# Chapter 2
# Exploiting Beneficial Traits of Plant-Associated Fluorescent Pseudomonads for Plant Health

**Anuradha Rai, Pradeep Kumar Rai, and Surendra Singh**

**Abstract** Plants have recently been recognized as meta-organisms harboring distinct microbiome and reveling close symbiotic relationship with the associated microflora. Each plant has a unique niche and possesses species-specific microbes to a certain proportion and majority of the ubiquitous microbes that fulfill important host as well as ecosystem function. Currently, agricultural crops are facing challenges due to imbalance of micronutrients, deterioration of soil health, fluctuating environmental conditions, and increasing pest and pathogen attack. The rhizosphere region of the plants is the most extensively studied area due to its remarkable microbial diversity. Fluorescent pseudomonads are Gram-negative, motile, rod-shaped bacteria predominantly inhabiting the vicinity of rhizosphere and sometimes even the root interior. They effectively colonize the plant roots and rhizosphere soil because of their excellent ability to utilize a variety of organic substrates exuded by the plant roots. The study on the role of fluorescent pseudomonads in agriculture has been a matter of great interest attributable to their ability to control plant diseases, maintain soil health, and influence the plant growth directly or indirectly. They directly promote the plant growth by producing secondary metabolites such as siderophores and phosphatases that can chelate iron and solubilize phosphorus, respectively, from the soil and make them available to the plants. They also produce indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate (ACC) deaminase that sequesters ACC, the precursor of ethylene. They also indirectly promote the plant growth mainly by suppressing the plant pathogens by producing an array of antibiotics and fungal cell wall degrading enzymes. Specific metabolites produced by fluorescent pseudomonads may elicit defense reactions and induce systemic resistance of the host plants. Introduction of such multifunctional rhizobacteria

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to the plant roots can lead to increased plant growth and protection against phytopathogens. This chapter reviews the beneficial traits of the fluorescent pseudomonads and their relationship to the functioning in the rhizosphere.

**Keywords** PGPR • Micronutrient • Medicinal plants • Fluorescent *Pseudomonas* • Rhizosphere

## 2.1 Introduction

Photosynthetic plants play a key role in ecosystems functioning (Hartmann et al. 2009). In plant-based ecosystems, they contribute to the establishment of unique microbial ecological niches. Recently, plants have been recognized as meta-organisms harboring distinct microbial community and reveling close symbiotic relationship with the associated microflora. Hence, such a microbial community associated with plant roots can be referred to as a microbiome (Chaparro et al. 2013). Each plant has a unique niche which possesses species-specific microbes to a certain proportion, and majority being the ubiquitous microbes that fulfill important host as well as ecosystem function. Plant roots are colonized by an outstanding number of bacteria. These bacteria have profound effects on plant growth and development and are known as plant growth promoting rhizobacteria (PGPR) (Kloepper et al. 1980). PGPR are heterogeneous in nature comprising bacteria, fungi, and actinomycetes that survive in and around the rhizosphere (Singh 2013, 2014). They colonize the root surface as well as interior of the roots (Gray and Smith 2005). PGPR function in three different ways: by synthesizing particular compounds for the plants, facilitating the uptake of certain nutrients from the soil, and lessening or preventing the plants from diseases. Bacteria of diverse genera have been identified as PGPR, of which *Bacillus* and *Pseudomonas* spp. are predominant (Podile and Kishore 2006). It is a well-established fact that only 1–2 % of bacteria promote plant growth in the rhizosphere (Antoun and Kloepper 2001).

In recent years, fluorescent pseudomonads have drawn the attention worldwide owing to their ability to produce secondary metabolites such as antibiotics, volatile compounds, hydrogen cyanide (HCN), siderophores, cell wall degrading enzymes, and phytohormones (Bakker and Schippers 1987; O'Sullivan and O'Gara 1992; Nielsen et al. 2000). Plant-associated *Pseudomonas* can be categorized into beneficial, deleterious, and neutral groups on the basis of their effects on plant growth although they may colonize the same ecological niche (Dobbelaere et al. 2003). Beneficial fluorescent pseudomonads include *Pseudomonas putida*, *Pseudomonas chlororaphis*, *Pseudomonas aureofaciens*, *Pseudomonas aeruginosa*, and *Pseudomonas syringae*. Fluorescent pseudomonads are diverse group of aerobic, gram-negative, chemoheterotrophic, and rod-shaped bacteria. They are characterized by production of water soluble yellow-green fluorescent pigments pyoverdins or pseudobactins under low iron condition. All fluorescent pseudomonads fall into one of the five rRNA groups. The G + C content of their DNA ranges from 58 to 68 mol% (Palleroni et al. 1973). They are heterogenous and ubiquitous in nature. They have simple nutritional requirements and are well adapted to numerous ecological niches (Stanier et al. 1966). Their universal distribution suggests a remarkable degree of their physiological and genetic adaptability (Spiers et al. 2005). Most species are saprophytic and commonly found in water and soil, and are used in biotechnological applications to improve plant growth and/or plant health and in the bioremediation of agricultural pollutants (Ramamoorthy et al. 2001). They are aggressive root colonizers of different crops and have a broad spectrum of antagonistic activity against a wide group of phytopathogens. Fluorescent pseudomonads are very common, diverse, and well-studied PGPR. *P. fluorescens* biovar III has been reported as the dominant group of bacteria among fluorescent pseudomonads associated with rhizosphere of rice (Sakthivel and Gnanamanickam 1987). Few members of this genus are associated with animal, plant and human diseases, and food spoilage. Fluorescent pseudomonads have been isolated from the rhizosphere of various crops and medicinal plants owing to their ability to utilize diverse organic substances and mobility. They have the ability to produce indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate (ACC) deaminase that sequesters ACC, the precursor of ethylene. They reside in the rhizospheric region and at times in the root interior. This review focuses on the plant-beneficial fluorescent pseudomonads interaction and its effect on the plant growth promotion and biocontrol potential. Both the aspects confer this bacterial group as an alternative to agrochemicals, which fit environment-friendly strategies to be implemented in a modern sustainable agriculture framework.

