Chapter 4
Mechanisms of Fluorescent Pseudomonads That Mediate Biological Control of Phytopathogens and Plant Growth Promotion of Crop Plants

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4.1 Introduction

Fluorescent pseudomonads are nonenteric, Gram-negative, aerobic, straight, or slightly curved rods, which are nonfermenting and motile belonging to γ-proteobacteria (Galli et al. 1992). They are pervasive bacteria which are common inhabitants of soil, water, and phyllosphere but predominant in plant rhizosphere due to the exudation of organic acids, sugars, and amino acids (Lugtenberg and Dekkers 1999). Fluorescent pseudomonads are the most promising group of plant growth-promoting rhizobacteria (PGPR) involved in biocontrol of plant diseases. This group of bacteria also includes a few pathogens and biodegraders. Saprophytic fluorescent pseudomonads are typical inhabitants of agricultural field soils and plant rhizosphere and are involved in several interactions with plants (Schroth et al. 1992). They are capable of utilizing many plant exudates as nutrient (Lugtenberg et al. 1999) and are known to possess important traits in bacterial fitness such as the ability to adhere to soil particles and to the rhizoplane, motility, and prototrophy (de Weger et al. 1994). Members of the genus *Pseudomonas* have very simple nutritional requirements and grow well under normal conditions in mixed populations with other types of microorganisms (Foster 1988). They are metabolically and functionally diverse and promote plant growth directly by phosphorus solubilization, sequestration of iron for plants by siderophores, production of phytohormones (Salisbury 1994; Ayyadurai et al. 2006, 2007; Ravindra Naik and Sakthivel 2006; Ravindra Naik et al. 2008), and lowering of plant ethylene levels (Glick 1995; Glick et al. 1999), and indirectly by suppressing pathogenic microorganisms through antibiotic production (Thomashow et al. 1990; Ayyadurai et al. 2006, 2007; Ravindra Naik and Sakthivel 2006; Ravindra Naik et al. 2008;

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Jha et al. 2009), reduction of iron available to phytopathogens in the rhizosphere (Scher and Baker 1982), synthesis of fungal cell wall-degrading enzymes, and competition with detrimental microorganisms for sites on plant roots. Additionally, fluorescent pseudomonads are capable of inducing a systemic resistance in plants against various phytopathogens (Van Loon et al. 1998; Pieterse et al. 2001). All these traits make fluorescent pseudomonads suitable for application as biological control agents (Sands and Rovira 1971).

Fluorescent pseudomonads are the extensively studied group within the genus *Pseudomonas*. They comprise *P. aeruginosa*, the type species of the genus; *P. aureofaciens*, *P. chlororaphis*, *P. putida* (two biotypes), *P. fluorescens* (four biotypes), and the plant pathogenic species *P. cichorii* and *P. syringae* (Leisinger and Margraff 1979). *Pseudomonas* strains are characterized on the basis of their nutritional features as well as by other phenotypic traits into species and species groups (Stanier et al. 1966). Conclusions of this study were supported by numerical analysis (Sneath et al. 1981) and DNA–DNA hybridization (Palleroni and Doudoroff 1972). The rRNA–DNA hybridizations that revealed five rRNA homology clusters: rRNA groups and all fluorescent pseudomonads fall into one of the five rRNA group (Palleroni et al. 1973). The Guanine-plus-Cytosine (G + C) content of their DNA ranges from 58 to 68 mol% (Palleroni 1975). *P. fluorescens* biovar III has been reported as dominant group of bacteria among fluorescent pseudomonads associated with rhizosphere of rice, the most important food crop of the world (Sakthivel and Gnanamanickam 1989). *P. fluorescens* biovar V constituted more than 75% of fluorescent pseudomonads in at least some areas of the world (Barrett et al. 1986) and represented as the predominant group in Australian soils and wheat rhizosphere (Sands and Rovira 1971). Nearly 90% of fluorescent pseudomonads in Colombia was reported to be *P. putida* (Hernandez et al. 1986). Thus, vast microbial diversity occurs among fluorescent pseudomonads in different geographic origins and this group of bacteria exhibits an array of mechanisms that mediate biocontrol of pathogens and growth promotion of crops.

4.2 Biocontrol Mechanisms

Biocontrol mechanisms such as production of fungal cell wall-degrading enzymes (Lim et al. 1991; Nielsen et al. 1998; Nielsen and Sorensen 1999; Ellis et al. 2000), antimicrobial compounds (James and Gutterson 1986; Gutterson et al. 1988; Thomashow et al. 1990; Natsch et al. 1994), namely, phenazines (Gurusiddaiah et al. 1986; Pierson and Thomashow 1992; Sunish Kumar et al. 2005), phloroglucinols (Dwivedi and Johri 2003), pyrrols (Homma and Suzui 1989; Pfender et al. 1993), polyketides (Kraus and Loper 1995), and peptides (Nielsen et al. 1999, 2000; Sorensen et al. 2001), hydrogen cyanide (Castric 1981; Bagnasco et al. 1998; Rodriguez and Fraga 1999; Siddiqui 2006), siderophores (Hamdan et al. 1991; Meyer et al. 2002), cell wall components (Meziane et al. 2005; Van Loon 2008), competition (van Loon et al. 1998), and induced resistance (van Loon et al. 1998) also have been identified. Sigma factor genes, *rpoD* and *rpoS*, have been reported to control antibiotic production and enhance the antagonistic activities of fluorescent *Pseudomonas* (Fujita et al. 1994).

