Plant Growth-Promoting Rhizobacteria: Harnessing Its Potential for Sustainable Plant Disease Management

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S. Harish, S. Parthasarathy, D. Durgadevi, K. Anandhi, and T. Raguchander

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Abstract

The sustainable plant disease management includes the use of beneficial microbes for the effective and sustained production of crop/plants. Numerous species of soil bacteria/rhizobacteria and fungi exist in the rhizosphere of plants which can counteract the pathogenic organisms and stimulate plant growth through direct/indirect mode of action. The plant growth-promoting rhizobacteria (PGPRs),

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S. Harish (✉)
Department of Plant Pathology, Agricultural College & Research Institute, Tamil Nadu Agricultural University, Madurai, Tamil Nadu, India

S. Parthasarathy · D. Durgadevi · T. Raguchander
Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

K. Anandhi
Krishi Vigyan Kendra, Agricultural College & Research Institute, Tamil Nadu Agricultural University, Madurai, Tamil Nadu, India

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viz., *Pseudomonas*, *Bacillus*, and *Streptomyces*, have been well exploited by scientists for the management of plant diseases in economically important agricultural and horticultural crops. In nature, interactions between the pathogenic and beneficial microbes take place which decides the existence of the pathogen in the rhizosphere region. Interaction of PGPR with pathogens in the rhizosphere may lead to an expression of innate immune response of defense genes in the plants which can counter the pathogen infection. This review helps in understanding the dynamics and existence of PGPR in the soil, their role in disease management, and their interaction with the pathogens which explore the possibility of identifying new proteins/genes in host-pathogen interaction. In addition, commercial production of bioagents with the suitable carrier material and delivery system play a major role in managing plant diseases under field conditions. The exploration for PGPR and study of their modes of action are escalating at a rapid pace, as efforts are made to exploit them commercially as bioinoculants.

Keywords

Antibiosis · *Bacillus* sp. · Competition · Induced systemic resistance · Lytic enzymes · *Pseudomonas* sp.

8.1 Introduction

Sustainable agriculture practices involves soil health maintanence, usage of minimal water, and minimize the pollution level in the environment which subsequently increases the food grain production in the country. During the cultivation of crops, biotic stress caused by plant pathogens is a major concern which incurs huge economical loss to the farmers. Various agrochemicals are being utilized by the farmers for the management of the diseases caused by plant pathogens. However, their use is increasingly restricted due to public concerns over toxic residues, development of resistance in the pathogens, and increased expenditure for plant protection. Exploitation of microbe-based management will be an alternative approach to control this disease. In nature, soil harbors numerous beneficial microorganisms with potential genes for governing resistance and promoting plant growth which can be well exploited for managing the plant diseases. The PGPR is currently applied in an extensive array of agri- and horticultural production systems in the form of bioinoculants in a variety of economically significant plants including cereals, millets, pulses, oilseeds, fiber crops, sugar crops, fruits, vegetables, medicinal crops, spices, condiments, ornaments, fodder, and cash crops for augmenting their growth and productivity. Free-living, nonpathogenic, root-colonizing bacteria have been studied for the past century as possible inoculants for increasing plant productivity (Kloepper et al. 1992).

In the last few decades, a large array of bacteria including species of *Alcaligenes*, *Aeromonas*, *Azotobacter*, *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Acinetobacter*, *Agrobacterium*, *Aneurinibacillus*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Gluconacetobacter*, *Gluconobacter*, *Herbaspirillum*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Rhodococcus*, *Saccharothrix*, *Serratia*, *Thiobacillus*, and *Variovorax* are considered as important PGPR (Dobbelaere et al. 2003; Crepin et al. 2012; Annapurna et al. 2013). These effective rhizobacteria are used in sustainable agriculture as biofertilizers and biocontrol agents (Babalola 2010). Several studies have depicted proteobacteria especially bacteria from family *Pseudomonadaceae* or *Burkholderiaceae* as dominant members of rhizosphere microflora in field conditions (Peiffer et al. 2013).

Rhizobacteria can survive in soil or seed, multiply in the spermosphere in response to seed exudates, get attached to the root surface (Suslow 1980), and later become endophytic by colonizing in root cortex region. They are sporadically dispersed along roots and are distributed in a lognormal pattern in the rhizosphere (Bahme and Schroth 1987). Various PGPR strains screened under laboratory, greenhouse, and field conditions against phytopathogens have been commercialized. The commercially utilized efficient PGPR strains include species of *Agrobacterium*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Delftia*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Rhizobium*, and *Serratia* (Glick 2012). Although various strains of PGPR have been isolated, there is a gap in identification of efficient crop-specific strain with good colonizing ability possessing antagonistic and growth-promoting genes. Also, the type of formulation used for mass multiplication of these biocontrol agents is more important which will help to establish itself in the field for a considerable period of time.

The molecular markers, of late, can be utilized for identification and screening of the efficient strain in a short span of time. Besides, understanding the mode of action of PGPR through genomic and proteomic approaches will help in depicting its role in plant disease management. With this background, this review will address the major PGPR strains utilized in agricultural and horticultural crops for plant disease management, highlight the various mode of action exhibited by these beneficial bacteria against soilborne diseases, and also discuss on the various bioformulations used for the management of plant diseases which will pay a way for sustainable agriculture.

8.2 PGPR in Plant Disease Management

PGPRs are the distinct group of microbes that suppress the deleterious pathogens in crop plants. The genera normally used as biocontrol agents are *Agrobacterium*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Streptomyces*, etc. Among the diversity of PGPR, *Pseudomonas* and *Bacillus* spp. have a wide distribution and are the extensively studied genera for PGPR as a biocontrol. In particular, the soilborne fluorescent pseudomonads have received particular interest due to its excellent root-colonizing abilities and their capacity to produce a wide range of antifungal metabolites (Olivain et al. 2004). These organisms combat the plant disease by competition, enzymatic lysis, production of antibiotics, hydrogen cyanide, siderophores, induced systemic resistance (ISR), or any other mechanisms. The rhizosphere soil is an active site with complex interactions between the root and the associated PGPR (Sylvia et al. 1998). At this point, the PGPR enhances plant growth and development by direct and/or indirect mechanisms. Direct mechanisms elicit growth promotion by biological nitrogen fixation (BNF), production of hormones such as indole-3-acetic acid (IAA), gibberellic acid (GA_3), cytokinin and phosphate, potassium and zinc solubilization or mobilization (Idris et al. 2008), production of siderophores for sequestering of iron (Fe) from the soil and supply it to the plants and synthesis of hydrogen cyanide, etc. (Keel and Defago 1997). Some strains improve the innate ability to tolerate the stresses like acidity, salinity, drought, etc., besides production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme to lower the ethylene synthesis and synthesis of fungal cell wall lytic enzymes.

