EPS), organic acids (OA), fix atmospheric nitrogen, and control plant diseases (Muleta et al. 2013; Rani et al. 2012). A large number of bacteria species have been studied for this purpose and many of them commercialized (Vejan et al. 2016). However, they are little utilized, this is because of their inconsistency that could influence crop production. Success through PGPR inoculation greatly depends on their survival in the rhizosphere, compatibility with crop and interactions with crop and other soil micro-flora (Compant et al. 2010). Another aspect is that the mode of action, which is diverse and vary from species to species of PGPR (Siddiqui 2005). This weakness limits the advantages of PGPR. Hence, the rivalry between chemical fertilizers and biofertilizer is believed redundant in the face of the worldwide agricultural productivity necessary to nurse the growing world's population (Lelieveld et al. 2015).

PGPR have been categorized based on their actions as biofertilizers, phytostimulators, rhizoremediators, and biopesticides (Antoun and Prévost 2005; Kloepper 2003; Vessey 2003). In general, PGPR may be categorized into extracellular (ePGPR) and intracellular (iPGPR) PGPR (Figueiredo et al. 2016; Bhattacharyya and Jha 2012). Most of the iPGPR are gram-negative rod-shaped bacteria, while some are gram-positive cocci or pleomorphic (Bhattacharyya and Jha 2012). Besides, many actinomycetes are also the dominant inhabitants of rhizosphere microbial community beneficial characters (Bhattacharyya and Jha 2012; Merzaeva and Shirokikh 2010). Among them, *Streptosporangium* sp., *Micromonospora* sp., *Thermobifida* sp., and *Streptomyces* spp., which have presented huge potential as bio-control agents contrary to a variety of root fungal pathogens (Franco-Correa et al. 2010).

12.4 PGPR and Their Mechanism of Action Under Drought Stress

One alternative treatment against drought is the application of PGPR to crops as they boost plant growth and increase drought tolerance either directly or indirectly (Bashan 1998; Cassán et al. 2014). This may be due to their ability for fixation of atmospheric nitrogen, production of different plant hormones including GA, IAA, and cytokinin, solubilization of inorganic phosphate and production of exopolysaccharides and siderophores (Mayak et al. 1999). In addition, PGPR is related to catabolism of molecules linked to stress-signaling in plants (Glick et al. 2007).

The rhizosphere is inhabited by millions of different microbes that form complex interactions with the plant (Berg 2009; Schmidt et al. 2014). Plant-associated PGPR adopt itself to stressful environmental conditions and thus improve the resistant of plants towards a variety of abiotic stressors which also promote plant health and yield (Schmidt et al. 2014; Yin et al. 2018). However, this depends on the distribution of microorganisms in the rhizosphere and endosphere. Differences in the bacterial population were experiential at the rhizosphere and in the soil nearby plant roots due to root exudates (Marasco et al. 2012).

Microbiome related to roots can improve micronutrient uptake or disturb the content of phytohormones or indirectly they arouse the plant immunity against phytopathogens (Balloi et al. 2010; Rolli et al. 2015; Berg et al. 2014). ACCdeaminase producing PGPR species have the ability to lesser stress and impart tolerance against that particular stress (Lucy et al. 2004). Similarly, *Acinetobacter* and *Pseudomonas* species significantly increased the shoot and leaf biomass the photosynthetic activity even in drought-sensitive grapevine plants grown under stress condition (Rolli et al. 2015). Similar results were noted by Khan et al. (2017) for drought-sensitive chickpea genotype. PGPR, *Stenotrophomonas rhizophila* DSM14405 triggered the expression of several functional genes responsible for stress protection, energy production and for motility of cells (Alavi et al. 2013). The extremely eroded region of southern Sonoran desert had been reinstated with

leguminous plants by the application of PGPR in combination with mycorrhizal fungi and compost (Bashan et al. 2012).

ACC-deaminase-producing bacteria results in more seed yield and enhance seed size and restore the process of nodulation even under unavailability of water (Dodd et al. 2005). These bacteria effectively reduced the negative effects of moisture stress in plants grown under field and pot condition (Arshad et al. 2008). Inoculation of a pea plant with ACC-deaminase producing *P. fluorescens* caused increase root system and improved nutrient uptake under water scarcity (Zahir et al. 2008; Rossi et al. 2012), whereas *V. paradoxus* augmented growth, yield, and water-use efficiency of droughty peas (Belimov et al. 2009). This PGPR augmented the soil drying-induced surge in the abscisic acid of xylem tissues and lessened soil drying-induced rise of xylem ACC (Dodd et al. 2005; Tiemann and Billings 2011). It has been reported that nitrogen-fixing PGPR prevents drought-induced decrease in nodules formation (Belimov et al. 2009) (Fig. 12.2).

PGPR were found responsive even at the transcriptional level in *Arabidopsis thaliana* where they improved the growth and tolerance (Timmusk et al. 2011). Six newly identified stress-related proteins were reported in plants after treatment with *B. licheniformis*. Among them the genes of Cadhn, VA, sHSP, and CaPR-10 showed 1.5-fold increase in inoculated plants than control (Lim and Kim 2013). Upregulation of stress-responsive genes was noted in the inoculated wheat plants, which also alleviated the harmful effect of drought stress (Kasim et al. 2013;

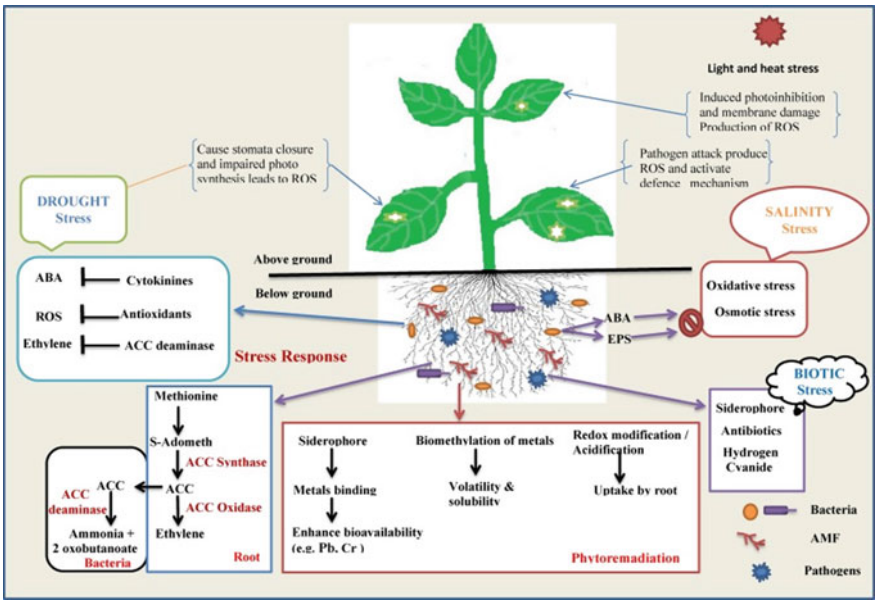

Fig. 12.2 Mechanism of action of ACC-deaminase-producing rhizobacteria for mitigating the adverse effects of drought stress (Kumar and Verma 2017)

Hecker et al. 1996). Similarly, a set of drought signaling responsive genes was downregulated in the *A. thaliana* treated with *P. chlororaphis* compared to those droughty plants lacking bacterial treatment (von Rad et al. 2008). Transcripts of the jasmonic acid (JA) marker genes were upregulated in the PGPR inoculated plants but varied in their reaction to water scarcity (Cho et al. 2013; Schimel et al. 2007).

Rhizobia are well-known mutualistic symbiotic bacteria, could create symbiotic relations with leguminous crops, and help them in fixing atmospheric nitrogen in specific root structures known as nodules. These bacteria are also equally beneficial in non-leguminous plants. Maize plants inoculated with PGPR under drought stress displayed lessen antioxidant enzyme activity as compared to un-inoculated plants (Sandhya et al. 2010; Conlin and Nelson 2007). Similarly, inoculated maize with *Bacillus* species developed resistance to drought by reducing the activities of the antioxidants (Vardharajula et al. 2011; Heidari et al. 2011; Placella et al. 2012). Reduction in the activity of apex, catalase, and GPX was noted in inoculated maize plants with EPS-producing bacteria resulting in stress tolerance in test plants (Naseem and Bano 2014). The effectivity of *B. thuringiensis* in lavender and in common sage under rainfed condition have been studied and was found a promising PGPR against drought stress (Armada et al. 2014; Gusain et al. 2015). These studies provide evidence regarding the advantageous effect of PGPR for drought tolerance in plants by altering the antioxidants activity under water-deficit conditions (Gusain et al. 2015) (Fig. 12.3).

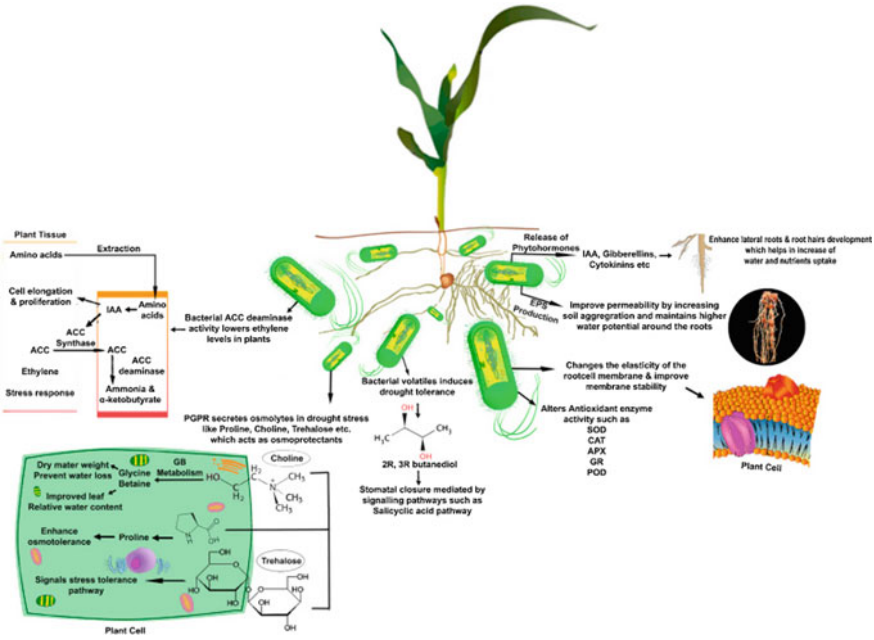

Fig. 12.3 Mechanism of plant drought tolerance induced by plant growth-promoting rhizobacteria (Dubey et al. 2019)

12.5 Conclusion

Water scarcity to the agriculture crops mainly in arid and semiarid regions decreasing crop production. PGPR are playing a significant role in the course of managing plant stresses. Enhanced production of exopolysaccharides, phytohormone, 1-aminocyclopropane- 1-carboxylate (ACC) deaminase, volatile compounds by PGPR underwent considerable increases in growth and yield of important cereals. There is recent urgent to explore the draught resistant mechanisms of PGPR to facilitate this plant protection and phytoremediation properties in order to sustain agriculture.

Conflict of Interest The author(s) have no conflict of interest.

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Chapter 13
Plant Growth Promotion and Suppression of Fungal Pathogens in Rice (*Oryza Sativa* L.) by Plant Growth-Promoting Bacteria

Hassan Etesami

Abstract Crop plants play an outstanding function in providing food and energy to humans. Rice (*Oryza sativa* L.) is one of the most important stable crops that have a role in providing the main food to more than half of the world's people. One of the important factors in increasing yield in rice is the balanced nutrition or supply of the required nutrients in the proper form and ratios. Chemical fertilizers are essential components of modern agriculture by providing essential plant nutrients. However, the overuse of these fertilizers causes serious environmental pollution. But threats of plant pathogens on the attack and damages on the crop productivity cannot be ruled out. Therefore, chemical-based pesticides are thought to be an effective and trustworthy agricultural management measure for repressing pests. Nowadays, the use of beneficial microorganisms and biological control agents are proved as good as synthetic pure/chemicals for the increased plant growth and yield. The diminished utilization of chemical fertilizers for the management of plant pathogens is considered as a secure and maintainable strategy for safe and rewarding agricultural productivity. Based on research conducted until this moment, rice-associated bacteria are encouraging alternatives to chemical fertilizers in an eco-friendly manner. In general, the application of plant growth-promoting bacteria (PGPB) could offer a cheaper and cost-effective approach to overcome the environmental problems caused by chemical fertilizers and their use in the form of biofertilizers and biopesticides could decrease our reliance on synthetic agrochemicals. This chapter highlights the importance of PGPB for enhancing sustainable rice production.

Keywords Sustainable agriculture · Biocontrol agents · PGPR · Biofertilizer · Co-inoculation

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13.1 Introduction

Cereals are the main source of nutrition for human beings in the world. Among the cereals, rice (*Oryza sativa* L.) is of great importance. Rice is a staple food in food diet over 40% of the world's population, especially, in Asia (Naureen et al. 2009a). Of the total energy produced by cereals per person per day, more of it is related to rice. This has made rice as the most important food product in developing countries. According to statistics, the world's rice cultivation area in 2009 was 153 million hectares, with a production of 585 million tons, which should increase to 800 million tons in 2025. In other words, in order to meet the food needs of this growing population, an increase of 70% in rice production is needed over the next few years. Rice is mostly produced in countries, whose population are growing rapidly and often are limited in terms of land and resources. Therefore, given the limiting factors of production (including decreasing the quality and quantity of agricultural land, reducing water resources and labor shortage), the only rational solution is to increase the yield of rice per unit area of land cultivation or use of high-yielding rice varieties to meet the demand for rice demanded in 2025 (Mishra et al. 2006). However, the use of these varieties requires extensive application of fertilizers such as nitrogen (N) and phosphorus (P) (Hazell 2010). Some of the main constraints on the growth of this crop can be inadequate fertilizer use, pest infestation, and growing of low-yielding traditional varieties, and paucity of water (Datta et al. 2017). In general, one of the most important factors in increasing the rice yield is the balanced nutrition or the supply of essential nutrients. Low-soil fertility is the most important factor which not only seriously affects the rice production but also reduces the quality of the rice (Vaid et al. 2014).

Chemical fertilizers are essential components of modern agriculture due to the provision of essential plant elements. However, the excessive use of these chemical fertilizers for greater production of crop plants including rice can cause unpredictable environmental impacts including leaching and runoff of nutrients, especially N and P, leading to environmental degradation (deterioration in air and water quality) (Gyaneshwar et al. 2002). In addition to essential nutrients, diseases are also among the most significant limiting factors that affect rice production, causing annual yield losses conservatively estimated at five percent (Song and Goodman 2001).

In agricultural systems, the utilization of plant growth-promoting bacteria (PGPB) is of particular consequence in augmenting crop production and preserving sustainable soil fertility (Bagyaraj and Balakrishna 2012). In the past decade, the use of PGPB as a biofertilizer or biological control agent in agriculture has been considered by many researchers. The growth of different crops by these bacteria has been proved in greenhouse and field experiments. Most studies show that these bacteria could have positive and economic effects on crop plants such as corn, wheat, and rice (Freitas and Germida 1990; Çakmakçı et al. 2007; Etesami et al. 2013, 2014a, c, 2015; Ghorchiani et al. 2018; Etesami and Maheshwari 2018) by mechanisms like increasing the availability of soil mineral elements (i.e., through

solubilizing insoluble P compounds and potassium (K)-bearing minerals and releasing P and K), producing plant growth-regulating hormones (i.e., indole-3-acetic acid, gibberellin, and cytokinin) and siderophores (increase in availability of Fe, Zn, etc.), producing ACC (1-aminocyclopropane-1-carboxylate) deaminase (decrease of stress ethylene), controlling pathogenic microorganisms (Etesami et al. 2017; Etesami and Maheshwari 2018), and nitrogen fixation (Bhattacharjee et al. 2008; Saharan and Nehra 2011).

It has been well proven that PGPB could increase plant growth and resistance to environmental stresses (Fig. 13.1) such as salinity (Dimkpa et al. 2009; Egamberdieva and Lugtenberg 2014; Paul and Lade 2014; Choudhary et al. 2016; Qin et al. 2016), drought (Timmusk et al. 2013; Choudhary et al. 2016; Kaushal and Wani 2016; Ngumbi and Kloepper 2016), heavy metal toxicity (Carmen and Roberto 2011; Sessitsch et al. 2013; Ullah et al. 2015), nutritional imbalance (Adesemoye and Kloepper 2009; Yang et al. 2009; Miransari 2013; Chakraborty et al. 2015; Pii et al. 2015; Choudhary et al. 2016), and plant pathogens (bacterium, virus, fungi, etc.) (Compant et al. 2005; Pal and Gardener 2006; Ryan et al. 2008) via miscellaneous mechanisms usually more than one action mechanism (Etesami and Maheshwari 2018). Despite these good reviews, there are a few review studies on PGPB-mediated nutrient availability and biological control of fungal pathogens in rice. Better understanding on interactions of rice with the plant-associated PGPB enhanced nutrient acquisition and controlled fungal rice pathogens is needed for increasing the efficiency of nutrient management and rice disease management in soil and also for promoting eco-friendly low-input sustainable agriculture. Therefore, the aim of this chapter was to reviews advances in research on PGPB

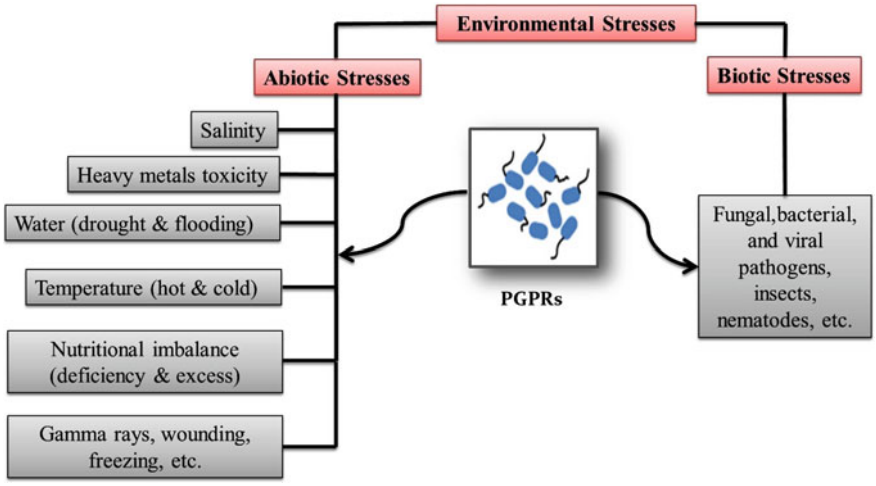

Fig. 13.1 Common abiotic and biotic stresses in agricultural environments alleviated by PGPR

capable of increasing the availability of soil insoluble nutrients, their mechanism of action, and their potential use for biofertilization of nutrients in rice and biological control of fungal rice pathogens (Table 13.1).

13.2 Nitrogen-Fixing Bacteria (NFB) in Nitrogen Nutrition

Nitrogen (N) is an important element in the plant and a component of chlorophyll molecules and therefore plays an important role in photosynthesis and in the production of proteins, nucleic acids, and coenzymes. Chemical N-fertilizers are one of the most influential factors in the production and yield of rice. Without the addition of chemical N-fertilizers, the yield of existing varieties is severely limited (Ladha et al. 1997). The excessive use of the chemical fertilizers for greater production of this crop has caused unpredictable environmental impacts. Currently, most of the N-fertilizers are produced through the Haber–Bosch process at chemical fertilizer factories. This process requires a large amount of energy (natural gas or oil), all of which are nonrenewable sources. It also generates carbon dioxide (CO_2), which is a greenhouse gas. In developing countries, the cost of purchasing N-fertilizers is usually higher than farmers' income, which limits yield potential of their crops. Approximately one-third of the applied N (urea-N or nitrate-N, which is applied as fertilizer) is consumed by the plant; the rest of the N can enter as nitrate form into underground waters and are a potential hazard to environmental health. Excess N can also produce nitrous oxide (N_2O), an effective greenhouse gas. In addition, since rice grows in an environment susceptible to N loss, more than half of the N-fertilizer used in the paddies is lost through denitrification, ammonia volatilization, and leaching/runoff (Ladha et al. 1997).

In general, the agrosystems that require a lot of N-fertilizers are not sustainable systems because they require the use of nonrenewable natural resources and can endanger the health and the environment (Yanni and Dazzo 2010). Reducing the amount of industrial N production for agricultural systems is one of the important goals of agricultural researchers. In the case of sustainable rice production, an important goal is to replace the industrial N fixation to biological N fixation (Yanni et al. 2001). Two basic ways to solve the problem of N-fertilizer loss in paddy fields can be proposed: One is the regulation of N application time based on rice needs, which increases the efficiency of plant use of applied N and another way is to increase the ability of the rice to biological nitrogen fixation. The second approach is a long-term strategy, but it has multiple environmental benefits and also helps low-income farmers. Additionally, farmers can easily adopt a variety of genotypes with useful features rather than conducting soil and crop management operations that are costly (Ladha et al. 1997).

