Use of Plant Growth-Promoting Rhizobacteria as Biocontrol Agents: Induced Systemic Resistance Against Biotic Stress in Plants

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Abstract Plant growth-promoting rhizobacteria (PGPR) are free-living bacteria able to colonize roots and soil around them that have a positive effect on plant growth, development, and health. One of the mechanisms by which PGPR exert a beneficial effect involves the capacity to control growth of deleterious organisms diminishing or preventing their negative effects on plant health and growth. Pathogen biocontrol implicates diverse features of bacteria; one of them is the antagonism that excludes pathogen due to the ability of some bacteria to colonize faster and more effectively a niche, reducing nutrient availability for the deleterious organism. Also some bacteria produce antibiotics, organic compounds that are lethal in low concentration for growth and metabolic activities of other microorganisms. Finally, the ability of bacteria to elicit a defense response in plant, called induced systemic resistance (IRS), involves the induction of synthesis of defense metabolites, but without causing a disease itself, enhancing the plant's defensive capacity. This chapter analyzed and discussed PGPR as biocontrol agent and the possibility to use them as ecological alternative to the use of agrochemicals, since they have been proved in different plant species in order to diminish the damage of pathogen and to reduce losses in crops.

1   Introduction

In nature, plants interact with a wide variety of microorganisms including soil bacteria. In the rhizosphere, that is, the soil/root interface, microorganisms are far more abundant than in bulk soil. This is because roots release significant part of

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their photo-assimilates as different metabolites, which are the main source of nutrients for bacteria that stimulate their copiousness in the rhizosphere (Hartmann et al. 2008; Diallo et al. 2011). In return, a number of them are able to exert a beneficial effect on plant growth playing a fundamental role in the adaptation of the plant to the environment (Hallman et al. 1997; Rodríguez and Fraga 1999; Hardoim et al. 2008). Kloepper and Schroth (1978) coined the term plant growth-promoting rhizobacteria (PGPR) to define free-living bacteria able to colonize roots and the soil around them that have a positive effect on plant growth and development (Fulchieri et al. 1993; Compant et al. 2005). Generally, different PGPR are associated with most, if not all, plant species and are present in almost all environments. Therefore, since PGPR were characterized as helpful for plants, different genera like *Azospirillum*, *Herbaspirillum*, *Bacillus*, *Pseudomonas*, *Burkholderia*, and *Gluconacetobacter* have been used to improve seedling establishment, weight enhancement, and yield increase and to help plants to cope with biotic stresses (herbivore and pathogen attack) in different plant species of economic importance (Lugtenberg and Kamilova 2009).

PGPR have direct and indirect mechanisms by which they interact positively with plants; the direct mechanisms are related to plant nutrition and development and include production of plant growth regulators such as abscisic acid (ABA), gibberellins (GAs), and indole acetic acid (IAA) (Bottini et al. 1989; Podile and Kishore 2006; Piccoli et al. 2011; Piccoli and Bottini 2013); nitrogen fixation that contributes to the accumulation of this element in soil; phosphate solubilization that makes P available for plant uptake (Rodríguez and Fraga 1999; Rodriguez et al. 2006); and siderophore production that improves Fe acquisition (Masalha et al. 2000; Miethke and Marahiel 2007). On the other hand, indirect mechanisms involve the capacity of several bacteria to control growth of deleterious organisms and so diminishing or preventing their negative effects on plant health (Haas and Défago 2005). The last mechanism has been defined as biocontrol and includes diverse metabolic features of the PGPR, which are subject of the present chapter.

