



Chatting With a Tiny Belowground Member of the Holobiome: Communication Between Plants and Growth-Promoting Rhizobacteria

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Abstract

As sessile organisms, plants have facilitated to actively protect themselves against biotic and abiotic stresses. For this, plants keep communicating with other organisms including insect and microbes inside and outside plant surface including root surface. In the area around the root referred to as the rhizosphere, diverse root-associated bacteria interact with plants with both positive and negative effects. In the past three decades, a group of rhizosphere bacteria known as plant growth-promoting rhizobacteria (PGPR) have been intensively studied for possible use in improving plant health. Here, we provide an overview of the current knowledge on the nature of PGPR, their signatures and their

roles in plant growth promotion and biological control against plant pathogens, as revealed by classic physiological and morphological observations and recent cutting-edge technology. We also discuss new information on insect–plant–PGPR tritrophic interactions, as well as technology transfer from the laboratory to the field. We use the new concept of the holobiome to help elucidate plant–PGPR interactions. Understanding plant root–bacterial communications in this novel framework may facilitate the improvement of plant health in agricultural production systems.



1. BELOWGROUND ZERO

The term ‘rhizosphere’ was first coined by Lorenz Hiltner in 1904 (Hartmann, Rothballer, & Schmid, 2007). This term refers to the narrow zone of soil around plant roots that is under the influence of root exudates chemically, physically and biologically. Plants deposit approximately 6–12% of their fixed carbon into the rhizosphere, mainly in the form of sugars and organic acids. Moreover, total nitrogen exudation comprises 10–16% of total plant nitrogen (Bais, Weir, Perry, Gilroy, & Vivanco, 2006; Dennis, Miller, & Hirsch, 2010). The amount of root exudate varies along the root, with the highest level found below the root tip and elongation zone. The volume of the rhizosphere, which is affected by soil type, plant species and phenological growth stage, ranges from less than 1 mm to several centimetres around the root system.

Compared to the surrounding (bulk) soil, the rhizosphere is a niche full of nutrients, which makes it attractive to soil microorganisms. The microbial population is 10–1000 times higher in the rhizosphere than in bulk soil (Haas & Defago, 2005). Microbial population levels are highest near the root, with the largest population (1×10^{12} CFU/g of soil) occurring within 50 μm of the root (Miransari, 2011; Pinton, Varanini, & Nannipieri, 2007). Bacterial populations in the rhizosphere are large, but since they belong to distinct genera and families of bacteria, their diversity is low in the rhizosphere (Lakshmanan, 2015; Lundberg et al., 2012), because the rhizosphere environment is highly competitive. Bacteria must have competitive and ecological advantages to thrive in this zone (Bulgarelli, Schlaeppi, Spaepen, Ver Loren van Themaat, & Schulze-Lefert, 2013). Several reports revealed that Proteobacteria, especially Pseudomonadaceae, comprise the highest bacterial population in the rhizosphere. High populations of Gram-positive Firmicutes and Actinobacteria are also present in the rhizosphere (Lareen, Burton, & Schafer, 2016; Lundberg et al., 2012). In one study, the largest populations in the rhizosphere included Proteobacteria (46% of the total),

followed by Firmicutes (18%), Actinobacteria (11%), Bacteroidetes (7%) and Acidobacteria (3%) (Weinert et al., 2011). Only small groups of these bacteria can enter the root tissues. These microorganisms are commonly known as root endophytes or endorhizosphere microbes. Populations of endophytic bacteria make up less than 10^4 CFU/g of root tissues (Bulgarelli et al., 2013). Actinobacteria, especially members of Streptomycetaceae, are the top colonizers of the endorhizosphere (Lundberg et al., 2012).

Single-plant species have specific root exudate profiles which allow them to support distinctive groups of microbes. Indeed, the diversity of the root microbiome (the total microbial community) differs when different plant species are cultivated in the same soil (Berg & Smalla, 2009). Even different cultivars of the same plant species have different microbial diversity when grown in the same soil (Raaijmakers & Mazzola, 2012). Three different wheat cultivars exhibited different abilities to recruit pseudomonads for biocontrol (Mazzola, Funnell, & Raaijmakers, 2004). Interestingly, plants under biotic stress attract specific microorganisms. Plants infected with the plant pathogen *Verticillium* spp. attracted 2,4-diacetylphloroglucinol (DAPG) producing fluorescent pseudomonads to control this fungal pathogen (Hartmann, Schmid, Tuinen, & Berg, 2008). DAPG is a phenolic antibiotic produced by various *Pseudomonas* species which exhibits antifungal activity against many fungal plant pathogens. Plants secrete different groups of root exudates with various effects on root microbiome diversity. In-depth studies showed that low molecular weight carbon exudates, especially organic acids, play a critical role in altering microbiome diversity in the rhizosphere. Citric acid treatment, 240 mg/g soil as standard concentration, increased the sizes of populations of beta and gamma Proteobacteria, especially members of Burkholderiales, and treatment with the same concentration of amino acid glycine increased the population sizes of Actinobacteria and Bradyrhizobiales (Eilers, Lauber, Knight, & Fierer, 2010). Malic acid was attractive to *Bacillus*, and quinolic acid increased Proteobacteria populations (Shi et al., 2011).

As mentioned earlier, plants release high amounts of carbon and nitrogen into the rhizosphere, which alters the rhizosphere microbiome. Does the plant benefit from this investment, and do rhizobacteria respond to this benevolence? The relationship between plants and rhizobacteria is more than just a cost–benefit relationship. Indeed, the plant–microbiome is considered to resemble an individual superorganism. This superorganism is described by the term holobiont, i.e., a superorganism of a host and its interacting microbes in the microbiome (Partida-Martinez & Heil, 2011).



