



Plant growth promoting rhizobacteria in sustainable agriculture: from theoretical to pragmatic approach

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Abstract

Plant growth promoting rhizobacteria (PGPR) are the residents of rhizosphere that are known to influence plant growth and survival through the production of various regulatory chemicals under a variety of circumstances. This growth promotion is accomplished by both direct and indirect means. Direct effects of PGPR encompass two major activities, that is, Bio-fertilization (Enhancement of nutrient uptake including nitrogen and phosphorous primarily) and phyto-stimulation (Production of plant growth promoting hormones). Indirect effects of PGPR are majorly contained within their ability as biocontrol agents that antagonize the growth and survival of phytopathogens either by the production of antagonizing chemicals (Local antagonism) or by the induction of systemic resistance throughout the plant against pathogens. The understanding of such diverse growth promoting abilities of PGPR has led to their application as potent biofertilizers for sustainable agriculture. However, further analyses of the agro-ecosystem with complex biotic and abiotic mechanisms should not be overlooked for their extensive commercial applications and future prospects.

Keywords PGPR · Bio-fertilization · Phytostimulation · ISR

1 Introduction

Plant growth promoting rhizobacteria (PGPR) are the bio-stimulants that exert beneficial effects to the host plant health and reduce environmental stress (Calvo et al. 2014). They are also known as Nodule promoting rhizobacteria (NPR) or plant health promoting rhizobacteria (PHPR) (Hayat et al. 2010). They influence the development of plant by synthesis of various phytochemicals and inhibiting phytopathogenic microorganisms (Son et al. 2014). PGPR have mutualistic association with plant roots that fulfill essential nutritional requirements for both plants and associated microorganisms (Atlas and Bartha 1998).

The rhizosphere microbial community comprises of bacteria, protozoa, algae, fungi and actinomycetes. However, rhizobacteria overwhelmingly exist in the rhizosphere (Vejan et al. 2016) and their density in this region is much high compared to the surrounding soil (Glick 2012). Only 4%–

10% of the actual surface of the plant root (rhizoplane) directly interacts with micro-organisms; they are mostly present in adjacent rhizosphere soil (Reddy et al. 2017). Plant roots predominantly influence the microbial population within the rhizosphere. The successional changes in the rhizosphere during plant development result in selection of rapidly growing and opportunistic microbial population (Atlas and Bartha 1998).

Depending on the proximity to plant roots, PGPR are characterized into extracellular PGPR (present in rhizoplane or rhizosphere) or intracellular PGPR (reside in nodules of plant cells to exchange metabolites directly (Gray and Smith 2005). PGPR are also characterized for their distinctive property to grow and compete with other microorganisms, the ability to colonize the plant roots and the efficiency to enhance plant growth (Kloepper 1994). On the other hand, they are functionally characterized as phyto-stimulators, biofertilizers, biopesticides and rhizoremediators, (Antoun and Prévost 2005). Some of these beneficial activities of PGPR have been demonstrated by many researchers in the past few years (Fatnassi et al. 2015; Huang et al. 2016; Adediran et al. 2016). Several species of *Pseudomonas*, *Xanthomonas*, *Bacillus*, *Bradyrhizobium*, *Enterobacter* and *Rhizobium* are considered as the most potent phytohormone producing rhizobacteria (Karnwal 2009). However, the different strains of *Pseudomonas* and *Bacillus*

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have mostly investigated for their distinctive plant growth promoting characteristics (Karnwal 2017).

Rhizobacteria act symbiotically with plant roots through two basic mechanisms to augment plant development and protection. The direct promotion involves the mechanisms to increase uptake of water and mineral nutrients, including Nitrogen fixation and phosphate solubilizing activity and the production of phytohormones and siderophores (Ryu et al. 2005). Indirect mechanisms involve the control of phytopathogens associated with various plant diseases by the production of antagonistic substances (such as antibiotics, lytic enzymes, bacteriocins) and by induced systemic resistance (Lugtenberg and Kamilova 2009) (Fig. 1).