## 2.2 Rhizosphere and Plant–Microbe Interaction

The term rhizosphere was first defined by Lorenz Hiltner as “the soil compartment influenced by the root” (Hiltner 1904). The rhizosphere is a hot spot for numerous organisms and is influenced by plant roots, and considered as one of the most complex ecosystems on Earth (Pierret et al. 2007; Jones and Hinsinger 2008; Raaijmakers et al. 2009; Singh et al. 2016a, b). From decades, it is known that an association exists between microbes and plants (Singh 2015a, b). All beneficial traits that fluorescent pseudomonads provide to plants would be useless if some fundamental requirements are not fulfilled (Singh et al. 2011a, b, c). They must be efficient root colonizers. They must persist, multiply, and compete with other microbiota. Plant roots synthesize, accumulate, and secrete a diverse array of compounds called root exudates (Walker et al. 2003). These compounds act as chemoattractants as well as repellents for a large number of heterogenous, diverse, and actively metabolizing soil microbes (Badri and Vivanco 2009). Root exudates are an immediate source of carbon, nitrogen, and energy. A wide range of chemical compounds of root exudates modifies physicochemical properties of the soil and regulates the composition of soil microbial community (Dakora and Phillips 2002). The chemical composition of

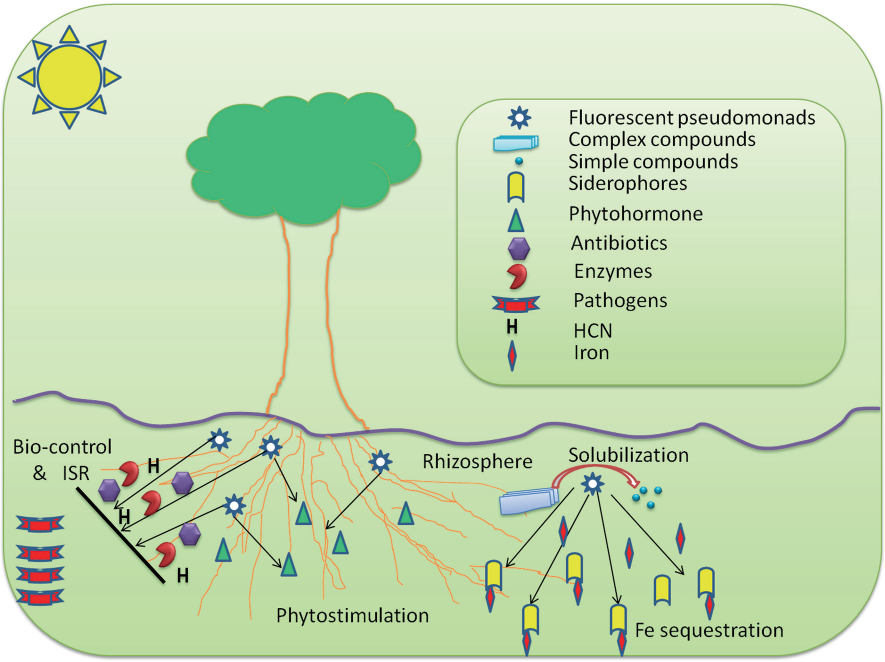


**Fig. 2.1** Diagrammatic representation of different mechanisms of fluorescent pseudomonads

the root exudates also depends on plant species and microbes (Kang et al. 2010). Bacteria compete with each other and with other soil microorganisms for these carbon resources. In addition, severe competition between microorganisms in the rhizosphere involves specific communication between microorganisms, including quorum-sensing (QS) and complex mechanisms that modulate it (Faure et al. 2009). Plants can produce and secrete various compounds that mimic QS signals of bacteria and, thereby, alter bacterial activities in the rhizosphere (Bauer and Mathesius 2004).