2. PLANT HOLOBIOME: DO PLANT-ASSOCIATED MICROBES AND THE HOST PLANT REPRESENT A SUPERORGANISM?

Symbiosis of plants or animals with microbes is thought to be the norm rather than the exception (Zilber-Rosenberg & Rosenberg, 2008). Indeed, if we consider all of the genes from all of the microbes (microbiome) that help plants acquire mineral nutrients, modulate growth and increase resistance against biotic and abiotic stresses, we find that a network of thousands of microbial genes work for plant fitness and vice versa. The holobionome refers to the sum of the plant and microbiome genomes. Van Der Heijden, Bardgett, and Van Straalen (2008) suggested that 20,000 plant species have obligatory beneficial relationships with microbes. Approximately 80% of plant nitrogen and 75% of phosphate are provided by such microorganisms. Plants in the Orchidaceae family do not have enough nutrients and energy for germination, making their relationship with specific symbiotic fungi called mycorrhizal fungi indispensable for germination (McCormick et al., 2012). Sometimes, bacteria from other holobionts can act as friends or foes of plants. The helper bacteria help mycorrhizal fungi to grow and colonize both the plant surface and its interior (Bonfante & Anca, 2009). *Rhizobium radiobacter* is an endosymbiont of the beneficial fungus *Piriformospora indica*. This bacterium exhibits plant growth-promoting and biocontrol activities in *P. indica* (Bonfante & Anca, 2009). In another example, microbial endosymbionts of aphids make them more attractive to aphid parasitoids (aphids' natural enemy). The bacterium also alters the host ranges of herbivorous insects (Sugio, Dubreuil, Giron, & Simon, 2014).

In the holobiont, the host plant and mutual rhizobacteria share their genetic capacities to reach their highest ecological competence and to undergo rapid evolution. These beneficial rhizobacteria are known as plant growth-promoting rhizobacteria (PGPR), a term coined by Kloepper, Schroth, and Miller (1980) to describe groups of rhizobacteria that colonize plants and improve their growth and resistance to biotic and abiotic stresses. Well-known genera of PGPR include the genera of *Pseudomonas*, *Bacillus*, *Azospirillum*, *Azotobacter*, *Streptomyces* and *Rhizobia* genera. PGPR improve plant growth and health by providing mineral nutrients, stimulating plant growth via the production of phytohormones, facilitate mycorrhizal formation, functioning in biological control of plant pathogens, increasing tolerance to abiotic stresses and functioning in the bioremediation of toxic compounds (Bonfante & Anca, 2009; Ruzzi & Aroca, 2015).



3. TINY ORGANISM WITH BIG ROLES IN PLANT HEALTH

PGPR play critical roles in providing nutrient elements for the host plant and enriching plant yields and the contents of mineral elements required for human. PGPR fix atmospheric nitrogen, solubilize phosphorous and produce iron and zinc chelates (known as siderophores). The application of PGPR might represent an alternative to chemical fertilization or at least reduce their application dose (Adesemoye, Torbert, & Kloepper, 2009; Miransari, 2011). Chemical fertilizers represent 30–35% of total agricultural input in some countries (Rose et al., 2014), whose less than 50% and 20% of the added nitrogen and phosphate are absorbed by the plant, respectively (Miransari, 2011). Excess phosphate adds to the inorganic phase of sediment, while excess nitrogen leaches out of the soil into the groundwater or emitted as nitrogen oxides (Eichner, 1990). The application of PGPR *biostimulants* represents a promising technology for reducing the negative effects of chemical fertilizers. In one study, the application of PGPR reduced the need for nitrogen fertilizers by about 50% of recommended amount (Rose et al., 2014), and, in another study, PGPR reduced the need for nitrogen and phosphate by approximately 20–30% in tomato (Adesemoye, Torbert, & Kloepper, 2008).

PGPR also help plants take up microelements such as Fe, Zn and Cu. These elements are abundant in soil, but the levels of soluble microelements are too low in normal agricultural soils with good aeration. The concentration of Fe is 10^{-10} to 10^{-18} in normal soils, but the proper concentration for easy absorption by plants and microbes should be 10^{-6} (Lemanceau, Expert, Gaymard, Bakker, & Briat, 2009). Bacteria produce siderophores with high affinity for iron such as pyoverdine, which solubilize iron and deliver it to producer microorganisms and host plants (Sharifi, Ahmadzadeh, Sharifi-Tehrani, & Talebi-Jahromi, 2010). PGPR also increase iron acquisition efficiency in plants. Volatiles of *Bacillus subtilis* GB03 increased the expression of plant genes encoding Fe-deficiency-induced transcription factor 1 and iron transporter1. They also decreased the rhizosphere pH by increasing proton release into the rhizosphere. Altogether, these mechanisms increased iron uptake and transport in *Arabidopsis*, which subsequently improved photosynthesis in PGPR-treated plants (Zhang et al., 2009).

PGPR use a chemical language to communicate with plants and to improve their growth and tolerance against biotic and abiotic stresses. In this chapter, we describe recent findings on this topic. First, we describe

how PGPR directly produce phytohormones or modulate plant hormone signalling to enhance root and shoot growth leading to plant growth promotion. Secondly, we discuss PGPR-elicited induced systemic resistance and induced systemic tolerance against biotic and abiotic stresses. We also describe bacterial determinants that activate plant defences against pests and pathogens, as well as plant defence mechanisms and signalling. Third, we introduce new data on insect-modulated plant root exudation resulting in rhizosphere bacteria that reengineer plant defence responses against insect herbivory. Finally, we evaluate technology transfer from scientists to farmers and provide examples. Since similar reviews focussing on Gram-negative PGPR, primarily *Pseudomonas* spp., have been published (Bloemberg & Lugtenberg, 2001; Van Loon, 2007), we will focus on the Gram-positive genus *Bacillus*. *Bacillus*-based products represent more than 70% of total microbial biopesticide sales (Ongena & Jacques, 2008). The capacity for endospore production makes *Bacillus* spp. easy to formulate, increases their shelf life and makes them durable (Schisler, Slininger, Behle, & Jackson, 2004). Furthermore, the multifaceted biocontrol and plant growth-promoting features of these bacteria made them good candidates for in-depth molecular research.