Secondly, indirect mechanisms include suppression of harmful/deleterious rhizosphere microbes through induced systemic resistance (ISR), which are normally recognized as having a role in biocontrol (Dobbelaere et al. 2003). Induced systemic resistance is based on the activation of plant defense mechanisms by rhizobacterial strains and is considered natural, eco-friendly, and safe besides providing resistance against a broad spectrum of pathogens (Sticher et al. 1997). The rhizobacteria need to colonize the roots to a sufficient level for induction of resistance in the host. For example, in radish, a minimal number of 10^5 colony-forming units (cfu) per g root of bacteria is required to induce resistance in the host (Raaijmakers et al. 1995). Colonization of plants by biocontrol agents induces cell wall modifications, viz., deposition of callose, pectin, cellulose, and phenolic compounds leading to the formation of a structural barrier at the site of potential attack by phytopathogens (Benhamou et al. 2000). Defense reaction occurs due to accumulation of PR proteins (chitinase, β-1,3-glucanase), phenylalanine ammonia lyase, peroxidase, phenolics, callose, lignin, and phytoalexins (Harish et al. 2009b).

The successful establishment of an introduced PGPR depends on its compatibility/establishment with the crop and also on its interaction with indigenous microflora. An ideal PGPR should be rhizosphere competent, enhance plant growth, be easy to mass multiply, possess broad spectrum of action, have consistent biological control activity, be safe to the environment, and be compatible with other rhizobacteria (Nakkeeran et al. 2005; Barea, 2015). Therefore, identification of a functional PGPR strain possessing the growth-promoting and broad-spectrum biocontrol activity is an ever-challenging one. Utilization of molecular tools to identify the antibiotic biosynthetic genes, quorum quenching/sensing genes, and growth-promoting genes in PGPR will pay way for the selection of efficient microbes in a short span of time (Fig. 8.1). Besides, updating the knowledge on the utilization of PGPR for plant disease management is the need of the day. This review, therefore, will focus on some novel and highly utilized PGPR in disease management with special reference to the genera *Pseudomonas* and *Bacillus*.

Various research groups throughout the world have utilized PGPR strains that were found to be successful in combating the major diseases of field and horticultural crops (Kloepper and Schroth 1978) through direct/indirect mode of action along with plant growth promotion activity (Tables 8.1 and 8.2). The enhancement

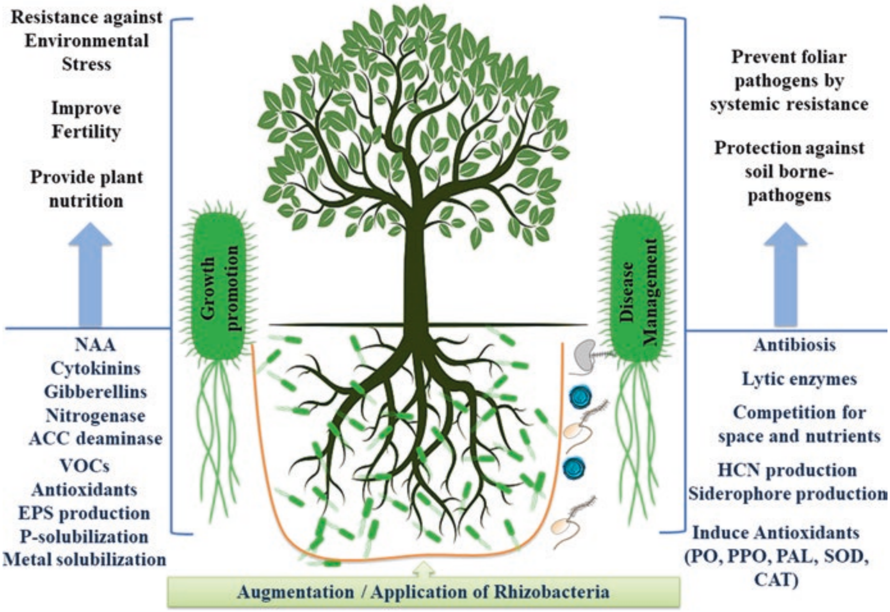

Fig. 8.1 Proposed model for PGPR-mediated plant growth promotion and disease management

of plant growth by PGPR indicates their potential as biofertilizers and biocontrol agents in the field of agriculture (Kloepper and Adesemaye 2009).

8.3 Plant Growth Promotion (PGP) Activities

The studies on the mechanism of growth promotion indicated that PGPR promotes plant growth directly by the production of plant growth regulators (PGR) or indirectly by stimulating nutrient uptake, by producing siderophores or antibiotics to protect plants from soilborne pathogens or deleterious rhizosphere organisms (Kavino et al. 2010). Barea et al. (2005) reported phosphate-solubilizing bacteria (PSB) positive for IAA, GA_3, and cytokinin production. Several isolates of *Pseudomonas* produced auxin or cytokinin and gibberellin.

Fluorescent pseudomonads increased the plant growth of rice and cotton by ~27% and 40%, respectively, when the bacteria were applied to the seed (Sakthivel and Gnanamanickam 1987). Seeds treated with fluorescent pseudomonads resulted in increased number of tillers and grain yield in addition to control of sheath blight disease in rice (Mew and Rosales 1992). An increase in germination of ~30 to 60% in maize by plant growth-promoting strains of *P. aeruginosa* strain 7NSK2 and *P. fluorescens* ANP15 was observed by Hofte et al. (1991). Fluorescent *Pseudomonas* strains improved vegetative sett germination, plant height, cane diameter, brix values, and cane weight in sugarcane (Viswanathan and Samiyappan 1999). Indirect