Recent advances in understanding the legume–rhizobium–symbiotic relationships at the molecular level and the ability to introduce new genes into the rice

Table 13.1 Potential of rice-associated bacteria in controlling some important fungal rice pathogens

Biocontrol PGPB	Pathogenic fungi	Effect	References
Streptomyces sp., *Pseudomonas* sp., *Ochrobactrum anthropic, Bacillus firmus*, *Pseudomonas aureofaciens,* and *Kocuria rhizophila*	*Alternaria* sp., *Fusarium oxysporum*, *Pyricularia oryzae* and *Sclerotium* sp.	In dual-culture technique, the siderophore-producing rhizobacteria showed a strong antagonistic effect against the *Alternaria* (35.4%), *F. oxysporum* (37.5%), *P. oryzae* (31.2%), and *Sclerotium* sp. (10.4%)	Chaiharn and Lumyong (2011)
Streptomyces globisporus	*Magnaporthe oryzae*	*S. globisporus* inhibited mycelial growth of *M. oryzae*, and histological investigations showed that conidial germination and appressorial formation of *M. oryzae* were suppressed on detached rice leaves. This bacterium could suppress disease incidence of rice blast caused by *M. oryzae*	Li et al. (2011)
Streptomyces sindeneusis	*Magnaporthe oryzae*	*S. sindeneusis* resulted in strong inhibition of the pathogen and suppression of leaf symptoms	Zarandi et al. (2009)
Streptomyces flavotricini	*Magnaporthe oryzae*	*S. flavotricini* showed the strongest antifungal activity against *M. oryzae;* the antifungal compound produced by *S. flavotricini* was successfully purified and identified as dihydroxy viridiofungin (C37H58N2O10)	Khalil et al. (2014)
Bacillus methylotrophicus BC79	*Magnaporthe oryzae*	This bacterial strain showed the highest efficiency for *M. oryzae*, with 84.8% biocontrol effect	Shan et al. (2013)

(continued)

Table 13.1 (continued)

Biocontrol PGPB	Pathogenic fungi	Effect	References
Bacillus spp.	*Rhizoctonia solani, Sclerotium rolfsii,* and *Sclerotium oryzae*	All *Bacillus* strains showed strongly inhibited (up to 90%) the growth of phytopathogens, were capable of enhancing the vegetative growth and yield parameters (shoot/root length, biomass, chlorophyll content and yield), and showed significant increase than non-inoculated control plants	Sethi and Mukherjee (2018)
Bacillus mojavensis, B. amyloliquefaciens, B. subtilis, and B. cereus	*Magnaporthe oryzae, M. salvinii, Fusarium verticillioides, F. fujikuroi,* and *F. proliferum*	These bacterial strains exhibited significant antifungal activity against these pathogens, with 70–90% inhibition of mycelial growth	Etesami and Alikhani (2017), Etesami and Alikhani (2016a), Etesami et al. (2014a),
Streptomyces sp. UPMRS4	*Pyricularia oryzae*	This bacterial strain was able to reduce 67.9% of disease severity and able to increase shoot height (15.13%), shoot dry weight (45.75%), leaf surface area (44.6%), root length (48.93), root dry weight (63.25%), number of tillers (42.26%), yield (36.96%), panicle length (15.4%), and the number of spikelet/panicles (29.39%) compared to the control plants at 3 months after inoculation	Awla et al. (2017)
Streptomyces philanthi RM-1-138	*Magnaporthe oryzae*	This bacterial strain exhibited significant antifungal activity against *M. oryzae* (*P. oryzae* PTRRC-18), with 88.73% inhibition of mycelial growth of the rice blast fungus	Boukaew and Prasertsan (2014)

(continued)

Table 13.1 (continued)

Biocontrol PGPB	Pathogenic fungi	Effect	References
Streptomyces philanthi RM-1-138	*Rhizoctonia solani, Pyricularia grisea*, *Bipolaris oryzae*, and *Fusarium fujikuroi*	Volatile organic compounds (VOCs) produced by *S. philanthi* inhibited mycelial growth of the rice pathogenic fungi. The inhibition was most pronounced on *R. solani* while the least inhibition was against *F. fujikuroi*	Boukaew et al. (2013)
Streptomyces vinaceusdrappus	*Magnaporthe oryzae, Curvularia oryzae, Bipolaris oryzae,* and *Fusarium oxysporum*	*S. vinaceusdrappus* showed maximal antagonistic activity against fungal pathogens *Curvularia oryzae*, *Bipolaris oryzae*, and *Fusarium oxysporum*. *S. vinaceusdrappus* inhibited the mycelial growth of P. oryzae by 53.5%, which was relatively good since more than 50% of the mycelial growth was inhibited	Ningthoujam et al. (2009)
P. fluorescens Aur6 and *Chryseobacterium balustinum* Aur9	*Magnaporte grisea*	Each strain individually protected rice against rice blast, but the combination of both strains was the most effective treatment (reaching 50% of protection against disease). A relation between protection and increase in rice productivity and quality was found	Lucas et al. (2009)
Streptomyces corchorusii UCR3-16	*Bipolaris oryzae, Pyricularia oryzae, Rhizoctonia solani, Rhizoctonia oryzae-sativae, Fusarium oxysporum,* and *Curvularia oryzae*	This bacterial strain exhibited significant biocontrol potential against rice fungal pathogens showing the highest inhibition against *Rhizoctonia solani*. The strain could significantly enhance the growth and grain yield production of rice plants under pot conditions	Tamreihao et al. (2016)

genome by transformation have made it an excellent opportunity to study the ability of N fixation in rice, although this has remained largely unfinished until now (Dawe 2000). There are such opportunities for cereals including rice. In general, the strategies enabling rice to fix nitrogen are complex and have a long-term nature, but if done, they can increase rice productivity, resource conservation, and environmental security. In addition to the strategies mentioned above, it has been well known that the use of nitrogen fixation technology can reduce the use of N-fertilizers in agricultural land, which can be effective at reducing environmental hazards. Biological nitrogen fixation in rice paddies has significantly contributed to the sustainable yield of these systems. Studies show that biological nitrogen fixation in rice paddies can produce up to 50 kg N per hectare (Elbeltagy et al. 2001). It has been well known that nitrogen fixation through the bacteria associated with rice (associative and free-living bacteria) has a high potential for supply of N for rice. For example, in a study, Mäder et al. (2011) observed an increase of 23% in rice yield obtained upon rice inoculation with N_2-fixing *Pseudomonas* sp. In another study, the co-inoculation of N_2-fixing bacteria (i.e., *Brevundimonas diminuta* PR7, *Anabaena oscillarioides* CR3, and *Ochrobactrum anthropi* PR10) remarkably augmented N, P, and K content and bettered rice yield by 21.2%, as compared to the utilization of recommended quantity of N, P, and K fertilizers (Rana et al. 2015). Due to having a very close relationship with the plant, as compared to other bacteria, endophytic bacteria can offer the fixed N to rice without its loss.

Endophyte bacteria seem to be more effective at supplying rice with N than other bacteria. The bacteria isolated from the internal tissues of the plant or isolated from the plants with sterilized surfaces that do not show any symptoms of the disease are regarded as endophytic bacteria (Di Fiore and Del Gallo 1995). It is well documented that a significant diversity of endophytic bacteria such as *Pantoea*, *Burkholderia, Azospirillum, Herbaspirillum, Rhizobium, Methylobacterium*, etc., is naturally associated with rice (Carvalho et al. 2014; Mano and Morisaki 2008). Diazotrophs that effectively colonized into rice roots can have a greater potential for N fixation. It has been reported that the contribution of endorhizosphere bacteria to N fixation is much more extensive than the contribution of rhizospheric bacteria because there is no competition in the endorhizosphere with other rhizosphere microorganisms, and carbon sources with low-pressure oxygen oscillations are provided (James et al. 2002). Several endophytic N_2-fixing bacteria have been isolated from various rice species including the genera *Klebsiella, Citrobacter, Enterobacter, Bacillus, Alcaligenes, Azospirillum, Rhizobium, Sphingomonas, Agrobacterium, Corynebacterium, Herbaspirillum, Azoarcus, Penibacillus, Microbacterium,* and *Burkholderia* (Reinhold-Hurek et al. 2007; Prayitno and Rolfe 2010; Yanni and Dazzo 2010; Gupta et al. 2012; Hongrittipun et al. 2014; Ji et al. 2014).

It has been found that the stimulation of growth of the crop plants (such as rice) inoculated with N_2-fixing bacteria may be due to other mechanisms like increasing the availability of soil mineral elements, producing plant growth-regulating hormones, siderophores, and ACC deaminase, and controlling pathogenic microorganisms (Etesami et al. 2017; Etesami and Maheshwari 2018) other than nitrogen

fixation (Bhattacharjee et al. 2008; Saharan and Nehra 2011). For example, previous studies have shown that nitrogen accumulation in inoculated non-leguminous plants can be due to either biological N fixation (Elbeltagy et al. 2001; Oliveira et al. 2002) or escalation in nitrogen uptake from soil (Prayitno et al. 1999; Yanni et al. 1997). In another study, Etesami and Alikhani (2016a) showed that bacterial IAA had considerable role in improving use efficiency of N and could increase N content of rice. In other works, Estrada et al. (2013) showed that P-solubilizing diazotrophic bacteria augmented nutrient uptake by rice plants. de Souza et al. (2013) showed that the bacteria (e.g., *Herbaspirillum* sp., *Burkholderia* sp., *Burkholderia* sp., *Pseudacidovorax* sp., and *Rhizobium* sp.) unable to solubilize phosphate in in vitro assay and reduce acetylene (low capacity to reduce acetylene) increased levels of N, P, and K in rice shoots. These observations could indicate that growth promotion mechanisms other than N_2 fixation such as IAA production and improved nutrient uptake balance (de Souza et al. 2013; Ji et al. 2014). The above studies show that if the purpose of rice inoculation with bacteria is to supply nitrogen to the plant, it is better to use nitrogen-fixing bacteria that have other PGP characteristics (such as IAA, ACC deaminase, siderophores, and phosphate solubilization) as well.

13.3 Phosphate-Solubilizing Bacteria (PSB) in Phosphorus Nutrition

After nitrogen (N), phosphorus (P), as a necessary nutrient and a macronutrient, is the most restricting nutrient for the plant (Schachtman et al. 1998; Theodorou and Plaxton 1993). Phosphorus plays several key roles in the plant, including participation in energy transfer reactions, photosynthesis, deformation of sugar into starch, key enzymatic reactions in important metabolic and signaling pathways, and transference of genetic characteristics in plants (Theodorou and Plaxton 1993). There has been an enduring increment in the application of P fertilizers in rice production (Syers et al. 2008) because it is one of the main restricting factors for upland rice production in many regions of the world (Sahrawat et al. 2001). Since water scarcity is becoming a major problem for agriculture, there is a pressing need to cultivate aerobic rice. Aerobic rice requires the same amount of nutrients as flooded rice, but there is a problem of P availability due to its rapid immobilization/fixation with elements such as calcium (Ca^{2+}), iron (Fe^{3+}), and aluminum (Al^{3+}) (Goldstein 1986; Othman and Panhwar 2014). The previous findings also suggest that P deficiency in aerobic crops is quite common (Fageria 2001).

Phosphorus is the most sensitive nutrient to soil pH. The best pH for P uptake by the plant is 6.5. In alkaline condition, P becomes insoluble by reacting with calcium (Ca^{2+}), whereas in acidic soils, it reacts with iron (Fe^{3+}) and aluminum (Al^{3+}) and becomes unavailable to the plants. The amount of P absorbed by the plant in the soil is controlled by several factors such as soil pH, calcium ion concentration, soil

organic matter, clay type, and clay amount, root density and exudates, and soil moisture and texture. In order to compensate for the shortage of P, large amounts of P fertilizers are added to the soil annually. The excessive use of P fertilizers and the subsequent accumulation of P in the soil, in addition to increasing costs, have a negative effect on uptake of micronutrients and also contribute to environmental pollution (e.g., eutrophication).

The majority of P fertilizers are adsorbed by solid particles and stored in a solid phase of soil. Most of the P in the fertilizer, after entering the soil, gradually turns into insoluble compounds and is stored as plant unavailable forms in the soil (Dey 1988). It has been reported that the P fertilizer use efficiency in calcareous and alkaline soils does not exceed 20%. The P mobility in the soil is very low and cannot respond to the rapid absorption of the plant. This leads to the emergence and development of phosphate-depleted areas adjacent to the contact surface of roots with soil. Under P-deficient conditions, by modifying root morphology, carbon metabolism; membrane structure, exudation of organic acids, protons, and enzymes; and association with mycorrhizal fungi, and harboring phosphate-solubilizing microorganisms (PSM), some plants have been able to somehow compensate for their lack of P (uptake of adequate P) (Begum and Islam 2005; Islam and Hossain 2012). Among these strategies, secretion of organic acids and association of mycorrhizal fungi are very poor in rice under flooding conditions (Begum et al. 2005; Islam and Hossain 2012). Therefore, the rice plants need an auxiliary system that can easily go beyond these depleted areas and, by developing a wide network around the root system, receive P from an exorbitant volume of adjoining soil.

PGPB such as phosphate-solubilizing bacteria (PSB) are considered to be the most effective plant assistants for the supply of P at the optimal level and seems to be another manner for P nutrition in rice under P-insufficient tropical soils (Islam and Hossain 2012). PSB have been able to dissolve insoluble phosphates through a set of mechanisms such as production of low-molecular-weight organic acids (i.e., gluconic, oxalic, 2-ketogluconic, citric, succinic, lactic, and malic), inorganic acids, siderophores, and exopolysaccharides (EPS), and secretion of hydrolytic enzymes (e.g., phosphatases and phytases, which convert the organic forms of P into P inorganic forms, and thereby increase plant growth under conditions of P deficiency) (Khan et al. 2007, 2014; Sharma et al. 2013). PSB have the ability to dissolve inorganic P in a range of 25–42 μg P ml^{-1} and organic P between 8 and 18 μg P ml^{-1} (Guang-Can et al. 2008). *Agrobacterium, Pseudomonas, Bacillus, Rhizobium, Flavobacterium, Acinetobacter, Micrococcus, Burkholderia, Achromobacter, Erwinia, Pantoea,* and *Streptomyces* are of the most important bacterial genera of solubilizing insoluble phosphates (Khan et al. 2007, 2014; Sharma et al. 2013).

In addition to improving soil P status, members of the bacterial genera such as *Burkholderia, Pseudomonas, Bacillus, Streptomyces,* and *Pantoea* could also suppress soil-borne pathogens (Islam and Hossain 2012; Rodríguez and Fraga 1999). PSB, which form less than one percent total bacterial populations in the soils (Kucey 1983), have been isolated from approximately all agricultural soils (both

fertile soils and P-deficient ones) (Oehl et al. 2001). Previous studies show that rhizosphere and endorhiza of rice plants also harbor the bacteria with a good potential for solubilizing insoluble phosphates such as *Bacillus* spp., *Pantoea agglomerans*, *Streptomyces anthocysnicus*, *Pseudomonas pieketti*, *P. aeroginosa, Acinetobacter* sp., *Klebsiella* sp., *Acinetobacter* sp., *Enterobacter* sp., *Microbacterium* sp., *Pseudomonas* sp., *B. megaterium, B. firmus, Erwinia, Serratia,* and *Staphylococcus epidermidis* (Etesami et al. 2014a; Islam and Hossain 2012; Naik et al. 2008; Panhwar et al. 2011a; Sapsirisopa et al. 2009; Thakuria et al. 2004; Zeng et al. 2012). Previous studies show that PSB alone or in combination with varying doses of P fertilizers could also increase soil available P and P content in the rice plant tissue (Duarah et al. 2011; Othman and Panhwar 2014; Panhwar et al. 2011a, b, 2013). There are reports that PSB also have the ability to increase the efficiency of P fertilizer and diminish about 25–50% of the required P to plants (Attia et al. 2009; Islam and Hossain 2012; Yildirim et al. 2011). In addition to increasing the efficiency of P fertilizer, PSB also increased total N, K, Ca, S, P, Mg, Fe, Mn, Zn, and Cu contents in plant tissues (Duarah et al. 2011; Gyaneshwar et al. 2002; Islam and Hossain 2012; Yildirim et al. 2011).

It is well known that PSB can increase plant seed germination (Duarah et al. 2011; Sapsirisopa et al. 2009), plant growth and development (i.e., augmented leaf chlorophyll content, leaf area index, tiller numbers, plant height, photosynthesis rate, root morphology, and plant biomass of aerobic rice genotypes) (Duarah et al. 2011; Panhwar et al. 2011a, b), and plant yield and quality (Islam and Hossain 2012), through other mechanisms such as phytohormone production, nitrogen fixation, urease activity, siderophore production, ACC deaminase, and/or antagonisms against phytopathogens, in addition to by solubilizing insoluble phosphates (Islam and Hossain 2012). In general, the above studies show that PSB have been found to have the ability to solubilize P in soil and could reduce fertilizers inputs in rice fields.

13.4 Plant Growth-Promoting Bacteria (PGPB) in Micronutrient Nutrition

Similar to macronutrients, micronutrients are also required for optimum plant growth. Micronutrient deficiencies are omnipresent (Das 2014). For example, 50% of world cereal soils are deficient in zinc (Zn) and 30% of cultivated soils globally are deficient in iron (Fe). Fe deficiency is common in upland, high pH, and aerobic soil due to the low solubility of the oxidized ferric form in aerobic environments (Das 2014; Samaranayake et al. 2012; Zuo and Zhang 2011). Rice is also substantially deficient in Fe (Bouis and Welch 2010). Toxicity of Fe is one of the major constraints to lowland rice production (Das 2014). Manganese (Mn) deficiency is also very common in upland rice (Das 2014). In general, micronutrients-deficient

soils hamper the growth of many plants including staple foods such as wheat, rice, corn and sugarcane (Kamran et al. 2017).

Use of micronutrients fertilizers may not be cost-effective in alleviating deficiency of these nutrients and increasing yield of these crop plants. It has been known that bacteria can cause a substantial increase in concentration of micronutrients in crop plants (Etesami and Maheshwari 2018) including in rice grains (Mäder et al. 2011; Pooniya et al. 2012) through various mechanisms such as acidification, production of organic acids/organic anions in soil, which sequester the cations of micronutrients and decrease the pH of the adjacent soil as well as chelate micronutrients and enhance the solubility of these nutrients, and production of siderophores, which mainly form the complexes with Fe(III) (Alexander 1977; Etesami and Maheshwari 2018; Jones and Darrah 1994; Kamran et al. 2017; Saravanan et al. 2007). For example, Zn-solubilizing bacteria such as *Pseudomonas fragi*, *Pantoea dispersa*, *Pantoea agglomerans*, *E. cloacae,* and *Rhizobium* sp. are potential alternatives for Zn supplementation and convert applied inorganic Zn to available forms (Kamran et al. 2017). In a study, Vaid et al. (2014) showed that Zn-solubilizing *Burkholderia* and *Acinetobacter* caused significant increase in productive tillers per plant (15.1%), number of panicles per plant (13.3%), total Zn uptake of rice (52.5%), the mean dry matter-yield per pot (12.9%), yield of straw (12.4%), yield of grain (17.0%), and number of grains per panicle (12.8%) relative to rice plants non-inoculated with the bacterial isolates in a Zn-deficient soil. It was reported that this increment might be due to solubilization of insoluble soil Zn via generating gluconic acid by these bacteria. In another study, co-inoculation of rice with *Providencia* sp. PR3, *Brevundimonas diminuta* PR7, and *Ochrobactrum anthropi* PR10 recorded an increment of 13–16% in Fe, Zn, Cu, and Mn concentrations, respectively, in rice grains (Rana et al. 2015). Adak et al. (2016) also observed 13–46% enhancement of Fe and 15–41% enhancement of Zn in rice grains through the use of cyanobacterial inoculants, under different modes of rice cultivation. The above studies indicate the potential of the PGPB associated with rice to be used as biofertilizer and overcome deficiency of micronutrients.

13.5 Silicate-Solubilizing Bacteria (SSB) in Silicon Nutrition

Silicon (Si) is known as the second most copious element in soils (Epstein 1994). Utilization of Si is known as an ecologically congenial and environmentally friendly technique to augment plant growth, attenuate miscellaneous environmental stresses (i.e., nutritional imbalance, salinity, drought, heavy metal toxicity, and pathogens) in plants, and enhance the plant resistance to multiple stresses (Etesami and Jeong 2018). Despite these benefits, Si is still not classified as an essential element but considered as a beneficial element. This element is useful for some plants such as monocotyledons and *Poaceae* species (Etesami and Jeong 2018; Epstein 1999; Ma et al. 2007). Rice is one of the plants that accumulate this element

(a Si-accumulator/a siliceous plant-containing Si up to 10% in shoots on a dry weight basis) and requires high Si content (a high Si-accumulating crop) (Ma and Takahashi 2002). Rice is known that the escalation in its yield per unit area is connected with Si depletion, which is a matter of concern (Savant et al. 1997). Due to being removed from the soil to produce every 100 kg brown rice (about 20 kg/hm^2 SiO_2) (Ma and Takahashi 2002), being exported from fields by removing straw residues with the harvest by farmers, and being connived the exogenous use of Si in rice cultivation, plant accessible Si in paddy fields is usually low (Cuong et al. 2017; Etesami and Jeong 2018; Ma and Takahashi 2002). This suggests that Si may become a yield-limiting element for rice production and its exogenous application may be necessary to Si-deficient paddy soil for an economic and sustainable rice production system (both high rice yield and disease resistance) (Bocharnikova et al. 2010; Ning et al. 2014). At the present time, Si-fertilizers are exerted in many countries for augmenting rice yield (Guntzer et al. 2012). In previous studies, the positive effects of Si on rice growth and yield have been reported (Detmann et al. 2012; Gerami et al. 2013; Etesami and Jeong 2018; Jawahar and Vaiyapuri 2013; Lavinsky et al. 2016; Liang et al. 1994; Pati et al. 2016; Prakash et al. 2011; Singh et al. 2005). For example, in a study, Cuong et al. (2017) showed that application of Si in combination with the recommended dose of N, P, and K fertilizers positively affected agronomic and yield-related traits, yield and nutrient uptakes of rice. Si had also beneficial effects on disease resistance of rice (i.e., brown spot caused by the fungus *Bipolaris oryzae*, rice blast caused by the fungus *Pyricularia grisea*, and sheath blight caused by *Rhizoctonia solani* Kuhn, which are becoming more severe on rice plants are grown in Si-depleted soils) (Abed-Ashtiani et al. 2012; Ashtiani et al. 2012; Cacique et al. 2012; Dallagnol et al. 2014; Fauteux et al. 2005; Hayasaka et al. 2005; Ning et al. 2014; Prabhu et al. 2001; Rodrigues and Datnoff 2005; Sakr 2016; Song et al. 2016; Van Bockhaven 2014) by various mechanisms such as maintaining mesophyll cells relatively intact, increasing the thickness of silicon layer, enhancing physiological or induced resistance to fungal colonization (Si acts as a modulator of host resistance to pathogen), depositing in host cell walls and papillae sites, which is the first physical barricade for fungal penetration (Ning et al. 2014), and accumulating phenolics and phytoalexins as well as with the activation of some PR-genes (Rodrigues and Datnoff 2005).

There are some bacteria like *Bacillus globisporus, B. mucilaginosus, B. flexus, B. megaterium, Burkholderia eburnean*, and *Pseudomonas fluorescens* that can mobilize K and Si from silicate minerals (i.e., feldspar, muscovite, and biotite) (Kang et al. 2017; Naureen et al. 2015a; Sheng et al. 2008; Vasanthi et al. 2018; Vijayapriya and Muthukkaruppan 2010) by various mechanisms such as producing excess proton, organic ligands, organic acids (i.e., gluconic acid), hydroxyl anion, extracellular EPS, and enzymes (Meena et al. 2014). Inoculation of rice with silicate-solubilizing bacteria (SSB) also caused a significant increase in growth and yield of this plant. In a study (Kang et al. 2017), when combined with silica fertilization, soil inoculation with *Burkholderia eburnean* CS4-2 promoted all rice growth attributes over those of the water-treated (control) and insoluble

silica-fertilized plants. In addition to solubilizing Si, K, and P (e.g., by competing with P fixation sites in soil and decreasing the availability of Fe and Mn in plants) (Kannan and Raj 1998; Sahebi et al. 2015), SSB were also capable of controlling the growth of fungal pathogens such as *Magnaporthae grisae, Rhizoctonia solani, Altarnaria alternata,* and *Macrophomina pheasolina* (Naureen et al. 2015a). In addition to the role of Si in increasing rice resistance to pathogens, SSB can antagonize fungal pathogens by the production of hydrolytic enzymes, HCN (hydrogen cyanide), siderophores, and antibiotics (Hassan et al. 2010; Naureen et al. 2015b, 2009b). In a previous study (Vijayapriya and Muthukkaruppan 2010), *B. mucilaginosus*, which was efficient in silicate solubilization, showed antagonistic activity against *Pyricularia oryzae*. The above studies indicate the potential of SSB to be used as biofertilizer for overcoming Si deficiency and as biocontrol agents for controlling fungal rice pathogens.

13.6 Combined Use of PGPB and Chemical Fertilizers for Rice Production

Application of biological fertilizers, in particular, GPGB, combined with the use of fertilizers, is the most important integrated plant nutrition strategy for sustainable agricultural management and increasing their production in a sustainable agricultural system with sufficient input (Bagyaraj and Balakrishna 2012; Etesami and Alikhani 2016b).

Beneficial effects of PGPB in increasing nutrient uptake by rice, including NPK uptake, have been reported in previous studies (Adesemoye and Kloepper 2009; Adesemoye et al. 2009; Biswas et al. 2000; Duarah et al. 2011; Etesami and Alikhani 2016a; Vessey 2003). It has been reported that the PGPB can diminish the exertion of chemical fertilizers without compromising with the growth and yield of rice under nutrient-poor soil conditions (Etesami and Alikhani 2016a; Khan et al. 2017). In a study, Etesami and Alikhani (2016a) showed that co-inoculation with endophytic (*Pseudomonas putida* REN5) and rhizosphere (*Pseudomonas fluorescens* REN1) bacteria can reduce application rates of N-fertilizer up to 25% for rice plant. These researchers showed that the compound application of *P. putida* REN5 and *P. fluorescens* REN1 and nitrogen fertilizer levels (50, 75, and 100% of the recommended N-fertilizer rate) compared to the application of these bacterial isolates with minimum nitrogen fertilizer (25% of the recommended N-fertilizer rate) and or control (25% of the recommended N-fertilizer rate) significantly increased the rice growth indices. It was found that 75% of the recommended fertilizer rate was the minimum level to diminish N-fertilizer. This indicates that nitrogen plays a key role in the growth of the rice plant, and the plant's yield decreases without the presence of nitrogen. de Souza et al. (2013, 2016) showed that rice plants inoculated with bacterial strains (*Herbaspirillum* sp. AG15, *Herbaspirillum* sp. AC32, *Pseudacidovorax* sp. AC32, *Burkholderia* sp. CA21,

Azospirillum sp. UR51, and *Rhizobium* sp. UR51), which were isolated from rice rhizosphere, with 50% of the recommended N-fertilizer rate achieved growth indices (i.e., shoot length and dry matter, the number of panicles, and plant yields) similar to those that received the full-fertilization dose without inoculation. Other researchers also confirmed that single PGPR or combinations of PGPR promoted the growth of rice, increased plant height, dry shoot matter, N, P, and K uptake and grain production even when the recommended amount of nitrogen fertilizer was reduced in half (Biswas et al. 2000; Duarah et al. 2011; Khorshidi et al. 2011; Yanni and Dazzo 2010). In addition, rice plants inoculated with these bacterial strains supplemented with 50% N fertilizer accumulated a higher amount of N and P than those that received 100% of N fertilizer alone (de Souza et al. 2016). Khan et al. (2017) also inoculated rice with *Burkholderia* sp. BRRh-4 and *Pseudomonas aeruginosa* BRRh-5 along with 50% of recommended N, P, and K fertilizers. Both bacterial strains generated equivalent or higher grain yield of rice relative to the control—plants grown with full recommended—fertilizer doses. The above studies show that PGPB can interact with rice plant under different nitrogen fertilizer levels, but this interaction can be much more productive when plants are treated with low levels of chemical N-fertilizers (de Souza et al. 2016).