4. PHYTOHORMONE PRODUCTION AND MODULATION BY RHIZOBACTERIA FOR DIRECT IMPROVEMENT OF PLANT GROWTH

PGPR, as part of a holobiont, improve plant fitness by producing plant hormones or modulating hormonal sensing and signalling in plants. PGPR can synthesize most critical hormones such as auxins, cytokinins, gibberellic acid, abscisic acid (ABA) and salicylic acid (SA) (Ortíz-Castro, Contreras-Cornejo, Macías-Rodríguez, & López-Bucio, 2009; Ruzzi & Aroca, 2015). Among these hormones, auxin production appears to be widespread in rhizobacteria. Approximately 80% of bacteria isolated from the rhizosphere can produce auxin (Glick, Cheng, Czarny, & Duan, 2007). Abbas-Zadeh et al. (2009) tested 40 strains of fluorescent pseudomonads for auxin production and found that all of them produced auxin *in vitro*.

Auxin: The role of auxin in plant–PGPR communications can be investigated by either examining the production of auxin in bacteria or by examining how PGPR modulate auxin signalling in plants. The role of PGPR-produced auxin in plant growth can be assessed by altering auxin production in rhizobacteria through mutation. *Pseudomonas putida*

GR12-2 produces high levels of auxin. The application of the wild-type strain increased plant growth by 35–50% more than that of the auxin mutant (Xie, Pasternak, & Glick, 1996). An auxin deficient mutant of *Bacillus amyloliquefaciens* failed to increase plant growth. *Pseudomonas thivervalensis* MLG45 increased *Arabidopsis* growth by up to 70%, but a mutation in an auxin biosynthesis gene compromised its plant growth-promoting activity (Dodd, Zinovkina, Safronova, & Belimov, 2010). However, some bacteria are unable to produce auxin but they can increase auxin biosynthesis in the host plant. For example, *Phyllobacterium brassicacearum* increased lateral root formation by up to 50% by modulating auxin biosynthesis in *Arabidopsis* (Contesto et al., 2010).

PGPR increase shoot growth but reduce primary root elongation by modulating auxin signalling (Shi, Park, Lee, Ryu, & Ryu, 2010). However, secondary root and hair root proliferation increase in plants treated with auxin-producing or auxin-modulating rhizobacteria. This increase in root surface area increases the absorption of minerals. In-depth investigations have also shown that rhizobacteria determinants such as volatile organic compounds (VOCs), acyl homoserine lactones and DAPG affect auxin signalling and transport in *Arabidopsis* and tomato, respectively (Bai, Todd, Desikan, Yang, & Hu, 2012; Brazelton, Pfeufer, Sweat, Gardener, & Coenen, 2008; Zhang et al., 2007).

Bacterial VOCs increase basipetal transport of auxin from shoot to root. Naphthylphthalamic acid, an inhibitor of auxin transport, abolishes the plant response to *B. subtilis* GB03 VOCs. Low concentrations of auxin are sufficient for improving the growth of the aerial parts of plants, but high concentrations can be suppressive. By contrast, root growth increases in response to higher concentrations of auxin. Therefore, basipetal transports of auxin favours either shoot or root growth. Search for specific volatile compound showed that indole plays an important role in the activation of auxin signalling. The greatest lateral root formation in *Arabidopsis* occurred in the presence of 600 µg of indole (Bailly et al., 2014).

Cytokinins: PGPR belonging to the genera *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea* and *Paenibacillus* produce cytokinin (Bishnoi, 2015). This hormone increases cell division, cell differentiation, stomatal opening, shoot elongation and root hair proliferation, but decreases primary and lateral root formation (Liu, Xing, Ma, Du, & Ma, 2013; Miri, Janakirama, Held, Ross, & Szczyglowski, 2016; Ortíz-Castro, Valencia-Cantero, & López-Bucio, 2008). Cytokinin can reduce root growth via activating the ethylene signalling. However, the holobiont has a strategy for bypassing the negative

effects of its cytokinin production on root growth. Treating plants with bacterial cytokinin (Zeatin) leads to increased cytokinin biosynthesis in the aerial parts of plants, but cytokinin production in roots is not affected by this treatment (Liu et al., 2013). Therefore, both root and shoot biomass increase in response to rhizobacteria. *Bacillus megaterium* has an effect on cytokinin perception. Single or multiple mutations in plant cytokinin receptors reduce the plant growth-promoting activity of this bacterium (Ortíz-Castro et al., 2008). In addition, plants with a mutation in *cre*, encoding a cytokinin receptor, are insensitive to *B. subtilis* GB03 volatiles indicating that bacterial volatiles increase plant growth through the cytokinin signalling pathway (Ryu, Farag, et al., 2003).

ABA: ABA increases drought tolerance in plants by promoting stomatal closure, which reduces evaporation through the stomata (Dodd et al., 2010). Furthermore, ABA increases primary root elongation to help the plant reach new sources of water. This hormone also reduces lateral root formation (Ruzzi & Aroca, 2015). PGPR increase ABA biosynthesis in plants under stress conditions, thereby reducing water evaporation in the stomata. Application of *Azospirillum brasilense* sp245 and *Burkholderia* increased ABA biosynthesis in *Arabidopsis* in drought stress conditions (Cohen, Bottini, & Piccoli, 2008; Ruzzi & Aroca, 2015). Treatment of grapevines with *Bacillus licheniformis* and *Pseudomonas fluorescens* under water stress increased ABA production by 70% and 40%, respectively. Plants inoculated with these strains lost 10% and 4% less water, respectively (Salomon et al., 2014). In one case, the application of *Burkholderia* LD-11 increased drought tolerance in plants but reduced ABA levels. Further work revealed that rhizobacteria increase the sensitivity of the ABA receptor, allowing plants to respond to low concentrations of ABA (Fan et al., 2015). In addition to its role in drought stress, ABA functions in the plant growth-promoting activity of rhizobacteria. *B. megaterium* treatment fails to increase plant growth in ABA mutants indicating that ABA is required for the activity of this bacterium. Indeed, bacteria treatment increases ethylene biosynthesis in ABA mutant plants (Porcel, Zamarreño, García-Mina, & Aroca, 2014).