Table 8.1 Plant growth-promoting rhizobacteria in field crop diseases management

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
Rice	*Magnaporthe grisea*	*Pseudomonas fluorescens*, *Bacillus polymyxa*, *P. fluorescens*	Gnanamanickam and Mew (1992), Vidhyasekaran et al. (1997), and Karpagavalli et al. (2002)
	Pyricularia oryzae	*P. fluorescens*, *Bacillus* sp., *Streptomyces sindeneusis*, *Bacillus amyloliquefaciens*, *Bacillus subtilis*, *Bacillus megaterium*, *Bacillus pumilus*, *Paenibacillus kribbensis*, *Pseudomonas aeruginosa*, *Pseudomonas putida*	Krishnamurthy and Gnanamanickam (1998), Vidhyasekaran and Muthamilan (1999), Nandakumar et al. (2001), Kanajanamaneesathian et al. (2007), Yang et al. (2009), Zarandi et al. (2009), Guo and Liao (2014), Srivastava et al. (2016), and Rais et al. (2017)
	Rhizoctonia solani	*P. fluorescens*, *B. subtilis*	Rabindran and Vidhyasekaran (1996) and Kumar et al. (2012)
	Sarocladium oryzae	*P. fluorescens*, *P. aeruginosa*	Sakthivel and Gnanamanickam (1987) and Sunish kumar et al. (2005)
	Xanthomonas oryzae pv. *oryzae*	*P. fluorescens*, *P. aeruginosa*, *B. subtilis*, *Lysobacter antibioticus*, *Bacillus lentus*, *Bacillus cereus*, *Bacillus circulans*	Vidhyasekaran et al. (2001). Velusamy and Gnanamanickam (2003), Ji et al. (2008), and Yasmin et al. (2016)
Wheat	*Tilletia laevis*	*P. fluorescens*	McManus et al. (1993)
	Helminthosporium sativum	*P. fluorescens*	Ping et al. (1999)
	Gaeumannomyces graminis var. *tritici*	*P. fluorescens*, *Pseudomonas chlororaphis*	Pierson and Thomashow (1992) and Mazzola et al. (2004)
	Microdochium nivale	*Pseudomonas brassicacearum*	Levenfors et al. (2008)
	Septoria tritici	*P. aeruginosa*	Flaishman et al. (1990)
	Fusarium culmorum	*P. fluorescens*	Khan and Doohan (2009)
	Fusarium graminearum	*Lysobacter enzymogenes*	Jochum et al. (2006)
	Mycosphaerella graminicola	*B. megaterium*	Kildea et al. (2008)
Barley	*Pythium ultimum*	*P. fluorescens*	Gutterson et al. (1986)
	F. culmorum	*P. fluorescens*	Khan and Doohan (2009)
	Pyrenophora teres	*P. fluorescens*	Khan et al. (2010)
Maize	*P. ultimum*, *Pseudomonas arrhenomanes*	*Burkholderia cepacia*	Mao et al. (1998)
	P. ultimum	*P. fluorescens*	Callan et al. (1990)

(continued)

Table 8.1 (continued)

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
	Peronosclerospora sorghi	*B. subtilis*, *P. fluorescens*	Sadoma et al. (2011)
	Fusarium verticillioides	*P. fluorescens*, *B. amyloliquefaciens*	Nayaka et al. (2009) and Pereira et al. (2010)
	F. culmorum	*P. fluorescens*	Khan and Doohan (2009)
	Helminthosporium maydis	*B. subtilis*, *B. cereus*	Lu et al. (2006) and Yun-feng et al. (2012)
	Erwinia carotovora	*Bacillus thuringiensis*	Dong et al. (2004)
	Stenocarpella maydis	*B. subtilis*, *P. fluorescens*, *Pantoea agglomerans*	Petatan-Sagahon et al. (2011)
	R. solani	*B. subtilis*	Muis and Quimiob (2006)
	Fusarium moniliforme	*Bacillus* sp., *Pseudomonas* sp.	Pal et al. (2001)
Sorghum	*P. ultimum*	*P. fluorescens*	Idris et al. (2008)
	Macrophomina phaseolina	*P. chlororaphis*	Das et al. (2008)
	Sclerospora graminicola	*B. pumilus*, *B. subtilis*	Raj et al. (2003)
	Erwinia carotovora subsp. *atroseptica*	*P. chlororaphis*	Das et al. (2008)
Pearl millet	*Sclerospora graminicola*	*P. fluorescens*	Umesha et al. (1998)
Ragi	*P. grisea*	*P. fluorescens*	Vanitha (1998)
Foxtail millet	*M. grisea*	*P. fluorescens*	Karthikeyan and Gnanamanickam (2008)
Pigeon pea	*Macrophomina phaseolina*	*P. fluorescens*	Siddiqui et al. (1998)
	Fusarium udum	*Bacillus licheniformis*	Singh et al. (2002)
Chickpea	*P. ultimum*	*B. pumilus*, *Streptomyces lydicus*, *Streptomyces griseoviridis*	Leisso et al. (2009)
	F. oxysporum f. sp. *ciceri*	*P. aeruginosa*, *Bacillus macerans*, *B. megaterium*	Anjaiah et al. (2003), Landa et al. (2004), and Saikia et al. (2006)
	M. phaseolina	*P. putida*, *P. polymyxa*	Akhtar and Siddiqui (2007)
	Rhizoctonia bataticola	*P. fluorescens*	Ahamad et al. (2000)
Mung bean	*M. phaseolina*	*Burkholderia* sp.	Satya et al. (2011)
Soya bean	*P. ultimum*	*P. putida*	Paulitz (1991)
	Sclerotinia sclerotiorum	*B. subtilis*	Zhang et al. (2011) and Zeng et al. (2012)
	F. oxysporum	*B. subtilis*	Zhang et al. (2009)
	F. graminearum		

(continued)

Table 8.1 (continued)

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
	Soyabean stunt virus	*P. aeruginosa*	Khalimi and Suprapta (2011)
Groundnut	*S. rolfsii*	*P. fluorescens*	Vanitha (1998), and Abd-Allah and El-Didamony (2007)
		B. subtilis	
	Aspergillus niger	*P. aeruginosa*, *Pseudomonas* sp.	Kishore et al. (2005a) and Anjaiah et al. (2006)
		Bacillus sp.	
	Aspergillus flavus	*B. megaterium*	Kong et al. (2010)
	Puccinia arachidis	*P. fluorescens*	Meena et al. (1999)
	M. phaseolina	*P. fluorescens*	Shanmugam et al. (2002)
Sesame	*P. ultimum*	*P. polymyxa*	Ryu et al. (2006)
	M. phaseolina	*P. fluorescens*	Jayashree et al. (2000)
Sunflower	*Plasmopara halstedii*	*B. pumilus*	Nandeeshkumar et al. (2008)
	Sunflower necrosis virus	*Streptomyces fradiae*, *B. licheniformis*	Srinivasan and Mathivanan (2011)
Safflower	*M. phaseolina*	*P. fluorescens*	Prashanthi et al. (2000)
Rapeseed	*S. sclerotiorum*	*B. subtilis*, *P. chlororaphis*	Fernando et al. (2007) and Yang et al. (2009)
		B. amyloliquefaciens	
Cotton	*P. ultimum*	*Enterobacter cloacae*, *Acinetobacter calcoaceticus*, *P. fluorescens*	Nelson (1988), van Dijk and Nelson (1998), and Hagedorn et al. (1990)
	Verticillium dahliae	*Pseudomonas* sp., *Serratia plymuthica*	Erdogan and Benlioglu (2010)
	Thielaviopsis basicola	*Paenibacillus alvei*	Schoina et al. (2011)
	R. solani	*P. fluorescens*, *Pseudomonas cepacia*	Hagedorn et al. (1990), Cartwright et al. (1995), and Ligon et al. (2000)
	X. campestris pv. *malvacearum*	*P. fluorescens*, *B. cereus*	Mondal et al. (2000) and Ishida et al. (2008)
Sugarcane	*Colletotrichum falcatum*	*P. putida*	Viswanathan and Samiyappan (2002)
Sugar beet	*Pythium ultimum* var. *ultimum*	*L. enzymogenes*	Palumbo et al. (2005)
	P. ultimum	*Stenotrophomonas maltophilia*	Dunne et al. (1998)
	R. solani	*P. fluorescens*	Nielsen et al. (1998)
	Cercospora beticola	*B. subtilis*	Collins and Jacobsen (2003)

