Review Article

Insight into the Interaction between Plants and Associated Fluorescent *Pseudomonas* spp.

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Fluorescent *Pseudomonas* are known for their plant growth promoting and disease protection abilities. In past years, a number of studies have focused on how these bacteria suppress disease and induce resistance. They are known to produce antibiotics and siderophores, promote growth, and induce systemic resistance in the host plant. This bacterium has come out as a model organism for ecological studies going on in rhizosphere and for studying plant-beneficial microbe interaction. This review focuses on the current state of knowledge on biocontrol potential of fluorescent *Pseudomonas* strains and the mechanisms adopted by them.

1. 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 [1] 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 [2, 3]. Studies on plant-microbe interaction have witnessed tremendous progress in the past two decades [4]. Plant associated microbes not only are stimulants to plant growth and soil health, but are also involved in abiotic and biotic stress tolerance [5, 6].

Plant growth promoting rhizobacteria (PGPRs) are diverse group of soil microorganisms that are huge contributors to enhanced plant health and induced systemic resistance (ISR) [7]. These PGPRs colonize the root surfaces closely adhering to soil interface, the rhizosphere [8]. There are wide mechanisms of biocontrol mediated by PGPR such as competition for nutrients and ecological niche, production of allelochemicals such as enzymes and antibiotics, induction of systemic resistance in plants against pathogens [9, 10], abiotic stress tolerance [11], and increasing population of other beneficial microorganisms [12]. This knowledge is still in

a latent phase and is yet to be fully exploited for maximizing agriculture benefits.

The genus *Pseudomonas* encompasses a group of ubiquitous microorganisms found in diverse ecological habitats such as water, soil, sediments, and plant surfaces maybe just because of their simple nutritional requirements. Fluorescent *Pseudomonas* spp. can be generally visually distinguished from other *Pseudomonas* by their ability to produce a water soluble yellow-green fluorescent pigment. It is common gram-negative, chemoheterotrophic, motile, rod shaped bacterium with polar flagella. The rhizosphere is a microbial hot spot zone in which root associated pseudomonads play a promising role as plant health managers [13, 14]. Although few of them like *Pseudomonas syringae* are well-known plant pathogens, other rhizosphere-inhabiting fluorescent pseudomonads have received much attention because of their ability to fight phytopathogens [15]. Beneficial pseudomonads are rapid root colonizers, directly and indirectly improving plant growth and yield [16, 17].

Their main mechanism of action involves production of a diverse group of metabolites, including antibiotics, and volatile compounds like hydrogen cyanide [18], competition for iron and other nutrients by production of siderophore, niche exclusion [2], and induction of systemic resistance [19, 20] (Figure 1). The present review discusses the various

FIGURE 1: Schematic representation of mechanism of action of fluorescent *Pseudomonas* in rhizosphere.

modes employed by fluorescent *Pseudomonas* in enhancing plant growth and disease resistance in different agricultural and horticultural crops. In addition, we will also discuss their interaction with other rhizospheric microorganisms.

2. Plant Disease Protection

2.1. Antibiosis. The significance of antibiotics produced by biocontrol agents and particularly fluorescent *Pseudomonas* is well known [2, 14]. The versatility in type of antibiotics produced is now being fully realized and compounds including phenazine-1-carboxylic acid [21], pyocyanin [22], pyrrolnitrin [23], and pyoluteorin [24] and 2,4-diacetylphloroglucinol (Phl) have been isolated from fluorescent pseudomonads. The antibiotic Phl produced by fluorescent *Pseudomonas* strains are of worldwide origin and are relatively well conserved [25, 26]. Phl is a phenolic metabolite with antibacterial, antifungal, anthelmintic, and phytotoxic properties [27]. HPLC/mass spectrometry was further used to elucidate the role of introduced and naturally occurring Phl-producing *Pseudomonas* spp. in biological control of soil-borne plant pathogens on roots of wheat plants grown in raw soil [28, 29]. On assessment of *P. fluorescens* B16 genomic library, pyrrolo-quinoline quinone (PQQ) biosynthetic genes were found responsible for enhancing plant health; PQQ was suggested to act as an antioxidant in plants [30]. Phenazine-producing *Pseudomonas* contributes to the natural suppression of *Fusarium* wilt in soils [31]. Mavrodi et al. [32] also found that the frequency of wheat root colonized by these phenazine-producing pseudomonads was inversely related to annual precipitation; some of these pseudomonads showed strong inhibitory activity against *Rhizoctonia solani* AG-8 both *in vitro* and *in situ*.

