Chapter 4
Biological Control of Pathogens and Plant Growth Promotion Potential of Fluorescent Pseudomonads

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4.1 Introduction

Modern agricultural practises have augmented the use of chemicals to enhance crop productivity. However, indiscriminate use of hazardous chemicals has resulted in soil pollution. Incorporation of harmful pesticides and insecticides as residues in our agricultural products has reached an alarming limit. Consequently, there has been a profound upward trend in the incidence of diseases associated with exposure to such toxic chemicals. Hence, recently the focus has shifted towards environment-friendly strategies to control devastating pathogens using inexpensive biocontrol microbes. These natural practises can preserve environment quality and conserve natural resources (Rigby and Caceres 2001; Lee and Song 2007). Fluorescent pseudomonads are promising microbial agents that offer dual benefits of enhancing the crop growth and productivity while suppressing plant pathogens. Among the diverse range of fluorescent pseudomonad bacteria, specific strains that belong to *Pseudomonas fluorescens*, *P. putida*, *P. aeruginosa* and *P. chlororapis* have the immense potential to be exploited for biological control because of their inherent capacity for the production of an array of metabolites (Thomashow et al. 1990; Sunish Kumar et al. 2005; Pathma et al. 2011) and enzymes (Salisbury 1994; Ayyadurai et al. 2006, 2007; Ravindra Naik et al. 2008) which mediate both plant growth-promotion (Sakthivel and Gnanamanickam 1987) and biological control of pathogens (Raaijmakers and Weller 1998; Rosales et al. 1995) in a wide variety of economically important agricultural crops.

Fluorescent pseudomonads possess many traits that make them well suited as biological control and growth-promoting agents. The beneficial attributes of fluorescent pseudomonads include (1) the ability to grow rapidly *in vitro* and *in vivo*,

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(2) the ability to utilise seed and root exudates, (3) the potential to colonise and multiply in the rhizosphere, (4) the capability to produce a wide spectrum of bioactive metabolites, (5) the competence with other microorganisms for rhizosphere niche and availability of nutrients and (6) the adaptability efficiently to environmental stresses. This article reviews the biological control and growth-promoting potential of specific beneficial group of fluorescent pseudomonad bacteria for the enhancement of crop production.

4.2 Biological Diversity of Pseudomonads

Pseudomonas is an enormously diverse genus of γ-*Proteobacteria* (Galli et al. 1992). This genus consists of ubiquitous saprophytic members of plant, animal and human pathogens. They are typically Gram-negative, chemoheterotrophic motile rods with polar flagella. 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). Den Dooren deJong (1926) first characterised *Pseudomonas* strains phenotypically on the basis of their nutritional features. The fundamental study on *Pseudomonas* resulted into an extensive phenotypic characterisation in which the genus was subdivided into species and species groups (Stanier et al. 1966). These characterisation studies were supported by numerical analysis (Sneath et al. 1981) and DNA–DNA hybridisation (Palleroni and Doudoroff 1972) and rRNA–DNA hybridisations (Palleroni et al. 1973) and pseudomonad bacteria were grouped into five groups based on the relatedness of their rRNA genes.

4.2.1 rRNA Groups of Pseudomonads

4.2.1.1 rRNA Group I

The largest rRNA group consists mostly of saprophytic bacteria (*P. fluorescens*, *P. putida*, *P. chlororaphis*) or pathogenic bacteria for humans (*P. aeruginosa*), plants (*P. cichorii*, *P. marginalis*, *P. syringae*, *P. savastanoi*) and mushrooms (*P. agarici*, *P. tolaasii*) and *P. stutzeri*, *P. mendocina*, *P. alcaligenes* and *P. pseudoalcaligenes*. Taxonomically the fluorescent pseudomonad bacteria such as *P. aeruginosa* and *P. fluorescens* are remarkably heterogeneous species (Doudoroff and Palleroni 1974; Palleroni 1992).

4.2.1.2 rRNA Group II

The second RNA group is called the *Pseudomallei-cepacia* group. It contains a group of pathogenic species, with an exception of *P. pichettii* (Ralston et al. 1973). The most remarkable species is *P. cepacia*, which is a plant pathogen and also a

significant human opportunistic pathogen (Ederer and Matsen 1972). This group also contains *P. marginata* (*P. glaioli*), *P. caryophylli*, *P. pseudomallei*, *P. mallei* and *P. solanacearum*.

4.2.1.3 rRNA Group III

The third rRNA group is represented by five species. Two of the species *P. acidovorans* (*Comamonas acidovorans*) and *P. testosteroni* (*Comamonas testosteroni*) have been shown to be so distantly related to other *Pseudomonas* sp. that a new genus, *Comamonas*, has been proposed (De Vos et al. 1985). The other three phytopathogenic species are *P. avenae*, *P. rubrilineans* and *P. konjaci*. These groups are phenotypically different from one another.

4.2.1.4 rRNA Group IV

Group IV comprises *P. diminuta* and *P. vesicularis*. These two strains stand as an out group and do not show affinity with any other *Pseudomonas* (Ballard et al. 1968).

4.2.1.5 rRNA Group V

The fifth rRNA homology group constitutes *P. maltophilia* (now S*tenotrophomonas maltophilia*) (Palleroni and Bradbury 1993) together with X*anthomonas* species. *P. maltophilia*, the saprophytic bacterium, can be found in many natural habitats and it is also frequently present in clinical specimens (Palleroni et al. 1973). A number of *Pseudomonas* species have not yet been assigned to RNA homology groups. The marine species, facultative autotrophs, the poly-β-hydroxyl butyrate utilising pseudomonads are among them.

In common with the other species of the genus *Pseudomonas*, the fluorescent pseudomonad bacteria are Gram-negative, strictly aerobic, polar flagellated rods. All fluorescent pseudomonad bacteria fall into one of the five rRNA groups (Palleroni et al. 1973) and the Guanine-plus-Cytosine (G + C) content of their DNA ranges from 58 to 68 mol% (Palleroni 1975).

4.3 Plant Growth-Promoting and Disease Management Mechanisms of Fluorescent Pseudomonads

There are various direct and indirect ways of plant growth-promotion and disease management by fluorescent Pseudomonads.

4.3.1 Phosphate Solubilisation

Phosphorus is an important macronutrient essential for plant growth and development. Soil contains a wide range of organic phosphorus substrates, but to make this form available for plant nutrition, it must be hydrolysed to inorganic phosphorus (Glass 1989). Also a large portion of soluble inorganic phosphate applied to soil as chemical fertiliser is rapidly immobilised soon after application and becomes unavailable to plants (Dey 1998). The principal mechanism for the mineralization of organic phosphorus is the production of organic acids and acid phosphatases. Most of the strains belonging to fluorescent pseudomonad species such as *P. chlororaphis*, *P. putida*, *P. aeruginosa P. monteilli*, *P. plecoglossicida*, *P. fluorescens P. fulva*, and *P. moselli* are among the most powerful phosphate solubilisers (Cattelan et al. 1999; Bano and Musarrat 2003; Sunish Kumar et al. 2005; Ravindra Naik et al. 2008; Jha et al. 2009). It has been reported that 41 % of fluorescent pseudomonad bacteria isolated from banana rhizosphere were found to be phosphate solubilising bacteria (Ravindra Naik et al. 2008).

4.3.2 Phytohormones

Phytohormones are involved in several stages of plant development like cell division, cell elongation, tissue differentiation and apical dominance. Fluorescent pseudomonads produce various phytohormones such as auxins, gibberellins, cytokinins and abscisic acid (Streit et al. 1996; Patten and Glick 2002). Auxin, indole-3-acetic acid (IAA), is an important phytohormone. Fluorescent pseudomonads are found to produce significant amount of IAA (Salisbury 1994; Sunish kumar et al. 2005) which stimulates the density and length of root hairs which improve plant uptake potential for water and other nutrients, thereby stimulating plant growth. In addition to IAA, several pseudomonad species also produce gibberellins and cytokinins. Cytokinins are believed to be the signals involved in mediating environmental stress from roots to shoots (Jackson 1993). Ethylene is a gaseous phytohormone commonly induced by wounding in plants (Salisbury 1994) which causes inhibition of root growth. Various strains of pseudomonads produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase (an enzyme which cleaves ACC), the immediate precursor to ethylene, thereby inhibiting ethylene production which in turn leads to an increase of root growth in plants. ACC deaminase gene of pseudomonads stimulates plant growth even in heavy metal (cadmium) contaminated soils (Belimov et al. 2001). List of phytohormones produced by fluorescent pseudomonad bacteria is given in Table 4.1.

Table 4.1 Phytohormones produced by fluorescent pseudomonads

Phytohormone	Producer strain	References
Auxin	*P. putida* GR12-2	Xie et al. (1996)
	P. monteilli	Ravindra Naik et al. (2008)
Cytokinins	*P. fluorescens*	Garcia de Salamone et al. (2001), Vessey (2003)
ACC deaminase	*P. fluorescens*	Wang et al. (2000)
	P. aeruginosa Pw60, 61	Ravindra Naik et al. (2008)
Gibberellins	*Pseudomonas* spp.	Gutierrez-Manero et al. (2001)

4.3.3 Iron Absorption

Iron is an essential nutrient of plants, but it is relatively insoluble in soil solutions. Plant roots can readily absorb ferrous (Fe^{2+}) ion, but ferric ion (Fe^{3+}) is the most prevalent form in soil (Salisbury and Ross 1992). Siderophores are small high affinity iron chelating compounds that facilitate the reduction of iron and hence favours easy absorption by plants. Under iron limiting conditions, several species of pseudomonads produce many fluorescent yellow siderophores such as pyoverdins (Budzikiewicz 1993, 1997), pyochelin (Cox et al. 1981), pseudomonine (Lewis et al. 2000; Mossialos et al. 2000; Mercado-Blanco et al. 2001), quinolobactin (Matthijs et al. 2007) and ornicorrugatin (Matthijs et al. 2008). The production of siderophores has been linked to the disease-suppressing ability of fluorescent pseudomonads (Loper 1988). Siderophore production by fluorescent pseudomonads is influenced by an array of factors, such as concentration of iron (Kloepper et al. 1980a, b); nature and concentration of carbon and nitrogen sources (Park et al. 1988); level of phosphates (Barbhaiya and Rao 1985); degree of aeration (Lenhoff 1963); presence of trace elements such as magnesium (Georgia and Poe 1931), zinc (Chakrabarty and Roy 1964) or molybdenum (Lenhoff et al. 1956) and temperature (Weisbeek et al. 1986). Different types of siderophores produced by fluorescent pseudomonad bacteria are presented in Table 4.2.

4.3.4 Nitrogen Fixation

Several species of pseudomonads are involved in the process of nitrogen fixation, thereby enhancing plant growth and productivity (Nicole et al. 2003). *Pseudomonas stutzeri* A1501 is found to be involved in denitrification under anaerobic conditions, nitrification under aerobic conditions and nitrogen fixation under microaerophilic conditions (Yan et al. 2010). Strains of *Pseudomonas* sp. (Raverkar and Konde 1988; Li and Alexander 1988) and *P. fluorescens* were reported for their ability to stimulate rhizobia–legume symbiosis in pea (Andrade et al. 1998), red clover (Marek-Kozaczuk and Skorupska 2001) and soybean (Li and Alexander 1988). Many reports indicate that various strains of pseudomonads possess *nif* genes, signifying their role in nitrogen fixation. Several species of pseudomonads are involved in the denitrification process (Gamble et al. 1977).

Table 4.2 Siderophores produced by fuorescent pseudomonads

Siderophore	Producer strain	References
Pyoverdins	*Pseudomonas* sp. B10	Budzikiewicz (1997), Kloepper et al. (1980a, 1980b)
	P. aeruginosa	Meyer (2000), Lamont and Martin (2003)
	P. fluoresens 3551	Loper et al. (2008)
	P. putida WCS358	Van Wees et al. (1997)
	P. fluorescens WCS374	Mohammad et al. (2009)
Pyochelin	*P. aeruginosa* PAO1	Cox et al. (1981), Buysens et al. (1996)
	P. fluorescens CHAO	Lewis et al. (2000)
	P. stutzeri KC	
	P. aeruginosa	Audenaert et al. (2002), Sun et al. (2006)
Pseudomonine	*P. stuzeri*, *P. putida*	Lewis et al. (2000), Mossialos et al. (2000)
	P. fluorescens	Mercado-Blanco et al. (2001)
	P. aeruginosa PUPa3	Sunish Kumar et al. (2005)
	P. aeruginosa FP10	Ayyadurai et al. (2006)
	P. fulva FP23	Ravindra Naik et al. (2008)
	*P. fluorescens*WCS374	Mohammad et al. (2009)
Yersiniabactin	*P. syringae*	Jones et al. (2007), Petermann et al. (2008)
	P. syringae DC300	Bultreys et al. (2001), Youard et al. (2007)
Quinolobactin	*P. fluorescens* 1740	Matthijs et al. (2007)
Achromobactin	*P. syringae* B728a	Franza et al. (2005), Berti and Thomas (2009)
Corrugatin	*P. fluorescens*	Matthijs et al. (2007)
Ornicorrugatin	*P. fluorescens* AF76	Matthijs et al. (2008)

4.3.5 Antimicrobial Compounds

Antibiotics are organic low molecular weight compounds produced by microorganisms, which even at low concentrations are deleterious to the growth and metabolism of other microorganisms. Antibiotic production of fluorescent pseudomonads is recognised as an important factor in the disease-suppressing ability of this group of bacteria (James and Gutterson 1986; Gutterson et al. 1988; Thomashow et al. 1990). Antibiotics produced by fluorescent pseudomonads include 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; Shanahan et al. 1992), pyrrole-type compounds (Homma and Suzui 1989; Pfender et al. 1993), polyketides (Nowak-Thompson et al. 1997; Kraus and Loper 1995) and peptides (Nielsen et al. 1999, 2000; Sorensen et al. 2001; de Bruijn et al. 2008; Loper et al. 2008). Different types of antibiotics produced by fluorescent pseudomonad bacteria are presented in Table 4.3.