In addition to chemotactic factors, bacterial lipopolysaccharides (LPS) and pilli can also contribute to root colonization in several PGPR. Fluorescent *Pseudomonas* chemotactically reaches root surfaces through flagella motility (De Weger et al. 1987; Turnbull et al. 2001a, b; De Weert et al. 2002). Different mechanisms of fluorescent pseudomonads in the rhizosphere have been diagrammatically represented in Fig. 2.1, and they are self-explanatory. Besides the flagella motility, O-antigenic side chain of LPS of *P. fluorescens* PCL1205 contributes to a major role in tomato root colonization (de Weger et al. 1989; Dekkers et al. 1998). *P. fluorescens* WCS365 strain isolated from potato (*Solanum tuberosum* L.) is a good colonizer of both potato (Brand et al. 1991) and tomato (*Lycopersicon esculentum* L.) (Simons et al. 1996) roots. The root colonization genes (*rhi*) associated with the colonization of *P. fluorescens* are specifically expressed by means of in vivo expression technology (IEVT) (Bloemberg and Lugtenberg 2001).

Microbes residing inside the plants go one step forward in their colonization ability compared to rhizospheric bacteria and almost all plants harbor endophytic bacteria (Singh and Singh 2013; Singh and Strong 2016; Singh and Gupta 2016; Singh et al. 2016a, b). Beneficial effects of *Pseudomonas* in combination with other endophytic bacterial genera have been reported in soybean (Kuklinsky-Sobral et al. 2004), rice (Adhikari et al. 2001), oilseed rape, tomato (Nejad and Johnson 2000), and hybrid spruce (Chanway et al. 2000).

## 2.3 Mechanisms of Plant Growth Promotion

PGPR enhance the plant growth and yield either directly or indirectly, without conferring pathogenicity (Hariprasad and Niranjana 2009). Indirect plant growth promotion includes the prevention of the deleterious effects of phytopathogenic organisms. This can be achieved by the production of siderophores, hydrogen cyanide (HCN), antibiotics, and fungal cell wall degrading enzymes, e.g., chitinase and ß-1, 3-glucanase. Direct plant growth promotion includes production of phytohormones and volatile compounds, nitrogen-fixation, and mineral nutrient solubilization that affect the plant signaling pathways. Whereas bacterial genera such as *Pseudomonas*, *Azospirillum*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Alcaligenes*, *Acinetobacter*, and *Flavobacterium* have been studied and used as PGPR inoculants, bacteria belonging to genera *Bacillus*, *Streptomyces*, *Pseudomonas*, *Burkholderia*, and *Agrobacterium* are, however, predominantly studied and increasingly marketed as biological control agents.

### *2.3.1 Phosphate Solubilization*

Phosphorus (P), the second most important plant growth limiting mineral nutrient next to nitrogen, is present in the form of insoluble phosphates which cannot be utilized by the plants (Pradhan and Sukla 2006). Plants absorb P in two soluble forms, the monobasic [phosphoric acid ($HPO_4^{2-}$)] and the dibasic [dihydrogen phosphate ($H_2PO_4^-$)] ions (Galleguillos et al. 2000). Indian soils are normally deficient in available phosphorus (Johri et al. 2003). Of the total P exists in a soluble form, only 0.1 % is available for plant uptake (Zhou et al. 2003) due to P fixation into an unavailable form. To overcome P deficiency in soils, available P level has to be maintained by adding chemical P fertilizers. Plants absorb only trace amounts of chemical P fertilizers whereas the rest is converted into insoluble complexes (Mckenzie and Roberts 1990). The regular application of phosphatic fertilizers poses adverse environmental impacts on soil health (Tilman et al. 2001), disturbing the microbial diversity. This has led to search for an ecologically safe and economically viable option for improving crop production in low P soils. Phosphate solubilizing microorganisms (PSMs) play an important role in supplying phosphate to plants through various mechanisms of solubilization and mineralization. Among the different organic acids, gluconic acid production seems to be the most common mechanism of phosphate solubilization used by *P. fluorescens* (Di Simine et al. 1998). A considerable population of PSMs is present in the rhizosphere and secretion of organic acids and phosphatases is commonly involved in facilitating the conversion of insoluble forms of P to plant available forms. Bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Aereobacter*, *Flavobacterium*, and *Erwinia* have the ability to solubilize insoluble form of P to a form available to plants (Rodriguez and Fraga 1999). Among PSB, fluorescent pseudomonads spp. such as *P. chlororaphis*, *P. putida*, *P. aeruginosa*, *P. monteilii*, *P. plecoglossicida*, *P. fluorescens*, *P. fulva*, and *P. mosselii* have been identified as the most potent phosphate solubilizers (Gaur 1990; Cattelan et al. 1999; Bano and Musarrat 2003; Sunish Kumar et al. 2005; Ravindra Naik et al. 2008; Jha et al. 2009). *P. fluorescens* solubilizes $ZnPO_4$ in the presence of glucose as the carbon source (Di Simine et al. 1998). Das et al. (2003) has reported that cold-tolerant mutants of *P. fluorescens* were more efficient solubilizers of tricalcium phosphate than their respective wild-type counterparts at low temperatures. *P. fluorescens* strain Psd isolated from the rhizosphere of *Vigna mungo* also has a significant phosphate solubilization ability in addition to IAA production.

