

Chapter 16

Production of Antibiotics from PGPR and Their Role in Biocontrol of Plant Diseases



Saima Hamid, Rafiq Lone, and Heba I. Mohamed

Contents

1	Introduction.....	441
2	Mechanism of Action of PGPR.....	443
3	Direct Mechanisms Involved in PGPR.....	443
3.1	Nutrient Acquisition.....	443
3.2	Nitrogen Fixation.....	444
3.3	Phosphate Solubilization.....	444
4	Major Antibiotics of PGPR.....	446
4.1	Nonvolatile Antibiotics.....	447
4.2	Volatile Antibiotics.....	448
5	Biostimulants of PGPR.....	449
6	Role of PGPR in Biocontrol of Plant Disease.....	451
6.1	Antibiotic Production.....	452
6.2	Induced Systemic Resistance (ISR).....	454
7	Conclusion.....	455
	References.....	455

1 Introduction

The symbiotic bacteria present around the roots of plants are called rhizobacteria which are free-living unswervingly correlated with root surface or dwell inter alia on the roots such as endophytic bacteria without adding any value to the soil (Kloepper and Beauchamp 1992). When rhizobacteria help plants to grow, they are defined as plant growth-promoting rhizobacteria (PGPRs) (Kloepper et al. 2004).

S. Hamid · R. Lone (✉)

Centre of Research for Development, University of Kashmir,
Srinagar, Jammu and Kashmir, India

H. I. Mohamed

Department of Biological and Geological Sciences, Faculty of Education, Ain Shams
University, Cairo, Egypt

© The Author(s), under exclusive license to Springer Nature
Switzerland AG 2021

H. I. Mohamed et al. (eds.), *Plant Growth-Promoting Microbes
for Sustainable Biotic and Abiotic Stress Management*,
https://doi.org/10.1007/978-3-030-66587-6_16

441

Bacteria must be competent for rhizosphere, i.e., capable of interacting with rhizosphere-based nutrients secreted from the root or from sites which can be occupied on the root, to exert their beneficial effects in the root system (Hao et al. 2012; Kim et al. 2012). Also, the characteristic inherence of PGPR is that it interacts with other microbes, such as arbuscular mycorrhizal fungi (AMF), to promote plant growth. In addition to soil-based microbes other than AMF, the plant-AMF relationship is mostly manipulated through indirect mechanisms by the increased availability of soil nutrients (Ghignone et al. 2012; Pii et al. 2015), while its impact directly is still under debate for plant-based growth (Glick 2012). A very favorable habitat for the growth of microorganisms in the rhizosphere, which covers a volume of root soil, which is chemically and physically affected by the plant root, can have a potential effect on plant health and soil fertility (Sorensen 1997). The microorganisms colonizing at root may be free, parasitic, and saprophytic, and their diversity remains varied because population and species abundance often change amino acid, monosaccharide, and organic acids into primary sources of nutrients released from a root environment which support the dynamic increase and activities of different microorganisms (Kunc and Macura 1988). It has been observed that in various plant species with aid of PGPR, plant growth has been improved in terms of an increase in seedlings, biomass, vigor, root system proliferation, and production. During the past 30 decades, various reports have been performed at a very exponential rate to identify PGPR in different agricultural systems and agroecological regions, as they are an important component of the root-colonizing microorganism (Podile 2006) (Table 16.1).

The protective effect of PGPR inoculated to seedlings was observed against soil-borne pathogens (Manjula and Podile 2001; Guo et al. 2004). Therefore, the role of PGPR as defense products for soil pathogens has been increased. However, in recent years, PGPR has once again been discovered as biofertilizers, and organic farming has become more important with minimum to no input. The requirement for a threshold point to sustain plant development for the initial bacterial inoculum indicates the quorum sensing of bacteria in plant-PGPR interactions plays a significant

Table 16.1 Commercially accessible PGPR strains, which are primarily assisted by mechanisms for direct plant production

PGPR strain	Trade name	Manufacturer	Recommended application
<i>Azotobacter</i> spp.	Bioplin	Kumar Krishi Mitra Bioproducts Pvt. Ltd., Pune, India	Soil drenching for sunflower, tomato, and another vegetable crops
<i>Bacillus subtilis</i>	Kodiak	GB03 Gustafson, LLC, Dallas, TX	Seed treatment in fruits and vegetables
<i>Bacillus</i> spp.	Bioyield	Gustafson, LLC, Plano, TX	Seed treatment in tomato, tobacco, cucumber, and pepper
<i>Bacillus</i> , <i>Pseudomonas</i> and <i>Streptomyces</i> spp.	Compete	Plant Health Care BV, CA Vught	Soil drenching for turfgrass, nursery, and greenhouse plantations

role (Teplitski et al. 2000). With understanding and knowledge of genetics, biochemical and physiological pathways aimed to help as to how PGPR can be used for plant growth promotion and disease control, hence with the goal of choosing and improving potential strains for crop improvement. PGPR innovation and distribution systems in various crop systems increase the rapid acceptance of strains and satisfy farmers by reducing costs in respect of chemical fertilizer.

2 Mechanism of Action of PGPR

PGPR-mediated growth in plants is promoted as per the reports of Kloepper and Schroth (1981), with the alteration in the rhizosphere niche of the entire microbial community through the formation of different compounds (Kloepper and Schroth 1981). In general, PGPR promotes plant growth through promoting either the production or regulation of the hormone levels of plants or indirectly interfering with the rhizosphere, by fixing nitrogen, solubilized phosphorus, and potassium, or the production of siderophore. Other biocontrol mechanisms, such as antibiotics (Chin-A-Woeng et al. 1998) and CNN (competition for nutrients and niches) (Validov et al. 2009), have been certainly required to create root colonization over the current years. The development of exopolysaccharides may be one of the potential explanations. Thus, produced exopolysaccharides reduce Na uptake by binding them and also by forming biofilms (Qurashi and Sabri 2012). Although there are two mechanisms involved for PGPR, mostly studied is the direct one which is also discussed below.

3 Direct Mechanisms Involved in PGPR

In the absence of pathogens, direct PGPR promotes plant production. According to Vessey (2003), plant rhizosphere soil bacterial species growing in, on, or around plant tissue enhance plant development and growth through a multitude of processes. In addition to supplying mechanical assistance and supporting water and nutrient absorption, rhizosphere microbial behavior influences the habits of rooting and the availability of nutrients to plants.

3.1 Nutrient Acquisition

A part of these organically grown plants are additionally metabolized by nearby microorganisms as carbohydrate and nitrogen sources and replanted for the growth and processing by certain microbiological molecules (Kang et al. 2010).

3.2 Nitrogen Fixation

Certain microorganisms are in a position to transform nitrogen to ammonia through the process of fixing nearly two-thirds of the global amount of nitrogen by means of complex enzyme mechanism known as nitrogenase (Kim and Rees 1994). There are two groups of microbes which fix atmospheric nitrogen into a usable form: (a) symbiotic nitrogen-fixing bacteria (Ahemad and Khan 2011) and *Frankia* (nonleguminous tree) and (b) nonsymbiotic nitrogen-fixing form such as cyanobacteria (Bhattacharyya and Jha 2012). Host plant, which is associated with nonsymbiotic nitrogen-fixing bacteria, fixes a minimal amount of nitrogen (Glick 2012). Diazotrophs are nitrogen-fixing microbes and contain molybdenum nitrogenase which is responsible for biological nitrogen fixation and other related activities (Bishop and Jorenger 1990). A variety of free-living bacteria, such as *Azospirillum* spp., in addition to *Rhizobia* spp., can also fix and distribute nitrogen to the plants (Wisniewski-Dyé et al. 2015). However, the bacteria which live freely produce only a small number of fixed nitrogen required by the bacterial host plant. Nitrogenases (*nif*) are also important for the fixation of nitrogen into structural genes, iron-protein activation genes, molybdenum cofactor genes, electron donations, and regulatory genes required for the synthesis and action of enzymes (Bruto et al. 2014). As with the NIF genes, they usually occur in a group of 7 operons between the dimensions of 10 and 20 kb, encoding 20 proteins (Glick 2012).