4.3.6 Lytic Enzymes

Apart from the production of antibiotics and other secondary metabolites, pseudomonads are found to produce an array of lytic enzymes by which they exert their ability to suppress phytopahogenic fungi (Martin and Loper 1999;

Table 4.3 Antibiotics produced by fluorescent pseudomonads

Antibiotics	Producer strain	References
Phenazine-1-carboxylic acid	*P. fluorescens* 2-79	Gurusiddaiah et al. (1986)
	P. fluorescens 2-79RN10	Weller and Cook (1983)
	P. aureofaciens 30-84	Thomashow et al. (1990)
	P. chlororaphis	Pierson and Thomashow (1992)
	P. putida P15	Pathma et al. (2011)
Dimer of phenazine-1-carboxylic acid	*P. fluorescens* Pf23	Sakthivel and Sunish Kumar (2008)
Phenazine-1-carboxamide	*P. aeruginosa* PUPa3	Sunish Kumar et al. (2005)
2-Hydroxyphenazine	*P. chlororaphis* PCL1391	Chin-A-Woeng et al. (1998)
Pyocyanin	*P. aeruginosa* PAO1	Baron et al. (1997)
Phloroglucinols		
2,4-diacetylphloroglucinol	*P. fluorescens* Pf-5, Q2-87, CHAO, PFM2, Q8r1-96	Howell and Stipanovic (1979), Vincent et al. (1991)
	P. fluorescens F113	Shanahan et al. (1992), Keel et al. (1992), Levy et al. (1992), Flaishman et al. (1990), Raaijmakers and Weller (1998)
Pyrrolnitrin	*P. fluorescens* BL914, 915	Kirner et al. (1998), Ligon et al. (2000)
	P. aureofaciens A10338.7	Elander et al. (1968)
	P. cepacia 5.5B	Cartwright et al. (1995)
Isopyrrolnitrin	*Pseudomonads* spp.	Hashimoto and Hattori (1966a)
Oxypyrrolnitrin	*Pseudomonads* spp.	Hashimoto and Hattori (1966b)
Monodechloro-pyrrolnitrin	*P. pyrrolnitrica*	Hashimoto and Hattori (1968)
Polyketides		
Pyoluteorin	*P. fluorescens* Pf-5, CHAO	Howell and Stipanovic (1979), 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		
Viscosinamide	*P. fluorescens* DR54	Nielsen et al. (1998)
Tensin	*P. fluorescens* 96.578	Nielsen et al. (2000)
Amphisin	*Pseudomonas* sp. DSS73	Sorensen et al. (2001)
Masstolides A	*P. fluorescens* SS101	de Bruijn et al. (2008)

Neilsen and Sorensen 1999; Picard et al. 2000). Chitinase, cellulase and glucanase enzymes hydrolyse chitin, cellulose and β-1,3-glucan which are major cell wall components of various phytopathogenic fungi. *P. cepacia* producing glucanase is found to inhibit the proliferation of pathogenic fungi such as *Rhizoctonia solani*, *Sclerotium rolfsii* and *Pythium ultimum* (Friedlender et al. 1993). Pseudomonads are also found to produce various enzymes such as protease, pectinase and xylanase which also contribute to disease suppression. A reduction in the activity of these enzymes correlates with a reduction in virulence (Beraha et al. 1983). Role of chitinase and glucanase in biological control has been well documented (Shapira et al. 1989; Nielsen et al. 1998; Lim et al. 1991). Pseudomonads are also found to produce enzymes such as peroxidase, polyphenol oxidase and phenyl alanine ammonia lyase which arrested the pathogen colonisation in crops such as sugarcane (Viswanathan et al. 2003).

4.3.7 Volatiles such as Hydrogen Cyanide

Hydrogen cyanide (HCN), a volatile compound produced by fluorescent pseudomonads, exerts biocontrol activity against plant pathogens (Sacherer et al. 1994; Bagnasco et al. 1998; Rodriguez and Fraga 1999; Siddiqui 2006). Production of HCN is found to be a common trait of *Pseudomonas* (88.89 %) (Ahmad et al. 2008). HCN inhibits the enzyme cytochrome oxidase and other metalloenzymes (Voisard et al. 1989) of the pathogens and hence assists the plants in the control of soil-borne diseases (Blumer and Haas 2000).

4.3.8 Induced Systemic Resistance

Induced systemic resistance (ISR) is a phenomenon wherein plant growth-promoting rhizobacteria activate an array of biochemical pathways to trigger the plant's defence mechanisms against a broad spectrum of phytopathogens (Van Loon et al. 1998). Signalling pathways involved are salicylic acid pathway and the pathway of ethylene and jasmonic acid (Pieterse et al. 2001). Seed treatment with *P. aeruginosa* resulted in the rapid accumulation of pathogenesis-related (PR) enzymes such as chitinase, β-1,3-glucanase, peroxidases and lyases. Bacterial determinants such as outer membrane lipopolysaccharides (LPS), flagella, iron-regulated metabolites, volatile compounds, antibiotics and cyclic lipopeptides are reported to activate ISR (Bakker et al. 2007; Iavicoli et al. 2003; Meziane et al. 2005; Ongena et al. 2008; Ryu et al. 2004; Tran et al. 2007). Fluorescent pseudomonad strains that show ISR against various plant pathogens are presented in Table 4.4.

Table 4.4 Induced systemic resistance by PGPR pseudomonads

Pseudomonad strain	Target pathogen	Host plant	References
Pseudomonas WCS417	*F. oxysporum*	Carnation	Van Peer et al. (1991)
Pseudomonas WCS374	*F. oxysporum*	Radish	Hoffland et al. (1996)
Pseudomonas WCS374	Turnip crinkle virus (TCV)	Arabidopsis	Mohammad et al. (2009)
P. putida 89B-27	*C. orbiculare*	Cucumber	Wie et al. (1991)
P. fluorescens strain S97	*P. syringae*	Bean	Alstrom (1991)
P. aeruginosa 7NSK2	*B. cinerea*	Grapevine	Verhagen et al. (2010)

4.4 Bacterisation Techniques

Bacterisation is the process of inoculating plant seeds, seed pieces or roots with inoculant bacteria to enhance plant growth and to suppress phytopathogens. Treatments with bacterial inoculants include drench application (Babalola et al. 2007b; Vleesschauwer and Hofte 2005), seed bacterisation (Babalola et al. 2007a; Kumar et al. 2009), seedling treatment (Babalola et al. 2007a), bioformulation, biopreparation, dual treatment (Lavania et al. 2006) and multiple delivery (Nakkeeran et al. 2005). The choice of the method depends on the crop, soil type and the nature of the bacterial inoculum. Many commercial preparations such as "Ecomonas" and "Florezen P" are available in the market which can be directly used. The efficacy of combined application method was comparable with fungicide treatments (Rabindran and Vidhyasekaran 1996). Beneficial microbial agents and biocontrol bacteria may be applied to the crops to be treated by one of the method.

4.4.1 Seed Bacterisation

In this method, bacterial suspension was prepared using the log phase cultures (10^{10} cells/ml) and the seeds were exposed in the above suspension for 30 min and then dried for 3 h before sowing (Babalola et al. 2007a; Kumar et al. 2009). Aqueous methyl cellulose is added to the bacterial suspension as an adhesive and preservative in commercial formulations. Seed treatment of maize with *Pseudomonas* spp. GRP3A, PRS9 and *P. chlororaphis* ATCC 9446 increased seed germination, shoot and root lengths and dry weight of seedlings (Sharma and Johri 2003). ISR, plant growth-promotion and sheath blight control were observed when rice seeds were treated with strains of *P. aeruginosa* (Saikia et al. 2006).

4.4.2 Direct Inoculation of Liquid Culture into Soil

In this method, the microorganism is multiplied in large quantity as liquid culture. These liquid cultures are either first mixed in the soil before sowing or applied in the furrows. In the case of rice, these are applied by sprinkling in the water-logged beds

(Wang et al. 2009). The in-furrow inoculants provide a larger amount of bacteria to the crop plant than seed inoculation. Mixing the potting soil with suspensions of *P. aeruginosa* mutants along with soil drench conferred resistance against blast and sheath blight diseases of rice by eliciting ISR (Vleesschauwer and Hofte 2005).

4.4.3 Seedling Treatment

Liquid culture containing the biocontrol bacteria in log phase is prepared. The seedlings and saplings are dipped in the above culture for about 30 min followed by immediate sowing (Babalola et al. 2007a; Kloepper et al. 1980a, b). This method is highly suited for rice, vegetable and fruit saplings (Niknam and Dawan 2003; Al-Taweil et al. 2009).

4.4.4 Foliar Application

This method is based on the fact that bacterial cells and exudates can be absorbed into plant via epidermal cells and stomatal pores from where they are transported to the growing zones of the plants, causing the desired effects. Application is more or less uniform when the bacterial cultures are spread on leaves as foliar spray. But the survival rates and the application efficiency are dependent on the microenvironment (Nakkeeran et al. 2005) and the time of application. Commercial formulation of *P. fluorescens* applied by foliar method conferred disease resistance and hence increased total grain yield (Vijay Krishna Kumar et al. 2009).

4.4.5 Carrier-Based Inoculation

In this method, bacterial cells mixed with carrier materials such as peat lignite, charcoal and farmyard manure (Rabindran and Vidhyasekaran 1996). Carrier material provides a conducive environment for the microorganisms to remain viable for a longer period. This method is mostly accepted and widely used because it supports transportation and retains cell viability. Microencapsulation is an advanced technology in which there is a controlled release of microbes from formulations (Fages 1992; Smith 1995; Rojan et al. 2011). In contrast, conventionally used solid and liquid formulations encompass several problems with respect to the low viability of microorganisms during storage and field applications.

4.5 Biocontrol of Plant Diseases and Yield Enhancement by Fluorescent Pseudomonads

Fluorescent pseudomonad bacteria are the most promising group of beneficial bacteria due to their multiple attributes for crop productivity. 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 (Table 4.5 and 4.6).

4.5.1 Wheat Diseases

Take-all disease of wheat is caused by the fungus *Gaeumannomyces graminis* var. *tritici*. Take-all is controlled by crop rotation, but it is also suppressed by continuous monoculture following an outbreak of the disease which is known as "Take-all decline" (TAD) (Andrade et al. 1995). Strains of *P. fluorescens* (2-79 and 13-79) from the USA were reported as biological control agents against *G. graminis* var. *tritici* (Capper and Higgins 1993). Take-all caused by the soil-borne fungal pathogen *G. graminis* var. *tritici* is one of the most destructive root diseases in wheat and other cereal grain crops. Take-all decline is strongly associated with the development of antagonistic microorganisms in the wheat rhizosphere. The most prominent antagonistic microorganisms are bacteria of the genus *Pseudomonas* which are able to suppress *G. graminis* var. *tritici* in both saprophytic and parasitic stages. Phenazine-1-carboxylic acid as a biocontrol determinant is produced by *P. fluorescens* 2-79 that controls take-all disease. The strain *P. fluorescens* 2-79, originally isolated from the rhizosphere of wheat, was found to suppress take-all disease (Thomashow and Weller 1988). *Fusarium culmorum* causes seedling blight, foot rot and head blight diseases of cereals, resulting in yield loss. *P. fluorescens* strains MKB 100 and MKB 249, *P. frederiksbergensis* strain MKB 202 and *Pseudomonas* sp. strain MKB 158 were effective in ameliorating the negative effects of *F. culmorum* on seedling germination of six wheat cultivars and on stem base infection of wheat cv. GK-Othalom. Chitosan has been shown to reduce Fusarium seedling blight disease of wheat caused by seed-borne *F. graminearum* (Reddy et al. 1999). It was found that even lower doses (1,000 versus 2,000–8,000 ppm) were effective in reducing *F. culmorum* seedling blight of wheat, both as a stem base treatment and as a soil amendment. Chitosan exhibited direct antifungal activity against *Candida albicans*, *F. oxysporum*, *Aspergillus fumigatus* and *Aspergillus parasiticus*. Chitosan induced systemic host resistance to *F. culmorum* against seedling blight. There are reports on chitosan-induced systemic resistance against different plant pathogens, including fungi, in a plant species-dependent manner. Soil amendment with chitosan or with culture filtrate of either *Pseudomonas* sp. strain MKB 158 or *P. fluorescens* strain MKB 249 was reported to reduce *Fusarium* seedling blight of wheat (Johansson et al. 2003; Khan et al. 2004).