Treatments with volatiles of *B. subtilis* GB03 were found to increase the chlorophyll content, the photosynthesis efficiency and the amount of hexose sugars (60%) in *Arabidopsis*. As treatment with GB03 volatiles also reduced ABA levels in plant shoots by 20–50%, it was proposed that this low level of ABA repressed sugar sensing, therefore preventing the feedback inhibition of photosynthesis by elevated photosynthate level (Zhang et al., 2008). The

application of exogenous ABA also removed this ability of *B. subtilis* GB03 volatiles.

Ethylene (ET): Ethylene is involved in senescence and abscission processes. In addition this phytohormone plays regulatory roles in seed germination, flowering, fruit ripening, defoliation, and it inhibits shoot and root growth (Glick, 2015). The role of PGPR in modulating plant ethylene levels was first described by Glick, Jacobson, Schwarze, and Pasternak (1994) who discovered the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase by rhizobacteria. Rhizobacterial ACC deaminase converts ACC, an immediate precursor of ET, to α -ketobutyrate, a carbon source for bacterial nutrition. ACC deaminase is widespread in both Gram-positive and Gram-negative bacteria; 18 of 20 species of *Burkholderia* can produce ACC deaminase (Onofre-Lemus, Hernández-Lucas, Girard, & Caballero-Mellado, 2009). Treatment with rhizobacteria alleviates the inhibitory effect of ET by repressing ethylene production in roots. ACC deaminase not only increases plant root biomass, but it also increases plant tolerance to abiotic stresses. Treatment of 55-day-old tomato plants with the ACC deaminase producer *P. putida* increased plant resistance to flooding. Transgenic tomato expressing a bacterial ACC deaminase gene showed increased tolerance to flooding (Grichko & Glick, 2001).



5. RELIEVING PLANT STRESS I: RHIZOBACTERIA ACTIVATE ABIOTIC TOLERANCE

Plants suffer much more from abiotic stress than from biotic challenges. The proportion of yield loss caused by abiotic and biotic stress was found to be 70% and 30%, respectively (Jewell, Campbell, & Godwin, 2010). The major abiotic stresses include high or low temperature, flooding or drought, deficiency or toxicity of minerals and soil salinity.

PGPR alleviates abiotic stress via various mechanisms, such as increasing micro- and macronutrient uptake, root volume and extracellular polysaccharide (EPS) production as well as modulating plant stress hormone levels. Ethylene and ABA are the main hormones that function in abiotic stress tolerance (Fig. 1). The roles of rhizobacterial hormones in stress tolerance are described earlier.

Cyanobacteria increased tolerance to salt stress by reducing soil pH and salt concentrations. They decreased pH from 5.0 to 8.8 and Na^+ level from 0.78 to 0.60 ppm (Singh, Pandey, & Singh, 2011). PGPR produce EPS, binding agents for the production of soil micro- and macroaggregates. These

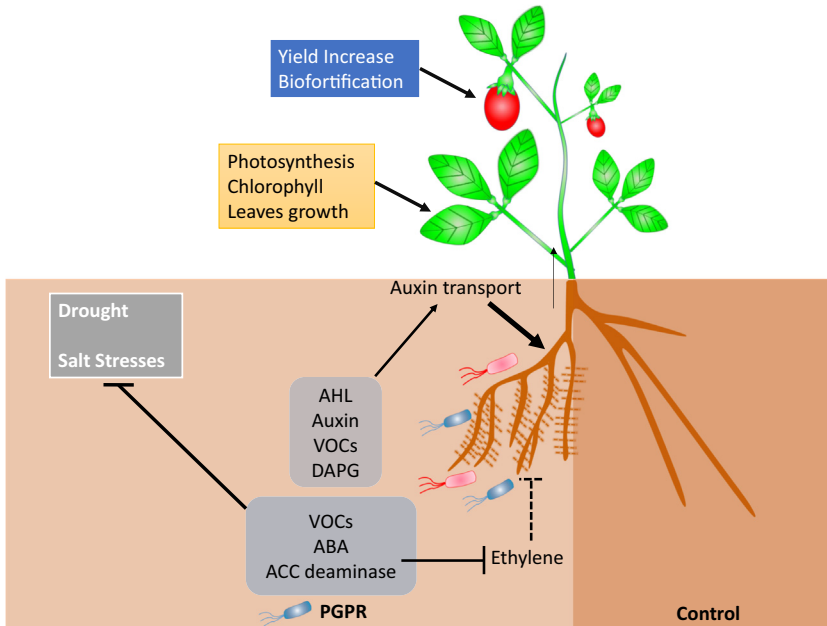


Figure 1 Plant growth-promoting rhizobacteria (PGPR) promote plant growth by providing nutrients, modulating hormone levels and alleviating abiotic stresses. Rhizobacteria produce volatile organic compounds (VOCs), acyl homoserine lactones (AHL) and the antibiotic diacetylphloroglucinol (DAPG) for modulating auxin homeostasis in plants. Auxin increases shoot growth, lateral root and root hair proliferation. Bacterial volatiles also increase chlorophyll content and photosynthesis efficiency by improving iron uptake and removing the negative impact of sugar accumulation on photosynthesis. The bacterial enzyme aminocyclopropane-1-carboxylate (ACC) deaminase represses the negative effect of ethylene on root growth by degrading the ethylene precursor ACC. Rhizobacteria increase plant tolerance against abiotic stresses such as drought, flooding and salt by modulating the levels of the hormones abscisic acid (ABA) and ethylene or diminishing Na^+ uptake in plants.

particles improve soil aeration and water capacity. In addition, EPS absorb Na^+ cations, making them unavailable for plants (Paul & Lade, 2014; Upadhyay, Singh, & Singh, 2011). *Pseudomonas aeruginosa*, with high EPS production, has high tolerance to salt compared to other strains. This strain increases plant tolerance to salt stress (Tewari & Arora, 2014). An EPS mutant of this bacterium failed to increase plant salt stress tolerance.