Apart from providing general functions of mechanical support and helping in nutrient and water uptake, plant roots help in symbiotic interaction by secreting different substances in the soil known as root exudate which acts chemical attractant for soil microbes. These compounds alter the physiochemical characteristics of the soil and effects soil microbial community (Walker et al. 2003; Ahemad and Kibret 2014). The exudation of these materials is demonstrated by the observation that bacteria present in the rhizosphere have distinctly different nutritional requirements compared to bacteria within root free soil (Atlas and Bartha 1998).

2 Direct effects of PGPRs

2.1 Bio-fertilization

PGPRs are known to improve the uptake of nutrients by the plants that are crucial to their optimal growth—an attribute

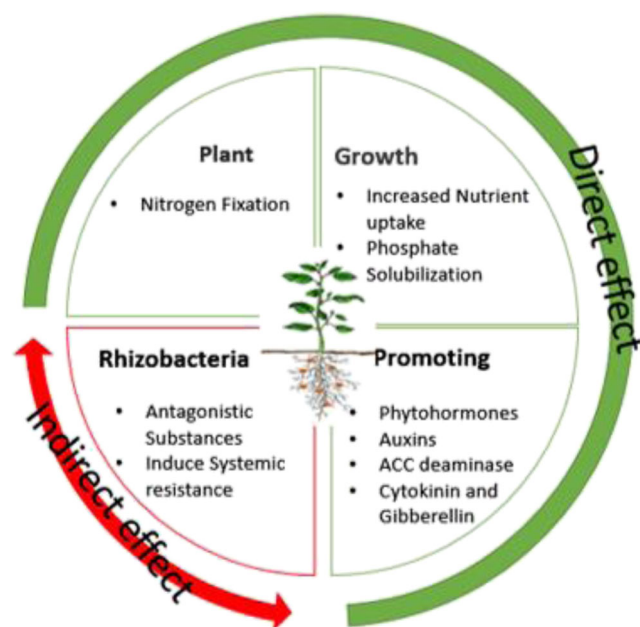


Fig. 1 Plant growth promoting bacteria and their effects

that allow them to undertake bio-fertilization. In this respect, these rhizospheric bacteria are involved in two major activities, that is, nitrogen fixation and phosphate solubilization.

1) Nitrogen fixation

Plant growth and development is contingent on an ample supply of nitrogen. Though atmosphere is much of nitrogen (nearly 78%), but this atmospheric N_2 is non-utilizable to the plants (Ahemad and Kibret 2014; Kim and Rees 1994). This situation led to the development of an intricate process of Biological Nitrogen Fixation (BNF) involving a great diversity of nitrogen fixing microflora primarily rhizobacteria populating the roots of plants. PGPRs carry out this process mainly by two means: either in a symbiotic relationship with the plants or in a non-symbiotic manner which can be of free-living, associative or endophytic in nature. Symbiotic bacteria reside within the host plant tissues and are involved in direct exchange of metabolites. So far, nearly all rhizobial species have been found associated to 11 genera of alpha- and 3 genera of beta-proteobacteria (Laranjo et al. 2014). Endosymbiotic rhizobacteria, for example, *Rhizobium*, *Bradyrhizobium* (Jordan 1982), *Sinorhizobium* (Chen et al. 1988) and *Mesorhizobium* (Jarvis et al. 1997) fix N_2 in the root nodules of legumes, while *Frankia* spp. in root nodules of non-leguminous plants. Non-symbiotic counterpart includes *Azoarcus*, *Azotobacter*, *Azospirillum*, *Gluconobacterium diazotrophicus*, *Enterobacter*, *Pseudomonas*, *Burkholderia* and cyanobacteria *Anabaena* and *Nostoc* (Ahemad and Kibret 2014). Yadegari et al. (2010) demonstrated the increment in symbiotic potential of *Rhizobium* with increased nodule number and shoot dry weight in addition to greater amount of fixed N_2 and better seed yield by co-inoculating the common bean with *Pseudomonas fluorescens* and *Azospirillum lipoferum*. The molecular machinery that forms the basis of BNF is nitrogenase enzyme system of nitrogen fixing microorganisms that converts the atmospheric N_2 to NH_3 which can then be assimilated by plants. Nitrogenase is a metallo-enzyme complex comprising of two subunits namely Dinitrogenase reductase—an Fe protein and Dinitrogenase having a metal cofactor. Based on the cofactor, three nitrogen-fixing systems have been classified as 1) Molybdenum (Mo) nitrogenase; 2) Vanadium (V) nitrogenase; and 3) Iron (Fe) nitrogenase. Different bacterial genera have different nitrogenase enzyme systems but most of the BNF is carried out by the Mo nitrogenase which is present in all diazotrophs (Hu and Ribbe 2016). Nitrogen fixation (*nif*) genes are present in both symbiotic and free-living bacteria. A *nif* gene cluster of 20 to 25 kb with seven operons is found in diazotrophs (Ahemad and Kibret 2014). The Mo nitrogenase system is encoded by *nifDK* and *nifH* genes. Dinitrogenase, which is a heterotetramer containing two α and two β ($\alpha_2\beta_2$) polypeptides, is encoded by *nifD* and *K* respectively. This

