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PGPR in biocontrol: mechanisms and roles in disease suppression

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Abstract

The ever increasing global population entails the need for uplifting agricultural productivity which is laden with hindrances such as crop nutritional deficiencies and diseases. Extensive use of chemical fertilizers and pesticides in overcoming these hurdles has come with a cost of irreparable damage to the environment and human health. As such, plant growth promoting rhizobacteria (PGPR) offers promise for establishing environment friendly sustainable agriculture systems and as a notable alternative to these harmful chemicals due to their wide range of direct and indirect mechanisms of plant growth promotion. In this review we focus on the indirect mechanisms, which involve plant growth promotion through disease suppression. Disease suppression mechanisms include antibiosis, Induced Systemic Resistance (ISR), high affinity siderophore production, competition for nutrient and niches and production of lytic enzymes. Disease suppression roles of these mechanisms have been illustrated in different strains of PGPR. Based on experimental evidences, PGPR, mostly *Bacillus* and *Pseudomonas* strains have been used as biocontrol agents as they demonstrate wide range of protection in a variety of plants. PGPR have huge prospects for use in eco-friendly sustainable agriculture for plant protection from a myriad of plant diseases.

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Introduction

The rhizosphere is the layer of soil under the influence of plant roots (Dobbelaere *et al.,* 2013). It is a hotspot for bacterial diversity as it harbors species which show a great deal of functional diversity and metabolic versatility (Rawat and Mushtaq, 2015). Diversity is partly owed to the wide range of compounds that are secreted as byproducts of plant metabolic activities through plant roots and are commonly known as root exudates which are nutrient source for microbial growth (Doornbos and Loon, 2012).

Around 5-21% of carbon fixed by plants is secreted as root exudates (Lugtenberg and Kamilova, 2009). Hence the microbial load in the rhizosphere is much higher (usually 10 to 100 times) than the bulk soil (Weller and Thomashow, 1994). Bacteria colonize the rhizosphere to use these exudates for their metabolism. In return there are valuable compounds in bacterial secretions, which are used up by plants, making this plant-microbe relationship a give and take phenomenon (Rovira, 1956; Kamilova *et al.,* 2006).

Plant associated bacteria that succeed in colonizing the roots are called rhizobacteria. They can be classified into beneficial, deleterious and neutral based on the effects they have on plant growth. The beneficial bacteria that colonize plant roots and promote its growth are termed as Plant Growth Promoting Rhizobacteria (PGPR) (Beneduzi, Ambrosini and Passaglia, 2012).

Some PGPR are involved in direct plant growth promotion in the absence of pathogens while others do so indirectly by inhibiting growth of phytopathogens in and around the rhizosphere (Lugtenberg and Kamilova, 2009). Direct plant growth promotion serves various purposes for plants which includes nitrogen fixation, increasing the availability of nutrients in the rhizosphere, positive effect on root growth and morphology and promotion of beneficial plant–microbe symbioses (Vessey, 2003). Increasing nutrient availability entails solubilization of unavailable nutrient forms such as phosphate, one of the primary nutrients for plant growth (Chabot *et al.,* 1996) . Furthermore, PGPR are responsible for the production of essential phytohormones such as abscisic acid, auxins and cytokinins (Remans *et al.,* 2007; Miransari *et al.,* 2012;). Other functions include siderophore production for the transport of sparingly soluble ferric ion, phytoremediation and increasing tolerance in plants against abiotic stresses such as drought, salinity and metal toxicity (Dimkpa *et al.,* 2009; Glick, 2010; Ambrosini and Beneduzi, 2012).

In the presence of pathogens, PGPR are involved in indirect plant growth promotion achieved primarily through disease suppression. PGPR lessens or prevents the deleterious effects of the pathogen through diverse mechanisms (Glick and Bashan, 1997). These traits have been exploited for use of PGPR as biocontrol agents for plant disease control (Weller, 2007). The present review focuses on several mechanisms that PGPR employ to suppress or inhibit plant diseases and instances of their use in pathogen control.