The production of metabolites such as the osmoprotectant trehalose-6-phosphate by rhizobacteria confers abiotic stress resistance to plants (Rodrigues, Bonifacio, De Araujo, Lira, & Figueiredo, 2015). Overexpressing trehalose-6-phosphate in *Rhizobium etli* increased drought

tolerance in common bean (Suárez et al., 2008). Plants inoculated by an overexpression mutant exhibited increased nodule formation and high nitrogenase activity compared to the control, but a mutation in trehalose-6-phosphate had a negative effect on these two factors. Transformation of *Azospirillum brasilense* with a trehalose-6-phosphate gene increased its tolerance to high salt levels compared to the wild type. Corn plants inoculated with this mutant exhibited increased drought tolerance of more than 85% compared to noninoculated plants. Application of a wild-type strain increased drought tolerance by only 55% compared to the noninoculated control (Rodríguez-Salazar, Suárez, Caballero-Mellado, & Iturriaga, 2009).



6. RELIEVING PLANT STRESS II: RHIZOBACTERIA ACTIVATE BIOTIC RESISTANCE

Plants and animals have been invaded by pests and pathogens throughout their evolutionary history and have therefore developed efficient strategies for defence against these enemies. Animals have innate and adaptive immunity based on mobile lymphocyte cells (Flajnik & Kasahara, 2010). Plants use pattern recognition receptors for non-self-detection of microbial molecular patterns in places of attack (Newman, Sundelin, Nielsen, & Erbs, 2013). Same as animals, plants recognize molecular determinants on the surfaces of pathogens. These patterns are known as microbe-associated molecular patterns (MAMPs). Well-studied MAMPs include molecules such as flagellin, chitin, peptidoglycan, lipopolysaccharide, siderophores and VOCs (Newman et al., 2013; Pieterse et al., 2014). After detecting MAMPs, plants use mobile signals such as SA, azelaic acid, pipelicolic acid and methyl-jasmonate (Me-JA) to spread the defence mechanism throughout the plant (Shah & Zeier, 2014).

In addition to using mobile signals, plants use defence hormones to regulate the expression of specific sets of defence genes. Two important pathways are involved in the regulation of defence gene: the SA and jasmonic acid (JA)/ET pathways (Pieterse, Van Der Does, Zamioudis, Leon-Reyes, & Van Wees, 2012). In the SA pathway, defence inducers such as SA, benzothiadiazole (BTH), necrotizing pathogens and some rhizobacteria increase SA biosynthesis in the cytoplasm. Accumulation of SA alters cytoplasmic redox and cleaves disulfide bonds in nonexpressor of PR genes1 (NPR1) oligomers. NPR1 monomers are transported to the nucleus, where they act as cotranscription factors with TGA transcription factors. This complex

activates genes such as *wrky70*, which subsequently activates a set of SA-dependent defence genes such as those encoding pathogenesis-related proteins (PRs). PR-1 is a marker for the activation of this pathway (Fu & Dong, 2013).

In the JA pathway, defence inducers such as JA, β -aminobutyric acid (BABA), and some rhizobacteria are perceived by plant cells, leading to an increase in JA biosynthesis. JAR1 convert JA to the highly active form, JA-isoleucine (Ile). JA-Ile mediates recognition and degradation of jasmonate ZIM-domain (JAZ) by the 26s proteasome. JAZ is a transcriptional repressor of JA-dependent genes (Katsir, Chung, Koo, & Howe, 2008). Thus, degradation of JAZ releases its repressive activity and activates JA transcription factors such as MYC2 and ERF1 for the expression of JA-dependent genes such as *pdf1.2* and *vsp2* (Pieterse et al., 2012).

The SA pathway is more effective against biotrophic pathogens, whereas the JA pathway is effective against necrotrophic pathogens and herbivorous insects (Glazebrook, 2005). Plants have the ability to fine-tune these two pathways. Most often, the activation of one of the pathways suppresses the other pathway. For example, the application of exogenous SA represses JA-dependent genes or the production of the JA-Ile mimic coronatine produced by *Pseudomonas syringae*, thereby repressing SA-dependent genes and sensitizing the plant to biotrophic pathogens (Brooks, Bender, & Kunkel, 2005). However, there are examples of synergistic activation of both pathways. Low concentrations of exogenous SA or JA activate both *PR-1* and *PDF1.2*. In addition, some rhizobacteria activate both pathways (Sharifi & Ryu, 2016), which is common in the genus *Bacillus* (Table 1).

High efficiency systemic defence against an array of pathogens has inspired chemical companies to release chemical inducers into the market. SA has negative effects on some plants, but its derivative BTH is more compatible with plants. Commercial formulations of BTH (BION and Actigard), Messenger and Laminarin have been introduced into the market as promising products for the control of plant disease (Leadbeater & Staub, 2007). However, it was later revealed that treating plants with these compounds has a negative impact on plant growth and yield (Goellner & Conrath, 2008). This finding indicates that plants have limited sources of nutrients, and activating thousands of defence genes diverts these resources away from plant growth and fitness. Constitutive activation of the SA pathway in the *cpr1* mutant of *Arabidopsis* reduces rosette volume and seed production (Heidel, Clarke, Antonovics, & Dong, 2004).