protein also contains two active metalloclusters iron-sulphur and iron-molybdenum cofactors. Fe-Mo cluster is the site of nitrogen reduction (Atlas and Bartha 1998). The symbiotic expression of *nif* genes is dependent on low level of O₂ which is regulated by *fix* genes which is found in symbiotic as well as free-living diazotrophs (Kim and Rees 1994).

2) Phosphate solubilization

Phosphorous (P) is considered as the second essential macronutrient for plant growth and development because it is involved virtually in all metabolic pathways in plants namely photosynthesis and respiration, cell signaling, energy transfer and biosynthesis of macromolecules (Khan et al. 2010). Both organic and inorganic forms of phosphorous are present in soil abundantly but they are sparingly obtainable by the plants generally at concentrations 1 mgkg⁻¹ or less of soil. The phosphorous when applied to the soil, 90–95% of it is rendered unavailable to the plants by its conversion to insoluble organic (inositol phosphate/soil phytate, phosphomono- and triesters) forms as well as inorganic minerals (phosphates of iron mainly apatite, calcium and aluminium) (Pandey and Maheshwari 2007). Plants take up two soluble forms, monobasic (H₂PO₄⁻) and dibasic (HPO₄²⁻) ions. PGPRs solubilize the insoluble phosphates primarily by two different strategies: 1) Release of chelating agents or mineral dissolving compounds like organic acid anions, hydroxyl or hydrogen ions and CO₂ to solubilize inorganic phosphate compounds; 2) Production of extracellular enzymes (phosphatases/phytases) that mineralize organic forms of phosphate by the hydrolysis of phosphoric esters (Glick 2012; Sharma et al. 2013). Phosphate-solubilizing bacteria (PSBs) are among the most potent biofertilizers and they have drawn attention as soil inoculums of agriculturists. PSBs among PGPRs belong to diverse bacterial genera like *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Rhizobium* and *Serratia* to name a few (Bhattacharyya and Jha 2012).

2.2 Phytohormone production/phytostimulation

1) Auxin

The most important plant growth regulator is the auxin referred to as Indole 3-acetic acid (IAA), which is naturally produced by plants. Nearly 80% of rhizospheric bacteria can also produce and liberate auxin as a secondary metabolite (Patten and Glick 1996). Some other indole derivatives such as indole-3-acetamide, indole-3-acetaldehyde, and indole-3-pyruvate are also known to have auxin activity (Olanrewaju et al. 2017). Auxin (IAA) acts as a notable signaling molecule in plant cell division, elongation and differentiation; in tropical responses (geo- and phototropism); apical dominance and root initiation

