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Use of Plant Growth-Promoting Rhizobacteria in Plant Disease Suppression: Characteristics and Mechanisms of Action

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The rhizosphere is the immediate area of soil which is in close association of plant roots (Dobbelaere *et al*., 2013). It is a hotspot for wide variety of bacterial diversity. The diversity is partly due to the wide range of compounds that are secreted as by-products of plant metabolic activities through plant roots and are commonly known as root exudates, which are a source of nutrients for microbial growth (Doornbos and Loon, 2012). Therefore, the microbial load in the rhizosphere is much higher (typically 10 to 100 times) as compared to bulk soil. Bacteria colonize the rhizosphere and use these exudates for their metabolism. In return, there are valuable compounds in bacterial secretions that are consumed by plants, making this plant-microbe relationship a give-and-take phenomenon (Kamilová *et al*., 2006). Bacteria associated with the plant that succeed in colonizing the roots are called rhizobacteria. They can be classified as beneficial, harmful and neutral, based on the effects they have on plant growth. Beneficial bacteria that colonize plant roots and promote their growth are called Plant Growth Promoting Rhizobacteria (PGPR). Some PGPRs are involved in directly promoting plant growth in the absence of pathogens, while others do so indirectly by inhibiting the growth of phytopathogens in and around the rhizosphere (Lugtenberg and Kamilová, 2009). In addition, PGPRs are responsible for the production of essential phytohormones such as abscisic acid, auxins and cytokinins (Miransari *et al*., 2012). In the presence of pathogens, PGPRs participate in the indirect support of plant growth achieved mainly by disease suppression. PGPR reduces or prevents the deleterious effects of the pathogen through various mechanisms (Glick and Bashan, 1997). These properties have been exploited for the use of PGPR as biocontrol agents for plant disease control (Weller, 2007). This chapter focuses on several mechanisms used by PGPR to suppress or inhibit plant diseases and their use in pathogen control.

Rhizobacteria as biological control agents

The antagonistic effects of PGPR on various phytopathogens strengthen the possibilities of their use as biocontrol agents (Lamsal *et al*., 2013). Recent findings suggest that competition for nutrients, niche exclusion, induced systemic resistance and production of metabolites such as antibiotics, siderophores and hydrogen cyanide are the main modes of biological control in PGPR (Ambrosini and Beneduzi, 2012). In order to exert their effects, the bacteria should be rhizosphere competent, *i.e.* able to efficiently colonize the plant rhizosphere. Successful root colonization is primarily required for mechanisms such as antibiosis and competition for nutrients and spaces.

Classification of Rhizobacteria

PGPRs have been recognized more as biological control agents of plant diseases than as a growth promoter andthey include bacteria such as *Bacillus subtilis* and *Pseudomonas*, which are antagonistic to the soil-borne plantpathogens (Kloepper *et al*., 1989). Few genera and species of PGPR are classified below:

Rhizobia: *Rhizobia* and *bradyrhizobia* are well known as symbiotic microbes of legumes that form N_2-fixingnodules. In fact, *rhizobia* can produce siderophores and HCN and can colonize the roots of many non-legume plants. Reitz *et al*. (2000) showed that *R. etli* G12 induce systemic resistance to infectionby cyst-forming nematode *Globodera pallida* in potato. It has been reported that under field conditions *R. leguminosarum*when used either as a seed dressing or as a soil drench, reduced infection by*Rhizoctonia solani*,*Macrophomina phaseolina* and *Fusarium* spp., in both leguminousand non-leguminous plants. *Rhizobia* have good potential for use as bio-control agents against some phytopathogens.

Bacillus: The majority (about 95%) of gram-positive bacteria in soils were found to be*Bacillus* species *viz*., *B. pumilus*,*B.mycoides*, *B.megaterium*,*B. thuringiensis* and *B. firmus*. Other gram-positive bacteria such as*Arthrobacter*spp. and *Frankia* spp. were 6% or even less. The best isolates to inhibit *Fusarium roseum*, the causal organism of dry rot of potato, belonged to the species *B. lentimorbus*,*B. cereus*and *B. licheniformis*.*Bacillus* spp. they are able to form endospores which enable them to do sosurvive for a long time in adverse environmental conditions. They have the ability to produce inhibitory volatiles and complexlytic chitinases which impart them antifungal activity. *Bacillusmegaterium* KL39, a bio-control agent against *Phytophthora*,produces an antifungal antibiotic effective against a wide range of plant pathogenic fungi. *B. subtilis* also synthesizes an antifungal antibiotic inhibiting *Fusarium oxysporum*,the causal agent of *Fusarium* wilt of chickpea (Kumar, 1999) and strain RB14 produces surfactinand antibioticsiturin-A inhibitory against several plant pathogens.