Table 8.2 Plant growth-promoting rhizobacteria in horticultural crop diseases management

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
Tomato	*P. ultimum*	*P. fluorescens*, *B. subtilis*	Hultberg et al. (2000) and Jayaraj et al. (2005)
	Pythium aphanidermatum	*P. fluorescens*	Ramamoorthy et al. (2001)
	Pythium splendens	*P. aeruginosa*	Buysens et al. (1994)
	Phytophthora infestans	*B. pumilus*, *P. fluorescens*	Yan et al. (2002)
	F. oxysporum f. sp. *lycopersici*	*P. fluorescens*, *S. griseoviridis*	Chin-A-Woeng et al. (1998), Dekkers et al. (2000), Khan and Akram (2000), Minuto et al. (2006), and Omar et al. (2006)
		P. fluorescens, *P. chlororaphis*	
		B. megaterium, *B. cepacia*	
	Alternaria solani	*P. fluorescens*	Geels and Schippers (1983)
	S. rolfsii	*P. fluorescens*, *B. amyloliquefaciens*	Thiribhuvanamala et al. (1999) and Jetiyanon et al. (2003)
	R. solani	*P. fluorescens*	Geels and Schippers (1983) and Szezech and Shoda (2006)
		B. subtilis	
	Ralstonia solanacearum	*P. putida*	Amith et al. (2004)
	X. axonopodis pv. *vesicatoria*	*B. pumilus*	Ji et al. (2006)
	Pseudomonas syringae pv. *tomato*	*P. syringae*, *P. putida*, *P. fluorescens*	Van Peer et al. (1991), Wilson et al. (2002), and Matilla et al. (2010)
	Clavibacter michiganensis subsp. *michiganensis*	*B. subtilis*	Utkhede and Koch (2004)
Potato	*P. ultimum*	*E. cloacae*	Kageyama and Nelson (2003)
	P. infestans	*P. fluorescens*, *S. plymuthica*	Glass et al. (2001) and Slininger et al. (2007)
	Phytophthora erythroseptica	*E. cloacae*, *Enterobacter* sp.	Schisler et al. (2009)
		Pseudomonas sp.	
	R. solani	*P. fluorescens*	Grosch et al. (2005)
	Fusarium sp.	*P. fluorescens*	Al-Mughrabi (2010)
	Verticillium dahliae	*P. fluorescens*	Uppal et al. (2008)
	F. roseum var. *sambucinum*	*B. licheniformis*, *B. cereus*	Sadfi et al. (2002)

(continued)

Table 8.2 (continued)

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
	Gibberella pulicaris	*P. agglomerans*	Schisler et al. (2000)
		P. fluorescens	
	Helminthosporium solani	*B. cereus*, *P. putida*, *Rhodococcus erythropolis*	Martinez et al. (2002)
		Rhodococcus globerulus	
	E. carotovora subsp. *atroseptica*	*P. fluorescens*	Cronin et al. (1997)
	Pectobacterium atrosepticum	*R. erythropolis*	Crepin et al. (2012)
	Streptomyces scabies	*Pseudomonas mosselii*	Singhai et al. (2011)
Carrot	*P. ultimum*	*E. cloacae*	Kageyama and Nelson (2003)
	Alternaria radicina	*B. cepacia*, *B. amyloliquefaciens*	Chen and Wu (1999)
Brinjal	*R. solanacearum*	*P. fluorescens*	Chakravarty and Kalita (2011)
Chillies	*Phytophthora capsici*	*Bacillus* sp.	Jiang et al. (2006)
		S. plymuthica	Kim et al. (2008)
		B. megaterium	Akgül and Mirik (2008)
	Colletotrichum capsici	*P. fluorescens*, *B. subtilis*	Bharathi et al. (2004)
	Colletotrichum sp.	*P. fluorescens*	Hegde and Anahosur (2001)
	Colletotrichum acutatum	*Myxococcus* sp.	Kim and Yun (2011)
	R. solani	*Chromobacterium* sp.	Kim et al. (2008)
	F. oxysporum f. sp. *capsici*	*B. licheniformis*, *P. fluorescens*, *Chryseobacterium balustinum*, *B. subtilis*, *B. amyloliquefaciens*	Domenech et al. (2006)
		P. fluorescens, *B. subtilis*	Sundaramoorthy et al. (2012)
	S. rolfsii	*Streptomyces philanthi*	Boukaew et al. (2011)
Onion	*Botrytis allii*	*B. licheniformis*, *B. amyloliquefaciens*	Lee et al. (2001)
	F. oxysporum	*B. amyloliquefaciens*	
Garlic	*Penicillium hirsutum*	*P. agglomerans*	Kim et al. (2006)
Cassava	*P. aphanidermatum*	*B. pumilus*	Pereira de Melo et al. (2009)
	R. solani		
	S. rolfsii		

(continued)

Table 8.2 (continued)

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
	X. campestris pv. *manihotis*	*B. cereus*, *B. subtilis*, *Pseudomonas* sp.	Amusa and Odunbaku (2007)
Pea	*P. ultimum*	*P. fluorescens*	Naseby et al. (2001)
	Pythium sp.	*P. cepacia*, *P. fluorescens*	Parke et al. (1991)
	P. infestans	*B. pumilus*	Yan et al. (2002)
	Aphanomyces euteiches	*B. mycoides*	Wakelin et al. (2002)
	P. syringae pv. *syringae*	*P. fluorescens*	Seuk et al. (2001)
Beans	*P. splendens*	*P. aeruginosa*	Anjaiah et al. (1998)
	Colletotrichum lindemuthianum	*P. chlororaphis*	Lagopodi (2009)
	Botrytis cinerea	*B. subtilis*	Ongena et al. (2007)
Radish	*F. oxysporum* f. sp. *raphani*	*P. fluorescens*	Leeman et al. (1996)
		P. putida	Scher and Baker (1982)
	P. ultimum	*E. cloacae*	Kageyama and Nelson (2003)
Beetroot	*P. debaryanum*, *P. ultimum*	*P. fluorescens*	Dodd and Stewart (1992)
Cabbage	*P. brassicae*	*Pseudomonas* sp.	Hjort et al. (2010)
Yam	*Botryodiplodia theobromae*	*B. subtilis*	Swain et al. (2008)
	F. moniliforme	*B. subtilis*	Okigbo (2002)
	Penicillium sclerotigenum	*Pseudomonas* sp.	
Lettuce	*R. solani*	*P. fluorescens*	Grosch et al. (2005)
	P. ultimum	*P. fluorescens*	Crawford et al. (1993)
Cauliflower	*F. moniliforme*	*P. fluorescens*	Rajappan and Ramaraj (1999)
Cucumber	*P. ultimum*	*P. fluorescens*	Georgakopoulos et al. (2002)
		E. cloacae	Kageyama and Nelson (2003)
	P. aphanidermatum	*L. enzymogenes*	Folman et al. (2004)
	Fusarium sp.	*P. fluorescens*	Brovko and Brovko (2000)
	F. oxysporum	*P. putida*	Park et al. (1988)
	F. oxysporum f. sp. *cucumerinum*	*P. aeruginosa*	Bradley and Punja (2010)
Cabbage	*X. campestris* pv. *campestris*	*Bacillus velezensis*	Liu et al. (2016)
Carnation	*F. oxysporum* f. sp. *dianthi*	*P. fluorescens*	Van Peer and Schippers (1992)
	P. cinnamomi	*P. fluorescens*	Sorokina et al. (1999)

