JOURNAL OF PURE AND APPLIED MICROBIOLOGY, Dec. 2014. Vol. **8**(6), p. 4947-4959

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.

(Received: 06 April 2014; accepted: 19 August 2014)

Key words: Rhizobacteria, environmental friendly, agriculture.

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 Kloepper 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

* 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 H^+ to H_2 bynitrogenase. ATP is wasted on the production of hydrogen and only 40–60% of the electron flux through the nitrogenase system is transferred to N_2, lowering the overall efficiency of nitrogen fixation. Some diazotrophic strains contain hydrogenase that can take up H_2 from the atmosphere and convert it into H^+ and 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 actinorrhizal 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 *Azoarcus* (Reinhold-Hurek *et al*., 1993), *Azospirillum* (Bashan and de- Bashan, 2010), *Burkholderia* (Estrada de los Santos *et al*., 2001), *Gluconacetobacter* (Fuentes-Ramírez *et al*., 2001) and *Pseudomonas* (Mirza *et al*., 2006) have been isolated from differentsoils. 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

Phosphate solubilization

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 ferric-siderophores 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), gibberellines (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 (Dobbelaere *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 ratioand 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- producting 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/genes 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 campestri* 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 butyrolactones, zwittermycin A, kanosamine, oligomycin A, oomycin A, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, viscosinamide, xanthobaccin, agrocin 84, agrocin 434, herbicolin

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*., 1997). In soils, it suppresses the growth of the wheat pathogenic fungus *Gaeumannomyces 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 aschitinase, 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 Fe^{3+} 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 Fe^{2+} 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 (Fravel *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 (Maurhofer *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).

REFERENCES

1. Abeles FB, Ethylene in plant biology.Academic, New York, p 302 (1973).
2. Ahmad, F., Ahmad, I., Khan, M.S. Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiol. Res.* 2008; **163**, 173–181.
3. Ahmad, F., Ahmad, I., Khan, M.S. Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities.*Microbiol. Res*.2008; **163**, 173–181.
4. Arkhipova TN, Prinsen E, Veselov SU, Martinenko EVA, Melentiev I, Kudoyarova GR. Cytokinin producing bacteria enhance plant growth in drying soil. *Plant Soil.* 2007; **292**:305–315.
5. Atzhorn R, Crozier A, Wheeler CT, Sandberg G, Production of gibberellins and indole-3-acetic acid by Rhizobium phaseoli in relation to nodulation of Phaseolus vulgaris roots. *Planta*, 1988; **175**: 532–538.
6. Avis TJ, Gravel V, Antoun H, Tweddell RJ, Multifaceted beneficial effects of rhizosphere 2008.
7. Azco´n-Aguilar C, Gianinazzi-Pearson V, Fardeau JC, Gianinazzi S, Effect of vesicular arbuscular mycorrhizal fungi and phosphate-solubilizing bacteria on growth and nutrition of soybean in a neutral-calcareus soil amended with 32P-45Ca-tricalcium phosphate. *Plant Soil*, 1986; **96**:3–15.
8. Babana AH, Antoun H, Effect of Tilemsi phosphate rock-solubilizing microorganisms on phosphorus uptake and yield of field-grown wheat (Triticum aestivum L.) in Mali. *Plant Soil,* 2006; **287**:51–58
9. Bakker PAHM, Pieterse CMJ, van Loon LC, Induced systemic resistance by fluorescent Pseudomonas spp. *Phytopathology,* 2007; **97**: 239–243.
10. Bakker PAHM, Pieterse CMJ, van Loon LC, Induced systemic resistance by fluorescent Pseudomonas spp. *Phytopathology,* 2007; **97**:239–243.
11. Bakker, A.W., Schippers, B. Microbial cyanide production in the rhizosphere in relation to potato yield reduction and *Pseudomonas* spp. mediated plant growth stimulation. *Soil Biol. Biochem.*, 1987; **19**, 249–256.
12. Bar-Ness E, Chen Y, Hadar H, Marschner H and Romheld V, Siderophores of *Pseudomonas putida* as an iron source for dicot and monocot plants. *Plant Soil,* 1991; **130**, 231–241.
13. Bashan Y, Holguin G, Proposal for the division

of plant growth-promoting rhizobacteriaminto two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. *Soil Biol Biochem,* 1998; **30**: 1225–1228.