Pseudomonads: The fluorescence producing *Pseudomonas* spp. had been long used for controlling various plant diseases and pathogens. This is largely due to the production of a new lipo-peptide antibiotic (AFCBC11)for the ability of *Pseudomonas* spp. to effectively control *Rhizoctoniasolani* (Kang *et al*., 1998). Many strains of pseudomonads can indirectly protectplants by inducing systemic resistance against various pests and. Using a bacterial mutant,Gallagher and Manoil (2001) were able to demonstrate that *P. aeruginosa* PAO1 killednematode *Caenorhabditis elegans* by cyanide poisoning. Several lines of evidence suggest that the production of siderophores were responsible for the antagonism by some strains of *P. aeruginosa* against *Pythium* spp. Pseudomonads are well known for their biologicalactivityagainst several phytopathogens. Fluorescent pseudomonads naturally suppress *Fusarium* wilt and have been successfully used to control *Fusarium* wilt of various plant species. In many pseudomonads, the production of metabolites, such as siderophores,antibiotics and hydrogen cyanide are the primary biological control mechanisms.

Diazotrophic PGPR: *Azospirillum* was isolated from the rhizosphere of grasses and cereals throughout the world, inboth tropical and temperate climates. This bacterium was originallyused for its ability to fix atmospheric nitrogen (N_2) and since the mid-1970s has consistently been researchedforbeing very promising PGPR. *Herbaspirillum* is an endophyte that colonizes maize,rice, sorghum and other cereals. *Azoarcus* spp.are strictly respiratory bacteria belonging to the subclass Proteobacteria.

Characteristics of an ideal PGPR

- High rhizosphere attachment ability
- Aid in plant growth
- Broad spectrum action

- Ease of mass multiplication
- Environment friendly
- Compatibility with other rhizobacteria
- Tolerance toheat, desiccation, UV radiations andoxidizing agents.

Mechanism of Plant Disease Control by PGPRs: PGPRshave been used successfully for bio-control of fungal, bacterial, nematodal and viral diseasesof plants in different parts of the world. The various modes used by different PGPRs have been described below:

Production of Antibiotics: In response to biotic stress conditions such as attack by plant pathogens, bacteria secrete several types of antibiotics having different specificities and mechanisms of action (Glick, 2012). Antibiotics are low molecular weight compounds that have severe impact on several microrganisms *viz*., bacteria, fungi, viruses, protozoa etc when applied at low concentrations (Maksimov *et al*., 2011). This antagonistic effect of one microbe against another is called antibiosis. Antibiotic synthesis is primarily attributed to stress conditions such as external stimuli and nutrient availability. In addition, the physiological state of the host plant also regulates antibiotic production (Picard *et al*., 2000). It was found thatroot colonization was necessary for antibiosis in *Pseudomonas chlororaphis* strain PCL1391, which produced phenazine-1-carboxamide antibiotic. The bacterial genus *Bacillus*is the most prevalent microbial group in soil producing approximately 167 different types of antibiotics (Maksimov *et al*., 2011). Antibiotics such ascirculin, polymyxin and colistin have reported to show inhibitory activity against plant pathogenic fungi*viz*.,*Aspergillus flavus*, *Alternaria solani*, *Botryosphaeria ribis*, *Colletotrichum gloeosporioides*, *Helminthosporium maydis* and *Fusarium oxysporium* as well as both gram-positive and gram-negative bacteria (Maksimov *et al*., 2011). Various rhizobacteria have been reported to produce antifungal metabolites such as phenazines, HCN, 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrin, viscosinamide, pyoluteorin, and tensin (Bhattacharyya and Jha, 2012). Phenazine is one of the important antibiotics that had been extensively studied for its antagonistic properties (Chin-a-woeng *et al*., 2000). It is an antibiotic produced by fluorescent strains of pseudomonads which had shown an increased level of disease suppression against *Fusarium* wilt. Considerable success has been observed in controlling plant pathogens but sometimes antibiotic resistance development has been reported in some pathogens. For overcoming this problem, biocontrol strains that produce hydrogen cyanide (HCN) along with other antibiotics have been used, resulting in improved disease control through synergistic effects of these two metabolites (Glick *et al*., 2012). Schouten *et al*., 2004 observed significant antagonistic activity of antibiotic DAPG against pathogen*F. oxysporum*. Evidence of biological control through antibiotics can be seen in *PaeniBacillus polymyxa* (AB15), which was tested for inhibitory effects on *Colletotrichum acutatum* causing anthracnose in pepper (Lamsal *et al*., 2012).