Generally speaking, it is believed that PGPB are more effectual in augmenting plant growth under restricting nutrient conditions. Besides, the colonization of the plant root by PGPR might have been repressed by the augmenting levels of nutrients (i.e., N) in the growth medium (Egamberdiyeva 2007; Shaharoona et al. 2008). It was also reported that these bacteria can be used as a supplement to chemical fertilizers to reduce the use of fertilizers but cannot replace nitrogen fertilizer in rice (Etesami and Alikhani 2016a). Generally speaking, the PGPB-based inoculation technology should be consumed along with desired levels of fertilization to achieve maximal benefits in terms of fertilizer savings, nutrient uptake, and rice plant growth (de Souza et al. 2016).

13.7 Biological Control of Fungal Rice Pathogens

Pathogenic microorganisms affecting plant fitness are an outstanding and chronic threat to food production and ecosystem steadfastness throughout the world (Compant et al. 2005). Diseases of fungal, bacterial, viral origin, and damage brought about by insects and nematodes can be led to a significant diminution in crop production. Diseases are one of the most important limiting factors affecting rice production, which reduces annual rice yield by about 5% (Song and Goodman 2001). More than 70% of the diseases caused by fungi, bacteria, viruses or nematodes have been reported in rice (Manandhar et al. 1998). In other words, rice is susceptible to diseases. Pathogenic fungi can reduce the quality and quantity of rice grain production (Chaiharn et al. 2009) and affliction with these fungi are among the most niggling of these diseases as it may result in remarkable crop yield losses (Chaiharn et al. 2009; Suprapta 2012). In addition, the consumption of

mycotoxins (e.g., aflatoxins, citrinin, ochratoxin A, fumonisins, and zearalenone)-polluted rice can be hazardous to human beings (Almaguer et al. 2012; Ferre 2016).

To control fungal diseases, fungal pathogens-resistant rice cultivars and fungicides are commonly used. But, due to the loss of resistance to pathogens, despite the high variability of disease agents of the pathogen population, the useful life of many pathogen-resistant cultivars is only several years. Use of fungicides is also expensive and environmentally unfriendly and has led to risks to human health, environmental pollution, residual toxicity, development of pesticide resistance, and other beneficial organisms in the soil (Komárek et al. 2010; Suprapta 2012; Yoon et al. 2013). These fungicides also reduced soil fertility and quality and damaged to natural ecosystems (Chaiharn et al. 2009). Furthermore, there are a number of painstaking diseases for which chemical solutions are few, unproductive, or nonexistent (Gerhardson 2002). Biocontrol is thus being considered as an alternative or a supplemental way of diminishing the utilization of chemicals in agricultural land (Compant et al. 2005, 2010; Etesami and Alikhani 2016b, 2016d; Gerhardson 2002; Pal and Gardener 2006; Suprapta 2012; Welbaum et al. 2004). Bacterial biocontrol agents can control plant pathogens including fungal pathogens by various mechanisms (Fig. 13.2). Various suitable nutrient-rich niches on/or inside roots attract a great diversity of microorganisms, including phytopathogens. Competition for the nutrients (root exudates including organic acids, amino acids, specific sugars, etc.) and niches is a underlying mechanism by which PGPB preserve plants from phytopathogens (Compant et al. 2005).

Biocontrol PGPB are aggressive root colonizers and play an important role in the biological control of plant diseases caused by soil-borne fungal pathogens (Chaiharn et al. 2009). Another mechanism of biological control by PGPR is production of allelochemicals like (i) iron(III)-chelating siderophores, which deprive pathogenic fungi of Fe since the fungal siderophores have lower affinity to Fe compared to bacterial siderophores (Loper and Henkels 1999; O'sullivan and O'Gara 1992; Van Loon and Bakker 2005); (ii) production of antibiotics such as amphisin, 2,4-diacetylphloroglucinol (DAPG), rhizoxin, oomycin A, phenazines, tensin, pyoluteorin, pyrrolnitrin, tensin, tropolone, oligomycin A, kanosamine, zwittermicin A, xanthobaccin, viscosinamide, and cyclic lipopeptides (Compant et al. 2005; de Souza et al. 2003; Défago 1993; Hashidoko et al. 1999; Joseph et al. 2012; Kai et al. 2009; Kim et al. 1999; Nain et al. 2012; Nielsen et al. 2002; Pal and Gardener 2006); (iii) biocidal volatiles like HCN and ammonia (NH_3) (Blumer and Haas 2000; Kai et al. 2009; Pal and Gardener 2006; Zou et al. 2007); (iv) lytic enzymes (Chernin and Chet 2002; Sindhu and Dadarwal 2001) such as chitinase (Ordentlich et al. 1988), which inhibits spore germination and germ-tube elongation (Frankowski et al. 2001), laminarinase, which digests and lyses mycelia of some fungi (Lim et al. 1991), β-1,3-glucanase, which lyses fungal cell walls of some fungi (Fridlender et al. 1993; Singh et al. 1999), glucanases, cellulases, and detoxification enzymes (Abbas-Zadeh et al. 2010; Fridlender et al. 1993; Kai et al. 2009; Nain et al. 2012; Pal and Gardener 2006; Sindhu and Dadarwal 2001; Zhao et al. 2010). ISR (induced systemic resistance) is an consequential mechanism by which PGPR in the rhizosphere prime the whole plant body for augmented defense

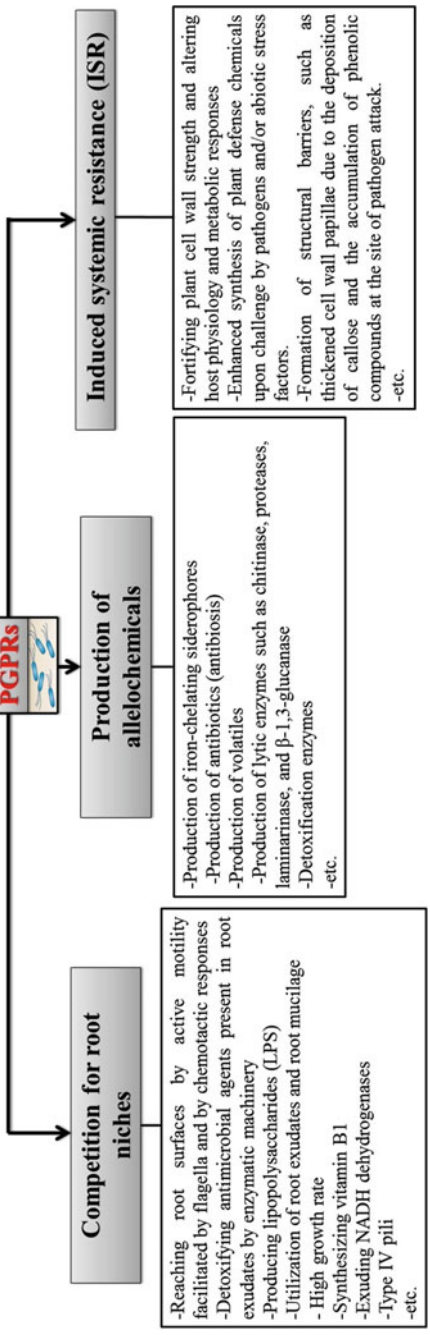

Fig. 13.2 Some of action mechanisms of PGPR in controlling plant pathogens

against a scopious range of pathogens and insect herbivores (Compant et al. 2005; Pal and Gardener 2006; Van Loon and Bakker 2005). Biocontrol PGPR, through different mechanisms such as production of siderophores, lipopolysaccharides (Leeman et al. 1995; Maurhofer et al. 1994; Meziane et al. 2005; Van Loon and Bakker 2005; Van Loon et al. 1998; Van Wees et al. 1997), volatile organic compounds (Ping and Boland 2004; Ryu et al. 2004), cyclic lipopeptides, 2,4-diacetylphloroglucinol, and homoserine lactones (Lugtenberg and Kamilova 2009), sensitize the plant immune system for enhanced defense without directly activating overpriced defenses (Pieterse et al. 2014).

Biocontrol PGPR-mediated control of several bacterial, fungal, and viral plant diseases in plants by this mechanism (ISR) has been reported (Leeman et al. 1995; Pal and Gardener 2006; Park et al. 2009). It has been also known that the ISR contains ethylene and jasmonate intracellular signaling, and these hormones stimulate host plant defense responses against plant diseases (Glick 2012). Biocontrol PGPR-mediated ISR also fortifies plant cell wall strength (Benhamou et al. 1996, 1998), alters host physiology and metabolic responses (Jeun et al. 2004; Park and Kloepper 2000), and increases accumulation of compounds (i.e., phenylalanine ammonia-lyase, peroxidase, phytoalexins, polyphenol oxidase, and/or chalcone synthase) (Chen et al. 2000; Ongena et al. 2000) that augment synthesis of plant defense chemicals upon challenge by plant pathogens (Compant et al. 2005; Nowak and Shulaev 2003; Ramamoorthy et al. 2001). The total of these changes lead to increased plant resistance to diseases. Generally speaking, the most effectual biological control agents (BCAs) studied to date appear to antagonize pathogens using multitudinous mechanisms (Iavicoli et al. 2003; Pal and Gardener 2006).

The ability of biocontrol PGPR to lessen or prevent the deleterious effects of certain fungal rice pathogens has been well documented (Amruta et al. 2018; Awla et al. 2017; Chaiharn et al. 2009; Etesami and Alikhani 2016b, 2016d, 2018; Velusamy and Gnanamanickam 2008; Verma et al. 2018).

Magnaporthe oryzae (anamorph *Pyricularia oryzae*), which causes diseases generically called "blast disease" or "blight disease—the most destructive disease of rice (Chaiharn et al. 2009; Dean et al. 2012) and attacks rice plants at all stages of development and infects the aerial parts of the rice plant—including leaves, nodes, stems, and panicles, bringing about annual losses of approximately 10–30% in miscellaneous rice—producing regions (Law et al. 2017), *Alternaria* sp., which cause leaf spots, *Fusarium* oxysporum, which cause root rot, *Sclerotium* sp., which cause stem rot (Chaiharn et al. 2009), *Bipolaris oryzae*, which causes brown spot disease, *Rhizoctonia solani*, which causes sheath blight disease, *Curvularia oryzae*, which causes leaf spot disease, *Gibberella fujikuroi*, which causes bakanae disease in rice seedlings, and *Rhizoctonia oryzae-sativae*, which causes aggregate sheath blight disease, have been reported as the most consequential fungal pathogen bringing about diseases in rice (Boukaew et al. 2013; Tamreihao et al. 2016). By a combination of different modes of action such as hydrogen ions and gaseous products including ethylene, HCN and NH_3, and siderophore (hydroxamate type), cell wall degrading enzymes (i.e., chitinase, protease, cellulase, β-1,3-glucanase, β-1,4-glucanase, and lipase) and antibiotics, biocontrol PGPB (e.g., *Streptomyces*

sp. *S. globisporus, S. sindeneusis, S. flavotricini*, *S. philanthi*, *S. vinaceusdrappus, S. corchorusii, Ochrobactrum anthropic*, *Bacillus* sp., *B. cereus*, *B. subtilis*, *B. methylotrophicus, Enterobacter* sp., *Pseudomonas aeruginosa*, and *Pseudomonas* sp.) significantly inhibited the mycelia growth of these fungi (Awla et al. 2017; Boukaew et al. 2013; Boukaew and Prasertsan 2014; Chaiharn et al. 2009; Khalil et al. 2014; Li et al. 2011; Ningthoujam et al. 2009; Prapagdee et al. 2008; Shan et al. 2013; Tamreihao et al. 2016; Tokpah et al. 2016; Zarandi et al. 2009).

In previous studies, Etesami and Alikhani (2016d), (2017), and Etesami et al. (2014b) investigated the potential of antifungal activity of the bacterial isolates isolated from rhizosphere and endorhiza of rice, oilseed rape (*Brassica napus* L.), and berseem clover (*Trifolium alexandrinum* L.), respectively, against five rice pathogenic fungi (*Magnaporthe oryzae, M. salvinii, Fusarium verticillioides, F. fujikuroi,* and *F. proliferum*—the most important pathogenic fungi of rice in Iran) under in vitro conditions. A considerable part of these isolates showed a good percentage of mycelial growth inhibition against all the tested major rice fungal pathogens in dual cultures on solid media (Fig. 13.3) (Etesami and Alikhani 2016d).

Bacillus species (*Bacillus mojavensis*, *B. amyloliquefaciens*, *B. subtilis*, and *B. cereus*) were reported as the most propitious bacterial biocontrol agents in rhizosphere and endorhiza of these plants (Etesami and Alikhani 2018). In addition, endophytic bacterial isolates were more effective at mycelial growth inhibition than rhizosphere bacterial isolates. Probably endophytic bacteria use mechanisms similar to PGPR to control plant fungal pathogens. Biocontrol activities of these

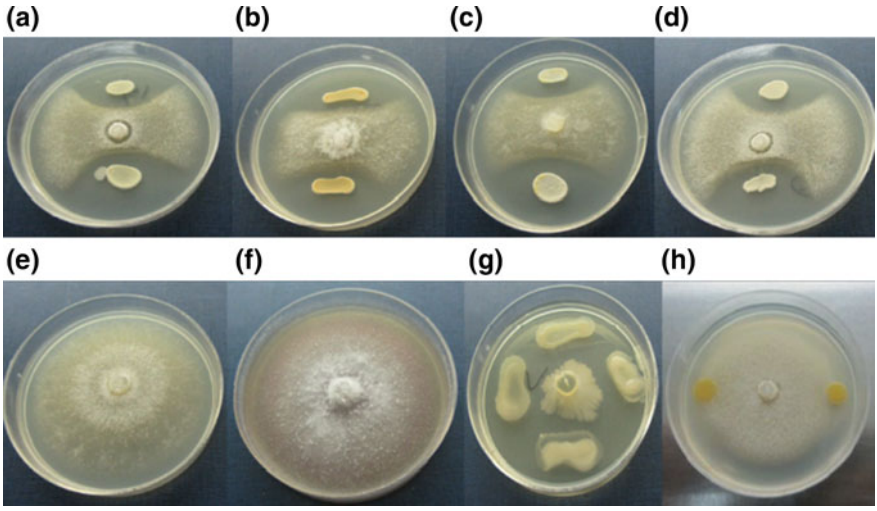

Fig. 13.3 Dual culture assay for in vitro inhibition of mycelia of fungal rice pathogens by the endophytic and rhizoshpere strains grown on PDA agar for 5 days. **a** endophytic strain *B. subtilis* CEN_3; **b** rhizosphere strain *B. cereus* CEN_5; **c** endophytic isolate; **d** rhizosphere isolate; **e** and **f** control (pathogen alone); **g** combination of endophytic and rhizosphere isolates with each other; and **h** rhizosphere isolate resulted in no inhibition zones

bacterial strains may be owing to the creation of antifungal metabolites, volatile organic compounds (VOCs), siderophores, and cell wall degrading enzymes (Etesami and Alikhani 2016c).

Among biocontrol bacteria, spore-forming *Bacillus* bacteria have properties that make them more suitable for development as biocontrol agents, including high resistance to stress, production of various secondary metabolites, induction of ISR in order to reduce the severity of the disease caused by a wide range of pathogens, stimulating plant growth, simplicity in cultivating and maintaining them, as well as use of them as spores on plant or seed inoculation (Alina et al. 2015; Shafi et al. 2017). Besides, *Streptomyces* bacteria also appear to be auspicious biocontrol agents against a wide range of phytopathogenic fungi due to generating various bioactive compounds such as antibiotics (e.g., Blasticidin S, Kasugamycin, Oligomycin A, geldanamycin, and nigericin) or antifungals which can inhibit or kill the pathogen (Copping and Duke 2007; González-Franco and Robles-Hernandez 2009; Law et al. 2017; Tapadar and Jha 2013; Trejo-Estrada et al. 1998; Yang et al. 2010), the release of extracellular lytic enzymes such as chitinases and glucanases, which play consequential roles in ruination of fungal cell walls (El-Tarabily et al. 2000; González-Franco and Robles-Hernandez 2009; Palaniyandi et al. 2013), and their colonization ability, competitive traits, and survival in various types of soil (ability to produce spores which allow them to survive longer and in various extreme conditions) (González-Franco and Robles-Hernandez 2009; Law et al. 2017; Ningthoujam et al. 2009). Under greenhouse conditions, *Streptomyces* could result in up to 88.3% disease diminution of rice blast (Law et al. 2017). Approximately, 75% commercially practicable antibiotics were derived from the genus *Streptomyces* (Kashif et al. 2016). Besides, *Streptomyces* produces spores that help dissemination and confer resistance to many hostile conditions (Goodfellow and Williams 1983). The biocontrol bacteria not only prevent the growth of pathogens, but also improve plant growth. These bacteria were also positive for different PGP traits such as IAA, ACC deaminase, siderophores, and phosphate solubilization, and could significantly enhance the growth and grain yield production of the plants (Alina et al. 2015; Etesami and Alikhani 2016c, 2017; Shafi et al. 2017; Tamreihao et al. 2016).

There are many studies that show bacterial biocontrol agents can be very promising antagonist candidates against plant pathogens which can be developed for sustainable plant diseases management. Despite these studies and the recent interest in bioassays of plant diseases, it is difficult to find examples of commercial use of biological control agents in controlling pathogens. This can be due to inappropriate screening systems that are used. In general, biocontrol PGPB by colonizing the root system of the plant prevent the establishment of harmful rhizospheric microorganisms on the root of the plant. These rhizobacteria must compete with indigenous microorganisms and effectively colonize the rhizosphere. In other words, the biocontrol agents and PGPB are influenced by native microbial communities. Generally, the antagonistic activity of biocontrol bacteria is tested through in vitro inhibition of fungal pathogens in dual cultures on solid media and then confirmed in bioassays on host plants. It has been reported that in vitro

evaluations have some limitations (Compant et al. 2005). Many biological control agents effectively control diseases in vitro conditions, but have not been successful in field conditions. The ineffectiveness of biocontrol bacteria in the field is often attributed to their inability to colonize the roots. Rhizosphere competence and colonization are considered as an important factor in controlling fungal pathogens by biocontrol bacteria because both organisms colonize the same ecology niche and use the same nutrient (Compant et al. 2005). Factors such as temperature, soil moisture, soil texture, and environmental stresses affect the survival and establishment of bacteria.

In general, in many studies, a single biological control agent is usually used to control a pathogen under controlled and greenhouse conditions. This can sometimes result in incompatible performance by the biological control agent under natural conditions because a biological control agent cannot be active in all types of soil environments/agricultural ecosystems (Raupach and Kloepper 1998) or against all pathogens that attack the host plant (there is usually more than one pathogen in the soil). Moreover, this may also be due to inadequate colonization, limited resistance to changes in environmental conditions, and fluctuations in the production of antifungal metabolites by this biological control agent (Dowling and O'Gara 1994). Several solutions have been proposed to overcome these problems including the combined use of two or more isolates in biological control (Raupach and Kloepper 1998). Mixtures of biological control agents with different plant colonization patterns or a biological control agent with antifungal activities against several pathogens (formulation of a biocontrol isolate is simpler and cheaper than that of multiple biocontrol isolates) can be useful for controlling the biological diversity of miscellaneous pathogens via assorted mechanisms of repression of the disease. In general, the use of a combination of bacterial antagonists for biological control of pathogens can expand the range of antifungal activities (protection of the plant against a wide range of fungal pathogens), increase the efficiency, sustainability, and effect of biological control agents, and combine different characteristics without applying genetic engineering. In addition, designing a combination of biocontrol isolates and the use of multiple antifungal properties demonstrated by these isolates can be useful in the sense that at least one of the biological control mechanisms among these isolates may exist under unpredictable field conditions. In addition, mixtures of biocontrol microorganisms can increase the genetic diversity of biological control systems that prolong the stay in the rhizosphere and use a spacious range of biological control mechanisms.

A higher efficiency of several isolates from biocontrol agents against plant pathogens has been reported in previous studies (Etesami and Alikhani 2016c; Lucas et al. 2009; Schisler et al. 1997). In addition to controlling the disease, the combination of biocontrol isolates has also increased plant growth in terms of germination, plant height, and yield. It is noteworthy that the compatibility of biocontrol isolates to be inoculated with each other on plant should be considered. The incompatibility of inoculants (biocontrol isolates) can sometimes prevent the growth of each other and target pathogens. Selection of effective biocontrol isolates of bacteria is also very important for the control of pathogens in plants.

The isolation of these bacteria from pathogens repulsive soils can increase the chance of isolating effective isolates. In order to obtain effective isolates, biocontrol bacteria should be isolated from the same environment that they are supposed to be used in it. Formulations and application methods are often of great importance in the effectiveness of biological control, which should pay attention to them. In general, according to the studies conducted on biological control of fungal pathogens in rice, it can be concluded that *Streptomyces* and *Bacillus* bacteria may be taken advantage of as a potential bioinoculant agent for biocontrol as well as rice plant growth promoter.

13.8 Conclusions and Future Prospects

Reviews of literature clearly show that rhizosphere and endorhiza of rice harbor bacteria with a potential in promoting rice growth and controlling fungal rice pathogens. The co-inoculation of rice with the PGPB, as an attractive technique for utilization in commercial inoculant formulations than sole-inoculation of these bacteria, could allow declines in the prevalent high rates of fertilizer and the succeeding environmental problems without making compromise plant productivity under in vitro and greenhouse conditions. One of the major challenges encountered during the selection of biocontrol agents and biofertilizers is that biocontrol agents/biofertilizers that appear efficacious based on in vitro and greenhouse experiments might not be effective at controlling plant diseases and increasing rice growth and yield under field conditions. This inefficiency of bacteria can be owing to the variations in environmental conditions in different locations. Therefore, the environmental factors at the location where biocontrol agents/biofertilizers will be applied should be taken into consideration during the selection of suitable biocontrol agents/biofertilizers. Ideally, the biocontrol agents/biofertilizers should be isolated from and applied to locations with similar environmental factors in order to achieve successful biological control/biofertilizers. Besides, the formulation such as liquid, powder, or granule and the method of use of biocontrol agents/biofertilizers such as seed inoculation, soil inoculation, and vegetative part inoculation should be inspected as they are consequential in specifying the outcomes of field experiments. In general, before PGPB can be regarded for agricultural practices, further studies are essential to evaluate the efficacy of PGPB on rice plants under field conditions where there are a variety of constraints such as soil conditions (i.e., pH, soil nutrients status, nutrients sorption capacity, organic matter, and moisture level of the soil, etc.), environmental stresses, and types of autochthonous microorganisms that can affect the survival and growth promotion activities of PGPB/biocontrol agents.

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Chapter 14
Plant Growth-Promoting Rhizobacteria-Induced Defense Against Insect Herbivores

Joseph Disi, Jocelyn Simmons and Simon Zebelo

Abstract Plant growth-promoting rhizobacteria (PGPR) improve plant health and productivity by providing protection to plants from diseases and pests and enhancing plant growth. PGPR induce systemic resistance (ISR) against microbial pathogens and herbivorous insects. There are limited studies that show the induction of systemic resistance in crop plants against insect pests. Commonly used PGPR genera in insect pest control include *Pseudomonas*, *Bacillus, Burkholderia, Xenorhabdus, Photorhabdus, Agrobacterium, Streptomyces,* etc. PGPR suppress the activity of insect pests by inducing systemic resistance that results in the production of secondary metabolites (terpenes, siderophores, hydrogen cyanide, etc.) and some display direct insect pathogenicity. This chapter focused on PGPR-induced defense against insect pest in field crops with emphasis on the mechanism of action involved against insect pests. PGPR-mediated biochemical and physical changes in the host plants that display insect pathogenicity, methods mixtures application, and challenges associated with their use of PGPR in sustainable agriculture.