Diseases caused by pathogens become relevant by affecting economically important species since they are responsible for significant loses in yield. Factually, different agrochemicals as well as genetic tools have been used in order to control diseases, but they are not always effective. Moreover, many agrochemicals are nondegradable and therefore harmful for the environment (Lugtenberg and Kamilova 2009). In the last decades, the use of PGPR as biocontrol agents became an environmentally friendly alternative to deal with diseases, thus decreasing the use of chemicals in agriculture (Gerhardson 2002). Pathogen control involves different aspect and features of bacteria; one mechanism is the pathogen exclusion based on the capability of some bacteria to colonize faster and more effectively a niche, thus reducing the nutrient availability for the deleterious organism. An important aspect of this mechanism includes Fe chelation by bacterial siderophores that makes the element unavailable for the pathogen (Whipps 2001; Podile and Kishore 2006; Singh et al. 2011). Other mechanism is the capacity to produce antibiotics which include a chemically heterogeneous group of organic compounds that are lethal in low concentration for growth and metabolic activities of other
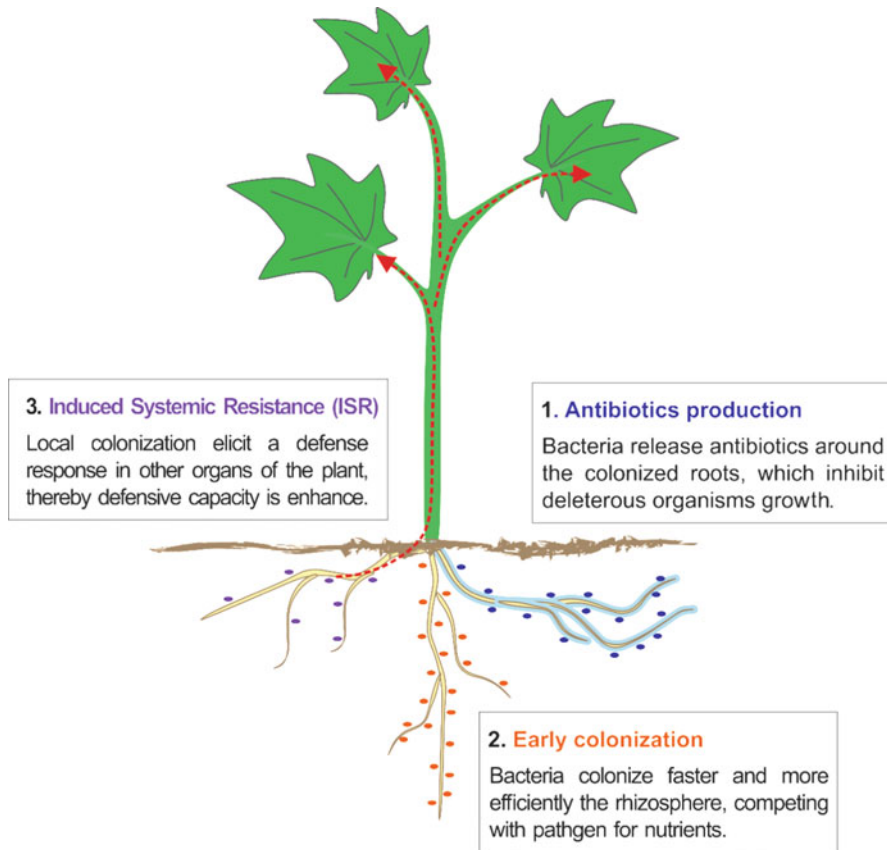
3. Induced Systemic Resistance (ISR)
Local colonization elicit a defense response in other organs of the plant, thereby defensive capacity is enhance.

1. Antibiotics production
Bacteria release antibiotics around the colonized roots, which inhibit deleterous organisms growth.

2. Early colonization
Bacteria colonize faster and more efficiently the rhizosphere, competing with pathgen for nutrients.

Fig. 1 Mechanisms of disease biocontrol by plant growth-promoting rhizobacteria. Adapted from Lugtenberg and Kamilova (2009)

microorganisms (Haas and Défago 2005). Besides the ability of bacteria to produce diverse compounds, PGPR can reduce the incidence of the pathogen attack by eliciting a defense response in plant, called induced systemic resistance (ISR) (Glick 2015). In these responses, PGPR elicit synthesis of different defense metabolites, but without causing a disease itself, which modify the physical and biochemical properties of the host enhancing the plants defensive capability (Kloepper et al. 2004). Figure 1 shows a diagram of the different mechanisms.

This chapter is focused in reviewing PGPR as biocontrol agents. The following sections are dedicated to different biocontrol mechanisms mentioned above and to analyze the effectiveness of PGPR in biocontrol, as well as the possibility of using PGPR as an ecological alternative in the management of plant diseases. Moreover, the advantages and disadvantages of their use will be discussed in the context of environmental impact.