Rhizobacteria as biocontrol agents

The antagonistic effects by PGPR over various phytopathogens bolster the possibilities for their use as biocontrol agents (Sang *et al.,* 2011; Lamsal *et al.,* 2013). Recent findings suggest that competition for nutrient, niche exclusion, induced systemic resistance and production of metabolites such as antibiotics, siderophores and hydrogen cyanide are the chief modes of biocontrol activity in PGPR (Ambrosini and Beneduzi, 2012). To exhibit their effects, the bacteria should be rhizosphere competent i.e. able to effectively colonize the plant rhizosphere. Successful root colonization is primarily required for mechanisms such as antibiosis and competition for nutrient and niches (Lugtenberg and Kamilova, 2009).

Antibiosis

In response to stressful conditions, bacteria secrete several types of antibiotics with varying specificity and modes of action (Glick, 2012). Antibiotics are low molecular weight oligopeptides which at low

concentration, confer deleterious effects on several microorganisms (Maksimov *et al.,* 2011). This antagonistic effect is termed as antibiosis. Antibiotic synthesis is primarily attributed to biotic conditions such as nutrient availability and external stimuli which dictates the metabolic status of the cell. In addition, the physiological status of the plant also regulates antibiotic production (Picard *et al.,* 2000).

Table 1. List of PGPR antagonistic to several phytopathogens and the mechanisms involved in pathogen suppression.

Bacteria	Mode of action	Phytopathogen	Disease	Crop	Reference
Bacillus subtilis BMB26	Production of antifungal metabolites	*Sclerotium rolfsii*	Sclerotium rot	Melon(*Cucumis melo* var. *amanta*	(Darma *et al.,* 2016)
Bacillus velezensis strain AP136 and AP305 and *Bacillus mojavensis* AP209	ISR	*Xanthomonas campestris* pv. *Campestris*	Black rot	Chinese cabbage	(Liu *et al.,* 2016)
Burkholderia cepacia MPC-7	Gluconic acid, alpha, 2-ketogluconic acid, benzoic acid, phenylacetic acid	*Phytopthora capsici*	Late blight	Pepper	(Sophereth *et al.,* 2013)
Paenibacillus polymyxa (AB15), *Bacillus subtilis* (AB14)	Antibiosis, ISR, production of volatiles	*Colletotrichum acutatum*	Anthracnose of pepper	Pepper(*Capsicum annuum)*	Lamsal *et al.,* 2012
Flavobacterium sp. strain GSE09 and *Lysobacter enzymogenes* strain ISE13	Production of volatiles	*Colletotrichum acutatum*	Pepper('Nockwang')	Pepper('Nockwang')	(Sang *et al.,* 2011)
Pseudomonas chlorororaphis PCL 1391	Production of antifungal metabolite (Phenazine-1-carboxamide)	*Colletotrichum lindemuthianum*	Bean anthracnose	Bean	(Lagopodi, 2009)
Pseudomonas chlororaphis	Siderophores, extracellular antibiotics, production of volatiles	*Erwinia carotovora* subsp atroseptics(Van Hall)	Charcoal rot of sorghum	Sorghum	(Das *et al.,* 2008)
Bacillus subtilis strain Bs2508	ISR	*Botrytis cinerea*	Grey Mould	Bean and tomato	(Ongena *et al.,* 2007)
Pseudomonas fluorescens MKB 100 and MKB 249, *P. frederiksbergensis* 202	ISR, production of antifungal metabolites	*Fusarium culmorum*	Fusarium seedling blight	Wheat and Barley	(Khan *et al.,* 2005)
Pseudomonas fluorescens (Trevisan) Migula F113	Production of antibiotic 2,4-diacetylpholorogluinol (DAPG)	*Erwinia carotovora* subsp atroseptics(Van Hall)	Soft rot	Potato	(Cronin *et al.,* 1997)

The necessity of root colonization for antibiosis was confirmed in *Pseudomonas chlororaphis* strain PCL1391 that expressed phenazine-1-carboxamide. Mutants impaired in root colonization but able in producing this antibiotic, failed to suppress the disease (Chin-a-woeng *et al.,* 2000). Antibiosis is one of the more significant traits that has been exploited for use in biological control of pant diseases by PGPR (Lamsal *et al.,* 2012; Darma *et al.,* 2016).

Diverse specificity of PGPR has been exploited for use in plant disease control.