of lateral and adventitious types (Gobelak et al. 2015). IAA influence these mechanisms by 1) altering the plant auxin pool; 2) increasing the root length and area which in turn causes greater absorption of soil nutrients; 3) loosening the plant cell wall causing greater exudation by the roots that facilitate the growth of rhizospheric microorganisms (Glick 2012). Tryptophan in root exudates acts as precursor for IAA biosynthesis which follows five different pathways. These are named for a key intermediate within the pathway as 1) Indole-pyruvate pathway; 2) Indole-acetamide pathway; 3) Indole-acetonitrile pathway; 4) Indole-acetaldehyde pathway; and 5) Tryptamine pathway (Duca et al. 2014). PGPRs such as *Rhizobium*, *Bradyrhizobium*, *Pseudomonas*, *Enterobacter* and *Klebsiella* undertake indole-pyruvate and indole-acetaldehyde pathways for IAA biosynthesis (Shilev 2013). Microbially synthesized phytohormones are effective as compared to their chemical counterparts owing to their slow but continuous release. Moreover, chemical phytohormones have a low threshold between their stimulatory and inhibitory levels.

2) ACC (1-Aminocyclopropane-1-carboxylate) deaminase

The phytohormone ethylene is crucial to normal plant growth and development as it is engaged in a diverse array of biological phenomena including promotion of root initiation and fruit ripening, stimulation of seed germination, lowering of wilting, promotion of leaf abscission and activation of production of other phytohormones (Glick et al. 2007). In addition to being produced endogenously, many biotic and abiotic processes can trigger ethylene production. Stress conditions like drought, water logging and salinity, heavy metal toxicity and pathogenic infections stimulate extraordinary levels of ethylene which have negative impacts on plant physiology, thus it is also referred to as ‘stress hormone’ (Ali et al. 2014; Saleem et al. 2007). Negative effects may include defoliation and diminished crop performance which can be prevented by the enzyme ACC deaminase. PGPRs that exhibit ACC deaminase activity are able to ease out plant growth and development by lowering ethylene levels thereby stimulating salt tolerance and diminishing drought stress in plants (Nadeem et al. 2009). Rhizobacterial strains with ACC deaminase activity are widely distributed among different genera including *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* (Kang et al. 2010; Shaharoon et al. 2007). These bacteria convert ethylene to α ketobutyrate and ammonia and prior root or seed inoculation of these PGPRs lowers ethylene production in response to a pathogenic infection, thus, releases stress among various positive effects such as root and shoot elongation, increased nodulation by rhizobacteria and increased nutrient (N, P, K) uptake (Ahemad and Kibret 2014; Glick 2012).

3) Cytokinins and Gibberellins

Though cytokinins are produced by algae, bacteria and higher plants, little is known about the bacterially-produced cytokinins. Cytokinin genes are evidently expressed in many PGPRs, and their application to the growing plants can modify the plants' phytohormone composition. PGPR strains capable of producing either cytokinins or gibberellins or both of these include *Azotobacter* sp., *Rhizobium* sp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis* and *Paenibacillus polymyxa* (Kang et al. 2010). Lettuce plant growth has been augmented by inoculating with *Bacillus subtilis*. Zeatine riboside (ZR) was the most prominent cytokinin that accumulated in roots and shoots of the plant thereby increasing root and shoot weight nearly 30% over a period of 8 days (Arkhipova et al. 2005). Cytokinin-producing PGPRs' potential has also been demonstrated to reduce drought stress in oriental thuja. Leaves inoculated with *Bacillus subtilis* showed a higher water level than that of non-inoculated ones. Root and shoot dry weights in drought seedlings were increased by 19.23% and 13.99%. This study reflects the prospective of such strains as drought stress inhibitors in arid environments (Liu et al. 2013). Purified cytokinins applied to individual plants have also been shown to delay senescence by accumulating chlorophyll, stimulating root development and elongation, root-hair formation, shoot initiation and leaf expansion (Olanrewaju et al. 2017). Four forms of gibberellins GAs (GA_1 , GA_3 , GA_4 , GA_{20}) are produced by bacteria with GA_1 and GA_4 being the most active (Gupta et al. 2016) PGPRs capable of synthesizing GAs *Achromobacter xylosoxidans*, *Gluconobacter diazotrophicus*, *Acinetobacter calcoaceticus*, *Rhizobia*, *Azotobacter* spp., *Bacillus* spp., *Herbaspirillum seropedicae*, and *Azospirillum* spp. (Deka et al. 2015; Olanrewaju et al. 2017). Exogenously-added purified GAs boosts up the activity of endogenous plant gibberellins thereby promoting plant growth. Specifically, they can induce shoot growth and development through the activity of DELLA repressor that regulates the activity of gibberellins activating genes (Nelson and Steber 2016).