4.5.2 Rice Diseases

Treatments with *P. fluorescens* 7-14 have been reported to control rice blast caused by *Magnaporthe grisea* (Chatterjee et al. 1996; Gnanamanickam and Mew 1992). Production of an antifungal antibiotic by *P. fluorescens* is the mechanism known to mediate the biological disease suppression. Biological suppression of blast disease of rice was afforded by bacteria applied either as seed treatment or as root-dip infiltration. Among these, Pf 7-14 applied as infiltration gave a maximum of 28.7 and 25.2 % blast disease control in the two separate field experiments. Root-dip applications also performed better than seed treatments. The blast lesions did not appear on the resistant rice cultivars (C101LAC and C101PKT). Rice stem and leaf but not root tissues which received Pf 7-14 and *P. putida* V14i showed increases in salicylic acid (SA) levels over the native SA levels found in the untreated controls. It has been proved that bacteria which are spatially separated from the pathogen are involved in the induction of ISR against the rice blast pathogen. SA levels which increase during bacteria-induced systemic resistance contribute to the suppression of rice blast by about 25 %. The results on disease suppression when taken together with limited bacterial migration would support the suggestion that the blast reductions are caused by the nonmigratory bacteria which remain on the roots or inside the rice stem. These data suggest that the benefits of bacterial treatments could only be realised through properly timed foliar spray applications of bacteria. Such applications will sustain adequate bacterial populations on the rice foliage and achieve maximum (70 $\pm$ 80 %) disease control (Chatterjee et al. 1996). SA-mediated ISR is caused by *P. fluorescens* 7-14 and *P. putida* V14i that are spatially separated from the rice blast pathogen *M. grisea* and plays a significant role in the biological control of rice blast disease (Krishnamurthy and Gnanamanickam 1997).

Rice sheath blight, caused by *Rhizoctonia solani* Kuhn (Sexual stage: *Thanetophorus cucumeris*), is one of the major production constraints in rice-growing countries and ranks next to blast in causing economical loss. Effective biological control of soil-borne diseases can be achieved by applying *P. fluorescens* that are insensitive to toxic metabolites produced by plant pathogens because of their ability to detoxify toxins. Several rhizobacteria are known to detoxify the toxins produced by fungal pathogens and they have been developed as biocontrol agents to control fungal diseases of crop plants. The rice sheath blight fungus, produces oxalic acid (OA). An OA-detoxifying strain of *P. fluorescens*, PfMDU2, was isolated from the rhizosphere of rice and its efficacy in controlling sheath blight of rice was demonstrated under greenhouse conditions. Strain of *P. fluorescens* PfMDU2 was isolated from the rhizosphere soil of rice amended with OA. This bacterium was tested for its ability to inhibit the mycelial growth of *R. solani in vitro* by the dual culture technique. PfMDU2 was highly effective in inhibiting the mycelial growth of *R. solani* and further, it was demonstrated that seed treatment followed by soil application with talc-based powder formulation of *P. fluorescens* PfMDU2 significantly reduced the severity of sheath blight by 75 % compared to untreated control plants. The mode of actions of *P. fluorescens* that inhibit various soil-borne plant

pathogenic fungi include biosynthesis of antibiotics, production of HCN, production of hydrolytic enzymes, production of siderophores and competition for substrates. Successful bacterial antagonists often show a combination of synergistic mechanisms (Nagrajkumar et al. 2005).

P. fluorescens strains PF1 and FP7 were reported as antagonistic bacteria for sheath blight of rice (Nandkumar et al. 2000). Suspension culture or a talc-based formulation of biocontrol bacteria was used to control disease severity and promote plant growth under glasshouse or field conditions. Upon challenge inoculation of the pathogen, the treated plants had smaller lesions compared to the untreated control plants. Furthermore, the plants grew faster and greener with longer roots and shoots than the untreated plants. *Pseudomonas*-treatment played a dual role by reducing disease severity and promoting the growth of the plant, resulting in increased biomass and yield. It has been established that fluorescent pseudomonad bacteria enhance plant growth in several ways by producing plant growth regulators, such as gibberellins, cytokinins and indole acetic acid, which can either directly or indirectly modulate the plant growth and development. These bacteria were also reported to produce chitinase in the culture medium which gets further accelerated when the medium was supplemented with chitin (Velazhahan et al. 1999; Viswanathan and Samiyappan 2000). The increased chitinase activity in chitin medium implies that *Pseudomonas* strains are able to degrade the complex chitin polymer, which is the major component of fungal cell walls. More chitinolytic activity in culture medium inoculated with FP7 suggested that the strain FP7 performed well with the addition of chitin as a substrate. Since the fungal cell wall contains chitin, the FP7 bacteria in the plant rhizosphere might have produced more chitinase, and the enhanced chitinase activity might be one of the reasons for the increased disease reduction indicated that induced systemic resistance in rice may be due to the elicitation of defence mechanisms involving peroxidase and chitinases. Fluorescent pseudomonads are also known to produce salicylic acid which acts as local and systemic signal molecules in inducing resistance in plants. PF1 strain had typical PGPR activity and induced both peroxidase and chitinase enzymes, while FP7-mediated ISR appears to be associated with the involvement of induced plant chitinase as well as its own chitinase to suppress the pathogen. Hence, the addition of chitin to the talc-based formulation may enhance the effect of ISR. Antibiotic production by *Pseudomonas* strains also revealed that FP7 and PF1 have the capacity to produce 2,4-diacetyl phloroglucinol (DAPG) and phenazine (Nandkumar et al. 2000).

4.5.3 Cotton Diseases

Damping-off is a disease of cotton incited by *P. ultimum*. Many rhizobacteria which are found in cotton rhizosphere exhibit potent inhibition against this pathogenic fungus by different mechanisms. These beneficial bacteria are mainly *P. fluorescens* type. Lopper (1988) reported a pseudomonad fluorescent strain 3551 which showed

antagonism against *Pythium* sp. It has been proved that strain 3551 inhibits the growth of *P. ultimum* due to its potential to produce siderophore. Mutant strain of this bacterium did not show the suppression of *Pythium*. Several studies showed the production of siderophores and secondary metabolites by fluorescent pseudomonad bacterium. Therefore, antagonistic effect of this strain also may be contributed by secondary metabolites. This biocontrol strain also induces the host resistance against this pathogen. Numerous studies have demonstrated the role of 2,4-DAPG-producing *Pseudomonas* spp. in the suppression of a wide variety of plant pathogens, including fungi, bacteria and nematodes. The sensitivity of various infectious propagules of *P. ultimum* var. *sporangiiferum* to 2,4-DAPG produced by *P. fluorescens* strain CHAO was studied in detail. The effects of pH and level of acetylation on activity of phloroglucinols against mycelial growth of *P. ultimum* were also assessed. It is shown that lower pH has a significant effect on the activity of 2,4-DAPG against mycelial growth of *P. ultimum*. Changes in pH in the rhizosphere of plants, growing in agricultural soils, by as much as 2 pH units may occur. In general, the pH changes induced by roots lead to acidification, with more pronounced effects observed for dicot plants. Also microorganisms, including pathogenic fungi, can alter the pH to make nutrients or trace elements more readily available. As a result of these changes in pH, the activity of antimicrobial compounds produced by competing microorganisms may also change. It has been observed that *P. ultimum* acidifies unbuffered, liquid medium (potato dextrose broth) in a 7-day period from pH 6.5 to 4.5. This reduction in pH and coordinate increase in toxicity of 2,4-DAPG may explain some of the discrepancies in inhibitory concentrations of 2,4-DAPG reported in the different experiments. Based on TEM observations, it appears that 2,4-DAPG does not affect the cell wall structure and composition of hyphal tips of *P. ultimum* (de Souza and Raaijmakers 2003).

4.5.4 Tomato Diseases

The root-knot nematode *Meloidogyne javanica* is one of the most economically important pest causing severe damages to a wide variety of crops, particularly to tomato. Certain root-associated strains of fluorescent pseudomonad bacteria produce and excrete metabolites that are inhibitory to soil-borne plant pathogens. Siddiqui and Shahid Shaukat (2003) showed that 2,4-DAPG-producing *P. fluorescens* CHAO could affect egg hatch and induce mortality in juveniles of *M. javanica*. Since natural soil with a large number of soil microorganisms including deleterious soil-borne plant pathogens was used in this study, it is not sure whether observed suppression of the root-knot nematode was solely due to the application of DAPG-producing *P. fluorescens* in such soil. It is clearly demonstrated that tomato plants treated with *P. fluorescens* strain CHAO reduced nematode penetration rates in roots. Results suggest that *P. fluorescens strain* CHAO reduces nematode infection by inducing systemic resistance in tomato plants against *M. javanica* because the bacteria and nematode were spatially

separated. Leeman et al. (1996) demonstrated that antibiotics and siderophores may function as stress factors or signals inducing local and systemic host resistance. These results suggest that CHAO releases 2,4-DAPG during early growth stages which elicit systemic resistance in tomato against nematode.

P. syringae pv. tomato causes bacterial speck disease of tomato and has been demonstrated to be virulent on *Arabidopsis* as well (Dong et al. 1991; Whalen et al. 1991). *P. fluorescens* strain WCS417 shows antagonistic activity against *P. syringae* by inducing systemic response in tomato. To demonstrate ISR activity of this antagonistic bacteria, *Arabidopsis*-based model system using *P. syringae* pv tomato as challenging pathogen and for induction, a rifampicin-resistant mutant of the PGPR strain WCS417 of *P. fluorescens* (*P. fluorescens* WCS417r; Van Peer et al. 1991) was used.

It was documented that *P. fluorescens* WCS417r effectively protects *Arabidopsis* against infection by *P. syringae* pv. tomato. Root colonisation by *P. fluorescens* WCS417r resulted in a marked delay in symptom development and reduction in disease severity. Challenge inoculation with *P. fluorescens* WCS417r reduced both the visible symptoms caused by *P. syringae* infection and the growth of this pathogen in the leaves. Because inducing bacteria and challenging pathogens remained spatially separated throughout the experiment, antagonism by direct interactions could be ruled out, demonstrating that *P. fluorescens* WCS417r-induced protection is plant mediated. Among the bacterial determinants implicated in eliciting metabolic events in plants is the outer membrane LPS (Graham et al. 1977; Mazzucchi et al. 1979; Dazzo et al. 1991; Newman et al. 1995). Earlier, it was demonstrated that the LPS of *P. fluorescens* WCS417r is involved in eliciting systemically enhanced resistance in carnation (Van Peer and Schippers 1992) and radish (Leeman et al. 1995), indicating that PGPR-mediated protection is accomplished by induction of ISR in the plant. In *Arabidopsis*, this resistance response is effective against bacterial leaf pathogen.

The plant growth-promoting rhizobacterium *P. aeruginosa* 7NSK2 produces three siderophores when iron is limited: the yellow-green fluorescent pyoverdin, the salicylate derivative pyochelin and salicylic acid. This *Pseudomonas* strain was shown to be an efficient antagonist against *P. splendens*, the causative agent of tomato damping-off. The role of pyoverdin and pyochelin in the suppression of *P. splendens* was demonstrated by using various siderophore-deficient mutants derived from *P. aeruginosa* 7NSK2. Mutant KMPCH inhibited *P. splendens* but was less active than the parental strain. This residual protection could be due to the production of salicylic acid. Salicylic acid is known to induce systemic acquired resistance in plants. A rise in the level of salicylic acid increases systemic acquired resistance. Salicylic acid produced by rhizobacteria might be taken up by plants, thereby inducing resistance systemically. Superoxide, hydrogen peroxide and hydroxyl free radicals represent reactive oxygen species (ROS) that are thought to be involved in induction of disease resistance in plants. It is attractive to hypothesise that active oxygen species generated by the pyochelin–pyocyanin interaction induce resistance in tomato plants, which results in an enhanced protection against *Pythium*-induced damping-off. It remains to be shown whether or not this phenomenon can occur on plant roots. Only pyochelin is reported to be

involved in free-radical formation. In fact, most iron chelators, including pyoverdin, appeared to have free-radical scavenging properties. The observed antagonism of *P. aeruginosa* 7NSK2 towards *P. splendens* could be explained by pyoverdin-mediated iron competition and induction of resistance by pyochelin (Saskia et al. 1995).

4.5.5 Sugarcane Diseases

Red rot of sugarcane caused by the fungus *Colletotrichum falcatum* Went (Perfect state: *Glomerella tucumanensis*) is one of the oldest recorded diseases and has caused significant losses both to the cane growers and to sugar factories in India and other countries. Various fungicides have been used to control the disease, but limited success was achieved under field conditions (Singh and Singh 1989). Hence, plant protection chemicals are not useful for managing the red rot disease. In this context, management of red rot disease through biocontrol agents is increasingly capturing the attention of scientists as an alternative, environment-friendly strategy for the disease management.

The PGPR strains SS1, SS2 and SS3 that belong to *P. fluorescens* native to sugarcane rhizospheric soil have been isolated and their efficacy against the pathogen was demonstrated under laboratory, greenhouse and field conditions. Application of fluorescent pseudomonads to rhizosphere region had induced several defence-related enzymes such as chitinase, β-1,3-glucanase, peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase in sugarcane stalks which arrested the colonisation and spread of pathogen in the stalk (Viswanathan et al. 2003). The red-rot pathogen *C. falcatum* Went is known to produce a phytotoxic metabolite, anthroquinone. It has been established that this toxic metabolite is host specific and produces part of the disease symptoms. Recently, specific strains of *Pseudomonas* spp. effective against the pathogen have been identified. Samples treated with *P. fluorescens* strains FP 7 and VPT 4 along with phytotoxic metabolites did not produce any symptom on the leaves. It suggests that the reduction of symptoms may be possibly due to inactivation of the toxic metabolite by bacterial inoculants. The PGPR formulation was applied three times, seed treatment while planting and soil application twice in the field. Talc formulation of PGPR strains significantly reduced red rot disease incidence when the treated canes were challenge inoculated with pathogen. When PGPR strains were evaluated for their efficacy against the disease in endemic locations, strains of *P. fluorescens* such as EP1, Pfl and CHAO and *P. putida* KKM1 strongly suppressed the red rot disease development in field experiments. In addition to their efficacy against red rot disease in sugarcane, the strains significantly improved seed germination, number of millable canes (NMC) and cane yield (Malathi et al. 2002).