Volatile Organic Compounds (VOCs): Recent findings supported by mass spectrometry (MS) and gas chromatography (GC) have revealed the ability of bacteria to produce large amounts of volatile compounds (Schulz and Dickschat, 2007; Kai *et al*., 2009). Bacterial VOCs are signaling molecules that bacteria use to communicate with external biota. Research results have so far identified 346 different types of VOCs released by bacterial species of the genera *Xanthomonas*, *Staphylococcus*, *Stenotrophomonas*, *Pseudomonas*, *Serratia*, *Bacillus*, *Burkholderia*, *Agrobacterium*,*Erwinia* and *Staphylococcus* (Kai *et al*., 2009). Evidence suggests a role for VOCs in suppression of phytopathogens through ISR (Santoro *et al*., 2015). Direct application of the bacterial volatile acetoin to roots under growth chamber conditions caused a significant reduction in pathogen growth 96 hrs after disease induction. The role of 2,3-butanediol produced by *Bacillus subtilis* GB03 and *B.amyloliquefaciens* IN937a in inducing systemic resistance in plants such as pepper, tomato, muskmelon, sugar beet, watermelon, tobacco, *Arabidopsis* spp., cucumber have been reported. All these instances proves that VOCs produced by PGPRs show promising results for enhancing plant immunity in modern agriculture.

Production of siderophores : Iron is an essential element for various metabolic activities in plants as well asin microorganisms. Although it is found abundantly in soil, Fe^{3+}(the bioavailable) form of iron is the poorly soluble (Lugtenberg and Berg, 2013). To use this poorly soluble form of iron, PGPR secretes siderophores. Siderophores are low molecular weight iron chelating compunds that provide high affinity for ferric ion incorporation (Wandersman and Delepelaire, 2004). Plants such as oats, cucumber, cotton, peanut, sorghum and sunflower demonstrate the ability to use microbial siderophores for iron uptake (Crowley *et al*., 1988; Dimpka *et al*., 2009). These high-affinity siderophores produced by PGPRs effectively bind available soil iron, thereby limiting its supply to nearby plant pathogens (Neilands, 1982). This creates competition among microorganisms to utilize the limited amount of iron present in the rhizospheric region. Rhizobacteria that excel in this competition may serve as biocontrol agents through a siderophore-mediated disease suppression mechanism. Different species of fluorescent pseudomonads synthesize high-affinity siderophores, such as pseudobactins or pyoverdins, which suppress various fungal plant pathogens and harmful microorganisms in iron-deprived environments (Lemanceau *et al*. 2009). *Pseudomonas* strain B10 suppressed *Fusarium* wilt of linseed caused by *Fusarium oxysporum* f. sp. *lini* due to production of pseudobactin, a highly potent siderophore that competitively complexed available iron leading to its reduced availability to the pathogen and subsequently inhibiting its growth (Kloepper *et al*., 1980). In addition, inhibition of *Colletotrichum gossypi* by siderophore-producing rhizobacteria stimulated increased growth of cotton seedlings.

Production of lytic enzymes: Extracellular hydrolytic enzymes such as glucanases, chitinases, lipases and proteases achieve disease suppression through lysis of cell walls of plant pathogenic fungi (Maksimov *et al*., 2011). The role of lytic enzymes such as β-1,3-glucanase and chitinase in the suppression of the anthracnose pathogen *Colletotrichum gloeosporioides* were determined (Vivekananthan *et al*., 2004). Furthermore, chitinase produced by *Serratia plymuthica* C48 was found to inhibit spore germination and germ tube elongation in *Botrytis cinerea* (Frankowski *et al*., 2001). Lysis of fungal cell walls is a direct method of pathogen inhibition.

