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Pseudomonas fluorescens PGPR bacteria as well as biocontrol agent: A review

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Abstract
Plant growth-promoting rhizobacteria (PGPR) are a diverse group of microorganisms that are increasingly appreciated for their contributions to primary productivity through promotion of growth and triggering of induced systemic resistance (ISR) in plants. By triggering plant defense, PGPR can make an important contribution to biocontrol of pests and pathogens of plants. Fluorescent *Pseudomonas* belong to plant Growth Promoting Rhizobacteria (PGPR) the important major group of bacteria that play a major role in the plant growth promotion, induced systemic resistance, biological control of pathogens. The ability of bacterial siderophores and antibiotics to suppress phytopathogens could be the significant agronomic importance. Both mechanisms have essential functions in microbial antagonism but also the mechanisms leads to elicit induced resistance. Resistance-inducing and antagonistic rhizobacteria might be useful in formulating new inoculants, offering an attractive alternate of environmentally friendly biological control of plant disease and improving the cropping systems into which it can be most profitably applied.

Keywords: PGPR, *Pseudomonas fluorescens*, induced systemic resistance, biocontrol

Introduction
One of the major challenges of the twenty-first century will be intensifying agricultural production. Therefore, environmentally sound crop protection methods are our future focus. Increasing concerns over the use of chemical fertilizers and pesticides (Leach and Mumford, 2008) [45]. Call for ecologically stable and sustainable modes for crop production. Biological control thus comes out as a nonhazardous strategy to reduce crop damage caused by plant pathogens (Weller, 1998; Cook, *et al.*, 1995) [84]. Studies on plant-microbe interaction have witnessed tremendous progress in the past two decades **(**Huang, *et al*.2013) [49]. Plant associated microbes not only are stimulants to plant growth and soil health, but are also involved in abiotic and biotic stress tolerance (Welbaum, *et al.*, 2004; Jain, 2012) [83, 35]. The crucial factor in the success of biological control by fluorescent *Pseudomonas* is their ability to colonize the rhizosphere and their persistence throughout the growing season, because they occur in the natural habitat of rhizosphere and when they are reintroduced to roots through seed or seed-piece inoculation, they colonize root surface profusely (Van-Loon *et al.*, 1998) [76].

Plant growth-promoting rhizobacteria (PGPR)
Plant growth-promoting rhizobacteria (PGPR) are a diverse group of microorganisms that are increasingly appreciated for their contributions to primary productivity through promotion of growth and triggering of induced systemic resistance (ISR) in plants. By triggering plant defense, PGPR can make an important contribution to biocontrol of pests and pathogens of plants. Biological control is a potential non-chemical means for plant disease management by reducing the harmful effects of a parasite or pathogen through the use of other living entities. However, the effectiveness of PGPR-triggered plant defense depends on a variety of genetic and biotic/abiotic environmental factors. PGPR naturally occur within a complex community of soil organisms inhabiting the rhizosphere. Hence, in order to understand the role of PGPR in influencing a plant's defense against pests and pathogens, it is important to understand how biotic interactions with these rhizosphere organisms will affect the ability of PGPR to enhance plant defense (Gera Hol, *et al.*, 2013) [26]**.** The rhizosphere is a nutrient-rich habitat and harbors a huge variety of bacteria and fungi that each can have neutral, beneficial or deleterious effects on the plant (Berendsen, *et al*., 2012) [37]. Some of these organisms can improve plant growth by different mechanisms (Lugtenberg and Kamilova, 2009; Van der, 2009) [52, 75].