Table 1 Signalling Pathways Involved in the Induction of Systemic Resistance by Gram-Positive Rhizobacteria

Strains	Plants	Pathogen	Signalling Pathway			References
			Salicylic Acid	Jasmonic Acid	Ethylene	
<i>Bacillus pumilus</i> SE34	Tobacco	<i>Peronospora tabacina</i> ^b	+	nd	nd	Zhang, Moyne, Reddy, and Kloepper (2002)
<i>B. pumilus</i> SE34	Tomato	<i>Phytophthora infestans</i> ⁿ	0	+	+	Yan et al. (2002)
<i>B. pumilus</i> SE34	<i>Arabidopsis</i>	<i>Pseudomonas syringae</i> pv. <i>tomato</i> ^h	++	+	0	Ryu, Hu, Reddy, and Kloepper (2003)
<i>Paenibacillus alvei</i> K165	<i>Arabidopsis</i>	<i>Verticillium dahliae</i> ^h	+	0	0	Tjamos, Flemetakis, Paplomatas, and Katinakis (2005)
<i>Paenibacillus polymyxa</i> E681	<i>Arabidopsis</i>	<i>Pseudomonas syringae</i> pv. <i>maculicola</i> ^h	+	+	+	Lee, Farag, et al. (2012)
<i>Streptomyces</i> sp. EN28	<i>Arabidopsis</i>	<i>Fusarium oxysporum</i> ^h	++	+	+	Conn, Walker, and Franco (2008)
<i>Streptomyces</i> sp. EN28	<i>Arabidopsis</i>	<i>Erwinia carotovora</i> ⁿ	0	+	+	Conn et al. (2008)
<i>Bacillus cereus</i> AR156	<i>Arabidopsis</i>	<i>P. syringae</i> pv. <i>tomato</i> ^h	+	+	+	Niu et al. (2011)
<i>B. cereus</i> AR156 Leaf Infiltration	<i>Arabidopsis</i>	<i>P. syringae</i> pv. <i>tomato</i> ^h	+	+	+	Niu et al. (2016)
<i>Bacillus amyloliquefaciens</i> KPS46	<i>Arabidopsis</i>	<i>P. syringae</i> pv. <i>tomato</i> ^h	+	+	+	Buensanteai, Yuen, and Prathuangwong (2009)
<i>B. amyloliquefaciens</i> KPS46	Soya bean	<i>Xanthomonas axonopodis</i> pv. <i>glycines</i> ^h	+	+	nd	Buensanteai et al. (2009)
Acetoin (Volatile From <i>Bacillus subtilis</i> FB17)	<i>Arabidopsis</i>	<i>P. syringae</i> pv. <i>tomato</i> ^h	+	+	+	Rudrappa et al. (2010)

(Continued)

Table 1 Signalling Pathways Involved in the Induction of Systemic Resistance by Gram-Positive Rhizobacteria—cont'd

Strains	Plants	Pathogen	Signalling Pathway			References
			Salicylic Acid	Jasmonic Acid	Ethylene	
3-Pentanol (Volatile From <i>Bacillus amyloliquefaciens</i> IN937a)	Pepper	<i>Xanthomonas axonopodis</i> pv. <i>vesicatoria</i> ^h	+	+	0	Choi et al. (2014)
3-Pentanol	<i>Arabidopsis</i>	<i>P. syringae</i> pv. <i>tomato</i> ^h	+	+	0	Song, Choi, and Ryu (2015)
<i>Bacillus vallismortis</i> EXTN-1	Tobacco	<i>Pepper mild mottle virus</i> ^b	+	+	+	Ahn, Park, and Kim (2002)
<i>B. vallismortis</i> EXTN-1	Potato	Potato virus Y ^b	+	+	nd	Park, Ryu, and Kim (2006)
<i>Bacillus cereus</i> UMAF8564	Cucurbits	<i>Powdery mildew</i> ^b	+	0	nd	Garcia-Gutierrez et al. (2013)
<i>Bacillus amyloliquefaciens</i> LJ02	Cucurbits	<i>Powdery mildew</i> ^b	+	nd	nd	Li et al. (2015)
Mycosubtilin From <i>Bacillus</i> sp.	Grapevine	<i>Botrytis cinerea</i> ⁿ	+	+	0	Farace et al. (2015)
<i>Bacillus subtilis</i> GB03	<i>Arabidopsis</i>	<i>B. cinerea</i> ⁿ	+	+	0	Sharifi and Ryu (2016)
<i>B. subtilis</i> GB03	<i>Arabidopsis</i>	<i>E. carotovora</i> ⁿ	0	0	+	Ryu et al. (2004)
C13 hexadecane	<i>Arabidopsis</i>	<i>E. carotovora</i> ⁿ	0	+	0	Park, Lee, Kloepper, and Ryu (2013)
<i>Bacillus amyloliquefaciens</i>	Tomato	<i>Ralstonia solanacearum</i> ⁿ	0	++	+	Tan et al. (2013)
<i>Bacillus</i> sp. JS	Tobacco	<i>Rhizoctonia solani</i> ⁿ	0	+	nd	Kim et al. (2015)
Surfactin from <i>Bacillus</i> FZB42	Lettuce	<i>R. solani</i> ⁿ	0	+	0	Chowdhury et al. (2015)

(+) positive effect, (−) negative effect, (0) no effect, (nd) no data. Superscript bold letters 'b' indicates biotroph, 'h' indicates hemibiotroph and 'n' indicates necrotroph.

Constitutive expression of the JA pathway via constitutive expression of *VSP1* (*cev1*) also has a negative effect on plant growth (Ellis & Turner, 2001).