Bacteria of *Bacillus* species are among the most predominant microbe in soil and they produce around 167 different antibiotic types (Maksimov *et al.,* 2011). Majority of *Bacillus* antibiotics including polymyxin, circulin, and colistin show activity against both gram-positive and gram-negative bacteria, and

plant pathogenic fungi *Alternaria solani*, *Aspergillus flavus*, *Botryosphaeria ribis*, *Colletotrichum gloeosporioides*, *Fusarium oxysporum*, *Helminthosporium maydis* (Maksimov *et al.,* 2011). Considerable success has been observed in the control of phytopathogens with limitations that include antibiotic resistance development in some pathogens. To overcome this problem, biocontrol strains that synthesize Hydrogen Cyanide (HCN) along with other antibiotics have been used which provides improved disease control through synergistic effects of the two metabolites (Glick *et al.,* 2012).

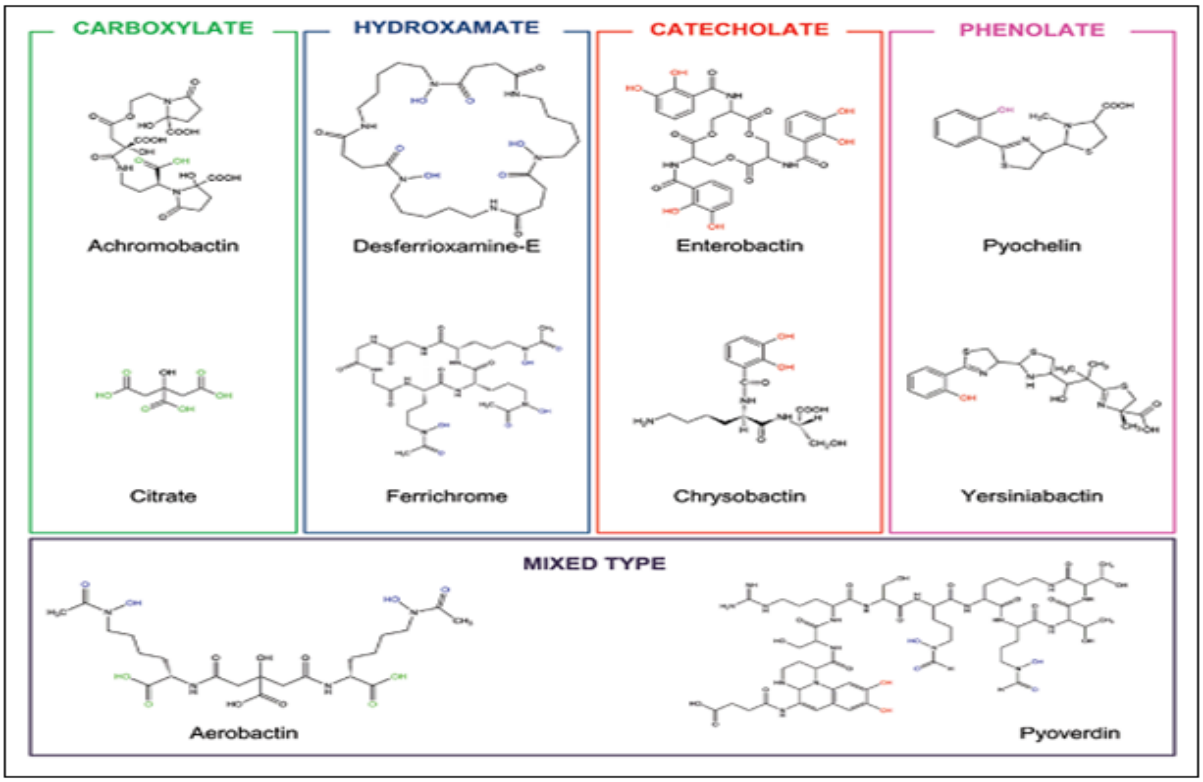

Fig. 1. Structures of different classes of bacterial and fungal siderophores and their functional groups involved in iron chelation (shown in color) (Aznar and Dellagi, 2015).

