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REVIEW

Plant growth promoting rhizobacteria as a biological tool for augmenting productivity and controlling disease in agriculturally important crops- A review

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Abstract

The ecological role of plant growth promoting bacteria associated with plant root environment is currently gaining increased attention. The tremendous use of chemical fertilizers and pesticides which are environmentally harmful can be replaced with the microbes generally called as Plant Growth Promoting Rhizobacteria (PGPR). These microbes can be developed as biofertilizers because they are eco-friendly, cost effective and are natural living organisms. The advantages of these microorganisms rely on their production of novel bioactive metabolites that inhibit various pathogens in the soil as well as their vast mechanisms in improving growth, productivity and yield in agriculturally important crops. Apart from this, their role in nutrient acquisition, soil fertility improvement and stress tolerance are also inevitable. This review represents the present scenario of beneficial bacteria as plant growth agents and disease control tools. They have been extensively studied for plant disease suppression, plant growth modulation, and interaction with plants. Here, some mechanisms employed by plant growth promoting bacteria from different environments are discussed.

Keywords: disease control, growth promotion, induction of systemic resistance, PGPR

Introduction

Rhizosphere is the term defined to the region of the soil bound by plant roots extending a few millimetres from root surface or in association with the roots and plant-produced materials (Arroyave *et al.* 2018). Studies based on metagenomics estimate that more than 5,000 microbial species are present per gram of soil, but a major portion of microbial population is unculturable. Plant root exudates such as sugars and aminoacids provide a rich supply of nutrients and energy for the development of various bacterial communities

in the rhizosphere, establishing more microbial populations in rhizosphere region. Hellriegel & Wilfarth (1888) discovered the root colonization of rhizobacteria in legumes and grasses which could convert atmospheric nitrogen to a usable form. Kloepper & Schroth (1978) coined the term 'rhizobacteria' based on their investigations on radishes. The term can be collectively applied to the soil bacterial community that colonises plant roots and stimulate growth and thereby diminishing the incidence of diseases. PGPR can be defined as the crucial part of rhizosphere region that when grown in symbiotic association with the host plants can trigger the growth of the host.

According to Whipps (2001), rhizobacterial interactions between the rhizobacteria and plants can be neutral, negative or positive. Beattie (2006) stated that the rhizobacteria associated with the plants are symbionts in which the rhizobacteria establish a healthy relationship with the host plants displaying no noticeable effect on the growth as well as the physiology of the host. In case of negative interactions, the pathogenic rhizobacteria produce toxic substances which negatively influence the growth and physiology of host plants. Apart from this, many beneficial PGPRs make use of a positive effect on the plant by many direct mechanisms *viz.*, solubilization of nutrients, production of growth regulators, nitrogen fixation, etc. or by indirect mechanisms *viz.*, suppression of phytopathogens, stimulation of mycorrhizae associations and removal of toxic substances (Fig. 1). Based on the degree of association with the plant roots, beneficial PGPRs can be divided into intracellular plant growth promoting rhizobacteria (iPGPR) and extracellular plant growth promoting rhizobacteria (ePGPR) (Ankati & Podile 2018). The iPGPRs generally exist inside the specialized structures of root cells, usually endophytes. On the other hand, the ePGPRs exist either in the rhizosphere or on rhizoplane or in the intercellular spaces of root cortex (Bhattacharyya & Jha 2012).

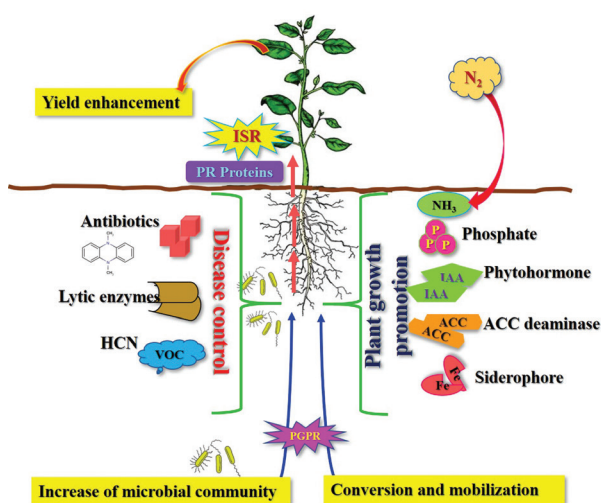Use of PGPRs as plant growth promoting agents and disease-suppressive agents is

Fig. 1. Mechanisms exhibited by plant growth promoting bacteria as plant growth promoters and disease suppressing agents

gaining attention nowadays to alleviate the toxic effects posed by chemical fertilizers and pesticides. These organisms support plants by modulating plant growth and other developmental processes thereby enhancing yield. Positive results mediated by these PGPR bacteria have been explained in a wide variety of plants cultivated under different stress conditions, including crops such as wheat (Kumar *et al.* 2018), maize (Berger *et al.* 2018; Ke *et al.* 2019), rice (Kotoky *et al.* 2019; Suarez Moreno *et al.* 2019), legumes (Sathya *et al.* 2017) and vegetable crops (Bader *et al.* 2019; He *et al.* 2019). Several PGPR formulations currently commercialized are meant for plant growth modulation as biofertilizers and plant disease suppression as bioprotectants or plant hormone production as biostimulants. Development of bioformulation has been most successful to deliver biological control agents *i.e.*, microbes capable of destroying phytopathogens to the agricultural fields. New reports related to PGPR role in plant growth promotion, nutrient management and disease resistance in various crops is depicted in Table 1.