3.3 Phosphate Solubilization

Phosphorus (P) is the second most important nutrient-restricting plant growth in soils, in both organic and inorganic forms, following nitrogen (Khan et al. 2009). The phosphorus mass of soil is found as an insoluble form when only the monobasic ions (H_2PO_4) and the diabolic ions are taken into consideration when absorbing plants in two soluble forms, although phosphorus is available to plants in minimal amounts (Bhattacharyya and Jha 2012). Phosphorus deficits are frequently used in soil fields because plants absorb lower phosphatic fertilizers and the remaining complexes quickly become insoluble when a reaction to other soil component phosphatic fertilizers is carried out (Mckenzie and Roberts 1990). However, routine treatments of phosphate fertilizers are both costly and unnecessary (Kaur and Reddy 2014). This led to the search for environmentally sustainable and affordable alternatives. Pyoluteorin was first isolated in tivo to grow crops in low phosphorus soils.

In this respect, a viable substitute for the chemical phosphatic fertilizers is provided by the phosphorus sources used by the plant (Khan et al. 2007). The microorganisms which can solubilize the phosphate are called phosphate solubilizing microorganism (PSM). Although the most potential biofertilizer of different PSMs inhabiting the rhizosphere was the use of phosphate-solubilizing bacteria (PSB), plants that can easily absorb via biological routes obtain a good amount of

phosphorus (Zaidi et al. 2009; Yadav et al. 2014). Kumar et al. (2001) put forward that many crops like radish, potato, tomato, and wheat are associated with microbial species which solubilizes phosphorus.

Therefore, it is very relevant for agricultural microbiologist that PGPRs can solubilize the mineral phosphate since they can boost phosphorus availability for effective plant development. PGPRs for the solubilization of precipitated plant phosphates were registered as a possible plant growth support mechanism in field conditions (Verma et al. 2001; Guo et al. 2015). The reason for the solubilization of inorganic phosphorus might be the organic acid synthesis by rhizospheric microbes (Barea and Richardson 2015). The commercial use of PGPR phosphate solubilization was unfortunately limited due to variable results (Ghosh et al. 2014).

Biological disease control is an attractive alternative strategy for the control of plant diseases. Meanwhile, it also provides practices compatible with the goal of a sustainable agricultural system. Understanding the mechanisms of biological control of plant diseases through the interactions between antagonists and pathogens may allow us to select and construct the more effective biocontrol agents and to manipulate the soil environment to create a conducive condition for successful biocontrol. Many factors have to be considered in deciding whether a biological system is feasible for the control of a particular pathogen. Of prime importance is the availability of a suitable antagonist capable of maintaining itself on the host plant. The environment under which the crop is grown will play a significant part in determining whether effective population levels of an antagonist can be established in competition with the existing microflora. Environment may also govern the choice of antagonist; for example, yeasts can survive on leaves more readily than non-spore-forming bacteria under adverse humidity conditions. It is essential that the primary mechanism by which antagonism is brought about should be known. A variety of biological controls are available for use, but further development and effective adoption will require a greater understanding of the complex interactions among plants, people and the environment (Nega 2014). Currently, agriculture faces challenges, such as soil fertility reductions, changes in climate, and increased pathogen attacks (Gopalakrishnan et al. 2015). In this way, our future main priorities are environmentally sustainable plant conservation strategies. There are growing questions about the use of chemical and synthetic fertilizers and pesticides and environmentally sustainable and effective approaches to crop growth and development. The sustainability and safety of the horticulture industry depend on eco-adaptation methods such as biopesticides, biofertilizers, and crop residues. PGPR is a big part of the conservation of crops, the development of growth, and the improvement of soil health (Beneduzi et al. 2012; Liu et al. 2017). Some of the exceptional PGPR strains that play a large part in inhibiting or destroying pathogens by making unique antibiotic mixtures are *Pseudomonas*, *Bacillus*, *Azospirillum*, and *Rhizobium*. In addition to chemical pesticides, the microbial antagonist is another way to suppress plant pathogen in crops. A broad variety of pathogens are regulated by PGPR, including bacteria, fungi, viruses, and nematode diseases (Liu et al. 2017).

4 Major Antibiotics of PGPR

In the management of plant diseases, PGPR plays a vital role in the production of antibiotics, and the system is called pathogenic microbes' inhibition or suppression. PGPR such as *Bacillus* species and fluorescent *Pseudomonas* help in the destruction of pathogens, generating inhibitory, antagonistic metabolites in their defense mechanism against harmful strains of microbes. Furthermore, in plant induced systemic resistance mechanism (ISR) antibiotics play a critical role in direct antagonistic action. Specific microorganisms can produce a range of antibiotic products, for example, PGPR produce multiple antibiotics (Table 16.2).

Antibiotic is defined as a heterogeneous community of low-molecular organic complexes that harm the production or metabolism of various microorganisms (Kumar et al. 2015). In vitro and in situ, the development of the target pathogen was smothered more effectively with the help of antibiotics. The formation of one or more antibiotics is the most crucial aspect of plant growth that promotes rhizopathological bacteria and promotes resistance to other pathogens (Glick et al. 2007). Moreover, the antibiotics are classified as volatile and nonvolatile, as aldehydes, alcohols, sulfides, ketones, and hydrogen cyanide come under the category of

Table 16.2 Antibiotics produced by PGPR

PGPR	Antibiotics
<i>Pseudomonas</i> sp.	Antifungal antibiotics
	Phenazines
	Phenazine-1-carboxylic acid
	Phenazine-1-carboxamide
	Pyrrolnitrin
	Pyoluteorin
	Cepaciamide A
	Oomycin A
	Viscosinamide
	Pyocyanin
	Antibacterial antibiotics
	Pseudomonic acid
	Azomycin
	Antitumor antibiotics
	FR901463
	Cepafungins
	Antiviral antibiotic
Karalicin	
<i>Bacillus</i> sp.	Kanosamine
	Zwittermicin A
	Iturin A (cyclopeptide)
	Bacillomycin
	Plipastatins A and B

volatile antibiotics, while the nonvolatile antibiotics include heterocyclic nitrogenous compound (Gouda et al. 2017; Fernando et al. 2018). Antibiotics promote plant growth and possess other potentially beneficial properties like antimicrobial, antiviral, and antioxidant (Ulloa-Ogaz et al. 2015; Fernando et al. 2018).

The antibiotics that play a critical role when plant pathogens are suppressed are classified into two groups: volatile and nonvolatile antibiotic products.

4.1 Nonvolatile Antibiotics

4.1.1 Polyketides (2,4-Diacetylphloroglucinol (DAPG or Phl))

DAPG or Phl is a phenolic polyketide compound which is obtained from fluorescent pseudomonas with antibacterial, antifungal, and antioxidant activities (Gaur 2002). Phl is a key determinant of plant growth-enhancing rhizobacteria's biocontrol activity. *Gaeumannomyces graminis* var. *tritici* is responsible to cause take-all diseases in wheat which can be suppressed by 2,4-DAPG antibiotic to act as take-all decline (TAD) which is produced from strains of *P. fluorescens* (Weller et al. 2007). The diseases are caused by some soil-borne pathogens and are prevented by some strains of *P. fluorescens* which also have nematicidal activity (McSpadden Gardener 2007; Meyer et al. 2009). As per reports of Dwivedi and Johri (2003), Phl's mode of action remains uncertain, although the interaction between root-associated Phl-producing microorganisms and pathogens is considered to be a significant cause of disease suppression. So, in plants, Phl elicits ISR microorganisms and, therefore, can serve as unique elicitors in plant disease management of the development of phytoalexins or other related molecules.

4.1.2 Pyoluteorin (Plt)

Pyoluteorin (Plt) is a natural antibiotic that is biosynthesized from a hybrid nonribosomal peptide synthetase (NRPS) and polyketide synthase (PKS) pathway (Fernando et al. 2005). Pyoluteorin was first isolated in the 1950s from *Pseudomonas aeruginosa* strains T359 and IFO 3455 and was found to be toxic against oomycetes, bacteria, fungi, and against certain plants (Kraus and Loper 1995). Plt inhibited most pathogens of oomycete, like *Pythium ultimum*. The severity of *Pythium* damping decreased when seeds are applied with *Pseudomonas* Plt producing, reported by now by Nowak-Thompson et al. (1999). Hassan et al. (2011) put forward that in sugarcane, *Glomerella tucumanensis* is responsible to cause disease, namely, red root rot, but pyoluteorin produced by *P. putida* has been found to be effective against this disease.