14. Bashan, Y., de-Bashan, L.E. How the plant growth-promoting bacterium Azospirillum promotes plant growth–a critical assessment. *Adv. Agron.*2010*;* **108**, 77–136.
15. Blaha D, Prigent-Combaret C, Mirza MS, Moe¨nne-Loccoz Y, Phylogeny of the 1-aminocyclopropane-1-carboxylic acid deaminase-encoding gene acdS in phyto beneficial and pathogenic Proteobacteria and relation with strain biogeography. *FEMS Microbiol Ecol,* 2006; **56**: 455–470
16. Bnayahu BY, Root excretions and their environmental effects: influence on availability of phosphorus. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Dekker, New York, 1991; 529–557.
17. Bnayahu BY, Root excretions and their environmental effects: influence on availability of phosphorus. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Dekker, New York,1991; 529–557.
18. Boopathi, E., Rao, K.S. A Siderophore from *Pseudomonas putida* type A1: structural and biological characterization. *BBA-Protein Struct. M*. 1999; **1435**, 30–40.
19. Bottini R, Cassa´n F, Piccoli P, Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. *Appl Microbiol Biotechnol,* 2004; **65**: 497–503.
20. Bottini R, Cassa´n F, Piccoli P, Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. *Appl Microbiol Biotechnol,* 2004; **65**: 497–503.
21. Boukhalfa H, Crumbliss AL, Chemical aspects of siderophore mediated iron transport. *Biometals*, 2002; **15**:325–339.
22. Braud A, Je´ze´quel K, Vieille E, Tritter A, Lebeau T, Changes in extractability of Cr and Pb in a polycontaminated soil after bioaugmentation with microbial producers of biosurfactants, organic acids and siderophores. *Water Air Soil Pollut,* 2006; **6**:261–279.
23. Budzikiewicz H, Siderophores of the Pseudomonadaceae sensu stricto (fluorescent and non fluorescent Pseudomonas spp.). In: Herz W, Falk H, Kirby GW (eds) Progress in the chemistry of organic natural products. Springer, Vienna, 2004; 81–237.
24. Burd GI, Dixon DG, Glick BR, A plant growth-promoting bacterium that decreases nickel toxicity in seedlings. *Appl Environ Microbiol,* 1998; **64**: 3663–3668
25. Burd GI, Dixon DG, Glick BR, Plant growth promoting bacteria that decrease heavy metal toxicity in plants. *Can J Microbiol,* 2000; **46**: 237–245
26. Carrillo-Castañeda, G., Juárez Muños, J., Peralta-Videa, J.R., Gomez, E., Tiemann, K.J., Duarte-Gardea, M., Gardea-Torresdey, J.L. Alfalfa growth promotion by bacteria grown under iron limiting conditions. *Adv. Environ. Res.* 2002; **6**, 391–399.
27. Chen, Y.P., Rekha, P.D., Arun, A.B., Shen, F.T., Lai, W-A., Young, C.C. Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. *Appl. Soil Ecol.* 2006; **34**, 33–41.
28. Chet I, Inbar J, Biological control of fungal pathogens. *Appl Biochem Biotechnol,* 1994; **48**: 37–43.
29. Chung, H., Park, M., Madhaiyan, M., Seshadri, S., Song, J., Cho, H., Sa, T. Isolation and characterization of phosphate solubilizing bacteria from the rhizosphere of crop plants of Korea. *Soil Biol. Biochem.* 2005; **37**; 1970– 1974.
30. Creus C, Sueldo R, Barassi C, Shoot growth and water status in Azospirillum-inoculated wheat seedlings grown under osmotic and salt stresses. *Plant Physiol Biochem,* 1997; **35**: 939–944.
31. Cronin, D., Moënne-Loccoz, Y., Fenton, A., Dunne, C., Dowling, D.N., O'gara, F. Role of 2,4-Diacetylphloroglucinol in the interactions of the biocontrol Pseudomonad strain F113 with the potato cyst nematode *Globodera rostochiensis*. *Appl. Environ. Microb.* 1997; **63**, 1357– 1361.
32. Crowley, D.E. Microbial siderophores in the plant rhizosphere. In: L.L. Barton, J. Abadía (eds). Iron Nutrition in Plants and Rhizospheric Microorganisms.Springer, Netherlands, 2006; 169-198.
33. Devi, K.K., Seth, N., Kothamasi, S., Kothamasi, D. Hydrogen cyanideproducing rhizobacteria kill subterranean termite *Odontotermes obesus* (Rambur) by cyanide poisoning under *in Vitro* conditions. *Curr.Microbiol.* 2007; **54**; 74–78.
34. Dobbelaere S, Croonenborghs A, Thys A, Vande Broek A, Vanderleyden J, Phytostimulatory effect of Azospirillum brasilense wild type and mutant strains altered in IAA production on wheat. *Plant Soil,* 1999; **212**: 155–164.
35. Dobbelaere, S., Vanderleyden, J., Okon, Y. Plant growth-promoting effects of diazotrophs in the rhizosphere. *Crit. Rev. Plant Sci,* 2003; **22**; 107–149.
36. Duff RB, Webley DM (1959) 2-Ketogluconic acid as a natural chelator produced by soil bacteria. *Chem Ind* 1959: 1376–1377.