### 2.3.2 Phytohormones

Phytohormones are compounds that are produced by plants, and are involved in the developmental activities of plant like cell division, tissue differentiation, cell elongation, nutrients movements, apical dominance, ripening, and abscission. In addition to plants, fluorescent pseudomonads also produce various phytohormones such as auxins, gibberellins, cytokinins, and abscisic acid (ABA). Among these, IAA is involved in growth and development throughout the plant cell cycle, root initiation, apical dominance flowering, fruit ripening, senescence, and stimulation of plant growth (Xie et al. 1996). It has been found that about 80 % of the PGPR are involved in IAA production (Khalid et al. 2004; Patten and Glick 2002). Cytokinins produced by fluorescent pseudomonads (Vessey 2003) are involved in promoting the cell division, root development, and root hair formation (Frankenberger and Arshad 1995). Cytokinins are also involved in inhibition of auxin-induced apical dominance, prevention of senescence of plant parts mainly in leaves, chloroplast differentiation, and stimulation of opening of stomata (Crozier et al. 2001). Gibberellins synthesized by fluorescence pseudomonads induce cell elongation within the subapical meristem resulting in stem elongation (Dobbelaere et al. 2003), affecting seed germination, pollen tube growth, and development of reproductive part of various plants (Crozier et al. 2001). No reports are available regarding the ABA production by fluorescent pseudomonads; however, *Azospirillum* sp. and *Rhizobium* sp. are reported to produce this phytohormone (Dobbelaere et al. 2003). Interestingly, almost all species of bacteria synthesize ethylene (Primrose 1979). The synthesis of

**Table 2.1** Hormones, siderophores, and enzymes produced by fluorescent pseudomonads

| Hormones | Fluorescent pseudomonads | References |
|---|---|---|
| Auxins | *P. putida* GR12-2 | Xie et al. (1996) |
| Cytokinins | *P. fluorescens* | Garcia de Salamone et al. (2001); Vessey (2003) |
| ACC deaminase | *P. fluorescens* | Wang et al. (2000) |
| Gibberellins | *Pseudomonas* spp. | Gutierrez-Manero et al. (2001) |
| *Siderophores* | | |
| Pyoverdins | *P. fluorescens* WCS374 | Mohammad et al. (2009) |
| Pyochelin | *P. aeruginosa* | Sun et al. (2006) |
| Pseudomonine | *P. fluorescens* WCS374 | Mohammad et al. (2009) |
| Yersiniabactin | *P. syringae* | Jones et al. (2007); Petermann et al. (2008) |
| Quinolobactin | *P. fluorescens* 1740 | Matthijs et al. (2007) |
| Achromobactin | *P. syringae* B728a | Berti and Thomas (2009) |
| Corrugatin | *P. fluorescens* | Matthijs et al. (2007) |
| Ornicorrugatin | *P. fluorescens* AF76 | Matthijs et al. (2008) |
| *Enzymes* | | |
| Chitinase | *P. stutzeri* YPL-1 | Lim et al. (1991); Ayyadurai et al. (2007) |
| | *P. aeruginosa* P10 | |
| β-1,3 glucanase | *P. cepacia* | Fridlender et al. (1993) |
| Laminarinase | *P. stutzeri* YPL-1 | Lim et al. (1991) |
| Phosphatase | *P. mosselii* FP13 | Jha et al. (2009) |
| Denitrifying enzymes | *P. aeruginosa* PUPa3 | Sunish Kumar et al. (2005) |
| | *P. aeruginosa* FP10 | Ayyadurai et al. (2006) |
| | *P.aeruginosa* FPB9, FPB15 | Ravindra Naik et al. (2008) |

ethylene is generally induced by wounding in plants and consequently it inhibits root growth development (Salisbury 1994). However, synthesis of ethylene induces ripening of fruits, senescence, development of adventitious root and root hair and breaks dormancy of seeds. Different strains of fluorescent *Pseudomonas* produce ACC deaminase, an enzyme that cleaves ACC, an immediate precursor of ethylene, resulting in the inhibition of ethylene production. The phytohormones produced by fluorescent pseudomonads are listed in Table 2.1.