4.1.3 Heterocyclic Nitrogenous Compounds

Heterocyclic nitrogen pigments called phenazines, which are low-molecular-weight compounds, were developed by a small group of bacterial species including *Pseudomonas*, *Burkholderia*, *Brevibacterium*, or *Streptomyces*, since more than 50 phenazine compounds occurring naturally were examined. Some bacterial strains will generate blends of different phenazine derivatives simultaneously (Guttenberger et al. 2017; Dasgupta et al. 2015). Like phenazine-1-carboxylic acid (PCA) found in *P. fluorescens* 2–79, however, *P. aureofaciens* 30–84 has been identified as a mixture of PCA along with a minimum amount of 2-hydroxyphenazine.

Several PGPR pseudomonad strains have antibiotic and antitumor features and are active in their ability to suppress pathogenic plant fungi and nematodes (Cezairliyan et al. 2013; Zhou et al. 2016). The disease caused by *G. graminis* var. *tritici* in wheat has been biocontrolled by compound known as phenazine-1-carboxylic acid (PCA) which is produced by *P. fluorescens* 2–79 and *P. aureofaciens* 30–84 (Thomashow and Weller 1988; Chin-A-Woeng et al. 2000; Shanmugaiyah et al. 2010; Ju et al. 2018). *P. aeruginosa* PNA1 (wild-type) phenazine-1-carboxylic acid and phenazine-1-carboxamide are important in controlling cocoyam root rot caused by *P. myriotylum* (Tambong and Hofte 2001). *P. aeruginosa* is known to produce pyocyanin and phenazine-1-carboxylic acid which are having antagonistic activity against *F. oxysporum*, *Aspergillus niger*, and other various pathogens (Rane et al. 2007; Abo-Zaid 2014). In *P. chlororaphis*, 30–84 phenazine derivatives have to be developed to prevent plant pathogens (Ju et al. 2018). Several volatile antibiotics, such as hydrogen cyanide, aldehydes, alcohols, ketones, and sulfides, are present in this region, but hydrogen cyanide is the most important metabolite (Yu et al. 2018).

4.2 Volatile Antibiotics

4.2.1 Hydrogen Cyanide (HCN)

Various Gram-negative bacteria, namely, *Chromobacterium violaceum*, *P. aeruginosa*, and *P. fluorescens*, produce cyanide as their secondary metabolite (Hass and Defago 2005). It has been reported by many workers that hydrogen cyanide (HCN) showed the nematicidal activity against *Meloidogyne hapla* as produced from the bacterial strain, namely, *P. chlororaphis* O6 (Kang et al. 2018). Sarhan and Shehata (2014) reported that in alfalfa, infection caused by *F. solani* can be stopped by generation of HCN from *F. solani*. Hydrogen cyanide (HCN) production is an essential determinant of biocontrol (Anderson and Kim 2018). The characterized hcnABC gene set was found to be responsible in Q2-87 and CHA0 for biosynthesis of HCN (Hass and Defago 2005).

4.2.2 Aldehydes, Alcohols, Ketones, and Sulfides

Mycelium formation, ascospore germination, and survival of sclerotia were entirely impeded by these substances. These volatiles come directly into contact with sclerotial structures that lead to a reduction in inoculum capacity, preventing the occurrence of the disease (Fernando et al. 2004). The pathogen *Erwinia carotovora* has been inhibited by bacterial volatiles such as 2,3-butadienol (Ryu et al. 2003).

5 Biostimulants of PGPR

Plant growth regulators or phytochemicals which include auxin (indole-3-acetic acid (IAA)), gibberellic acid (GA), cytokinins (CK), and ethylene are organic chemical compounds that are known to regulate plant growth and development. Throughout the years, these chemical molecules became known as the main biochemical, physiological, and morphological hormones required for growth. PGPR species of the genera *Azospirillum*, *Pseudomonas*, *Xanthomonas*, *Rhizobium*, and *Bradyrhizobium* can form phytohormones (Mohamed and Goma 2012).

Auxin is a vital hormone, which controls most plant processes directly or indirectly. Being the first phytohormone identified in the *Phalaris canariensis* seeds by Darwin (1887), it has since paved the way for further exploration leading to the detection of the most active and prominent plant hormones in the auxin community, namely, indole-3-acetic acid (IAA). No matter how the plants can synthesize this chemical compound (endogenous supply), their success still depends entirely on external (exogenous) supply. PGPR is mainly supervised and is correlated with soil bacteria in this external gathering (Khalid et al. 2006). The cell function of auxin ranges from distinguishing the vascular tissue, initiating lateral and adventitious roots, stimulating the division of cells, and elongating the growth of the shoots and roots (Glick 1995). PGPR is significant in the development of the stage cum availability of nutrients in the rhizosphere for more efficient IAA production, considering the type of species and strain it cultivates, the condition, and the development (Ashrafuzzaman et al. 2009). While plants have now recognized other auxins including indole-3-butyric acid (IBA) and phenylacetic acid (PAA) (Normanly 1997), researchers also need to learn their structure mechanism of action and functioning. In comparison, in the soil-plant auxin pool and L-tryptophan (L-TRP) as a substitute for the production of the auxin, IAA producers are found to be more prevalent. The results indicate a rise in the L-tryptophan level that raises the biochemical and metabolic activities of bacterial BIPs or APBs, with subsequent root length reactions and root architecture modifications. Tryptophol, tryptamine, indole-3-pyruvic acid (IPA), and indole-3-acetamide are the primary metabolic pathways (Bartel 1997). Emergent evidence demonstrates that species that produce low auxins due to the lack of L-tryptophan are likely to grow high auxins when increased by L-tryptophan, especially in the presence of a viable strain of *Rhizobium* (Zahir et al. 2010). Importantly, it is important to notice that plant-based indigenous

auxin (IAA) might still not be automatically adequate to achieve maximum plant performance but should contribute to plant growth (Pilet and Saugy 1987). Therefore, it is important to explain the chemical 130 messengers (IAA produced by PGPR) with an exogenous need to bring about optimum plant development, growth, and adaptation to the stressful setting.

It is not well known yet what exact pathways PGPR stimulate to promote plant growth through the synthesis of gibberellic acid (Kang et al. 2009). GA is a group of diterpenes which greatly affect the processes of sprouting, leaf growth, elongation of the root, extension of the lateral root, fruit development, flowering, and initiation of trichomes (Yamaguchi 2008). Gibberellins and genera are the primary targets during environmental stress conditions because of the important role played by them in improving effective photosynthetic processes in plants, and they are a major plant growth biological regulator, which can enhance stress tolerance in many crops. The exogenous application of these growing hormones can be useful in soil shift and crop production improvements (Iqbal et al. 2011). Gibberellins are essentially interested in the alteration of plant morphology and promote the production of an aerial component, (Van Loon 2007) and has also been given to their effect in increasing tolerance of abiotic and biotic stresses. At the cellular level, the growth rate is regulated by the combined activity of two processes: cell proliferation and expansion. Gibberellins (GA) are plant specific hormones that play a central role in the regulation of growth and development with respect to environmental variability. It is well established that GA promotes growth through cell expansion by stimulating the destruction of growth-repressing DELLA proteins (DELLAs) and promotes chloroplast biogenesis, shoot proliferation, senescence, apical dominance, development of anthocyanin, and photomorphogens (Davies 2004). This also contributes to the susceptibility to vascular changes, proliferation of root hair, and suppression of the development of lateral root and main elongation (Aloni et al. 2006), and this molecule can be obtained by either plants or PGPR in an endogenous and exogenous way.

Plants improve the absorption through biosynthesis of endogenous cytokinin (Pospíšilová 2003). Studies have shown that cytokinin perfectly regulates plant adaptation, especially in salt-exposed areas, during plant growth (Hadiarto and Tran 2011). Through a biochemical test, cytokinin is a major antagonist of abscisic acid (ABA), resulting in certain phytohormone regulation (Pospíšilová 2003). The cytokinin content of the plant declines significantly during water scarcity, resulting in a favorable rise in ABA concentration. The evaluation of the development in broth media for plant hormones by various streptomycin strains indicates that cytokinin and gibberellin are synthesized by both strains (Mansour et al. 1994). While essential to phyto-development, it does not yet have a well-defined mechanism of action. The cytokinin in the receptor gene is regulated by changes in osmotic conditions (Merchan et al. 2007). Various studies have shown that the plants are immune to environmental stress by inoculating seedlings with cytokinin strains of *Bacillus subtilis*.