(continued)

Table 8.2 (continued)

Crop	Pathogen	Plant growth-promoting rhizobacteria	References
Tea	*Exobasidium vexans*	*P. fluorescens*	Saravanakumar et al. (2007b)
Peppermint	*R. solani*	*P. fluorescens*	Kamalakannan et al. (2003)
Mango	*Colletotrichum gloeosporioides*	*P. fluorescens*	Koomen and Jeffris (1993) and Vivekananthan et al. (2004)
	Lasiodiplodia theobromae	*P. fluorescens*, *B. subtilis*	Parthasarathy et al. (2016)
Banana	*BBTV*	*P. fluorescens, Bacillus sp.*	Harish et al. (2008a)
Apricot, peach	*Leucostoma cinctum*	*P. fluorescens*	Rozsnyay et al. (1992)
Apple	*Venturia inaequalis*	*P. fluorescens*	Kucheryava et al. (1999)
Grapevine	*Plasmopara viticola*	*B. subtilis*	Furuya et al. (2011)
Raspberry	*Phytophthora fragariae* var. *rubi*	*Streptomyces* sp.	Valois et al. (1996)
Arabidopsis	*P. syringae* pv. *lachrymans*	*P. putida*	Wei et al. (1996)
	P. aphanidermatum	*Peanibacillus polymyxa*	Timmusk et al. (2009)
	Hyaloperonospora parasitica	*P. fluorescens*	Iavicoli et al. (2003)
Asparagus	*Phytophthora megasperma*	*P. chlororaphis*	Carruthers et al. (1995)
Chrysanthemum	*P. aphanidermatum*, *Pythium dissotocum*	*P. fluorescens*	Liu et al. (2007)
Mushroom	*Pseudomonas tolaasii*	*P. fluorescens*	Bora et al. (2000)
Tobacco	*P. ultimum*	*P. fluorescens*	Howell and Stipanovic (1979)
	Peronospora tabacina	*S. marcescens*	Zhang et al. (2001)

stimulus of plant growth contains a range of mechanisms by which the bacteria protect plants from phytopathogens (Glick 2012). The PGPR strains, viz., *Paenibacillus* sp. *Azospirillum brasilense*, *B. subtilis* subsp. *subtilis*, *B. kururiensis*, and *P. stutzeri*, enhanced biomass production in several trees and nursery saplings (Radhapriya et al. 2018). Also, the application of *Bacillus* spp. in the plant system facilitates plant growth promotion (Gange and Gadhave 2018). The enzyme ACC deaminase secreted by PGPR lowers the plant ethylene levels that are produced during stress conditions and thus directly protects the plant from retardation (Glick 1995). The significance of ACC deaminase gene has been documented in many of the crops which promote plant growth under various conditions (Mayak et al. 2004). Seed bacterization with fluorescent pseudomonads GRC2 resulted in improved seed germination, pod yield, and reduced charcoal rot disease incidence caused by *M. phaseolina* in peanut (Gupta et al. 2002). Similarly, application of *P. fluorescens* Pf1 as seed treatment followed by soil application enhanced the plant growth and has better native rhizobium nodulation and grain yield in legumes (Jayashree et al. 2000). Thus application of PGPR strain promoted the growth of crop by direct and indirect means and thus compensates the loss caused due to pathogens.

8.4 Antibiosis

Antibiotics are mostly deliberated to be low molecular weight organic compounds produced by beneficial microbes and is considered as one of the most important traits of PGPR. Antibiosis shows a vital role in the biocontrol of plant disease which often acts in concert with competition and parasitism. Dennis and Webster (1971) first described the antagonistic properties of *Trichoderma* in terms of antibiotic production which included both nonvolatiles and volatiles. Certain PGPR strains are capable of producing volatile and nonvolatile antibiotics and are important feature for suppression of plant pathogens (Table 8.3). Some of these antibiotic-producing strains were also shown to suppress fungal plant disease in vitro (Whipps 2001).

Several strains of *Pseudomonas* and *Bacillus* spp. have been shown to produce wide array of antibiotics which includes ammonia, butyrolactones, 2–4 diacetylphloroglucinol, kanosamine, oligomycin A, oomycin A, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, tropolone, pyocyanin, iturin, surfactin, viscosinamide, zwittermicin A, agrocin 84, as well as several other uncharacterized moieties (Nyfeler and Ackermann 1992; Keel and Defago 1997; Nielsen et al. 1999; Whipps 2001). Burkhead et al. (1994) reported that *P. cepacia* B37W produced pyrrolnitrin antibiotic inhibitory to *Fusarium sambucinum*. Michereff et al. (1994) could correlate the in vitro inhibition of *Pythium* and *Rhizoctonia* by 2,4-diacetylphloroglucinol, an antibiotic produced by *P. fluorescens* PF5 and in vivo control of *C. graminicola*, incitant of sorghum anthracnose. *P. fluorescens* (Trevisan) Migula F113 was shown to control the potato soft rot pathogen, *E. carotovora* subsp. *atroseptica* (van Hall) Dye, by the production of antibiotic 2,4-diacetylphloroglucinol (DAPG) (Cronin et al. 1997). Some evidence was also obtained that siderophore production by *P. fluorescens* F113 may play a role in biocontrol of potato soft rot.

Bacillus cyclic lipopeptides belong to three major families, the iturins (bacillomycins, iturins, and mycosubtilins), the fengycins (plipastatins), and the surfactins (bamylocin A, esperins, lichenysins, pumilacidins, and surfactins) (Jacques 2011). Iturins and fengycins possess antifungal activity against a wide range of phytopathogens, while surfactins are mostly antibacterial (Ongena and Jacques 2008). Bacilysin is a dipeptide composed of an L-alanine and the unusual amino acid L-anticapsin and one of the simplest peptide antibiotics known with antifungal and antibacterial activities. Difficidin and bacilysin from *B. amyloliquefaciens* FZB42 have antibacterial activity against *X. oryzae* in rice (Wu et al. 2015). *B. subtilis* CMB32 produced antifungal lipopeptides which was found to be antagonistic against *C. gloeosporioides* (Kim et al. 2010). Thus antibiotics secreted by the biocontrol agents were found to inhibit the plant pathogens and thus play an important role in disease management.