Bacteria as PGPRs

Bacteria belonging to the genus *Alcaligenes, Agrobacterium, Azospirillum, Azoarcus, Azotobacter, Arthrobacter, Bacillus, Brevibacterium,*

Table 1. Recent reports of different PGPRs in plant growth promotion, nutrient management and disease resistance in various crops

PGPR strain/s	Mode of application	Crop/s	PGPR effects
Pseudomonas putida PSDM3, *Proteus penneri* PSDM6, *Enterobacter hormaechei* PSDM10, *Advenella* sp. PSDM17	5×10^8 CFU cell suspension	spring wheat	Crop protection from disease
Acinetobacter BS17, *Rahnella aquatilis* PGP27	5 mL of bacterial consortium plot^{-1}	*Vicia faba* L. and *Triticum durum* L.	Improved crop productivity and soil fertility
Paenibacillus sp. IITISM08, *Bacillus* sp. PRB77, *Bacillus* sp. PRB101	10 mL cell suspension kg^{-1} sterilized soil	*Helianthus annuus* (Sunflower)	Improved biomass production and enhanced remediation of endosulfan contaminated soil
Bacillus megaterium CAM12 *Pantoea agglomerans* CAH6	10^8 CFU mL^{-1} cell suspension as seed inoculation	*Vigna radiata*	Tolerance to abiotic stress and better growth
Serratia marcescens S2I7	Cell suspension introduced in pots	*Oryza sativa* L	Alleviated Cd-induced phytotoxicity and promoted the growth
Paenibacillus polymyxa Sx3	10^8 CFU mL^{-1} cell suspension as seed inoculation	*O. sativa* L	Promote plant growth and suppress bacterial leaf blight
Streptomyces A20 and *Streptomyces* 5.1	Cell suspension containing 10^3 CFU mL^{-1} of each strain under gnotobiotic conditions	*O. sativa* L	Biocontrol against bacterial panicle blight caused by *Burkholderia glumae* and plant growth promotion
S. violaceusniger AC12AB	Pots were inoculated by drenching with 10^6 CFU mL^{-1} bacterial suspension	Potato	Biocontrol against *Streptomyces scabies*, and plant growth promotion, yield in potato
S. lydicus A01	Mycelia were mixed with the soil	Tomato	Increased mineralization, nutrient accumulation, degradation of toxic and hazardous substances
S. variabilis, *S. fradiae*	The plantlet rhizosphere area was inoculated with 10 mL of 10^8 CFU mL^{-1}	*Stevia rebaudiana* L. Bertoni	Plant growth and salt tolerance improvement
Curtobacterium albidum SRV4	Seeds were treated in double volume of bacterial suspension of 10^8 CFU mL^{-1}	*O. sativa* L	Improved photosynthetic efficiency, modulation of osmolytes and antioxidative enzymes, development of induced systemic tolerance and alleviating salt stress in paddy plants

Bradyrhizobium, Burkholderia, Caulobacter, Chromobacterium, Leucobacter, Enterobacter, Erwinia, Flavobacterium, Herbaspirillum, Klebsiella, Shewanella, Mesorhizobium, Micrococcus, Pantoea, Pseudomonas, Paenibacillus, Providencia, Rhizobium, Stenotrophomonas, Rhodococcus, Serratia, Streptomyces and *Variovorax* are those bacterial species that reported for plant growth enhancement and yield (Ahemad & Kibret 2014). They are generally isolated from the rhizoplane or rhizosphere soil as root activities are higher in this area. Other than culturable bacteria, unculturable genera such as *Aquificae, Cholorobi, Bacteroidetes, Deinococcus-Thermus, Firmicutes, Chloroflexi, Gemmatimonadetes, Fusobacteria, Nitrospira, Proteobacteria, Spirochaetes, Planctomycetes* and *Verrucomicrobiae* have also been reported (Goel *et al*. 2018). Many of the genera also exist as endophytes which inhabit inside the plant parts. Many actinobacteria are also reported for the interaction with plants including endophytes (Palaniyandi *et al*. 2013a). Among the actinobacterial group, *Actinomadura, Actinoplanes, Corynebacterium, Microbispora, Micromonospora, Mycobacterium, Nocardiopsis, Nonomurea, Rhodococcus, Saccharopolyspor*a, *Streptomyces* and *Verrucosispora* have been greatly studied and explored for various applications (Sathya *et al*. 2017). They are found abundantly in bulk or rhizospheric soils and inhabit as either epiphyte or endophyte in different plant tissues including rice, barley, wheat, maize, soybean, ginger, cowpea, chickpea, banana, tomato, mangroves and medicinal plants.

Fungi as plant growth promoters

Most of the plant growth promoting fungi are endophytes that inhabit the internal tissues of plants without imparting any deleterious effects. The genera such as *Trichoderma, Fusarium, Penicillium* and *Phoma* are considered as source of novel bioactive compounds, however, the full potential of endophytic fungi remains underexplored (Shah *et al*. 2019). Most endophytic fungi isolated from plants are members of the *Ascomycota,* or their anamorphs, with only a few reports of mycorrhizal fungi

(Varma *et al*. 2012). For the first time ever, some fungal species like *Aspergillus awamori, Acremonium terricola, Piriformospora indica, Phomatropica, Tetraploaaristata* and *Trichoderma virens* were isolated as plant growth promoting fungi (Contreras-Cornejo *et al*. 2009; Yadav 2019).

PGP traits of microbes

Production of plant growth regulators

Auxins

Plant hormones (phytohormones) play a major role in plant growth and development. Auxin, one of the main phytohormone also referred as indole-3-acetic acid (IAA) has been produced by more than 80% of rhizospheric as well as endophytic bacteria since it is very essential for plant-rhizobacterial interactions. L-tryptophan is the main precursor for IAA synthesis and there are different pathways such as indole-3-acetamide, indole-3-pyruvate, tryptamine, indole-3-acetonitrile and tryptophan side-chain oxidase pathways discovered in many microorganisms (Numponsak *et al.* 2018). This phytohormone is involved in cell division and differentiation, seed stimulation and tuber germination, development of adventitious and lateral roots, effect light and gravity responses, photosynthesis, pigment formation, synthesis of various metabolites and resistance to biotic as well as abiotic stresses (Spaepen & Vanderleyden 2011).