2 PGPR as Biocontrol Agents

2.1 *Antibiotic Production*

In agriculture, plant cultivars have been selected in order to optimize crop yield (quantity and quality); therefore, genetic variability and resistance to diseases are frequently decreased in comparison with wild-type ancestors. Plant diseases cause severe losses in crop production, and a variety of chemical pesticides are used to control maladies, but chemicals are often harmful for the environment and farmer's and consumer's health and even for the crops themselves. The excessive use of pesticides also increases resistance of the pathogen with the outcome of resistant strains (Burketova et al. 2015). Taking this in consideration, compounds of natural origin are expected to have lower environmental impact than synthetic pesticides, mainly because they are easier to biodegrade (Couillerot et al. 2014). In such a venue, a more sustainable alternative seems to be the use of microbial pesticides, like metabolites usually produced by bacteria and fungi. Some advantages of microbial antibiotics in comparison to chemical products have been reported. They may have low persistence in the environment, higher specificity against the pathogen target, minor induction of pathogen resistance, and low production cost (for instance, direct infection of the plant with the microbial producer may work). However, scientific evidence indicates that these advantages are not always achieved. On the other hand, disadvantages include that the level of protection can vary between crop species, they are highly influenced by environmental factors, and aspects of biosafety and impact on ecosystems have to be evaluated (Burketova et al. 2015; Bonaterra et al. 2012; Lagerlöf et al. 2015).

Microbial antibiotics are bioactive metabolites produced by bacteria and fungi that in certain concentration suppress disease agents (Fig. 1, item 1). It has been demonstrated, however, that in subinhibitory concentration these products can produce other side effects on the pathogen, such as changes in gene transcription, virulence, motility, and biofilm formation (Raaijmakers and Mazzola 2012). Chemical classes of secondary metabolites reported as having antibiotic effect are diverse, and they are not produced by a single strain since each strain usually produces more than one antibiotic. As is shown in Table 1, *Pseudomonas fluorescens* strains have an important role as biocontrol agents in plants due to their ample production of antimicrobial metabolites. In this section some antibiotics will be considered, especially those reported for *Pseudomonas* spp. and *Bacillus* spp. like 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrins, pyoluteorins, phenazine, iturins (cyclic lipopeptide), and hydrogen cyanide (HCN) (Ahmadzadeh and Tehrani 2009; Blumer and Haas 2000; Costa et al. 2009; Kennedy et al. 2015; Morohoshi et al. 2013; Pieterse et al. 2014).

Phenazines are nitrogen-containing heterocyclic pigmented compounds, known for their broad-spectrum antifungal activity, synthesized by a wide range of bacterial genus, including *Pseudomonas*, *Burkholderia*, *Brevibacterium*, *Streptomyces*, *Nocardia*, *Erwinia*, *Vibrio*, *Pelagiobacter*, and some Actinomycetales like

Table 1 Bacterial antibiotics and pathogen antagonism

Biocontrol agent	Antibiotic produced	Pathogen	Reference
Chaetomium globosum NM0066	Gliotoxin	*F. oxysporum f.* sp. *vasinfectum* *F. graminearum* *F. sulphureum* *Cercospora sorghi* *B. cinerea* *Alternaria alternata*	Li et al. (2011)
Chryseobacterium wanjuense KJ9C8	Hydrogen cyanide	*Phytophthora capsici*	Kim et al. (2012)
Burkholderia cepacia	Pyrrolnitrin	*Rhizoctonia solani*	Hwang et al. (2002)
B. pyrrocinia 2327T	Pyrrolnitrin	*Trichophyton* *Rhizoctonia solani*	Kwak and Shin (2015) Costa et al. (2009)
P. brassicacearum J12	DAPG Hydrogen cyanide	*Ralstonia solanacearum*	Zhou et al. (2012)
P. chlororaphis subsp. *aurantiaca* StFRB508	Phenazine	*F. oxysporum* f. sp. *conglutinans*	Morohoshi et al. (2013)
Pantoea agglomerans	Pantocins Herbicolins Microcins Phenazines	*Erwinia amylovora*	Braun-kiewnick et al. (2012), Smith et al. (2013)
P. fluorescens *P. fluorescens* 2-79 *P. fluorescens* Psd *P. fluorescens* Pf-5 *P. fluorescens* WCS417r	Phenazine Pyrrolnitrin Pyoluteorin dimethylhexadecylamine DAPG	*Gaeumannomyces graminis var. tritici* *Pythium ultimum* *B. cinerea* *P. syringae* pv. *tomato*	Mazzola et al. (1992) Upadhyay and Srivastava (2011) Howell and Stipanovic (1980) Hernández-león et al. (2015) Weller et al. (2012)
P. aureofaciens 30-84	Phenazine	*F. oxysporum*	Mazzola, et al. (1992)
P. protegens	DAPG		Ramette et al. (2011)
Bacillus subtilis	Iturin Fengycin	*Podosphaera fusca*	Romero et al. (2007)
B. amyloliquefaciens	Iturin A	*Rhizoctonia solani*	Yu et al. (2002)
B. thuringiensis UM96	Chitinase	*B. cinerea*	Martínez-absalón et al. (2014)