Induced systemic resistance (ISR): Plant beneficial bacteria interact with plants in the rhizosphere region to stimulate a defense response against a range of pathogens. This heightened state of defense in host plants is termed “induced systemic resistance” (ISR) (Pieterse *et al*., 2014). It strengthens the innate defense capability of plants that protects them from probable future infection (Loon *et al*., 1998). ISR requires jasmonic acid (JA) and ethylene (ET) for its signaling mechanism (Yan *et al*., 2002). ISR is one of the primary mechanisms of action in disease suppression by PGPR. It induces defense reactions in plants against a diverse range of pathogens. PGPR strains such as *Serratia marcescens* and *Pseudomonas fluorescens* effectively induced systemic resistance in cucumber plants against anthracnose (Liu *et al*., 2016). Rhizobacterial isolates of *Micrococcus luteus* strain TRK2-2, *Pseudomonas putida* strain TRL2-3 and *Flexibacteraceae* bacterial strain MRL412 were able to trigger ISR in potato plants against potato blight (Kim and Jeun, 2006). The role of ISR has been studied in systems where the pathogen and bacteria remain spatially separated on the plant. Spatial separation is achieved by inoculating two microorganisms into different plant parts such as root and leaves. Such a method of co-inoculation precludes direct interactions between the two populations of microbes, and the subsequent suppression of the disease must occur through the induction of resistance in plants, *i.e.* ISR induced by *Pseudomonas* bacteria. In addition, several *Bacillus* strains such as *B. amyloliquefaciens* and *B. subtilis* induced a significant reduction in disease incidence in several host plants

(Kloepper *et al*., 2004). ISR has been reported to be the sole mechanism of action for several *Bacillus* species used as biocontrol agents (Ongena *et al*., 2007). Colonization of roots is vital for the emergence of antibiosis, and therefore poor root colonizers of the genus *Bacillus* that exhibit biological control properties must act through ISR.

Competition for nutrients and niches: The rhizosphere is a nutrient basin that serves for a vast array of nutrient-rich compounds (Weller and Thomashow, 1994). These compounds attract various microbial life forms including plant pathogens, which compete for available nutrients and niches or sites. PGPR strains that are able to compete with these pathogens for nutrient and space can serve as a biocontrol agent, thereby creating competition as an indirect mechanism of disease suppression (Lugtenberg and Kamilová, 2009). Competition for nutrients and niches is believed to be the primary mechanism of action by which PGPR protects plants from phytopathogens. The importance of competitive colonization of root tips by *Psuedomonas* species in protecting tomato plants against tomato root rot has been demonstrated (Beneduzi *et al*., 2012). Such evidence further illustrates the role of competitive PGPR strains in plant disease suppression.

