Plant Growth Promoting Rhizobacteria -
A Promising Tool for Eco-friendly Agriculture

D.G. Panpatte*, H.N. Shelat, R.V. Vyas and Y.K. Jhala
Department of Agricultural Microbiology, B. A. College of Agriculture,
Anand Agricultural University, Anand, Gujrat, India.

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Worldwide agricultural practice is moving to a more sustainable and environmental friendly approach due to increasing demand of safe food and awareness of the environmental and human health damage induced by overuse of pesticides and fertilizers (Avis et al., 2008). In this context, soil microorganisms with beneficial activity on plant growth and health represent an attractive alternative to conventional agricultural. In recent years, several microbial inoculants have been formulated, produced, marketed, and applied successfully by an increasing number of growers (Reed and Glick 2004). Although all parts of the plant are colonized by microorganisms, the rhizosphere represents the main source of bacteria with plant-beneficial activities. These bacteria are generally defined as plant growth promoting rhizobacteria (PGPR) (Bashan and Holguin, 1998). Plant growth promoting rhizobacteria (PGPR) influence plant health and productivity by two prime mechanisms- 1) Direct mechanism viz. increased nutrient availability and phytohormone production 2) Indirect mechanism involving control of phytopathogens. Research on PGPR has been increasing at an ever increasing rate since the term was first used by Kloeppeper and coworkers in the late 1970s (Kloepper and Schroth, 1978). Today PGPR are commonly used in developing countries, and inoculants are used on millions of hectares of land (Zehnder et al., 2001). Nevertheless, implementation of this biotechnology has been hindered by the lack of consistency and variation in responses that are obtained in field trials from site to site, year to year, or for different crops (Lambert and Joos, 1989). PGPR have been subjected to numerous investigations focused on biotechnological applications in agriculture, horticulture, forestry and environmental protection (Zahir et al., 2004). PGPR strains are broadly distributed among many taxa including Actinobacteria, Bacteroidetes, Cyanobacteria, Firmicutes and Proteobacteria (Tilak et al., 2005).

PGPR for improvement of plant nutritional status
The means by which PGPR enhance the nutrient status of host plants can be achieved by three main mechanisms : (1) biological nitrogen fixation (2) increasing the availability of nutrients in the rhizosphere (3) phytohormone production which thereby increase root surface area for nutrient absorption

Biological nitrogen fixation
Nitrogen-fixing (diazotrophic) bacteria fix atmospheric nitrogen by means of the enzyme nitrogenase, a two component metalloenzyme composed of (a) dinitrogenase reductase and (b) the dinitrogenase. Since nitrogen fixation requires a large amount of ATP, it would be advantageous if rhizobial carbon resources were directed toward oxidative phosphorylation, which results in the

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* To whom all correspondence should be addressed. E-mail: dgpanpatte@gmail.com
synthesis of ATP, rather than glycogen synthesis, which results in the storage of energy as glycogen. An undesirable side reaction of nitrogen fixation is the reduction of H2 to H+. ATP is wasted on the production of hydrogen and only 40–60% of the electron flux through the nitrogenase system is transferred to N2, lowering the overall efficiency of nitrogen fixation. Some diazotrophic strains contain hydrogenase that can take up H2 from the atmosphere and convert it into H+. The presence of a hydrogen uptake system in a symbiotic diazotroph improves its ability to stimulate plant growth by binding and then recycling the hydrogen gas that is formed inside the nodule by the action of nitrogenase.

There are two types of biological fixation: symbiotic and nonsymbiotic. The first is the most important mechanism by which most atmospheric N is fixed, but it is limited to legume plant species and various trees and shrubs that form actinorhizal roots with Frankia. This process is carried out in well-defined nodule structures. Among the most studied symbiotic bacteria are Rhizobium, Bradyrhizobium, Sinorhizobium, and Mesorhizobium (Zahran, 2001). Although the beneficial effects of the symbiotic association of rhizobia with legume plants is known, these bacteria are not considered PGPR, except when associated with non-legume plants (Dobbelaere et al., 2003). Non-symbiotic N-fixing rhizospheric bacteria belonging to genera including Azotococcus (Reinhold-Hurek et al., 1993), Azospirillum (Bashan and de-Bashan, 2010), Burkholderia (Estrada de los Santos et al., 2001), Gluconacetobacter (Fuentes-Ramirez et al., 2001) and Pseudomonas (Mirza et al., 2006) have been isolated from different soils. Due to the high energy requirement for N fixation and relatively low metabolic activity of free living organisms that must compete for root exudates outside anodule environment, the ability of non-symbiotic bacteria to fix significant quantities of N is limited. The presence of a diazotrophic bacterium in the rhizosphere of a certain plant is no longer considered to imply that such bacteria make a substantial contribution to N fixation and N supply for plant growth. Although the N-fixing capacity of certain bacteria can easily be demonstrated under in vitro conditions, its demonstration in greenhouse and field studies is more complex and highly variable. Nevertheless, studies in sorghum, maize and wheat inoculated with Azospirillum have revealed a contribution of only 5 kg N ha−1 yr−1 (Okon and Lanbandera-Gonzalez, 1994).