A large number of fluorescent pseudomonad species such as *P. putida* (de Freitas and Germida 1991), *P. fluorescens* (Sakthivel and Gnanamanickam 1987), *P. aeruginosa* (Anjaiah et al. 2003; Sunish Kumar et al. 2005), *P. aureofaciens* (now considered as *P. chlororaphis*) (Chin-A-Woeng et al. 1998), and *P. pyrrocinia* (de Weger et al. 1986) have been well documented for their antagonistic potential. Specific strains such as *P. fluorescens* 2-79, Pf-5, 96.578, DR 54, *P. aeruginosa* 7NSK2, PNA1, *P. aureofaciens* 30-84, and *P. chlororaphis* PCL1391 suppress disease severities caused by plant pathogens in cotton (Howell and Stipanovic 1980), rice (Mew and Rossales 1986; Sakthivel and Gnanamanickam 1987; Rosales et al. 1995), wheat (Weller and Cook 1983; Weller et al. 1985; Rovira and McDonald 1986), barley (Rovira and McDonald 1986; Iswandi et al. 1987), tomato (Buysens et al. 1996; Chin-A-Woeng et al. 1998), potato (Burr et al. 1978; Kloepper et al. 1980; Bakker and Schippers 1987), radish (Kloepper and Schroth 1978; Homma and Suzui 1989), sugar beet (Suslow and Schroth 1982; Nielsen et al. 2000; Thrane et al. 2000, 2001), cassava (Hernandez et al. 1986), chickpea (Anjaiah et al. 2003), soybean (Cattelan et al. 1999), tobacco (Keel et al. 1990), and apple and pears (Jamisiewicz et al. 1991). Antimicrobial metabolites and enzymes produced by fluorescent pseudomonads are listed in Table 4.1.

4.2.1 Fungal Cell Wall-Degrading Enzymes

Production of fungal cell wall-degrading enzymes by microorganisms is frequently involved in the attack of phytopathogenic fungi (Martin and Loper 1999; Nielsen and Sorensen 1999; Picard et al. 2000). Lysis by cell wall-degrading enzymes excreted by microorganisms is a well-known feature of mycoparasitism. Chitinase, β-1,3 glucanase, and cellulase are especially important fungus controlling enzymes due to their ability to degrade the fungal cell wall components such as chitin, β-1,3 glucan, and glucosidic bonds (Potgieter and Alexander 1966; Bartnicki-Garcia and Lippman 1973; Schroth and Hancock 1981; Chet 1987; Lorito et al. 1996). Chitinase excreting microorganisms have been reported as efficient biocontrol agents (Sneh 1981; Ordentlich et al. 1988; Inbar and Chet 1991). Role of chitinase in biological control as well as in plant defense mechanisms has been documented well (Shapira et al. 1989). Nielsen et al. (1998) reported that in the sugar beet rhizosphere fluorescent pseudomonads inhibit plant pathogenic fungi *Rhizoctonia solani* by production of cell wall-degrading endochitinase. Biological control of *Fusarium solani*, mainly via laminarinase and chitinase activities of *P. stutzeri* YPL-1, has been reported (Lim et al. 1991). Fridlender et al. (1993) reported that β-1,3 glucanase-producing *P. cepacia* decreased the incidence of diseases caused by *R. solani*, *S. rolfsii*, and *P. ultimum*.

Table 4.1 Antimicrobial metabolites and enzymes produced by fluorescent pseudomonads

Metabolite/enzymes	Producer strain	References
Fungal cell wall-degrading enzymes		
	P. stutzeri YPL-1	Lim et al. (1991)
Chitinase	*P. aeruginosa* P10	Ayyadurai et al. (2007)
β-1,3 Glucanase	*P. cepacia*	Fridlender et al. (1993)
Laminarinase	*P. stutzeri* YPL-1	Lim et al. (1991)
Phenazines		
	P. fluorescens 2-79	Thomashow and Weller (1988)
Phenazine-1-carboxylic acid	*P. aureofaciens* 30-84	Pierson and Thomashow (1992)
Phenazine-1-carboxamide	*P. aeruginosa* PUPa3	Sunish Kumar et al. (2005)
Dimer of phenazine-1-carboxylic acid	*P. fluorescens* Pf23	Sakthivel and Sunish Kumar (2008)
Pyocyanin	*P. aeruginosa* PAO1	Baron et al. (1997)
Phloroglucinols		
	P. fluorescens Pf-5	Howell and Stipanovic (1979)
	P. fluorescens Q2-87	Vincent et al. (1991)
	P. fluorescens CHAO	Keel et al. (1992)
	P. fluorescens PFM2	Levy et al. (1992)
	P. fluorescens Q8r1-96	Shanahan et al. (1992); Flaishman et al. (1990)
2,4-Diacetyl phloroglucinol	*P. fluorescens* F113	Raaijmakers and Weller (2001)
Pyrrols		
	P. fluorescens BL914	Kirner et al. (1998)
	P. aureofaciens A10338.7	Elander et al. (1968)
	P. cepacia 5.5B	Cartwright et al. (1995)
Pyrrolnitrin	*P. fluorescens* BL915	Ligon et al. (2000)
Polyketides		
	P. fluorescens Pf-5	Howell and Stipanovic (1979)
Pyoluteorin	*P. fluorescens* CHA0	Keel et al. (1992)
Mupirocin	*P. fluorescens* NCIMB10586	El-Sayed et al. (2003)
2,3-Deepoxy-2,3-didehydro rhizoxin	*P. borealis* MA342	Tombolini et al. (1999)
Rhizoxin analogues	*P. fluorescens* Pf-5	Loper et al. (2008)
Peptides		
Tensin	*P. fluorescens* 96.578	Nielsen et al. (2000)
Viscosinamide	*P. fluorescens* DR54	Nielsen et al. (1998)
Amphisin	*Pseudomonas* sp. DSS73	Sorensen et al. (2001)
Masstolides	*P. fluorescens* SS101	de Bruijn et al. (2008)
Volatiles		
	P. fluorescens Pf-5	Voisard et al. (1981)
	P. fluorescens P5, P7, P8, P21	Ayyadurai et al. (2007)
Hydrogen cyanide	*P. pseudoalcaligenes* P4	Ayyadurai et al. (2007)