Strains of *Pseudomonas* spp. have also been found to induce systemic resistance against *C. falcatum* (Viswanathan and Samiyappan 1999a). Suppression of C. *falcatum* by the bacterial strains may be due to the production of antifungal secondary metabolites or by the bacterial strains-induced chitinases in sugarcane (Viswanathan and Samiyappan 1999b).

4.5.6 Banana Diseases

Bunchy top caused by Banana bunchy top virus (BBTV) is one of the most destructive diseases of banana. BBTV infects almost all banana cultivars, retarding the growth of infected plants and causing substantial economic losses. Two strains of the PGPR *P. flourescens* (Pf1 and CHAO) formulated with the carrier chitin for the ability to promote the growth of banana plants were investigated for their efficacy in controlling BBTV. Banana plants treated at planting and at the third, fifth and seventh month after planting had significantly reduced bunchy top incidence under field conditions, compared with the control treatment. The reduction in disease incidence was more pronounced with the chitin-amended CHAO strain. The chitin-amended CHAO strain also increased the leaf nutrient status and enhanced growth, bunch yield and the quality of the fruits compared to untreated plants. *P. fluorescens* strains CHAO and Pf1 and in combination with chitin were investigated for their biocontrol efficacy against BBTV. Bioformulation of *P. fluorescens* CHAO with chitin was effective in reducing the BBTV incidence under glasshouse and field conditions. *P. fluorescens* strains might stimulate the production of biochemical compounds associated with the host defence. The presence of phenolic compounds in plants or their synthesis in response to infection has often been associated with resistance (Ingham 1972). It is well known that resistant plants contain more phenols or produce polyphenols more rapidly than susceptible ones. Multifold increase in phenol content was observed in *P. fluorescens*-treated plants along with pathogen inoculation compared with the infected control plants. *P. fluorescens* strains are capable of inducing high levels of defence enzymes in banana, and it could be speculated that induced enzyme activities by *P. fluorescens* may be associated with the biosynthesis of phenolic compounds that have been considered as major determinants in inducing systemic resistance against BBTV disease, besides increasing the bunch yield. Banana plants treated with *P. fluorescens* CHAO alone or in combination with chitin showed an increase in PR-2 (β-1,3-glucanase) and PR-3 (chitinase) proteins. Thus, the induction of PR-proteins corresponding to a reduction in BBTV infection in banana supports the hypothesis that the resistance induced by fluorescent pseudomonad strains are systemic (Kavino et al. 2007; Mathiyazhagan et al. 2008).

4.5.7 Sugar Beet Diseases

The important root pathogenic fungi of sugar beet are the oomycetes, *Aphanomyces cochleoides* and *P. ultimum* and the basidiomycete *R. solani*. Antagonistic fluorescent pseudomonad bacteria producing antifungal substances have shown a potential for biological control of the pathogen *P. ultimum* in sugar beet. *P. fluorescens* DR54 was isolated as an antifungal agent towards plant pathogens causing damping-off in sugar beet. The antifungal activity of *P. fluorescens* DR54 towards both *P. ultimum*

and *R. solani* was primarily determined by production of the cyclic lipopeptide, viscosinamide. This cyclic lipopeptide was also produced in the spermosphere and rhizosphere of sugar beet when the seedlings were treated with *P. fluorescens* DR54 and grown in soil microcosms. Pot and microcosm experiments supported the field observations, demonstrating a clearly improved emergence of healthy sugar beet seedlings in the presence of the *P. fluorescens* DR54 inoculant, which established in the rhizosphere surrounding the seedling roots. The observation that low disease level in presence of *P. fluorescens* DR54 concurred with reduced mycelial biomass and sclerotia formation by *R. solani*. *R. solani* growth may be exerted by antagonistic mechanisms such as production of antibiotic (viscosinamide) and hydrolytic, cell wall-degrading enzyme (chitinase). Direct surface attachment and microcolony growth of *P. fluorescens* DR54 cells on the surface of *R. solani* hyphae were observed using Gfp-labelling of bacteria (Thrane et al. 1999, 2000; Nielsen et al. 2002).

4.5.8 Tobacco Diseases

Strain CHAO of *P. fluorescens* suppressed black root rot of tobacco, caused by *Thielaviopsis basicola*, under gnotobiotic conditions in an artificial soil containing vermiculite as clay mineral. Many facts indicate that competition for iron is not the mechanism of suppression of tobacco black root rot, caused by *T. basicola*, in the gnotobiotic system. The siderophore-negative mutant CHA400 suppressed disease as effectively as the wild-type strain CHAO in the soils containing vermiculite, and strain CHAO suppressed disease more effectively in the iron-rich soil (vermiculite) than in the iron-poor soil (illite); the addition of $FeCl_3$ to vermiculite did not reduce the capacity of the bacteria to suppress disease; the addition of $FeCl_3$ to illite increased it; iron-free siderophores did not inhibit the growth of *T. basicola* in vitro. The endoconidia of *T. basicola* may contain enough endogenous iron to initiate germination and infection. The addition of $FeCl_3$ to illite increased the capacity of strain CHAO and its siderophore-negative mutant CHA400 to suppress disease. This indicates that the bacteria need sufficient iron to suppress disease (Keel et al. 1989). Maurhofer et al. (1994) indicated that induced protection of tobacco against tobacco necrosis virus by *P. fluorescens* CHAO was associated with the production of pyoverdine. Thus, systemic resistance by bacteria appears to involve multiple mechanisms.

4.6 Concluding Remarks

Overuse of chemicals is reported to affect plant nutrition and subsequently reduce the total yield. Phytopathogens are becoming increasingly tolerant to chemicals and emerged as a major threat for crop productivity. Modern agricultural practises helped to increase the food production, but still 10–16 % of the harvest is lost

Table 4.5 Biological control of phytopathogens by fluorescent pseudomonads

Biocontrol strain	Crop	Disease	Pathogen	References
P. fluorescens BL915	Cotton	Seedling damping-off	*Rhizoctonia solani*	Ligon et al. (2000)
P. cepacia 5.5B	Cotton	Damping-off	*R. solani*	Cartwright et al. (1995)
P. fluorescens Pf-5	Tobacco	Black root rot	*Pythium ultimum*	Howell and Stipanovic (1979)
	Cotton	Damping-off	*R. solani*	Howell and Stipanovic (1979)
P. fluorescens CHAO	Tobacco	Black root rot	*P. ultimum*	Keel et al. (1992)
	Tomato	Damping-off	*P. splendens*	Buysens et al. (1994)
	Wheat	Take-all	*Gaeumannomyces graminis graminis* var. *tritici*	Keel et al. (1992)
P. fluorescens 3551	Cotton	Damping-off	*P. ultimum*	Lopper (1988)
Pseudomonas spp.	Cucumber	Damping-off	*P. aphanidermatum*	Elad and Chet (1987)
P. putida NIR	Soyabean	Damping-off	*P. ultimum*	Paulitz (1991)
P. aeruginosa 7NSK2	Tomato	Damping-off	*P. splendens*	Buysens et al. (1994)
P. fluorescens Hv37a	Barley	Damping-off	*P. ultimum*	Gutterson et al. (1986)
P. fluorescens DR54	Sugar Beet	Damping-off	*R. solani*	Nielsen et al. (1999)
P. fluorescens 2-79,13-79	Wheat	Take-all	*G. gramnis var. tritici*	Thomashow and Weller (1988)
P. fluorescens PfMDU	Rice	Sheath blight	*R. solani*	Nagrajkumar et al. (2005)
P. putida KKM1	Sugarcane	Red rot	*Colletotrichum. falcatum*	Malathi et al. (2002)
P. fluorescens PGS12	Corn	Damping off	*F. oxysporum*	Georgakopoulos et al. (1994)
P. chlororaphis 30-84	Wheat	Take-all	*G. gramini* var. *tritici*	Pierson and Thomashow (1992)
P. putida	Cucumber	Fusarium wilt	*Fusarium oxysporum*	Park et al. (1988)
Pseudomonas spp.	Cucumber	Fusarium wilt	*F. oxysporum* f. sp. *cumuerinum*	Sneh et al. (1984)
P. aeruginosa PNA1	Chickpea	Damping-off	*F. oxysporum*	Anjaiah et al. (1998, 2003)
P. chlororaphis PCL1391	Tomato	Root rot	*F. oxysporum* f. sp. *radicis-lycopersici*	Chin-A-Woeng et al. (1998)
P. fluorescens	Rice	Sheath rot	*Sarocladium oryzae*	Sakthivel and Gnanamanickam (1987)
P. aeruginosa PUPa3	Rice	Sheath rot	*S. oryzae*	Sunish kumar et al. (2005)
		Sheath blight	*R. solani*	
P. aeruginosa	Wheat	Foliar disease	*Septoria tritici*	Baron et al. (1997), Flaishman et al. (1990)
P. fluorescens Q8r1-96	Wheat	Take-all	*G. gramini* var. *tritici*	Raaijmakers and Weller (1998)
F113	Sugar beet	Damping-off	*P. ultimum*	Shanahan et al. (1992)
PFM2	Wheat	Foliar disease	*S. tritici*	Levy et al. (1992)
P. putida	Radish	Fusarium wilt	*F. oxysporum*	Scher and Baker (1982)

Table 4.6 Enhancement of crop growth and productivity by fluorescent pseudomonad bacteria

Bacterial strain	Crop	Enhancement of plant growth and yield	References
Pseudomonas sp.	Potato	Increase in root dry weight (44–201 %) Stem length increase (26–28 %) Increase in lignin up to 43 % Enhancement of stem hair formation (55–110 %)	Frommel et al. (1991)
Pseudomonas sp.	Wheat	Increase in yield up to 27 % and control of Take-all	De Freitas and Germida (1990)
P. cepacia	Wheat	Stimulation of plant growth	De Freitas and Germida (1990)
P. fluorescens		Biocontrol against pathogen, *Rhizoctonia solani*	
P. putida		Suppression of the growth of pathogen, *Leptosphaera maculans*	
P. cepacia MR85, R85 *P. putida* MR111, R105	Wheat	Increase in grain yield	De Freitas and Germida (1992b)
P. cepacia R55, R85	Wheat	Increase in dry weight (62–78 %), root weight (92–128 %)	De Freitas and Germida (1991)
P. putida R104		Increase in dry shoot weight (28–48 %) Antagonism against pathogen, *Rhizoctonia solani*	
P. cepacia R85 *P. fluorescens* R104, 105 *P. putida* R111	Wheat	Increase in grain yield (46–75 %)	De Freitas and Germida (1992a)
P. chlororaphis 2E3, O6	Wheat	Increase in growth (8–6 %) Inhibition against pathogen, *Fusarium culmorum*	Kropp et al. (1996)
P. corrugate	*Amaranthus paniculatus*	Increase in plant growth and nitrogen content	Pandey et al. (1999)
P. fluorescens *P. putida* TL3, BK1	Potato	Increase in tuber yield (14–33 %)	Burr et al. (1978)
P. fluorescens	Wheat	Increase in seedling height and number of heads and yield in *Pythium*-contaminated sites	Weller and Cook (1986)
*P. fluorescens*63-28 R17-FP2, QP5, R15-A4	Tomato	Increase in yield up to 18.2 %	Gagne et al. (1993)

P. corrugate 13	Cucumber	Increase in yield	McCullagh et al. (1996)
P. fluorescens 63-28			
P. fluorescens 63-49	Cucumber	Increase in fruit number (18 %)	McCullagh et al. (1996)
P. fluorescens Pf5	Blueberry	Leaf area and stem diameter increase	de Silva et al. (2000)
P. putida	Canola	Increase in yield up to 57 %	Kloepper et al. (1988)
P. putida biovar B			
P. fluorescens	Canola	Increase in yield (6–13 %)	Kloepper et al. (1988)
P. putida	Cucumber	Increase in root length	Uthede et al. (1999)
P. putida GR12-2	Canola	Increase in root elongation Greater phosphate uptake and growth	Lifshitz et al. (1987)
P. putida GR12-2	Canola Lettuce Tomato Barley Wheat Oat	Increase in root elongation Reduction in ethylene synthesis (ACC deaminase)	Hall et al. (1996)
P. putida W4P63	Potato	Increase in yield (10.2–11.7 %) Suppression of potato soft rot	Xu and Gross (1986)
Pseudomonas sp.	Canola	Increase in root dry weight (11–52 %)	Bertrand et al. (2001)
Pseudomonas sp. PsJN	Potato	Increase in plant dry weight	Frommel et al. (1993)
Fluorescent pseudomonad strains A1, B10, TL3,BK1, E6	Potato	Significant yield increase	Kloepper et al. (1980a, 1980b)
Fluorescent pseudomonad strains A1, B2, B4, E6.RV3, SH5	Sugar beet	Increase in seedling mass	Suslow and Schroth (1982)
Pseudomonas sp.	Potato	Increase in yield (10–37 %)	Howie and Echandi (1983)
Pseudomonas sp.	Potato	Increase in yield (9–20 %)	Geels et al. (1986)
Pseudomonas sp.	Potato	Increase in yield (14–33 %)	Kloepper et al. (1989)

(continued)

Table 4.6 (continued)

Bacterial strain	Crop	Enhancement of plant growth and yield	References
P. fluorescens	Rice	Increase in plant height, tiller number and grain yield (3–160 %)	Sakthivel and Gnanamanickam (1987)
Pseudomonas sp.	Canola	Increase in growth	Kloepper et al. (1988)
Pseudomonas sp.	Lettuce Canola Cucumber Tomato	Increase of root and shoot weights	Van Peer and Schippers (1988)
Pseudomonas sp. 7NSK2	Maize Barley Wheat	Increase in yield (15–25 %)	Iswandi et al. (1987)
Pseudomonas W34	Lettuce Tomato	Increase in seedling biomass in soils infested with *Meloidogyne incognita*	Hoffmann-Hergarten et al. (1998)
Pseudomonas sp.	Maize	Increase in yield (8–14 %)	Lalande et al. (1989)
P. syringae pv. *phaseolicola*	Bean	Increase in protein	Alstrom (1995)

due to plant diseases. As the communities of bacteria on the plants are complex, in-depth understanding of the dynamics of the plant–bacterial interaction is required to exploit them for biological control. Strategies that would lead to the development of more consistent and reliable methodology for the selection and application of fluorescent pseudomonad bacteria to inhibit crop pathogens and subsequent enhancement of crop productivity may be envisaged.