IAA formation through indole-3-pyruvic acid and indole-3-acetic aldehyde pathway have been reported in many bacteria such as *Erwinia herbicola* and certain representatives of *Agrobacterium, Azospirillum, Bradyrhizobium, Enterobacter, Klebsiella, Pseudomonas* and *Rhizobium*. The conversion of tryptophan into indole- 3-acetic aldehyde involve an alternative pathway where tryptamine is produced as found in pseudomonads and azospirilla. On the other hand, IAA synthesis *via* indole-3-acetamide pathway is reported

in bacteria such as *A. tumefaciens*, *E. herbicola* and *Pseudomonas syringae*, *P. fluorescens* and *P. putida*. IAA biosynthesis involving tryptophan conversion to indole-3-acetonitrile is reported in a cyanobacterium, *Synechocystis*. A tryptophan-independent pathway commonly found in plants is also present in azospirilla and cyanobacteria (Prasanna *et al.* 2010).

In *Streptomyces*, IAA production is through indole-3-acetamide via L-tryptophan dependent pathway as described by Lin & Xu (2013). An endophytic *Streptomyces* strain isolated from *Azadirachta indica* has been reported to induce plant growth in tomato plants as described by Verma *et al.* (2011). Myo *et al.* (2019) investigated the optimization of IAA production from *Streptomyces fradiae* NKZ-259 and its formulation as a plant growth promoter to enhance economic and agricultural development. It is also noted that the lateral root development, root hair formation and release of nutrients are the responses of IAA in plants as reported by Davies (2004). Root colonizing bacteria depends on sugars exuded from the plant roots as a nutrient source (Dakora & Phillips 2002) and affirm the advantage of plant growth and disease suppression (Kunkel & Harper 2017).

Ethylene

Ethylene is also important to plant growth and development because it is involved in many biological phenomena such as root initiation, seed germination, fruit ripening, lowering of wilt incidence, production of various phytohormones and leaf abscission promotion (Glick *et al.* 2012). One of the direct effects of PGPRs is the biosynthesis of ACC (1-aminocyclopropane-1-carboxylate deaminase), an enzyme that control ethylene production by catalysing ACC (precursor of ethylene biosynthesis) into α-ketobutyrate and ammonia. Jaemsaeng *et al.* (2018) investigated *Streptomyces* sp. GMKU which improved salt tolerance in rice as well as enhanced flood tolerance in mung bean through conversion of ACC into ammonia and α-ketobutyrate thereby reducing the ethylene level. Since ethylene is

required for the induction of systemic resistance in plants elicited by pathogens, it is assumed that treating plants with ethylene-lowering bacteria would prevent this induction (Ghosh *et al.* 2018). Ethylene is also called stress hormone (Abeles *et al.* 1992) and the increased synthesis is typically associated with various environmental stresses such as extreme temperatures, intensified light, flood, drought, presence of organic pollutants and toxic metals, radiation, wound, insect attack, high salinity and attack of phytopathogens (Glick 2012).

Cytokinins and gibberellins

Some PGPR strains are also capable to produce cytokinins and gibberellins and their application to the growing plants can modify plant's phytohormone composition. Cytokinins stimulate plant cell division, enlargement and tissue expansion and also modulate stomatal conductivity. Selvakumar *et al.* (2018) reported that inoculation of tomato seedlings with a cytokinin producing plant growth promoting rhizobacterium *B. amyloliquefaciens* enhanced tomato growth and alleviated water stress. Cytokinin has also been shown to be produced by several PGPRs. This hormone has been identified in some strains of *Azotobacter* spp., *Bacillus subtilis*, *Paenibacillus polymyxa*, *Pantoea* spp., *Pseudomonas fluorescens*, *Rhizobium* spp., *Rhodospirillum rubrum* and *Streptomyces* (Joshi &Loria 2007). Nonetheless, it should be noted that PGPRs produce lower cytokinin levels than phytopathogens so that the effect of the PGPRs on plant growth is stimulatory. On the other hand, the action of the cytokinins from pathogens is inhibitory. But, a detailed understanding of the mode of action of bacterially synthesized hormones and how the these plant hormone production is regulated is not currently known (Kunkel & Harper 2017).

Conversion and mobilization of nutrients

Phosphate solubilization

Organic phosphorus is the predominant form of phosphorus and contribute up to 90% of the total P in soil (Khan *et al.* 2009).

Therefore, P mineralisation is a prerequisite for conversion of organic P into a plant available form and the reaction is catalysed by extracellular phosphatases produced by some microorganisms and plants. Further, much of the soluble inorganic phosphorus to be used as chemical fertiliser is immobilised soon after it is applied to soil. Many PGPRs possess the capacity to solubilise insoluble inorganic phosphates such as dicalcium phosphate, tricalcium phosphate, rock phosphate and hydroxyapatite. Organic acids produced by these bacteria convert the insoluble phosphorus compounds to di- and mono-basic phosphates that can easily be absorbed by the plant. Bacterial genera such as *Achromobacter*, *Agrobacterium*, *Bacillus*, *Burkholderia*, *Erwinia*, *Flavobacterium*, *Micromonospora*, *Pseudomonas*, *Rhizobium* and *Streptomyces* are reported as phosphate solubilizers (Roychowdhury *et al.* 2015). Phosphate solubilization has been reported in actinobacteria such as *Kitasatospora*, *Micrococcus* and *Thermobifida* (Franco-Correaa *et al.* 2010). On the other hand, Phosphorus-Mobilizing Bacteria (PMB) can effectively mobilize phosphorus through solubilization of phosphorus pools and mineralization of organic phosphorus compounds which are not readily available to the plant. Therefore, application of phosphate solubilizing bacteria to agriculture soils will be a promising approach for improvement of phosphorus fertilization in fields.