4.2.2 Antifungal Metabolites

Production of an array of antifungal metabolites (James and Gutterson 1986; Gutterson et al. 1988; Thomashow et al. 1990) by fluorescent pseudomonads is considered one of the most important biocontrol traits. With the advent of recombinant DNA technologies, the importance of antibiotic production in biocontrol of fluorescent pseudomonads has been demonstrated using antibiotic-deficient mutants and concerted efforts have been made to study the antifungal metabolites such as phenazines (Gurusiddaiah et al. 1986; Thomashow and Weller 1988; Pierson and Thomashow 1992; Chin-A-Woeng et al. 1998), phenolics (Keel et al. 1990, 1992; Vincent et al. 1991), pyrrole-type compounds (Homma and Suzui 1989; Pfender et al. 1993), polyketides (Nowak-Thompson et al. 1994; Kraus and Loper 1995), and peptides (Nielsen et al. 1999, 2000; Sorensen et al. 2001). Antibiotic producing fluorescent pseudomonads, *P. fluorescens* 2-79, Pf-5, CHA0, 96.578, DR 54 (Thomashow et al. 1990; Keel et al. 1992; Nowak-Thompson et al. 1994; Nielsen et al. 1999, 2000), *P. aureofaciens* 30-84 (Pierson and Thomashow 1992), and *P. chlororaphis* PCL1391 (Chin-A-Woeng et al. 1998) with varying degree of biocontrol ability have been reported.

4.2.2.1 Phenazines

Phenazines are intensely colored N-containing heterocyclic pigments synthesized by different bacterial strains (Leisinger and Margraff 1979; Budzikiewicz 1993; Stevans et al. 1994). Phenazines exhibit broad-spectrum activity against bacteria and fungi (Sunish Kumar et al. 2005; Ayyadurai et al. 2006, 2007; Ravindra Naik and Sakthivel 2006; Ravindra Naik et al. 2008). Phenazines also play an important role of microbial competition in rhizosphere, including survival and competence (Mazzola et al. 1992). Phenazine-1-carboxylic acid (PCA) has been reported from fluorescent pseudomonads such as *P. fluorescens* (Gurusiddaiah et al. 1986), *P. chlororaphis* (Pierson and Thomashow 1992), and *P. aeruginosa* (Anjaiah et al. 1998). PCA was demonstrated to be effective against various fungal pathogens such as *Gaeumannomyces graminis* var. *tritici*, *Pythium* sp., *Polyporus* sp., and *R. solani* and bacterial pathogens such as *Actinomyces viscosus*, *Bacillus subtilis*, and *Erwinia amylovora* (Gurusiddaiah et al. 1986; Thomashow et al. 1990). Production of phenazine-1-carboxamide (PCN) had been reported in fluorescent pseudomonads such as *P. aeruginosa* and *P. chlororaphis* (Chin-A-Woeng et al. 1998; Mavrodi et al. 2001; Sunish Kumar et al. 2005). PCN differs from PCA with a carboxamide ($CONH_2$) group replacing the carboxyl (COOH) group at the first position of the phenazine core. PCN is more stable than PCA and exhibits antifungal activities even in alkaline pH (Chin-A-Woeng et al. 1998). Pyocyanin is bluish colored (1-hydroxy-5-methyl-phenazine) and predominantly produced by *P. aeruginosa* (Demange et al. 1987). The antibiotic cyanomycin, from *Streptomyces cyanoflavus* (Funaki et al. 1958), is also known as pyocyanin (Turner and Messenger

1986). Pyocyanin is toxic to a wide range of fungi including *Septoria tritici* and bacteria (Baron et al. 1989; Baron and Rowe 1981; Flaishman et al. 1990; Hassan and Fridovich 1980). Broad-spectrum antifungal activity of PCN has been shown toward the phytopathogens *Pythium*, *Fusarium oxysporum* f.sp. *radiciopersici*, *Sarocladium oryzae*, and *R. solani* (Chin-A-Woeng et al. 1998; Sunish Kumar et al. 2005).

4.2.2.2 Phloroglucinols

Phloroglucinols are broad-spectrum antibiotics produced by a variety of bacterial strains. Phloroglucinols are known to induce systemic resistance in plants, thus serving as a specific elicitor of phytoalexins and other similar molecules (Dwivedi and Johri 2003). Production of phenolic antibiotic, 2,4-diacetylphloroglucinol (DAPG), has been reported from *P. fluorescens* Pf-5, *P. fluorescens* CHA0, and *P. fluorescens* Q2-87 (Fenton et al. 1992; Rosales et al. 1995). The broad-spectrum antimicrobial activity of DAPG produced by fluorescent pseudomonads has drawn great attention in agriculture due to its ability to suppress plant pathogens and play a key role in the biological control (Keel et al. 1992; Thomashow and Weller 1988; Duffy and Defago 1997; Duffy et al. 2004). DAPG-producing strains such as *P. fluorescens* Pf5, CHA0, F113, Q2-87, and Q8r1-96 (Howell and Stipanovic 1980; Vincent et al. 1991; Harrison et al. 1993; Pierson and Weller 1994; Cronin et al. 1997; Raaijmakers and Weller 1998; Duffy and Defago 1999) have been used to suppress the black root rot of tobacco, root rot of tomato, *Pythium* damping-off of cucumber and sugar beet, cyst nematode and soft rot of potato, and take-all disease of wheat. The antagonistic fluorescent pseudomonads producing DAPG that inhabit in banana rhizosphere have been studied earlier (Banerjee and Langhe 1985; Sutra et al. 2000). DAPG is found to exhibit antifungal, antibacterial, and antihelminthic activities (Vincent et al. 1991; Keel et al. 1992; Levy et al. 1992; Harrison et al. 1993; Nowak-Thompson et al. 1994; Bangera and Thomashow 1996; Abbas et al. 2002) as well as phytotoxic properties (Reddi et al. 1969). The compound also exhibits herbicidal activity resembling 2,4-dichlorophenoxyacetic acid (2,4-D), a commonly used post-emergence herbicide for the control of many annual broad leaf weeds of cereals, sugarcane, and plantation crops.