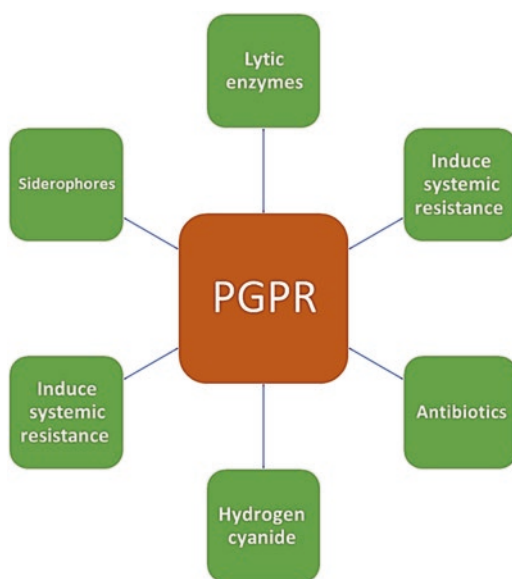
Ethylene which is a special phytohormone has a wide spectrum of chemical activity as at low concentrations the useful function of this biomolecule is better

reported. This impairs certain significant developmental features, e.g., root elongation, defoliation, and other cellular processes, which lead to reduced crop production at high concentrations (Bhattacharyya and Jha 2012). An enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase is required to resolve these troubling effects. The biocatalyst's function is to degenerate the ACC plant which is the direct precursor to α -ketobutyrate and ammonium for ethylene synthesis on the plant (Glick et al. 2007). The decay results from the decrease of plant production of ethylene by a variety of pathways, while PGPR producing ACC deaminase controls the amount of ethylene of plants and stops high levels of ethylene from inhibiting development (Noumavo et al. 2016). However, this vaporous hormone also governs the initiation, maturation, and germination of the seeds and abscission of the leaf and wilting (Kaur et al. 2016).

6 Role of PGPR in Biocontrol of Plant Disease

The greatest danger to food security worldwide is the loss of crops from plant diseases. The losses vary from small reductions in plant growth to major damage resulting in plant death and reduced yields (Savary et al. 2012). Many methodologies were studied to avoid or control these pathogens, including the production of resistant varieties by plant breeding, the production of GMO plants, as well as the chemical enrollments such as fungicides. Furthermore, there could be a detrimental effect on the health of humans through the presence of pesticide and fungicide leftovers. Due to the imperatives on antibiotic development in standard environments,

Fig. 16.1 Model to illustrate the role of PGPR in plant protection



the role of antibiotics in biocontrol and microbial antagonism has been discussed. PGPR is a biocontrol agent with the ability to kill a large variety of potential species with plant disease. PGPR must use one of the following mechanisms to be an effective biocontrol agent against pathogenic microbes: antibiotic formation, systemic resistance induction, hydrogen cyanide formation, and lytic enzyme formation (Fig. 16.1) (Lugtenberg and Kamilova 2009). According to reports by Junaid et al. (2013), key organisms which attack the plants typically include, in host plants, bacteria, fungus, and nematodes which cause bad diseases. Thereby, rhizobacteria or their metabolites are known to function as a sort of protection against disease.

6.1 Antibiotic Production

Antibiotic production by PGPR is one of the essential components for the promotion of plant growth and antimicrobial activity (Table 16.3). These antibiotics have been shown to play a part in disease concealment through mutant study and biochemical exams using distilled antibiotics in various biocontrol frameworks. These antimicrobial mixes can track pathogenic plant microbes or their growth by inhibiting the germination of spores and fungal mycelia lysis (Adhya et al. 2018; Ulloa-Ogaz et al. 2015). PGPR is known as a biocontrol agent due to the generation of antibiotics which includes known examples, i.e., DAPG, phenazine, cyclic lipopeptides, and amphisin (Loper and Gross 2007), while there is certain list of antibiotics which includes zwittermicin A, oligomycin A, xanthobaccin, and kanosamine known to be generated by *Pseudomonas strains*, *Bacillus*, *Streptomyces*, and *Stenotrophomonas* sp. (Compant et al. 2005). However, these biochemicals are found to be regulated by abiotic, biotic, and other environmental factors, and diseases caused by pathogens can be suppressed by low-weight-molecular compounds known as antibiotics as various good known drugs from PGPR as biocontrol agents which have been utilized for the disease control include 2-hexyl-5-propyl resorcinol (HPR), 2-hydroxymethyl-chroman-4-one, D-gluconic acid, hydrogen cyanide (HCN), and phloroglucinols (Phl) (Cazorla et al. 2006). To maintain other microbes in the soil as niche competition in the field will have passed, and the fundamental path to decreasing the incidence of disease in plants will be followed by *Rhizobacteria* with a view to nutrient supply and spatial abundance (Kamilova et al. 2005, b). If an association of competent microbes flourishes in the rhizosphere and affects the radically colonized PGPR by releasing noxious metabolites or compounds, it thus impedes the root absorption capacity to assimilate growing and developing nutrients. Apart from the ability to survive in the nutrients of PGPR, flagellum, lipopolysaccharide, chemotaxis, and root exudate secretion enhance its longevity (Lugtenberg and Kamilova 2009). According to Saraf et al. (2011), it is important in heme growth the reduction of ribotide precursors of DNA and ATP synthesis that siderophores are synthesized in PGPR with iron chelation when not present in pathogenic fungal species of plant. Space exposure is thus a significant factor in the thriving and dominant role of PGPR over pathogens in niche competition, and the rhizosphere role plays a vital role in supplying plant nutrient exposure (Heydari and Pessarakli 2010).

Table 16.3 Generation of antibiotics for soil-borne diseases via the PGPR microorganism

Antibiotics/functions	PGPR	Pathogen/disease	References
Phenazine, 2,4-diacetylphloroglucinol (DAPG)	<i>Pseudomonas fluorescens</i>	<i>Meloidogyne incognita</i> <i>Fusarium oxysporum</i>	Meyer et al. (2016)
Surfactin Iturin Fengycin	<i>Bacillus velezensis</i>	<i>Ralstonia solanacearum</i> <i>Fusarium oxysporum</i>	Cao et al. (2018)
Volatile antibiotics	<i>Bacillus amyloliquefaciens</i> subsp. <i>plantarum</i> XH-9	<i>Fusarium oxysporum</i>	Wang et al. (2018)
Bacilysin	<i>B. subtilis</i>	<i>Phytophthora infestans</i>	Caulier et al. (2017)
Hydrogen cyanide Phenazine	<i>Fluorescent pseudomonads</i>	<i>Pythium aphanidermatum</i>	Prabhukarthikeyan and Raguchander (2016)
Pyrrolnitrin	<i>Pseudomonas aeruginosa</i>	<i>Rhizopus microsporus</i> , <i>Fusarium</i>	Uzair et al. (2018)
<i>Bacillus</i> Peptide Antibiotics	<i>Bacillus</i>	<i>Fusarium graminearum</i>	Khan et al. (2017)
Surfactin Iturin A Iturin D Fengycin Bacillomycin D	<i>Bacillus subtilis</i>	Wilt and root rot	Smitha et al. (2017)
Bacillomycin D Fengycin A	<i>B. subtilis</i>	<i>Sclerotinia sclerotiorum</i>	Abdeljalil et al. (2016)
Pyrrolnitrin Hydrogen cyanide	<i>Pseudomonas chlororaphis</i>	<i>Sclerotinia sclerotiorum</i>	Nandi et al. (2015)
Triterpenoid soyasapogenol	<i>Rhizobium leguminosarum</i> bv. <i>viciae</i>	<i>Didymella pinodes</i>	Ranjbar Sistani et al. (2017)
Fengycin	<i>Bacillus amyloliquefaciens</i> subsp. <i>plantarum</i>	<i>Rhizomucor variabilis</i>	Zihahirwa Kulimushi et al. (2017)
Iturin Bacilysin Bacillomycin Surfactin Subtilin Subtilosin	<i>B. amyloliquefaciens</i>	<i>Sclerotinia sclerotiorum</i>	Vinodkumar et al. (2017)