Zinc solubilization

The importance of zinc (Zn) in plants corresponds to nodulation process, nitrogen fixation, modulation of plant growth as well as yield. Zinc is present in the unavailable form in soil. Unfortunately, only a small portion of soil microbes can transform insoluble Zn to an available form. PGPRs with Zn solubilization potential can act as alternatives for Zn supplements in agricultural fields. Microorganisms such as *B. subtilis*, *Pseudomonas* sp., *Thiobacillus thiooxidans* and *Saccharomyces* sp. help in the solubilization of zinc from compounds such as zinc oxide (ZnO), zinc carbonate ($ZnCO_3$) and zinc sulfide (ZnS) (Saravanan *et al.* 2011).

Potassium mobilization

Microorganisms involving in the solubilization of potassium (K) are known as Potassium Solubilizing Microorganisms (KSM). Various genera of *Aspergillus*, *Azospirillum*, *Clostridium*, *Bacillus*, *Phosphobacteria*, *Paenibacillus*, *Azotobacter* and *Rhizobacteria* are reported so far to possess this trait (Velázquez *et al.* 2016). *Frateuria aurantia* was also shown to solubilize K into an usable form. In another study, *B. pseudomycoides* isolated from tea growing soil could mobilize K from bound form in soil when applied along with mica waste (Pramanik *et al.* 2019). The mechanism of K solubilization and perspectives of KSM is best reviewed by Sattar *et al.* (2019).

Silicate solubilization

Silicon (Si) also act as advantageous plant nutrient functioning as plant growth enhancer and contributor of tolerance to both biotic and abiotic stresses. This insoluble, polymeric silica found in soils is solubilised during weathering process to release monosilicic acid, the available form of silicon to be absorbed by the plants. Microbes such as *Bacillus globisporus* Q12, *Bacillus* sp. and *Rhizobium* sp. are known for silicate solubilization (Chandrakala *et al.* 2019).

Nitrogen fixation

Nitrogen (N_2) is the main plant nutrient and a limiting factor in agricultural ecosystems because of the loss through mineral leaching or rainfall. Nitrogen fixation is the process whereby atmospheric nitrogen is converted to ammonia which can be utilized by plants for the synthesis of various nitrogenous compounds. Different PGPR strains like *Azoarcus* sp., *Beijerinckia* sp., *Frankia* sp., *Klebsiella* sp., *Pantoea* sp., *Rhizobium* sp. and *Streptomyces* sp. are reported to fix atmospheric N_2 in soil (Jiao *et al.* 2015; Gopalakrishnan *et al.* 2015). Nitrogen fixing organisms are generally divided into symbiotic N_2 fixers including members of the *Rhizobiaceae* that forms symbiotic association (e.g. rhizobia) with many leguminous plants and non-leguminous trees (e.g. *Frankia*). *Frankia* is the

best studied actinobacteria that live in symbiosis with many dicot plants called actinorhizal plants by the formation of root nodules with nitrogen fixing ability (Yamaura *et al.* 2010).

Azotobacter is a genus of non-symbiotic, aerobic, free-living heterotrophic N_2 fixing bacteria. This bacterium colonizes the plant roots and fixes N_2 and the yield in these crops can be increased up to 50% (Kızılkaya 2008). *Azotobacter vinelandii*, *A. beijerinckii*, *A. armeniacus*, *A. insignis*, *A. nigricans*, *A. chroococcum*, *A. paspali* and *A. macrocytogenes* are commonly employed as biofertilizers. *Azotobacter* was used for plant growth as well as yield improvement in both cereal and millet crops like rice, wheat, sorghum, sugarcane, maize, pearl, millet, sesame, cotton and vegetables (Wani *et al.* 2007). Moreover, actinobacteria such as *Streptomyces*, *Thermomonosporaceae* and *Micromonosporaceae* were also reported for their nitrogen fixing capacity in different crop plants (Valdés *et al.* 2005).

Siderophore production

Iron, despite the fact that it is the fourth most abundant element on earth, it is not readily absorbed by either plants or bacteria because of the predominant insoluble form, Fe^{3+} (ferric ion). In nature, the amount of available iron for assimilation by living organisms is very low. Microorganisms as well as plants require high iron concentration and obtaining the same is tricky in the rhizosphere since plant, bacteria and fungi compete for iron. In order to survive with such a limited supply of iron, bacteria synthesize low-molecular mass siderophores (~400-1500 Da) as well as membrane receptors that are able to bind the Fe-siderophore complex, thereby facilitating iron uptake (Hider & Kong 2010). Currently, there are over 500 known siderophores and the chemical structures of 270 of these compounds have been determined (Fig. 2).

PGPR secrete low molecular weight siderophores with iron-chelating ability, making it very difficult for other microbes to access iron.
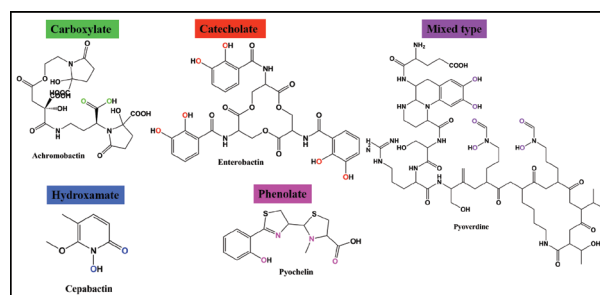

Fig. 2. Various siderophore structures discovered in different bacteria. The chemical structures were drawn with Chem DrawPro12.0 Cambridgesoft, USA.