**Increased availability of nutrients in rhizosphere**

The major mechanism used by PSB for solubilization of inorganic P is based on the synthesis of low molecular weight organic acids such as gluconic and citric acid (Bnayahu, 1991; Rodriguez et al., 2004). These organic acids bind phosphate with their hydroxyl and carboxyl groups thereby chelating cations and also inducing soil acidification, both resulting in the release of soluble phosphate (Kpomblekou and Tabatabai, 1994; Bnayahu, 1991). Other mechanisms that have been implicated in solubilization of inorganic phosphate are the release of H+ (Illmer and Schinner, 1992), the production of chelating substances (Sperber, 1958; Duff and Webley, 1959) and inorganic acids (Hopkins and Whiting, 1916). In addition, exopolysaccharides synthesized by PSB participate indirectly in the solubilization of tricalcium phosphates by binding free P in the medium, affecting the homeostasis of P solubilization (Yi et al., 2008).

These bacteria have been characterized as members of the Bacillus, Burkholderia, Enterobacter, Klebsiella, Kluyvera, Streptomyces, Pantoea and Pseudomonas genera, (Chung et al., 2005: Hariprasad and Niranjana, 2009; Oliveira et al., 2009) in various studies of P solubilizing bacteria from different rhizospheric soils. These microorganisms grow in media with tricalcium phosphate or similar insoluble materials as the only phosphate source and not only assimilate the element, but also solubilize quantities in excess of their nutritional demands, thereby making it available for plants (Chen et al., 2006).

The mineralization of organic P occurs through the synthesis of phosphatases, including phosphomonoesterase, phosphodiesterase, and phosphotriesterase, catalysing the hydrolysis of phosphoric esters (Rodriguez and Fraga, 1999). In addition, P solubilization and mineralization can coexist in the same bacterial strain (Tao et al., 2008). Among the phytase producing rhizobacteria, species belonging to Bacillus, Burkholderia, Enterobacter, Pseudomonas, Serratia and Staphylococcus genera are the most common.
culturable bacteria (Richardson and Hadobas, 1997; Hussin et al., 2007; Shedova et al., 2008). Many of these bacteria are remarkably efficient.

The role of phosphate solubilization in plant growth promotion is often overshadowed by other plant beneficial activities expressed by the PSB. When Poonguzhali et al. (2008) selected ten pseudomonads on the basis of their high phosphate solubilization activity on tricalcium phosphate and inoculated seeds with these strains, which also synthesize indole-3-acetic acid, ACC deaminase, and siderophores, the plants showed increased root elongation and biomass, however, under the conditions employed, P uptake was unaffected. The highest efficiency in stimulating plant growth was observed when PSB were co-inoculated with bacteria with other physiological capabilities such as N fixation (Rojas et al., 2001; Valverde et al., 2006; Matias et al., 2009), or with mycorrhizal (Ray et al., 1981; Azco’n-Aguilar et al., 1986; Toro et al., 1997; Babana and Antoun 2006; Matias et al., 2009) or nonmycorrhizal fungi (Babana and Antoun 2006). Thus, the use of mixed inocula with different plant beneficial activities appears to be a promising strategy.