Streptomyces (Kennedy et al. 2015; Mavrodi et al. 2010; Morohoshi et al. 2013). The principal effect of phenazines is to generate reactive oxygen species (ROS) and to uncouple oxidative phosphorylation. Although these effects increase virulence and pathogenesis, the primary role of phenazines is as antibiotic that inhibits fungal pathogens; they also induce protein of defense pathways, iron chelation, biofilm formation, and modulation of gene expression (Pierson and Pierson 2010). Other antibiotics are pyrrolnitrins and pyoluteorins, which are tryptophan-derived metabolites produced mainly by Gram-negative bacteria, as *Pseudomonas* spp.

Burkholderia spp., and *Serratia* spp. Pyrrolnitrins are monochlorinated heteroaromatic pyrrole rings, while pyoluteorins possess dichlorinated rings (Pang et al. 2015; Schmidt et al. 2009). No mode of action has been published for pyoluteorin, although pyrrolnitrin has been reported to inhibit respiratory electron transport and synthesis of proteins; they also combine with cell membrane phospholipids, thus affecting transport (Haas and Défago 2005; Nose and Arima 1969; Tripathi and Gottlieb 1969). DAPG is a benzenetriol in which two of the ring hydrogens are replaced by acetyl groups. Troppens et al. (2013) demonstrated that DAPG produced by *Pseudomonas fluorescens* alters mitochondrial morphology, with loss of the membrane potential and increase of cytosolic Ca_2^+ in *Neurospora crassa*. Hydrogen cyanide is generated due to oxidation of glycine that produces HCN and CO_2 by a membrane-bound flavoenzyme (HCN synthase). It is a potent inhibitor of cytochrome c oxidase and several other metalloenzymes (Blumer and Haas 2000). The HCN and pyrrolnitrins produced by *Pseudomonas chlororaphis* strain PA23 have repellent and nematicidal activity against *Caenorhabditis elegans* (Nandi et al. 2015). Iturins are lipo-polypeptides (heptapeptides) with a β-amino fatty acid that exhibit strong antifungal activity (Arrebola et al. 2010). These antibiotics have been studied mainly in *Bacillus* spp., and it has been proposed that the antimicrobial activity of iturins relies predominantly on their capability to augment membrane permeability due to strong interaction with the phospholipids and sterols (Zhang et al. 2013). Figure 2 shows the structure of some of the mentioned antibiotics.

Generally, pesticides produced by microbes may play an important role in sustainable agriculture, with competitive advantages, although their application at the moment is limited. These antibiotics are lesser aggressive to environment than synthetics, and also application of biocontrol microorganism has some other advantages that benefit crops like nutrition increase and growth promotion. However, the knowledge of the mechanisms for microbial biocontrol is a key factor to achieve. There is limited evidence so far regarding in situ antibiotics produced by soil bacteria at concentrations to achieve anti-pathogenic effects.

2.2 Nutrient Competition and Siderophore Production

Another mechanism of phytopathogen antagonists is production of siderophores (Beneduzi et al. 2012). Under limited conditions bacteria with high capability to compete for nutrient uptake can restrict growth of minor contenders. In the rhizosphere, competition for niches, also called niche exclusion, has been described as a mode of biocontrol (Beattie 2007). In roots surface exist niches with high nutrient content (as it was mentioned root exudates are rich in amino acids, monosaccharides, and organic acids), which are attractive to organisms, including pathogens. PGPR compete with other microorganisms including pathogens for these nutrients, although not killing them (Fig. 1, item 2). For example, *Kloeckera apiculata* strain 34–9, isolated for its biocontrol effectiveness against *Penicillium italicum*,
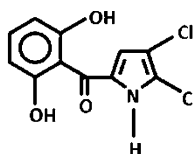
Fig. 2 Examples of antibiotic structures produced by PGPR. Each structure was redrawn from Moran et al. (2009), Haas and Défago (2005), and Pang et al. (2015)
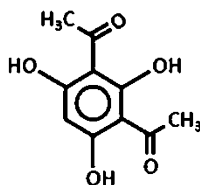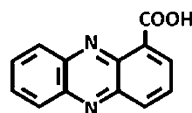