References

Ahmad F, Ahmad I, Khan MS (2008) Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. Microbiol Res 163(Suppl 2):173–81

Alstrom S (1991) Induction of disease resistance in common bean susceptible to halo blight bacterial pathogen after seed bacterization with rhizosphere pseudomonads. J Gen Appl Microbiol 37:495–501

Alstrom S (1995) Evidence of disease resistance induced by rhizosphere pseudomonad against *Pseudomonas syringae* pv. *phaseolicola*. J Gen Appl Microbiol 41:315–325

Al-Taweil HI, Osman MB, Hamid AA, Wan Yusouff WM (2009) Development of microbial inoculants and the impact of soil application on rice seedling growth. Am J Agric Biol Sci 4(1):79–82

Andrade G, Azcdn R, Bethlenfalvay GJ (1995) A rhizobacterium modifies plant and soil responses to the mycorrhizal fungus *Glomusmossae*. Appl Soil Ecol 2:195–202

Andrade G, DeLeij FA, Lynch JM (1998) Plant mediated interactions between *Pseudomonas fluorescens*, *Rhizobium leguminosarum* and arbuscular mycorrhizae on pea. Lett Appl Microbiol 26:311–316

Anjaiah V, Koedam N, Nowak-Thompson B, Loper JE, Hofte M, Tambong JT, Cornelis P (1998) Involvement of phenazines and anthranilate in the antagonism of *Pseudomonas aeruginosa* PNA1 and Tn5 derivatives toward *Fusarium* spp. and *Pythium* spp. Mol Plant Microbe Interact 11:847–854

Anjaiah V, Cornelis P, Koedam N (2003) Effect of genotype and root colonization in biological control of fusarium wilts in pigeonpea and chickpea by *Pseudomonas aeruginosa* PNA1. Can J Microbiol 49:85–91

Audenaert K, Pattery T, Cornelis P, Hofte M (2002) Induction of systemic resistance to *Botrytis cinerea* in tomato by *Pseudomonas aeruginosa* 7NSK2: role of salicylic acid, pyochelin, and pyocyanin. Mol Plant Microbe Interact 15:1147–1156

Ayyadurai N, Ravindra Naik P, Sreehari Rao M, Sunish Kumar R, Samrat SK, Manohar M, Sakthivel N (2006) Isolation and characterization of a novel banana rhizosphere bacterium as fungal antagonist and microbial adjuvant in micropropagation of banana. J Appl Microbiol 100:926–937

Ayyadurai N, Ravindra Naik P, Sakthivel N (2007) Functional characterization of antagonistic fluorescent pseudomonads associated with rhizospheric soil of rice (*Oryza sativa* L.). J Microbiol Biotechnol 17:919–927

Babalola OO, Berner DK, Amusa NA (2007a) Evaluation of some bacterial isolates as germination stimulants of *Striga hermonthica*. Afr J Agric Res 2(1):27–30

Babalola OO, Sanni AI, Odhiambo GD, Torto B (2007b) Plant growth-promoting rhizobacteria do not pose any deleterious effect on cowpea and detectable amounts of ethylene are produced. World J Microbiol Biotechnol 23(6):747–752

Bagnasco P, De La Fuente L, Gaultieri G, Noya F, Arias A (1998) Fluorescent *Pseudomonas* spp. as biocontrol agents against forage legume root pathogenic fungi. Soil Biol Biochem 30:1317–1323

Bakker PAHM, Pieterse CMJ, Van Loon LC (2007) Induced systemic resistance by fluorescent *Pseudomonas* spp. Phytopathology 97:239–243

Ballard RW, Doudoroff M, Stanier R, Mandel M (1968) Taxonomy of the aerobic Pseudomonads: *Pseudomonas diminuta* and *P. vesiculare*. J Gen Microbiol 53:349–361

Bano N, Musarrat J (2003) Characterization of a new *Pseudomonas aeruginosa* strain NJ-15 as a potential biocontrol agent. Curr Microbiol 46:324–328

Barbhaiya HB, Rao KK (1985) Production of pyoverdine, the fluorescent pigment of *Pseudomonas aeruginosa* PAO1. FEMS Microbiol Lett 27:233–235

Baron SS, Teranova G, Rowe JJ (1997) Molecular mechanism of the antimicrobial action of pyocyanin. Curr Microbiol 18:223–230

Belimov AA, Safronova VI, Sergeyeva TA, Matveyeva VA, Egorova TN, Tsyganov VE, Borisov AY, Tikhonovich IA, Kluge C, Preisfeld A, Dietz KJ, Stepanok VV (2001) Characterization of plant growth promoting rhizobacteria isolated from polluted soils and containing 1-aminocyclopropane-1-carboxylate deaminase. Can J Microbiol 47:642–652

Beraha L, Wisniewski V, Garber ED (1983) Avirulence and reduced extracellular enzyme activity in *Geotrichum candidum*. Bot Gaz 144:461–465

Berti AD, Thomas MG (2009) Analysis of achromobactin biosynthesis by *Pseudomonas syringae pv. syringae* B728a. J Bacteriol 191:4594–4604

Bertrand H, Nalin R, Bally R, Cleyet-Marel JC (2001) Isolation and identification of the most efficient plant growth-promoting bacteria associated with canola *Brassica napus*. Biol Fertil Soils 33:152–156

Blumer C, Haas D (2000) Mechanism, regulation, and ecological role of bacterial cyanide biosynthesis. Arch Microbiol 173:170–177

Budzikiewicz H (1993) Secondary metabolites from fluorescent pseudomonads. FEMS Microbiol Rev 104:209–228

Budzikiewicz H (1997) Siderophores of fluorescent pseudomonads. Z Naturforsch 52:713–720

Bultreys A, Gheysen I, Maraite H, de Hoffmann E (2001) Characterization of fluorescent and non fluorescent peptide siderophores produced by *Pseudomonas syringae* strains and their potential use in strain identification. Appl Environ Microbiol 67:1718–1727

Burr TJ, Schroth MN, Suslow T (1978) Increased potato yields by treatment of seed pieces with specific strains of *Pseudomonas fluorescens* and *P. putida*. Phytopathology 68:1377–1383

Buysens S, Poppe J, Hofte M (1994) Role of siderophores in plant growth stimulation and antagonism by *Pseudomonas aeruginosa* 7NSK2. In: Ryder MH, Stephens PM, Bowen GD (eds) Improving plant productivity with rhizosphere bacteria. CSIRO, Adelaide, pp 139–141

Buysens S, Heungens K, Poppe J, Hofte M (1996) Involvement of pyochelin and pyoverdine in suppression of *Pythium*-induced damping-off of tomato by *Pseudomonas aeruginosa* 7NSK2. Appl Environ Microbiol 62:865–871

Capper AL, Higgins KP (1993) Application of *Pseudomonas fluorescens* isolates to wheat as potential biological control agents against Take-all. Plant Pathol 42:560–567

Cartwright DK, Chilton WS, Benson DM (1995) Pyrrolnitrin and phenazine production by *Pseudomonas cepacia*, strain 5.5B, a biocontrol agent of *Rhizoctonia solani*. Appl Microbiol Biotechnol 43:211–216

Cattelan AJ, Hartel PG, Fuhrmann FF (1999) Screening for plant growth promoting rhizobacteria to promote early soybean growth. Soil Sci Soc Am J 63:1670–1680

Chakrabarty AM, Roy SC (1964) Effects of trace elements on the production of pigments by a pseudomonad. Biochem J 93:228–231

Chatterjee A, Valasubramanian R, Vachani A, Mau WL, Gnanamanickam SS, Chatterjee AK (1996) Biological control of rice diseases with *Pseudomonas fluorescens* 7–14: isolation of ant mutants altered in antibiotic production, cloning of ant$^+$ DNA and an evaluation of a role for antibiotic production in the control of blast and sheath blight. Biol Control 7:185–195

Chin-A-Woeng TFC, Bloemberg GV, Van der Bij AJ, Van der Drift KMGM, Schripse-ma J, Kroon B, Scheffer RJ, Keel C, Bakker PAHM, Tichy H, de Bruijn FJ, Thomas-Oates JE, Lugtenberg BJJ (1998) Biocontrol by phenazine-1-carboxamide-producing *Pseudomonas*

chlororaphis PCL1391 of tomato root rot caused by *Fusarium oxysporum* f. sp. *radicis-lycopersici*. Mol Plant Microbe Interact 11:1069–1077

Cox CD, Rinehart KL, Moore ML, Cook JC (1981) Pyochelin: novel structure of an iron chelating growth promoter for *Pseudomonas aeruginosa*. Proc Natl Acad Sci USA 78:4256–4260

Dazzo FB, Truchet GL, Hollingsworth RI, Hrabak EM, Pankratz HS, Philip-Hollingsworth S, Salzwedel JL, Chapman K, Appenzeller L, Squartini A, Gerhold D, Orgambide G (1991) *Rhizobium* lipopolysaccharide modulates infection thread development in white clover root hairs. J Bacteriol 173:5371–5384

de Bruijn I, de Kock MJD, de Waard P, Van Beek TA, Raaijmakers JM (2008) Massetolide A biosynthesis in *Pseudomonas fluorescens*. J Bacteriol 190(8):2777–2789

De Freitas JR, Germida JJ (1990) Plant growth promoting rhizobacteria for winter wheat. Can J Microbiol 36:265–272

De Freitas JR, Germida JJ (1991) *Pseudomonas cepacia* and *Pseudomonas putida* as winter wheat inoculants for biocontrol of *Rhizoctonia solani*. Can J Microbiol 37:780–784

De Freitas JR, Germida JJ (1992a) Growth promotion of winter wheat by fluorescent pseudomonads under growth chamber conditions. Soil Biol Biochem 24:1127–1135

De Freitas JR, Germida JJ (1992b) Growth promotion of winter wheat by fluorescent pseudomonads under field conditions. Soil Biol Biochem 24:1137–1146

de Silva A, Patterson K, Rothrock C, Moore J (2000) Growth promotion of highbush blueberry by fungal and bacterial inoculants. Hortic Sci 35:1228–1230

de Souza JT, Raaijmakers JM (2003) Polymorphisms within the prnD and pltC genes from pyrrolnitrin and pyoluteorin-producing *Pseudomonas* and *Burkholderia* spp. FEMS Microbiol Ecol 43:21–34

de Vos P, Kersters K, Falsen E, Pot B, Gillis M, Segers P, De Ley J (1985) *Comamonas* Davis and Park 1962 gen. nov. nom. rev. emend and *Comamonas terrigena* Hugh 1962 sp. nov. nom. rev. Int J Syst Bacteriol 35:443–453

den Dooren de Jong LE (1926) Bijdrage tot de kennis van het mineralisatieproces. Dissertation. Technische Hogeschool, Delft. Nijgh and van Ditmar, Rotterdam, the Netherlands

Dey KB (1998) Phosphate solubilizing organisms in improving fertility status. In: Sen SP, Palit P (eds) Biofertilizers: potentialities and problems. Plant Physiology Forum, Naya Prokash, Calcutta, pp 237–248

Dong X, Mindrinos M, Davis KR, Ausubel FM (1991) Induction of *Arabidopsis* defense genes by virulent and avirulent *Pseudomonas syringae* strains and by a cloned avirulence gene. Plant Cell 3:61–72

Doudoroff M, Palleroni NJ (1974) Genus I. *Pseudomonas migula*. 1894. Addendum IV. In: Bergey's manual of determinative bacteriology. Williams and Wilkins, Baltimore, MD, pp 241–242

Ederer GM, Matsen JM (1972) Colonization and infection with *Pseudomonas cepacia*. J Infect Dis 125:613–618

Elad Y, Chet I (1987) Possible role of competition for nutrients in biocontrol of *Pythium* damping-off by bacteria. Phytopathology 77:190–195