Various rhizobacteria have been reported to produce antifungal metabolites like, HCN, phenazines, pyrrol-nitrin, 2,4-diacetylphloroglucinol (DAPG), pyoluteorin, viscosinamide and tensin (Bhattacharyya and Jha, 2012). Phenazine is an important antibiotic that has been extensively studied for its antagonistic property (Chin-a-woeng *et al.,* 2000), an antibiotic produced by fluorescent *pseudomonads* strains showed increased level of disease suppression against *Fusarium* wilt. The primary role of phenazine in disease suppression was confirmed by results that showed phenazine deficient mutant's inability to suppress the same disease (Mazurier *et al.,* 2009). Schouten observed substantial antagonistic activity against pathogenic *F. oxysporum* (Schouten *et al.,* 2004), by the antibiotic DAPG. Furthermore, population of DAPG-producing *pseudomonads* were highly enriched in a soil naturally suppressive to Fusarium wilt of peas (Landa *et al.,* 2002). Evidences of bioconrol through antibiotics can be observed in *Paenibacillus polymyxa* (AB15) which was tested for inhibitory effects on *Colletotrichum acutatum* that causes anthracnose in pepper (Lamsal *et al.,* 2012).

High affinity siderophore production

Iron is an essential element for metabolic activities in plants and microorganisms. Although it is abundant in soil, the bio-available form of iron is ferric ion (Fe^{3+}) which is sparingly soluble i.e. around 10^{-18} M at pH 7.4 (Lugtenberg and Berg, 2013). To use this meagerly soluble form of iron, PGPR secrete siderophores. Siderophores are low molecular weight peptide molecules that provide a high affinity set of ligands to incorporate ferric ions (Wandersman and Delepelaire, 2004).

Although plants have their specific iron carriers called phytosiderophores, they are able to utilize the bacterial siderophore-iron complexes (Reichman and Parker, 2005). Plants such as Cucumber, Oats, Sorghum, Cotton, Peanut, Sunflower demonstrate the ability to use microbial siderophores for iron uptake (Crowley *et al.,* 1988; Bar-Ness *et al.,* 1991; Dimpka *et al.,* 2009).

Moreover, high affinity siderophores (K_d= 10^{-20} to 10^{-50} for iron) produced by certain PGPR effectively bind iron available in soil, thereby limiting its supply for phytopathogens in the vicinity (Neilands, 1982; Schippers, Bakker and Bakker, 1987).