The resource base in the rhizosphere is highly complex (Loper, *et al*., 1984; Lynch and Whipps, 1991) [51, 53] and accordingly, the composition of the rhizosphere microorganisms undergoes a dynamic change, and accordingly, the composition of the rhizosphere microorganisms undergoes a dynamic change. Among the microbial population in rhizosphere, the bacteria have received most attention. However, a marked rhizosphere effect also occurs with actinomycetes, fungi, nematodes, protozoa and other microflora and fauna (Bowen and Rovira, 1999) [9]. Certain members of the *P. fluorescens* have been shown to be potential agents for the biocontrol which suppress plant diseases by protecting the seeds and roots from fungal infection. Known to enhance plant growth promotion and reduce severity of many fungal diseases (Hoffland, *et al*., 1996, Wei *et al*., 1996) [34, 82]. Specific strains of *Pseudomonas fluorescens* and *P. putida* group were shown to readily colonize the growing roots and cause statistically significant yield increases (Schroth and Hancock, 1982) [68]. This effect is the result of the production of a number of secondary metabolites including antibiotics, siderophores and hydrogen cyanide (O'Sullivan and O'Gara, 1992) [57]. They are Fluorescent *Pseudomonas* are important groups of plant growth-promoting microorganism reported to protect plants against pathogens by evolving various mechanisms such as antagonism, competition and Induced systemic resistance (ISR) (Harman, *et al*., 2004; Kloepper, 1980, Marx, 2004, Van Loon, *et al*., 1998; Vinale *et al.* 2008) [29, 41, 54, 76, 78]. Species of fluorescent *Pseudomonas* are known to produce phytohormones like indole-acetic acid (IAA), cytokinins, gibberellins, and inhibitors of ethylene production, which may indirectly help in increasing the absorptive surface of plant roots for uptake of water and nutrients (Nihorimbere, *et al*. 2011) [56]. *P. fluorescens* and related species may act directly on the growth and physiological and nutritional status of plant they colonize. *P. fluorescens* with ACC deaminase activity (Blaha, *et al*., 2006) [8] can be important for biological control as they diminish the quantity of plant aminocyclopropane-1-carboxylic acid deaminas (ACC) left for ethylene synthesis (Glick, 2005) [27]. *Pseudomonas fluorescens* encompasses a group of common, nonpathogenic saprophytes that colonize soil, water and plant surface environments. It is a common gram negative, rod-shaped bacterium. As its name implies, it secretes a soluble greenish fluorescent pigment called fluorescein, particularly under conditions of low iron availability. *Pseudomonas fluorescens* has simple nutritional requirements and grows well in mineral salts media supplemented with any of a large number of carbon sources (Palleroni, 1984) [60]. In the past three decades, numerous strains of fluorescent *Pseudomonas* have been isolated from the rhizosphere soil and plant roots by several workers and their biocontrol activity against soil-borne and foliar pathogens were reported (Vivekananthan *et al.*, 2004) [79]. The plant growth-promoting traits by a comparative genomics analysis of four representative *pseudomonas* PGPR strains. The genes that were conserved among the different *Pseudomonas* species have provided clues to the common characteristics of *pseudomonas* PGPR, such as rhizosphere competence traits (nutrient catabolism and transport, resistance to various environmental stresses and rhizosphere colonization). Genetic modification may accelerate the commercialization of PGPR as biocontrol agents, which could further contribute to sustainable development of agriculture (Shen, *et al*. 2013) [69].

Mechanisms of bio-control *Pseudomonas fluorescens* against different plant pathogens

For achieving biological control, antagonists should have the ability to colonize the root system effectively (Weller, 1988; Parke, 1990) [85, 61] and to produce certain antagonistic secondary metabolites (Defago and Haas, 1990) [17]. These beneficial bacteria suppress the plant pathogens by producing one or more of a variety of mechanisms and metabolites that include antibiotics (Fravel, 1988; Thamashow and Weller, 1990; Keel, *et al.*,1992) [23, 74, 39], siderophores (Kloepper, *et al*., 1980; Leong, 1986; Schippers, *et al.*, 1987) [41, 47, 87], parasitism and lysis (Ordentich, *et al.*, 1987; Campbell and Ephgrave, 1983) [58, 11], volatile substances such as cyanide (Voisard *et al*., 1989) [80] or induced systemic resistance or ISR (van Loon *et al*., 1998) [76].