**Increased iron availability**

Both microbes and plants have a quite high iron requirement, and this condition is more accentuated in the rhizosphere where plant, bacteria, and fungi compete for iron (Guerinot and Ying, 1994; Loper and Buyer, 1991). To survive with a limited supply of iron, in bacteria, cellular iron deficiency induces the synthesis of low-molecular weight siderophores, molecules with an extraordinarily high affinity for Fe$^{3+}$ (Ka ranging from 1023 to 1052) as well as membrane receptors able to bind the Fe–siderophore complex, thereby allowing iron uptake by microorganisms (Neilands, 1981). Some rhizospheric bacteria also produce siderophores and there is evidence that a number of plant species can absorb bacterial Fe$^{3+}$ siderophore complexes (Bar-Ness et al., 1991; Wang et al., 1993). Many Pseudomonas spp. and related genera produce yellow–green, water soluble, fluorescent pigments collectively called pyoverdines, composed of a quinoleinic chromophore bound together with a peptide and an acyl chain, conferring a characteristic fluorescence to the bacterial colonies (Meyer and Abdallah, 1978). About 100 different pyoverdines have been identified (Budzikiewicz, 2004; Meyer et al., 2008) and represent about 20% of the microbial siderophores that have been characterized (Boukhalfa and Crumbliss, 2002). Pyoverdine-mediated iron uptake confers a competitive advantage on to fluorescent pseudomonads over other microorganisms (Mirleau et al., 2000, 2001). Regulation of pyoverdine synthesis is not only based on iron availability but also on quorum sensing whereby cell-to-cell communication mediated by N-acyl homoserines lactones occurs activating siderophore synthesis (Stintzi et al., 1998). Siderophores are involved both in plant growth promotion and health protection (Robin et al., 2008). The benefits of microbial siderophores have been demonstrated by supplying radiolabeled ferrisiderophores to plants as a sole source of iron (Jin et al., 2006). In addition, by supplying iron to the plants, siderophores may help to alleviate the stresses imposed on plants by high soil levels of heavy metals (Braud et al., 2006). *Kluyvera ascorbata*, a PGPB able to synthesize siderophores was able to protect canola, Indian mustard, canola, and tomato from heavy metal (nickel, lead, and zinc) toxicity (Burd et al., 2000). The siderophore overproducing mutant SUD165/26 of this bacterium provided even greater protection, as indicated by the enhanced biomass and chlorophyll content in plants cultivated in nickel contaminated soil (Burd et al., 2000).

**Phytohormone production**

The production of phytohormones by PGPR is now considered to be one of the most important mechanisms by which many rhizobacteria promote plant growth (Spaepen et al., 2007). Studies have demonstrated that the PGPR can stimulate plant growth through the production of auxins (indole acetic acid) (Spaepen et al., 2008), gibberellin (Bottini et al., 2004) and cytokinins (Timmusk et al., 1999) or by regulating the high levels of endogenous ethylene in the plant (Glick et al., 1998).

**Indole 3 acetic acid**

Many actual and putative biofertilizing-PGPR produce phytohormones that are believed to be related to their ability to stimulate plant growth. In most cases these phytohormones are believed to be changing assimilate partitioning patterns in plants and affecting growth patterns in
roots to result in bigger roots, more branched roots, and/or roots with greater surface area. Indole-3-acetic acid is a phytohormone which is known to be involved in root initiation, cell division, and cell enlargement (Salisbury, 1994).

Many important plant-microbial interactions center on the production of auxins, IAA being the main plant auxin. The IAA is responsible for the division, expansion and differentiation of plant cells and tissues and stimulates root elongation. Most commonly, IAA-producing PGPR are believed to increase root growth and root length, resulting in greater root surface area which enables the plant to access more nutrients from soil. The ability to synthesize IAA has been detected in many rhizobacteria as well as in pathogenic, symbiotic and free living bacterial species (Tsavkelova et al., 2006). At present, auxin synthesizing rhizobacteria are the most well-studied phytohormone producers (Tsavkelova et al., 2006; Spaepen et al., 2007). Production of other phytohormones by biofertilizing- PGPR has been identified, but not nearly to the same extent as bacteria which produce IAA. Among PGPR species, Azospirillum is one of the best studied IAA producers (Dobbelkaere et al., 1999). Other IAA producing bacteria belonging to Aeromonas (Halda-Alija, 2003), Azotobacter (Ahmad et al., 2008), Bacillus (Swain et al., 2007), Burkholderia (Halda-Alija, 2003), Enterobacter (Shoebitz et al., 2009), Pseudomonas (Hariprasad and Niranjana, 2009) and Rhizobium (Ghosh et al., 2008) genera have been isolated from different rhizosphere soils. Inoculation with IAA producing PGPR has been used to stimulate seed germination, to accelerate root growth and modify the architecture of the root system, and to increase the root biomass. In recent studies, Tsavkelova et al. (2007) have extended beyond individual strains as inoculants and reported an increase in the germination of orchid seeds (Dendrobium moschatum) inoculated with Sphingomonas sp. and IAA producing Mycobacterium sp. In addition to stimulating root growth, IAA producing bacteria can also be used to stimulate tuber growth. Swain et al. (2007) reported a positive effect of Bacillus subtilis IAA producing strains on the edible tubercle Dioscorea rotundata L in one of their studies. They applied a suspension of B. subtilis on the surface of the plants, which resulted in an increase in stem and root length, increased fresh weight of the stem and root, an increase in the root:stem ratio and increased numbers of sprouts as compared with non-inoculated plants.