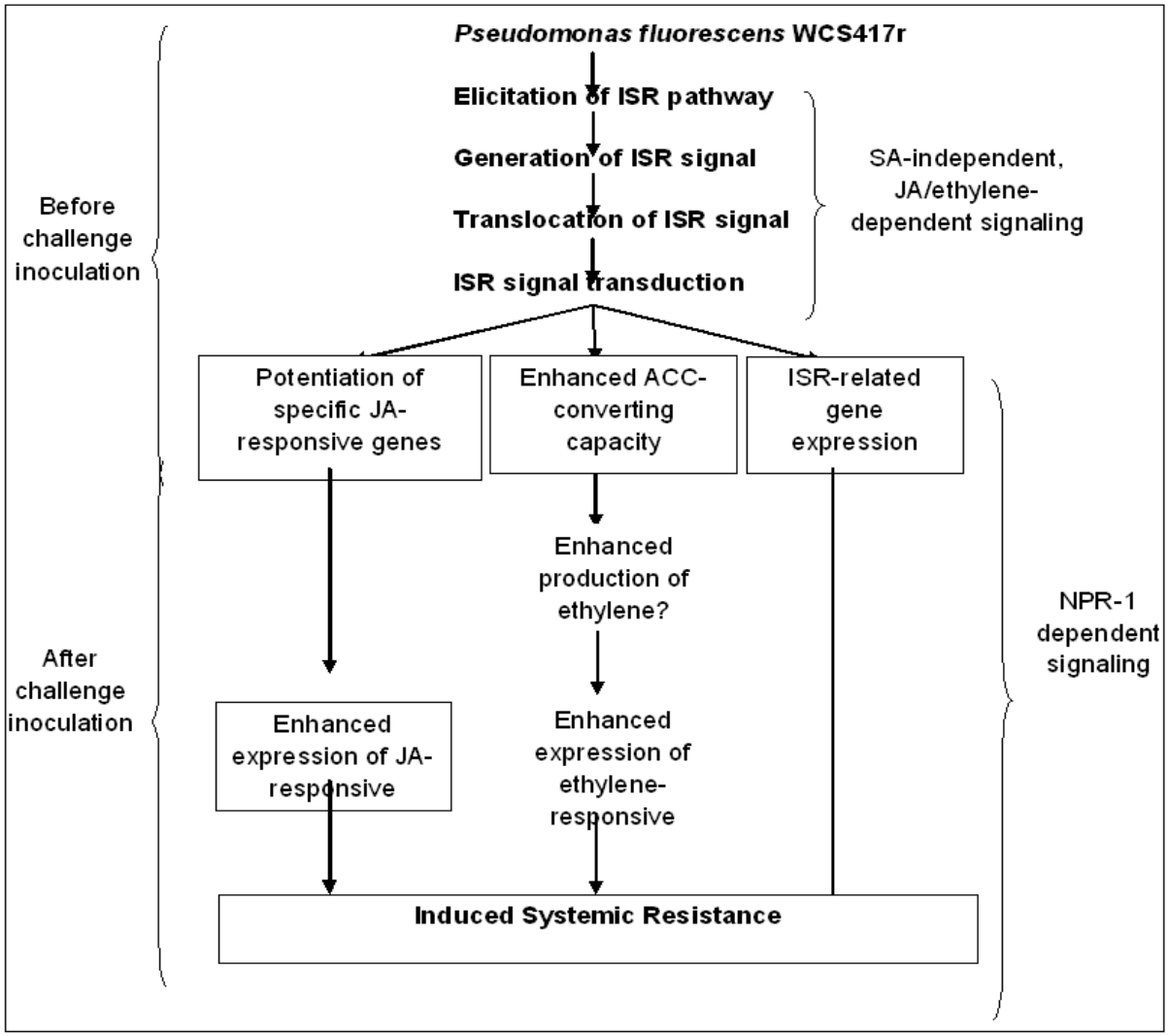

Fig. 2. Figurative illustration of the possible involvement of JA and ethylene in ISR by *P. fluorescens* WCS417r in Arabidopsis.

The signaling pathway triggered after colonization of Arabidopsis roots by WCS417r requires responsiveness to JA and ethylene. Components of JA and ethylene responses are involved in ISR pathway, which leads to a systemic resistance similar to SAR and is controlled by the regulatory factor NPR1. Although ethylene responsiveness is required at the site of ISR induction, the latter stages of ISR pathway might require the involvement of JA and ethylene individually or in combination. A specific set of JA-responsive genes is potentiated in ISR-expressing plants which allows for higher level of expression after challenge inoculation. In addition, ISR-expressing plants possess higher capacity to convert ACC to ethylene. Upon challenge, such plants have improved potential to produce ethylene. Hence, ISR-expressing plants are better suited to express JA and/or ethylene dependent defence reactions faster and at higher levels after pathogen attack (Pieterse, 2001).

Siderophores are generally categorized based on their into three groups: i) hydroxamate (Griffiths *et al.,* 1984); ii) catecholate (includes phenolate) and iii) carboxylate (or hydroxycarbolates) (Aznar and Dellagi, 2015). Different siderophore classes are shown in figure 1.

Bacterial siderophores are diversely distributed in different species, with more than 500 different kinds that have been characterized (Boukhalfa and Crumbliss, 2002). Some of the molecules exhibit antagonistic properties against plant pathogens. Rhizosphere shelters a diverse range of microorganisms and is usually in an iron deprived condition compared to bulk soil. Hence, there is competition between microorganisms to use the limited iron present in the rhizosphere. Rhizobacteria that excel in this competition can serve as biocontrol agents through a siderophore mediated disease suppression mechanism. Different species of fluorescent *pseudomonads* synthesize high affinity siderophores such as pyoverdines or pseudobactins that suppress fungal phytopathogens and deleterious microorganisms in an iron deprived environment (Lemanceau *et al.* 2009). *Pseudomonas* strain B10 suppressed Fusarium wilt caused by *Fusarium oxysporum* f. sp. *lini*. Disease suppression was partly due to psuedobactin, a highly efficient siderophore that competitively complexed available iron, thereby limiting its availability to the pathogen and subsequently inhibiting its growth (Kloepper *et al.,* 1980). Furthermore, inhibition of *Colletotrichum gossypi* by siderophore producing rhizobacteria prompted increased growth in cotton seedlings (Freitas and Pizzinato, 1997). Siderophore mediated competition for iron is a major arm for PGPR against plant diseases. However, there is lot more to be explored regarding its production and role in plant disease suppression.