Table 8.3 Antibiotics produced by PGPR

Target group	PGPR	Antibiotics	References
Oomycetes, fungi	*P. fluorescens*	2,4-diacetylphloroglucinol	Shanahan et al. (1992)
		Phenazine-1-carboxylic acid	Gurusiddaiah et al. (1986)
		Dimer of phenazine-1-carboxylic acid	Sakthivel and Sunish Kumar (2008)
		Pyrrolnitrin	Ligon et al. (2000)
		Pyoluteorin	Keel et al. (1992)
		Mupirocin (pseudomonic acid A)	El-Sayed et al. (2003)
		Rhizoxin analogues	Loper et al. (2008)
		Viscosinamide	Nielsen et al. (1998)
		Tensin	Nielsen et al. (2000)
		Masstolides A	de Bruijn et al. (2007)
	P. aeruginosa	Phenazine-1-carboxamide	Sunish Kumar et al. (2005)
		Pyocyanin	Baron et al. (1997)
	Pseudomonas aureofaciens	Phenazine-1-carboxylic acid	Thomashow et al. (1990)
		Pyrrolnitrin	Elander et al. (1968)
	P. chlororaphis	Phenazine-1-carboxylic acid	Pierson and Thomashow (1992)
		2-hydroxyphenazine	Chin-A-Woeng et al. (1998)
	P. putida	Phenazine-1-carboxylic acid	Pathma et al. (2011)
	P. cepacia	Pyrrolnitrin	Cartwright et al. (1995)
	Pseudomonas pyrrolnitrica	Monodechloro-pyrrolnitrin	Hashimoto and Hattori (1968)
	Pseudomonas borealis	2,3-deepoxy-2,3-didehydro-rhizoxin	Tombolini et al. (1999)
	Pseudomonas spp.	Isopyrrolnitrin	Hashimoto and Hattori (1966a)
		Oxypyrrolnitrin	Hashimoto and Hattori (1966b)
		Amphisin	Sorensen et al. (2001)
		Oomycin A	Kim et al. (2000)
		Cepaciamide A	Howie and Suslow (1991)
		Ecomycins	Jiao et al. (1996)
		2,3-deepoxy-2,3-didehydro-rhizoxin	Miller et al. (1998)
		Butyrolactones	Thrane et al. (2000)
		N-butylbenzene	Gamard et al.(1997)
		Sulphonamide	Kim et al. (2000)

(continued)

Table 8.3 (continued)

Target group	PGPR	Antibiotics	References
	B. amyloliquefaciens	Bacillomycin D	Gu et al. (2017)
	B. cereus	Kanosamine	Milner et al. (1996)
		Zwittermicin A	Silo-Suh et al. (1994)
	B. subtilis	Kanosamine	Vetter et al. (2013)
		Iturin A (cyclopeptide)	Constantinescu (2001)
		Plipastatins A and B	Volpon et al. (2000)
		Fengycins	Zhang and Sun (2018)
Bacteria	*P. fluorescens*	Mupirocin (pseudomonic acid A)	Fuller et al. (1971)
		Azomycin	Shoji et al. (1989)
Virus	*Bacillus* sp.	Karalicin	Lampis et al. (1996)
	B. amyloliquefaciens	Mersacidin	Chatterjee et al. (1992)

8.4.1 Hydrogen Cyanide (HCN) Production

HCN is a volatile, secondary metabolite that overwhelms the growth of microbes and that also disturbs deleteriously the growth and development of plants (Siddiqui et al. 2006). Several studies feature a disease defensive effect to HCN, e.g., in the suppression of "root-knot" and black rot in tomato and tobacco root caused by the nematodes *Meloidogyne javanica* and *Thielaviopsis basicola*, respectively (Voisard et al. 1989).

8.4.2 Siderophore Production

Iron (Fe) is an essential element to virtually all forms of life and plays an important role in different physiological processes such as respiration, photosynthesis, DNA synthesis, and defense against reactive oxygen species. However, its availability is extremely limited by the very low solubility of ferric hydroxide complexes at neutral pH. To survive in such an environment, plant-associated PGPRs have different strategies for obtaining iron from the soil, which includes the synthesis of low molecular weight siderophores, viz., catechols, pyoverdin, and hydroxamate, which are selective ferric ion chelators. These compounds are secreted in response to iron deficiency. Siderophore-producing PGPR can prevent the multiplying of pathogens by repossessing ferric iron in the root zone (Siddiqui 2005). Iron depletion in the rhizosphere does not harm the plants, as the low iron level occurs at microsites of high microbial movement during the establishment of the pathogens.

Plants can utilize various fungal and bacterial siderophores as source of iron, while the total iron levels are too low to pay substantially to plant iron uptake. Plants also use their innate mechanisms to gain iron, dicots via a root membrane reductase protein that converts insoluble Fe^{3+} ion into the more soluble Fe^{2+} ion or in the case of monocots by the production of plant siderophores (Crowley 2006).

Siderophore-secreting microbial strains own iron-regulated outer membrane proteins (IROMPs) on their cell surface that carriage ferric iron complex to the respective cognate membrane; iron thus becomes accessible for metabolic processes (Johri et al. 2003). Siderophore-producing fluorescent pseudomonads are ahead commercial importance as they are harmless, do not prime to biomagnification, and also deliver iron nourishment to the plants, thereby stimulating plant growth (Sayyed et al. 2005). Carrillo-Castaneda et al. (2003) reported encouraging effects on alfalfa plantlet development after the inoculation of siderophore-producing genus such as *Azospirillum*, *Pseudomonas*, and *Rhizobium* grown in iron-starved cultures. The bacterized alfalfa seeds improved their germination as well as the root and stem dry weight. Iron-chelating hydroxamate siderophores of *P. aeruginosa* showed inhibitory action against *R. solani* and *C. gloeosporioides* in chili (Sasirekha and Srividya 2016). Also, inoculation of siderophore-producing rhizobacteria and their consortium increased the growth of wheat plant (Kumar et al. 2018). Nevertheless, as with other PGPR, the growth elevation that occurred may be due to other mechanisms or combinations of one or two mechanisms that rise nutrient availability, subdue pathogens, or upset root growth via hormone production.