**Gibberellins**

Gibberellins affect cell division and elongation and are involved in several plant developmental processes, including seed germination, stem elongation, flowering, fruit setting, and delay of senescence in many organs of a range of plant species (MacMillan, 2002). Gibberellins have also been implicated in promotion of root growth since they regulate root hair abundance (Bottini et al., 2004). The ability of bacteria to synthesize gibberellins-like substances was first described in Azospirillum brasilense (Tien et al., 1979) and Rhizobium (Williams and Sicardi de Mallorca, 1982). Plant growth promotion by gibberellin-producing PGPR has positive effect on plant biomass (Atzhorn et al., 1988; Gutierrez-Manero et al., 2001; Joo et al., 2009; Kang et al., 2009). Azospirillum spp. is a nitrogen fixing and IAA-producing PGPB that is well known to induce enhancement of plant growth and yield (Okon and Labandera-Gonzalez, 1994) under both non-stressed as well as stressful conditions such as drought (Creus et al., 1997). Besides improving N nutrition under some conditions, plant growth promotion activity by Azospirillum spp. may also be related to gibberellin synthesis.

**Cytokinins**

Cytokinins play significant role in a wide range of physiological processes such as plant cell division, interruption of the quiescence of dormant buds, activation of seed germination, promotion of branching, root growth, accumulation of chlorophyll, leaf expansion, and delay of senescence (Salisbury and Ross, 1992). Many PGPR including Azotobacter, Azospirillum, Rhizobium, Bacillus, and Pseudomonas spp., have been found to produce cytokinine (Salamone et al., 2001). Various environmental stresses such as drought may also cause plant cytokinin levels to become elevated (Arkhipova et al., 2007), often inducing an increase in plant ethylene levels which in turn inhibits root elongation (Werner et al., 2003). A positive correlation has been observed in several legume species between the level of cytokinins in plants and the ability of Rhizobia to form nodules on the roots of those plants (Lorteau et al., 2001).
In addition, cytokinins are believed to be involved in rhizobial infection and nodule differentiation (Frugier et al., 2008). A strain of Rhizobium sp., impaired in the synthesis of the Nod factor (Nod-) and therefore unable to nodulate its legume host, but genetically modified for the production of the cytokinin transzeatin, induced the formation, on Medicago sativa roots, of a nodule-like structure which remained uncolonized by Rhizobia, suggesting that cytokinins can mimic some of the morphogenetic effects of Nod factors.