Induced systemic resistance (ISR)

Plant beneficial bacteria interact with plants in the rhizosphere microbiome to stimulate a defense response against a number of pathogens. This enhanced state of defensive ability is termed as "Induced Systemic Resistance" (ISR) (Pieterse *et al.,* 2014)**.** It enhances the innate defense mechanism of plants that protects them from future infection (Van Loon *et al.,* 1998). It is similar to the pathogen induced "Systemic Acquired Resistance" (SAR) in plants as both render uninfected plant parts more resistant to a broad spectrum of pathogens. Yet, there are certain differences and similarities in the SAR and ISR signaling pathways (Pieterse and Wees, 2015). SAR occurs through salicylic acid (SA) mediated signaling pathway while ISR requires jasmonic acid (JA) and ethylene (ET) for its signaling mechanism (Yan *et al.,* 2002; Fu and Dong, 2013). The role of the possible involvement of JA and ethylene is shown in figure 2.

ISR is one of the primary mechanisms of action in disease suppression by PGPR. It induces defense responses in plants against a diverse range of pathogens. PGPR strains such as *Serratia marcescens* and *Pseudomonas fluorescens* have effectively induced systemic resistance in cucumber plants against anthracnose disease at certain concentrations (Liu *et al.,* 1995). Rhizobacterial isolates *Pseudomonas putida* strain TRL2-3, *Micrococcus luteus* strain TRK2-2 and *Flexibacteraceae* bacterium strain MRL412 have been able to trigger ISR in potato plants against late blight in potato (Kim and Jeun, 2006). The role of ISR has been studied in systems where the pathogen and the bacteria remain spatially separated on the plant (Bakker, Pieterse and Loon, 2007). Spatial separation is achieved by inoculating the two microorganisms in different plant parts like root and leaves or by using a split root system. Such manner of co-inoculation excludes direct interactions between the two population of microbes and the subsequent disease suppression has to occur through resistance induction in plants i.e. ISR induced by *Pseudomonas* bacteria.

Furthermore, several strains of *Bacillus* like *B. amyloliquefaciens* and *B. subtilis* have elicited 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 (Kloepper *et al.,* 2004; Ongena *et al.,* 2007).

Root colonization is vital for antibiosis to occur and hence poor root colonizers of *Bacillus* species that exhibit biocontrol properties must act through ISR. The fact that certain antifungal metabolites induce resistance in plants explains the role of ISR in antagonism shown by plants inoculated with these bacteria (Lugtenberg and Kamilova, 2009).

Volatile Organic Compounds (VOCs)

Recent findings aided by gas chromatography (GC) and mass spectrometry (MS) has revealed capabilities of bacteria to produce a wealth of volatile compounds (Schulz and Dickschat, 2007; Bunge *et al.,* 2008; Kai *et al.,* 2009). Bacterial VOCs are signaling molecules bacteria use for communication with the external biota (Farag, Zhang and Ryu, 2013). Research findings till date have identified 346 distinct VOCs released by bacterial species of the genera *Staphylococcus, Xanthomonas, Stenotrophomonas, Serratia, Pseudomonas, Bacillus, Burkholderia, Erwinia*, *Agrobacterium* and *Staphylococcus* (Kai *et al.,* 2009). Evidences suggest the role of VOCs in plant growth promotion through ISR and phytopathogen suppression (Santoro *et al.,* 2015). Bacterial volatiles, produced by *Bacillus* spp., have been shown to promote plant growth in *A. thaliana* with the highest level of growth promotion observed with 2,3- butanediol and its precursor acetoin (Ryu *et al.,* 2003). Direct application of the bacterial volatile, acetoin to roots under growth chamber conditions has produced significant reductions in pathogen growth at 96 hr post disease induction (Rudrappa *et al.,* 2010). The role of 2,3- butanediol produced by *B. subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a in inducing systemic resistance in plants such as tomato, bell pepper, muskmelon, watermelon, sugar beet, tobacco, Arabidopsis sp., cucumber have also been reported (Ryu *et al.,* 2004). Extensive research is still warranted regarding specific roles of bacterial volatiles on plant growth and metabolism (Santoyo *et al.,* 2012). Yet, VOCs produced by PGPR show biological and ecological promise for enhancing plant self-immunity in modern agriculture.