Siderophores bind the soluble form of iron from soil to make it available to plants and this siderophore-Fe complex is taken up by plant roots making the soil environment Fe-deficient for phytopathogens. Under Fe limiting conditions, many pathogens especially fungi are unable to thrive under normal conditions. Siderophores synthesized by *Pseudomonads* have high Fe chelating ability and thus make them potential biocontrol agents (Chincholkar *et al.* 2000). Siderophores secreted by many microorganisms include *Pseudomonas* (pyoverdins), *Agrobacterium* (catechols), *Erwinia* (catechols and hydroxamates) and *R. meliloti* (rhizobactin). *Arthrobacter maltophilia* has also been reported to reduce Fe^{3+} to Fe^{2+} which enhances bioavailability of Fe and promote growth in many plants (Valencia-Cantero *et al.* 2007). Many root colonizing actinobacteria were also reported to produce siderophores as suggested by Palaniyandi *et al.* (2013a). Improved iron acquisition and wheat growth promotion under saline conditions by a siderophore-producing *Streptomyces* strain designated as C is reported by Sadeghi *et al.* (2012). In this case, application of strain C to wheat plants enhanced N, P, Fe and Mn concentrations in their shoots, when grown in normal and saline soil though, there were no significant differences in the concentration of macro and micronutrients in wheat shoots treated with this strain.

Enhancement of microbial community

PGPRs play an important role in developing the

indigenous microbial community structure in their habitat. Piromyou *et al.* (2011) reported the positive effect of putative genera *Pseudomonas* sp. SUT 19 and *Brevibacillus* sp. SUT 47 in species diversity of the rhizosphere and demonstrated that dominant species in microbial community structure were not interfered by PGPR, but strongly influenced by plant development. Recently, Luo *et al.* (2019) showed that inoculation with plant growth promoting *Sphingomonas* sp. Cra20 changed *Arabidopsis thaliana* rhizosphere indigenous bacterial community under salt stress.

Plant disease suppression and induction of systemic resistance

Many PGPR genera have been well exploited by many researchers for the management of plant diseases in economically important agricultural and horticultural crop plants. In nature, interactions between the pathogenic and beneficial microbes decides the survival of the pathogen in rhizosphere. This interaction can lead to the development of innate immunity responses through the expression of defence related genes in host plants thereby diminishing pathogen infection.

In nature, plants exhibit a non-specific defence which give resistance to a broad spectrum of pathogens attacking them. These responses are of two types *viz.*, induced systemic resistance (ISR) and systemic acquired resistance (SAR). ISR is the term used for resistance induced by rhizobacteria and the one induced by plant pathogens is called SAR (Schuhegger *et al.* 2006). ISR does not target specific pathogens whereas it is effective in controlling diseases caused by different pathogens. On the other hand, induced systemic resistance does not need any direct interaction between PGPRs and pathogen. Usually, ISR mediates through jasmonate and ethylene signalling pathways in host plants and these hormones trigger the host's defence responses to pathogen. Along with ethylene and jasmonate, other bacterial molecules such as *O*-antigenic side chain of lipopolysaccharide (LPS) region of bacterial outer membranes,

flagellar proteins, pyoverdine, *β*-glucans, chitin, cyclic lipopeptides and surfactants have all been reported to act as signals for the induced systemic resistance.

Sharma *et al.* (2019) showed that seed inoculation with a halotolerant rhizobacteria, *Klebsiella* MBE02 provided systemic resistance to the peanut plants against *Aspergillus* infection under controlled as well as field environment. Another report by Zhao *et al.* (2012) exhibited that *Streptomyces bikiniensis* HD-087 was able to induce systemic resistance against *Fusarium* wilt in cucumber plants caused by *F. oxysporum* f. sp. *cucumerinum*. The treatment increased different enzyme activities such as phenylalanine ammonia-lyase (PAL), peroxidase (POX) and *β*-1,3 glucanase in cucumber leaves. The levels of total chlorophyll and soluble sugars were also found to be increased in this investigation. Mishra *et al.* (2014) confirmed that the tea cuttings treated with two fluorescent *Pseudomonas* strains and fungal pathogens responsible for brown root rot (*Fome slamoensis*) and charcoal stump rot (*Ustulina zonata*) resulted in better plant growth promotion and disease suppression under both gnotobiotic and nursery conditions. In another investigation, Dutta *et al.* (2008) reported the induction of systemic resistance against wilt caused by *Fusarium udum* in pigeon pea with the application of BS 03 (*Bacillus cereus*), RRLJ 04 (*Pseudomonas aeruginosa*) and RH 2 (Rhizobial strain). The levels of defence-related enzymes such as peroxidase (POX), phenylalanine ammonia lyase (PAL), and polyphenol oxidase (PPO), were also increased in inoculated plants.

Production of antibiotics

Antibiotic production is an indirect mechanism of plant growth promotion where PGPRs produce bioactive metabolites like antibiotics to suppress phytopathogens by competing for nutrients in plant exudates. This phenomenon becomes beneficial to the plant because this will suppress the incidence of disease. Antibiotics produced by antagonist bacteria include volatile compounds (alcohols, aldehydes, hydrogen cyanide, sulphides and

ketones) and non-volatile antibiotics such as polyketides (diacetyl phloroglucinol, DAPG and mupirocin), heterocyclic nitrogenous compounds like pyocyanin, phenazine-1-carboxylic acid (phenazine derivatives) and hydroxy phenazines (Bouizgarne 2013). It is discovered that the *Bacillus* strains could produce a variety of lipopeptide antibiotics such as bacillomycin, iturins, surfactin, and Zwittermicin A (Sansinenea & Ortiz 2011).