Elander RP, Mabe JA, Hamill RH, Gorman M (1968) Metabolism of tryptophans by *Pseudomonas aureofaciens VI*. Production of pyrrolnitrin by selected *Pseudomonas* species. Appl Microbiol 16:753–758

El-Sayed AK, Hothersall J, Cooper SM, Stephens E, Simpson TJ, Thomas CM (2003) Characterization of the mupirocin biosynthesis gene cluster from *Pseudomonas fluorescens* NCIMB 10586. Chem Biol 10:410–430

Fages J (1992) An industrial view of *Azospirillum* inoculants: formulation and application technology. Symbiosis 13:15–26

Flaishman M, Eyal Z, Voisard C, Haas D (1990) Suppression of Septoria triticii by phenazine or siderophore-deficient mutants of Pseudomonas. Curr Microbiol 20:121–124

Foster RC (1988) Microenvironments of soil microorganisms. Biol Fertil Soils 6:189–203

Franza T, Mahe B, Expert D (2005) *Erwinia chrysanthemi* requires a second iron transport route dependent of the siderophore achromobactin for extracellular growth and plant infection. Mol Microbiol 55:261–275

Friedlender M, Inbar J, Chet I (1993) Biological control of soilborne plant pathogens by a β-1,3-glucanase-producing *Pseudomonas cepacia*. Soil Biol Biochem 25:1211–1221

Frommel MI, Nowak J, Lazarovitis G (1991) Growth enhancement and developmental modifications of in vitro grown potato *Solanum tuberosum* ssp. *tuberosum*. Plant Physiol 96:928–936

Frommel MI, Nowak J, Lazarovitis G (1993) Treatment of potato tubers with a growth promoting *Pseudomonas* sp.: plant growth responses and bacterium distribution in the rhizosphere. Plant Soil 150:51–60

Gagne S, Dehbi L, Le Quere D, Cayer F, Morin J, Lemay R, Fournier N (1993) Increase of greenhouse tomato fruit yields by plant growth-promoting rhizobacteria PGPR inoculated into the peat-based growing media. Soil Biol Biochem 25:269–272

Galli E, Barbieri P, Bestetti G (1992) Potential of pseudomonads in the degradation of methylbenzenes. In: Galli E, Silver S, Witholt B (eds) Pseudomonas: molecular biology and biotechnology. American Society for Microbiology, Washington, DC, pp 268–276

Gamble TN, Betlach MR, Tiedje JM (1977) Numerically dominant denitrifying bacteria from world soils. Appl Environ Microbiol 33:926

Garcia de Salamone IE, Hynes RK, Nelson LM (2001) Cytokinin production by plant growth promoting rhizobacteria and selected mutants. Can J Microbiol 47:404–411

Geels FP, Lamers JG, Hoekstra O, Schippers B (1986) Potato plant response to seed tuber bacterization in the field in various rotations. Neth J Plant Pathol 92:257–272

Georgakopoulos DG, Hendson M, Panopoulos NJ, Schroth MN (1994) Analysis and expression of a phenazine biosynthesis locus of *Pseudomonas aureofaciens* PGS12 on seeds with a mutant carrying a phenazine biosynthesis locus-ice nucleation reporter gene fusion. Appl Environ Microbiol 60:4573–4579

Georgia FR, Poe CP (1931) Study of bacterial fluorescence in various media. 1. Inorganic substances necessary for bacterial fluorescence. J Bacteriol 22:349–361

Glass ADM (1989) Plant nutrition: an introduction to current concepts. Jones and Bartlett, Boston, MA, p 234

Gnanamanickam SS, Mew TW (1992) Biological control of blast disease of rice (*Oryza sativa* L.) with antagonistic bacteria and its mediation by a *Pseudomonas* antibiotic. Ann Phytopathol Soc Jpn 58:380–385

Graham TL, Sequeira L, Huang TSR (1977) Bacterial lipopolysaccharides as inducers of disease resistance in tobacco. Appl Environ Microbiol 34:424–432

Gurusiddaiah S, Weller DM, Sarkar A, Cook RJ (1986) Characterization of an antibiotic produced by a strain of *Pseudomonas fluorescens* inhibitory to *Gaeumannomyces graminis* var. *tritici* and *Pythium* spp. Antimicrob Agents Chemother 29:488–495

Gutierrez-Manero FJ, Ramos B, Probanza A, Mehouachi J, Talon M (2001) The plant growth promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. Physiol Plant 111:206–211

Gutterson N, Layton TJ, Ziegle JS, Warren GJ (1986) Molecular cloning of genetic determinants for inhibition of fungal grwoth by a fluorescent pseudomonad. J Bacteriol 165:696–703

Gutterson MB, Ziegle JS, Warren CJ, Layton TL (1988) Genetic determinants for catabolic induction of antibiotic biosynthesis in *Pseudomonas fluorescens* HV37a. J Bacteriol 170:380–385

Hall JA, Peirson D, Ghosh S, Glick BR (1996) Root elongation in various agronomic crops by the plant growth promoting rhizobacterium *Pseudomonas putida* GR12-2. Isr J Plant Sci 44:37–42

Hashimoto M, Hattori K (1966a) Oxypyrrolnitrin:a metabolite of *Pseudomonas*. Chem Pharm Bull 14:1314–1316

Hashimoto M, Hattori K (1966b) Isopyrrolnitrin: a metabolite from *Pseudomonas*. Bull Chem Soc Jpn 39:410

Hashimoto M, Hattori K (1968) A new metabolite from *Pseudomonas pyrrolnitrica*. Chem Pharm Bull 16:1144

Hoffland E, Hakulinen J, Van Pelt JA (1996) Comparison of systemic resistance induced by avirulent and nonpathogenic *Pseudomonas* species. Phytopathology 86:757–762

Hoffmann-Hergarten S, Gulati MK, Sikora RA (1998) Yield response and biological control of *Meloidogyne incognita* on lettuce and tomato with rhizobacteria. J Plant Dis Protect 105:349–358

Homma Y, Suzui T (1989) Role of antibiotic production in suppression of radish damping-off by seed bacterization with *Pseudomonas cepacia*. Ann Phytopathol Soc Jpn 55:643–652

Howell CR, Stipanovic RD (1979) Control of *Rhizoctonia solani* on cotton seedlings with *Pseudomonas fluorescens* with an antibiotic produced by the bacterium. Phytopathology 69:480–482

Howie WJ, Echandi E (1983) Rhizobacteria: Influence of cultivar and soil type on plant growth and yield of potato. Soil Biol Biochem 15:127–132

Iavicoli A, Boutet E, Buchala A, Métraux JP (2003) Induced systemic resistance in *Arabidopsis thaliana* in response to root inoculation with *Pseudomonas fluorescens* CHAO. Mol Plant Microbe Interact 16:851–858

Ingham JL (1972) Phytoalexins and other natural products as factors in plant disease. Bot Rev 38:343–424

Iswandi A, Bossier P, Vandenbeele J, Verstraete W (1987) Effect of seed inoculation with the rhizopseudomonad strain 7NSK2 on the root microbiota of maize *Zea mays* and barley *Hordeum vulgare*. Biol Fertil Soils 3:153–158

Jackson MB (1993) Are plant hormones involved in root to shoot communication. Adv Bot Res 19:103–187

James DW, Gutterson NI (1986) Multiple antibiotics produced by *Pseudomonas fluorescens* HV37a and their differential regulation by glucose. Appl Environ Microbiol 52:1183–1189

Jha BK, Pragash MG, Cletus J, Raman G, Sakthivel N (2009) Simultaneous phosphate solubilisation potential and antifungal activity of new fluorescent pseudomonad strains, *Pseudomonas aeruginosa*, *P. plecoglossicida* and *P. mosselii*. World J Microbiol Biotechnol 25:573–581

Johansson PM, Johnsson L, Gerhardson B (2003) Supression of wheat-seedling diseases caused by *Fusarium culmorum* and *Microdochium nivale* using bacterial seed treatment. Plant Pathol 52:219–227

Jones AM, Lindow SE, Wildermuth MC (2007) Salicylic acid, yersiniabactin, and pyoverdin production by the model phyto-pathogen *Pseudomonas syringae* pv. tomato DC3000: synthesis, regulation, and impact on tomato and *Arabidopsis* host plants. J Bacteriol 189:6773–6786

Kavino M, Harish S, Kumar N, Saravanakumar D, Damodaran T, Soorianathasundaram K (2007) Rhizosphere and endophytic bacteria for induction of systemic resistance of banana plantlets against bunchy top virus. Soil Biol Biochem 39:1087–1098

Keel C, Voisard C, Berling CH, Kahr G, Défago G (1989) Iron sufficiency, a prerequisite for suppression of tobacco black root rot by *Pseudomonas fluorescens* strain CHAO under gnotobiotic conditions. Phytopathology 79:584–589

Keel C, Wirthner P, Oberhansli T, Voisard C, Burger U, Haas D, Defago G (1990) Pseudomonads as antagonists of plant pathogens in the rhizosphere: role of the antibiotic 2,4-diacetylphloroglucinol in the suppression of black root rot of tobacco. Symbiosis 9:327–341

Keel C, Schnider U, Maurhofer M, Voisard C, Laville J, Burger U, Wirthner P, Haas D, Defago G (1992) Suppression of root diseases by *Pseudomonas fluorescens* CHAO: importance of the bacterial secondary metabolite 2,4-diacetylphloroglucinol. Mol Plant Microbe Interact 5:4–13

Khan NI, Schisler DA, Boehm MJ, Lipps PE, Slininger PJ (2004) Field testing of antagonists of Fusarium head blight incited by *Gibberella Zeae*. Biol Control 29:245–255

Kirner S, Hammer PE, Hill DS, Altmann A, Fischer I, Weislo LJ, Lanahan M, van Pee KH, Ligon JM (1998) Functions encoded by pyrrolnitrin biosynthetic genes from *Pseudomonas fluorescens*. J Bacteriol 180:1939–1943

Kloepper JW, Leong J, Teintze M, Schroth MN (1980a) Enhanced plant growth by siderophores produced by plant growth promoting rhizobacteria. Nature 286:885–886

Kloepper JW, Schoth MN, Miller TD (1980b) Effects of rhizosphere colonization by plant growth-promoting rhizobacteria on potato plant development and yield. Phytopathology 70:1078–1082

Kloepper JW, Hume DJ, Scher FM, Singleton C, Tipping B, Laliberte M, Frauley K, Kutchaw T, Simonson C, Lifshitz R, Zaleska I, Lee L (1988) Plant growth-promoting rhizobacteria on canola rapeseed. Plant Dis 72:42–46

Kloepper JW, Lifshitz R, Zablotowicz RM (1989) Free-living bacterial inocula for enhancing crop productivity. Trends Biotechnol 7:39–43

Kraus J, Loper JE (1995) Characterization of a genomic region required for production of the antibiotic pyoluterin by the biological control agent *Pseudomonas fluorescens* Pf5. Appl Environ Microbiol 61:849–854

Krishnamurthy K, Gnanamanickam SS (1997) Biological control of sheath blight of rice: Induction of systemic resistance in rice by plant-associated *Pseudomonas* spp. Curr Sci 72:331–334

Kropp BR, Thomas E, Pounder JI, Anderson AJ (1996) Increased emergence of spring wheat after inoculation with *Pseudomonas chlororaphis* isolate 2E3 under field and laboratory conditions. Biol Fertil Soil 23:200–206

Kumar KV, Srivastava S, Singh N, Behl HM (2009) Role of metal resistant plant growth promoting bacteria in ameliorating fly ash to the growth of *Brassica juncea*. J Hazard Mater 170:51–57

Lalande R, Bissonette N, Coutlée D, Antoun H (1989) Identification of rhizobacteria from maize and determination of the plant-growth promoting potential. Plant Soil 115:7–11

Lamont IL, Martin LW (2003) Identification and characterization of novel pyoverdine synthesis genes in *Pseudomonas aeruginosa*. Microbiology 149:833–842

Lavania M, Chauhan PS, Chauhan SVS, Singh HB, Nautiyal CS (2006) Induction of plant defense enzymes and phenolics by treatment with plant growth-promoting rhizobacteria *Serratia marcescens* NBRI1213. Curr Microbiol 52:363–368

Lee JY, Song SH (2007) Evaluation of groundwater quality in coastal areas: implications for sustainable agriculture. Environ Geol 52(7):1231–1242

Leeman M, Van Pelt JA, Den Ouden FM, Heinsbroek M, Bakker PAHM, Schippers B (1995) Induction of systemic resistance against Fusarium wilt of radish by lipopolysaccharides of *Pseudomonas fluorescens*. Phytopathology 85:1021–1027

Leeman M, Den Ouden FM, Van Pelt JA, Dirkx FPM, Steijl H, Bakker PAHM, Schippers B (1996) Iron availability affects induction of systemic resistance to Fusarium wilt of radish in commercial greenhouse trials by seed treatment with *Pseudomonas fluorescens* WCS374. Phytopathology 85:149–150

Lenhoff HM (1963) An inverse relationship of the effects of oxygen and iron on the production of fluorescein and cytochrome C by *Pseudomonas fluorescens*. Nature 199:601–602

Lenhoff HM, Nicholas DJD, Kaplan NO (1956) Effects of oxygen, iron and molybdenum on routes of electron transfer in *Pseudomonas fluorescens*. J Biol Chem 220:983–995