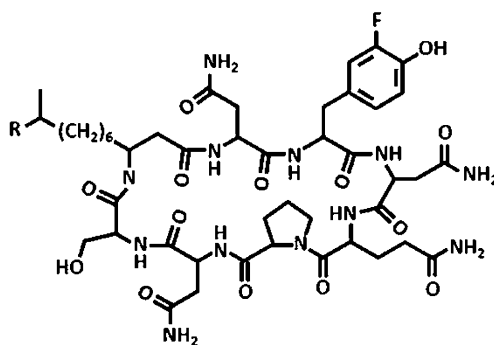2,4-diacetylphloroglucinol
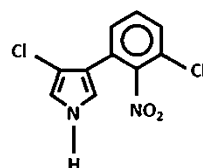
Pyrrolnitrin

Pyoluteorin

Phenazine

Iturin A

competes with the phytopathogen for nutrients and vitamins, inhibiting conidial germination of the pathogen albeit it is not able to kill the spores (Liu et al. 2013). Bencheqroun et al. (2007) provided in vitro and in situ evidence for nutrient competition in apple (mainly amino acids), as the most important mechanism of biocontrol activity of *Aureobasidium pullulans* strain Ach1-1 against *Penicillium expansum* on harvested apple fruits. Also, competition for nitrogen and carbon sources, secretion of hydrolytic enzymes, and elicitation of ISR play an important role in the biocontrol mechanism of *Pichia guilliermondii* M8 against *Botrytis cinerea* (Zhang et al. 2011). Regarding nutrient competition, root exudates are not the only factor, since essential soil nutrients like Fe are important too.

Fe is the second most abundant metal in the Earth crust and is essential to almost all organisms, since it has a crucial role in primary metabolism, oxygen transport and respiration, electron transfer, DNA synthesis, oxidative stress responses, and secondary metabolism (Abd-alla 1998; Ams et al. 2002; Braun 2001). Many environments tend to be a limitation and its deficiency is very common. The low Fe bioavailability is due mainly to the low solubility of Fe oxides, especially in alkaline and aerobic conditions. To increase Fe assimilation, organisms developed several strategies, and the most common is the production of extracellular siderophores (Rajkumar et al. 2010; Sahu and Sindhu 2011). Siderophores are low molecular mass compounds with high iron affinity and are typically produced in secondary metabolism by bacteria, fungi, and monocotyledonous plants in response to Fe stress (Gasser et al. 2015). Siderophores can chelate Fe^{+3} with high affinity, solubilizing and extracting it from most mineral or organic complexes. Siderophores have higher affinity to Fe^{+3} than to Fe^{+2}, because it is difficult to discriminate Fe^{+2} from other cations (Cu^{+2}, Zn^{+2}, Mn^{+2}, Ni^{+2}), but there are few biologically important trivalent cations (e.g., Co^{+3}), so in biological media, the selectivity to Fe^{+3} will be more effective (Hider and Kong 2010). There are basically four chemical classes of bacterial siderophores: phenol-catecholates, hydroxamates, rhizobactins, and hydroxycarboxylates. Phenol-catecholates have the highest Fe affinity, but is labile and unstable. Examples of this class are enterobactin, produced by *Escherichia* spp., *Enterobacter* spp., *Pseudomonas* spp., *Bacillus* spp., and *Agrobacterium* spp.; mycobactin, produced by *Mycobacterium* spp., *Nocardia* spp., and *Rhodococcus* spp.; and pyochelins, produced by *Pseudomonas* spp. On the other hand, hydroxamates are divided in citrate type (schizokinen, aerobactin), produced by *Bacillus* spp., *Aerobacter* spp., *Enterobacteriaceae* spp., and *Arthrobacter* spp., and ferrioxamines, produced by *Actinomyces* spp., *Streptomyces* spp., *Nocardia* spp., and *Arthrobacter* spp. Rhizobactins are produced by nodular bacteria, and finally hydroxycarboxylates, like pyoverdine (Pvd), are produced principally by *Azotobacter* spp. and *Pseudomonas* spp. Fungal siderophores mostly include three types: the rhodotorulic (hydroxamates), ferrichrome type, and fusarinines. Almost all fungal siderophores are hydroxamates, e.g., *Penicillium* spp. and *Aspergillus* spp. (Crowley 2006; Liu et al. 2015; Zheng and Nolan 2012; Raines et al. 2015). See Fig. 3 for siderophores structures.