Various species belonging to *Pseudomonas* genera also produce several antibiotic molecules with antifungal abilities *in vitro*. Phenazines produced by fluorescent pseudomonads were described as biocontrol agents of different plant diseases (Weller & Cook 1983). Other antibiotic producers are actinomycetes, which produce about 45% of the antibiotics used now a days (Berdy 2012). From actinomycetes, antibiotics like cycloheximide and streptomycin produced by *Streptomyces griseus* were the first to be used as biocontrol agents against fungal and bacterial diseases in plants (Leben & Keitt 1954). Phenazine like antibiotics produced by *Streptomyces griseoluteus* P510 as reported by Luo *et al.* (2015) exhibited strong antifungal activity against plant pathogens. Calderon *et al.* (2019) investigated the production of 2-hexyl-5-propyl resorcinol (HPR) by a rhizobacterium *Pseudomonas chlororaphis* PCL1606 and its role in fungal antagonism against *Rosellinia necatrix* and biocontrol activity in protecting avocado plants. Structures of some bioactive metabolites produced by *Bacillus* sp., *Pseudomonas* sp. and *Streptomyces* sp. are illustrated in Fig. 3.

Production of volatile antibiotics

Volatile HCN production is a mechanism exhibited by beneficial bacterial strains to protect plants from pathogenic attack (Ahmad *et al.* 2008). Voisard *et al.* (1989) reported that *P. flourescens* can excrete several bioactive molecules such as pyoverdine, DAP, pyoluteorin, and HCN with antifungal properties. Moreover, this strain exhibited enhanced root growth in tobacco plants and inhibition of *Thielaviopsis basicola* responsible for tobacco black root rot under
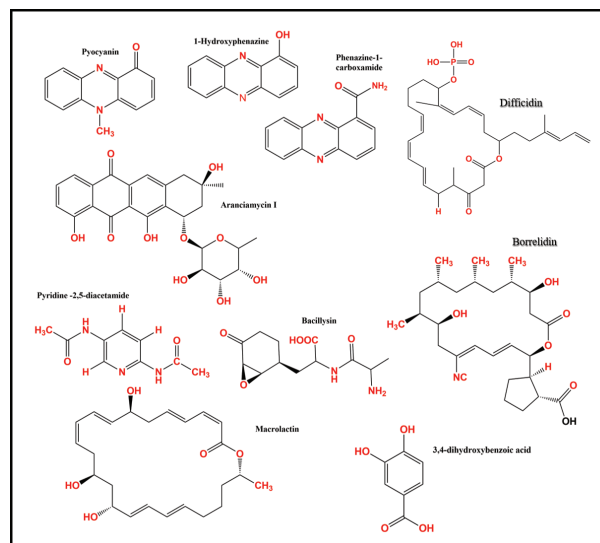

Fig. 3. Some of the bioactive metabolites produced by *Bacillus* sp. (Bacillysin, Difficidin, Macrolactin and 3,4-dihydroxybenzoic acid), *Pseudomonas* sp. (Pyocyanin, 1-hydroxyphenazine and Phenazine 1-carboxamide) and *Streptomyces* sp. (Aranciamycin I, Pyridine-2,5-Diacetamide and Borrelidin). The chemical structures were drawn using Chem Draw Pro12.0 Cambridgesoft, USA.

gnotobiotic conditions. It was also proposed that HCN might induce a stress in plants, increasing their resistance to fungal diseases. Similarly, volatile compounds produced by *Streptomyces* sp. also have great potential as biofumigants in agriculture. For example, volatile compounds produced by *Streptomyces alboflavus* TD-1 suppressed the growth of storage fungi such as *Aspergillus flavus*, *A. ochraceus*, *A. niger*, *Fusarium moniliforme* and *Penicillum citrinum in vitro*. Furthermore, GC-MS analysis detected 27 different compounds including dimethyl disulfide which proved inhibition towards *F. moniliforme in vitro* (Wang *et al.* 2013). Boukaew *et al.* (2013) studied *Streptomyces philanthi* RM-1-138 having inhibitory action towards many phytopathogens such as *Bipolaris oryzae*, *Fusarium fujikuroi*, *R. solani* and *Pyricularia grisea*.

Production of cell wall degrading enzymes

Pal & Gardener (2006) showed that biocontrol strains that produce hydrolytic enzymes are capable of attacking fungal and bacterial

cell walls, cell membrane proteins and some extracellular virulence factors have been involved in the management of plant diseases. Enzymes such as cellulase, chitinase, protease, glucanase and phospholipase are produced by many biocontrol agents. They can destroy spores of pathogenic fungi and influence both spore germination and germ-tube formation in contributing to the biocontrol properties. Akocak *et al.* (2015) observed a positive relationship between antifungal activity and chitinase enzyme production in *P. fluorescens*. Likewise, the biocontrol property of *S. cavourensis* SY224 has been attributed to glucanase and chitinase production against the causative agent for anthracnose in pepper (Lee *et al.* 2012). In another study, a chitinolytic actinomycete strain *Streptomyces vinaceusdrappus* S5MW2 isolated from Chilika Lake, India with *in vitro* antifungal activity against the sclerotia producing pathogen *R. solani* in a dual culture assay has been reported. Here chitinase enzyme played significant role in resistance in tomato plants (Yandigeri *et al.* 2015). Some of the plant growth and biocontrol traits exhibited by PGPRs are illustrated in Fig. 4. Chalotra *et al.* (2019) detected Pseudomonads possessing biocontrol properties with the production of chitinase, lipase and protease cell wall/coat protein hydrolysing enzymes.