**Ethylene**

Ethylene is the only gaseous phytohormone. It is also known as the ‘wounding hormone’ because its production in the plant can be induced by physical or chemical perturbation of plant tissues (Salisbury, 1994). Ethylene is essential for the growth and development of plants, but it has different effects on plant growth depending on its concentration in root tissues. At high concentrations, it can be harmful, as it induces defoliation and cellular processes that lead to inhibition of stem and root growth as well as premature senescence, all of which lead to reduced crop performance (Li et al., 2005). The term “stress ethylene” (Abeles, 1973), describes the increase in ethylene synthesis associated with environmental stresses including extremes of temperature, high light, flooding, drought, the presence of toxic metals and organic pollutants, radiation, wounding, insect predation, high salt, and various pathogens including viruses, bacteria, and fungi (Morgan and Drew, 1997). The increased level of ethylene formed in response to environmental stresses can exacerbate symptoms of stress or it can lead to responses that enhance plant survival under adverse conditions. Thus, stress ethylene has been suggested to both alleviate and exacerbate some of the effects of the stress, depending upon the plant species, its age and the nature of the stress (Van Loon and Glick, 2004). Glick et al. (1998) put forward the theory that the mode of action of some PGPR was the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme which could cleave ACC, the immediate precursor to ethylene in the biosynthetic pathway for ethylene in plants. They submitted that ACC deaminase activity would decrease ethylene production in the roots of host plants and result in root lengthening. The growth promotion effects of ACC deaminase-producing PGPR appear to be best expressed in stressful situations such as flooded (Grichko and Glick, 2001) or heavy metal-contaminated soils (Burd et al., 1998). Bacterial ACC deaminase activity is relatively common. ACC deaminase activity genotypes were found in a wide range of bacterial isolates including Azospirillum, Rhizobium, Agrobacterium, Achromobacter, Burkholderia, Ralstonia, Pseudomonas, and Enterobacter (Blaha et al., 2006). Grinchko and Glick (2001) inoculated tomato seeds with the ACC deaminase expressing bacteria Enterobacter cloacae and Pseudomonas putida and registered an increase in plant resistance on 55 days of age to 9 consecutive days of flooding. Ghosh et al. (2003) found ACC deaminase activity in three Bacillus species (Bacillus circulans DUC1, Bacillus firmus DUC2 and Bacillus globisporus DUC3), which stimulated root elongation of Brassica campestris plants. Mayak et al. (2004) evaluated tomato plants inoculated with the bacterium Achromobacter piechaudii under water and saline stress conditions. The authors reported a significant increase in fresh and dry weight of inoculated plants. In soils with a high copper content, Reed and Glick (2005) reported an increase in dry matter content of the root and the air part in raps seeds inoculated with the ACC deaminase producing bacterium Pseudomonas asplenii.

**PGPR for biocontrol of phytopathogens**

A large number of mechanisms are involved in biocontrol and can involve direct antagonism via production of antibiotics, siderophores, HCN, hydrolytic enzymes (chitinases, proteases, lipases, etc.), or indirect mechanisms in which the biocontrol organisms act as a probiotic by competing with the pathogen for a niche (infection and nutrient sites). Biocontrol can also be mediated by induced systemic resistance (ISR) responses (van Loon, 2007) in the plant tissues.

**Antibiotic production**

The synthesis of antibiotics is prime mechanism of biocontrol exerted by PGPR (Mazurier et al., 2009). The antibiotics synthesized by PGPR include butyro lactones, zwittermycin A, kanosamine, oligomycin A, oomycin A, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, viscosinamide, xanthobaccin, agrocin 84, agrocin 434, herbicolen
and 2,4-diacetyl phloroglucinol (2,4-DAPG) (Whipps, 2001). The last is one of the most efficient antibiotics in the control of plant pathogens (Fernando et al., 2006) and can be produced by various strains of Pseudomonas, one of the most common bacterial species of the rhizosphere (Rezzonico et al., 2007). The 2,4-DAPG has a wide spectrum of properties in that it is antifungal (Loper and Gross, 2007; Rezzonico et al., 2007), antibacterial (Velusamy et al., 2006) and antihelmintic (Cronin et al., 2007). In soils, it suppresses the growth of the wheat pathogenic fungus Gaecumonomyces graminis var. tritici, Raaijmakers et al. (1999) reported a production of 0.62 ng 2,4-DAPG per 105-107 CFU g−1 root by P. fluorescens, strain Q2-87.

Production of cell wall degrading enzymes:

The other mechanism by which PGPR behave as biocontrol agents is the production of cell wall degrading enzymes such ashtinase, cellulose, b-1,3 glucanase, protease, or lipase, that induce lysis of fungal cell walls (Chet and Inbar, 1994). In particular, chitinase is considered crucial for the biocontrol activity exhibited by PGPR against phytopathogenic fungi.

Production of hydrogen cyanide

Hydrogen cyanide (HCN) is a volatile, secondary metabolite that suppresses the development of microorganisms HCN is a powerful inhibitor of many metal enzymes, especially copper containing cytochrome C oxidases. To date many different bacterial genera have shown to be capable of producing HCN, including species of Alcaligenes, Aeromonas, Bacillus, Pseudomonas and Rhizobium (Devi et al., 2007; Ahmad et al., 2008). HCN production is a common trait within the group of Pseudomonas present in the rhizosphere, with some studies showing that about 50% of pseudomonads isolated from potato and wheat rhizosphere are able to produce HCN in vitro (Bakker and Schippers, 1987; Schippers et al., 1990). Various studies attribute a disease protective 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 basicota, respectively (Voisard et al., 1989; Siddiqui et al., 2006). The subterranean termite Odontotermes obesus, an important pest in agricultural and forestry crops in India, is also controlled by HCN (Devi et al., 2007).