### *2.3.3 Siderophores*

Siderophores are water soluble, low molecular weight, organic compounds synthesized by many microorganisms under iron-deficient condition. These molecules show high affinity with ferric irons ($Fe^{3+}$) and form a stable chelate for transport into the cell (Neilands 1981). $Fe^{3+}$ is the most abundant form of iron in soil and an essential nutrient for the development of plants (Salisbury and Ross 1992). $Fe^{3+}$ concentration along with ferric oxide hydrates is about $10^{-17}$ M in soil having neutral pH (Budzikiewicz 2010). However, rhizobacteria require iron concentrations higher than $10^{-6}$ M, and when its concentration declines below this level, they start producing siderophores (Miethke and Marahiel 2007). Various species of fluorescent pseudomonads produce fluorescent yellow siderophores such as pyoverdins (Budzikiewicz 1993, 1997), pseudomonine (Lewis et al. 2000; Mercado-Blanco et al. 2001), quinolobactin (Matthijs et al. 2007), pyochelin (Cox et al. 1981), and ornicorrugatin (Matthijs et al. 2008). These siderophores trap the limited iron in the rhizosphere and make it unavailable to deleterious fungi, resulting in the inhibition of fungal growth (Keel et al. 1992). Around 500 different siderophores with known structures have been reported (Boukhalfa and Crumbliss 2002) and many of them have been purified (Hider and Kong 2010). Siderophores produced by fluorescent pseudomonads are listed in Table 2.1.

### *2.3.4 Antibiotics*

Fluorescent pseudomonads play an active role in the suppression of pathogenic microorganisms by secreting antibiotics. These antibiotics are low molecular weight organic compounds and are deleterious to the growth and metabolism of pathogenic microorganisms, even at low concentrations. Production of antibiotics by fluorescent pseudomonads is an important factor in the disease-suppressing ability of this group of bacteria (Thomashow et al. 1990). Antibiotics namely phenazines (Thomashow et al. 1990), pyoluteorin (Howell and Stipanovic 1980), 2,4-diacetylphloroglucinol (DAPG) (Shanahan et al. 1992), and pyrrolnitrin (Hammer et al. 1997) are produced by fluorescent pseudomonads. Some of the antibiotics have broad-spectrum activity and inhibit the growth of different groups of macro- and microorganisms. For example, DAPG produced by the fluorescent pseudomonads exhibits antibacterial, antifungal, and antihelminthic activities (Thomashow and Weller 1996). These antibiotics are grouped into nonvolatile and volatile antibiotics. Volatile antibiotics are alcohols, aldehydes, HCN, sulfides, and ketones. Nonvolatile antibiotics are DAPG, mupirocin, pyocyanin, phenazine-1-carboxylic acid, hydroxy phenazines (de Souza and Raaijmakers 2003), and phenylpyrrole (pyrrolnitrin) (Ahmad et al. 2008). Soilborne plant diseases are also suppressed by the introduction of antagonistic fluorescent pseudomonads into the rhizosphere. The extracellular secretion of antibiotics by pseudomonads also triggers the induced systemic resistance (ISR) in plants leading to protection from pathogens. Some important antibiotics produced by fluorescent pseudomonads are listed in Table 2.2.

**Table 2.2** Some important antibiotics produced by fluorescent pseudomonads

| Fluorescent pseudomonads | Antibiotics | Target pathogens | References |
|---|---|---|---|
| *P. fluorescens* F113 | 2,4-diacetylphloroglucinol | *Pythium* sp. | Shanahan et al. (1992) |
| *P. fluorescens* 2-79 | Phenazines | *Gaeumannomyces graminis var. tritici* | Thomashow et al. (1990) |
| *P. fluorescens* | Pyoluteorin | *Py. ultimum* | Howell and Stipanovic (1980) |
| *P. aureofaciens* | Phenazine-1-caboxylate | *Sclerotinia homeocarpa* | Powell et al. (2000) |
| *P. chlororaphis* | Phenazine-1-carboxamide | *Fusarium oxysporum* f. sp. *radicis-lycopersici* | Chin-A-Woeng et al. (1998); Bolwerk et al. (2003) |
| *P. fluorescens* | Viscosinamide | *R. solani* | Nielsen et al. (2002) |
| *P. fluorescens* | Amphisin | *Py. ultimum* and *R. solani* | Andersen et al. (2003) |
| *P. fluorescens* | Aerugine | *Phytophthora, Colletotrichum orbiculare* | Lee et al. (2003) |
| *P. fluorescens, P. cepacia* | Pyrrolnitrin | *Rhizoctonia solani, F. sambucinum* | Hammer et al. (1997); Burkhead et al. (1994) |
| *P. agglomerans* EH318 | Pantocin A, B | *Erwinia herbicola* | Wright et al. (2001) |