8.5 Competitions

Effective colonization and perseverance in the rhizosphere are essential for PGPR to utilize their positive consequence on plants (Elliot and Lynch 1995). Several reports indicate the importance of colonization of the biocontrol agents in rhizosphere and endorhizosphere regions of plant (Forlani et al. 1999). Competition for nutrients, primarily carbon, nitrogen, and iron, might result in biocontrol of soil-borne plant pathogens (Benson and Baker 1970). Suppression of damping off of peas by *P. cepacia* showed a significant relationship between population size of the biocontrol agent and the degree of disease suppression (Parke et al. 1991). The bacterial antagonist *P. fluorescens* effectively suppressed the green mold pathogen *P. digitatum* by means of competition and induced systemic resistance on citrus peels (Wang et al. 2018).

Also, suppression of take-all of wheat and *Fusarium* wilt of radish was correlated with the colonization of roots by *Pseudomonas* strains (Bull et al. 1991). Scher et al. (1985) reported that disease suppression by fluorescent pseudomonads depends mainly on its ability to colonize rhizosphere. Introduction of sss gene encoding rhizosphere colonization ability into poor colonizer strain of *P. fluorescens* WCS 307 increased competitive rhizosphere colonization ability in tomato root tip resulting in increased protection against *F. oxysporum* f. sp. *lycopersici* (Dekkers et al. 2000). So, the microbial ability to colonize rhizosphere and their persistence throughout the growing season has become the crucial factor for the selection of effective antagonistic organism. Dekkers et al. (1998b) showed that the gene encoding NADH dehydrogenase I plays an important role in root colonization. Another gene required for efficient colonization is the sss gene, encoding a site-specific recombinase of the lambda integrase family which helps in adapting cells to rhizosphere conditions (Dekkers et al. 1998a).

8.6 Lytic Enzymes

The antagonistic process relies on the production of hydrolytic enzymes which enhances penetration of the host mycelium and partial degradation of its cell wall via secretion of mycolytic enzymes, viz., chitinases and glucanases. The pathogenic microbes that have shown susceptibility to these hydrolytic enzymes include *B. cinerea*, *F. oxysporum*, *Phytophthora* spp., *P. ultimum*, *R. solani*, and *S. rolfsii* (Glick 2012). The roles of each protein in the enzymatic complex of *Pseudomonas* appear to be different, and enzymes with different or complementary modes of action appear to be required for maximal antifungal effect on different pathogens (Viswanathan and Samiyappan 2002). Minaxi et al. (2012) described that *B. subtilis* solubilized phosphorus, exhibited 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, and produced ammonia and indole-3-acetic acid. Various microbes secrete and excrete array of metabolites that can hamper pathogen growth and other activities. Numerous microbes produce and release hydrolytic enzymes that can lyse a wide range of polymers, including chitin, cellulose, hemicellulose, proteins, and nucleic acid (Table 8.4).

Expression and secretion of these hydrolytic enzymes by beneficial microbes can sometimes result in the suppression of plant pathogen activities directly. Several microbes like *B. subtilis*, *B. cereus*, *B. thuringiensis*, and *S. marcescens* have a potential to secrete hydrolytic enzymes for the biocontrol of phytopathogens (Jadhav and Sayyed 2016). Lytic enzymes can reduce different polymeric substances such as chitin, proteins, cellulose, hemicellulose, and DNA (Vivekananthan et al. 2004). Chitinase produced by *S. plymuthica* C48 inhibited spore germination and germ tube elongation in *B. cinerea*, but *S. marcescens* was considered to produce extracellular chitinases which act as antagonists against *S. rolfsii* (Frankowski et al. 2001). It was demonstrated that extracellular chitinase and laminarinase synthesized by *P. stutzeri* lyse mycelia of *F. solani* (Compant et al. 2005).

8.7 Induced Systemic Resistance

The PGPR induces systemic resistance (ISR) through invigorating the physical and mechanical integrity of cell wall as well as altering physiological and biochemical response of host leading to the synthesis of defense molecules against challenge inoculation of plant pathogens. ISR mechanism in plants was imparted by several PGPR determinants, viz., lipopolysaccharides, lipopeptides, salicylic acid, massetolide A, 2,3-butanediol, hexenal, and iron-regulated metabolite Cx (Pal and Gardener 2006). Followed by the interaction of PGPR determinants with plants, several defense reactions occur due to the accumulation of pathogenesis-related (PR) proteins (chitinase and β-1,3-glucanases), peroxidase, polyphenol oxidase,

Table 8.4 Lytic enzymes produced by plant growth-promoting rhizobacteria

Enzymes	Producer	Target pathogen	References
Chitinase	*S. plymuthica*	*B. cinerea*	Frankowski et al. (2001)
		S. sclerotiorum	Kamensky et al. (2003)
	S. marcescens	*S. rolfsii*	Ordentlich et al. (1988)
		Phaeoisariopsis personata	Kishore et al. (2005b)
	S. lydicus	*Pythium* sp.	Mahadevan and Crawford (1997)
	B. cereus	*R. solani*	Chernin et al. (1997)
	Paenibacillus illinoisensis	*R. solani*	Jung et al. (2003)
Endochitinase	*P. fluorescens*	*Tobacco necrosis virus*	Maurhofer et al. (1994)
		F. oxysporum f. sp. *pisi*	Benhamou et al. (1996)
β-1,3-glucanase	*Paenibacillus* sp.	*F. oxysporum* f. sp. *cucumerinum*	Singh et al. (1999)
	P. cepacia	*S. rolfsii*	Fridlender et al. (1993)
	Streptomyces spp.	*P. fragariae* var. *rubi*	Valois et al. (1996)
	Streptomyces sioyaensis	*P. aphanidermatum*	Hong and Meng (2003)
Laminarinase	*Pseudomonas stutzeri*	*F. solani*	Lim et al. (1991)
Proteases	*Stenotrophomonas maltophilia*	*P. ultimum*	Dunne et al. (1998)

phenylalanine ammonia lyase, chalcone synthase, catalase, phenolics, callose, lignin, and phytoalexins. Kloepper et al. (1992) reported that five of six rhizobacteria induced systemic resistance in cucumber which exhibited both external and internal root colonization. Seed treatment of radish with resistance inducing *P. fluorescens* strain WCS374 reduced *Fusarium* wilt in naturally infested field soil upto 50 percent (Leeman et al. 1995).

Chitinolytic enzymes together with β-1,3-glucanases or cellulases are most frequently considered to play a vital role in biocontrol (Chet et al. 1998). The enzymes like chitinases and β-1,3-glucanases lyse the host cell wall and lead to the leakage of protoplasmic contents which are in turn used as a food material for the multiplication of the antagonist. Biological control agents, namely, *P. fluorescens* 89B-27 and *S. marcescens* 90–166, were observed to induce resistance in cucumber against bacterial pathogen *P. syringae* pv. *lachrymans* and fungal pathogens, *F. oxysporum* f. sp. *cucumerinum* and *Colletotrichum orbiculare* (Liu et al. 1995). ISR by PGPR has been achieved in large number of crops including potato (Doke et al. 1987), radish (Leeman et al. 1996), cucumber (Wei et al. 1996), bean (de Meyer and Hofte 1997), tobacco (Troxler et al. 1997), tomato (Duijff et al. 1993), chilli, brinjal (Ramamoorthy et al. 2001), banana (Harish et al. 2009a, b), sugarcane (Viswanathan and Samiyappan 1999), rice (Harish et al. 2008b), and mango (Parthasarathy et al. 2016) against broad spectrum of pathogens including fungi (Leeman et al. 1995), bacteria (Liu et al. 1995), and viruses (Kandan et al. 2005).