Keywords PGPR · Induced systemic resistance · Entomopathogen · *Pseudomonas* · *Bacillus* · Insect pests

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14.1 Introduction

There are one million described insect species in our planet earth, but less than one percent of species are crop pests. Insect pests cause considerable losses in crop production. Crop producers typically rely on chemical insecticides to protect their crops against herbivorous insects. Approximately two million tons of insecticides applied to control insect pests' worldwide (Aktar et al. 2009). This intensive use of insecticides have negative impacts such as toxicity to humans and animals, environmental pollution, effects on nontarget species and development of resistance. The backlash of the negative impact of insecticides leads to the increasing demand from consumers to reduce the use of chemical insecticides in crop production and protection from deleterious pest and pathogens. Biological control using biopesticides are promising alternative to chemical insecticides. Particularly, the microbial pesticides have peculiar advantages, because they have unique mode of action. In many cases, they are species specific and have reduced toxicity. One such approach involves treating crops with Plant Growth-Promoting Rhizobacteria (PGPR) for induced defense against herbivores insects.

PGPR are specific strains of root-colonizing bacteria which can elicit increased rates of plant growth, suppress soil pathogens and induce systemic resistance (ISR) against diseases and insect pests. The effect of PGPR on insect pests could be indirect via ISR and/or direct as an entomopathogen. The indirect effect of PGPR against insects initiated through recognition of the microbes by the host plant, elicitation of specific hormonal signal pathways that might lead to the biosynthesis of defense-related chemical compounds, enzymes, protein, secondary metabolites, and volatile organic compounds (VOCs) against insect herbivores (Pineda et al. 2010, 2013; Van Oosten et al. 2008; Zamioudis and Pieterse 2012; Zebelo et al. 2016). Some PGPR strains exhibited direct insect pathogenicity. The most commonly used entomopathogenic bacteria, are *Bacillus thuringiensis* and *Photorhabdus*/*Xenorhabdus* species. These bacteria developed as an alternative to chemical pesticides. They are host specific and efficient to control insect pests. But these bacteria have two limitations. (1) They lack persistence in the environment and (2) their dependence in vectoring agents to infect hosts (e.g., nematodes). Interestingly, select PGPR strains display direct entomopathogenicity. Their high environmental persistence and ability to penetrate insect cuticle makes them the preferred candidate bio-insecticides for protection of plants against root-feeding insects (Kupferschmied et al. 2013) and nematodes (Wahla et al. 2012).

There are limited studies on PGPR-mediated plant–insect interaction. Zehnder et al. (1997a) elegantly demonstrated that PGPR could trigger ISR against insects using PGPR strain INR-7 (*Bacillus pumilus*) using Cucumber (*Cucumis sativus* L.) as a model system. *C. sativus* plants treated with INR-7 were less attractive to spotted cucumber beetle, *Diabrotica undecimpunctata* Howardi (Coleoptera: Chrysomelidae) and the striped cucumber beetle, *Acalyma vittatum* Fabricius (Coleoptera: Chrysomelidae), as a result, reduced the number of beetles recorded in INR-7-treated plants than the untreated control plants. In a similar study, Zehnder

et al. (1997b) conclude that the reduced number of beetles on PGPR-treated plants was due to decreased production of curcubitacin (insect-feeding stimulant). Hanafi et al. (2007) reported that PGPR (*Bacillus subtilis*) treated tomato plants showed lower whitefly populations under greenhouse conditions. In an unrelated study jasmonic acid (JA) pathway involved in the reduction of whitefly population in PGPR-treated plants (Valenzuela-Soto et al. 2010). The reduction of insect pest population in PGPR-treated plants clearly showed that these bacteria might induce resistance in plants against important insect pests.

The genera of PGPR commonly used as biocontrol agents include *Pseudomonas*, *Bacillus, Burkholderia, Agrobacterium, Streptomyces*, etc. (Dey et al. 2014) either alone or in combination forming a consortium of strain, which triggers multiple beneficial effects to the growing plants. This chapter focused on the indirect and direct impact of PGPR on insect pests, induced defense against insect pest in plants.

14.2 PGPR-Mediated Plant–Insect Interactions

PGPR can enhance plant growth and health by fixing atmospheric nitrogen, increasing nutrient availability and uptake (Spaink 2000), involved in biosynthesis of essential plant growth-related hormones including Indole-3-acetic acid (IAA), cytokinins, auxins, gibberellins etc. (Contreras-Cornejo et al. 2009; van Loon 2007). Some PGPR strains promote plant growth via the biosynthesis of secondary metabolites and enzymes (Vacheron et al. 2013; Zhang et al. 2008). Rhizobacteria also increases plant health and trigger resistance to plant pathogens and insect herbivores by ISR (Hossain et al. 2016; Rashid and Chung 2017). Some of the PGPR promotes plant growth that could result in improved nutrient composition of the plants (Pandey et al. 2018) and this could affect insect performance (Schoonhoven and Dicke 2005). Insect pests might be attracted and take advantage of increased availability of nutrients in PGPR-treated plants (Schoonhoven and Dicke 2005). PGPR enhances plant tolerance through the regeneration of herbivore injured plant tissue as a result of increased nutrient and water uptake (Rashid and Chung 2017). Thus, PGPR augments plant resistance against insect pest, disease, and weeds by increasing nutrient availability and absorption, the production of secondary plant metabolites, and growth hormones, these phenomena either directly or indirectly induce defense in plants.

14.3 PGPR-Mediated ISR Against Insect Pests

At the heart of PGPR-mediated ISR is priming. Conrath (2011) defined priming as a physiological process by which plants prepare to initiate defense in plants against pathogens and insect herbivores. Pieterse et al. (2014) showed that PGPR prime

plants are tolerant of various pathogens and insect herbivores. PGPR triggered ISR leads to jasmonic acid (JA) and ethylene (ET) in cross talk with salicylic acid (SA) independent and dependent pathways. Systemic Acquired Resistance (SAR) is the activation of pathogenesis-related (PR) proteins as a result of SA-dependent signaling pathway and necrotizing pathogens (Conrath et al. 2002; Hammerschmidt 2009).

PGPR triggered ISR involves jasmonic acid (JA) and ethylene (ET) independently or in cross talk with salicylic acid (SA)-dependent pathways. Through these signaling pathways, PGPR regulates plant hormones (JA, ET, and SA) that affect how insects interact with host plants (Shavit et al. 2013; Van Oosten et al. 2008). Chewing herbivorous trigger JA-pathways (Pineda et al. 2010). Zebelo et al. (2016) reported higher levels of JA and JA-related gene expression in PGPR-treated cotton plant that was injured by beet armyworm. The PGPR, *P. fluorescens* strain SS101 activates ISR against chewing insect through JA- and ET-dependent mechanisms (van de Mortel et al. 2012). Furthermore, higher expression of the JA/ET-dependent *ORA59* pathway than the JA-dependent *MYC2* pathway reported in Arabidopsis plants treated with *Pseudomonas simile* WCS417r was implicated in the induction of resistance against the cabbage moth larvae (Pangesti et al. 2016).

PGPR elicited ISR against phloem-feeding insects is dependent on both the JA/ET- and SA-signaling pathways (Niu et al. 2011). Valenzuela-Soto et al. (2010) demonstrated JA-dependent ISR and increased expression of JA-independent genes including terpenoid biosynthetic pathways genes, and photosynthetic genes by *Bacillus subtilis* against the phloem sucking insect whitefly on tomato plants (*Solanum lycopersicum*). *Arabidopsis* roots treated with *P. fluorescens* WCS417r were highly susceptible to the phloem-feeding aphid *Myzus persicae*, although they showed increased expression of *PDF1.2* and *LOX2* genes after insect attack (Pineda et al. 2012). These studies are examples of the role of different rhizobacteria genera, including *Pseudomonas* and *Bacillus,* have against phloem-feeding insects. This could be explained that microbe-associated molecular patterns (MAMPs) of different beneficial microbes recognized by plant root receptors leading to the production of specific hormonal signals. MAMPs of beneficial microbes including flagellin, secondary metabolites, and lipopolysaccharides activate MAMP-triggered immunity (MTI) that modulate hormonal signals in plants (Hermosa et al. 2012; Jacobs et al. 2011; Zamioudis and Pieterse 2012). For instance, lipopeptides of *B. amyloliquefaciens* S499 induced the expression of defense-related genes lipoxygenase D, and F (*LOXD*, *LOXF*)-induced ISR in tomato plants (Cawoy et al. 2014). The early event in rhizobacteria–plant interaction is the recognition of MAMPs of the rhizobacteria by plant root receptors and leads to the generation of a distinct ISR signal in the roots. The signal induced by MAMPs transport upward to shoots to trigger ISR in the leaves instantaneously activate the SA-, JA-, and ET-dependent signaling pathways. These signaling pathways expressed genes that regulate the production of defensive compounds such as enzymes, defensive proteins, and secondary metabolites (alkaloids, phenols, nonvolatile terpenes and VOCs). For example, the primed plants release VOCs upon herbivore damage (HD); these

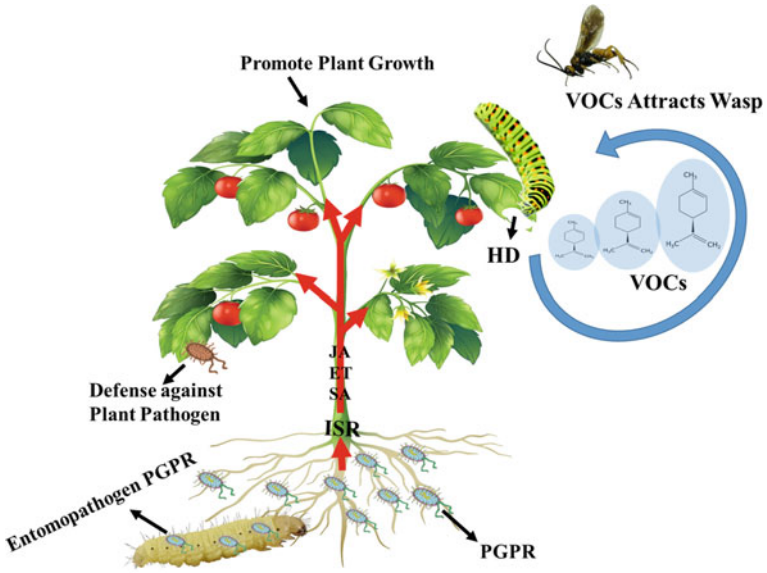

Fig. 14.1 PGPR prime the host plant to increase the defense against various pathogens and insect herbivores by the mechanism of induced systemic resistance (ISR) to produce the defensive compounds. The early event in rhizobacteria–plant interaction is the recognition of microbe-associated molecular patterns (MAMPs) of the rhizobacteria by plant root receptors and leads to the generation of a distinct ISR (red arrow) signal in the roots. The signal transport upward to shoots to trigger ISR in the leaves by instantaneously activating the SA, JA, and ET-dependent signaling pathways. These signaling pathways lead to the expression of genes that regulates the production of defensive compounds such as enzymes, defensive proteins, and secondary metabolites (alkaloids, phenols, nonvolatile terpenes and VOCs). For example, the primed plants release VOCs upon herbivore damage (HD), these VOCs might attract natural enemies of the herbivore (e.g., wasps) and pollinators or repel the herbivore directly. Some PGPR strains serves as an entomopathogen and causes disease root herbivores

VOCs might attract natural enemies of the herbivore (e.g., wasps) and pollinators or repel the herbivore directly (Fig. 14.1). Currently, there is no precise information on how the MAMPs of beneficial microbes modify phytohormone signaling pathways during plant–insect interactions.

14.3.1 PGPR-Mediated Antibiosis Compounds Biosynthesis

Antibiosis is one of the reported forms of PGPR-mediated host plant resistance mechanisms against herbivorous insects. Through elevated or compromised production of allelochemicals, insect-resistant crops reduce growth, inhibit reproduction,

alter physiology, delay maturation, and induce various physical or behavioral abnormalities in insect herbivores that ultimately suppress insect pest abundance. Several studies show that PGPR triggers the biosynthesis of plant defense-related compounds against insects through various plant defense signaling pathways (Pangesti et al. 2016; van de Mortel et al. 2012). For example, plant hormones such as JA, ET, and SA discussed above regulate the key defense-related chemical compounds that include, but not limited to, flavonoids, lignin, and other secondary metabolites. Most of these defense-related compounds have been shown to have broad-spectrum properties, against plant pathogens and insect herbivores (Campos et al. 2014; Valenzuela-Soto et al. 2010; Zebelo et al. 2016). Biosynthesis of camalexin and glucosinolates is one way PGPR regulate plant defenses against plant pathogens and insect herbivores (Clay et al. 2009; Kim Jae et al. 2008; Mewis et al. 2005; Muller et al. 2010). Pangesti et al. (2016) reported that the *Arabidopsis* plants treated with PGPR activate JA/ET pathway that leads to the biosynthesis of camalexin and glucosinolates, which triggers ISR against chewing insects. Zebelo et al. (2016) showed that cotton plants inoculated with mixtures of PGPR *Bacillus* spp. increased transcript level of JA-related genes *GhLOX1, GhAOS,* and *GhOPR3*, and gossypol biosynthesis genes including the (+)-δ- cadinene synthase (CAD1) gene family (*Cdn1- A, CAD1-C1, Cdn1-C3,* and *Cdn1-C14*). Consequently, the level of gossypol was elevated in PGPR-treated plants and the herbivory by beet armyworm larvae was significantly reduced, suggesting that the high level of gossypol in PGPR-treated plants might have contributed to the induced resistance of cotton plants against beet armyworm larvae. Gossypol is a phenolic sesquiterpenoid aldehyde with the insecticidal property. High production of phenolic compounds (secondary metabolites) induces resistance against pathogens and insects (Sharma et al. 2009; Usha Rani and Jyothsna 2010) Remarkably high levels of gossypol in cotton reduces the growth and development of *Heliothis* and *Helicoverpa* (Noctuidae) larvae (Du et al. 2004; Stipanovic et al. 2006). JA treatment increases the level of gossypol in cotton plant, and this was correlated with reduced growth, and development of the mealybug, *Phenacoccus solenopsis* (Zhang et al. 2011). High level of phenolic compounds was reported in rice plants treated with PGPR, *P. fluorescens* WCS374r (De Vleesschauwer and Höfte 2009). Furthermore, flavonoids are commonly known as insect-feeding inhibitor (Schoonhoven and Dicke 2005). Arabidopsis plants treated with *Bacillus* and *Actinomycetes* increases the transcript levels of five transcription factors (*TT8, EGL3, MYB12, MYB114,* and *MYB113*) that regulates the genes for flavonoid biosynthesis pathways (Ali and McNear 2014). The transcription factor *MYC2* controls JA-signaling pathways upon herbivory, and *MYC2* also regulates flavonoids and anthocyanin biosynthesis pathways (De Vos et al. 2005; Dombrecht et al. 2007; Verhage et al. 2011).

14.3.2 Structural Modification of Plant Cells by PGPR

Proteins like lipoxygenase (LOX), lignin and lectins are associated with various defense-related processes, which include the formation of cell wall structure, stress adaptation, resistance to pathogens and insects in several crops (Pauwels et al. 2009; Xiaohong et al. 2012). Rice plants colonized by *P. fluorescens* triggers ISR against the leaf folder larvae by the activation of several enzymes including LOX, chitinases and trypsin inhibitors (Commare et al. 2002; Saravanakumar et al. 2007; Saravanakumar et al. 2008). Al Atalah et al. (2014) reported that the jacalin-related lectins display insecticidal activity against different types of insects. The lectin-induced in soybean plants during interaction with bacterial pathogens including *Xanthomonas axono podis* pv. Glycines, *P. syringae* pv. Tomato, and *B. amyloliquefaciens* KPS46 (Buensanteai et al. 2009). Lignin being a recalcitrant confers resistance to insect herbivores (Barakat et al. 2010). The lignin content in plant cell wall directly related with plant leaf hardiness when lignin content increases in the plant cell wall the leaf hardiness also increases for insect herbivores (Johnson et al. 2009). Peroxidase (POD) and polyphenol oxidase (PPO) catalyze the biosynthesis of lignin and different oxidative phenols that are involved in plant defense against insect pests (Bhonwong et al. 2009; Gulsen et al. 2010). For example, *P. fluorescens* strains Pf1, TDK1 and PY15 display ISR against the leaf folder larvae (*Cnaphalocrocis medinalis*) due to the activation of PPO in rice plants (Saravanakumar et al. 2008). The mechanism of induced resistance against insects by PGPR related to lignin biosynthesis remains unclear. However, PGPR-mediated plant defenses against insect herbivores can be induced through biochemical and physical changes in plants. For example, the induced production of a chemical, such as a flavonoid, is not only a chemical inhibitor of insects. Instead, it may be linked to physical modifications of the cell wall by lignification. PGPR modulated ISR might lead to the production of both chemical and physical barriers that might have antibiotic and antixenosis effect on insect herbivores.

14.3.3 Effect of PGPR in Sucking and Chewing Insects

Induced systemic resistance works by potentiating plants' innate immunity which is effective against insect herbivores. An insect with biting and chewing mouthparts typically induce responses similar to induced systemic resistance that is dependent upon jasmonic acid as a signaling molecule and may promote induced resistance against subsequent insect herbivores (Gatehouse 2002). Insects with piercing and sucking mouthparts tend to inflict limited tissue damage through feeding and are often able to evade the wound-induced defense response. These insects may activate defenses similar to systemically acquired resistance responses that are dependent upon salicylic acid as a signaling molecule (Walling 2000). PGPR mediated ISR might vary by insect species and their feeding guilds.

14.3.3.1 Sucking Insects

Induced systemic resistance by PGPR against sucking insects are plant or beneficial microbe specific. This effect also depends on whether the targeted insects are specialist or generalist feeders. For instance, commercial *Bacillus* species applied in mixtures in bell pepper was shown to induce tolerance to *Myzus persicae* Sulzer (Boutard-Hunt et al. 2009; Herman et al. 2008). Similarly, Fahimi et al. (2014) reported the adverse effect on the population of *Aphis gossypii* feeding on cucumber plants treated with *P. fluorescens* strain UTPF. Treatment of *Arabidopsis thaliana* with *P. fluorescens* strain WCS417r and then subsequently feeding the plant to the generalist aphid, *M. persicae* positively affected growth and development of the aphid, but no effect documented on the crucifer aphid *Brevicoryne brassicae* that fed on the same plant (Pineda et al. 2012). However, treatment of the aphid host plant (crucifer) with single and mixtures of *Bacillus* species suppressed the growth and development of *B. brassicae* (Gadhave et al. 2016a; Gadhave and Gange 2016). This indicates a plant-specific or microbial species effect. Valenzuela-Soto et al. (2010) showed that treatment with *Bacillus subtilis* reduced the development of *Bemisia tabaci* on tomato plants, contrary to a work by Shavit et al. (2013) who found that *B. tabaci* nymphs had higher survivorship after they fed on *Bacillus subtilis* WCS417r-treated tomato plants.

14.3.3.2 Chewing Insects

There are several examples of PGPR-mediated plant defenses on the behavior of chewing insects that cut across Lepidoptera, Coleoptera, and Diptera insect orders. Zehnder et al. (1997b) observed a reduction in the number of cucumber beetles (*Diabrotica undecimpunctata* Hawardi (Barber) on cucumber plants or seedlings treated with *Bacillus pumilus* strain INR-7 by reducing the production of phagostimulants. A similar effect was reported on other aboveground and belowground-feeding coleopterans in different field crops (Santos et al. 2014; Coy et al. 2017; Disi et al. 2018b). Studies suggested that PGPR modified behavior of root-feeding insects via enhanced emission of volatile organic compounds even though different PGPR genera used in these separate independent studies. In the study by Santos et al. (2014) root colonization by *Azospirillum braslense* negatively affected weight gain and preference by *Diabrotica* speciose on maize via increased emission of (*E*)-β-caryophyllene but root colonization did not cause increased growth of the plant. Similarly, treatment of maize seeds with *Bacillus pumilus* strain INR-7 had an adverse effect on weight gain and preference of *Diabrotica virgifera virgifera* but no growth promotion was recorded for this bacterial species (Disi et al. 2018b). Chiriboga et al. (2018) reported the enhanced expression of a gene involved in the production of (*E*)-β-caryophyllene which correlated with the significantly enhanced emission of (*E*)-β-caryophyllene in *Pseudomonas protegens* CHA0 and *Pseudomonas chlororaphis* PCL1391 treated maize exposed to infestation by *Diabrotica balteata* larvae.

Van Oosten et al. (2008) revealed adverse impact by *P. fluorescens* WCS417r on *Spodoptera exigua*, a generalist chewing herbivore. Pangesti et al. (2015a) reported that a generalist caterpillar, *Mamestra brassicae* weighed less upon feeding on roots of *A. thaliana* treated with *P. fluorescens* WCS417r, but there was no effect on the weight of the specialist *Pieris brassicae*. Application of *P. fluorescens* (Pf1 and TDK1) and *Beauveria bassiana* (B2) in combination with chitin affected the production of defense enzymes in groundnut plants and concomitantly reduced infestation by a leaf miner (*Aproaerema modicella*) and a pathogen (*Sclerotium rolfsii*) (Senthilraja et al. 2013). Zebelo et al. (2016) showed that mixture of *Bacillus* PGPR strains (Blend-8 and Blend-9) enhanced the level of gossypol in cotton leaves with consequence on growth and development of *S. exigua* larvae and pupae. Application of *Pseudomonas putida* and Rothia sp. on tomato seeds affected the production of proteins and defense-related enzymes in tomato plants after the plants infested with *Spodoptera litura* (Bano and Muqarab 2017). Disi et al. (2018a) reported reduction in emission of maize volatiles treated by single and mixture of *Bacillus* PGPR species that deterred *Ostrinia nubilalis* oviposition, suggesting that manipulation of secondary metabolites may be a common mechanism of PGPR-mediated ISR against insects (Zehnder et al. 1997a; Santos et al. 2014; Zebelo et al. 2016; Chiriboga et al. 2018).

14.4 The Entomopathogenicity of PGPR

Entomopathogen defined as the pathogens that can cause disease and kill insects. An entomopathogen could be fungus, bacteria, virus, nematode or protozoans. The entomopathogenic bacteria promote plant growth, enhance plant health via ISR and display insect pathogenicity. Kupferschmied et al. (2013) reviewed broadly about the potential insect pathogenicity of some PGPR strains. The non-PGPR entomopathogenic bacteria, mainly *Bacillus thuringiensis* (*Bt*), *Photorhabdus* sp., and *Xenorhabdus* sp. are commonly used as entomopathogens. Efficiently controls insect pests in laboratory, greenhouse and field conditions. For example, *Bt* is commercially available as topical sprays and has several advantages over chemical insecticides. *Bt* attacks specific insect species, and its application is considered to be environmentally sound and harmless to humans and other mammals (Kupferschmied et al. 2013). However, the use of *Bt* to control insect pests has limitations. *Bt* has limited persistence on the surface of plant leaves, this is due to sensitivity to solar irradiation as well as to the chemical environment on plant leaves, and unlike PGPR strains, *Bt* is not a competitive plant colonizer (Bizzarri and Bishop 2008; Raymond et al. 2010). Because the susceptible stages of the pest insects are during the early instar larvae, *Bt* provides only short-term crop protection in the field and requires precise application practices (Bravo et al. 2011). Similarly, the use of *Photorhabdus* sp. and *Xenorhabdus* sp. as biocontrol depends on nematode vector (*Steinernena* spp.) for insect infection. Intriguingly, certain strains of PGPR *Pseudomonas* spp. and *Streptomyces* spp. display insect

pathogenicity and thus could be formulated to extend the present range of bio-insecticides for protection of plants against insect pests. These entomopathogenic PGPR strains have the remarkable ability to suppress soil-borne plant pathogens, promote plant growth, and induce systemic plant defenses against insect pests. Recently, at Auburn University, Department of Entomology and Plant pathology, Drs. Fadamiro and Kloepper screened more than three hundred strains of PGPR Bacillus spp. for their entomopathogenicity against beet armyworm, several strains showed toxicity against beet armyworm (unpublished data). *Pseudomonas* spp. and *Streptomyces* spp. are relatively well documented as an entomopathogen of several insect species.