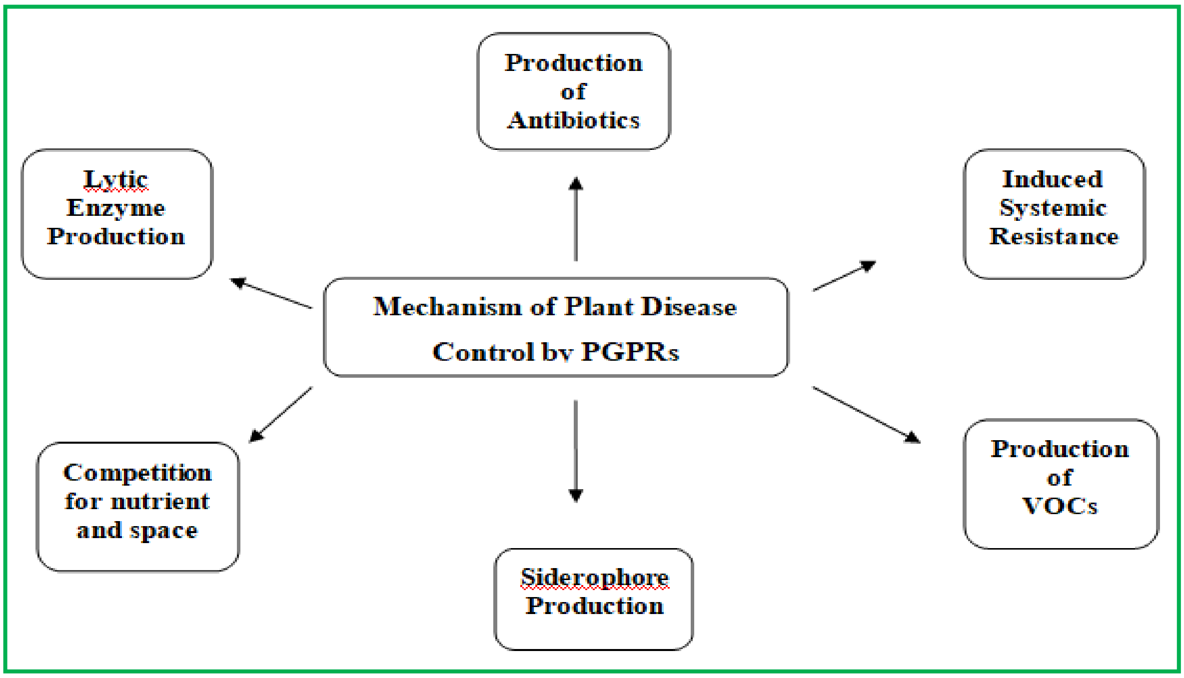

Fig 1: Different mechanism of plant disease suppression by PGPRs

Commercial products of PGPR: Research inventions from various countries during the early 1950 have proved the potential use of bacteria in plant disease management. Owing to the potential of PGPR, the first commercial product of *B. subtilis* was introduced during 1985 for the use of growers by Gustafson Inc. (Plano, Texas) in US. The strains of *B. subtilis* A-13, GB03, GB07 were sold for the management of soil-borne pathogens under the trade names of Quantum, Kodiak and Epic respectively. Release of *Bacillus* based products during 1985 has resulted in the increase in market size for the usage of bacterial products in crop disease management. The registered commercial products of PGPR are listed in Table 1.

Future Perspectives of use in modern agriculture

The success achieved with PGPR in *in-vitro* and greenhouse tests is often not really reflected in the fields. Discrepancies occur due to environmental factors such as diversity of soil texture, different microclimates, moisture content,salinity and unpredictable weather conditions that contribute to the field ineffectiveness of PGPR (Okon, 1994). In addition, lack of maximum quality in the experimental design and inadvertent errors in the analysis of the results add to the problem. A comprehensive study of the ecological properties of pathogens and beneficial bacteria will open up possibilities for the formulation of active substances for biological control in the future. Screening for beneficial strains that can act in coordination with each other to provide plants with a broad range of protection against pathogens will increase the efficacy of biocontrol strains.

Table 1: Various commercially available plant growth promoting rhizobacteria

Product	Target Pathogen	Host Plants
Campanion (*B. subtilis* GB03)	*Rhizoctonia, Fusarium, Phytophthora, Pythium*	Horticultural crops
Conquer (*P. flourescens*)	*P. tolassii*	Mushrooms
Bioject spotless (*P. aureofaciens*)	*Pythium aphanidermatum*	Turf crops
Deny (*P. cepacia*)	*Rhizoctonia, Fusarium, Phytophthora, Pythium*	Barley, Cotton. Sorghum. Vegetable crops
Biojet (*Pseudomonas* + *Azospirillum*)	*Clarireedia homoeocarpa*	Turf grass
Intercept (*P. cepacia*)	*Rhizoctonia, Pythium, Fusarium*	Cotton and Maize
Kodiak (*B. subtilis* GB03)	*Alternaria, Aspergillus, Rhizoctonia, Fusarium,*	Legumes and Cotton
Bio yield (*B. subtilis* + *B. amyloliquefaciens*)	*Rhizoctonia, Fusarium, Phytophthora, Pythium*	Tomato, Pepper, Cucumber

Conclusion

Growing world population means the need of increased agricultural productivity. The widespread use of chemical fertilizers and pesticides to increase crop yields has caused significant impacts on the environment and human health. With the growing awareness of these issues, the need for organic farming practices is well justified. Plant growth-promoting rhizobacteria (PGPR) with their diverse modes of action in plant disease management appear to provide an effective long-term solution for preventing crop losses caused by plant pathogens. A combinatorial approach using several PGPR strains to maintain an extended level of protection against pathogens in plants will help achieve high yields without harming the environment. Regardless of some challenges in the implementation of PGPR as biological control agents, there are huge prospects for its use in sustainable agriculture.

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