## *2.3.5 Enzymes*

Fluorescent *Pseudomonas* secretes several enzymes such as chitinases, proteases, pectinases, cellulases, xylanase, β-1, 3-glucanases, and some others, which can inhibit the growth and activities of pathogens. *P. fluorescens* CHA0 produces extracellular proteases and acts as an important biocontrol agent against the root-knot nematode disease caused by *Meloidogyne incognita* (Siddiqui and Shaukat 2005). *P. fluorescens* Pf-5 produces extracellular hydrolases and provides benefits to plant nutrition (Paulsen et al. 2005). Fluorescence pseudomonads strain, *Pseudomonas* GRC 2, produces chitinases (Gupta et al. 2001). This enzyme along with other secondary metabolites causes destruction and production of deformities of hypha, mycelia, and sclerotia of *Macrophomina phaseolina* and *Sclerotinia sclerotiorum. P. cepacia* produces β-1,3 glucanase which inhibits the growth and pathogenicity of *S. rolfsii*, *P. ultimum*, and *R. solani* (Fridlender et al. 1993). Rhizospheric fluorescent pseudomonads also produce cell wall degrading enzyme endochitinase which inhibits the pathogenicity of *R. solani* in sugar beet (Nielsen et al. 1998). In addition to enzyme production, *P. fluorescens* also induces the activity of laccase which is involved in the pathogenicity of *R. solani* (Crowe and Olsson 2001). Enzymes produced by fluorescent pseudomonads are listed in Table 2.1. In addition to the above discussed enzymes, fluorescent pseudomonads also produce ACC deaminase, which helps in plant growth promotion by inhibiting the biosynthesis of ethylene in roots of plant, resulting in increase in the lengthening of root and root hairs. The production of ACC deaminase has also been reported from wild-type and genetically modified fluorescent pseudomonads (Ravindra Naik et al. 2008). ACC deaminase promotes the PGPR activity in *Arabidopsis thaliana* by reducing the ethylene concentration in root system (Desbrosses et al. 2009).

### *2.3.6 Hydrogen Cyanide*

Hydrogen cyanide (HCN), a volatile compound which acts as an important biocontrol agent against plant pathogens, is produced by fluorescent pseudomonads (Rodriguez and Fraga 1999; Siddiqui 2006). HCN inhibits the cytochrome oxidase and metalloenzymes (Voisard et al. 1989) of pathogenic organisms and is highly toxic to all aerobic microorganisms at very low concentration. This helps fluoroscent pseudomonads protect plants from soilborne diseases (Blumer and Haas 2000). *P. fluorescens* CHA0 produces HCN and suppresses the black root rot of tobacco caused by the fungus *Thielaviopsis basicola* and take-all disease of wheat caused by *G. graminis* var. *tritici* (Defago et al. 1990). HCN synthase is an important enzyme responsible for HCN production, and is encoded by three different genes *hcn* A, *hcn* B, and *hcn* C (Ramette et al. 2003). HCN causes death of the organisms by inhibiting electron transport resulting in loss of energy production inside the cell.

## 2.4 Induced Systemic Resistance

Development of a state of enhanced defensive capacity using external agents without modifying the genome of the plants is called induced systemic resistance (ISR) (Van Loon et al. 1998). These external agents may be a chemical or extracts of cells of living organisms or microorganisms (Romeiro 2000). The fluorescent pseudomonads and other PGPR have been reported to induce systemic resistance in the plants against bacterial, fungal, and viral diseases (Kloepper et al. 1996). ISR can be local or systemic and provides protection against a broad spectrum of phytopathogens (Jamsen 2000). Bacterial components such as LPS, flagella, siderophores, cyclic lipopeptides, 2, 4-diacetylphloroglucinol, homoserine lactones, and volatiles like acetoin and 2, 3-butanediol induce ISR in plants (Lugtenberg and Kamilova 2009).

The plant–microbe association involves molecular recognition between the two partners through a signaling network mediated by the plant hormones salicylic acid (SA), jasmonic acid (JA), and ethylene. JA and ethylene have been described as signal transduction molecules for ISR due to the effect of beneficial microbes, and the signal transduction pathway through SA accumulation is found in the systemic acquired resistance (SAR) induced by the attack of pathogens. The increased amount of SA, a putative resistance signal in leaves, is correlated with the root colonization of *P. fluorescens* CHA0 and its derivatives (Maurhofer et al. 1994). The application of PGPR results in several biochemical or physiological changes in plants. ISR-mediated enhanced resistance by PGPR is achieved by the accumulation of pathogenesis-related (PR) proteins and induction of defense compounds of the phenylpropanoid pathway. A correlation exists between the colonization of bean root by fluorescent bacteria and induction of PR proteins along with systemic resistance against *Botrytis cinerea* (Zdor and Anderson 1992). ISR triggered in some rhizobacterial strains depends on SA signaling in the plants. Induced resistance by *P. aeruginosa* 7NSK2 was found to be iron regulated and involved three siderophores, pyoverdin, pyochelin, and SA. SA is also a precursor in the production of SA-containing siderophores, such as pseudomonine in *P. fluorescens* WCS374 (Audenaert et al. 2002). *P. fluorescens* WCS417r-mediated ISR has been found effective against a wide range of pathogens, namely, *F. oxysporum* causing vascular wilts in *Arabidopsis* (Pieterse et al. 1996), *Alternaria brassicicola* and *Pseudomonas syringae* pv. tomato causing necrotic lesions in radish (Hoffland et al. 1996). *P. putida* 89 B–27 offered resistance against *Colletotrichum orbiculare* (Wei et al. 1991). Increased activity of penylalanine ammonia lyase (PAL) was observed in *P. fluorescens*-treated tomato and pepper plants in response to infection by *F. oxysporum* f. sp. *lycopersici* and *Colletotrichum capsici* (Ramamoorthy et al. 2001). PAL is the first enzyme involved in phenylpropanoid pathway and plays a key role in the biosynthesis of phenolics and phytoalexins.