(continued)

Table 16.3 (continued)

Antibiotics/functions	PGPR	Pathogen/disease	References
DAPG	<i>Pseudomonas</i> sp. LBUM300	<i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i>	Lanteigne et al. (2012)
2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin (PLT) pyrrolnitrin (PRN)	<i>Pseudomonas fluorescens</i>	<i>Botrytis cinerea</i> <i>Monilinia fructicola</i>	Zhang et al. (2020)

6.2 Induced Systemic Resistance (ISR)

To combat pathogenic bacteria, fungi, and viruses, PGPR activates some form of protection mechanism. This will improve and adapt the plant much better (Van Loon 2007). The gene and gene products have not been well established for this form of biological control phenomenon. Unlike systemic acquired resistance (SAR), a protection state is triggered in the entire plant following primary pathogen infections (Bakker et al. 2013). To act against plant pathogens, a mechanism called induced systemic resistance (ISR) uses plant hormones like jasmonic acid (JA), salicylic acid (SA), and ethylene and other organic acids for the stimulation and signaling in host plant for the defense purpose (Pieterse et al. 2000). This mechanism is mediated through JA, ethylene, and SA biosynthesis pathways (Dempsey and Klessig 2012). The interaction of these hormones is either antagonistic or synergistic to change the mechanism of defense (Nassem and Dandekar 2012). A large number of secondary metabolites that have antibiotic activity (phenolic, flavonoids, alkaloids, cyanide glycosides, etc.) were identified as an ISR mechanism in noninfected crops following receipt of chemical signals from infected plants, with volatile methyl salicylic acid as a signal (Dempsey and Klessig 2012). Antimicrobial active ingredients, such as phenols, can inhibit microbial development, and different phenolic metabolic cells that are less harmful to plant cells accumulate in the cells than aglycones. After infection, aglycone is released by hydrolysis which is toxic to both plant cells and microbes (Kenawy 2016). The defense response in the plant system can cause cell wall thickening and lignification, callus deposition, a buildup of phytoalexins, and synthesis of many lytic enzymes (Sticher et al. 1997).

According to Labuschagne et al. (2010), to cope up with environmental stress, PGPR reaction toward ISR can be achieved through adjustment of physical and biochemical reaction to environmental stress and also by increasing physical and mechanical vigor of the cell wall, and it has been observed that certain molecules such as lipopolysaccharide, *N*-acyl homoserine lactone (AHL), salicylic acid, etc. are antibiotic forms of ISR in PGPR (Van Loon 2007). There are certain bacterial species which are found to be involved in the process to biocontrol including *Pseudomonas* sp., *Bacillus pumilus*, and *Enterobacteriaceae* (Jourdan et al. 2009). Zehnder et al. (2001) found that ISR has wider scope when applied PGPR strain is used as a seed coat against *Pseudomonas syringae* causing angular leaf spot, *Colletotrichum lagenarium* causing anthracnose in cucumber, and *Erwinia tracheiphila* leading to bacterial wilt.

Besides, *P. fluorescens* has protected tomatoes from wilt diseases and may serve as an ISR signal to cause DAG pools in tomato root rhizosphere (Haas and Keel 2003).

7 Conclusion

Over the last century, the effective application of organic fertilizers, herbicides, and pesticides should not be overlooked in an agricultural environment. They help plant growth initially while having a long-term negative impact. This practice not only affects the land and its inhabitants but also threatens people's lives through the food chain. The soil has become extremely infertile and unproductive due to the rise in soil pollution, condition of climate, soil pathogens, and extensive land overuse. Food insecurity and the increasing population are evident at the low agro-yield. To achieve auto-sufficiency, a wide understanding of the microbial interaction and its mechanism of action must be made, particularly in the tropic world, to be essential to scientific knowledge. Not only does this lead to bumper crops but also keeps the ground healthy and safe. Although the PGPR campaign has been in progress for decades, in Africa, it has not been adopted due to a lack of understanding and governmental policies. Nonetheless, efforts will be based on the replacement of bio-product agrochemicals such as biofertilizers, bioinsecticides, and bioherbicides by a supportive PGPR consortium. To boost crop yield while preserving the soil conditions, farmers must carefully define and recognize the benefits of these bioinoculants in terms of improved plant nutrients and biocontrol through the introduction of systemic resistance and nutrients or space rivalry. This approach is to mitigate soil degradation, habitat change, and land flora and fauna loss by genetically modified processing of PGPR as an essential compound of modern food production. Finally, this technology, especially in developed countries, must be used and implemented to curb the possible humanitarian (famine) crisis in areas ravaged by war and terrorism, thus stimulating the production of food and improving our community's environmental safety.

References

- Abdeljalil NOB, Vallance J, Gerbore J, Bruez E, Martins G (2016) Characterization of tomato-associated rhizobacteria recovered from various tomato-growing sites in Tunisia. *J Plant Pathol Microbiol* 7(351):2
- Abo-Zaid GA (2014) Scaling-up production of biocontrol agents from *Pseudomonas* spp. Faculty of Agriculture, Alexandria University, Alexandria
- Ashrafuzzaman M, Hossen FA, Ismail MR, Hoque MA, Islam ZM, et al. (2009) Efficiency of Plant Growth-Promoting Rhizobacteria (PGPR) for the enhancement of rice growth. *Afr J Biotech* 8:1247–1252
- Adhya TK, Lal B, Mohapatra B, Paul D, Das S (2018) *Advances in soil microbiology: recent trends and future prospects*. Springer, Singapore

- Ahemad M, Khan MS (2011) Toxicological assessment of selective pesticides towards plant growth promoting activities of phosphate solubilizing *Pseudomonas aeruginosa*. *Acta Microbiol Immunol Hung* 58:169–187
- Aloni R, Aloni E, Langhans M, Ullrich CI (2006) Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism. *Ann Bot* 97(5):883–893
- Anderson AJ, Kim YC (2018) Biopesticides produced by plant-probiotic *Pseudomonas chlororaphis* isolates. *Crop Prot* 105:62–69
- Bakker PA, Doornbos RF, Zamioudis C, Berendsen RL, Pieterse CMJ (2013) Induced systemic resistance and the rhizosphere microbiome. *Plant Pathol J* 29(2):136–143
- Barea JM, Richardson AE (2015) Phosphate mobilisation by soil microorganisms. In: Lugtenberg B (ed) *Principles of plant-microbe interactions*. Springer, Heidelberg, pp 225–234
- Bartel B (1997) Auxin biosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 48:51–66 . PMID: 15012256. <https://doi.org/10.1146/annurev.arplant.48.1.51>
- Beneduzi A, Ambrosini A, Passaglia LMP (2012) Plant growth-promoting rhizobacteria: their potential as antagonists and biocontrol agents. *Genet Mol Biol* 35(4):1044–1051
- Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World J Microbiol Biotechnol* 28:1327–1350
- Bishop PE, Jorger RD (1990) Genetics and molecular biology of an alternative nitrogen fixation system. *Plant Mol Biol* 41:109–125
- Bruto M, Prigent-Combaret C, Muller D, Moëgne-Loccoz Y (2014) Analysis of genes contributing to plant-beneficial functions in plant growth-promoting rhizobacteria and related Proteobacteria. *Sci Rep* 4:6261
- Cao Y, Pi H, Chandransu P, Li Y, Wang Y, Zhou H, Cai Y (2018) Antagonism of two plant-growth promoting *Bacillus velezensis* isolates against *Ralstonia solanacearum* and *Fusarium oxysporum*. *Sci Rep* 8(1):4360
- Caulier S, Gillis A, Colau G, Licciardi F, Liépin M, Desoignies N, Bragard C (2017) Versatile antagonistic activities of soil-borne *Bacillus* spp. and *Pseudomonas* spp. against *Phytophthora infestans* and other potato pathogens. *Front Microbiol* 9:143
- Cazorla FM, Duckett SB, Bergstrofm ET, Noreen S, Odijk R, Lugtenberg BJJ, Thomas-Oates J, Bloemberg GV (2006) Biocontrol of avocado dematophora root rot by antagonistic *Pseudomonas fluorescens* PCL1606 correlates with the production of 2-hexyl 5-propyl resorcinol. *Mol Plant Microbe Interact* 19:418–428
- Cezairliyan B, Vinayavekhin N, Grenfell-Lee D, Yuen GJ, Saghatelian A, Ausubel FM (2013) Identification of *Pseudomonas aeruginosa* phenazines that kill *Caenorhabditis elegans*. *PLoS Pathog* 9:e1003101
- Chin-A-Woeng TF, Bloemberg GV, Van der Bij AJ, Van der Drift KM, Schripsema J, Kroon B, de Bruijn FJ (1998) Biocontrol by phenazine-1-carboxamide-producing *Pseudomonas chlororaphis* PCL1391 of tomato root rot caused by *Fusarium oxysporum* f. sp. *radicis-lycopersici*. *Mol Plant* 11(11):1069–1077
- Chin-A-Woeng TF, Bloemberg GV, Mulders IH, Dekkers LC, Lugtenb BJ (2000) Root colonization by the phenazine-1-carboxamide producing bacterium *Pseudomonas chlororaphis* PC3L1391 is essential for biocontrol of tomato foot and root rot. *Am Phytopathol Soc* 13:1340–1345
- Compant S, Duffy B, Nowak J, Clément C, Barka EA (2005) Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl Environ Microbiol* 71:4951–4959
- Darwin F (1887) *The life and letters of Charles Darwin*, London: John Murray. Volume 3.
- Dasgupta D, Kumar A, Mukhopadhyay B, Sengupta TK (2015) Isolation of phenazine 1,6-dicarboxylic acid from *Pseudomonas aeruginosa* strain HRW.1-S3 and its role in biofilm-mediated crude oil degradation and cytotoxicity against bacterial and cancer cells. *Appl Microbiol Biotechnol* 99:8653–8665
- Davies PJ (2004) *Plant hormones: biosynthesis, signal transduction, action*. Kluwer Academic Publishers, Dordrecht