14.4.1 Pseusomonas *spp. as an Entomopathogen*

Pseudomonas fluorescens is an entomopathogeic PGPR used against termites (Devi and Kothamasi 2009), phytophagous ladybird beetles (Otsu et al. 2004), and aphids (Hashimoto 2002). *P. fluorescens* bacteria has been used successfully against herbivorous insects and as biological control of fungal plant pathogens (Commare et al. 2002; Karthiba et al. 2010; Péchy-Tarr et al. 2008). *P. fluorescens* infects the mid-gut of larvae, pupae, and adults within the Lepidopteran (Tang et al. 2012), Dipteran (Bansal et al. 2011; Corby-Harris et al. 2007), Coleopteran (Arias-Cordero et al. 2012; Saitou et al. 2009), Hemipteran species (Hashimoto 2002; Lacava et al. 2007), and Hymenopteran (Li et al. 2012; Mohr and Tebbe 2006).

Pseudomonas luminescens toxify insects through a single toxin gene called *makes caterpillars' floppy* (mcf). This mcf gene regulates a persuasive insect toxin Mcf1 (Péchy-Tarr et al. 2008). *Mcf1* is toxic to the midgut epithelial cells, and high expression leads to the floppy nature of the insect infected with *P. luminescens*. This potent insect toxin of *P. luminescens* might suppress immune response activity (Kupferschmied et al. 2013).

Similarly, the *mcf1*-related gene of *P. fluorescens* strain Pf-5 and CHA0, a part of the eight-gene cluster called *fit* for *P. fluorescens* insecticidal toxin (Péchy-Tarr et al. 2008). Kupferschmied et al. (2013) reported that the gene *fitD*, encodes for the actual insect toxin, fitABC and E genes encodes a type I secretion system and fitFGH genes encodes the regulatory proteins. Because the presence of potent Mcf1 toxin in the gene cluster in the Fit toxin, it is conceivable that *FitD* induces apoptosis in insect as in *P. luminescens*.

The Fit toxin gene detected in few PGPR strains, *P. protegens*, and *P. chlororaphis* showed high toxicity toward larvae of lepidopteran insects (Flury et al. 2016; Loper et al. 2012; Shen et al. 2013). Further, *P. protegens* strains CHA0 and Pf-5 were lethal to tobacco hornworm larvae, *Manduca sexta* and the greater wax moth *Galleria mellonella* (Péchy-Tarr et al. 2008). In a laboratory assay using artificial diet and leaves treated with *P. protegens* strain CHA0 and *P. chlororaphis* strain PCL1391 were shown insecticidal activity (Flury et al. 2016). Plants sprayed

with a low concentration of CHA0 and Pf-5 strains that contain Fit toxin shown insecticidal activity against *Spodoptera littoralis* (cotton ballworm), *Heliothis virescens* (tobacco budworm), and *Plutella xylostella* (diamondback moth). (Kupferschmied et al. 2013). In contrast, fit-deficient *P. fluorescens* failed to toxicity against insects in the same assay (Ruffner et al. 2013). Ruffner et al. (2013) performed host specificity test and examined the potential side effects of the *Pseudomonads* toward beneficial insects; the Fit toxin had no oral toxicity toward the important pollinator, bumblebee *Bombus terrestris*. Further research might be needed to confirm host specify of diverse species of *Pseudomonads* to that of other beneficial arthropods.

The potential of entomopathogenic PGPR demonstrated impressively by feeding Chinese cabbage leaves containing suspension of GFP (green fluorescent protein)-tagged *P. protegens* CHA0 to larvae of the large cabbage white *Pieris brassicae* (Fig. 14.2a, b) (Kupferschmied et al. 2013). The bacteria colonize the insect gut and subsequently translocated into the hemocoel by so far unknown means, where they multiply and cause disease (Fig. 14.2b). Quick invasion of the bacteria into the insect blood system indicates the level of virulence of the microorganisms, which suggests that these bacteria should be considered for pest management (Kupferschmied et al. 2013).

Regardless of the insecticidal activity of Fit toxin, when Fit toxin gene knocks out from some isolates of *P. protegens* or *P. chlororaphis* strains, is not sufficient to reduce the toxic effects of Fit toxins to insects (Maria et al. 2013; Ruffner et al. 2013). Further studies might be required to discover the virulence factors in these insecticidal pseudomonads. Candidate virulence factors that might play a role in insect pathogenicity in some of these strains are the so-called toxin complexes (Tc), first identified in *P. luminescens*. They are large multimeric insecticidal protein complexes displayed on the surface of these bacteria (Ffrench-Constant et al. 2007). Remarkably, Tc-related genes found also in some of the strains of *P. chlororaphis* and *P. fluorescens* (Loper et al. 2012) but their role in insect pathogenicity yet to be investigated.

Despite the above successful findings of pseudomonads PGPR as entomopathogen to many insect pests, no insecticidal products exist on the market for biopesticides. Pseudomonads PGPR are successfully used as bio-fungicides in agriculture, specifically for crop protection (Ahmadzadeh et al. 2006; Siddiqui et al. 2008). Thus, these entomopathogenic *Pseudomonas* fit well into integrated pest management (IPM) programs (Dotta 2015).

14.4.2 Streptomyces *spp. as an Entomopathogen*

Another important PGPR with entomopathogenic characteristic are the Actinobacteria mostly in the genera Streptomyces. *Streptomyces* spp. are notable for their toxic activity against pathogens (e.g., Breza-Boruta et al. 2004) and herbivores especially the order Lepidoptera (Arasu et al. 2013; Kaur et al. 2014;

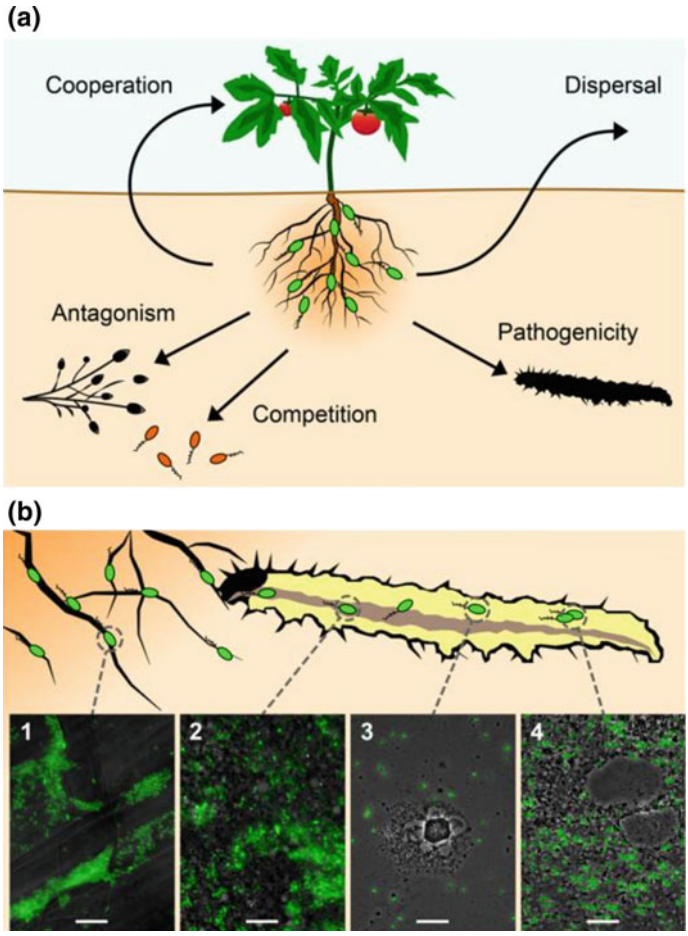

Fig. 14.2 Certain plant root-associated *Pseudomonas* bacteria exhibit insect pathogenicity as an additional trait to the well-studied biocontrol activity against phytopathogens. **a** The most important interactions of these plant-beneficial *pseudomonads* (in green) include cooperation with the plant host (growth promotion and induction of systemic resistance) and competition with and antagonism of soil-borne phytopathogens. In addition, they show insecticidal activity and can use insects as vectors for dispersal. **b** Certain strains of *Pseudomonas protegens* and *Pseudomonas chlororaphis* are capable of infecting and efficiently killing insect larvae after oral uptake. *P. protegens* strain CHA0 (here tagged with GFP for microscopical visualization) typically forms microcolonies on roots (1) of various plant species (here tomato). Following ingestion by herbivorous insects, the entomopathogenic *P. protegens* strain is able to colonize the midgut (2) of pest insect larvae (here the large cabbage white *Pieris brassicae*), possibly by competing with the intestinal microbiota. By a so far unknown mechanism CHA0 cells then cross the intestinal epithelial barrier and invade the hemocoel within less than 1 day after oral infection (3). Once in this body compartment, the bacteria proliferate, resist uptake and elimination by hemocytes and cause disease (4). Bars represent 10 μm (Adopted from Kupferschmied et al. (2013))

Vijayabharathi et al 2014; Goda et al. 2015; Sathya et al. 2016). Kaur et al. (2014) showed that high doses of secondary metabolites from *Streptomyces hydrogenas* DH16 increased mortality of *Spodoptera litura* (Fab.) larvae and lower doses prolonged development time in larvae and pupae. Polyketide metabolites from *Streptomyces* sp. AP-123 caused antifeedant and larvicidal activity on *Helicoverpa armigera* and *Spodoptera litura* larvae. Similar effects by *Streptomyces* sp. CAI-155 (Gopalakrishnan et al. 2012, 2016) and *Streptomyces griseoplanus* SAI-25 (Sathya et al. 2016) against *H. armigera* have also been documented on chickpea. These studies show that Actinobacteria have a strong potential as a biological control agent.

D-endotoxin proteins and Avermectins from *Bacillus thuringiensis* and *Streptomyces avermitilis*, respectively, are the two most toxic compounds against herbivores that have ever been identified from soil microbes. Of these two, avermectins is believed to have broad-spectrum activities against pathogens and herbivores and it is a gamma-amino butyric acid (GABA) receptor antagonist. It binds to the GABA receptor, leading to increased flow of chlorine into the muscle and subsequent muscle relaxation and eventual death of exposed organism (Ishaaya and Horowitz 1998). Since its discovery, insecticidal activities of Avermectins has been reported for insect pests from several orders and families (Lasota and Dybas 1991; Jacob and Sudini 2016; Hariprasad 2016). Negative effect of commercialized derivatives of Avermectins such as emamectin benzoate on *Cydia pomonella* and *Cydia molesta* (Ioriatti et al. 2009) and ivermectin on biology of the Indian Owlet-moth, *Spirama retorta* (Roychoudhury and Joshi 2011) is well documented. Ioriatti et al. (2009) reported that emamectin benzoate was effective at causing high mortalities to larva stages of codling moths both in laboratory and semi-field trials but minimal ovicidal effect was observed. Similarly, high mortality was recorded by invermectin on *S. retorta* a foliar pest of *Albizia* plants. However, a study showed that abamectin is very toxic to predators. Azod et al. (2016) reported 100% mortality of aphidophagous lady beetle, *Menochilus sexmaculatus* after feeding on the common pistachio psylla, *Agonoscena pistaciae*. Further studies are needed on a large scale to determine how best Avermectins and its derivatives can be integrated into current IPM systems as Coccinellids and other predators constitute a significant part of predators in agro landscapes.

14.5 PGPR Formulations for Insect Pest Control

PGPR formulations can come in ambient of different forms depending on their application. Although beneficial PGPR group of bacteria are used to ameliorate environmental degradation (Bashan et al. 2014), those for crop-specific agricultural use have been limited (Kloepper et al. 2004; Liu et al. 2016). The role of their formulation and application for agricultural needs broadly covered (Bashan et al. 2014). Depending on the availability of materials, formulations can be in liquid, solid dry powder, etc.(Arora et al. 2008; Atieno et al. 2012;

Bhattacharjya and Chandra 2013). The carrier materials can be organic (sawdust, vermicompost, peat, poultry manure, etc.) or inorganic (talc, perlite, clay soil, kaolin, etc.) or polymers (e.g., alginate), and these also depend on the need for the formulation (Bashan et al. 2002). Another determinant of the inoculum formulation depends on the characteristics of the bacteria.

There are only a few formulated PGPR inoculant for controlling insect pests in various field crops expect those commercially available for growth promotion and control of other foliar pathogens (Boutard-Hunt et al. 2009; Herman et al. 2008). However, the understanding of the "broad-spectrum" activity of many soil-inhabiting PGPR leads in this direction. The laboratory, greenhouse and field-based studies reported PGPR and some none-growth-promoting bacteria mediated plant–insect interactions with a focus on formulation media/carriers (Table 14.1). Further, as shown, most formulation was liquid and solid meant yet to address fundamental research. Only a few of the studies utilizing the various formulations [e.g., Gadhave et al. (2016a)] were conducted in the field, and very few showed carrier based formulations reported had good shelf-life (Sarma et al. 2011).

14.6 Application of PGPR Mixture

Application of PGPR depends on formulations (liquid, dry, slurry or pellets), the carrier material used for the formulations and the need-based requirement of farmers.. Given the complication of bacterial–plant–insect species specificity, PGPR is either applied singly or in the mixture (Domenech et al. 2006; Liu et al. 2016; Pangesti et al. 2013; Pineda et al. 2013; Pineda et al. 2010; Gadhave and Gange 2016; Raupach and Kloepper 1998). Certain PGPR strains promote growth of plants, but others induce resistance inplants. Targeting this discrepancy in the formulation of PGPR mixture should always inform the rationale or one of the most important reasons for formulating the product, but quite a few workers suggested that. PGPR mixture may provide broad-spectrum combination based qualities from individuals that make up the mixture with multifarious in nature. Several published works showed that application of PGPR mixture was more targeted on improvement of plant growth and yield (Cassán et al. 2009; Requena et al. 1997; Sandheep et al. 2013; Yadav and Verma 2014) except a few studies that demonstrated that a mixture of different microorganisms (*Azotobacter, Pseudomonas, and Bacillus*) enhanced their competitiveness compared to indigenous bacteria in the soil (e.g., Đalovic et al. 2013).

Table 14.1 Studies showing PGPR formulations used to test effects on insects: A few examples

PGPR strain(s)	Formulation medium/carrier	Plant species	Insect species tested	References
Pseudomonas putida 89B-61, *Serratia marsescens* 90–166, *Flavomonas oryzihatans* INR-5, *Bacillus pumilus* strain INR-7	Tryptic soybean broth (TSB)	Cucumber	*Diabrotica undecimpunctata howardi* and *Acalymma vittatum* (F.)	(Zehnder et al. 1997a)
Pseudomonas fluorescens PF1 and FP7, single and in mixture	Talc-based powder	Rice	*Cnaphalocrocis medinalis*	(Commare et al. 2002)
Pseudomonas fluorescens Pf1, TDK1 and PY15	Talc-based powder	Rice	*Cnaphalocrocis medinalis*	(Saravanakumar et al. 2007, 2008)
Bacillus subtilis strainGB03 Bacillus amyloliquefaciens IN937a	Commercial formulation	Pepper	*Myzus persicae*	(Herman et al. 2008)
Paenobacillus macerans GB122 and *Bacillus amyloliquefaciens* GB99	Commercial formulation	Pepper	*Myzus persicae*	(Boutard-Hunt et al. 2009)
Pseudomonas fluorescens (PGPR) *Beauveria bassiana* (Fungi)	Talc-based powder	Rice	*Cnaphalocrocis medinalis*	(Karthiba et al. 2010)
Bacillus subtilis BEB-DN (*Bs*DN)	Potato infusion medium	Tomato	*Bamisia tabaci*	(Valenzuela-Soto et al. 2010)
Pseudomonas fluorescens Pf1 and TDK1	Talc-based powder	Groundnut	*Aproaerema modicella*	(Senthilraja et al. 2013)
Pseudomonas fluorescens WCS417r	$MgSO_4$	*Arabdopsis*	Myzus persicae and *Diaeretiella rapae*	(Pineda et al. 2013)
Pseudomonas fluorescens WCS417r	$MgSO_4$	Tomato	*Bamisia tabaci*	(Shavit et al. 2013)
Pseudomonas fluorescens UTPF68, UTPF1, UTPF6 and CHA0	Methylcellulose solution	Cucumber	*Aphis gossypii*	(Fahimi et al. 2014)
Azospirillum brasilense	Nitro 1000	Maize	*Diabrotica speciosa*	(Santos et al. 2014)
Pseudomonas fluorescens WCS417r and *P. simiae* WCS417r	$MgSO_4$	*Arabdopsis*	*Mamestra brassicae, Pieris brassicae* and *Microplitis mediator*	(Pangesti et al. 2015a, b, 2016)

(continued)

Table 14.1 (continued)

PGPR strain(s)	Formulation medium/carrier	Plant species	Insect species tested	References
Pseudomonas putida and *Rothia* sp.	Water	Tomato	*Spodoptera litura*	(Bano and Muqarab 2017)
Bacillus cereus, *Bacillus subtilis* and *Bacillus amyloliquefaciens*	Saline water	Cucumber	*Brevicoryne brassicae*	(Gadhave and Gange 2016, 2016a, b)
Bacillus pumilis, Blend-8 and Blend-9 (both blends contained four strains)	Water	Cotton	*Spodoptera exigua*	(Zebelo et al. 2016)
Bacillus pumilis, MC1, MC2, MC3, MC4, Blend 8, Blend 18, Blend 19, Blend 20	Water	Bermudagrass	*Spodoptera frugiperda*	(Coy et al. 2017)
Bacillus velezensis YC7010	$MgSO_4$	*Arabdopsis*	*Myzus persicae*	(Rashid et al. 2017)
Bacillus pumilis, Blend-8 and Blend-9 (both blends contained four strains)	Water	Maize	*Ostrinia nubilalis* and *Diabrotica virgifera virgifera*	(Disi et al. 2018a, b)

14.7 Challenges Associated with the Use of PGPR in Sustainable Agriculture

The commercial success of PGPR strains needs economic and feasible market demand, consistent and broad-spectrum action, safety and stability, longer shelf-life, low capital costs and easy availability of career materials (Dey et al. 2014). The success and commercialization of PGPR strains depend on the collaborative work between the scientific institutions and chemical industries. These collaborative works mainly focused on the process of marketing include isolation of antagonist strains, screening, fermentation methods, mass production, formulation viability, toxicology, industrial linkages, quality control, and field efficacy. Though PGPR has potential use in sustainable agriculture and commercialization, the threat of certain PGPR (*P. aeruginosa, P. cepacia* and *B. cereus*) to impart toxicity to animals and pathogenic to human beings as opportunistic pathogens has to be clarified before large-scale acceptance (Nakkeeran et al. 2006). For example, volatile production of cyanide by some PGPR strains. Cyanide involves in growth promotion as well as a growth inhibition characteristic during PGPR–plant interactions. Moreover, cyanide acts as a biocontrol agent against specific plant pathogens (Ramette et al. 2006); likewise, cyanide can also cause adverse effects on plant growth and the environment (Solomos and Laties 1976). Potential PGPR

strains must pass through several regulatory measures to be commercially viable. The PGPR strains should not pose any threat to human and animal health and should not be an environmental hazard. Unlike the commercialization of PGPR strains used to control plant pathogens, information concerning PGPR strains used to control insect pest is very limited. Despite that PGPR have been discovered and studied for last three decades, the widespread use of these products is yet to be seen. The use of PGPR as biocontrol of pests in sustainable agriculture remains underutilized.

14.8 Concluding Remarks and Future Perspectives

This chapter highlights PGPR mediated plant–insect interactions. The interaction between PGPR–plant–insect resulted to plant growth promotion and induced defenses against insect herbivores. The effect of PGPR-induced systemic resistance against microbial pathogens has been studied for many years, but relatively little is known about the effect of ISR on herbivorous insects. Inducing resistance against herbivores is not the only mechanism through which PGPR affect plant–insect interactions. Intriguingly, certain strains of plant root-colonizing *Pseudomonas* bacteria display insect pathogenicity. There is evidence that PGPR enhance the effectiveness of natural enemies by manipulating the production of VOCs, this can also decrease herbivore pressure (Disi et al. 2018b). It is important to note that even the direct and indirect effect of PGPR-mediated defenses decreased and the herbivore pressure increases, PGPR can enhance plant biomass and yield, increasing plant tolerance against insect herbivores. Moreover, PGPR-treated plants might attract other beneficial organisms, particularly pollinators and natural enemies of herbivores, the impact of PGPR on pollinators and natural enemies might need further studies.

Beneficial microbes have an enormous contribution that ranges from increasing nutrient and moisture uptake to induction of plant defense against plant pathogens and insect herbivores. Considering this vast importance beneficial microbes might also contribute to the bio-diversification of plants. Beneficial microbes modulate plant–insect interactions, and plant genotype is vital for the successes of these mutualistic interactions. It is recommended that breeders might include traits that enhance plant–microbe interactions in their selection process. Due to the extended persistence of beneficial microbes in the environment, they can be an integral part of sustainable integrated pest management programs.

PGPR has the potential to be used in integrated pest management (IPM), with the progress of agriculture toward sustainability, PGPR will find greater use as biocontrol agents. However, we should be genuine with thoughtfulness. Numerous studies have been done over the past several decades about the potential applications of a PGPR strains of biocontrol agents in managing a number of plant disease

and pests, not much significant success achieved yet for application at field level and commercialization of PGPR products. Rigorous efforts will be required to demonstrate the benefits of the PGPR as biocontrol of plant disease and insect pests by conducting trials on farmers' field.

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Chapter 15
Potential Effect of Plant Growth-Promoting Rhizobacteria (PGPR) on Enhancing Protection Against Viral Diseases

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Abstract Plant viruses spread around the globe and have been considered one of the most critical plant pathogens, leading to severe economic losses in crop productivity and yield quality. Unlike pests, fungi, and bacteria, no direct control methods can use against viruses. Managing to plant viral diseases depends primarily on the genetic resistance of host plants and their environment, as well as on the performance of synthetic pesticides to control vectors, an essential strategy for managing viral diseases. Effective plant viral disease pesticides are available, but because residual poisoning persists, they are not considered useful in a long-term solution because of environmental hazards and public health problems. So, new ways were appealed to complement existing strategies to manage the viral disease for better and more sustainable viral disease control. The use of bioinoculants is one of the ways to protect crops that can reduce viral infection to enhance plant growth, resulting in a significant economic return for growers. In recent years, PGPR-systemic resistance to plant viruses has trended toward viral disease management, although many PGPR-ISR studies have centered on several pathogens of fungi and bacteria. This chapter will address the spectrum of PGPR-mediated ISR

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against some plant viruses including banana bunchy top virus, bean common mosaic virus strain blackeye cowpea mosaic, bean yellow mosaic virus, bitter gourd yellow mosaic virus, cucumber green mottle mosaic virus, cucumber mosaic virus, papaya ringspot virus, pepper mild mottle virus, potato virus X, potato virus Y, sunflower necrosis virus, tobacco mosaic virus, tobacco necrosis virus, tomato chlorotic spot virus, tomato mosaic tobamovirus, tomato mottle virus, tomato spotted wilt virus, tomato yellow leaf curl virus, urdbean leaf crinkle virus, and watermelon mosaic virus.