2.2. HCN Production. HCN has been long known for its role in disease suppression [33]. The production of HCN is one of the mechanisms involved by fluorescent pseudomonads in disease suppression [34]. HCN production has been shown to have a beneficial effect on the plants [35]. 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 biocontrol fluorescent pseudomonads are implicated for their role in the induction of resistance against diseases caused by phytopathogenic fungi, such as *Thielaviopsis basicola* on tobacco [34, 35], *Septoria tritici*, and *Puccinia recondita* f. sp. *tritici* on wheat [36]. HCN inhibits the terminal cytochrome c oxidase in the respiratory chain [37] and binds to metalloenzymes [38]. However, apart from its beneficial role in plant disease protection, microbial HCN may have deleterious effects on several plants [39, 40]. HCN production by *Pseudomonas* spp. is known to have a negative effect on growth of lettuce and bean [41]. In a study conducted by Kremer and Souissi [42] deleterious HCN-producing strains were exploited for biological control of weeds. Siddiqui et al. [43] reviewed the role of cyanide in controlling root knot disease of tomato. A close relationship is hypothesized to be present between the biocontrol activity of fluorescent pseudomonads and their HCN production ability [44]. Ramatte et al. [45] found positive correlations between *in vitro* HCN production and plant protection in the cucumber/*Pythium ultimum* and tomato/*Fusarium oxysporum* f. sp. *radicis-lycopersici* pathosystems.

2.3. Siderophore Production. Iron is an important micronutrient required by the microbes and being highly insoluble is

often a limiting condition in the rhizosphere. Some microorganisms, including fluorescent *Pseudomonas*, produce 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 [40]. These siderophores either are not produced by pathogens or if produced are of lower affinity than that of beneficial microorganisms, thus making iron unavailable to phytopathogens [46]. Kloepper et al. [47] were the first to isolate fluorescent siderophore from strain B10 with disease suppression activity. A Tn5-induced siderophore-negative fluorescent *Pseudomonas* spp. strain WCS358 lost the ability to promote growth of potato [48]. Therefore, it restricts the growth of deleterious microbes by limiting iron availability [49]. 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 [50].

2.4. 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 [51] 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 [52]. 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 [53] and endophytic colonization of roots of tomato by PGPR *P. fluorescens* WCS417r [54]. The ability of PGPRs to colonize roots is related to their ability to secrete a site-specific recombinase [53]. 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 exoenzymes and competition for spaces and nutrients [55].

2.5. Cellular Communication. Quorum sensing (QS) in *P. fluorescens* within spatially structured bacterial communities in the rhizosphere is found to be possible. QS signalling is mainly affected by (i) cell density, (ii) spatial distribution, and (iii) mass transfer [56]. 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 [57]. Pyoverdine has been found to have role in bacterial motility as mutation in pvdQ which codes

for a cycle involved in pyoverdine biosynthesis made bacteria unable to show motility [58].

3. Plant Growth Promotion

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 [59]. *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 [60] can be important for biological control as they diminish the quantity of plant aminocyclopropane-1-carboxylic acid deaminase (ACC) left for ethylene synthesis [61]. Fluorescent *P. aeruginosa* PJHU15 was found to produce IAA and solubilise phosphate *in vitro* using plate assays [62]. The same fluorescent *P. aeruginosa* in consortium with *Trichoderma harzianum* and *Bacillus subtilis* also showed improved plant health, induction of systemic resistance, and proteome level changes upon challenge with *Sclerotinia sclerotiorum* [6, 12, 62, 63]. The same combination of microbes also modulated nutritional and antioxidant quality of pea seeds and pericarp [64].

4. Induction of 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 [6, 12, 65, 66]. Fluorescent *P. aeruginosa* also suppressed oxalic acid production by *S. sclerotiorum* in pea plants alone or/and in consortia with other microbes [67]. The involvement of ISR is typically studied in fluorescent *Pseudomonas*-pathogen interaction [68].

Substances involved in ISR are partly the same with those involved in microbial antagonisms: siderophores, antibiotics, AHLs, and volatile compounds. In a previous report, pseudobactin 358 producing *P. putida* WCS358 has been shown to trigger ISR in tomato while a pseudobactin mutant failed to do so [69]. Lowering iron availability for *P. fluorescens* WCS374 and WCS417 increased suppression of ISR-mediated disease by triggering of ISR by the siderophores produced by these strains [70]. Similarly, Phl produced by *P. fluorescens* CHA0 is involved in ISR against *Peronospora parasitica* [71]. ISR in *P. fluorescens* WCS417r was seen to involve phytohormones jasmonate and ethylene as signals [19]. Sarvanakumar and Kavino [72] observed an increase in proline content in green gram plants bacterized with *P. fluorescens* Pfl.

TABLE 1: Microbial consortia with fluorescent *Pseudomonas* as one of the components and mechanisms involved in disease suppression.