- Dempsey DA, Klessig DF (2012) SOS—too many signals for systemic acquired resistance? *Trends Plant Sci* 17(9):538–545
- Dwivedi D, Johri BN (2003) Antifungal from fluorescent pseudomonads: biosynthesis and regulation. *Curr Sci* 85:1693–1703
- Fernando WGD, Nakkeeran S, Zhang Y (2004) Ecofriendly methods in combating *Sclerotinia sclerotiorum* (Lib.) de Bary. *Rec Res Dev Environ Biol* 1:329–347
- Fernando W, Nakkeeran S, Zhang Y, Savchuk S (2018) Biological control of *Sclerotinia sclerotiorum*(lib.) de Bary by *Pseudomonas* and *Bacillus* species on canola petals. *Crop Prot* 26:100–107
- Fernando WDG, Nakkeeran S, Zhang Y (2005) Biosynthesis of antibiotics by PGPR and its relation in biocontrol of plant diseases. In: Siddiqui ZA (ed) *PGPR: Biocontrol and Biofertilizer*. Springer, Dordrecht, pp 67–109
- Gaur R (2002) Diversity of 2,4-diacetylphloroglucinol and 1-aminocyclopropane 1-carboxylate deaminase producing rhizobacteria from wheat rhizosphere. PhD thesis, G.B. Pant University of Agriculture and Technology, Pantnagar
- Ghignone S, Salvioli A, Anca I, Lumini E, Ortu G, Petiti L, Bonfante P (2012) The genome of the obligate endobacterium of an AM fungus reveals an interphylum network of nutritional interactions. *ISME J* 6(1):136–145
- Ghosh UD, Saha C, Maiti M, Lahiri S, Ghosh S, Seal A, Mitra Ghosh M (2014) Root associated iron-oxidizing bacteria increase phosphate nutrition and influence root to shoot partitioning of iron in tolerant plant *Typha angustifolia*. *Plant Soil* 381(1–2):279–295
- Glick BR (1995) The enhancement of plant growth by free-living bacteria. *Can J Microbiol* 41:109–117
- Glick BR (2012) Plant growth-promoting bacteria: mechanisms and applications. *Scientifica* 2012:963401
- Glick BR, Cheng Z, Czary J, Duan J (2007) Promotion of plant growth by ACC deaminase-producing soil bacteria. *Eur J Plant Pathol* 119:329–339
- Gopalakrishnan S, Sathya A, Vijayabharathi R, Varshney RK, Gowda CL, Krishnamurthy L (2015) Plant growth-promoting rhizobia: challenges and opportunities. *3 Biotech* 5(4):355–377
- Gouda S, Kerry RG, Das G, Paramithiotis S, Shin HS, Patra JK (2017) Revitalization of plant growth-promoting rhizobacteria for sustainable development in agriculture. *Microbiol Res* 206:131–140
- Guo JH, Qi HY, Guo YH, Ge HL, Gong LY, Zhang LX, Sun PH (2004) Biocontrol of tomato wilt by plant growth-promoting rhizobacteria. *Biol Cont* 29:66–72
- Guo JK, Ding YZ, Feng RW, Wang RG et al (2015) *Burkholderia metalliresistens* sp. nov., a multiple metal-resistant and phosphate-solubilising species isolated from heavy metal-polluted soil in Southeast China. *Antonie van Leeuwenhoek* 107(6):1591–1598
- Guttenberger N, Blankenfeldt W, Breinbauer R (2017) Recent developments in the isolation, biological function, biosynthesis, and synthesis of phenazine natural products. *Bioorg Med Chem* S0968–S0896:31180–31844
- Haas D, Keel C (2003) Regulation of antibiotic production in root-colonizing *Pseudomonas* spp. and relevance for biological control of plant disease. *Annu Rev Phytopathol* 41:117–153
- Hadiarto T, Tran LS (2011) Progress studies of drought-responsive genes in rice. *Plant Cell Rep* 30:297–310
- Hao X, Xie P, Johnstone L, Miller SJ, Rensing C, Wei G (2012) Genome sequence and mutational analysis of plant-growth promoting bacterium *Agrobacterium tumefaciens* CCNWGS0286 isolated from a zinc-lead mine tailing. *Appl Environ Microbiol* 78:5384–5394
- Hass D, Defago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonads. *Nat Rev Microbiol* 3:307–319
- Hassan MN, Afghan S, Hafeez FY (2011) Biological control of red rot in sugarcane by native pyoluteorin-producing *Pseudomonas putida* strain NH-50 under field conditions and its potential modes of action. *Pest Manag Sci* 67:1147–1154