Hyperparasitism

Both bacteria and fungi exhibit hyperparasitism on various phytopathogenic fungi. In case of bacteria, hyperparasitism is rarely reported. Davies (2009) studied *Pasteuria penetrans*, an endospore forming bacterium, a hyperparasite of root nematode, *Meloidogyne* spp. an important pest of a wide range of crops. A biocontrol actinobacteria, *Streptomyces griseus* has been recorded to parasitize *Colletotrichum lindemuthianum* and exhibited a sponge-like appearance and growth on the hyphal surface. This strain also exhibited internal parasitism of host which resulted in the formation of several blebs like structures in hyphae. Another strain, *S. griseoviridis* penetrated the mycelial wall with disintegration of *Pythium* hyphae. Palaniyandi
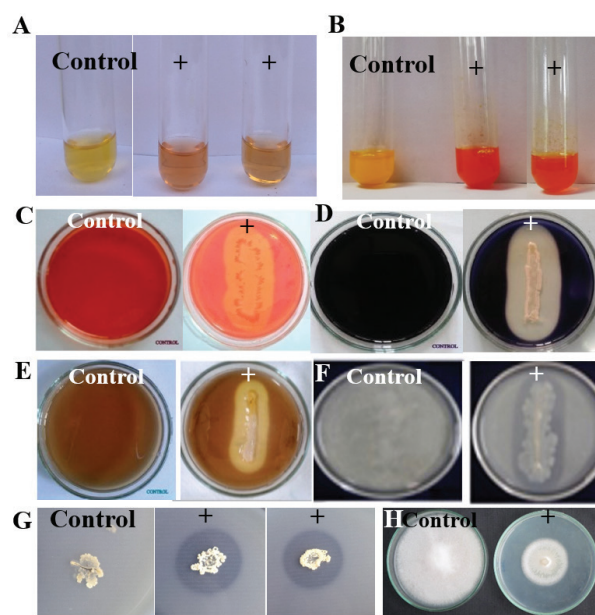

Fig. 4. Plant growth promotion attributes exhibited by PGPRs. A, IAA production; B, Ammonia production; C, cellulase production; D, amylase production; E, Pectinase production; F, protease production; G, phosphate solubilization and H, volatile production; + indicates positive production.

et al. (2013b) demonstrated mycoparasitism by *S. phaeopurpureus* ExPro138 as a mechanism of inhibition towards plant fungal pathogens. This is supported by mycoparasitism exhibited by *S. kanamyceticus* B-49 and *S. flavotricini* Z-13 as reported by Xue *et al.* (2013).

Competition

Plant root surfaces are rich in several nutrients such as amino acids, sugars, organic acids, vitamins, nucleosides, enzymes, inorganic ions and gases, phenolics, flavonoids, phytosiderophores and root border cells (Dakora & Phillips 2002). Out of these substances, phenolics and flavonoids influence symbiosis with beneficial rhizobacteria. On the other hand, compounds such as aminoacids, organic acids, inorganic ions, sugars, purines, and vitamins act as essential nutrients for rhizosphere microorganisms. These microorganisms compete for these essential nutrients which serve as one of the mechanisms of suppression of phytopathogens. Inhibition of the pathogens by

rhizobacteria is mostly achieved by production of antibiotics (Fig. 5) and/or hydrolytic enzymes. Neeno-Eckwall *et al.* (2001) reported that competition and antibiosis by non-pathogenic *S. scabies* and *S. diastatochromogenes* are responsible for the suppression of potato scab disease.

Another type of competition was examined in pathogen suppression upon competition for iron through the production of siderophores. Several rhizobacteria are involved in the suppression of pathogens through the production of siderophores (Verma *et al.* 2011). As reported by Macagnan *et al.* (2008), siderophores produced by *Streptomyces* sp. can inhibit the germination of *Moniliophthora perniciosa*. In another investigation, application of *Sphingomonas* sp. protected *Arabidopsis* plants from developing disease symptoms caused by *Pseudomonas syringae* pv. tomato under gnotobiotic system (Innerebner *et al.* 2011).

Plant - microbe interactions

The most important factor of soil quality lies in the diversity of microbial community present in it. Any alteration in the activity of microbes is proposed to be a sensitive indicator of human interactions on soil ecology (Shi *et al.* 2002). Interaction of plant and microbes can occur at endosphere, phyllosphere and rhizosphere. Phyllosphere is the term for the aerial parts of a plant and endosphere is its internal transport system. Plant-root interactions occur

at rhizosphere are categorized as root-microbe, root-root and root-insect interactions. This interaction leads to the production of more root exudates that results in maximum microbial populations in this region known as rhizosphere engineering. There are different molecular techniques merged to study the changes in root associated community structures including 'omics' tools employing polymerase chain reaction (PCR) followed by sequencing and phylogenetic analysis (Krishna *et al.* 2019). Better understanding of the microbial community structure provides an insight into the interaction between the plants and the environment and thus essential for beneficial interactions of plants with soil-borne microorganisms. The root associated bacteria may depend on other microbes for nutrients because one microbe may convert plant exudates into a usable form. Hence, rhizosphere region has appeared as a dynamic environment of profound plant-microbe interactions exploiting essential macro and micro-nutrients affecting plant growth (Haldar & Sengupta 2015). It is also noted that the root colonization process is related to different parameters such as biotic and abiotic factors and bacterial traits. In many rhizospheric interactions, rhizobacteria are known to colonize plant roots and stimulate the plant growth. The colonization of rhizosphere by various genera such as *Azospirillum* sp., *Bacillus* sp., and *Pseudomonas* sp., has been well studied so far. Investigation by Lugtenberg *et al.* (2001) reported many cell surface

Fig. 5. Suppression of *Rhizoctonia solani,* a causative agent of sheath blight disease in rice by some plant growth promoting strains

molecules responsible for better rhizosphere colonization. Thus, rhizospheric colonization is considered as a critical step in the application of microorganisms for biotechnological scopes like phytoremediation, biofertilization, biocontrol, phytostimulation, etc. It is noted that the colonization of rhizosphere by PGPRs is not an uniform process. For example, in case of *Kluyvera ascorbata*, it colonized the upper two-thirds of the surface of canola roots, but no bacteria were detected around the root tips as described by Wenbo *et al.* (2001). Plant growth promotion exhibited by some PGPR strains in rice is shown in Fig. 6.