37. Fernando, W.G.D., Nakkeeran, S., Zhang, Y. Biosynthesis of antibiotics by PGPR and its relation in biocontrol of plant diseases. In: Z.A. Siddiqui (ed).PGPR: Biocontrol and Biofertilization. Springer, Netherlands, 2006; 67–109.
38. Fravel D, Olivain C, Alabouvette C, Fusarium oxysporum and its biocontrol. *New Phytol* , 2003; **157**: 493–502.
39. Frugier F, Kosuta S, Murray JD, Crespi M, Szczyglowski K, Cytokinin: secret agent of symbiosis. *Trends Plant Sci*, 2008; **13**:115–120.
40. Fuentes-Ramírez, L.E., Bustillos-Cristales, R., Tapia-Hernández, A., Jiménez-Salgado, T., Wang, E.T., Martínez-Romero, E., Caballero-Mellado, J. Novel nitrogen-fixing acetic acid bacteria, Gluconacetobacter johannae sp. nov., and Gluconacetobacter azotocaptans sp. nov., associated with coffee plants. *Int. J. Syst. Evol. Micr.,* 2001; **51**; 1305–1314.
41. Ghosh S, Penterman JN, Little RD, Chavez R, Glick BR, Three newly isolated plant growth promoting bacilli facilitate the seedling growth of canola, Brassica campestris. *Plant Physiol Biochem,* 2003; **41**: 277–281
42. Ghosh, S., Sengupta, C., Maiti, T.K., Basu, P.S. Production of 3-indolylacetic acid in root nodules and culture by a *Rhizobium* species isolated from root nodules of the leguminous pulse *Phaseolus mungo*. *Folia Microbiol.* 2008; **53**: 351–355.
43. Glick B R, Penrose D M and Li J P, A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. *J. Theor. Biol.*, 1998; **190**, 63–68.
44. Glick BR, Patten CL, Holguin G, Penrose DM, Biochemical and genetic mechanisms used by plant growth promoting bacteria. Imperial College Press, London 1999.
45. Glick BR, Penrose DM, Li J, A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. *J Theor Biol*, 1998; **190**: 63–68.
46. Grichko VP, Glick BR, Amelioration of flooding stress by ACC deaminase-containing plant growth-promoting bacteria. *Plant Physiol Biochem,* 2001; **39**: 11–17
47. Guerinot ML, Ying Y, Iron: nutritious, noxious, and not readily available. *Plant Physiol*, 1994; **104**: 815–820
48. Gutierrez-Manero FJ, Ramos-Solano B, Probanza A, Mehouachi J, Tadeo FR, Talon M. The plant-growth-promoting rhizobacteria Bacillus pumilis and Bacillus licheniformis produce high amounts of physiologically active gibberellins. *Physiol Plant,* 2001; **111**: 206–211.
49. Halda-Alija, L. Identification of indole-3-acetic acid producing freshwater wetland rhizosphere bacteria associated with *Juncus effusus* L. Can. *J. Microbiol.,* 2003; **49**, 781–787.
50. Hariprasad, P., Niranjana, S.R. Isolation and characterization of phosphate solubilizing rhizobacteria to improve plant health of tomato. *Plant Soil,* 2009*;* **316**; 13–24.
51. Hariprasad, P., Niranjana, S.R. Isolation and characterization of phosphate solubilizing rhizobacteria to improve plant health of tomato. *Plant Soil* , 2009; **316**; 13–24.
52. Hopkins CG, Whiting AL; Soil bacteria and phosphates. III. *Agric Exp Stn Bull*, 1916; **190**: 395–406.
53. Hussin, A.S.M., Farouk, A-E., Greiner, R., Salleh, H.M., Ismail, A.F. Phytate degrading enzyme production by bacteria isolated from Malaysian soil. *World J. Microb.Biot.,* 2007; **23**, 1653–1660.
54. Iavicoli A, Boutet E, Buchala A, Me´traux JP, Induced systemic resistance in Arabidopsis thaliana in response to root inoculation with Pseudomonas fluorescens CHA0. *Mol Plant Microbe Interact*, 2003; **16**: 851–858.
55. Illmer P, Schinner F, Solubilization of inorganic phosphates by microorganisms isolated from forest soil. *Soil Biol Biochem*, 1992; **24**: 389–395
56. Jin CW, He YF, Tang CX, Wu P, Zheng SJ, Mechanisms of microbially enhanced Fe acquisition in red clover (Trifolium pratense L.). *Plant Cell Environ,* 2006; **29**: 888–897.
57. Joo GJ, Kang SM, Hamayun M, Kim SK, Na CI, Shin DH, Lee IJ, Burkholderia sp. KCTC 11096BP as a newly isolated gibberellin producing bacterium. *J Microbiol*, 2009; **47**: 167–171.
58. Kang SM, Joo GJ, Hamayun M, Na CI, Shin DH, Kim HY, Hong JK, Lee IJ, Gibberellin production and phosphate solubilization by newly isolated strain of Acinetobacter calcoaceticus and its effect on plant growth. *Biotechnol Lett,* 2009; **31**:277–281.
59. Khandelwal, S.R., Manwar, A.V., Chaudhari, B.L., Chincholkar, S.B. Siderophoregenic bradyrhizobia boost yield of soybean. *Appl. Biochem. Biot.* 2002; **102–103**, 155–168.
60. Kloepper J W and Schroth M N, Plant growth-promoting rhizobacteria on radishes. In Proceedings of the 4th International Conference on Plant Pathogenic Bacteria. 1978 ;879–882. Gilbert-Clarey, Tours, France.
61. Kpomblekou K, Tabatabai MA, Effect of organic acids on release of phosphorus from phosphate rocks. *Soil Sci*, 1994; **158**: 442–453.