- Heydari A, Pessarakli M (2010) A review on biological control of fungal plant pathogens using microbial antagonists. *J Biol Sci* 10:273–290
- Iqbal N, Nazar R, Iqbal MRK, Masood A, Nafees AK (2011) Role of gibberellins in regulation of source sink relations under optimal and limiting environmental conditions. *Curr Sci* 100:998–1007
- Jourdan E, Henry G, Duby F, Dommes J, Barthelemy JP, Thonart P, Ongena M (2009) Insights into the defense-related events occurring in plant cells following perception of surfactin-type lipopeptide from *Bacillus subtilis*. *Mol Plant Microbe Interact* 22:456–468
- Ju M, Wang D, Pierson L, Pierson E (2018) Disruption of MiaA provides insights into the regulation of phenazine biosynthesis under suboptimal growth conditions in *Pseudomonas chlororaphis* 30-84. *Microbiology* 163:94–108
- Junaid JM, Dar NA, Bhat TA, Bhat AH, Bhat MA (2013) Commercial biocontrol agents and their mechanism of action in the management of plant pathogens. *Int J Mod Plant Anim Sci* 1:39–57
- Kang S, Joo GJ, Hamayun M (2009) Gibberellin production and phosphate solubilization by newly isolated strain of *Acinetobacter calcoaceticus* and its effect on plant growth. *Biotech Lett* 31: 277–281
- Kang BR, Anderson AJ, Kim YC (2018) Hydrogen cyanide produced by *Pseudomonas chlororaphis* 06 exhibits nematicidal activity against *Meloidogyne hapla*. *Plant Pathol J* 34:35–43
- Kamilova F, Validov S, Azarova T, Mulders I, Lugtenberg B (2005) Enrichment for enhanced competitive plant root tip colonizers selects for a new class of biocontrol bacteria. *Environ Microbiol* 7:1809–1817
- Kang BG, Kim WT, Yun HS, Chang SC (2010) Use of plant growth-promoting rhizobacteria to control stress responses of plant roots. *Plant Biotechnol Rep* 4(3):179–183
- Kaur G, Reddy MS (2014) Influence of P-solubilizing bacteria on crop yield and soil fertility at multilocational sites. *Eur J Soil Biol* 61:35–40
- Kaur H, Kaur J, Gera R (2016) Plant growth promoting rhizobacteria: a boon to agriculture. *Int J Cell Sci Biotechnol* 5:17–22
- Kenawy AMA (2016) characterization of two udp glycosyltransferase genes from hybrid poplar, MSc thesis, Faculty of Forestry, The University of British Columbia, Vancouver, Canada
- Khalid A, Akhtar MJ, Mahmood MH, Arshad M (2006) Effect of substrate-dependent microbial ethylene production on plant growth. *Microbiology* 75:231–236
- Khan MS, Zaidi A, Wani PA, Oves M (2009) Role of plant growth-promoting rhizobacteria in the remediation of metal contaminated soils. *Environ Chem Lett* 7:1–19
- Khan N, Maymon M, Hirsch AM (2017) Combating *Fusarium* infection using bacillus-based antimicrobials. *Microorganisms* 5(4):75
- Khan MS, Zaidi A, Wani PA (2007) Role of phosphate-solubilizing microorganisms in sustainable agriculture - A review. *Agron Sustain Dev* 27: 29–43
- Kim J, Rees D (1994) Nitrogenase and biological nitrogen fixation. *Biochemistry* 33:389–397
- Kim BK, Chung JH, Kim SY, Jeong H, Kang SG, Kwon SK, Kim JF (2012) Genome sequence of the leaf-colonizing bacterium *Bacillus* sp. strain 5B6, isolated from a cherry tree. *J Bacteriol* 194(14):3758–3759
- Klopper JW, Beauchamp CJ (1992) A review of issues related to measuring colonization of plant roots by bacteria. *Can J Microbiol* 38(12):1219–1232
- Klopper JW, Schroth MN (1981) Plant growth-promoting rhizobacteria and plant growth under gnotobiotic conditions. *Phytopathology* 71:642–644
- Klopper JW, Ryu CM, Zhang S (2004) Induced systemic resistance and promotion of plant growth by *Bacillus* spp. *Phytopathology* 94:1259–1266
- Kraus J, Loper JE (1995) Characterization of a genomic locus required for the production of the antibiotic pyoluteorin by the biological control agent *Pseudomonas fluorescens* Pf-5. *Appl Environ Microbiol* 61:849–854
- Kumar V, Behl RK, Narula N (2001) Establishment of phosphate solubilizing strains of *Azotobacter chroococcum* in the rhizosphere and their effect on wheat cultivars under greenhouse conditions. *Microbiol Res* 156:87–93

- Kumar A, Vandana RS, Singh M, Pandey KD (2015) Plant growth-promoting rhizobacteria (PGPR). A promising approach to disease management. *Microbes and environmental management*. Studium Press, New Delhi, pp 195–209
- Kunc F, Macura J (1988) Mechanisms of adaptation and selection of microorganisms in the soil. In: Vancura V, Kunc F (eds) *Soil microbial associations*. Amsterdam, Elsevier, pp 281–299
- Labuschagne N, Pretorius T, Idris AH (2010) Plant Growth Promoting Rhizobacteria as Biocontrol Agents Against Soil-Borne Plant Diseases. In: *Plant Growth and Health Promoting Bacteria*, Microbiology Monographs, Maheshwari, D.K. (Ed.), SpringerVerlag Berlin Heidelberg, pp:211–230
- Lanteigne C, Gadkar VJ, Wallon T, Novinscak A, Filion M (2012) Production of DAPG and HCN by *Pseudomonas* sp. LBUM300 contributes to the biological control of bacterial canker of tomato. *Phyto Pathol* 102:967–973
- Liu K, McInroy JA, Hu C-H, Kloepper JW (2017) Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. Department of Entomology and Plant Pathology, Auburn University, Auburn
- Lugtenberg B, Kamilova F (2009) Plant-growth-promoting bacteria. *Annu Rev Microbiol* 63:541–555
- Loper JE, Gross H (2007) Genomic analysis of antifungal metabolite production by *Pseudomonas fluorescens* Pf-5. *Eur J Plant Pathol* 119: 265–278
- Manjula K, Podile AR (2001) Chitin-supplemented formulations improve biocontrol and plant growth promoting efficiency of *Bacillus subtilis* AF 1. *Can J Microbiol* 47:618–625
- Mansour FA, Ildesuguy HS, Hamedo HA (1994) Studies on plant growth regulator and enzyme production by some bacteria. *J. Qatar Univ Sci* 14:81–288
- McKenzie RH, Roberts TL (1990) Soil and fertilizers phosphorus update. In: *Proceedings of Alberta soil science workshop proceedings*, Edmonton, Alberta, Feb 20–22, pp 84–104
- McSpadden Gardener BB (2007) Diversity and ecology of biocontrol *Pseudomonas* in agricultural systems. *Phytopathology* 97:221–226
- Merchan F, de Lorenzo L, González-Rizzo S, Niebel A, Megías M, Frugier F, Sousa C, Crespi M (2007) Analysis of regulatory pathways involved in the reacquisition of root growth after salt stress in *Medicago truncatula*. *Plant J* 51:1–17
- Meyer SLF, Halbrendt JM, Carta LK, Skantar AM, Liu T, Abdelnabby HME, Vinyard BT (2009) Toxicity of 2,4-diacetylphloroglucinol (DAPG) to plant-parasitic and bacterial-feeding nematodes. *J Nematol* 41:274–280
- Meyer SL, Everts KL, Gardener BM, Masler EP, Abdelnabby HM, Skantar AM (2016) Assessment of DAPG-producing *Pseudomonas fluorescens* for management of *Meloidogyne incognita* and *Fusarium oxysporum* on watermelon. *J Nematol* 48(1):43
- Mohamed HI, Goma EZ (2012) Effect of plant growth promoting *Bacillus subtilis* and *Pseudomonas fluorescens* on growth and pigment composition of radish plants (*Raphanus sativus*) under NaCl stress. *Photosynthetica* 50(2):263–272
- Nandi M, Selin C, Brassinga AKC, Belmonte MF, Fernando WD, Loewen PC, De Kievit TR (2015) Pyrrolnitrin and hydrogen cyanide production by *Pseudomonas chlororaphis* strain PA23 exhibits nematicidal and repellent activity against *Caenorhabditis elegans*. *PLoS One* 10:e0123184
- Nega A (2014) Review on Concepts in Biological Control of Plant Pathogens. *J Biol Agri Healthcare* 4(27): 33–54
- Nassem M, Dandekar T (2012) The role of auxin-cytokinin antagonism in plant pathogen interactions. *PLoS Pathog* 8:1–4
- Normanly J (1997) Auxin metabolism. *Physiol Plant* 100:431–442
- Noumavo PA, Agbodjato NA, Baba-Moussa F, Adjanohoun A, Baba-Moussa L (2016) Plant growth-promoting rhizobacteria: beneficial effects for healthy and sustainable agriculture. *Afr J Biotechnol* 15(27):1452–1463
- Nowak-Thompson B, Chancey N, Wing JS, Gould SJ, Loper JE (1999) Characterization of a pyoluteorin biosynthetic gene cluster of *Pseudomonas fluorescens* Pf-5. *J Bact* 181:2166–2174