Keywords Plant viruses · Biocontrol · Crops management · PGPR · SAR · ISR

15.1 Introduction

Biotic and abiotic stresses adversely affect plant growth parameters, quality, and quantity based on the plants and stage(s), where average productivity of plant can be reduced between 65 and 87% (Gursoy et al. 2012). Plant viruses have occurred worldwide and are the most critical plant pathogens responsible for severe economic losses in the productivity and quality of many crops (Balconi et al. 2012). In contrast to pests, fungi, or bacteria, no direct control methods are evolved against viruses so far. Management of plant viral diseases depends mainly on host plants genetic resistance and their environment as well as synthetic pesticides to control vectors where it is an essential strategy in viral management (Srinivasan and Mathivanan 2009). Effective plant viral disease pesticides are available, but because residual poisoning persists, they are not considered useful in a long-term solution because of environmental health hazards (Srinivasan and Mathivanan 2009). The ever-increasing costs of pesticides, on the one hand, and consumer demand for food without pesticides, on the other, have resulted in seeking replacements for these chemical products (Gerhardson 2002). On the other hand, there are also specific diseases such as caused by certain viruses and viroids that have few, ineffective or inexistent chemical solutions (El-Dougdoug et al. 2012a; Gerhardson 2002; Sofy et al. 2013a, 2012, 2014b). It is, therefore, investigate for plant viral diseases management by inducing natural defenses of plants, e.g., systemically acquired resistance (SAR) (Ryals et al. 1994). In recent years, plant growth-promoting bacteria (PGPR)-systemic resistance to plant viruses has trended in the management of viral diseases, despite the fact that many PGPR-ISR studies have centered on several pathogens of fungi and bacteria (Kloepper et al. 2004a, b; van Loon et al. 1998), but available literature revealed the limited information on viral disease management by using PGPR and other beneficial microorganisms. Furthermore, some PGPRs stimulate plant growth, resulting in significant economic returns for growers (Babalola 2010).

15.2 PGPR-Induced Systemic Resistance Against Plant Viruses

There are two types of pathogen-induced resistance [Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR)] defined as "the activation of the host plant's chemical or physical defense mechanism by an inducer" that leads to multiple pathogens being controlled (Kloepper 1993; Kloepper et al. 1992). The ISR's expression in response to the pathogen inoculation challenge is similar to that of SAR due to reduced disease severity or reduced number of diseased plants (Van Loon and Bakker 2005). This reduction is often related to a reduction in pathogen growth and reduction of tissue invasion in induced tissues, showing that the plant can better withstand the pathogen (Van Loon 2000; Van Loon and Bakker 2005).

PGPRs are saprophytic bacterial microorganisms that are free-living in the rhizosphere and colonize the root system aggressively (Ramjegathesh et al. 2013). They can provide plants with beneficial effects through additional secretion such as vitamin, hormone, growth factors that help enhances plant growth and productivity (Babalola 2010). Several bacteria including the species of *Aeromonas*, *Agrobacterium*, *Arthrobacter*, *Alcaligenes*, *Azospirillum*, *Azoarcus*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Bradyrhizobium*, *Comamonas*, *Cyanobacteria* (predominantly *Anabaena* and *Nostoc*), *Enterobacter*, *Gluconacetobacter*, *Herbaspirillum*, *Klebsiella*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Variovorax*, *Streptomyces*, and *Xanthomonas* have been reported as PGPR (Vessey 2003). Some of these genera such as *Azoarcus*, *Burkholderia*, *Gluconacetobacter*, and *Herbaspirillum* established in cells and tissues of higher plants thus are called include endophytic species (Vessey 2003). However, the majority of PGPR strains registered are *Pseudomonas* and *Bacillus* species (Ramamoorthy et al. 2001). PGPRs are regarded as inducing systemic resistance, which can reduce the severity of some diseases in crop plants, termed as PGPR-induced systemic resistance (Kloepper et al. 1992).

Salicylic acid (SA) is a key signaling molecule that works locally in intracellular signal transduction (Shirasu et al. 1997). It may enhance the release of H_2O_2 and H_2O_2-derived active oxygen and induce activities of defense-related genes (Shirasu et al. 1997). Two downstream signaling pathways of salicylic acid reported as the defense mechanism, where the first pathway triggers fungal and bacterial resistance through *PR* and *NPR1* genes expression, and the other stimulates resistance to viral infection through alternative oxidase (Murphy et al. 1999). Since hormones primarily regulate plant defense against viruses, first relying on salicylic acid and second on jasmonic acid (Alazem and Lin 2015). On the other hand, due to the link between SA-mediated defense and siRNA antiviral mechanism, salicylic acid is considered to be extremely important for the resistance (local & systemic), where it participates in basal immune responses and *R*-gene resistance (Alamillo et al. 2006; Alazem and Lin 2015; Baebler et al. 2014; Beris et al. 2018). The defense response based on salicylic acid involves mitogen-activated kinase activation leading to increased *NPR1* regulation, thereby induces *PR* genes transcription (Beckers et al.

2009; Gkizi et al. 2016; Hirt et al. 2013; Kohler et al. 2002; Yi et al. 2015). Further, the treatment with salicylic acid or biologically active salicylic acid analogs led to the expression of the gene *NtRDRP1* (Beris et al. 2018). The gene *NtRDRP1* triggered following infection with many viruses is an essential element in the defense of plants against viral infection (Beris et al. 2018; Xie et al. 2001). PGPR activates ISR in salicylate-dependent and -independent manners and intersects somewhat with the jasmonate/ethylene pathway (Niu et al. 2011; Ryu et al. 2004; van Wees et al. 2000). Multiple strains of rhizobacteria were observed to produce salicylic acid (Van Loon and Bakker 2005). There are two criteria for clarifying whether these strains elicit ISR via SAR pathway activation depending on SA; first, *PRs* induction must be related to ISR; second, induced systemic resistance and *PRs* induction must be nullified in NahG plants (Van Loon and Bakker 2005). Experiments by De Meyer et al. (1999) with transformed tobacco of NahG (SA hydroxylase gene transgenic) revealed that salicylic acid accumulation in plants resulting from induced resistance of *Pseudomonas aeruginosa* strain 7NSK2 is due to its expression, but not due to its induction, and is therefore identical to SAR induced by tobacco mosaic virus (TMV), which is also not expressed in NahG tobacco (Gaffney et al. 1993). The characteristic, salicylic acid-stimulating *PRs* in tobacco plants were expressed when ISR was elicited against TNV via *Pseudomonas fluorescens* strain CHA0 (Maurhofer et al. 1994). Similarly, the expression of biosynthetic genes of salicylic acid (*pchA* & *pchB*) in the salicylic acid negative, root-colonizing *P. fluorescens* strain P3 considerably enhanced its capacity to trigger resistance against TNV in tobacco, confirming that salicylic acid induces SAR against viruses (Maurhofer et al. 1998). Unlike salicylic acid-producing *Pseudomonas fluorescens* strain CHA0, when the genes (*pchA* & *pchB*) were introduced, salicylic acid production increased but didn't enhance ISR in tobacco against TNV (Maurhofer et al. 1998). On the other hand, root application of *Bacillus subtilis* strain G1 triggered ISR against TMV by activating the signaling defense genes (*PR-1a* and *PR-1b*), and regulatory genes (*NPR1* and *Coi1*) indicating salicylic acid signaling pathway activation (Wang et al. 2009). However, unlike SAR, resistance induced by *P. aeruginosa* strain 7NSK2 during the TMV challenge time was not linked to the expression of *PR1a* (De Meyer et al. 1999). So, De Meyer et al. (1999) suggested that treatment with strain 7NSK2 would only enhance expression of the systemic tissue defense gene, which also explains why its resistance level is lower than in case of SAR. On the other hand, SA elicitation and ethylene signaling indicate expression patterns of encoding the osmotin-like protein (*CaPR5*) and the encoding of putative antifungal protein (*CaPR4*) (Choi and Hwang 2014). Similarly, the characteristic, SA-inducible PRs (*CaPR4*, *CaPR5*, and *CaPR10*) expressed in pepper plants when ISR was triggered by *Bacillus amyloliquefaciens* strain 5B6 against CMV (Lee and Ryu 2016). Beris et al. (2018) experiments also showed that after treatment with *B. amyloliquefaciens* strain MBI600, the salicylic acid signaling pathway induction in tomato plants and various patterns of gene expression of tomato defense-related genes have been detected against potato virus Y (PVY) and tomato spotted wilt virus (TSWV) infection. Beris et al. (2018) revealed this through transcriptional analysis of a group of genes

connected with SA-related defense [*SlRdR1* (Xie et al. 2001), *SlNPR1* (Kohler et al. 2002), *SlPR1b.1* (Block et al. 2005)] or JA-related defense [*SlLoxD* (Hu et al. 2015) and *SlCOI1* (Xie et al. 1998)], priming [*SlNPR1* (Yi et al. 2015), *SlMPK3* (Beckers et al. 2009)], or RNAi basal defense against viruses [*SlRdR1* (Xie et al. 2001)] (Beris et al. 2018). In comparison, *B. amyloliquefaciens* strain EXTN-1 treated *Arabidopsis* wild-type Col-0 plants resulted in the simultaneous activation of two representative molecular markers (*PR-1* & *PDF1.2*), indicating that strain EXTN-1 induces systemic resistance through SA-dependent and JA-dependent pathways (Ahn et al. 2002). Similarly, experiments of Park et al. (2006) with *B. vallismortis* strain EXTN-1 in transgenic tobacco have proved that there was activation of *PR-la* and *PDF1.2* defense genes upon treatment with EXTN-1 indicating involvement of a salicylic acid (SA) and jasmonic acid (JA) dependent pathway, where *PR-la* and *PDF1.2* genes frequently used as SA and JA signaling indicators, respectively (Reymond and Farmer 1998). Indeed, tobacco plants treatment with *B. amyloliquefaciens* strain EXTN-1 resulted in earlier and increased expression of defense-associated genes (HMGR, PAL, and *PR-1a*) in the presence of pepper mild mottle virus infection at non-inoculated, upper leaves; hence, resistance phase established by EXTN-1 treatment developed locally and systemically (Ahn et al. 2002). On the other hand, treatment with *B. amyloliquefaciens* strain EXTN-1 alone did not induce such strong gene activation (Ahn et al. 2002). 3-hydroxy-3-methylglutaryl CoA reductase (HMGR), phenylalanine ammonia-lyase (PAL), and *PR-1a* genes perceived as the reliable molecular markers, wherein tobacco defense system(s) via salicylic acid-dependent pathway was activated or not (Ahn et al. 2002). Since the expression of these genes was induced within a short time after TMV infection under the tobacco *N* gene-activated state (Kang et al. 1998). Further, mRNA accumulations of these genes also induced by the salicylic acid treatment (Klessig et al. 1994).

Conversely, Ryu et al. (2004) reported that *Arabidopsis thaliana* is protected by *Serratia marcescens* strain 90-166 from cucumber mosaic virus (CMV) through a virus protection signaling pathway in which *NPR1*- and SA are independent, but JA-dependent. Since the severity of CMV symptoms in NahG and Col-0 plants has been reduced with strain 90-166 and its SA-deficient mutant 90-166-1441, in addition to the absence of induction of the *PR-1* gene through strain 90-166, which is generally used as a salicylic acid signaling indicator, indicating that resistance has occurred via a salicylic acid-independent pathway against CMV (Ryu et al. 2004).

Hydrogen peroxide (H_2O_2) is a systemic source of the early molecular signal that strengthens apoptotic tissue and causes cell infection apoptosis (Ahn et al. 2011). H_2O_2 is a standard response to plant pathogens, a key signal that stimulates defensive responses (Zhang et al. 2009). PGPR-triggered ISR is also related to activation for increased cell defensive responses to pathogen attacks, like accelerated accumulation of H_2O_2 (Conrath et al. 2002; Niu et al. 2011; Van Wees et al. 2008). Li et al. (2016a) reported that *Enterobacter asburiae* BQ9 initiated the tomato plants to accelerate and improve the ability to activate cellular defense responses systemically (production of H_2O_2) triggered only via the attack of tomato yellow leaf curl virus (TYLCV). A large number of ISR-related defense enzymes include PAL, polyphenol oxidase (PPO), ascorbate peroxidase (ASC), peroxidase

(POD), superoxide dismutase (SOD), glutathione reductase (GR), lipoxygenase (LOX), catalase (CAT), chitinase, β-1,3-glucanase, and proteinase inhibitors (Van Loon and Bakker 2005). Furthermore, these enzymes give rise to molecules liberation that generates the primary steps in resistance induction, because of phenolic compounds and phytoalexins (Chen et al. 2000; Sofy et al. 2014a, b, 2018a, b; Vanitha and Umesha 2011). The phenolic compounds are oxidized by peroxidase into their quinone derivatives, which inhibits viruses through viral RNA inactivation (Lamb and Dixon 1997).

In *Phaseolus vulgaris, Bacillus globisporus* and *Pseudomonas fluorescens*–treated leaves showed increased activity of peroxidase and β-1,3-glucanase, respectively in pathogen-inoculated leaf sheaths, tobacco necrosis virus (TNV) (Shoman et al. 2003). On the other hand, polyacrylamide-gel electrophoretic analysis detected two similar induced proteins in *Phaseolus vulgaris* leaves treated with culture filtrates of *Streptomyces gibsonii* and *P. fluorescens* compared to the control (water-treated), which may play a role in defense mechanism in P. vulgaris plants against TNV (Shoman et al. 2003). PAL has a vital function in multiple secondary metabolites synthesis, such as phenylpropanoids and phenols, as well as salicylic acid derivatives and lignin, which imparts immunity to plants and stimulates PGPR-triggered resistance (Gerasimova et al. 2005; Harish et al. 2008; Li et al. 2016a). Since secondary metabolites accumulation is intended to limit the invasion of viruses (Lian et al. 2011). So, induction of defense enzymes (POD, PPO, and PAL), and *PR* proteins by application of *P. fluorescens* strains can improve plants to be resistant to banana bunchy top virus (BBTV) (Harish et al. 2008) and tomato spotted wilt virus (TSWV) (Kandan et al. 2005). Likewise, in *Bacillus*-treated tobacco plants challenged with tomato spotted wilt virus, the defense enzyme (POD, PPO, and PAL) amount and *PR* proteins have been increased significantly compared to control (Lian et al. 2011). Damayanti et al. (2007) reported that *Bacillus* sp. strain I-6, *Bacillus cereus* strain I-35, and *Brevibacterium sanguinis* strain I-16 increased the POD activity in hot pepper plants after TMV inoculation, suggested that these rhizobacteria might able to enhance plant's defense response through high POD activity. Similarly, increased total phenols and activity of defense enzymes (POD & PPO) observed in *Streptomyces griseorebens* and *S. cavourensis*-treated cucumber plants challenged with *Cucumber mosaic virus* (Shafie et al. 2016).

Also, *Rhizobium leguminosarum* bv. *viceae* (mixtures of ICARDA-441 and ARC-202) induced systemic resistance against bean yellow mosaic virus (BYMV) via seed treatment, where enhanced levels of defense enzymes activities (peroxidase and polyphenol oxidase), total phenols, and free proline observed in faba bean (Sofy et al. 2014a). Further stated five unique (polypeptide markers) induced in *R. leguminosarum* bv. *viceae* (ICARDA-441 + ARC-202)-treated faba bean plants inoculated with the BYMV (Sofy et al. 2014a). One of the first plant responses to bacterial, fungal and viral infections is active oxygen species production, whereas superoxide dismutase, a significant antioxidant enzyme, provides cell protection in plants from active oxygen species by converting $O2^{-}$ to H_2O_2 and O_2 (Fridovich 1986; Mehdy 1994; Vanacker et al. 2000). Recently Li et al. (2016a) noted that

Enterobacter asburiae BQ9 generated systemic acquired resistance in tomato plants against TYLCV, where the activities of PAL, POD, CAT, and SOD were significantly increased in TYLCV-challenged *E. asburiae* BQ9-pretreated plants. Furthermore, *PR1* (*PR1a* and *PR1b*) gene transcriptions of BQ9-treated tomato plants, which were challenged by TYLCV, were faster and broader than untreated plants. Li et al. (2016a, b further noted that the replication of cucumber green mottle mosaic virus (CGMMV) in pretreated cucumber plants with *Stenotrophomonas maltophilia* strain HW2 was delayed for more than three days, as well as increased expression of both defense-associated genes (*PR1* and *PR5*) and defense-associated enzymes (CAT and SOD), resulting in increased cucumber resistance.

15.3 Viral Protection Spectrum via PGPR

Lately, research on the ISR-mediated PGPR scope against viruses in various plants has gained significance. Several species of (PGPR) are used as microbiological inoculants for protecting plants from virus infection and enhancing crop yield as shown in the Table (15.1).

15.3.1 Banana Bunchy Top Virus

Banana bunchy top virus (BBTV), a member of the *Nanoviridae* family (*Babuvirus* genus), causes the bunchy top disease, a serious banana virus disease (*Musa* spp., *Musaceae*) (Dale 1987; Harding et al. 1991). It is transmitted in a persistent circulative and non-replicative manner by the aphid vector *Pentalonia nigronervosa* Coq. (Hu et al. 1996). The disease is difficult to eradicate and manage, where there are no possible strategies currently available to protect these plants against BBTV completely (Harish et al. 2008). Nevertheless, another way of integral management of this disease is for ISR to use in vitro virus-free micropropagated banana plantlets with rhizobacteria (PGPR) and endophyte bacteria (PGPE) to strengthen the plant against the virus (Harish et al. 2008). For instance, the application of *Streptomyces chibaensis* culture filtrate ten days prior to BBTV inoculation highly inhibited BBTV infection (Hewedy et al. 2008). In field conditions, the treatment of plants with a mixture formulated as (EPB5 + EPB22 + Pf1 + CHA0) was also very successful in limiting BBTV, where the mixture consisted of one strain of endophytic *Pseudomonas* (EPB5), one strain of endophytic *Bacillus* (EPB22), and two strains of rhizobacterial *P. fluorescens* (Pf1 & CHA0) (Harish et al. 2008). Further, Kavino et al. (2007a, b) indicated the effective use of a mixture beneficial microbes (EPB22 + Pf1 + CHA0) in reducing the disease incidence of BBTV in tissue culture banana plantlets. Also, according to Kavino et al. (2009), the two chitin-formulated *P. fluorescens* strains (Pf1 and CHA0) have demonstrated their effectiveness in BBTV control. In another study, under greenhouse and field

Table 15.1 Management of plant viruses using PGPR

Virus	Plant	Potential PGPR	References
Banana bunchy top virus (BBTV)	Banana (*Musa* spp.)	*Streptomyces chibaensis*	(Hewedy et al. 2008)
		Pseudomnas (EPB5) + *Bacillus* (EPB22) + *P. fluorescens* (Pf1 + CHA0)	(Harish et al. 2008)
		Bacillus (EPB22) + *P. fluorescens* (Pf1 + CHA0)	(Kavino et al. 2007a, b)
		P. fluorescens (Pf1 + CHA0)	(Kavino et al. 2009)
		Bacillus (EPB22) + *P. fluorescens* (Pf1)	(Harish et al. 2009a)
Bean common mosaic virus strain blackeye cowpea mosaic (BCMV-BlCM)	Cowpea (*Vigna unguiculata*)	*B. subtilis* (GB03) + *B. pumilus* (T4)	(Shankar et al. 2009)
Bean yellow mosaic virus (BYMV)	Faba bean (*Vicia faba*)	*P. fluorescens* (FB11)	(Elbadry et al. 2006)
		*R. leguminosarum*bv. *viceae* (FBG05)	
		*R. leguminosarum*bv. *viceae* (ICARDA-441 + ARC-202)	(Sofy et al. 2014a)
		Microbien (*Azotobacter* sp. + *Asosprillum* sp. + *B. megaterium* + *P. fluorescens* + *R. leguminosorum*)	(Hilal et al. 2016)
Bitter gourd yellow mosaic virus (BGYMV)	Bitter gourd (*Momordica charantia*)	*P. chlororaphis*	(Rajinimala et al. 2009)
		P. fluorescens	
Cucumber green mottle mosaic virus (CGMMV)	Cucumber (*Cucumis sativus*)	*Stenotrophomonas maltophilia* (HW2)	(Li et al. 2016b)
	Watermelon (*Citrullus lanatus*)	*P. oleovorans* (KBPF-004)	(Kim et al. 2017)
Cucumber mosaic virus (CMV)	Cucumber (*Cucumis sativus*)	*P. syringae* pv. *lachrymans*	(Bergstrom et al. 1982)
		P. fluorescens	(Raupach et al. 1996)
		Serratia marcescens	
		B. pumilus (SE49) + *B. amyloliqefaciens* (IN937a)	(Jetiyanon and Kloepper 2002)
		B. pumilus (SE49 + IN937b)	(Jetiyanon et al. 2003; Jetiyanon and Kloepper 2002)
		B. pumilus (SE34 + IN937b)	(Jetiyanon et al. 2003)
		Streptomyces violaceusniger	(Galal 2006)
		Azotobacter chroococcum	(El-Borollosy and Oraby 2012)
		P. fluorescens	
		Streptomyces calvus	(El-Dougdoug et al. 2012b)
		Streptomyces canarius,	
		Streptomyces vinaceusdrappus	
		Streptomyces nogalater	
		Streptomyces viridosporus	
		Streptomyces griseorebens	(Shafie et al. 2016)
		Streptomyces cavourensis	

(continued)

Table 15.1 (continued)

Virus	Plant	Potential PGPR	References
	Tomato (*Solanum lycopersicon* L.)	*Pseudomonas fluorescens*	(Raupach et al. 1996)
		Serratia marcescens	
		B. amyloliquefaciens (IN937a)	(Zehnder et al. 2000, 2001)
		B. subtilus (IN937b)	
		B. pumilus (SE34)	
		B. amyloliquefaciens (IN937a) + *B. subtilis* (GB03)	(Murphy et al. 2003)
		Azospirillum lipoferum (MRB16) + *A. brasilienses* (SP7) + *A. brasilienses* (N040) + *Anabena oryzae* Fritsch	(Dashti et al. 2007)
		P. aeruginosa + *Stenotrophomonas rhizophilia*	(Dashti et al. 2012)
	Pepper (*Capsicum annuum*)	*B. amyloliquefaciens* strain 5B6	(Lee and Ryu 2016)
	Tobacco (*Nicotiana tabacum*)	*B. pumilus* (SE34)	(Kloepper et al. 2004b)
		Pseudomonas chlororaphis (O6)	(Ryu et al. 2007a)
		Paenibacillus lentimorbus (B-30488)	(Kumar et al. 2016)
	Arabidopsis thaliana	*Serattia marcescens* (90-166)	(Ryu et al. 2004)
		B. pumilus (SE34)	
		B. subtilis (GB03) + *B. amyloliquefaciens* (IN937a)	(Ryu et al. 2007b)
Papaya ringspot virus (PRSV)	Squash	*B. pumilus* (SE34) + *B. amyloliquefaciens* (IN937a)	(Abdalla et al. 2017)
		B. pumilus (SE34) + *B. sphaericus* (SE56) + *B. amyloliquefaciens* (IN937a)	
Pepper mild mottle virus (PMMoV)	Tobacco (*Nicotiana tabacum*)	*B. amyloliquefaciens* (EXTN-1)	(Ahn et al. 2002)
	Pepper (*Capsicum annuum*)	*P. oleovorans* (KBPF-004)	(Kim et al. 2017)
Potato virus X (PVX)	Tobacco (*Nicotiana tabacum* L. cv. White Burley)	*Streptomyces afghanensis*	(Hussein 1992)
	Potato (*Solanum tuberosum*L.) variety Daeseo	*B. vallismortis* (EXTN-1)	(Park et al. 2006)
Potato virus Y (PVY)	*Chenopodium quinoa*	*Streptomyces erythraeus* (QS01)	(Mohamed and Galal 2005)
		Streptomyces erythraeus (QS02)	
		Streptomyces naganishii (QS03)	
		Streptomyces michigansis (QS04)	
	Potato (*Solanum tuberosum* L. variety Daeseo)	*B. vallismortis* (EXTN-1)	(Park et al. 2006)
	Tomato (*Solanum lycopersicon* L.)	*B. amyloliquefaciens* (MBI600)	(Beris et al. 2018)

(continued)

Table 15.1 (continued)