## 2.5 Biological Control of Plant Pathogens

PGPR play a major role in the biocontrol of plant pathogens by suppressing a broad spectrum of bacterial, fungal, viral, and nematode diseases and also providing protection against viral diseases. Fluorescent pseudomonads are the most promising group of beneficial bacteria due to their multiple attributes for crop productivity and ability to suppress a wide variety of plant diseases. This specific group of bacteria could be used as prospective agents due to their ability to maintain soil health, promote plant growth, and suppress phytopathogens. Certain plant-associated fluorescent pseudomonads produced DAPG, a phenolic molecule that has antifungal, antibacterial, antihelminthic, and phytotoxic properties. *P. fluorescens* strain CHA0 suppressed black root rot of tobacco caused by *Thielaviopsis basicola* and take-all disease of wheat caused by *Gaeumannomyces graminis* var. *tritici* due to the production of DAPG (Keel et al. 1992). Several strains of fluorescent pseudomonads produce antifungal metabolites such as phenazines, a nitrogen-containing pigment having broad-spectrum antibiotic activity (Thomashow et al. 1997). Suppression of take-all disease of wheat by *P. fluorescens* strain 2-79 was mainly due to the production of antibiotic phenazine carboxylic acid (Thomashow et al. 1990).

Siderophores are low molecular weight molecules secreted by microorganisms with a high affinity for $Fe^{3+}$. Siderophores show antagonistic activity by sequestering iron from the environment and thereby limiting the iron availability for pathogens (Bakker et al. 1986; Loper and Buyer 1991). Lemanceau and Alabouvette (1992, 1993) have reported that the capacity to produce pseudobactin 358 by *P. putida* WCS358 is responsible for the suppression of *Fusarium* wilt of carnation. Apart from antibiotic production, fluorescent *Pseudomonas* produces several lytic enzymes that can hydrolyze a wide range of polymeric compounds and consequently suppress phytopathogenic fungi directly or indirectly (Martin and Loper 1999; Picard et al. 2000). Chitinase producing *Serratia plymuthica* C48 inhibited the spore germination and germ tube elongation in *B. cinerea* (Frankowski et al. 2001). HCN, a volatile compound produced by fluorescent pseudomonads, was found to have antagonistic activity against plant pathogen (Rodriguez and Fraga 1999; Siddiqui 2006). *P. fluorescens* CHA0 played an indispensable role in suppression of *Thielaviopsis basicola*, casual organism of black root rot of tobacco, mainly by producing HCN (Voisard et al. 1989). Fluorescent pseudomonads also produce an array of cyclic lipopeptides (CLPs) which are peptide antibiotics (Nielsen et al. 2002), which play a significant role in biocontrol. Tensin, a CLP, produced by *P. fluorescens*, exhibited potent antagonistic activity against *R. solani* infection in sugar beet (Nielsen et al. 2000). Fluorescent *Pseudomonas* also produce pyrrolnitrin and pyoluteorin of which pyoluteorin is a broad-spectrum antifungal metabolite inhibiting the growth of *Phytophthora capsici*, the pathogen on black pepper (Paul and Sarma 2006). Application of *P. fluorescens* 7-14 as a biocontrol agent controls the rice blast disease caused by *Magnaporthe grisea* (Gnanamanickam and Mew 1992; Chatterjee et al. 1996) (Table 2.3).

## 2.6 Fluorescent Pseudomonads in Agriculture and Plant Health

Pest and disease management is a vital part of sustainable agriculture and this includes the use of beneficial microorganisms for the effective and sustained production of agricultural and horticultural crops. PGPR, viz., *Pseudomonas*, *Bacillus*, and fungal antagonist *Trichoderma*, have been well exploited for the management of plant diseases. They may play a regulatory role in plant growth and development (Schippers et al. 1987; Fravel 2005). They also protect plant root surfaces from colonization of pathogenic microbes through direct competitive effects and production of antimicrobial agents. PGPR have been used as soil inoculants intended to improve the supply of various nutrients like phosphorus, nitrogen, and potassium to crop plants. PGPR can either increase plant health or protect them from diseases, and thus their commercial application depends on the type of PGPR. The extensive colonization and biocontrol ability of rhizospheric fluorescent pseudomonads have generated increased interest in their use as crop protectants (Schippers et al. 1987;