4.2.2.3 Pyrrols

Pyrrolnitrin (PRN) (3-chloro-4-(2′-nitro-3′-chlorophenyl) pyrrole) is a broad-spectrum antifungal metabolite first described by Arima et al. (1964). PRN is a secondary metabolite derived from L-tryptophan. It is produced by fluorescent pseudomonads such as *P. fluorescens* (Kirner et al. 1998) and *P. aureofaciens* (Elander et al. 1968). Other variants of PRN such as isopyrrolnitrin, oxypyrrolnitrin, and monodechloropyrrolnitrin have lower antifungal activity. PRN is active against a wide range of deuteromycete, ascomycete, and basidiomycete fungi. PRN has found its applications in agricultural fungicide as a clinical compound. *P. fluorescens* BL915 has been reported as biocontrol agent in cotton for the suppression of *R. solani* (Ligon et al. 2000). *P. cepacia* 5.5B showed a broad-spectrum antifungal activity toward phytopathogenic fungi including *R. solani* (Cartwright et al. 1995). PRN was also reported as a topical antimycotic for human use and served as a lead molecule for pharmaceutical research.

4.2.2.4 Polyketides

Pyoluteorin (PLT) is the chlorinated antifungal metabolite of mixed polyketide/amino acid origin produced by certain strains of *Pseudomonas* spp. including soil bacterium, *P. fluorescens* Pf-5 (Maurhofer et al. 1992, 1994a; Kraus and Loper 1995; Nowak-Thompson et al. 1997). Strains producing PLT suppress several soil-borne plant diseases (Howell and Stipanovic 1980; Defago et al. 1990; Maurhofer et al. 1994b). PLT is found to be more effective against the damping-off disease causing oomycete, *P. ultimum* (Maurhofer et al. 1992). The mode of its antimicrobial activity is by the selective inhibition of bacterial isoleucyl-tRNA synthetase (Bennett et al. 1999). Mupirocin, the naturally occurring polyketide antibiotic of fluorescent pseudomonads, is also known as pseudomonic acid. Mupirocin produced by *P. fluorescens* NCIMB 10586 is highly active against *Staphylococcus aureus* and a variety of Gram-positive organisms (El-sayed et al. 2003). Mupirocin is also used as a tropical and intranasal antibiotic (Carcanague 1997). The metabolite 2,3-deepoxy-2,3-didehydrorhizoxin (DDR) produced by *P. chlororaphis* MA342 is effective against several phytopathogenic fungi, including net blotch of barley caused by the fungus *Drechslera teres* (Tombolini et al. 1999). Through the insertional mutagenesis and subsequent metabolite profiling in *P. fluorescens* Pf-5, five analogues of rhizoxin, a 16-member macrolides with antifungal, phytotoxic, and antitumor activities were identified as products synthesized from a hybrid polyketide synthase or nonribosomal peptide synthetase gene clusters. The five rhizoxin analogues were reported to show differential toxicity toward two agriculturally important plant pathogens: *Botrytis cinerea* and *Phytophthora ramorum*. The rhizoxin analogues were also reported to cause swelling of rice roots, a symptom characteristic of rhizoxin itself, but were less toxic to pea and cucumber roots. The predominant compound WF-1360 F rhizoxin analogue and the newly described compound 22*Z*-WF-1360 F were reported as most toxic against the two plant pathogens and three plant species. Upon further testing against a panel of human cancer lines, rhizoxin analogues reported to exhibit potent but nonselective cytotoxicity (Loper et al. 2008).

4.2.2.5 Peptide Antibiotics

Peptide antibiotics are predominately produced in both Gram-positive (Katz and Demain 1977) and Gram-negative bacteria (Dowling and O'Gara 1994) by a nonribosomal multienzymatic peptide synthesis (Kleinkauf and von Dohren 1990). Recently, it has been observed that fluorescent pseudomonads produce a number of different cyclic lipopeptides (CLPs), which are useful in biological control. It is also found that CLP production is a common trait among fluorescent pseudomonads isolated from sugar beet rhizosphere (Nielsen et al. 2002). Cyclic lipodecapeptide, tensin, is produced by *P. fluorescens* 96.578 (Nielsen et al. 2000). Tensin showed potent antagonistic activity against the basidiomycete fungus, *R. solani*. Significant reduction of *R. solani* infection was found in sugar beet seeds treated with tensin-producing strain *P. fluorescens* 96.578 (Nielsen et al. 2000). The mode of action of tensin on *R. solani* is still not clearly perceived. However, it is proposed that the activity might be in synergism with chitinolytic or cell wall-degrading enzymes produced by *P. fluorescens* 96.578 (Nielsen and Sorensen 1999; Nielsen et al. 2000). Viscosinamide is a cyclic lipopeptide produced by *P. fluorescens* DR54 (Nielsen et al. 1999). This compound shows prominent antifungal and biosurfactant properties (Nielsen et al. 2000, 2002; Thrane et al. 2000). It is highly effective against *R. solani*. When *R. solani* mycelium was challenged with purified viscosinamide under in vitro conditions, a number of growth modifications at hyphal tips such as increased branching, swelling, and septation leading to inhibition in radial growth were observed (Thrane et al. 2000). In soil conditions, viscosinamide-producing *P. fluorescens* DR54 is found to reduce the mycelial biomass and sclerotia formation by *R. solani* close to the seed or seedling root surfaces, thus making the fungal biomass inadequate for infection (Thrane et al. 2001). Amphisin is a lipoundecapeptide originating from the nonribosomal biosynthesis by *Pseudomonas* sp. DSS73 (Sorensen et al. 2001). The primary structure is β-hydroxydecanoyl-D-Leu-D-Asp-D-*allo*-Thr-D-Leu-D-Leu-D-Ser-L-Leu-D-Gln-L-Leu-L-Ile-L-Asp.The peptide is a lactone, linking Thr4 Oγ to the C-terminal. It is a close analogue of the cyclic lipopeptides tensin and polypeptin produced by *P. fluorescens* (Nielsen et al. 2000; Sorensen et al. 2001). The antifungal activity of amphisin is found to be more than that of other fluorescent pseudomonad peptide antibiotics such as tensin and viscosinamide (Nielsen et al. 2002). Massetolides are cyclic lipopeptide antibiotics produced by various *Pseudomonas* strains. Three genes were found to be involved in the massetolide A biosynthesis in *P. fluorescens* strain SS101. Massetolide A production is essential in swarming motility of *P. fluorescens* SS101 and plays an important role in biofilm formation (de Bruijn et al. 2008).