2.3 Siderophore production

Iron is an important micro-nutrient for the growth of all life forms. Despite of being fourth abundant element on earth, it is rendered unavailable to bacteria and plants in aerobic soils owing to the presence of its predominant trivalent form (Fe^{3+}) which is sparsely soluble and hence not readily absorbed by these organisms (Rajkumar et al. 2010). To overcome this problem, microorganisms have evolved to produce low molecular weight (nearly 200 to 2000 Da) iron scavengers named as siderophores that chelate iron and transport it into their cells (Ahmed and Holmström 2014). PGPR-produced

siderophores bind to iron with a very high affinity with a dissociation constant (Kd) of 10^{-20} to 10^{-50} . The siderophore-Fe complex interacts with special receptors on bacterial cell surface, internalized and then assimilated by either reducing into divalent form (Fe^{2+}) or cleavage of the siderophore moiety (Saha et al. 2013). On the basis functional groups, siderophores have been categorized into three major groups: 1) Hydroxamate-type siderophores (produced mainly by fungi); 2) Catecholate-type siderophores (produced mainly by bacteria and have higher Fe binding affinity than hydroxamates); 3) Carboxylate-type siderophores (commonly produced by plants) (Saha et al. 2016). Different PGPR strains can produce different types of siderophores, for example, *Rhizobium* and *Mesorhizobium* produce catecholate-type while *Pseudomonas putida* siderophore analysis by TLC revealed the presence of both hydroxamate and catecholate iron chelating moieties (Sarode et al. 2007) Siderophore-producing bacteria associated to a variety of plant species have been isolated including Pseudomonads, *Bacillus*, *Rhizobium*, *Bradyrhizobium*, *Serratia* and *Streptomyces* (Kuffner et al. 2008). Pii et al. (2015) demonstrated the restoration of cucumber plants from iron deficiency symptoms in Fe-deficient soils. Inoculating the plants with PGPR *Azospirillum brasilense* resulted in increased chlorophyll content and biomass and improved iron content of the leaves. In addition to iron, siderophores can chelate other heavy metals and hence allow the plants to cope up with stress induced by heavy metal toxicity. Inoculation of *Brassica juncea* with two rhizobial strains allowed the plants to grow under chromium stress (Ahemad and Kibret 2014; Rajkumar et al. 2005).

3 Indirect effects

Bacterial genera including *Pseudomonas*, *Bacillus*, *Serratia*, *Burkholderia*, *Staphylococcus*, *Enterobacter*, *Herbaspirillum*, *Stenotrophomonas* and *Ochrobactrum*, are well known for potential inhibitory effects against phytopathogens (Soylu et al. 2005; Tariq et al. 2010). They produce various antagonistic substances for their defense essentially antibiotics including (Hydrogen cyanide), hydrolytic enzymes and bacteriocins (Beneduzi et al. 2012) Moreover, rhizobacteria combat with other microbes for nutrients and niches to control their growth. PGPR also reduce the activity of pathogens by induce systemic resistance (Van Loon et al. 1998)