Antibiosis

Antibiotics are defined as heterogeneous group of low-molecular-weight organic compounds that are deleterious or harmful to the growth or metabolic activities of other microorganisms. The antibiotics were more effective in suppressing the growth of target pathogen *in vitro* and *in situ.* The production of one or more antibiotics is the most important mechanism of plant growth promoting rhizobacteria which facilitates the antagonistic against many phytopathogens (Glick, *et al.*, 2007) [28]. Six classes of antibiotic compounds are better associated with biocontrol of plant disesases: Phloroglucinol, phenazines, pyrrolnitrin, pyoluteorin, cyclic lipopeptides and hydrogencyanide (Haas and Defago, 2005) [31]. The important antibiotic 2, 4-diacetylphlroglucinol (DAPG) produced by *Pseudomonas* has effectively cause membrane damage to *Pythium* spp. and particularly has inhibitory action against zoospores of *Pythium spp*. (de souza, *et al*., 2003) [15]. *Pseudomonas* are potential biocontrol agents, that showing competitive interactions with other micro organisms including fungi, bacteria, protozoa and nematodes by producing lipopeptide bio-surfactants (de Bruijn *et al*., 2007; Raaijmakers, *et al*.,2010) [14, 62]. *Pseudomonas* has the capacity to produce phenazine antibiotic, showing antagonistic activity against *Fusarium oxysporum* and *Gaeumannomyces gramini* (Chin-Awoeng *et al*., 2003) [12]. This phenazine antibiotic plays a role in mobilization of iron in soils at neutral soil pH, where iron is present in insoluble ferric form and this was experimentally proven with *Pseudomonas chlororaphis* PCL1391 strain isolated from rhizosphere of tomato plants (Hernandez *et al*., 2004; Haas and Defago, 2005) [31]. The relative importance of antibiotic production by bacterial bio-agents has been demonstrated, where one or more genes responsible for biosynthesis of the antibiotics have been manipulated. For example, mutant strains incapable of producing phenazines (Thomashow and Weller, 1988) [85, 73] or phloroglucinols (Keel, *et al.* 1992, Fenton, *et al*., 1992) [39, 21] have been shown to be equally capable of colonizing the rhizosphere but much less capable of suppressing soil borne root diseases than the corresponding wild-types and the capacity to produce multiple classes of antibiotics, that differentially inhibit different plant pathogens, is likely to enhance biological control effectively. *Pseudomonas putida* WCS358r strains were shown the capacity of phenazine and DAPG production by genetic engineering with corresponding genes and showed improved capacity to suppress or inhibit plant diseases in wheat crop (Glandorf *et al*., 2001; Bakker, *et al*., 2002) [25, 4].

Competition for Root Niches and Nutrients

Soil microorganisms are highly dependent on plants for the nutrients they secrete in the rhizosphere. The surface surrounding rhizosphere is significant carbon sinks (Rovira, 1969) [65] and provides a large number of other important nutrients such as H+, free oxygen iron, water, enzymes, mucilage, antimicrobials vitamins, plant growth regulators, and other secondary metabolites. Thus, the root attracts a great diversity of microorganisms, including pathogens, creating competition for these nutrients and niches. Fluorescent *Pseudomonas* and some other fast growing PGPRs adapt themselves to such condition and they thus become competitive with pathogens. They move using their flagella and are guided through chemotactic responses and reach root surfaces by active motility facilitated by flagella (De Weert, *et al*., 2002) [16]**.** Bacterial lipopolysaccharides, in particular the O-antigen chain, can contribute to root colonization. The O-antigenic side chain of *P. fluorescens* PCL1205 has been found to be involved in tomato root colonization (Dekkers, *et al*., 1998) [18]. Endo-phytic colonization of roots of tomato by PGPR *P. fluorescens*WCS417r (Duijff, *et al.,* 1998) [19]. The ability of PGPRs to colonize roots is related to their ability to secrete a site-specific recombinase **(**Dekkers, *et al*. 1998) [18]. Endophytic *P. fluorescens* strain ALEB 7B isolated from *Atractylodes lancea* significantly inhibited the growth of *Athelia rolfsii* strain SY4 by secretion of antibiotics and lytic exo-enzymes and competition for spaces and nutrients (Zhou, *et al*., 2014) [88].