4.2.3 Hydrogen Cyanide

Certain strains such as pseudomonads produce hydrogen cyanide (HCN), a volatile antibiotic (Castric 1981), which helps in disease suppression (Bagnasco et al. 1998; Rodriguez and Fraga 1999; Siddiqui 2006; Voisard et al. 1981; Sacherer et al. 1994). HCN and CO_2 are formed from glycine and catalyzed by HCN synthase (Castric 1994). HCN was recognized as the biocontrol factor of *P. fluorescens*

CHA0 as it played an indispensible role in suppression of black root rot of tobacco caused by the fungus *Thielaviopsis basicola* (Voisard et al. 1981) and take-all disease of wheat caused by *G. graminis var. tritici*. However, few reports indicated that the HCN production was detrimental to growth of certain plants and it resulted in reduction of potato yields (Bakker and Schippers 1987). Few strains of fluorescent pseudomonads which failed to exhibit any antagonism in vitro toward *Pythium* and *Rhizoctonia* established successful biological control toward them in field (Kloepper et al. 1991; Lifshitz et al. 1987). Thus, disease suppression by HCN-producing fluorescent pseudomonads may be in part due to the induction of plant resistance (O'Sullivan and O'Gara 1992). Nearly a total of 800 plant species have been reported to liberate cyanide when wounded or attacked by a phytopathogen and thus suppress the cyanide-sensitive pathogens (Mansfield 1983). However, few fungal pathogens of cyanogenic plants are tolerant to cyanide because they can detoxify it by converting it to formamide (Van Etten and Kistler 1984).

4.2.4 Siderophores and Pathogen Suppression

Several species of fluorescent pseudomonads produce a range of iron complexing agents, the siderophores, under iron-limiting conditions, which have a very high affinity for ferric iron. Siderophores reported from pseudomonads so far include pyoverdines, pyochelin, quinolobactin, and ornicorrugatin. Several pyoverdines consisting of a shared dihydroxy-quinoline chromophore joined to an acyl (carboxylic acid or amide) group and a 6–12 amino acid type-specific peptide have been characterized (Budzikiewicz 1993; Meyer 2000; Lamont and Martin 2003). Pyoverdines and pseudobactins produced by a single strain have the same peptide but differ in the nature of acyl group. Fe^{3+} binding sites of pyoverdine are present in the quinoline chromophore and the peptide chain (Budzikiewicz 1993). Strains of pseudomonads utilize heterologous pyoverdines and pseudobactins for iron acquisition and the spectrum of ferrisiderophores used forms the basis of strain identification method termed siderotyping (Meyer et al. 2002; Lamont and Martin 2003). Pyoverdines can be identified by their UV Visible absorption spectrum. The Fe^{3+} complexes show absorption maximum at 400, 320, and 280 nm in correlation with the quinoline system (Poppe et al. 1987). Pyochelins frequently accompany pyoverdines and seem to be responsible for second iron transport system. Pyochelins are implicated to have similar antifungal activities to that of pyoverdines through minimizing availability of iron to other plant deleterious microorganisms. The abundant production of pyochelins was reported in *P. aeruginosa* (Cox et al. 1981). *P. fluorescens* ATCC 17400 has shown to produce quinolobactin siderophore in addition to pyoverdine, which itself results from the hydrolysis of the unstable molecule thioquinolobactin.

P. fluorescens ATCC 17400 was identified as antagonist against the oomycete, *Pythium* sp., which is repressed by iron, suggesting the involvement of siderophores

(Matthijs et al. 2007). A new class of lipopeptidic siderophore, ornicorrugatin, was known to be produced by a pyoverdine-negative mutant of *P. fluorescens* AF76. It is structurally related to the siderophore of *P. corrugata* differing in the replacement of one Dab unit by Orn (Matthijs et al. 2008). Siderophores are thought to sequester the limited iron supply available in the rhizosphere making it unavailable to harmful pathogenic fungi and thereby suppressing fungal growth (Keel et al. 1992). Siderophores such as pyoverdine and pyochelin have been documented well for suppression of *Pythium*-induced damping-off disease of tomato (Buysens et al. 1996). However, it is generally suggested that siderophores of fluorescent pseudomonads do not play a role in biocontrol in iron-rich soils (Campbell et al. 1986). The bacterial iron complexing agents, pyoverdine and salicylate may also act as elicitors for inducing systemic resistance against pathogens in tobacco (Maurhofer et al. 1998; van Loon et al. 1998).