As PGPR can improve plant health by acting as antagonists of pathogens by mechanisms such as solubilizing Fe and P, N fixation, antibiotic, and hormone productions, some evidences show that competition for Fe, N, and carbohydrates on leaves could limit the conditions for infection processes (Halfeld-vieira et al. 2015; Parangan-Smith and Lindow 2013; Smith et al. 2013). Siderophore production by PGPR confers them competitive advantages to colonize roots and exclude other microorganisms from this ecological niche. Some siderophores, like pyoverdine (Pvd), might compete at a distance depriving pathogens of Fe, thus showing bacteriostatic and fungistatic activities (Haas and Défago 2005). The ability to acquire Fe by microbial siderophores may determine the ability of the bacteria to
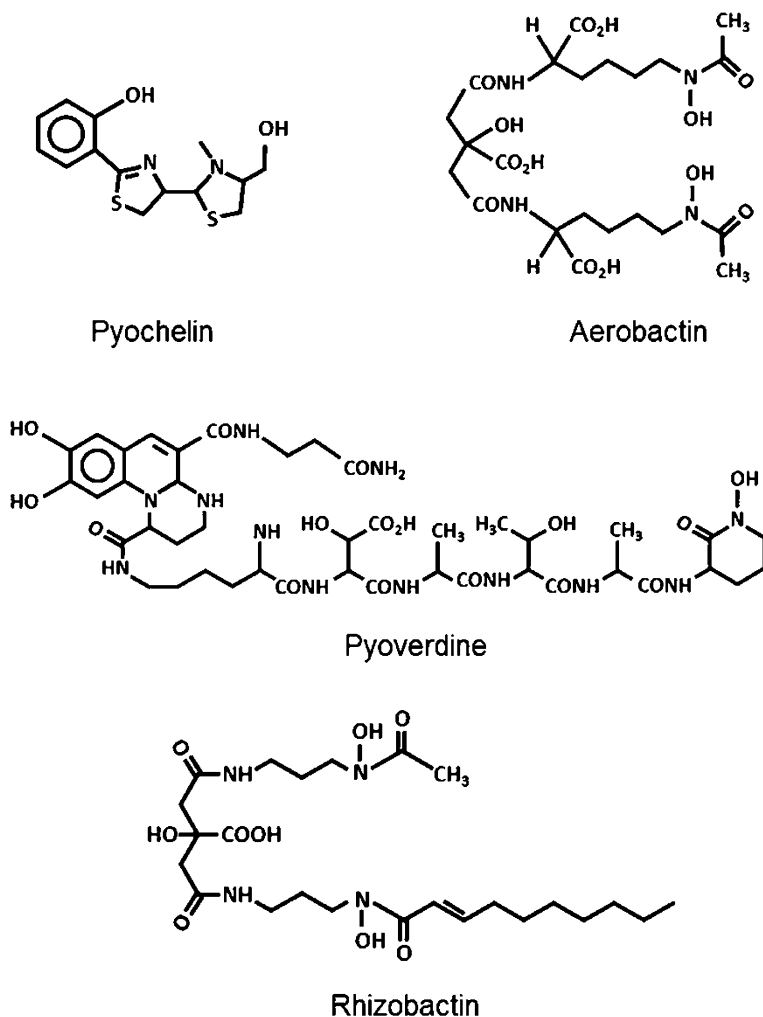
Fig. 3 Examples of siderophore structures produced by PGPR. Each structure was redrawn from Zheng and Nolan (2012), Hider and Kong (2010), and Permark et al. (1993)

compete for nutrient, like C source and even Cu or Zn, enhancing iron uptake by plant too (Beneduzi et al. 2012).

The genus *Pseudomonas* is one of the most studied as control disease agent because its ability to produce siderophores. Kloepper et al. (1980) suggested that disease suppression is caused in part by microbial pseudobactin produced by *Pseudomonas fluorescens* strains. Siderophores efficiently complex Fe (III) in soils, making it unavailable to pathogens, inhibiting their growth. *Arthrobacter* spp., *Curtobacterium* spp., *Enterobacter* spp., *Microbacterium* spp., *Pseudomonas* spp., or *Stenotrophomonas* spp. presented antagonism against the pathogen

Xanthomonas axonopodis pv. passiflorae, which is explained by competition for Fe and N-compounds on leaves of passion fruit (Halfeld-vieira et al. 2015). The catecholic siderophore producer *Bacillus subtilis* CAS15 significantly inhibited the mycelial growth of 15 different plant pathogens of *Fusarium* spp., *Colletotrichum* spp., *Pythium* spp., *Magnaporthe* spp., and *Phytophthora* spp. and also showed plant growth promotion effects in pepper. After treatment with Fe, the suppression by CAS15 on *Fusarium* wilt was significantly diminished, which indicate siderophore production as control mechanism (Yu et al. 2011). Finally, the effects of siderophores on control of phytopathogens may not be direct; De Vleesschauwer et al. (2008) showed the ability of *Pseudomonas fluorescens* WCS374r to trigger induced systemic responses in rice. They found that pseudobactin-type siderophore was responsible for ISR elicitation. Application of WCS374r-derived pseudobactin in roots activated multiple defense responses, enhancing resistance level against the leaf blast pathogen *Magnaporthe oryzae* (Table 2).