Levy E, Gough FJ, Berlin DK, Guiana PW, Smith JT (1992) Inhibition of *Septoria tritici* and other phytopathogenic fungi and bacteria by *Pseudomonas fluorescens* and its antibiotics. Plant Pathol 41:335–341

Lewis TA, Cortese MS, Sebat JL, Green TL, Crawford RL, Lee CH (2000) A *Pseudomonas stutzeri* gene cluster encoding biosynthesis of the CC_{l4}-dechlorination agent pyridine-2, 6-bis (thiocarboxylic acid). Environ Microbiol 2:407–416

Li DM, Alexander A (1988) Co-inoculation with antibiotic-producing bacteria to increase colonization and nodulation by rhizobia. Plant Soil 108:211–219

Lifshitz R, Kloepper JW, Kozlowski M, Simonson C, Tipping EM, Zaleska I (1987) Growth promotion of canola rapeseed seedlings by a strain of *Pseudomonas putida* under gnototropic conditions. Can J Microbiol 23:390–395

Ligon JM, Hill DS, Hammer PE, Torkewitz NR, Hofmann D, Kempf HJ, van Pee KH (2000) Natural products with antifungal activity from *Pseudomonas* biocontrol bacteria. Pest Manage Sci 56:688–695

Lim H, Kim Y, Kim S (1991) *Pseudomonas stutzeri* YLP-1 genetic transformation and antifungal mechanism against *Fusarium solani*, an agent of plant root rot. Appl Environ Microbiol 57:510–516

Loper JE, Paulsen I, Bruck DJ, Pechy-Tarr M, Keel C, Gross H (2008) Genomics of secondary metabolite production by *Pseudomonas fluorescens* Pf-5. Phytopathology 98(6S):94

Lopper JE (1988) Role of fluorescent siderophore production in biological control of *Pythium ultimum* by a *Pseudomonas fluorescens* strain. Phytopathology 78:166–172

Malathi P, Viswanathan R, Padmanaban P, Mohanraj D, Ramesh Sundar A (2002) Microbial detoxification of *Colletotrichum falcatum* toxin. Curr Sci 83:6

Marek-Kozaczuk M, Skorupska A (2001) Production of B-group vitamins by plant growth-promoting *Pseudomonas fluorescens* strain 267 and the importance of vitamins in the colonization and nodulation of red clover. Biol Fertil Soils 33:146–151

Martin FN, Loper JE (1999) Soilborne plant diseases caused by *Pythium* spp.: ecology, epidemiology, and prospects for biological control. Crit Rev Plant Sci 18:111–181

Mathiyazhagan K, Sankarasubramanian H, Neelakandan K, Duraisamy S, Ramasamy S (2008) Induction of systemic resistance in banana (*Musa* spp.) against Banana bunchy top virus (BBTV) by combining chitin with root-colonizing *Pseudomonas fluorescens* strain CHAO. Eur J Plant Pathol 120(4):353–362

Matthijs S, Tehrani KA, Laus G, Jackson RW, Cooper RM, Cornelis P (2007) Tioquinolobactin a *Pseudomonas* siderophore with antifungal and anti-Pythium activity. Environ Microbiol 9:425–434

Matthijs S, Budzikiewicz H, Schafer M, Wathelet B, Cornelis P (2008) Ornicorrugatin, a new siderophore from *Pseudomonas fluorescens* AF76. Z Naturforsch C 63:8–12

Maurhofer M, Hase C, Meuwly P, Métraux JP, Défago G (1994) Induction of systemic resistance of tobacco to tobacco necrosis virus by the root-colonizing *Pseudomonas fluorescens* strain CHAO: influence of the *gac*A gene of pyoverdine production. Phytopathology 84:139–146

Mazzucchi U, Baui C, Pupillo P (1979) The inhibition of susceptible and hypersensitive reactions by protein-lipopolysaccharide complexes from phytopathogenic pseudomonads: Relationship to polysaccharide antigenic determinants. Physiol Plant Pathol 14:19–30

McCullagh M, Utkhede R, Menzies JG, Punja ZK, Paulits TC (1996) Evaluation of plant growth promoting rhizobacteria for biological control of *Pythium* root rot of cucumbers grown in rockwool and effects on yield. Eur J Plant Pathol 102:747–755

Mercado-Blanco J, van der Drift KMGM, Olsson PE, Thomas-Oates JE, van Loon LC, Bakker PAHM (2001) Analysis of the *pmsCEAB* gene cluster involved in biosynthesis of salicylic acid and the siderophore pseudomonine in the biocontrol strain *Pseudomonas fluorescens* WCS374. J Bacteriol 183:1909–1920

Meyer JM (2000) Pyoverdins: Pigments siderohores and potential taxonomic markers of fluorescent pseudomonas species. Arch Microbiol 174:135–142

Meziane H, Van der Sluis I, Van Loon LC, Höfte M, Bakker PAHM (2005) Determinants of *Pseudomonas putida* WCS358 involved in inducing systemic resistance in plants. Mol Plant Pathol 6:177–185

Mohammad D, Jesus MB, Van Loon LC, Bakker PAHM (2009) Analysis of determinants of *Pseudomonas fluorescens* WCS374r involved in induced systemic resistance in *Arabidopsis thaliana*. Biological control of fungal and bacterial plant pathogens. IOBC/WPRS Bull 43:109–112

Mossialos D, Meyer JM, Budzikiewicz H, Wolff U, Koedam N, Baysse C (2000) Quinolobactin, a new siderophore of *Pseudomonas fluorescens* ATCC 17400 whose production is repressed by the cognate pyoverdine. Appl Environ Microbiol 66:487–492

Nagrajkumar M, Jayaraj J, Muthukrishnan S, Bhaskaran R (2005) Detoxification of oxalic acid by *P.fluorescens* strain PfMDU2: implication for the biocontrol of rice sheath blight caused by *Rhizoctonia solani*. Microbiol Res 160:291–298

Nakkeeran S, Dilantha FWG, Sidduqui ZA (2005) Plant growth promoting rhizobacteria formulations and its scope in commercialization for the management of pests and diseases. In: Siddiqui ZA (ed) PGPR: biocontrol and biofertilization. Springer, Netherlands, pp 257–296

Nandkumar R, Babu S, Vishwanath R (2000) Induction of systemic resistance in rice against sheath blight disease by *Pseudomonas fluorescens*. Soil Biol Biochem 33:603–612

Neilsen MN, Sorensen J (1999) Chitinolytic activity of *Pseudomonas fluorescens* isolated from barley and sugar beet rhizosphere. FEMS Microbiol Ecol 30:217–227

Newman MA, Daniels MJ, Dow JM (1995) Lipopolysaccharide from *Xanthomonas campestris* induces defense-related gene expression in *Brassica campestris*. Mol Plant Microbe Interact 8:778–780

Nicole D, Min L, Xianwu G, Luyan M, Ricardo C-L, Claudine E (2003) Nitrogen fixation genetics and regulation in a *Pseudomonas stutzeri* strain associated with rice. Microbiology 149:2251–226

Nielsen MN, Sorensen J, Fels J, Pedersen HC (1998) Secondary metabolite and endochitinase dependent antagonism toward plant-pathogenic microfungi of *Pseudomonas fluorescens* isolates from sugar beet rhizosphere. Appl Environ Microbiol 64:3563–3569

Nielsen TH, Christophersen C, Anthoni U, Sorensen J (1999) Viscosinamide, a new cyclic depsipeptide with surfactant and antifungal properties produced by *Pseudomonas fluorescens* DR54. J Appl Microbiol 86:80–90

Nielsen TH, Thrane C, Christophersen C, Anthoni U, Sørensen J (2000) Structure, production characteristics and fungal antagonism of tensin—a new antifungal cyclic lipopeptide from *Pseudomonas fluorescens* strain 96.578. J Appl Microbiol 89:992–1001

Nielsen TH, Sorensen D, Tobiasen C, Andersen JB, Christophersen C, Giskov M, Sorensen J (2002) Antibiotic and biosurfactant properties of cyclic lipopeptides produced by fluorescent *Pseudomonas spp*. from the sugar beet rhizosphere. Appl Environ Microbiol 68:3416–3423

Niknam GR, Dawan SC (2003) Effect of seed bacterization and methods of application of *pseudomonas fluorescens* on the control of *Rotylenchulus reniformis* infecting tomato. Nematol Medit 31:231–237

Nowak-Thompson B, Gould SJ, Loper JE (1997) Identification and sequence analysis of the genes encoding a polyketide synthase required for pyoluteorin biosynthesis in *Pseudomonas fluorescens* Pf-5. Gene 204:17–24

Ongena M, Jourdan E, Adam A, Schäfer M, Budzikiewicz H, Thonart P (2008) Amino acids, iron, and growth rate as key factors influencing production of the *Pseudomonas putida* BTP1 benzylamine derivative involved in systemic resistance induction in different plants. Microb Ecol 55:280–292

Palleroni NJ (1975) General properties and taxonomy of the genus *Pseudomonas*. In: Clarke PH, Richmond MH (eds) Genetics and biochemistry of *Pseudomonas*. Wiley, Baltimore, MD, pp 1–36

Palleroni NJ (1992) Introduction to the family Pseudomonadaceae. In: Balows A, Truper HG, Dworkin M, Harder W, Schleifer KH (eds) The prokaryotes: a handbook on the biology of bacteria: ecophysiology, isolation, identification, identification, applications. Springer, New York, pp 3071–3085

Palleroni NJ, Bradbury JF (1993) *Stenotrophomonas*, a new bacterial genus for *Xanthomonas maltophilia* (Hugh 1980) Swings et al. 1983. Int J Syst Bacteriol 43:606–609

Palleroni NJ, Doudoroff M (1972) Some properties and taxonomic subdivisions of the genus *Pseudomonas*. Annu Rev Phytopathol 10:73–100

Palleroni N, Kunisawa R, Contopoulou R, Doudoroff M (1973) Nucleic acid homologies in the genus *Pseudomonas*. Int J Syst Bacteriol 23:333–339

Pandey A, Durgapal A, Joshi M, Palni LMS (1999) Influence of *Pseudomonas corrugate* inoculation on root colonization and growth promotion of two important hill crops. Microbiol Res 154:259–266

Park CS, Paulitz TC, Baker R (1988) Biocontrol of Fusarium wilt of cucumber resulting from interactions between *Pseudomonas putida* and nonpathogenic isolates of *Fusarium oxysporum*. Phytopathology 78:190–194

Pathma J, Rahul GR, Kamaraj Kennedy R, Subashri R, Sakthivel N (2011) Secondary metabolite production by bacterial antagonists. J Biol Control 25(3):165–181

Patten CL, Glick BR (2002) Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. Appl Environ Microbiol 68:3795–3801

Paulitz TC (1991) Effect of *Pseudomonas putida* on the stimulation of *Pythium ultimum* by seed volatiles of pea and soyabean. Phytopathology 81:1282–1287

Petermann SR, Sherwood JS, Logue CM (2008) The *Yersinia* high pathogenicity island is present in *Salmonella enterica* Subspecies I isolated from turkeys. Microb Pathog 45:110–114

Pfender WF, Kraus J, Loper JE (1993) A genomic region from *Pseudomonas fluorescens* Pf-5 required for pyrrolnitrin production and inhibition of *Pyrenophora tritici-repentis* in wheat straw. Phytopathology 83:1223–1228

Picard C, Di Cello F, Ventura M, Fani R, Guckert A (2000) Frequency and biodiversity of 2,4-diacetylphloroglucinol-producing bacteria isolated from the maize rhizosphere at different stages of plant growth. Appl Environ Microbiol 66:948–955

Pierson LS, Thomashow LS (1992) Cloning of heterologous expression of phenazine biosynthesis locus from *Pseudomonas aureofaciens* 30–84. Mol Plant Microbe Interact 53:330–339

Pieterse CMJ, Ton J, Van Loon LC (2001) Cross-talk between plant defence signalling pathways: boost or burden? Ag Biotech Net 3:1–7

Raaijmakers JM, Weller DM (1998) Natural plant protection by 2,4-diacetylphloroglucinol-producing *Pseudomonas* spp. in take-all decline soils. Mol Plant Microbe Interact 11:144–152

Rabindran R, Vidhyasekaran P (1996) Development of a formulation of *Pseudomonas fluorescens* pfALR2 for management of rice sheath blight. Crop Prot 15:715–721

Ralston E, Palleroni NJ, Doudoroff M (1973) *Pseudomonas pickettii*, a new species of clinical origin related to *Pseudomonas solanacearum*. Int J Syst Bacteriol 23:15–19

Raverkar KP, Konde BK (1988) Effect of *Rhizobium* and *Azospirillum lipoferum* inoculation on the nodulation, yield and nitrogen uptake of peanut cultivars. Plant Soil 106:249–25

Ravindra Naik P, Raman G, Badri Narayanan K, Sakthivel N (2008) Assessment of genetic and functional diversity of phosphate solubilizing fluorescent pseudomonads isolated from rhizospheric soil. BMC Microbiol 8:230

Reddy RM, Reddy PG, Seenayya G (1999) Enhanced production of thermostable β-amylase and pullanase in the presence of surfactants by *Clostridium thermosulfurogenes* SV2. Process Biochem 34:87–92

Rigby D, Caceres D (2001) Organic farming and the sustainability of agricultural systems. Agric Syst 68(1):21–40

Rodriguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol Adv 17:319–339

Rojan P, John GS, Anisha K, Nampoothiri M, Pandey A (2011) Micro and macroalgal biomass: a renewable source for bioethanol. Bioresour Technol 102:186–193