4.2.5 Competition

Biocontrol competition refers to the ability of the beneficial organisms to compete with other harmful organisms and effectively scavenge and utilize the available nutrients and suitable niches, so that it constitutes a significant proportion of the rhizosphere–rhizoplane population (Hattori 1988). Competition for nutrients varies between different rhizospheres depending on the available sources of carbon, nitrogen, sulfur, phosphate, and micronutrients. Competitive exclusion of deleterious organisms in the plant rhizosphere by fluorescent pseudomonads is considered as a significant pathogen-suppressive biocontrol trait (O'Sullivan and O'Gara 1992). Biocontrol of *Fusarium* (Elad and Baker 1985) and *Pythium* (Elad and Chet 1987) species by fluorescent *Pseudomonas* spp. involves competition. Variations occur in the ability of different fluorescent pseudomonads to colonize a particular root niche (de Weger et al. 1987; Kloepper et al. 1980; Loper et al. 1985; Stephens et al. 1987; van Peer and Schippers 1988). Better root-colonizing ability of the strain is an integration of various factors (de Weger and Lugtenberg 1990; Lam 1990; Weller 1988). Also, various environmental factors such as water content, temperature, pH, soil types, composition of root exudates, mineral content, and other microorganisms confront an organism when it colonizes the root. Fluorescent pseudomonad strain in potato rhizosphere was greater by tenfold in a sandy loam soil than in a clay loam soil (Bahme and Schroth 1987). Variations in colonization potential of different strains of fluorescent pseudomonads can be due in part to specific cell killing by other biological entities such as predaceous protozoans (Acea and Alexander 1988), bacteriophages (Stephens et al. 1987), and *Bdellovibrio* sp., an obligate parasite of some soil Gram-negative bacteria (Scherff 1973). Flagellation is another important requirement for good colonization under certain circumstances (O'Sullivan and O'Gara 1992).

4.2.6 Cell Wall Components

Cell surface components, namely, lipopolysaccharides (LPS) and flagellins have been reported as potent determinants of ISR in plants (Meziane et al. 2005; Van Loon 2008). LPS are indispensable cell wall components of Gram-negative bacteria and have been implicated in the induction of systemic resistance (Dow et al. 2000; Leeman et al. 1995b; Van Loon et al. 1998). Flagellins, the main components of bacterial flagella, are reported to elicit defense responses in plants (Gomez-Gomez and Boller 2000; Zipfel et al. 2004). The outer membrane LPS of biocontrol strains *P. putida* WCS358 (Bakker et al. 2003; Meziane et al. 2005), *P. fluorescens* WCS374 (Leeman et al. 1995b, 1996), and *P. fluorescens* WCS417 (van Peer and Schippers 1992; Leeman et al. 1995a, 1996) and the flagella of *P. putida* WCS358 (Bakker et al. 2003; Meziane et al. 2005) are reported as important components involved in elicitation of ISR. *P. putida* WCS358 and *P. fluorescens* WCS417 and WCS374 were reported to show differential resistance-inducing activities on arabidopsis, tomato, and bean (Bakker et al. 2007). LPS of *P. fluorescens* WCS374 apart from inducing systemic resistance against *Fusarium* wilt diseases of radish (Leeman et al. 1995b) also enhanced its colonization in tomato (Dekkers et al. 1998). The O-antigen of LPS has been shown to be involved in induced systemic resistance of plants, thereby enhancing defense activities against pathogen attack (Van Peer and Schippers 1992). Also, LPS and flagellin are stronger inducers of the oxidative burst, which in turn elicits plants defense mechanisms (Van Loon 2008).

4.2.7 Induced Systemic Resistance

Colonization of the rhizosphere by certain bacteria such as nonpathogenic *Pseudomonas* can trigger a systemic resistance in plants by activating the plants' defense mechanisms phenotypically similar to pathogen-induced systemic acquired resistance (SAR) and this form of induced resistance is referred as rhizobacteria-mediated induced systemic resistance (ISR). Bacterial LPS, siderophores, and salicylic acid (SA) are found to be determinants of ISR. Similar to SAR, ISR is effective against different types of pathogens but differs from SAR in that the inducing PGPRs do not cause visible symptoms on the host plant (van Loon et al. 1998). Scientific studies shows that when PGPRs are applied to seeds or roots, their defense mechanisms are activated (Van Peer et al. 1991). Fluorescent pseudomonads are also involved in the induction of plant resistance against insects and nematodes (Renwick et al. 1991; Zahnder et al. 2001) and specific metabolites produced by these bacteria have been involved in elicitation of defense reactions of the host plants (Van Loon et al. 1998). Similar to classical induced resistance, PGPR-induced resistance is known to produce broad-spectrum resistance, which is correlated with increased amounts of pathogenesis-related (PR) proteins, peroxidases, chitinases, and β-1,3-glucanase in plant tissue. Root colonization by

P. fluorescens CHAO and its derivatives correlates with increased amounts of salicylic acid, a putative resistance signal in leaves (Maurhofer et al. 1994a). ISR is effective under field conditions and offers a natural mechanism for biological control of plant disease.

Research findings revealed that *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), carnation (Van Peer et al. 1991), and radish (Leeman et al. 1996), *Alternaria brassicicola* and *Pseudomonas syringae pv. tomato* causing necrotic lesions in radish (Hoffland et al. 1996), and *P. syringae pv. tomato* causing bacterial speck in *Arabidopsis* (Pieterse et al. 1996). *P. putida* 89B–27 offered resistance against *Colletotrichum orbiculare* (Wei et al. 1991), Cucumber mosaic virus (Raupach et al. 1996), *Erwinia tracheiphila* (Kloepper et al. 1993), *F. oxysporum* f.sp. *cucumerinum* (Liu et al. 1995a), and *F. oxysporum* f.sp. *lachrymans* (Liu et al. 1995b) in cucumber. *P. fluorescens* CHAO induced systemic resistance against disease caused by *Thielaviopsis basicola* (Troxler et al. 1997) and Tobacco necrosis virus (Maurhofer et al. 1994a) in tobacco. *P. aeruginosa* 7NSK2 provided resistance against Tobacco mosaic virus (De Meyer and Hofte 1997), while *P. corrugata* 13 and *P. fluorescens* C15 induced resistance in cucumber to crown rot caused by *Pythium aphanidermatum* (Zhou and Paulitz 1994).