In summary, several bacteria develop iron chelating mechanisms that capture Fe from the environment and make it unavailable to competitors. Several studies indicate that control of plant diseases by using siderophore-producing bacteria could be a better remedy than administering antibiotics. Siderophores have also been examined for their role in plant Fe acquisition and for their capacity to mobilize heavy metals. Rhizospheric microorganisms are ideal as biocontrol agents, since they could reduce environmental impact and application costs, replacing chemical compounds as well as promoting plant nutrition.

Table 2 Bacterial siderophore and pathogen antagonism

Biocontrol agent	Siderophore produced	Pathogen	Reference
Arthrobacter Curtobacterium Enterobacter Microbacterium Pseudomonas Stenotrophomonas		*Xanthomonas axonopodis* pv. *passiflorae*	Halfeld-vieira et al. (2015)
Rhodotorula glutinis	Rhodotorulic acid (hydroxamate)	*Penicillium expansum*	Calvente et al. (1999)
P. putida Pp17		*Ralstonia solanacearum*	Kheirandish and Harighi (2015)
P. putida	Pseudobactin	*F. oxysporum* f. sp. *lini Gaeumannomyces graminis* var. *tritici*	Kloepper et al. (1980)
P. fluorescens WCS374r	Pseudobactin	*Magnaporthe oryzae*	De Vleesschauwer et al. (2008)
B. subtilis	Catecholate	*Fusarium*	Yu et al. (2011)

2.3 Induced Systemic Resistance (IRS)

Plants respond to local herbivore or pathogen attack by synthesizing de novo compounds in order to inhibit or at least reduce its incidence (Heil and Bostock 2002). There are some bacteria able to elicit similar responses that increase the defense and resistance of the plant against viral, bacterial, and/or fungal pathogens, but without causing a disease by themselves. As mentioned before, this is called induced systemic resistance (IRS) and is one of the mechanisms included in biocontrol (Fig. 1, item 3). When PGPR have elicited an IRS, the basal defense of the plant is enhanced; so after a pathogen infection this is evidenced with reduced rate of disease development, and in consequence, a lesser number of plants are affected, and/or the severity of the damage is lower (Van Loon et al. 1998; Kloepper et al. 2004). Thereby, PGPR are capable to pre-sensitize plant cell metabolism, and by consequence these plants are able to respond faster and more effectively when they are expose to a biotic stress than those that were not previously stimulated (Compant et al. 2005; Harish et al. 2008). This phenomenon is called "priming," and although it is a different protective mechanism against pathogen attack as compared with direct defense, both have a similar phenotypic response (Verhagen et al. 2011).

Bacteria release different compounds in the rhizosphere that act as elicitors, and some of them are perceived by the plant roots as signals that trigger defense responses (Gray and Smith 2005; Bais et al. 2006); to make it happens, plant roots have to be capable to perceive and recognize those elicitors similarly to how they perceive pathogen elicitors (Van Loon 2007; Thakur and Sohal 2013). These compounds belong to different chemical groups such as polysaccharides, lipids, glycopeptides, glycoproteins, and volatiles, and even antibiotics and siderophores can act as elicitors (Van Loon and Bakker 2005; Thakur and Sohal 2013). After they are perceived by plant roots, signal transduction pathways are activated to trigger the synthesis of different phytoalexins, defense enzymes, pathogenesis-related proteins (PR proteins), and cell wall reinforcement (Liu et al. 1995; Van Loon 1997; Heil and Bostock 2002; Magnin-Robert et al. 2007). An important feature of the ISR is that the bacteria responsible of eliciting the response must stay spatially separate of the pathogen, for example, the bacteria interact with roots while the response is located in the aerial part of the plant where the pathogen is located (Liu et al. 1995; Van Loon 2007; Rudrappa et al. 2010).