Virus	Plant	Potential PGPR	References
Sunflower necrosis virus (SNV)	Sunflower (*Helianthus annuus* L.)	PGPMC-1 [*Streptomyces fradiae* (MML1042) + *B. licheniformis* (MML2501) + *Bacillus* (MML2551) + *P. aeruginosa* (MML2212)]	(Srinivasan and Mathivanan 2009)
Tobacco mosaic virus (TMV)	Tobacco (*Nicotiana tabacum*)	*P. syringae*	(Loebenstein and Lovrekovich 1966)
		B. uniflagellatus	(Mann 1969)
	Datura metel	*Streptomyces rochei*	(Mansour et al. 1988)
	Tobacco (*Nicotiana tabacum*)		
	Tobacco (*Nicotiana tabacum* L. cv. White Burley)	*Streptomyces afghanensis*	(Hussein 1992)
	Tobacco (*Nicotiana tabacum* L. cv. White Burley)	*P. aeruginosa* (7NSK2)	(De Meyer et al. 1999)
	Tobacco (*Nicotiana glutinosa*)	*Streptomyces erythraeus* (QS01)	(Mohamed and Galal 2005)
		Streptomyces erythraeus (QS02)	
		Streptomyces naganishii (QS03)	
		Streptomyces michigansis (QS04)	
	Hot Pepper	*B. cereus* (I-35)	(Damayanti et al. 2007)
	Tomato (*Lycopersicon esculentum*)	*Pseudomonas* spp. (B-25)	(Kirankumar et al. 2008)
	Tobacco (*N. tabacum* cv. NC89)	*B. subtilis* (G1)	(Wang et al. 2009)
		B. amyloliquefaciens (FZB24)	
	Tobacco (*Nicotiana tabacum*)	*B. subtilis* (SW1)	(Lian et al. 2011)
		B. pumilus (EN16)	
	Tobacco (*N. tabacum* cv. Xanthi-nc)	*P. chlororaphis* (O6)	(Park et al. 2012)
	Tobacco (*Nicotiana tabacum*)	*B. amyloliquefaciens* (Ba33)	(Shen et al. 2013)
	Tobacco (*N. tabacum*cv. Xanthi-nc)	*P. oleovorans* (KBPF-004)	(Kim et al. 2017)
Tobacco necrosis virus (TNV)	Tobacco (*Nicotiana tabacum*)	*P. fluorescens* (CHA0)	(Maurhofer et al. 1994, 1998)
		P. fluorescens (P3)	(Maurhofer et al. 1998)
	Bean (*Phaseolus vulgaris*)	*P. fluorescens*	(Shoman et al. 2003)
		Streptomyces gibsonii	
Tomato chlorotic spot virus	Tomato (*Solanum lycopersicon* L.)	*B. amyloliquefaciens* (IN937a)	

(continued)

Table 15.1 (continued)

Virus	Plant	Potential PGPR	References
(TCSV)		*B. pumilus* (SE34) + *B. amyloliquefaciens* (IN937a)	(Abdalla et al. 2017)
		B. pumilus (SE34) + *B. sphaericus* (SE56) + *B. amyloliquefaciens* (IN937a)	
Tomato mosaic tobamovirus (ToMV)	Tobacco (*Nicotiana tabacum* L. cv. White Burley)	*Streptomyces afghanensis*	(Hussein 1992)
	Datura metel	*P. fluorescens 2*	(Megahed et al. 2013)
		B. circulans	
Tomato mottle virus (ToMoV)	Tomato (*Lycopersicon esculentum*)	*B. amyloliquefaciens* (IN 937a)	(Murphy et al. 2000; Zehnder et al. 2001)
		B. subtilis (IN 937b)	
		B. pumilus (SE34)	
Tomato spotted wilt virus (TSWV)	Tomato (*Lycopersicon esculentum* cv. Co-3)	*P. fluorescens* (CHA0)	(Kandan et al. 2002; 2005)
		P. fluorescens (CHA0 + CoT-1)	
		P. fluorescens (CHA0 + CoT-1 + CoP-1)	
	Tomato (*Solanum lycopersicon* L.)	*B. amyloliquefaciens* (MBI600)	(Beris et al. 2018)
Tomato yellow leaf curl virus (TYLCV)	Tomato (*Lycopersicon esculentum* cv. Hezuo 903)	*Enterobacter asburiae* (BQ9)	(Li et al. 2016a)
Urdbean leaf crinkle virus (ULCV)	Blackgram (*Vigna mungo*)	*P. fluorescens* (pf1)	(Karthikeyan et al. 2009)
		P. fluorescens (CHA0)	
Watermelon mosaic virus (WMV)	Pumpkin (*Cucurbita maxima*)	*B. pumilus* 293 (B2)	(Elbeshehy et al. 2015)

conditions, mixture application (EPB22 + Pf1) increased yield by reducing the BBTV incidence (Harish et al. 2009a). Since bacterized plants significantly activate PR proteins, defense enzymes (PPO, POD, PAL, chitinase, and ß-1,3-glucanase) and phenolic compounds, thereby inducing resistance to BBTV (Harish et al. 2009a, b; Kavino et al. 2007b).

15.3.2 Bean Common Mosaic Virus Strain Blackeye Cowpea Mosaic

Bean common mosaic virus strain blackeye cowpea mosaic (BCMV-BlCM), a member of the family *Potyviridae* (genus *Potyvirus*) in cowpea (*Vigna unguiculate*, *Fabaceae*) is seed-transmitted, where the frequency of transmission is as high as

31%, and economic yield losses encountered, whenever virus-infected seed is used (Puttaraju et al. 2002; Zettler and Evans 1972). Also, BCMV-BlCM is aphid-transmitted in the field through *Aphis crassivora* and *Myzus persicae* in a nonpersistent manner (Murphy et al. 1987). Both aphid- and seeds-transmitted can lead to high yield losses, requiring the use of chemical control in aphids or the production of virus-free seeds or disease management through induced systemic resistance using PGPR (Hao et al. 2003). Shankar et al. (2009) used seven PGPR strains [*Bacillus pumilus* (T4), *B. amyloliquefaciens* (IN937a), *B. pumilus* (INR7), *B. subtilis* (SE34), *B. subtilis* (IN937b), *B. subtilis* (GB03), and *Brevibacillus brevis* (IPC11)] as promising inducers against BCMV-BlCM. All PGPR strains showed a significant increase in seed germination and seedling vigor and a decrease in the incidence of BCMV compared to untreated control under both greenhouse and field conditions (Shankar et al. 2009). Since under greenhouse conditions, the strains (GB03 and T4) provided 41 and 42% protection, respectively, in the treated cowpea seeds against BCMV-BlCM, whereas the strain (GB03) provided 34% under field conditions (Shankar et al. 2009). On the other hand, application of a combination of the two strains (GB03 + T4) registered the highest protection of 69 and 62% against BCMV-BlCM under greenhouse and field conditions, respectively (Shankar et al. 2009).

15.3.3 Bean Yellow Mosaic Virus

Bean yellow mosaic virus (BYMV), a member of the *Potyviridae* family (*Potyvirus* genus), is transmitted by many aphid species in a nonpersistent manner, one of the most frequently found and probably most damaging viruses affecting the production of field-grown legumes and some non-legumes (Bos 1970; Boswell and Gibbs 1983; Edwardson and Christie 1991; Fauquet et al. 2005). Faba bean (*Vicia faba* L., *Fabaceae*) is considered the most important nutritious popular food crop in Egypt and other countries around the world (Elbadry et al. 2006; Sofy et al. 2014a). Makkouk et al. (2003) recorded BYMV in 89% of the samples collected from surveyed Egyptian faba bean fields with high-level BYMV symptoms (80–100% infection). Controlling of BYMV is difficult due to its quite broad host range and its ability to be transmitted in a nonpersistent manner by many aphid species and also through seeds in certain legume species (Berlandier et al. 1997; Frison et al. 1990). Elbadry et al. (2006) investigated ISR in faba bean against BYMV through seed bacterization with *Rhizobium leguminosarum* bv. *viceae* strain FBG05, and *Pseudomonas fluorescens* strain FB11 individually or in combination. The results showed a decrease in the concentration of BYMV (ELISA) and the percentage of disease incidence (PDI) in the BYMV-challenged plants treated individually with strains (FBG05 and FB11) compared to non-bacterized and control-challenged plants (Elbadry et al. 2006). Co-inoculant preparation of the two strains (FBG05 + FB11) revealed an insignificant additional reduction of the ELISA value or PDI compared to the strain (FB11) alone which caused a marked reduction

(Elbadry et al. 2006). Also, Sofy et al. (2014a)_ENREF_44 investigated the mixture of two *R. leguminosarum* bv. *viceae* strains (ICARDA-441 + ARC-202) that triggered ISR against BYMV-induced bean yellow mosaic disease with significant increases in the levels of abscisic acid, salicylic acid, jasmonic acid in addition to total phenol, free proline and the activities of peroxidase and polyphenol oxidase enzymes compared to the non-bacterized and controlled challenged plants. Hilal et al. (2016) also observed induced systemic protection using five formulations of PGPR [Biogen (*Azotobacter* sp.), Cerealin (*Azotobacter* sp. + *Asosprillum* sp. + *Bacillus polymixa*), Microbien (*Azotobacter* sp. + *Asosprillum* sp. + *B. megaterium* +*Pseudomonas fluorescens*+ *Rhizobium leguminosorum*), Nitrobien (*Azotobacter* sp. + *Asosprillium* sp.) and Rhizobacterin (*Azotobacter* sp. + *Asosprillum* sp. + *R. leguminosarum*)] as foliar spraying or seed soaking of faba bean against *Botrytis fabae* and BYMV. Interestingly, Microbien's foliar treatment significantly reduced the incidence and severity of the disease for both *Botrytis fabae* and BYMV (Hilal et al. 2016). Therefore, PGPR strain could be used in the same crop to cause resistance to several pathogens (Ramamoorthy et al. 2001).

15.3.4 Bittergourd Yellow Mosaic Virus

Bitter gourd (*Momordica charantia* L., *Cucurbitaceae*) is considered an ancient species native to tropical Asia and Africa (Behera et al. 2010). It is widespread in China, Malaysia, India, and tropical Africa (Behera et al. 2010). Bitter gourd yellow mosaic virus (BGYMV), a member of the *Geminiviridae* family (*Begomovirus* genus) is one of the viruses that affect the bitter gourd causing severe yield loss due to its vector whitefly *Bemisia tabaci* (Rajinimala et al. 2005, 2009). Induction of systemic disease resistance in bitter gourd plants against BGYMV is one of the methods used for controlling the disease (Rajinimala et al. 2003, 2009). Seed treatment with *P. chlororaphis* and *P. fluorescens* has consistently reduced the disease incidence at 45 days after sowing (DAS), and further, it is significantly reduced at 75 DAS compared to inoculated untreated control (Rajinimala et al. 2009). The mean plant height of *P. chlororaphis*- and *P. fluorescens*-treated plants at 75 DAS was higher than in the inoculated control, as well as significantly increased phenol content, peroxidase activity, and polyphenol oxidase activity (Rajinimala et al. 2009).

15.3.5 Cucumber Green Mottle Mosaic Virus

Ainsworth (1935) first described the cucumber green mottle mosaic virus (CGMMV), a member of the *Virgoviridae* family (*Tobamovirus* genus), when it was found to cause cucumber disease in England. It also affects other vegetable

crops such as squash, pumpkin, zucchini, and gherkin, and the fruit cucurbits of watermelon and melon (Dombrovsky et al. 2017). As a result of increased trade between different regions, CGMMV spread rapidly through mechanical means, seeds, soil, pollen, and other propagating materials (Liu et al. 2014, 2016c; Reingold et al. 2015). Li et al. (2016b) used *Stenotrophomonas maltophilia* strain HW2 to control CGMMV, where it demonstrated its ability to promote the growth of cucumber plants, colonize effectively in cucumber rhizosphere, and its effectiveness against CGMMV was good. Li et al. (2016b) found that the replication of CGMMV in pretreated cucumber plants with the strain (HW2) delayed for more than three days and that the expression of viral protein genes in the leaf was inhibited compared to the control. Additionally, the expression of both defense-associated genes (*PR1* and *PR5*) and defense-associated enzymes (CAT & SOD) increased by the strain (HW2) resulting in increased cucumber resistance (Li et al. 2016b). On the other hand, Kim et al. (2017) evaluated the antiviral activity of *Pseudomonas oleovorans* strain KBPF-004 in CGMMV seed transmission compared to strain ATCC 8062 (control strain). Since virus-infected seeds harvested from infected watermelon plants were treated with cell-free culture supernatant of each strain before planting compared to untreated CGMMV-infected seeds (Kim et al. 2017). Kim et al. (2017) found that strain KBPF-004 reduced the rate of GGMMV seed transmission to 15.8% compared to 59.7% for strain ATCC 8062, indicating that the viability of GGMMV was adversely affected by strain KBPF-004.

15.3.6 Cucumber Mosaic Virus

Cucumber mosaic virus (CMV), a member of the *Bromoviridae* family (*Cucumovirus* genus), has a host range of more than 1200 plants in over 100 families worldwide, including crops, vegetables, ornamentals, and woody plants, where it is transmitted in a nonpersistent manner by at least 75 species of aphid (El-Dougdoug et al. 2014a; Megahed et al. 2012; Mochizuki and Ohki 2012; Palukaitis et al. 1992; Sofy and Soliman 2011; Tóbiás et al. 1982).

Several authors studied the induction of systemic disease resistance against CMV in plants such as cucumber, tomato, pepper, tobacco, and *A. thaliana* as follows. Bergstrom et al. (1982) were the first to show that the cucumber leaves treated with *P. syringae* pv. *lachrymans* induced systemic resistance to CMV. The number of chlorotic and primary lesions in CMV-inoculated decreased and systemic mosaic symptoms delayed (Bergstrom et al. 1982). Also, seed treatment of cucumber or tomato with *S. marcescens* 90-166, and *P. fluorescens* 89B-27 reduced the mean number of CMV symptomatic plants resulting in systemic resistance (Raupach et al. 1996). Protection against CMV PGPR seed treatment has either eliminated the development of viral symptoms in cucumber cotyledons or reduced disease severity in tomato (Raupach et al. 1996). Similarly, *S. marcescens* strain 90-166 and *B. pumilus* strain SE34 systemically protect *A. thaliana*, by reducing the

severity of the CMV symptoms and significantly reducing its accumulation in systemically infected leaves (Ryu et al. 2004). Further, Ryu et al. (2007a) noted that the *GacS* global regulator's role in the rhizosphere-competent *P. chlororaphis* strain O6 is relevant in stimulating growth promotion and inducing resistance in tobacco cv. Samsun. El-Borollosy and Oraby (2012) recommended the use of *Azotobacter chroococcum* followed by *P. fluorescens* to promote cucumber growth and induce systemic resistance against CMV. Whereas, two types of treatment were performed: (i) healthy cucumber plants were sprayed and subsequently inoculated with CMV after spraying at intervals (5 and 10 days) and (ii) healthy cucumber seeds were irrigated every 3 days–15 days with two hundred ml of each bacterial culture or supernatants and afterward inoculated with CMV (El-Borollosy and Oraby 2012).

Several authors characterized the role of *Streptomyces* isolates as PGPR in ISR against CMV. Galal (2006) found that the foliage treatment with culture filtrates of the five *Streptomyces* strains (*S. violarus*, *S. nasri* strain H35, *Streptomyces* sp., *S. aureofaciens*, and *S. violaceuisniger*) resulted in 50–85% reduction of the mosaic symptoms. Application of bacterial filtrate before CMV inoculation showed a higher level of antiviral activity than after CMV inoculation when the most favorable incubation period was after 6 h of incubation (Galal 2006). On the other hand, seeds soaking in the bacterial filtrate for 2 h achieved the highest viral inhibition (Galal 2006). Of all the strains tested, *S. violaceusniger* significantly inhibited the virus with the highest percentage (Galal 2006). El-Dougdoug et al. (2012b) also identified five Egyptian *Streptomyces* isolates (*S. calvus*, *S. canarius*, *S. vinaceusdrappus*, *S. nogalater*, and *S. viridosporus*) capable of producing an antiviral component in culture filtrate that was not phytotoxic and effective in local and systemic control of CMV infection. Both *S. canarius* and *S. viridosporus* showed a maximum reduction in the percentage of local lesions produced on the *Chenopodium amaranticolor* by CMV (El-Dougdoug et al. 2012b). Recently, Shafie et al. (2016) reported that foliage treatment with *S. griseorebens* and *S. cavourensis* culture filtrates resulted in a significant reduction in the severity of CMV infection disease and inhibitory effect when applied 48 h before virus inoculation.

On the other hand, due to its long shelf life, stability, and efficiency, several *Bacillus* species have been widely assessed as practical biological management agents (Kloepper et al. 2004a). Lee and Ryu (2016) demonstrated that foliar application of *B. amyloliquefaciens* strain 5B6 mediated ISR against CMV in pepper. Since the relative RNA content of CMV coat protein was considerably reduced in a 3-year field trial through the treatment with the strain (5B6) compared to water control, as demonstrated by qRT-PCR (Lee and Ryu 2016). On the other hand, Jetiyanon and Kloepper (2002) demonstrated that eleven mixtures of PGPR and one single strain treatment significantly reduced CMV of cucumber. Since seed treatment with [*B. pumilus* strain (SE49) + *Bacillus amyloliqefaciens* strain (IN937a)], [*B. pumilus* strains (SE49 +IN937b)], (*B. pumilus* strains (SE34 + IN937b)], [*B. pumilus* strain (SE49) + *B. sphaericus* strain (SE56)], [*B. amyloliqefaciens* strain (IN937a) + *B. pumilus* strain (IN937b)], [*B. pumilus* strain (INR7) + *B. amyloliqefaciens* strain (IN937a)], [*B. pumilus* strains (INR7 + T4)],

[*B. pumilus* strains (IN937b + T4)], [*B. pumilus* strain (IN937b) + *B. sphaericus* strain (SE56)], [*B. amyloliqefaciens* strain (IN937a) alone], [*B. pumilus* strains (IN937b + INR7)] and [*B. pumilus* strains (SE34 + T4)], reduced mean numbers of CMV symptomatic plants as a result to induced systemic resistance with 0.8, 0.8, 1.0, 1.0, 1.2, 1.4, 1.4, 1.6, 1.6, 1.6, 1.8, and 2, respectively, compared to the sodium phosphate buffer control treatment (3.0) (Jetiyanon and Kloepper 2002). In another study, Jetiyanon et al. (2003) reported that consortia (strain SE49 + strain IN937b) and (strain SE34 + strain IN937b) offered nearly 80% suppression of disease, while consortia (strain IN937a + strain IN937b, strain INR7 + strain T4, and strain IN937a alone) offered nearly 60% suppression of disease compared to the control.

Zehnder et al. (2000, 2001) identified PGPR strains that protect tomato plants under greenhouse and field conditions from CMV systemic infection. Initially, 26 PGPR strains were evaluated in greenhouse experiments to induce systemic resistance to CMV in tomatoes (Zehnder et al. 2000, 2001). Since four PGPR strains [*B. pumilus* (SE34), *B. subtilus* (IN937b), *B. amyloliquefaciens* (IN937a), and *Kluyvera cryocrescens* (IN114)] selected for field trials and their effectiveness assessed on the basis of symptomatic plant percentages ranged from 32 to 58% of the most effective PGPR treatments compared to 88 to 98% of the challenged control (Zehnder et al. 2000, 2001). In field experiments, three PGPR strains (*B. amyloliquefaciens* strain IN937a, *B. subtilus* strain IN937b, and *B. pumilus* strain SE34) reduced the development of CMV symptoms and the incidence of disease (Zehnder et al. 2000, 2001). Likewise, Murphy et al. (2003) evaluated six combined formulations with the carrier chitosan that included *Bacillus subtilis* strain GB03 together with one of *B. amyloliquefaciens* (IN937a), *B. pumilus* (SE34), *B. pumilus* (INR7), *B. pumilus* (T4), or *B. subtilis* (IN937b) as promising inducers against CMV in tomato. A mixture of PGPR [*B. amyloliquefaciens* (IN937a) + *B. subtilis* (GB03)] showed the ability to protect tomato from CMV (Murphy et al. 2003). This mixture also triggered ISR against CMV and encouraged plant growth in *Arabidopsis thaliana* (Ryu et al. 2007b). Likewise, *B. pumilus* strain SE34 elicited ISR against CMV in tobacco (Kloepper et al. 2004b). Kumar et al. (2016) suggested that *P. lentimorbus* strain B-30488 induce resistance against CMV in tobacco (*N. tabacum* cv. White Burley). The strain (B-30488) was isolated from cow's milk, which increased plant strength, while the accumulation of RNA virus and virulence in CMV infected tobacco plants systemic leaves decreased significantly by about 12-fold (91%) compared to control plants (Kumar et al. 2016). The strain (B-30488) was isolated from cow's milk, where the strain increased plant strength, while the accumulation of RNA virus and virulence in CMV infected tobacco plant systemic leaves decreased significantly by 91% compared to control plants (Kumar et al. 2016).

On the other hand, the mixing culture of *Azospirillum lipoferum* strain MRB16, *A. brasilienses* strain SP7, *A. brasilienses* strain N040, and *Anabena oryzae* Fritsch showed the ability to protect tomato against CMV containing viral satellite RNA (CARNA 5) leading to increased fruit yield both in the greenhouse and in the field (Dashti et al. 2007). Also, Dashti et al. (2012) observed that a PGPR mixture

containing *P. aeruginosa* and *S. rhizophilia*, with a mild strain of CMV associated with viral satellite RNA (CMV-KU1) enhanced the growth of tomato plants protected from the severe CMV-16 with 91.3% disease prevention.

15.3.7 Papaya Ringspot Virus

Papaya ringspot virus (PRSV) a member of the *Potyviridae* family (*Potyvirus* genus), causes a destructive disease and is the main restrictive agent in the cultivation of cucurbit or papaya throughout the world, where it is transmitted in a nonpersistent manner by multiple species of aphids (Gonsalves et al. 2010; Tripathi et al. 2008). The PRSV has two types in which the first type called PRSV-P affects both cucurbit and papaya and the second type only affects cucurbit but does not affect papaya and is called PRSV-W, previously known as watermelon mosaic virus-1 (Bateson et al. 2002; Gonsalves et al. 2010; Tripathi et al. 2008). Quite recently, Abdalla et al. (2017) reported that mixing either two PGPR strains [*B. pumilus* (SE34) + *B. amyloliquefaciens* (IN937a)] or three strains [*B. pumilus* (SE34) + *B. sphaericus* (SE56) + *B. amyloliquefaciens* (IN937a)] significantly reduced the severity of PRSV-W disease in squash plants 3 and 6 weeks after virus inoculation compared to infected untreated control. Since soil drenching is the more effective method observed by Abdalla et al. (2017), then root dipping and seed coating treatment.

15.3.8 Pepper Mild Mottle Virus

Pepper mild mottle virus (PMMoV), a member of the *Virgaviridae* family (*Tobamovirus* genus), is one of the most important pathogens of pepper crops, where infection can reach 100% in the field (Green 2003; Wetter and Conti 1988). PMMoV is easily transmitted by grafting, mechanical contact and PMMoV-infected seed coats (Genda et al. 2005; Svoboda et al. 2006). *B. amyloliquefaciens* strain EXTN-1 trigger ISR in tobacco against PMMoV through salicylate-dependent and jasmonate-dependent pathways (Ahn et al. 2002). On the other hand, Kim et al. (2017) evaluated the antiviral activity of *Pseudomonas oleovorans* strain KBPF-004 in PMMoV seed transmission compared to strain ATCC 8062 (control strain). Since virus-infected seeds harvested from infected pepper plants were treated with cell-free culture supernatant of each strain before planting compared to untreated PMMoV -infected seeds (Kim et al. 2017). Kim et al. (2017) found that strain KBPF-004 reduced the rate of PMMoV seed transmission to 15.5% compared to 61.9% for strain ATCC 8062, indicating that the viability of PMMoV was adversely affected by strain KBPF-004.

15.3.9 Potato Virus X

Potato virus X (PVX), a member of the *Alphaflexiviridae* family (*Potexvirus* genus), is a major pathogen of potato crops worldwide, infecting a wide range of hosts, notably within the *Solanaceae* family (Aboul-Ata et al. 2011; King et al. 2011). It has been included among pathogens with significant economic impact and can cause significant economic losses in synergistic co-infection with potato virus Y (Khurana and Singh 1988; Vance 1991). Hussein (1992) reported that both concentrated metabolites and their acetone extract of *Streptomyces afghanensis* (Egyptian isolate) inhibited the development of local lesions caused by PVX-infected *N. tabacum* L. cv. White Burley, where the maximum antiviral effect was observed 2 h after infection. On the other hand, the potato plants treated (seed treatment) with *Bacillus vallismortis* strain EXTN-1 increased the yield to untreated control by up to 45% (Park et al. 2006).