4.3 Plant Growth Promotion Mechanisms

Plant growth-promoting ability of these bacteria is due to the production of siderophore (Neilands and Leong 1986; Becker and Cook 1988; Loper 1988), phosphatase (Katznelson and Bose 1959), phytohormones (Keel et al. 1992; O'Sullivan and O'Gara 1992; Salisbury 1994; Patten and Glick 2002), 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Preisfeld et al. 2001; Penrose and Glick 2003), and cytokinins (Garcia de Salamone et al. 2001). A number of different fluorescent pseudomonad species such as *P. putida* (Scher and Baker 1982), *P. aeruginosa* (Bano and Musarrat 2003; Sunish Kumar et al. 2005), *P. chlororaphis* (Chin-A-Woeng et al. 1998), and *P. cepacia* (Cattelan et al. 1999) have been reported as PGPR as well as biocontrol strains against phytopathogenic fungi (Garcia de Salamone et al. 2001). Pigments, enzymes, and hormones produced by fluorescent pseudomonads that promote plant growth are listed in Table 4.2.

4.3.1 Phosphate Solubilization

Phosphate solubilizing bacteria are common in the rhizosphere. Secretion of organic acids and phosphatase are common methods of facilitating the conversion of insoluble forms of phosphorus to plant-available forms (Kim et al. 1998; Richardson et al. 2001). Fluorescent pseudomonad species such as *P. chlororaphis*,

Table 4.2 Pigments, enzymes and hormones by fluorescent pseudomonads

Pigments/enzymes/hormones	Producer strain	References
Siderophores		
	P. fluorescens 3551	Loper (1988)
	P. fluorescens CHAO	Maurhofer et al. (1994b)
Pyoverdine	*P. putida* WCS358	Van Wees et al. (1997)
	P. aeruginosa PAO-1	Cox et al. (1981)
	P. fluorescens CHAO	Buysens et al. (1996)
Pyochelin	*P. aeruginosa* 7NSK2	Buysens et al. (1996)
	P. stutzeri KC	Lewis et al. (2000)
	P. fluorescens ATCC 17400	Mossialos et al. (2000)
Pseudomonine	*P. fluorescens* WCS374	Mercado-Blanco et al. (2001)
	P. chlororaphis GN212	Cattelan et al. (1999)
	P. aeruginosa NJ-15	Bano and Musarrat (2003)
	P. aeruginosa PUPa3	Sunish Kumar et al. (2005)
	P. aeruginosa FP10	Ayyadurai et al. (2006)
	P. monteilii FPB59, FPB63	Ravindra Naik et al. (2008)
	P. plecoglossicida FPB31	Ravindra Naik et al. (2008)
	P. fluoresens FP7, FP14	Ravindra Naik et al. (2008)
	P. fulva FP23	Ravindra Naik et al. (2008)
	P. putida FP2, FP3	Ravindra Naik et al. (2008)
Phosphatase	*P. mosselii* FP13	Jha et al. (2009)
	P. stutzeri	Gamble et al. (1977)
Denitrifying enzymes	*P. fluorescens* YT101, RTC01	Philippot et al. (1995)
	P. putida GR12-2	Patten and Glick (2002)
	P. aeruginosa PUPa3	Sunish Kumar et al. (2005)
	P. aeruginosa FP10	Ayyadurai et al. (2006)
	P. aeruginosa FPB9, FPB15	Ravindra Naik et al. (2008)
	P. mosselli FP13	Ravindra Naik et al. (2008)
Indole-3-acetic acid	*P. monteilii* FPB21	Ravindra Naik et al. (2008)
Cytokinins	*P. fluorescens* G20-18	Garcia de Salamone et al. (2001)
1-Aminocyclopropane-1-carboxylate deaminase	*P. putida* GR12-2	Glick et al. (1994)
	P. aeruginosa Pw60, Pw61	Ravindra Naik et al. (2008)

P. putida, *P. aeruginosa*, *P. monteilii*, *P. plecoglossicida*, *P. fluorescens*, *P. fulva*, and *P. mosselii* have been identified as phosphate solubilizing rhizobacteria (Gaur 1990; Cattelan et al. 1999; Bano and Musarrat 2003; Sunish Kumar et al. 2005; Ravindra Naik et al. 2008; Jha et al. 2009).

4.3.2 Denitrification

Denitrification is an important microbial process in which oxidized nitrogen compounds are used as alternative electron acceptors for energy production when oxygen is limited. Denitrification consists of four reactions by which nitrates are reduced to dinitrogen by the metalloenzymes such as nitrate reductase, nitrite reductase, nitric oxide reductase, and nitrous oxide reductase. Fluorescent pseudomonads are the most common denitrifiers isolated from temperate soils (Gamble et al. 1977). Fluorescent pseudomonads are able to adapt to limited oxygen conditions by using nitrogen oxides as alternative electron acceptors (Stewart 1988). Respiratory nitrate and nitrite reductase have been described to implicate in the competitiveness of model strains of fluorescent pseudomonad in soil (Philippot et al. 1995; Ghiglione et al. 2000).

4.3.3 Siderophores and Growth Promotion

As described in the earlier section, siderophores are low-molecular-weight ferric-specific chelation agent synthesized and secreted to solubilize iron (Neilands 1981; Abd-Alla 1998). These microbial siderophores stimulate plant growth directly by increasing the iron availability in rhizosphere soil and indirectly by competitive inhibition of growth of phytopathogen with less efficient iron uptake system (Marek-Kozaczuk et al. 1996). Microbial siderophores play an important role in Fe nutrition of plants in neutral and basic soils (Shenker et al. 1992, 1995). Several species of fluorescent pseudomonads produce siderophores and there is evidence that a number of plant species can absorb these bacterial Fe^{3+} siderophore complexes (Becker and Cook 1988; Loper 1988; Bitter et al. 1991). Fluorescent yellow green siderophores have been named as pyoverdines (PVDs) or pseudobactins (Budzikiewicz 1993, 1997). Besides PVD, *P. aeruginosa* produces another siderophore called pyochelin with a lower affinity for iron (III) (Cox et al. 1981). Fluorescent pseudomonad species such as *P. fluorescens*, *P. stutzeri*, and *P. putida* produce pseudomonine (isoxazolidone) (Lewis et al. 2000; Mossialos et al. 2000; Mercado-Blanco et al. 2001).