Rosales AM, Thomashow L, Cook RJ, Mew TW (1995) Isolation and identification of antifungal metabolites produced by rice-associated antagonistic *Pseudomonas* spp. Phytopathology 85:1028–1032

Ryu CM, Farag MA, Hu CH, Reddy MS, Kloepper JW, Paré PW (2004) Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiol 134:1017–1026

Sacherer P, Defago G, Haas D (1994) Extracellular protease and phospholipase C are controlled by the global regulatory gene *gacA* in the biocontrol strain *Pseudomonas fluorescens* CHAO. FEMS Microbiol Lett 116:155–160

Saikia R, Kumar R, Arora DK, Gogoi DK, Azad P (2006) *Pseudomonas aeruginosa* inducing rice resistance against *Rhizoctonia solani*. Production of salicylic acid and peroxidases. Folia Microbiol 51:375–380

Sakthivel N, Gnanamanickam SS (1987) Evaluation of *Pseudomonas fluorescens* for suppression of sheath rot disease and for enhancement of grain yields in rice (*Oryza sativa* L.). Appl Environ Microbiol 53:2056–2059

Sakthivel N, Sunish Kumar R (2008) Dimer of phenazine-1-carboxylic acid and to the process of preparation thereof. USPTO 7,365,194 B2

Salisbury FB (1994) The role of plant hormones. In: Wilkinson RE (ed) Plant–environment interactions. Marcel Dekker, New York, pp 39–81

Salisbury FB, Ross CW (1992) Plant physiology, 4th edn. Wadsworth, Belmont, CA, p 682

Saskia B, Kurt H, Joseph P, Monica H (1995) Involvement of pyochelin and pyoverdin in suppression of *Pythium*-induced damping-off of tomato by *Pseudomonas aeruginosa* 7nsk2. Appl Environ Microbiol 62:865–871

Scher FM, Baker R (1982) Effect of *Pseudomonas putida* and a synthetic iron chelator on induction of soil suppressiveness to Fusarium wilt pathogens. Phytopathology 72:1567–73

Shanahan P, Sullivan DJO, Simpson P, Glennon JD, Gara FO (1992) Isolation of 2,4- diacetylphloroglucinol from a fluorescent pseudomonad and investigation of physiological parameters influencing its production. Appl Environ Microbiol 58:353–358

Shapira R, Ordentlich A, Chet I, Oppenheim AB (1989) Control of plant diseases by chitinase expressed from cloned DNA in *Escherichia coli*. Phytopathology 79:1246–1249

Sharma A, Johri BN (2003) Growth promoting influence of siderophore-producing *Pseudomonas* strains GRP3A and PRS9 in maize (*Zea mays* L.) under iron limiting conditions. Microbiol Res 158:243–248

Siddiqui ZA (2006) PGPR: prospective biocontrol agents of plant pathogens. In: Siddiqui ZA (ed) Biocontrol and biofertilization. Springer, Amsterdam, pp 111–142

Siddiqui IA, Shahid Shaukat S (2003) Suppression of root-knot disease by *Pseudomonas fluorescens* CHAO in tomato: importance of bacterial secondary metabolite, 2,4-diacetylpholoroglucinol. Soil Biol Biochem 35(12):1615–1623

Singh K, Singh RP (1989) Red rot. 111. In: Ricaud C, Egan BT, Gillaspie AG Jr, Hughes CG (eds) Diseases of sugarccule: major diseases. Elsevier, Amsterdam, pp 169–188

Smith RS (1995) Inoculant formulations and applications to meet changing needs. In: Tikhonovich IA, Provorov NA, Romanov VI, Newton WE (eds) Nitrogen fixation: fundamentals and applications. Kluwer Academic, Dordrecht, pp 653–657

Sneath PHA, Stevens M, Sackin MJ (1981) Numerical taxonomy of *Pseudomonas* based on published records of substrate utilization. Anton Von Leeuwenhook 47:423–448

Sneh B, Dupler M, Elad Y, Baker R (1984) Chlamydospore germination of *Fusarium oxysporum* f. sp. *Cucumerinum* as affected by fluorescent and lytic bacteria from fusarium-suppressive soil. Phytopathology 74:1115–24

Sorensen D, Nielsen TH, Christophersen C, Sorensen J, Gajhede M (2001) Cyclic lipoundecapeptide amphisin from *Pseudomonas* sp. strain DSS73. Acta Crystallogr Sect Cryst Struct Commun 57:1123–1124

Stanier RY, Palleroni NJ, Doudoroff M (1966) The aerobic pseudomonads: a taxonomic study. J Gen Microbiol 43:159–271

Streit WR, Joseph CM, Phillips DA (1996) Biotin and other water-soluble vitamins are key growth factors for alfalfa root colonization by *Rhizobium meliloti* 1021. Mol Plant Microbe Interact 9:330–338

Sun GX, Zhou WQ, Zhong JJ (2006) Organotin decomposition by pyochelin, secreted by *Pseudomonas aeruginosa* even in an iron-sufficient environment. Appl Environ Microbiol 72:6411–6413

Sunish Kumar R, Ayyadurai N, Pandiaraja P, Reddy AV, Venkateswarlu Y, Prakash O, Sakthivel N (2005) Characterization of antifungal metabolite produced by a new strain *Pseudomonas aeruginosa* PUPa3 that exhibits broad-spectrum antifungal activity and biofertilizing traits. J Appl Microbiol 98:145–154

Suslow TV, Schroth MN (1982) Rhizobacteria of sugar beets: effects of seed application and root colonization on yield. Phytopathology 72:199–206

Thomashow LS, Weller DM (1988) Role of a phenazine antibiotic from *Pseudomonas fluorescens* in biological control of *Gaeumannomyces graminis* var. *tirtici*. J Bacteriol 170:3499–3508

Thomashow LS, Weller DM, Bonsall RF, Pierson LS (1990) Production of the antibiotic phenazine-1-carboxylic acid of fluorescent *Pseudomonas* species in the rhizosphere of wheat. Appl Environ Microbiol 56:908–912

Thrane C, Olsson S, Nielsen TH, Sorensen J (1999) Vital fluorescent stains for detection of stress in *Pythium ultimum* and *Rhizoctonia solani* challenged with viscosinamide from *Pseudomonas fluorescens* DR54. FEMS Microbiol Ecol 30:11–23

Thrane C, Nielsen TH, Nielsen MN, Sørensen J, Olsson S (2000) Viscosinamide-producing *Pseudomonas fluorescens* DR54 exerts a biocontrol effect on *Pythium ultimum* in sugar beet rhizosphere. FEMS Microbiol Ecol 33:139–146

Tombolini R, van der Gaag DJ, Gerhardson B, Jansson JK (1999) Colonization pattern of the biocontrol strain *Pseudomonas chlororaphis* MA342 on barely seeds visualized by using green fluorescent protein. Appl Environ Microbiol 65:3674–3680

Tran H, Ficke A, Asiimwe T, Hofte M, Raaijmakers JM (2007) Role of the cyclic lipopeptide massetolide A in biological control of *Phytophthora infestans* and in colonization of tomato plants by *Pseudomonas fluorescens*. New Phytol 175:731–742

Uthede RS, Koch CA, Menzies JG (1999) Rhizobacterial growth and yield promotion of cucumber plants inoculated with *Pythium aphanidermatum*. Can J Plant Pathol 21:265–271

Van Loon LC, Bakker P, Pieterse CMJ (1998) Systemic resistance induced by rhizosphere bacteria. Annu Rev Phytopathol 36:453–483

Van Peer R, Schippers B (1988) Plant growth responses to bacterization with selected *Pseudomonas* spp. strains and rhizospheres microbial development in hydroponic cultures. Can J Microbiol 35:456–463

Van Peer R, Schippers B (1992) Lipopolysaccharides of plant growth-promoting *Pseudomonas* sp. strain WCS417r induce resistance in carnation to fusarium wilt. Neth J Plant Pathol 98:129–139

Van Peer R, Niemann GJ, Schippers B (1991) Induced resistance and phytoalexin accumulation in biological control of Fusarium wilt of carnation by *Pseudomonas* sp. strain WCS417r. Phytopathology 81:728–734

Van Wees SCM, Pieterse CMJ, Trijssenaar A, Van T, Westende YAM, Hartog F, van Loon LC (1997) Differential induction of systemic resistance in *Arabidopsis* by biocontrol bacteria. Mol Plant Microbe Interact 10:716–724

Velazhahan R, Datta SK, Muthukrishnan S (1999) The PR-5 family: thaumatin-like proteins. In: Datta SK, Muthukrishnan S (eds) Pathogenesis-related proteins in plants. CRC, Boca Raton, FL, pp 107–129

Verhagen BWM, Trotel-Aziz P, Couderchet M, Hofte M, Aziz A (2010) *Pseudomonas* spp.-induced systemic resistance to *Botrytis cinerea* is associated with induction and priming of defence responses in grapevine. J Exp Bot 61:249–260

Vessey KJ (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Vijay Krishna Kumar K, Krishnam Raju S, Reddy MS, Kloepper JW, Lawrence KS, Groth DE, Miller ME, Sudini H, Binghai D (2009) Evaluation of commercially available PGPR for control of rice sheath blight caused by *Rhizoctonia solani*. J Pure Appl Microbiol 3:485–488

Vincent MN, Harrison LA, Brackin JM, Krovacevich PA, Mukerji P, Weller DM, Pierson EA (1991) Genetic analysis of antifungal activity of a soilborne *Pseudomonas aurofaciens* strain. Appl Environ Microbiol 57:2928–2934

Viswanathan R, Samiyappan R (1999a) Induction of systemic resistance by plant growth-promoting rhizobacteria against red rot disease caused by *Colletotrichum falcatum* went in sugarcane. Proc Sugar Technol Assoc India 61:24–39

Viswanathan R, Samiyappan R (1999b) Identification of anti-fungal chitinases from sugarcane. ICAR News 5:1–2

Viswanathan R, Samiyappan R (2000) Antifungal activity of chitinases produced by some fluorescent pseudomonas against Colletotrichum falcatum Went causing rot disease in sugarcane. Microbiol Res 155:1–6

Viswanathan R, Rajitha R, Ramesh Sundar A, Ramamoorthy V (2003) Isolation and identification of endophytic bacterial strains from sugarcane stalks and their *In Vitro* antagonism against the red rot pathogen. Sugarcane 5:25–29

Vleesschauwer DD, Hofte M (2005) Bacterial determinants involved in systemic resistance in rice. In: Gnanamanickam SS, Balasubramanian R, Anand N (eds) Asian conference on emerging trends in plant-microbe interactions, Chennai, India, pp 1–4

Voisard C, Keel C, Haas D, Defago G (1989) Cyanide production by *Pseudomonas fluorescens* helps suppress black root rot of tobacco under gnotobiotic conditions. EMBO J 8:351–358

Wang C, Knill E, Glick BR, Defago G (2000) Effect of transferring 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase genes into *Pseudomonas fluorescens* strain CHA0 and its derivative CHA96 on their growth-promoting and disease-suppressive capacities. Can J Microbiol 46:1–10

Wang R, Korboulewsky N, Prudent P, Baldy V, Bonin G (2009) Can vertical-flow wetland systems treat high concentrated sludge from a food industry? A mesocosm experiment testing three plant species. Ecol Eng 35:230–237

Weisbeek PJ, van der Hofstad GAJM, Schippers B, Marugg JD (1986) Genetic analysis of the iron uptake system of two plant growth promoting *Pseudomonas* strains. NATO ASI Ser A 117:299–313

Weller DM, Cook RJ (1983) Suppression of take-all of wheat by seed treatments with fluorescent pseudomonads. Phytopathology 73:463–469

Weller DM, Cook RJ (1986) Increased growth of wheat by seed treatment with fluorescent pseudomonads, and implications of *Pythium* control. Can J Microbiol 8:328–334

Whalen M, Innes R, Bent A, Staskawicz B (1991) Identification of *Pseudomonas syringae* pathogens of *Arabidopsis thaliana* and a bacterial gene determining avirulence on both Arabidopsis and soybean. Plant Cell 3:49–59

Wie G, Kloepper JW, Tuzun S (1991) Induction of systemic resistance of cucumber to *Colletotrichum orbiculare* by select strains of plant growth-promoting rhizobacteria. Phytopathology 81:1508–1512

Xie H, Pasternak JJ, Glick BR (1996) Isolation and characterization of mutants of the plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2 that overproduce indoleacetic acid. Curr Microbiol 32:67–71

Xu GW, Gross DC (1986) Field evaluations of the interactions among fluorescent pseudomonads, *Erwinia caratovora* and potato yields. Phytopathology 76:423–430

Yan Y, Ping S, Peng J, Han Y, Li L, Yang J, Dou Y, Li Y, Fan H, Fan Y, Li D, Zhan Y, Chen M, Lu W, Zhang W, Cheng Q, Jin Q, Lin M (2010) Global transcriptional analysis of nitrogen fixation and ammonium repression in root-associated *Pseudomonas stutzeri* A1501. BMC Genomics 11:11

Youard ZA, Mislin GL, Majcherczyk PA, Schalk IJ, Reimmann C (2007) *Pseudomonas fluorescens* CHAO produces enantio- pyochelin, the optical antipode of the *Pseudomonas aeruginosa* siderophore pyochelin. J Biol Chem 282:35546–35553