Interestingly, rhizobacteria activate plant defence responses against several invaders. Not only do these bacteria have no negative effect on plant growth, but they actually improve plant growth and yield significantly. Indeed, plants treated with PGPR do not exhibit noticeable changes in defence gene expression, but, after pathogen challenge, they respond more rapidly and strongly than nontreated plants. This phenomenon is known as priming of defence (Conrath et al., 2006). Priming makes the plant ready for battle. Recent studies shed light on some molecular aspects of priming. Treating plants with priming inducers increased the expression of mitogen-activated protein kinases, MPK3 and MPK6, key signalling molecules in plant defence, in *Arabidopsis* (Conrath, Beckers, Langenbach, & Jaskiewicz, 2015). However, these molecules were in the nonphosphorylated, inactive form. After pathogen attack, plants do not need to spend time synthesizing these signalling molecules; they are present in the proper amounts. Epigenetic regulation is also important in defence priming. Methylation of siRNA, histone modification and chromatin modification are involved in the priming of resistance; see Conrath et al. (2015) for a more comprehensive review of the molecular mechanisms of defence priming. Examples of priming of resistance by PGPR or their metabolites are given in Table 1. As shown in this table, rhizobacteria utilize different signalling pathways with the type of signalling pathway depending on the type of pathosystem. Resistance against biotrophs is commonly mediated by modulation of the SA pathway. Biotrophic pathogens include powdery and downy mildews, viruses and rusts, as well as hemibiotrophs such as *P. syringae*, *Xanthomonas* and *Colletotrichum*. However, modulation of plant defence is not limited to rhizobacteria, pathogens also modulate plant defence as virulence mechanism. Some strains of *P. syringae* produce coronatine, which activates the JA pathway and represses the SA pathway (Brooks et al., 2005). Rhizobacteria also activate the JA pathway against necrotrophic pathogens such as *Rhizoctonia solani*, *Ralstonia solanacearum*, *Pectobacterium carotovorum* and *Botrytis cinerea*. However, *B. cinerea* can activate the SA pathway by producing an exopolysaccharide as virulence factor (El Oirdi et al., 2011). As shown in Table 1, the activation of both JA and SA signalling is common in Gram-positive bacteria.

7. YOU ARE NOT ALONE! – PLANTS CRY FOR HELP FROM RHIZOBACTERIA UNDER INSECT ATTACK

As mentioned earlier, rhizobacteria are attracted by root exudates in the rhizosphere. Plants can change the microbiome by changing their exudates. Some exudates are attractive and some are repulsive to specific groups of microbes. [Carvalhais et al. \(2015\)](#) showed that mutation in two branch of JA signalling in *Arabidopsis* had different exudate profiles and attracted specific groups of microbes. A mutation in *med25* increased the population sizes of *Bacillus* and *Streptomyces*, and a mutation in *myc2* increased the abundance of members of Enterobacteriaceae. Application of exogenous Me-JA also altered the populations of bacteria and Archaea.

Aphid and whitefly infestation of the aerial parts of pepper increases the abundance of Gram-positive PGPR bacteria and fungi, as shown in [Fig. 2](#). The insects activate SA and JA signalling pathways in aboveground and belowground plant parts ([Lee, Lee, & Ryu, 2012](#); [Yang et al., 2011](#)). Sometimes, plants challenged by invaders recruit specific biocontrol agents for defence against the invaders, a phenomenon known as cry for help. Aphid infestation in sweet pepper activates the SA and JA pathways. These plants actively recruit *B. subtilis* GB03 to colonize their roots ([Lee, Farag, et al., 2012](#)). Moreover, infection with *Pseudomonas syringae* pv. tomato DC3000 in aerial parts of plants increases the population of *Bacillus subtilis* FB17 in roots. Infected *Arabidopsis* plants secrete malic acid into the rhizosphere; this organic acid specifically attracts *B. subtilis* FB17 to the root ([Fig. 2](#)). FB17 induces systemic resistance against *P. syringae* pv. tomato DC3000 ([Rudrappa, Czymmek, Paré, & Bais, 2008](#)). Organic acids are the main root exudates that alter bacterial abundance. Malic acid affects chemotaxis in bacteria, and fumaric acid improves biofilm formation ([Yuan et al., 2015](#)). Cucumber plants inoculated with *Fusarium oxysporum* f.sp. *cucumerinum* exhibit increased fumaric acid secretion and improved colonization by *Bacillus amyloliquefaciens* SQR9 ([Yuan et al., 2015](#)).

8. FROM THE PETRI DISH TO THE FIELD: COMMERCIAL APPLICATIONS OF RHIZOBACTERIA

The demand for organic farming and healthy foods has increased in recent years, prompting researchers to develop safer chemical pesticides or biopesticides. Moreover, the cost of agrochemical discovery and the period of their registration have increased rapidly due to stricter legislation, both of

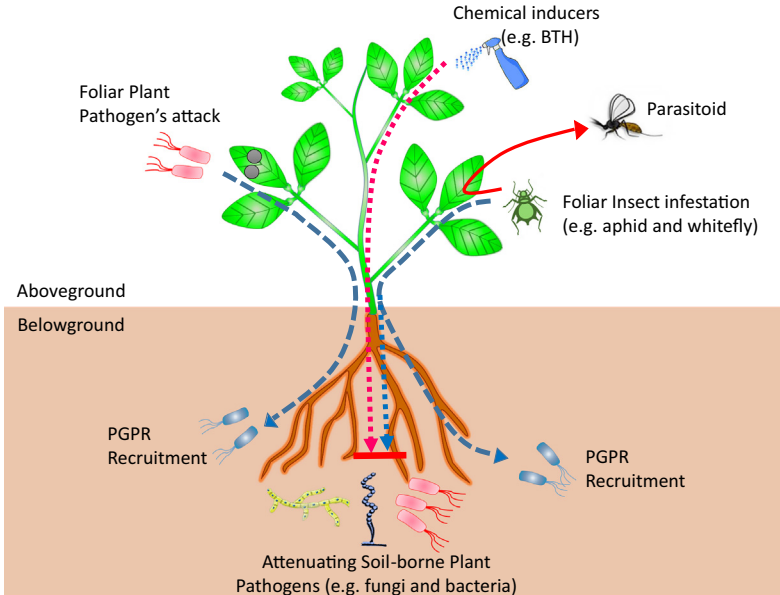


Figure 2 Plants link aboveground and belowground. Infestation with insects such as aphids and whiteflies or even treatment with chemical inducers modulates the levels of defence hormones jasmonic acid and salicylic acid in plants. Whitefly infestation increases the population of Gram-positive plant growth-promoting rhizobacteria (PGPR) [blue colour], and benzothiadiazole (BTH) increases the abundance of Gram-negative PGPR [pink colour] and fungi in the rhizosphere. Aphid damage induces the production of specific volatiles in the plant that function as signals for the attraction of aphid parasitoids. Inoculation of plants with the plant pathogen *Pseudomonas syringae* recruits biocontrol bacterium *Bacillus subtilis* to colonize plant roots and induce resistance against the pathogen.