Production of siderophores

Siderophores are low molecular weight iron chelating compounds. These compounds are produced by various types of bacteria in response to iron deficiency which normally occurs in neutral to alkaline pH soils, due to low iron solubility at elevated pH (Sharma and Johri, 2003). Iron is essential for cellular growth and metabolism, such that Fe acquisition through siderophore production plays an essential role in determining the competitive fitness of bacteria to colonize plant roots and to compete for iron with other microorganisms in the rhizosphere. Siderophore producing PGPR can prevent the proliferation of pathogenic microorganisms by sequestering Fe3+ in the area around the root (Siddiqui, 2006). Fe depletion in the rhizosphere does not affect the plant, as the low Fe concentrations occur at microsites of high microbial activity during establishment of the pathogen. Many plants can use various bacterial siderophores as iron sources, although the total concentrations are probably too low to contribute substantially to plant iron uptake. Plants also utilize their own mechanisms to acquire iron; dicots via a root membrane reductase protein that converts insoluble Fe3+ into the more soluble Fe2+ ion, or in the case of monocots by production of phytosiderophores (Crowley, 2006). Various studies have isolated Siderophore producing bacteria belonging to the Bradyrhizobium (Khandelwal et al., 2002), Pseudomonas (Boopathi and Rao, 1999), Rhizobium (Roy and Chakrabartty, 2000), Serratia and Streptomyces (Kuffner et al., 2008) genera from the rhizosphere. Carrillo-Castañeda et al. (2002) reported positive effects on alfalfa plantlet growth after the inoculation of siderophore producing Pseudomonas, Rhizobium and Azospirillum grown in iron limited cultures. The inoculated alfalfa seeds increased their germination as well as the root and stem dry weight. Nevertheless, as with other PGPR, the growth promotion that occurred may be due to other mechanisms or combinations of mechanisms that increase nutrient availability, suppress pathogens, or affect root growth via hormone production.

Competitive colonization of roots

Competitive colonization of the root system and successful establishment in the zones of the roots that are preferentially colonized by the pathogen is a prerequisite for effective biocontrol
(Weller, 1988). In addition, the synthesis of several antagonistic molecules through quorum sensing is directly linked to the proliferation of the PGPB on the roots. Moreover, PGPB can out compete some pathogens by degrading organic compounds or sequestering micronutrients (i.e., iron), which are also required for the growth and the development of deleterious microorganisms (Faravel et al., 2003). A number of factors such as soil composition, temperature, relative humidity, composition of root exudates, presence of recombinant plasmids as well as the interactions with other soil biota can affect the persistence of a PGPB on the root system making it difficult to predict the behavior of the bacterial strain under natural conditions. Therefore, PGPB that are effective in the laboratory frequently do not show any significant impact on plants in the field (Glick et al., 1999).

**Induced systemic resistance**

Some PGPR can trigger the phenomenon of induced systemic resistance (ISR) which involves jasmonate and ethylene signaling within the plant that stimulates the host plant’s response to a range of pathogens without requiring direct interaction between the resistance-inducing microorganisms and the pathogen (Bakker et al., 2007). Besides ethylene and jasmonate, other bacterial molecules such as the O-antigenic side chain of the bacterial outer membrane protein lipopolysaccharide (Leeman et al., 1995), flagellar fractions (Zipfel et al., 2004), pyoverdine (Maurohofer et al., 1994), DAPG (Iavicoli et al., 2003; Siddiquiand Shoukat, 2003), cyclic lipopeptide surfactants (Ongena et al., 2007; Tran et al., 2007) and, in some instances, salicylic acid (van Loon et al., 1998) have been implicated as signals for the induction of systemic resistance. Most studies of systemic resistance have been carried out using fungal pathogens; however, this approach may also have potential in the control of bacterial pathogens such as *P. syringae pv. lachrymans*, the causal agent of bacterial angular leaf spot (Liu et al., 1995). ISR can induce alterations to host physiology leading to an overe xpression of plant defensive chemicals including pathogenesis-related proteinssuch as chitinases, peroxidases, superoxide dismutase phenylalanine ammonia lyase, phytoalexins, and polyphenol oxidase enzymes (Bakker et al., 2007).

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