4.3.4 Phytohormones and Enzymes

Direct promotion of plant growth entails either providing the plant with a compound that is synthesized by the bacterium or facilitating the uptake of certain nutrients from the environment. Fluorescent pseudomonads also produce phytohormone, indole-3-acetic acid (IAA) cytokinins, and vitamins (Salisbury 1994; Streit et al. 1996; Patten and Glick 2002). Fluorescent pseudomonad bacteria also produce ACC deaminase that sequesters the ethylene precursor ACC (Belimov et al. 2001; Penrose and Glick 2003). Due to their potential to enhance plant growth, and participate in carbon, nitrogen, and phosphorous cycling in nature (O’Sullivan and O’Gara 1992), the role of fluorescent pseudomonads in agriculture and environment has been a matter of interest.

4.3.4.1 Indole-3-Acetic Acid

The phytohormone, IAA, is known to be involved in root initiation, cell division, and cell enlargement (Salisbury 1994). This hormone is commonly produced by specific strains of PGPR type of fluorescent pseudomonads (Barazani and Friedman 1999; Sunish Kumar et al. 2005; Ravindra Naik et al. 2008). IAA-producing rhizobacteria have been known to increase root growth and root length, resulting in greater root surface area, which enables the plant to access more nutrients from soil. Patten and Glick (2002) reported the role of IAA-producing *P. putida* in development of the host plant root system.

4.3.4.2 Cytokinins

Cytokinins are a class of phytohormones, which are known to promote cell divisions, cell enlargement, and tissue expansion (Salisbury 1994). Cytokinins are believed to be the signals involved in mediating environmental stress from roots to shoots (Jackson 1993). Production of cytokinins and enhancement of plant growth by strains *P. fluorescens* have been reported (Garcia de Salamone et al. 2001).

4.3.4.3 1-Aminocyclopropane-1-Carboxylate Deaminase

Ethylene is the only gaseous phytohormone. It is also known as the “wounding hormone” because its production in the plant can be induced by physical or chemical perturbation of plant tissues (Salisbury 1994). Among its myriad of effects on plant growth and development, ethylene production can cause an inhibition of root growth. Glick et al. (1998) put forward the theory that the mode of action of some PGPR was the production of ACC deaminase, an enzyme that could cleave ACC, the immediate precursor to ethylene in the biosynthetic pathway for ethylene in plants. ACC deaminase activity would decrease ethylene production in the roots of host plants and result in root lengthening. Wild-type and genetically modified fluorescent pseudomonads were reported as ACC deaminase producers (Glick et al. 1994; Ravindra Naik et al. 2008). Transforming *Pseudomonas* spp. strains with a cloned ACC deaminase gene enabled the bacteria to grow on ACC as a sole source of nitrogen and to promote the elongation of seedling roots (Shah et al. 1998). The growth promotion effects also expressed in stressful situations such as flooded (Grichko and Glick 2001) or heavy metal-contaminated soils (Burd et al. 1998; Belimov et al. 2001).

4.3.5 Vitamins

Vitamins are organic nutritional factors that influence the growth of living organisms. Plants synthesize vitamins (Arrigoni et al. 1992; De Gara et al. 1993) and their root exudates contain B-group vitamins that enhance the growth of rhizosphere bacteria (Rovira and Harris 1961; Mozafar and Oertli 1993; Azaizeh et al. 1996; Streit et al. 1996). In addition, most soil bacteria and fungi also produce the B-group vitamins (Dahm et al. 1993; Deryło and Skorupska 1993; Rodelas et al. 1993; Sierra et al. 1999; Strzelczyk and Leniarska 1985) that are beneficial for plant growth (Azaizeh et al. 1996; Mozafar and Oertli 1993; Rovira and Harris 1961). These water-soluble vitamins are known to act synergistically with other biologically active substances stimulating growth of plants and microbes (Oertli 1987). Bacterial vitamin production might be one of the several factors affecting microbial competition for root colonization (Streit et al. 1996), bacterial growth stimulation (Marek-Kozaczuk and Skorupska 2001), and symbiotic nitrogen fixation (Deryło and Skorupska 1993). *P. fluorescens* 267 was reported to produce several B-group vitamins, i.e., biotin, thiamine, cobalamine, pantothenic acid, and niacin, which influenced its colonization on clover roots (Marek-Kozaczuk and Skorupska 2001). Several reports demonstrating the beneficial effect of rhizosphere pseudomonad strains on leguminous plants are available (De Freitas et al. 1993; Deryło and Skorupska 1993; Grimes and Mount 1987; Polonenko et al. 1987). Coinoculation of legumes with plant growth-promoting rhizobacteria increased the green and dry matter per plant, the number and weight of nodules, and symbiotic N fixation (Deryło and Skorupska 1993). Under controlled conditions, coinoculation of clover with biotin auxotroph *Rhizobium leguminosarum* bv. *trifolii* and vitamin-producing *P. fluorescens* strain 267 stimulated the growth and symbiotic N fixation of clover (Deryło and Skorupska 1993; Marek-Kozaczuk et al. 1996).

4.4 Concluding Remarks

Flourescent pseudomonads are the predominant group of rhizobacteria. This group of bacteria is metabolically and functionally diverse and exhibits multiple mechanisms that mediate their ability to suppress phytopathogens and to promote crop growth and yield. Specific strains of fluorescent pseudomonads could be used as biocontrol agents and biofertilizers in sustainable agriculture. Beneficial effects of fluorescent pseudomonads on plant growth and yield result from competition, root-colonizing potential, phosphate solubilization, sequestration of iron, production of plant growth regulators, vitamins, enhancement of plant nutrient uptake, production of antibiotics, synthesis of fungal cell wall-degrading enzymes, suppression of pathogenic or deleterious microorganisms, and induction of systemic resistance against phytopathogens. Strains that exhibit biocontrol mechanisms and plant growth promotion traits could be used to achieve biological control of phytopathogens. Knowledge of different mechanisms involved in plant growth promotion and disease suppression is essential for the selection and utilization of appropriate biocontrol strains for sustainable agriculture.

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