HCN Production

HCN has been long known for its role in disease suppression (Keel, *et al.,* 1989) [38]**.** The production of HCN is one of the mechanisms involved by fluorescent *Pseudomonas* in disease suppression (Laville, *et al.* 1992) [48]**.** HCN production has been shown to have a beneficial effect on the plants (Voisard *et al.* 1989) [80]**.** The rate of HCN production by microbes may also vary depending upon the crop species probably due to difference in amino acid composition of root exudates. Certain HCN-producing bio-control fluorescent *pseudomonas* are implicated for their role in the induction of resistance against diseases caused by phytopathogenic fungi, such as *Thielaviopsis basicola* on tobacco (Laville, *et al.,* 1992; Voisard, *et al.,* 1989) [48, 80]**,** *Septoria tritici*, and *Puccinia recondita* f. sp. *tritici* on wheat (Flaishman, *et al.* 1996) [22]**.** HCN inhibits the terminal cytochrome c oxides in the respiratory chain (Knowles, 1976) [42]. However, apart from its beneficial role in plant disease protection, microbial HCN may have deleterious effects on several plants (Schippers, *et al.*, 1990; O'Sullivan and O'Gara, 1992) [66, 57]. HCN production by *Pseudomonas* spp. is known to have a negative effect on growth of lettuce and bean (Alstrom and Burns, 1989) [1]**.** In a study conducted by (Kremer and Souissi, 2001) [43] deleterious HCN-producing strains were exploited for biological control of weeds. (Siddiqui, *et al.,* 2006) [70]. Reviewed the role of cyanide in controlling root knot disease of tomato. A close relationship is hypothesized to be present between the bio-control activity of fluorescent *Pseudomonas* and their HCN production ability (Ellis, *et al* 2000) [20]. Found positive correlations between *in vitro* HCN production and plant protection in the cucumber/*Pythium ultimum* and tom ato/*Fusarium oxysporum* f. sp. *radicis-lycopersici* pathosystems (Ramatte *et al*. 2003) [63].

Siderophore Production

Synthesis of iron-chelating compounds, such as siderophores, by *Pseudomonas* is a characteristic feature visible in some isolates from bulk or rhizosphere soils. In culture media with trace amounts of iron, a yellow-green halo can be observed, which may be fluorescent under ultraviolet light (Budzikiewicz, 1993) [10]. Iron is an important micronutrient required by the microbes and being highly insoluble is often a limiting condition in the rhizosphere. Iron binding ligands (siderophores) for iron acquisition to have a competitive advantage over other microorganisms. These siderophores bind to ferric iron in the soil or the root zone and are then taken up using outer membrane receptors. Their different affinity to ferric iron depends on their structural, that is, hydroxymate- and phenolate/catecholate-type structures, classified as either pyoverdins or pseudobactins (Weller *et al.* 2004) [86]**.** The ability of bacterial siderophores to suppress phytopathogens could be the significant agronomic importance (Beneduzi, *et al*. 2013) [6]. (Kloepper, *et al*., 1980) [41]. Were the first to isolate fluorescent siderophore from strain B10 with disease suppression activity. A Tn5-induced siderophore-negative fluorescent *Pseudomonas* spp. strainWCS358 lost the ability to promote growth of potato (Bakker, *et al*., 1986) [3]. Therefore, it restricts the growth of deleterious microbes by limiting iron availability (Loper and Buyer 1991) [50]. Interestingly, siderophore-mediated iron competition by *P. fluorescens* may also be useful to prevent growth of human pathogen *Escherichia coli* O157:H7 growing on food products (McKellar and Nelson, 2003) [55].

Induced systemic resistance

Colonization of plants with some plant growth promoting microorganisms may lead to ISR and protection of plants against various pathogens. ISR is generated in response to an external stimulus that provides plants with defensive immune capacity. The mechanisms of ISR include (1) growth promotion, (2) physiological tolerance, (3) induction of cell wall reinforcement, and (4) increase in production of phytoalexins, defense enzymes, antioxidants, proline, pathogenesis related proteins, lignin deposition, and modulation of phenols with antimicrobial and antioxidant properties **(**Jain**,** *et al.,* 2012; Jain**,** *et al.,* 2013; Jain**,** *et al.,* 2015; Singh, 2014) [35, 37, 36, 71]. Fluorescent *P. aeruginosa* also suppressed oxalic acid production by *S. sclerotiorum* in pea plants alone or/and in consortia with other microbes (Jain**,** *et al.,* 2013) [37]. The involvement of ISR is typically studied in fluorescent *Pseudomonas* pathogen interaction (Bakker, *et al.,* 2007) [5]. Antibiotics are also play key role in inducing resistance in plants and the importance of DAPG production in ISR was further supported by observations that mutants which were unable to produce DAPG, not having the capacity to induce resistance and finally concluded that antibiotics are major components for triggering ISR (Weller, *et al.,* 2004) [86]. (Van Peer, *et al*., 1991) [77] reported that *Pseudomonas* strain WCS417 induced resistance in carnation against wilt caused by *Fusarium oxysporum* f. sp. *dianthi* when the roots were inoculated with bacteria 1 week prior to stem inoculation with the pathogen. This strain was isolated from the wheat rhizosphere and also promoted the growth of several crops subsequently, strains WCS417 and WCS374 were shown to induce resistance in radish against *F. oxysporum f. sp. Raphani* and other pathogens (Hoffland, *et al.,* 1996) [34]. The O-antigenic side chain of the lipopolysaccharide, present on the outer membrane of strains WCS374 and WCS417, appeared to be the determinant