ISR has been studied in several species, both model plants (like *Arabidopsis thaliana*), and economic important crops summarized in Table 3. In those studies, *Pseudomonas* spp. and *Bacillus* spp. have been mainly used (Liu et al. 1995; Haas and Défago 2005; Kloepper et al. 2004; Van Loon and Bakker 2005; Van Loon 2007; Liu et al. 2009; Podile and Kishore 2006). As examples, in *A. thaliana*, *Bacillus* spp. triggered IRS by releasing 2,3-butanediol, while *Pseudomonas* spp. by production of 2,4-diacetylphloroglucinol (Iavicoli et al. 2003; Ryu et al. 2004). In grapevine, Salomon et al. (2014) have shown that root inoculation with *P. fluorescens* as well as *B. licheniformis*, besides improving plant growth, elicited

Table 3 Induced systemic resistance elicited by plant growth-promoting rhizobacteria

PGPR strain	Plant species	Disease (pathogen)	Reference
B. subtilis GB03 *B. subtilis* Sb4-23, Mc5-Re2, Mc2-Re2 *B. amyloliquefaciens* IN937a *B. mycoides* *B. cereus* AR156 *B. lipopeptides*	*Arabidopsis* Sugar beet Tomato	*Erwinia carotovora* subsp. *carotovora* *Cercospora beticola* *P. syringae* pv. *tomato* *Polymyxa betae* *Meloidogyne incognita*	Ryu et al. (2004) Bargabus et al. (2002) Niu et al. (2011) Desoignies et al. (2013) Adam et al. (2014)
P. fluorescens CHA0 *P. fluorescens*	*Arabidopsis* Tomato	*P. syringae* pv. *tomato* *Peronospora parasitica* *Meloidogyne javanica*	Pieterse et al. (1998) Iavicoli et al. (2003) Siddiqui and Shaukat (2004) Weller et al. (2012)
P. fluorescens *B. licheniformis*	Grapevine	*B. cinerea*	Salomon et al. (2014)
P. fluorescens 89B61 *P. aeruginosa* 7NSK2	Tomato	*Phytophthora infestans* *B. cinerea*	Yan et al. (2002) Audenaert et al. (2002)
P. putida BTP1	Bean	*B. cinerea*	Ongena et al. (2004)
Pseudomonas *Pantoea* *Acinetobacter*	Grapevine	*B. cinerea*	Verhagen et al. (2010) Magnin-Robert et al. (2013)

de novo synthesis of the monoterpenes α-pinene, terpinolene, 4-carene, limonene, eucalyptol, and lilac aldehyde A, as well as the sesquiterpenes α-bergamotene, α-farnesene, nerolidol, and farnesol in leaves. The synthesis of terpenes in plant tissues have been associated with defense responses to deleterious organisms (Neri et al. 2006; Leitner et al. 2008; Escoriaza et al. 2013), and their antimicrobial properties have been demonstrated (Machida et al. 1998; Brehm-Stecher and Johnson 2003; Semighini et al. 2006; Park et al. 2009). Also, other studies showed that grapevine leave extracts from inoculated plants have enhanced antioxidant properties due in part to terpenes (Salomon et al. 2016). Moreover, strains of *Pseudomonas* spp., *Pantoea* spp., and *Acinetobacter* spp. elicited synthesis of chitinases and β-1,3-glucanases that enhance tolerance to *B. cinerea* infection in leaves, reducing the lesion diameter (Verhagen et al. 2010; Magnin-Robert et al. 2013). In other crops as bean, a nonpathogenic *P. putida* strain increased hexenal levels (volatile antifungal compound) and the expression of enzymes involved in its synthesis, thereby reducing the incidence of *B. cinerea* infection (Ongena et al. 2004). In tomato, different strains of *Pseudomonas* spp. elicited IRS against both fungal and nematode diseases (Audenaert et al. 2002; Yan et al. 2002; Siddiqui and Shaukat 2004). Additional examples are shown in Table 3.

3   Conclusion

In literature, there is a plethora of information about PGPR as biocontrol agents in which bacteria have shown positive effects in a variety of crops. All the mechanisms have been extensively analyzed, mainly in short-scale trials. The use of natural products as antibiotics and/or siderophores as well as the capability to elicit ISR by bacteria is a positive ecological alternative to the use of agrochemicals, since there are evidences that the impact on environment is lower as compared with agrochemicals. But besides the extent literature about this topic, other studies about impact on the environment and the potential large-scale use of these technologies are still needed. In order to be able to commercialize PGPR to control diseases, biosafety and environmental impact have to be deeply analyzed, and regulation rules established accordingly. In this regard, several features of the biocontrol agents released to the environment, such as stability, impact on other beneficial microorganisms, and effect on human health, have to be considered for adequate implementation and use.

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