Microbial consortia involving fluorescent <i>Pseudomonas</i>	Disease/pathogen	Mechanisms involved	Reference
<i>T. harzianum</i> and <i>P. fluorescens</i>	<i>Aphanomyces euteiches</i> f. sp. <i>pisi</i>	Siderophore, ISR, and plant growth promotion	[78]
<i>P. fluorescens</i> and <i>Stenotrophomonas maltophilia</i>	<i>Pythium ultimum</i>	ISR	[79]
<i>P. fluorescens</i> NBRI-N6 and <i>P. fluorescens</i> NBRI-N	<i>Sclerotium rolfsii</i>	ISR	[80]
<i>P. fluorescens</i> and <i>T. viride</i>	<i>Rhizoctonia solani</i>	ISR and plant growth promotion	[81]
<i>P. fluorescens</i> EBC5 and EBC6	<i>Pythium aphanidermatum</i>	ISR	[82]
<i>T. harzianum</i> , fluorescent <i>Pseudomonas</i> , and <i>G. intraradices</i>	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Plant growth promotion and increased nutrient uptake	[83]
Fluorescent <i>P. aeruginosa</i> , <i>Mesorhizobium</i> spp.	<i>S. rolfsii</i>	ISR	[20, 66]
Fluorescent <i>P. aeruginosa</i> , <i>T. harzianum</i> , and <i>Bacillus subtilis</i>	<i>Sclerotinia sclerotiorum</i>	ISR, increase in plant growth, and suppression of oxalic acid production	[6, 12, 62–64, 67]

ISR: induced systemic resistance.

5. Compatible Interactions with Other Microbes

A large number of success stories of fluorescent *Pseudomonas* consisting consortia for disease management are reported (Table 1). In a previous study, it has been demonstrated that some *Pseudomonas* stimulate nodulation of legumes by *Rhizobium* and *Bradyrhizobium* [73, 74]. It is also reported that their positive effects may be due to indirect growth promotion via protection from pathogen infection and not due to enhancement or stimulation of nodulation [75]. Molecular level studies also confirmed the enhanced biocontrol potential of *P. fluorescens* and *Trichoderma atroviride* in consortia [76]. Similarly, interaction between *P. fluorescens* CHA0 and 7NSK2 was found to trigger an oxidative burst and the phytoalexin accumulation in grape leaves upon challenge with *Botrytis cinerea* [77].

In a study comprising chickpea plants treated with a consortium of fluorescent *P. aeruginosa*, *T. harzianum*, and *Mesorhizobium* sp., increase in plant growth and modulation of phenolics was observed compared to individual and two-way combination of antagonist mixtures after challenge inoculation with *Sclerotium rolfsii* [20]. Application of *P. fluorescens* and *T. viride* in combination with chitin induced accumulation of phenols and activities of PR proteins in coconut palm as compared to single-microbe-treated and control plants [84]. Recent studies by our group on pea plant treated with consortia of fluorescent *P. aeruginosa*, *B. subtilis*, and *T. harzianum* and challenged with *S. sclerotiorum* under greenhouse conditions showed decrease in plant mortality and increase in activities of defense-related and antioxidant enzymes and phenols and suppression of oxalic acid induced cell death [6, 12, 62, 67]. Also, proteome level study using 2D gel electrophoresis on the same system showed 30 differential protein spots, 25 of which were identified by MALDI TOF

MS/MS to be involved in photosynthesis, respiration, disease resistance, and stress alleviation [63]. Such reports support the beneficial effect of fluorescent *Pseudomonas* in consortia mode with other microorganisms in root colonization, increasing plant growth and activities of defense-related enzymes, and induction of phenylpropanoid pathway and therefore it may also be expected to alter the production and composition of secondary metabolites in plants [10].

6. Conclusion and Future Prospects

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 [85]. Strain discovery from diverse ecological niche's targeting selections of specific biosynthetic genes may be fruitful. Identification of new metabolites and finding mechanisms involved may further increase our knowledge. Factors that stimulate antibiotics and enzyme productions can be exploited by targeting inoculants suitable for particular soil condition and more likely to support biocontrol by having insights into physicochemical properties of soil involved for, for example, giving soil amendments like substrates and minerals [86]. The future relies on the development of microbial consortia which can provide a more stable ecological community by improving plant growth and working effectively against a broad spectrum of pathogens [12, 67].

Along with basic science, genetic engineering can be coupled by having strains with multiple modes of action [87, 88]; for example, *P. fluorescens* CHAO has increased plant growth promotion and biocontrol activity by transforming the 1-ACC gene, which cleaves the immediate precursor of ethylene [89]. Exploiting molecular tools and techniques to study the genome expression and proteome level changes modulated by plant-fluorescent *Pseudomonas* interaction and pathogen-fluorescent *Pseudomonas* interaction will provide a complete picture of rhizosphere biodiversity. Future studies require identification of genes and gene products in the genotypes and in plants that govern efficient rhizosphere colonization and improved biocontrol potential. Advances in ISR based research using fluorescent *Pseudomonas* would provide exciting new insights into various mechanisms of action working together and the underlying defense signalling network involved.

Abbreviations

ISR: Induced systemic resistance
PGPRs: Plant growth promoting rhizobacteria
Phl: 2,4-Diacetylphloroglucinol.

Competing Interests

The authors declare that they have no competing interests.

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