- Pieterse CMJ, Van Pelt JA, Ton J, Parchmann S, Mueller MJ, Buchala AJ, Métraux JP, Van Loon LC (2000) Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* requires sensitivity to jasmonate and ethylene but is not accompanied by an increase in their production. *Physiol Mol Plant Pathol* 57:123–134
- Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C (2015) Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process—a review. *Biol Fertil Soil* 51:403–415
- Pilet PE, Saugy M (1987) Effect of root growth of endogenous and applied IAA and ABA. A critical reexamination. *Plant Physiol* 83:33–38
- Podile AR (2006) Seed bacterization with *Bacillus subtilis* AF 1 enhances seedling emergence, growth and nodulation of pigeonpea. *Indian J Microbiol* 35:199–204
- Pospíšilová J (2003) Interaction of cytokinins and abscisic acid during regulation of stomatal opening in bean leaves. *Photosynthetica* 41:49–56
- Prabhukarthikeyan SR, Raguchander T (2016) Antifungal metabolites of *Pseudomonas fluorescens* against *Pythium aphanidermatum*. *J Pure Appl Microbiol* 10(1):579–585
- Qurashi AW, Sabri AN (2012) Bacterial exopolysaccharide and biofilm formation stimulate chickpea growth and soil aggregation under salt stress. *Braz J Microbiol* 11:83–91
- Rane MR, Sarode PD, Chaudhari BL, Chincholkar SB (2007) Detection, isolation and identification of phenazine-1-carboxylic acid produced by biocontrol strains of *Pseudomonas aeruginosa*. *J Sci Ind Res* 66:627–631
- Ranjbar Sistani N, Kaul HP, Desalegn G, Wienkoop S (2017) Rhizobium impacts on seed productivity, quality, and protection of *Pisum sativum* upon disease stress caused by *Didymella pinodes*: phenotypic, proteomic, and metabolomic traits. *Front Plant Sci* 8:1961
- Ryu CM, Farag MA, Hu CH, Reddy MS, Wei HX, Pare PW, Kloepper JW (2003) Volatiles produced by PGPR elicit plant growth promotion and induced resistance in *Arabidopsis*. In: Proceedings of the 6th international workshop on plant growth promoting rhizobacteria, pp 436–443
- Saraf M, Jha CK, Patel D (2011) The role of ACC deaminase producing PGPR in sustainable agriculture. In: Maheshwari DK (ed) Plant growth and health promoting bacteria microbiology. Steinbuchel A (series ed) Monographs, vol 18. Springer, Berlin, pp 365–386
- Sarhan EAD, Shehata HS (2014) Potential plant growth-promoting activity of *Pseudomonas* spp. and *Bacillus* spp. as biocontrol agents against damping-off in alfalfa. *Plant Pathol J* 13:8–17
- Savary S, Ficke A, Aubertot JN, Hollier C (2012) Crop losses due to diseases and their implications for global food production losses and food security. *Food Secur* 4:519
- Shanmugaiah V, Mathivanan N, Varghes B (2010) Purification, crystal structure and antimicrobial activity of phenazine-1-carboxamide produced by a growth-promoting biocontrol bacterium, *Pseudomonas aeruginosa* MML2212. *J Appl Microbiol* 108:703–711
- Smitha K, Mohan R, Devadason A, Raguchander T (2017) Exploiting novel rhizosphere *Bacillus* species to suppress the root rot and wilt pathogens of chickpea. *Afr J Microbiol Res* 9:1098–1104
- Sorensen J (1997) The rhizosphere as a habitat for soil microorganisms. In: van Elsas JD, Trevors JT, Wellington EMH (eds) Modern soil ecology. Marcel Dekker, New York, pp 21–46
- Sticher L, Mauch-Mani B, Métraux JP (1997) Systemic acquired resistance. *Annu Rev Phytopathol* 35:235–270
- Tambong JT, Hofte M (2001) Phenazines are involved in biocontrol of *Pythium myriotylum* on cocoyam by *Pseudomonas aeruginosa* PNA1. *Eur J Plant Pathol* 107:511–521
- Thomasow LS, Weller DM (1988) Role of a phenazine antibiotic from *Pseudomonas fluorescens* in biological control of *Gaeumannomyces graminis* var. *tritici*. *J Bact* 170:3499–3508
- Teplitski M, Robinson JB, Bauer WD (2000) Plants secrete substances that mimic bacterial nacyl homoserine lactone signal activities and affect population density-dependent behaviour in associated bacteria. *Mol Plant Microbe Interact* 13:637–648
- Ulloa-Ogaz AL, Muñoz-Castellanos LN, Nevárez-Moorillón GV (2015) Biocontrol of phytopathogens: antibiotic production as a mechanism of control. The battle against microbial pathogens: basic science, technological advances, and educational programmes. *Formatex Research Center, Badajoz*, pp 305–309

- Uzair B, Kausar R, Bano SA, Fatima S, Badshah M, Habiba U, Fasim F (2018) Isolation and molecular characterization of a model antagonistic *Pseudomonas aeruginosa* divulging in vitro plant growth-promoting characteristics. *Biomed Res Int* 2018:6147380
- Validov SZ, Kamilova F, Lugtenberg BJ (2009) *Pseudomonas putida* strain PCL1760 controls tomato foot and root rot in stonewool under industrial conditions in a certified greenhouse. *Biol Control* 48(1):6–11
- Van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. *Eur J Plant Pathol* 119:243–254
- Verma SC, Ladha JK, Tripathi AK (2001) Evaluation of plant growth-promoting and colonization ability of endophytic diazotrophs from deep water rice. *J Biotechnol* 91(2):127–141
- Vessey JK (2003) Plant growth-promoting rhizobacteria as biofertilizers. *Plant Soil* 255:571–586
- Vinodkumar S, Nakkeeran S, Renukadevi P, Malathi VG (2017) Biocontrol potentials of antimicrobial peptide producing *Bacillus* species: multifaceted antagonists for the management of stem rot of carnation caused by *Sclerotinia sclerotiorum*. *Front Microbiol* 8:446
- Wang X, Wang C, Ji C, Li Q, Zhang J, Song X, Jun Kang S, Liu Z, Liu X (2018) Isolation and characterization of antagonistic bacteria with the potential for biocontrol of soil-borne wheat diseases. *bioRxiv preprint first posted online 18 May 2018*
- Weller DM, Landa BB, Mavrodi OV, Schroeder KL, De La Fuente L, Bankhead SB, Molar RA, Bonsall RF, Mavrodi DV, Thomashow LS (2007) Role of 2,4-diacetylphloroglucinol-producing fluorescent *Pseudomonas* spp. in the defense of plant roots. *Plant Biol* 9:4–20
- Wisniewski-Dyé F, Vial L, Burdman S, Okon Y, Hartmann A (2015) Phenotypic variation in *Azospirillum* spp and other root-associated bacteria. In: De Bruijn FJ (ed) *Biological nitrogen fixation*. Wiley, Hoboken, pp 1047–1054
- Yadav J, Verma JP, Jaiswal DK, Kumar A (2014) Evaluation of PGPR and different concentration of phosphorus level on plant growth, yield and nutrient content of rice (*Oryza sativa*). *Ecol Eng* 62:123–128
- Yamaguchi S (2008) Gibberellin metabolism and its regulation. *Annu Rev Plant Physiol* 59:225–251
- Yu JM, Wang D, Pierson LS, Pierson EA (2018) Effect of producing different phenazines on bacterial fitness and biological control in *Pseudomonas chlororaphis* 30–84. *Plant Pathol* J34:44–58
- Zahir ZA, Shah MK, Naveed M, Akhtar MJ (2010) Substrate dependent auxin production by *Rhizobium phaseoli* improve the growth and yield of *Vigna radiate* L. under salt stress conditions. *J Microbiol Biotechnol* 20:1288–1294
- Zaidi A, Khan MS, Ahemad M, Oves M (2009) Plant growth promotion by phosphate solubilizing bacteria. *Acta Microbiol Immunol Hung* 56:263–284
- Zehnder GW, Murphy JF, Sikora EJ, Klopper JW (2001) Application of rhizobacteria for induced resistance. *Eur J Plant Pathol* 107:39–50
- Zhang QX, Kong XW, Li SY, Chen XJ, Chen XJ (2020) Antibiotics of *Pseudomonas protegens* FD6 are essential for biocontrol activity. *Aust Plant Pathol* 49:307–317
- Zhou L, Jiang HX, Sun S, Yang DD, Jin KM, Zhang W, He YW (2016) Biotechnological potential of a rhizosphere *Pseudomonas aeruginosa* strain producing phenazine-1-carboxylic acid and phenazine-1-carboxamide. *World J Microbiol Biotechnol* 32:50
- Zihalirwa Kulimushi P, Argüelles Arias A, Franzil L, Steels S, Ongena M (2017) Stimulation of fengycin-type antifungal lipopeptides in *Bacillus amyloliquefaciens* in the presence of the maize fungal pathogen *Rhizomucor variabilis*. *Front Microbiol* 8:850