3.1 Antagonistic substances

Antibiotics are the low molecular weight organic molecules that act by inhibiting the metabolic activities of other microorganisms. The synthesis of antibiotic compounds is highly

effective to control and prevent pathogen growth (Tariq et al. 2010). The mode of action of the antibiotics isolated from bacterial and fungal genera includes inhibition of cell wall or cell membrane synthesis and blocking of 30s ribosomal RNA initiation complexes (Maksimov et al. 2011). Six classes of antibiotics like phenazines, phloroglucinols, pyrrolnitrin, cyclic lipopeptides and hydrogen cyanide (HCN) are evidenced as more efficient towards biocontrol of root diseases (Haas and Défago 2005). Aldehyde, alcohol, ketones and sulphides also produce effective volatile antimicrobials (Table 1). The antibiotic compounds produced by *Pseudomonas* species include Pyocyanin, phenazine-1-carboxamide, viscosinamide, Cepaciamide A, Rhamnolipids, Oomycin A, phenazine-1-carboxylic acid, Butyrolactones, Ecomycins, sulphonamide N-butylbenzene and 2,4 Diacetyl phloroglucinol with antifungal activity; Karalicin with antiviral activity; Azomycin and Pseudomonic acid with antibacterial activity; Cepafungins with antitumour activity. Whereas, the several antibiotic metabolites synthesized by *Bacillus* are the following Kanosamine, Plipastatins A and B, Zwittermycin A, Bacillomycin and Iturin A (Fernando et al. 2005).

Moreover, PGPR synthesize various hydrolytic enzymes for instance protease, lipase, glucanase, chitinase and cellulases to suppress phytopathogens growth rate. The biocontrol ability of hydrolytic enzymes was found against fungal species of *Rhizoctonia solani*, *Botrytis cinerea*, *Sclerotium rolfisii*, *Pythium ultimum*, *Phytophthora sp.* and *Fusarium oxysporum* (Singh et al. 1999; Frankowski et al. 2001). These lytic compounds damage the fungal cell wall and help in releasing biotic stress of host plant (Neeraja et al. 2010; Maksimov et al. 2011). Microorganisms known for production of lytic enzymes include *Serratia marcescens* with effectiveness against *Sclerotium rolfisii* by synthesis of chitinase hydrolytic enzyme (Ordentlich et al. 1988), *Lysobacter* inhibit *Bipolaris* and *Pythium spp.* by producing glucanase (Palumbo et al. 2005) and *Myxobacteria* with antagonistic activity against fungal phytopathogens (Kobayashi and Nour 1996; Bull et al. 2002).

PGPR also produce antagonistic substances such as bacteriocins which have inhibitory activity against only closely related species. Interestingly, bacteriocins produced by *Bacillus sp.* have been found with broad spectrum lethal activity (Abriouel et al. 2011). They are ribosomally synthesized proteinaceous antimicrobial agents. Some bacteriocins originated from Gram-negative microorganisms are recombinantly synthesized by existing bacteriocins (Riley 1993). Colicins synthesized by certain *Escherichia coli* strains are the most representative bacteriocins. Some other examples of bacteriocins include marcescins from *Serratia marcescens*, megacins from *B. megaterium* and pyocins from *P. pyogenes* strains and cloacins from *Enterobacter cloacae* (Cascales et al. 2007).

Table 1 Common antibiotics produced by PGPR strains and their mode of action

Antibiotic	Origin	Mode of action	Pathogen	Disease	Reference
Phenazines	<i>Pseudomonas</i> spp.	Inhibition of oxidative phosphorylation reaction and accumulation of toxic superoxide radicals	<i>Gaeumannomyces graminis</i> var. tritici	Take all of wheat	Dowling and O'Gara 1994; Fernando et al. (2005)
Pyrolnitrin	<i>Pseudomonas</i> spp.	Not well demonstrated	<i>Pythium</i> spp.	Seedling decay of crops (sugar beet and radish)	Tripathi and Gottlieb (1969)
Phloroglucinols	<i>Pseudomonas</i> spp.	Membrane damage	<i>Pythium</i> spp.	Root rot of crop	de Souza et al. (2003)
Pyrrolnitrin	<i>Pseudomonas fluorescens</i> BL915	Inhibit fungal respiratory chain	<i>Rhizoctonia solani</i>	Seedling decay of crops	Tripathi and Gottlieb (1969); Dowling and O'Gara (1994)
Cyclic lipopeptides	fluorescent <i>Pseudomonas</i> spp.	Damages membranes and alters its function and have surfactant properties	<i>Pyrenophora tritici-repentis</i> <i>Pythium ultimum</i>	Tan spot of wheat Damping off	Haas and Défago (2005); Fernando et al. (2005)
Volatile antibiotic compounds	<i>Pseudomonas</i> spp. (mainly <i>Pseudomonas aeruginosa</i>), <i>Chromobacterium</i> spp. and <i>Rhizobium</i>	Inhibit cytochrome C oxidase and other metal containing enzymes	<i>Thielaviopsis basicola</i>	black root rot of tobacco	Blumer and Haas (2000)
Aldehydes, alcohols, ketones and sulfides	<i>Pseudomonas chlororaphis</i> (PA23)	deconstruct the structure of sclerotial bodies	<i>Sclerotinia sclerotiorum</i>	white mold	Fernando et al. (2005)