responsible for the induction of resistance in radish (Leeman, *et al.,* 1995) [46]. Under iron limited conditions several *Pseudomonas* produce salicylic acid which in turn play a major role in SA-dependent signal transduction pathway. However, ISR by SA producing Pseudomonas strains does not depend on SA but it is frequently observed in Siderophores (Ran, *et al.,* 2005) [64]. Induced systemic resistance is broadly defined as activation of latent defense mechanisms in plants prior to pathogenic attack. The mechanism has been hypothesized rhizobacterial systems. Induced systemic resistance is associated with increased synthesis of certain enzymes such as peroxidase (Langrimini and Rothstein, 1987) [44], increased levels of certain acid soluble proteins (Zdor and Anderson, 1992) [87] and the accumulation of phytoalexins in the induced plant tissue (Van peer *et al.,* 1991) [77]. The seed bacterization of common bean with *P. fluorescens* S97 was reported to suppress the halo blight caused by *P. syringe* pv. *phaseolicola* through induced systemic resistance mechanism (Alstrom, 1991) [2].

Quorum sensing (QS) Cellular Communication

Many host-associated bacteria use chemical signals to monitor their own species population density and to control expression of specific genes in response to population density. This type of gene regulation is termed quorum sensing (Fuqua, *et al*., 1997) [24]. Quorum sensing (QS) in *P. fluorescens* within spatially structured bacterial communities in the rhizosphere is found to be possible (Hense, *et al*., 2007) [32]. QS Signaling is mainly affected by cell density, spatial distribution, and mass transfer. In gram-negative bacteria, the most common QS system is regulated by the *N*-acyl homoserine lactone-signalling molecules (AHLs). Bacterial motility on semisolid surfaces is mediated by flagella and type IV pili in pseudomonads (Overhage, *et al*., 2008) [59]. Pyoverdine has been found to have role in bacterial motility as mutation in pvdQ which code for a cycle involved in pyoverdine biosynthesis made bacteria unable to show motility (Sio, *et al.,* 2006) [72].

Conclusion

Plant disease control, now become heavily dependent on fungicides to combat the wide variety of fungal diseases that threaten agricultural crops. The governments of many countries are increasingly aware of the drawbacks of many chemical pesticides, in terms of their effect on the environment, as well as on the growers and consumers of agricultural products. Studies aimed at replacing pesticides with environmentally safer methods are currently being conducted at many research centers. The heightened scientific interest in biological control of plant pathogens is partly a response to growing public concerns over chemical pesticides. Biological control is a potent means of reducing the damage caused by plant pathogens. The inconsistency in performance of these bio-control agents over time and space in comparison to chemical pesticides is a major impediment to their large scale use in commercial agriculture. Thus the use of bio-control agents is being tried in a system where chemical fungicides provide a better and more economical result *i.e.*, the bio-control agents are tried to fit in to a chemical paradigm (Harman, 2000) [30]. IAA, as IAA positively influences root growth and development, thereby enhancing nutrient uptake (Khalid, *et al.,* 2004) [40]. To exploit this organism to its fullest it is required to have greater understanding of mechanisms underlying plant growth promotion and dimensions involved in disease suppressions by them. Knowing that rhizospheric competence as a prerequisite of effective biological control, knowledge about cell-to-cell communication, root-microbe communication, microbe-microbe interaction, and genetic and environmental factors affecting growth will help in providing a better understanding of the mechanisms adopted. Strategic approach and designing models will improve efficacy of this wonderful microbe.

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