15.3.10 Potato Virus Y

Potato virus Y (PVY), a member of the *Potyviridae* family (*Potyvirus* genus), is a serious pathogen infecting several important crop species in the night shad family, including potato, tomato, tobacco, and pepper, resulting in significant yield losses and quality degradation (El-Dougdoug et al. 2014b; Glais et al. 2002; Sofy et al. 2013b). Mohamed and Galal (2005) observed that both the culture filtrates with pellets (cells of streptomycetes) of four Egyptian halotolerant *Streptomyces* isolates (*S. erythraeus* strain QS01, *S. erythraeus* strain QS02, *S. naganishii* strain QS03, and *S. michigansis* strain QS04) isolated from Qaroon Lake showed a decrease in the number of local necrotic lesions produced by PVY on *Chenopodium quinoa*. On the other hand, potato plants treated with *Bacillus vallismortis* strain EXTN-1 increased yields of up to 45% and chlorophyll content compared to the untreated control by protecting plants against potato virus Y (Park et al. 2006). Also, the application of *B. amyloliquefaciens* strain MBI600 decreased the accumulation of PVY during early infection and overdue detection of PVY in apical leaves (Beris et al. 2018). Where, in addition to the length of the tomato plants treated with the strain (MBI600), the fresh and dry weight after 30 days of inoculation was significantly higher than that of water and BTH treatments (Beris et al. 2018).

15.3.11 Sunflower Necrosis Virus

Sunflower necrosis virus (SNV) is a strain of tobacco streak virus (TSV), a member of the *Bromoviridae* family (*Ilarvirus* genus) that has recently caused significant crop loss in sunflower in India (Chavhan et al. 2017; Ravi et al. 2001). Although

Ilarvirus transmitted through seeds (van Regenmortel et al. 2000), SNV transmission not confirmed by sunflower seeds (Srinivasan and Mathivanan 2009). Insecticides are mainly used to control the SNV carrier (thrips) for disease management as observed by Srinivasan and Mathivanan (2009). On the other hand, the application of two PGPR microbial consortia [PGPMC-1 (*Streptomyces fradiae* strain MML1042 + *Bacillus licheniformis* strain MML2501 + *Bacillus* strain MML2551 + *P. aeruginosa* strain MML2212), and PGPMC-2 (strains MML2501 + MML2551 + MML2212)] to the sunflower plants in two different formulations in powder and liquid forms resulted in increased efficiency of ISR against SNV (Srinivasan and Mathivanan 2009). In addition to a significant reduction in disease, plants treated with PGPMC-1 liquid formulation registered an increase in seed germination, plant height and yield parameters with a higher income and benefit–cost ratio (Srinivasan and Mathivanan 2009).

15.3.12 Tobacco Mosaic Virus

Tobacco mosaic virus (TMV), a member of the *Virgoviridae* family (*Tobamovirus* genus), is a global plant virus infecting many horticultural crops and one of the most destructive plant diseases, resulting in severe losses (Sutic et al. 1999). Several studies have shown that individual PGPR strains could result in ISR against TMV as follows. Loebenstein and Lovrekovich (1966) noted that, injecting heat-killed cells of *P. syringae* into the intracellular spaces of *N. tabacum* var. Samsun NN leaves 0–7 days before inoculation with TMV reduced TMV lesions to 3–12% compared with water-injected control leaves. Whereas heat-killed bacteria were injected 5–72 h after inoculation with TMV, the number of lesions decreases by 86% and the area per lesion by 95–33% (Loebenstein and Lovrekovich 1966). Knowledge of this kind of resistance came mainly from the work of several authors including Loebenstein and Lovrekovich (1966). Also, De Meyer et al. (1999) showed that root colonization with *P. aeruginosa* strain 7NSK2 triggered ISR in tobacco against TMV, which is phenotypically similar to SAR TMV. *Pseudomonas* spp. strain B-25 treatment significantly improved growth components and fruit yield of TMV-challenged tomato plants, whereas at 60 DAT (days after transplanting); plant height, the number of branches, number of leaves, total biomass, chlorophyll content, and fruit yield were increased by 44.8, 69.9, 59.5, 52.2, 158.2 and 102%, respectively, over challenged control (TMV only) (Kirankumar et al. 2008). Also, treatment with the strain (B-25) increased NPK uptake in TMV-challenged tomato plants, where N, P, and K uptake were increased by 78.6, 84.5 and 80.3%, respectively, and higher than challenged control (Kirankumar et al. 2008). *P. chlororaphis*strain strain O6 has been shown to have ISR activity against cucumber mosaic virus, where the global *GacS* regulator is considered necessary for strain (O6) to stimulate ISR determinants (Ryu et al. 2007a). The nature of antiviral components in O6 against TMV identified by Park et al. (2012) as a cyclic peptide with molecular formula $C_{39}H_{67}N_9O_{12}S$ composed of seven different amino

acids and called "Peptamine." Peptamine (1000 μg/ml) exhibited more than 95% of disease suppression on the leaves treated with the mixture of TMV (Park et al. 2012). Recently, Kim et al. (2017) reported that *P. oleovorans* strain KBPF-004 cell-free culture diluted supernatant (1/20) treated *N. tabacum* cv. Xanthi-nc leaves showed the highest, i.e., 96% antiviral activity against mechanical transmission of TMV, whereas strain ATCC 8062 showed 19.7% compared to untreated leaf regions (control).

Long back, Mann (1969) showed that the applied culture of *Bacillus uniflagellatus* used as a soil drench method induces systemic resistance to TMV and reduces the number of lesions. Similarly, Fahmy and Mohamed (1984) found that the culture filtrate of certain microorganisms containing *B. subtilis* reduced the local lesions produced by TMV on the tobacco cv. Samsun. Damayanti et al. (2007) reported that *Bacillus* sp. strain I-6, *B. cereus* strain I-35, and *Brevibacterium sanguinis* strain I-16 protected hot pepper plants from TMV and attained maximally by strain 1-15. Wang et al. (2009) assessed that individual strains (*B. amyloliquefaciens* strains FZB24 and FZB42 and *B. subtilis* strains G1 and B3) could induce resistance against TMV and decrease the severity of the disease 28 days post-inoculation. However, the effect of *B. amyloliquefaciens* (FZB24) and *B. subtilis* (G1) treatments was most significant (Wang et al. 2009). Furthermore, western blot analysis confirmed that tobacco plants treated with *B. amyloliquefaciens* (FZB24) and *B. subtilis* (G1) contained a lower amount of the TMV coat protein compared to tobacco plants treated with *B. amyloliquefaciens* (FZB42) and *B. subtilis* (B3) (Wang et al. 2009). Tobacco plants treated with *B. pumilus* strain EN16 or *B. subtilis* strain SW1 also offered protection of 52% and 71%, respectively, at 14 d of inoculation (Lian et al. 2011). The amount of virus detected by ELISA decreased in tobacco plants treated with EN16 or SW1 (Lian et al. 2011). Further, after 5 d and 7 d intervals between PGPR treatment and TMV inoculations, respectively, strain EN16 and SW1 induce optimal resistance (Lian et al. 2011). Shen et al. (2013) recommended the use of *B. amyloliquefaciens* strain Ba33 as a soil disinfectant and an antiviral agent against TMV, where Ba33 treatments decreased the number of local necrotic lesions and disease index. The best treatment was spraying *N. tabacum* with strain Ba33 simultaneously with TMV inoculation in field trials comparable to ningnanmycin registered and established as an antiviral agent in tobacco (Shen et al. 2013).

Mansour et al. (1988) Observed inhibition of TMV (from *Datura metel* leaves) using *Streptomyces rochei*, while *S. rimosus*or and *S. gougerotti* caused weak inhibition. Both the concentrated metabolites and their acetone extract of *Streptomyces afghanensis* (Egyptian isolate) inhibited the development of local lesions caused by TMV-infected *N. tabacum* L. cv. White Burley, where the maximum antiviral effect was observed 2 h after infection (Hussein 1992). Similarly, the culture filtrates with cell pellets of four Egyptian halotolerant *Streptomyces* isolates (*S. erythraeus* strain QS01, *S. erythraeus* strain QS02, *S. naganishii* strain QS03, and *S. michigansis* strain QS04) showed a decrease in the number of local necrotic lesions produced by TMV on *N. glutinosa* (Mohamed and Galal 2005).

15.3.13 Tobacco Necrosis Virus

Tobacco necrosis virus (TNV), a member of the *Tombusviridae* family (*Necrovirus* genus), is a plant virus has an extensive host range including many cultivated species, where it is infectious to 298 species of 167 genera belonging to 54 families (Edwardson and Christie 1997). The virus occurs in plant roots and is transmitted in a nonpersistent manner by the chytrid fungus vector *Olpidium*, especially *O. brassicae* and *O. bornavirus* (Fry and Campbell 1966; Hull 2002; Sutic et al. 1999). The soil application of *P. fluorescens* strain CHA0 which produces salicylic acid naturally under iron-limited conditions exhibits induced systemic protection against TNV in tobacco, where the incidence of leaf necrosis in tobacco plants is reduced after inoculation with TNV (Maurhofer et al. 1994, 1998). While the introduction of the salicylic acid biosynthetic genes (*pchA* and *pchB*) into *P. fluorescens* strain CHA0 that produces salicylic acid increased salicylic acid production in tobacco rhizosphere and in vitro, it did not improve ISR in tobacco against TNV (Maurhofer et al. 1998). On the other hand, the introduction of salicylic acid biosynthetic genes into *P. fluorescens* strain P3 which does not produce salicylic acid gives this strain the ability to produce salicylic acid in vitro and significantly enhances its capability to ISR in tobacco against TNV (Maurhofer et al. 1998). Foliage treatment with *B. globisporus*, *P. fluorescens*, or *S. gibsonii* culture filtrate profoundly reduced the local lesions number in *Phaseolus vulgaris*, where *P. fluorescens* and *S. gibsonii* showed the highest inhibitory effect of TNV infection by 91.5% and 97.2%, respectively (Shoman et al. 2003).

15.3.14 Tomato Chlorotic Spot Virus

Tomato chlorotic spot virus (TCSV), a member of the *Bunyaviridae* family (*Tospovirus* genus), is transmitted by thrips (*Thysanoptera*: *Thripidae*) in a persistent and propagative manner, where the most efficient TCSV vectors are the dark form of *Frankliniella schultzei* followed by *Frankliniella occidentalis* (King et al. 2011; Martínez et al. 2018; Peters et al. 1996; Polston et al. 2013). TCSV causes diseases associated with significant losses in overall yield and quality in both agricultural and ornamental crops (Pappu et al. 2009; Polston et al. 2013). Application of *Bacillus amyloliquefaciens* strain IN937a reduced the severity of TCSV disease in tomato plants by almost 50% compared to infected untreated control (Abdalla et al. 2017). Whereas soil drenching application of mixture of either two PGPR strains [*Bacillus pumilus* (SE34) + *B. amyloliquefaciens* (IN937a)] or three strains [*B. pumilus* (SE34) + *B. sphaericus* (SE56) + *B. amyloliquefaciens* (IN937a)] showed the highest reduction of TCSV disease severity at 3 and 6 weeks after virus inoculation compared to infected untreated control in both first and second trials (Abdalla et al. 2017).

15.3.15 Tomato Mosaic Tobamovirus

Tomato mosaic tobamovirus (ToMV), a member of the *Virgaviridae* family (*Tobamovirus* genus), is found in tomatoes around the world where it can be seed-borne and spread very quickly through mechanical transmission by grafting or contaminated tools and workers, resulting in significant losses (Adams et al. 2012; Broadbent 1965). Egyptian isolate of *Streptomyces afghanensis* has an antiviral effect against ToMV, that inhibited local lesion produced on *N. tabacum* L. cv. White Burley (Hussein 1992). Recently, Megahed et al. (2013) mentioned that the liquid culture, cells and culture filtrate of individual *P. fluorescens* 2, and *B. circulans* imparted ISR on tomato plants and reduced the ToMV symptoms and ToMV local lesions produced on *Datura metel* as ToMV indicator host. The seed treatment with an individual liquid culture, microbial culture filtrate and microbial cells of *P. fluorescens* 2 profoundly reduced the local lesions number by 49.2, 57.7, and 58.5%, respectively, compared to infected untreated control, while *B. circulans* reduced the local lesions number by 42.3, 46.8, and 47.3%, respectively, compared to infected untreated control (Megahed et al. 2013). Interestingly, *P. fluorescens* proved better than *B. circulans* during field trials (Megahed et al. 2013).

15.3.16 Tomato Mottle Virus

Tomato mottle virus (ToMoV), a member of the *Geminiviridae* family (*Begomovirus* genus), transmitted through whitefly B biotype, *Bemisia tabaci* (Gennadius), was a primary limiting agent of tomato yields (Kring et al. 1991; Polston et al. 1993; Simone et al. 1990). ToMoV management was limited due to the ability of its vector to acquire insecticide resistance and lack of genetically resistant tomatoes (Denholm et al. 1996; Stansly et al. 1991). In 1997, Murphy et al. (2000) and Zehnder et al. (2001) noted that the severity ratings of ToMoV disease were significantly less in the plants treated with powder-based treatments of *B. amyloliquefaciens* strain IN937a, and *B. subtilus* strain IN937b compared to the control. Consequently, in all powder-based treatments, the Southern blot analysis showed a lower percentage of ToMoV-infected tomato plants compared to plants undergoing seed treatment singly or control treatment (Murphy et al. 2000; Zehnder et al. 2001). Further, Murphy et al. (2000) and Zehnder et al. (2001) used *B. pumilus* strain SE34 instead of *Bacillus amyloliquefaciens* strain IN937a, where the severity symptom ratings of ToMoV were notably reduced in plants treated as seed treatment alone with *B. subtilis* (IN937b), in addition to plants treated as powder treatment alone and seed + powder treatment with *B. pumilus* (SE34) compared to control (Murphy et al. 2000; Zehnder et al. 2001).

15.3.17 Tomato Spotted Wilt Virus

Tomato spotted wilt virus (TSWV), a member of the *Bunyaviridae* family (*Tospovirus* genus), ranks among the top 10 most economically important plant viruses worldwide with a broad host range of up to 1000 plant species (Mumford et al. 1996; Naidu et al. 2008; Parrela et al. 2003). TSWV transmitted by western flower thrips, *Frankliniella occidentalis* (Pergande) as the primary vector in a persistent and propagative manner (Ogada et al. 2013; Whitfield et al. 2005), as well as transmitted by multiple species of thrips (Ullman et al. 1997). It causes severe damages to crops grown in greenhouses, and open fields in all climate zones (German et al. 1992; Peters et al. 1996). Treatment of seeds, seedlings, soil or foliar applications with *P. fluorescens* strains (CHA0, CoT-1, and CoP-1) either alone or in mixtures has triggered ISR against TSWV infection in tomato under both greenhouse and field conditions (Kandan et al. 2002, 2005). They found that the mixture of (CHA0 + CoT-1 + CoP-1) decreased disease maximum by 84%, followed by the strain (CHA0) individually or in combined with the strain (CoT-1) by 80% compared to the untreated control plants (Kandan et al. 2002, 2005). This is why *P. fluorescens* strains treated tomato plants demonstrated increased growth promotion compared to untreated control plants under both greenhouse and field conditions (Kandan et al. 2002, 2005). On the other hand, Beris et al. (2018) demonstrated that under two different environmental conditions, the application of *B. amyloliquefaciens* strain MBI600 as foliar, drench, or soil amendment reduced the TSWV incidence by up to 80%.

15.3.18 Tomato Yellow Leaf Curl Virus

Tomato yellow leaf curl virus (TYLCV), a member of the *Geminiviridae* family (*Begomovirus* genus), is a plant virus spread throughout the world and can be found in most places where tomatoes are grown and is considered one of the most destructive plant diseases in the world leading to severe losses (Navas-Castillo et al. 2011; Rybicki 2015; Sofy et al. 2017). TYLCV transmitted by the whitefly *Bemisia tabaci* (Hemiptera; *Aleyrodidae*) in a circulative and persistent manner (Gotz et al. 2012). *Enterobacter asburiae* strain BQ9-elicited ISR against tomato yellow leaf curl disease of TYLCV-induced tomato was investigated by Li et al. (2016a) who observed a significant 42% decrease in the disease even after 45 days of inoculation leading to long-term plant protection against TYLCV, in addition to increased growth parameters compared to mock treatment plants (Li et al. 2016a). Moreover, viral load in BQ9-pretreated tomato plants was reduced after 9 days by nearly 1/3 of viral control (Li et al. 2016a). In addition to the production of H_2O_2, the expression of both defense-associated genes and defense enzymes was associated with BQ9-induced ISR against TYLCV (Li et al. 2016a).

15.3.19 Urdbean Leaf Crinkle Virus

Urdbean leaf crinkle virus (ULCV) has not been assigned to any genus and family until now and is a plant virus that causes urdbean leaf crinkle disease (ULCD) which is also considered to be very severe among viral diseases (Gautam et al. 2016; Ravinder Reddy et al. 2005). The disease is more severe in blackgram than mungbean under field conditions, where the virus is transmitted by seed, grafting, and sap inoculation, as well as by insects, whiteflies, and aphids (Gautam et al. 2016). Karthikeyan et al. (2009) reported that foliar- and soil-applied *P. fluorescens* (strain pf1 or strain CHA0) 24 h prior to virus inoculation triggered ISR against ULCV in blackgram, significantly reducing ULCV infection. The strain (Pf1) was highly effective in reducing the percentage of ULCV infection by 9.33% for foliar application or soil application compared to 74.50% for the control (Karthikeyan et al. 2009). Whereas, foliar- and soil-applied strain (CHA0) reduced the percentage of ULCV infection by 17.31%, and 20%, respectively, compared to the control by 77.16% (Karthikeyan et al. 2009). Furthermore, the strain (Pf1) increased the activity of POD, PAL, and PPO and induced the phenolics accumulation in blackgram plants against ULCV, thus helping the host plants to resist the disease (Karthikeyan et al. 2009).

15.3.20 Watermelon Mosaic Virus

Watermelon mosaic virus (WMV), a member of the *Potyviridae* family (*Potyvirus* genus), is a plant virus mostly distributed in temperate and Mediterranean regions with broader host range than most *Potyviruses*, resulting in severe losses to all cucurbit plants (Desbiez et al. 2009; Desbiez and Lecoq 2008; Moradi 2011). A strategic approach to plant management of watermelon mosaic virus disease is based on the use of insecticides to control its vectors (whites and aphids) and the cross-protection of genetically engineered plants (Elbeshehy et al. 2015; Lomonossoff 1995). Elbeshehy et al. (2015) investigated the induction of systemic disease resistance in pumpkin against WMV by soil application with two PGPR strains (*B. subtilis* 281 strain B1 and *B. pumilus* 293 strain B2) either individually or in combination. They found that the strain (B2) suppressed disease by approximately 77.7% significantly higher than plants treated with the strain (B1) and mixture (B1 + B2) that suppressed disease by 33.3% and 66.6%, respectively (Elbeshehy et al. 2015). Furthermore, in plants treated with the strain (B2) or a mixture of strains (B1 + B2), the concentration of WMV measured by ELISA was 0.16 and 0.34, respectively, which was significantly lower compared to plants treated with strain (B1) and untreated WMV control than 0.75 and 1.366, respectively (Elbeshehy et al. 2015).

15.4 Conclusion

Viral diseases are difficult to eradicate and manage, where there are currently no strategies to completely protect plants from viruses. PGPRs are considered to induce systemic resistance, which can reduce the severity of certain diseases in crop plants, known as PGPR-induced systemic resistance. Although PGPR-ISR studies have centered on several pathogens of fungi and bacteria, several species of PGPR are used as microbial inoculants to protect plants from virus infection and improve crop yield. Since once resistance induced, it will provide nonspecific protection against viruses. This chapter deals with several studies highlighting the importance of several PGPR species against the viral infection of different plants. This approach is, therefore, one of the methods of environmentally friendly prevention and sustainable development.

Conflict of Interest The author(s) have no conflict of interest.

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Chapter 16
Conclusion

Piyush Pandey

Abstract The beneficial microorganisms, majorly PGPR are helpful in the improvement of plant growth and enhanced crop productivity. The future of organic agriculture is bound to be dominated by the application of PGPR. This book has been brilliantly carved out with the information on the mechanisms of interactions, and cross talk of PGPR with plants, that will be useful in designing the strategies of their application. Application of PGPR for biocontrol, as biopesticides, is another domain that has translated in profitable industry, yet the information on their use against viral infections is fascinating. Further, phytoremediation of heavy metal from contaminated soil has been discussed in this book. In fact, the sustainable management of field crops by PGPR triumph its merit, for ensuring the food security in eco-friendly manner, and this book is a valuable collection of information for its application and success.

Keywords PGPR · Biocontrol · Plant immunity · Cereals crops · Horticulture crops

"*A reasonable agriculture would do its best to emulate nature. Rather than change the earth to suit a crop… it would diversify its crops to suit the earth*"—this quote by Klinkenborg (2013) reflects the necessity of agricultural technologies to proceed toward green and sustainable agri practices. This book, has been complemented with elaborated discussions, which has come up as an excellent cumulative effort of scientists from different expertise, and single goal, i.e. promotion of PGPR for better crop productivity and management.

A couple of chapters is focused on using different combinations of organisms like various rhizobacteria, or PGPR with mycorrhizae, for the improvement of plant growth. In fact, the term consortium was given in the last part of nineteenth century for symbiotically living two or more bacteria, but the applications of such relations in soil is recently becoming popular among users, which is supposed to provide

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better results. Not only it provides relatively more functional genes in system, but also ensures the stability and survival of inoculated PGPR in new environment (Pandey and Maheshwari 2007).

There are another two contributions which discuss the use of PGPR in vegetables. While one of these is specifically focused on cucurbitaceous vegetables, while another one describes the significance of PGPR in productivity and disease management in tomato, pepper, melon, radish, and lettuce. In fact, the importance of horticultural crops in food safety is less realized, but these crops are important not only for economic reasons but also as a source of nutrition to large population. PGPR shall play a significant role in improving the quality of produce, along with economic benefits.

The cross talk between PGPR and host plant have been a very interesting aspect for research. It has been realized that the chemical communications between soil bacteria and host plants may induce the plants to tolerate abiotic stress such as salt and drought stress. In fact, differentially expressed stress proteins had been identified in the treated host plants and expression of stress-specific genes had been found to increase by 1.5-fold in *PGPR*-treated plants (Lim and Kim 2013). Such facts make use of PGPR even more interesting where the direct mechanisms of plant growth are further strengthened by the indirect benefits to plants. Similarly, phytoremediation of heavy metal contaminated soil is coming up as another applied aspect of PGPR (Kotoky and Pandey 2018), and this required a systematic discussion, which has been incorporated in this book.

The PGPR are versatile organisms. Their competitive physiological skills of PGPR in rhizosphere also provide them the ability to remove some phytopathogenic parasites from the soil. This indirect mechanism of growth promotion has been utilized for the formulation of PGPR-based biopesticides. Considering the benefits of biological control, it is appropriate to understand the molecular and physiological mechanisms of interactions, to obtain maximum benefits (Backer et al. 2018). The biological control of fungal phytopathogens has been relatively studied more, yet it's stimulating and thought-provoking to read a chapter on the protection of plants from viral diseases, primarily by the mechanism of induced systemic resistance. There might be several checkpoints to understand the underlying mechanism, such as de novo production of pathogenesis-related proteins, modifications in cell wall composition and/or synthesis of phytoalexins, yet there is a possibility to find many other compounds, which are likely to exist but have not been identified (Heil and Bostock 2002).

This book will be useful not only to the researchers, but also to each and every stakeholder that contributes toward food security and green agriculture. The enriched efforts of contributors and editorial team have resulted in a volume, which systematically describes to different issues, and applications of PGPR in sustainable agriculture. Needless to mention, that maybe, such volumes will be needed to place the PGPR technology in field to its potential, but this particular book stands on its merit for the information and contents, which will be useful to all.

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