3.2 Induced systemic resistance

PGPR indirectly aid in plant development by increasing its defensive activity against harmful microorganism through the phenomenon of induce systemic resistance (ISR) and inhibiting subsequent attack by pathogen through systemic acquired resistance (SAR) (Van Loon 2007). Plants synthesize antagonistic substances phytoalexins (proteinaceous antimicrobial compounds, polyphenolic and flavonoid) directly at the site of microbial infection and spread its synthesis to the adjacent cells. This mechanism not only restraint the plant disease but also protect plant from further infection (SAR). Additionally, plants cause the rapid local necrosis and death of infected cells which leads to invade the pathogen (Atlas and Bartha 1998). SAR is potentiated by pathogen and can be regulated by virulent microorganisms (induce using salicyclic acid SA pathway) and avirulent microorganisms (SA independent pathway). In contrast, ISR nor directly involve the pathogen rather respond to prevent its deleterious effects. Both ISR and SA-independent pathway are triggered by ethylene. ISR is also dependent on jasmonic acid that stimulates defense response by the plant. But unlike SAR, induce systemic resistance does not rely on pathogenic protein (glucanase,

chitinase) and salicyclic acid. In addition, outer membrane Lipopolysaccharide, chitin, flagella, cyclic lipopeptide, pyoverdine, $\beta\beta$ -glucans also act as triggering agents for ISR (Glick 2012). The best characterized strains for the stimulation of ISR are *Pseudomonas spp.*, and some bacillus species including *Bacillus sphaericus*, *Bacillus subtilis*, *Bacillus mycoides*, *Bacillus amyloliquifaciens*, *Bacillus pasteurii*, *Bacillus pumilus* and *Bacillus cereus* (Choudhary et al. 2007). ISR is quite stable indicating that once resistance is induced, the plants can withstand the biotic challenges manifested by pathogen and suppress the disease for considerable time. ISR can be stimulated by avirulent microorganisms as well as by simulating conditions which initiate the similar response in the plant (Van Loon et al. 1998).

4 Commercialization and challenges

High yield crops along with eco-friendly fertilizers are the basic need of developing world. Because of the plentiful benefits, PGPR has become successful to attain the attentions of agricultural scientists (Tewari and Arora 2013). A lot of work has been done to find out different attributes of PGPR and