which favour investment in the production of biopesticides. The annual growth rate of the biopesticide market is more than 15%, but that of chemical pesticides has been declining by 1.5% annually (Thakore, 2006). Biopesticide companies such as Gustafson, Agroquest, Certis, Becker Underwood, BioWorks, ABiTEP GmbH, Marrone Bio Innovation and Prophyta have released effective biopesticides to the market. Agrochemical supercompanies such as Bayer CropScience have also been interested in the biopesticide market. Bayer CropScience acquired Agroquest in 2012 at a price of 425 million US dollars (Kling, 2012). One year later, Bayer also signed an agreement to acquire Prophyta GmbH. BASF, the giant chemical pesticide company, acquired Becker Underwood in 2013.

Nowadays, effective PGPR formulations such as Kodiak, Serenade, Sonata, Yieldshield and Rhizovital are available. Some of these products, such as Serenade and Kodiak, can also induce systemic resistance in plants. Serenade activates JA- and ethylene-dependent genes and increases PAL activity in canola (Lahlali et al., 2013). *B. subtilis* GB03, the active ingredient of Kodiak and Quantum, activates defence against multiple pathogens. Combining two or more PGPR strains is likely to enhance their effects (Raupach & Kloepper, 1998). However, these bacilli strains must have no negative effects on each other and must have different modes of action in the promotion of plant growth or biocontrol of pests and pathogens. BioYield is a mixture of *B. subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a with the carrier chitosan. This formulation induces systemic resistance against two plant pathogens. The type of defence signalling depends on the type of pathogen (Ryu, Murphy, Reddy, & Kloepper, 2007). In addition to combining strains, it is possible to combine PGPR strains with plant activators. The plant activator BTH, a derivative of SA, has a negative effect on plant growth, but treatment of BTH combined with *Bacillus pumilus* INR7 diminishes the negative effect of BTH on plant growth under field conditions (Yi, Yang, & Ryu, 2013).

The increasing information about the molecular biology of plant–PGPR interactions has opened up a new window for improving commercial biocontrol products by genetic engineering. For successful and sustainable application of PGPR, it is important to consider three factors: soil quality, PGPR and plants. The soil should be amended to support physical and biochemical bases for holobiome establishment. Application of compost, vermicompost, sewage sludge, green manure or biochar and good cultural practices will improve soil quality to support the holobiome. Biochar amendment in soil improves soya bean growth either directly or by shifting the microbiome in favour of PGPR (Egamberdieva, Wirth, Behrendt, Abd Allah, & Berg, 2016). On the plant side, root exudation could be engineered. As stated earlier, organic acids such as malic acid and citric acid influence the rhizobacterial population. Overexpressing the pyrophosphatase gene in *Arabidopsis* increased the levels of these two organic acids in exudates. Treating *Arabidopsis* with the toxin coronatine or with flagellin from *Pseudomonas syringae* pv. tomato induced malic acid secretion, which subsequently increased the population size of the biocontrol agent *Bacillus subtilis* (Rudrappa et al., 2008). On the bacterial side, there are several examples of genetic engineering of PGPR to enhance their rhizosphere competence. As noted earlier, overexpressing a trehalose-6-phosphate

synthase gene in *R. etli* improved its ability to induce drought stress tolerance in common bean (Suárez et al., 2008). Expressing *Rhizobium leguminosarum*-derived ACC deaminase in *Sinorhizobium meliloti* increased its nodulation in alfalfa (Ma, Charles, & Glick, 2004). Expressing this gene in *Mesorhizobium ciceri* also reduced the negative effects of osmotic stress in chickpea (Brígido, Nascimento, Duan, Glick, & Oliveira, 2013). However, attention should also be paid to the holobiont when applying PGPR or releasing genetically engineered organisms due to the possibility of ecologically disturbing the shaping of each component in the holobiome. To avoid this pitfall, the impact of genetically engineered plants and microbes must be carefully evaluated. Any alteration in a component of the holobiont may have adverse effects on the other components. For example, plants under attack by the insect *Diabrotica virgifera* recruited entomopathogenic nematodes in wild maize, but not in new American hybrid maize lines (Rasmann et al., 2005). Subsequently, the gene corresponding to the determinant of recruitment of entomopathogenic nematodes was introduced into American maize, resulting in protection against insect herbivory. Breeding programmes that take this concept into consideration may greatly improve the control of plant pathogens and insects.



9. PERSPECTIVES

In this review, we explained in detail the process and molecular mechanisms involved in plant–PGPR communications. This advanced knowledge has inspired scientists and has provided a basis for discovery and field application of novel disease-protecting agents. Rhizobacterial determinants are another source of new plant activators. For example, 3-pentanol, a volatile of *Bacillus*, suppresses multiple diseases on pepper in the field (Choi, Song, Yi, & Ryu, 2014). This compound induced the SA and JA signalling pathways. Another bacterial volatile, 2-butanone, induced plant defence against bacteria and aphids under field conditions. This compound also increased the population of beneficial lady bird beetles in the field (Song & Ryu, 2013).

In this new millennium, the strong demand for reducing the use of chemical pesticides and carbon consumption and our concern about environmental side effects must be balanced with the need to produce healthy plants to feed the world's population. In this chapter, we described the many potential applications of a group of rhizosphere bacteria (PGPR), from mechanisms to field applications. We hope that this information

broadens our understanding and will be of interest to a general audience. Finally, we again emphasize that we hope we have provided a fresh point of view about the roles of PGPR in plant health based on bacterium–plant communications.

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