The ISR shares many properties with innate immunity in humans (Lugtenberg and Kamilova 2009). When plants grow, their roots enter quickly into a symbiosis with diverse microbes. This symbiosis may play the role of beneficial (aid in the uptake of water and minerals, such as phosphate, and protection of biotic and abiotic stress) or pathogenic agents in the development of plants (Gnanamanickam 2006). In case of pathogenic bacteria, the immune response of the plant is characterized by the production of salicylic acid, which in revenge induces a set of genes encoding pathogenesis-related proteins in the plant (Gnanamanickam 2006). ISR was observed first with *Pseudomonas* sp. strain WCS417r against *Fusarium* wilt of carnations and by selected rhizobacteria against the fungus *C. orbiculare* in cucumber (Compant et al. 2005). Available reports showed that in rice, seed treatment followed by root dipping and a foliar spray with *P. fluorescens* strains Pf1 and FP7 induces systemic resistance against the sheath blight pathogen, *R. solani* (Jayashree et al. 2000). Thus ISR plays a major role in combating the pathogen during the host-pathogen-biocontrol interaction.

8.8 Formulations of PGPR

Potential PGPR needs to be formulated with suitable carriers for mass multiplication and broad-scale application in fields. Mass multiplication of PGPR in a suitable medium and development of a powder formulation were first carried out in 1980. A dried powder formulation of PGPR is especially important for seed treatment and soil application. Among the various bioformulations, talc- and liquid-based formulations were extensively used in agriculture and horticulture crops for managing diseases (Table 8.5). Although this type of formulation can be produced in large quantity, it may be difficult to store and have a relatively short shelf life, poor quality, and low field performance. Development of bioformulation with short shelf life was possible by using vegetative cells of the antagonists as the active ingredient in the formulations (Kanjanamaneesathian et al. 2007). Various solid formulations, such as floatable granules, floatable pellets, and effervescent fast-disintegrating granules, have been developed for the management of sheath blight disease under controlled conditions (Wiwattanapatapee et al. 2013). These carrier-based formulations help in improving the shelf life, protecting the viability, and easy delivery of the bacterial cells to the targeted sites in the plant system and long-term survival in the soil. Thus formulations with longer shelf life need to be targeted as they can establish in the soil, survive for a considerable period of time, and improve the soil fertility besides protecting from harmful pathogens.

Table 8.5 Different types of formulations from PGPR

Formulation	PGPR	Crop	Disease	References
Talc	*P. fluorescens*	Blue pine	Nursery diseases	Ahangar et al. (2012)
		Chillies	Fruit rot	Bharathi et al. (2004)
		Muskmelon	*Fusarium* wilt	Bora et al. (2004)
		Rice	Sheath blight	Radjacommare et al. (2002)
		Tomato	*TSWV*	Kandan et al. (2005)
		Mung bean	*Macrophomina* root rot	Saravanakumar et al. (2007a)
		Rice	Sheath rot	Saravanakumar et al. (2007b)
		Tea	Blister blight	Saravanakumar et al. (2009)
		Sugarcane	Red rot	Viswanathan and Samiyappan (2002)
		Mango	Anthracnose	Vivekananthan et al. (2004)
		Rice	Sheath blight	Vidhyasekaran and Muthamilan (1999)
Lignite	*P. fluorescens*	Rice	Sheath blight	Vidhyasekaran and Muthamilan (1999)
Peat	*P. fluorescens*	Rice	Sheath blight	Vidhyasekaran and Muthamilan (1999)
	P. chlororaphis, *B. subtilis*	Turmeric	Rhizome rot	Nakkeeran et al. (2004)
Chitin	*B. subtilis*	Groundnut	Crown rot	Manjula and Podile (2001)
		Pigeon pea	*Fusarium* wilt	
Vermiculate	*P. fluorescens*	Rice	Sheath blight	Vidhyasekaran and Muthamilan (1999)
Charcoal	*Bacillus* sp.	Mung bean	Wilt	Pahari et al. (2017)
Wheat bran	*B. subtilis*, *P. putida*	Lettuce, cucumber	Root rot	Amer and Utkhede (2000)
EB™	*P. fluorescens*	Sugar beet	Damping-off	Moenne-Loccoz et al. (1999)
Alginate	*P. fluorescens*	Sugar beet	*Pythium* rot, *Rhizoctonia* rot	Russo et al. (2001)
	Streptomycetes sp.	Tomato	Damping-off	Sabaratnam and Traquair (2002)
Liquid	*P. fluorescens*	Tomato	*Fusarium* wilt	Manikandan et al. (2010)
		Mango	Stem end rot	Parthasarathy et al. (2016)
Water in oil	*Fluorescent pseudomonads* (FP7)	Banana	Anthracnose	Faisal et al. (2014)

8.9 Concluding Remarks and Future Directions

Historically, emphasis in crop science has been placed on the discovery of new disease resistance genes through molecular breeding techniques rather than using the resistance potential already present in plants. The resistance in the plants can be induced by means of beneficial microbes present in the soil rhizosphere. The recent demonstration of the use of biocontrol agents in the laboratory and field situations presents exciting opportunities for the control of plant diseases by multiple mechanisms. Various field experiments with crop plants have shown that eco-friendly approaches using microbial bioagents can lead to long-lasting, broad-spectrum disease control and can be used preventively to bolster general plant health. However, application of bacterial bioformulation in the field at times may exhibit inconsistency in the efficacy due to short shelf life in the environment and their susceptibility to unfavorable environmental conditions. The survival and competitive ability of the microbial strains to be introduced must be improved as very little information is known about the competitiveness of the microbes and factors governing it. In order to harness the potential benefits of bioagents in commercial agriculture, the consistency of their performance must be improved. Development of quality inoculum with increased shelf life and user-friendly formulation are important factors essential for the success of bioinoculant technology. Besides, the molecular mechanisms underlying the host-pathogen-biocontrol interaction should be unraveled through genomic and proteomic approaches to identify the defense genes in the plants. These genes can be exploited for the management of plant diseases. Molecular markers, e.g., reporter gene tagging, PCR, or serological markers, can be used for studying the competence of the inoculated PGPR strains. Once these factors are identified, it may be possible to manipulate them in the field to enhance the stability of their performance. Thus the PGPR possessing the useful biosynthetic genes can be screened through molecular markers and can be exploited for sustainable plant disease management.

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