Table 2 List of different commercially available PGPR products

Commercially available products	PGPR strain	Crop	Mode of action	Producer
Cedomon, Cerall	<i>Pseudomonas chlororaphis</i>	barley and oats Wheat	biopesticide	Lantmännen BioAgri AB, Sweden
Cedress		Pea, carrot		
AMASE	<i>Pseudomonas azotoformans</i>	cucumber, lettuce, tomato, peppers, eggplant, cabbage and broccoli	Phytostimulators	Lantmännen BioAgri AB, Sweden
Amnite A100	<i>Azotobacter</i> , <i>Bacillus</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> and <i>Chaetomium</i> genera	Cucumbers, tomatoes, lettuce, capsicums, ornamental flowers and herbs	Biofertilizer and biopesticide	Cleveland Biotech Ltd.
BactoFil A10	<i>Azospirillum brasilense</i> , <i>Azotobacter vinelandii</i> , <i>Paenibacillus polymyxa</i> , <i>Bacillus megaterium</i>	monocotyledonous plants (maize, corms)	Biofertilizer	AGRObio Hungary
BactoFil B 10	<i>Azotobacter vinelandii</i> , <i>Paenibacillus polymyxa</i> , <i>Bacillus megaterium</i> , <i>B. subtilis</i>	sunflower, sugar beet, rape,	Biofertilizer	AGRObio Hungary
BactoFil CELL	<i>Cellvibrio ostraviensis</i>	Corn	Biofertilizer	AGRObio Hungary
BactoFil Soya	<i>Bradyrhizobium japonicum</i>	Soya	Biofertilizer (nitrogen fixation)	AGRObio Hungary
Compete Plus	<i>Bacillus</i> strains	Field Crop	Biofertilizer	Plant Health care USA
Inomix series	<i>Azotobacter vinelandii</i> , <i>Bacillus amyloliquefaciens</i> , <i>B. licheniformis</i> , <i>B. megaterium</i> , <i>B. polymyxa</i> , <i>B. subtilis</i> , <i>P. fluorescens</i>	Cereals	Biofertilizers, Phytostimulator	IAB, Spain

different strains of PGPR showed impressive results in promoting growth of different plants. Commercialization of these strains is the foremost need of the present time, for which the connection between research scientists and industries is vital. Identification and selection of the effective strain of PGPR for commercialization is also one of the big challenges (Nelson 2004). Although many PGPR execute well under laboratory settings, their commercialization calls for maximum functionality in the fields as well. In addition, the worthwhile market demand, effective and consistent activity, longer stability, low cost and informal availability is also required. The affectivity and consistent activity of PGPR products depend upon the farmer's understanding, while at same time it is not easy to educate them properly. One of the added challenges is the regulatory policies regarding bio-products. Each country has its own risk assessments policies so that they can avoid unconstrained issue of possibly destructive biological entities. Hence, PGPR products have to pass through different obstacles before reaching the market (Tabassum et al. 2017).

Many products of PGPR are already available in the market. They are already being used in different countries like Sweden, Finland, Switzerland, Austria, Lithuania, Denmark, Belgium, The Netherlands, Italy, Spain, Portugal, Germany, France, UK, and Austria. They are applied as biofertilizers, phytostimulators, rhizoremediators and bio-pesticides to attain varied benefits for better plant growth (Antoun and Prévost 2005). Famous commercially available PGPR include *Azospirillum*, *Pseudomonas*, *Bacillus*, *Burkholderia*, *Azotobacter*, *Rhizobium*, and *Serratia* (Nandakumar et al. 2001). Different commercialized PGPR based products along with their intended crops are mentioned in Table 2.

5 Future perspectives

Future perspectives involve the use of biotechnological and molecular biological approaches to get genetically modified PGPR. Genetically modified PGPR can boost the production of plant much better as compared to normal PGPR (Denton 2007). Work should be done to engineer different PGPR to avoid different soil pollutants, phytopathogens and to increase the water absorbing capacity (Wu et al. 2006). Fresh alternative PGPR should also be considered which can enhance the yield much efficiently. More work should be done on ice-nucleating plant growth promoting rhizobacteria that have the capability to increase plant growth at low temperature (Nadeem et al. 2013). There are some reported PGPR like *Azoarcus*, *Exiguobacterium*, *Methylobacterium*, *Paenibacillus* and *Pantoea* etc., which have shown very productive results for effective growth of plants. Work should be done for their commercialization as well (Chauhan et al. 2015). In short, the future success of this industry needs productive research, effective screening, proper interaction,

appropriate communication, inventive business organization and product marketing.

6 Conclusion

The phytopathogens, being a great threat for plant health and longevity, need to be controlled and restricted for invasion. Using eco-friendly indigenous soil microorganisms can be of great benefit to combat with these potential pathogens. The deliberate administration of rhizobacteria in soil can be of worth importance as their intricate symbiotic and antagonistic relationships with plants and plant pathogens respectively, are vital to plant growth and survival. However, prior to incorporation, the safety aspects should be considered and standards should be maintained.

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