**Table 2.3** Fluorescent pseudomonads mediated induced systemic resistance and biocontrol activity against phytopathogens

| Fluorescent pseudomonads | Pathogens | Diseases | Plants | References |
|---|---|---|---|---|
| *P. fluorescens* S97 | *P. syringae* pv. *phaseolicola* | Halo blight | Bean | Alstrom (1991) |
| *P. aeruginosa* 7NSK2 | *Botrytis cinerea* | Grey mold | Bean | De Meyer and Hofte (1997) |
| *P. aureofaciens* 25-33 | *Colletotrichum orbiculare* | Anthracnose | Cucumber | Wei et al. (1991) |
| *P. corrugata* 13 | *Pythium aphanidermatum* | Crown rot | Cucumber | Chen et al. (2000) |
| *P. fluorescens* WCS374 | *F. oxysporum raphani* | Vascular wilt | Radish | Leeman et al. (1995) |
| *P. fluorescens* WCS417 | *Alternaria brassicicola* | Necrotic lesions | Radish | Ton et al. (2002) |
| *P. fluorescens* WCS417 | *F. oxysporum* f. sp. *lycopersici* | Vascular wilt | Tomato | Duijff et al. (1998) |
| *P. putida* | *F. oxysporum* | Fusarium wilt | Radish | Scher and Baker (1982) |
| *P. fluorescens* Q8r1-96 | *Gaeumannomyces gramini* var. *tritici* | Take-all | Wheat | Raaijmakers and Weller (1998) |
| *P. aeruginosa* | *Septoria tritici* | Foliar disease | Wheat | Baron et al. (1997); Flaishman et al. (1990) |
| *P. fluorescens* Pf-5 | *Pythium ultimum*, *R. solani* | Seedling diseases of cotton | Cotton | Howell and Stipanovic (1979, 1980) |
| *P. cepacia* 5.5B | *R. solani* | Damping-off | Cotton | Cartwright et al. (1995) |
| *P. fluorescens* CHA0 | *P. splendens* | Damping-off | Tomato | Buysens et al. (1994) |
| *P. putida* NIR | *P. ultimum* | Damping-off | Soybean | Paulitz (1991) |
| *P. fluorescens* Hv37a | *P. ultimum* | Damping-off | Barley | Gutterson et al. (1986) |
| *P. fluorescens* DR54 | *R. solani* | Damping-off | Sugar beet | Nielsen et al. (1999) |
| *P. fluorescens* PfMDU | *R. solani* | Sheath blight | Rice | Nagrajkumar et al. (2005) |
| *P. putida* KKM1 | *C. falcatum* | Red rot | Sugarcane | Malathi et al. (2002) |
| *P. fluorescens* PGS12 | *F. oxysporum* | Damping-off | Corn | Georgakopoulos et al. (1994) |
| *P. aeruginosa* PNA1 | *F. oxysporum* | Damping-off | Chickpea | Anjaiah et al. (1998, 2003) |

Weller 1988; Lam and Gaffney 1993; Fravel 2005). Rice plants treated with bioformulation containing *P. fluorescens* strains Pf1 and AH1 and *Beauveria bassiana* isolate B2 showed a greater accumulation of defense enzymes, lipoxygenase and chitinase against leaf folder (Karthiba et al. 2010). Siderophore-mediated competition for iron between the two biocontrol agents *P. putida* WCS358 and *P. fluorescens* WCS374 decreased the colonization of radish roots by *P. fluorescens* WCS374 (Raaijmakers et al. 1995a, b). Combination of chitinase-producing *Streptomyces* spp., *Bacillus cereus*, and antibiotic-producing *P. fluorescens* and *Burkholderia cepacia* had a synergistic effect on the suppression of rice sheath blight (Sung and Chung 1997). Treatments of seed, soil, or root by *P. fluorescence* could control the foliar diseases and could also protect the leaves of cucumber (Wei et al. 1991).

The combined use of PGPR and specific contaminant-degrading bacteria can successfully remove complex contaminants (Huang et al. 2005). ACC deaminase containing plant growth promoting fluorescent pseudomonads could suppress accelerated endogenous ethylene synthesis and thus may facilitate root elongation, nodulation and improve growth and yield of plant (Zafar-ul-Hye 2008). Co-inoculation studies with PGPR and rhizobia have shown increased plant nodulation and $N_2$ fixation in leguminous plants such as soybean, pea, peanut, and alfalfa (Vessey and Buss 2002; Figueiredo et al. 2007). Co-inoculation of *P. fluorescens* and *Azospirillum* also stimulated root growth in spring wheat (Combes-Meynet et al. 2011).

## 2.7 Conclusions

Increased concern about the cleaner environment and excessive and deliberate use of chemicals in modern agriculture has necessitated the search for eco-friendly alternatives. PGPB offer an attractive alternative for sustainable agriculture and are gaining worldwide importance and acceptance in agriculture. Rhizospheres inhabiting fluorescent pseudomonads are a metabolically and functionally diverse group of bacteria which exhibit multiple mechanisms that mediate their ability to both suppress phytopathogens and promote crop growth and yield. Fluorescent pseudomonads provide benefit to the plants by various mechanisms which include competitive root colonization, phosphate solubilization, iron sequestration, production of plant growth regulators, enhancing nutrient uptake via mineral solubilization and synthesis of lytic enzymes along with the induction of ISR against phytopathogens. A better understanding of different mechanisms involved in the plant–microbe interaction is a prerequisite and necessarily required to develop new strategies for improving crop yields. These microorganisms can be used as model systems for providing novel genetic constituents and bioactive chemicals and can be used as a potential tool for sustainable agriculture.

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