Production of lytic enzymes

Extracellular hydrolytic enzymes such as chitinases, glucanases, proteases and lipases, achieve disease suppression through lysis of pathogenic fungal cell walls (Neeraja *et al.,* 2010; Maksimov *et al.,* 2011). Except oomycetes, cell walls of most phytopathogenic fungi are made up of chitin ($C_8H_{13}O_5N$), an unbranched, longchain polymer of glucose derivatives, composed of β-1,4-linked units of the amino sugar N-acetyl D-glucosamine (NAG) (Shaikh and Sayyed, 2015). Chitinase activity of PGPR has been well explored for suppression of fungal phytopathogens (Singh *et al.,* 1999; Frankowski *et al.,* 2001; Kim *et al.,* 2008). The role of lytic enzymes such as chitinase and β-1,3-glucanase in suppression of anthracnose pathogen *Colletotrichum gloeosporioides* Penz. have been established (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 which indirectly promotes plant growth.

Competition for nutrients and niches

The rhizosphere is a nutrient basin which serves a vast array of nutrient rich compounds (Weller and Thomashow, 1994). These compounds attract different microbial life forms including phytopathogens who compete for the available nutrients and sites or niches. PGPR strains that are able to compete with these pathogens can serve as biocontrol agent, establishing competition as an indirect mechanism of disease suppression (Lugtenberg and Kamilova, 2009). Competition for nutrient and niches has been believed to be a fundamental mechanism of action by which PGPR protect plants from phytopathogens, but conclusive experimental results regarding the primary role of competition in biocontrol are difficult to establish. Molecular studies suggest the role of fatty acid (lineloic acid) inactivation by *Enterobacter cloacae* strain EcCT-501 in inhibiting germination of *Pythium* spp. spores (Dijk and Nelson, 1998). Importance of competitive root tip colonization by *Psuedomonas* species in protecting tomato plants from tomato foot and root rot (TFRR) has also been demonstrated (Beneduzi *et al.,* 2012). Such evidences further illustrate the role of competition based PGPR strains in plant disease suppression.

Instances of the roles of various modes of action of disease suppression by PGPR are shown in table 1.

Prospects for use in sustainable agriculture

The success obtained with PGPR in in-vitro and greenhouse assays are not often truly reflected in the fields. Discrepancies occur due to environmental factors such as varying microclimates, diversity of soil texture, salinity and moisture content, and unpredictable weather conditions which contribute to field inefficacies of PGPR (Okon, 1994). Furthermore, lack of utmost quality in experimental design and unintentional errors in result analysis contribute their bit to the problem. Recent advances in functional genomics, genome sequencing and microbial ecology have allowed for a better understanding of these microbes and their interaction with plants and phytopathogens (Beattie, 2006). Comprehensive study of ecological traits of pathogen and beneficial bacteria will open up possibilities for formulating effective biocontrol agents in the future. Screening beneficial strains that can act in co-ordination with each other to confer a wide range of pathogen protection in plants will increase efficacies of biocontrol strains.

Conclusion

The increasing world population implies the need of increasing agricultural productivity. Extensive use of chemical fertilizers and pesticides to increase crop yield has caused significant impacts on the environment and human health. With increasing awareness regarding these issues, the need for eco-friendly agricultural practice is well justified. Plant growth promoting rhizobacteria, with its diverse mode of actions in plant disease management seem to provide an efficient long term solution in avoiding crop losses to phytopathogens. Combinatorial approach using several PGPR strains to maintain an extended level of pathogen protection in plants will help achieve high yields without causing harm to the environment. Regardless of certain challenges in establishing PGPR as biocontrol agents, there are huge prospects for its use in sustainable agriculture.

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