Formulations

As discussed earlier, PGPRs exhibit many mechanisms of biocontrol and plant growth promotion. Formulation is necessary for sustainable agriculture practices in order to utilize the beneficial effects exerted by these bacteria. Formulation is the act of mixing microbes or its products such as their bioactive secondary metabolites and/or cell wall-degrading enzymes with inactive substances to boost their viability as well as activity during storage and field applications. There are several studies attributed to the loss of bioformulation and its consistency under field conditions due to the lack of suitable formulations.

If PGPR suspensions are inoculated into the soil without a suitable carrier, the applied bacterial population may decline rapidly. This can lead to less bacterial biomass production and the physiological status of the introduced bacteria at the time of application, can prevent the development of sufficient PGPR population in the rhizosphere. The heterogeneity in soil microbial population is the key obstacle, where introduced microbes sometimes cannot cope with the new environmental conditions and survive in the soil. The introduced bacteria must compete with the native microbial population and overcome predation by soil microfauna. Hence, proper formulation of inoculants plays a pivotal role in providing more suitable microenvironment as well as physical protection for a prolonged period to suppress a rapid decline of introduced bacteria (Bashan *et al.* 2014).

Formulations using *Rhizobium* are commercially produced worldwide, especially in developed countries. But most developing countries are facing problems with no or little impact on productivity under field conditions with inoculant technology, especially with PGPR. A suitable bioformulation should have the property of improving the growth of specific microorganisms and ensuring viable counts for a particular period. The formulation should also release enough beneficial bacteria at the time of application. Moreover, the type of formulation relies on the nature of the biocontrol agent, site of application and the susceptibility to target pathogen. Usually, bioformulations are
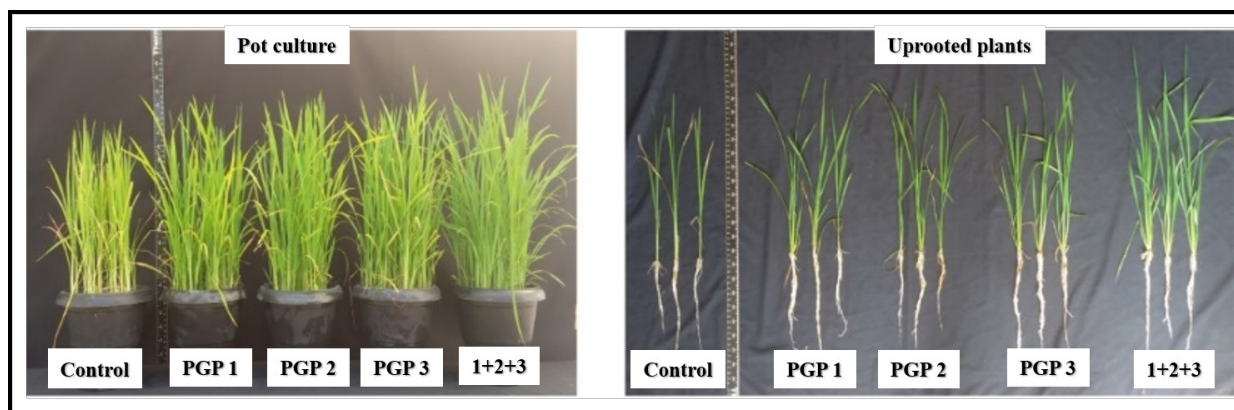

Fig. 6. Plant growth promotion exhibited by some PGPR strains (individual and in combination) in *O. sativa* (rice plant) after 28 days of treatment compared to control

prepared as liquids or powders. Formulations in dry form are usually acceptable because of easy transportation, ease of use as this can be dispersed in either water or oil and extended shelf life. Moreover, an efficient bioformulation must not be toxic, compatible with other fertilizers, inexpensive, soluble in water and withstand adverse environmental conditions. Mycostop containing *S. griseoviridis* was the first actinobacterial bioformulation developed for crop protection against soil borne pathogens such as *Alternaria*, *Fusarium*, *Pythium* and *Rhizoctonia* and marketed as wettable powder. Other than live microbes, the secondary metabolites like phytohormones, lipochito-oligosaccharides were also employed for the development of bioformulations (Morel *et al.* 2016).

Conclusion and future prospects

The use of PGPRs is an important part of agricultural practices which is not new to the world. It clearly appears that microorganisms exhibit diverse mechanisms in their interaction with plants. More studies are required to establish a strong involvement of PGPR strains in agriculture. In addition to this, physiological and molecular studies on the interaction between bacterial endophytic isolates and host plants are also required. Development of suitable formulations and scale up of microbial strains for the enhancement of disease suppression and plant growth promotion in various agricultural crops have been successfully tested. However carefully controlled field trials of crop plants inoculated along with rhizobacterial strains are necessary for their application as bioinoculants for plant growth promotion and disease control.

Furthermore, research should focus on improved innovative techniques in root environments, especially with respect to the mode of action and adaptability to stress conditions. Use of rhizo-engineering, meta-transcriptomics, next generation sequencing and DNA microarrays will be the focus areas of the researchers in the near future.

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