62. Kuffner, M., Puschenreiter, M., Wieshammer, G., Gorfer, M., Sessitsch, A. Rhizosphere bacteria affect growth and metal uptake of heavy metal accumulating willows. *Plant Soil,* 2008; **304**, 35–44.
63. Lambert, B., Joos, J. Fundamental aspects of rhizobacterial plant growth promotion research. *Trends Biotechnol.*, 1989; **7**; 215–219.
64. Leeman M, van Pelt JA, Denouden FM, Heinsbroek M, Bakker PAHM, Schippers B. Induction of systemic resistance against Fusarium wilt of radish by lipopolysaccharides of Pseudomonas fluorescens. *Phytopathology,* 1995; **85**: 1021–1027.
65. Li, Q., Saleh-Lakha, S., Glick, B.R. The effect of native and ACC deaminase-containing Azospirillum brasilense Cd1843 on the rooting of carnation cuttings.*Can. J. Microbiol.* 2005; **51**; 511–514.
66. Liu L, Kloepper JW, Tuzun S, Induction of systemic resistance in cucumber against bacterial angular leaf spot by plant growth-promoting rhizobacteria. *Phytopathology,* 1995; **85**: 843–847.
67. Loper JE, Buyer JS, Siderophores in microbial interactions on plant surfaces. *Mol Plant Microbe Interact,* 1991; **4**: 5–13
68. Loper, J.E., Gross, H. Genomic analysis of antifungal metabolite production by *Pseudomonas fluorescens* Pf-5. *Eur. J. Plant Pathol.* 2007; **119**, 265–278.
69. Lorteau MA, Ferguson BJ, Guinel FC, Effects of cytokinin on ethylene production and nodulation in pea (Pisum sativum cv. sparkle). *Physiol Plant,* 2001; **112**: 421–428.
70. MacMillan J, Occurrence of gibberellins in vascular plants, fungi, and bacteria. *J Plant Growth Regul,* 2002; **20**: 387–442.
71. Matias SR, Pagano MC, Carvalho-Muzzi F, Oliveira CA, Almeida-Carneiro A, Horta SN, Scotti MR, Effect of rhizobia, mycorrhizal fungi and phosphate-solubilizing microorganisms in the rhizosphere of native plants used to recover an iron ore area in Brazil. *Eur J Soil Biol,* 2009; **45**: 259–266
72. Matias SR, Pagano MC, Carvalho-Muzzi F, Oliveira CA, Almeida-Carneiro A, Horta SN, Scotti MR, Effect of rhizobia, mycorrhizal fungi and phosphate-solubilizing microorganisms in the rhizosphere of native plants used to recover an iron ore area in Brazil. *Eur J Soil Biol,* 2009; **45**: 259–266
73. Maurhofer M, Hase C, Meuwly P, Metraux JP, De´fago G, Induction of systemic resistance of tobacco to tobacco necrosis virus by the root-colonizing Pseudomonas fluorescens strain CHA0: influence of the gacA gene and of pyoverdine production. *Phytopathology,* 1994; **84**: 139–146.
74. Mayak S, Tirosh T and Glick B R, Effect of wild-type and mutant plant growth- promoting rhizobacteria on the rooting of mung bean cuttings. *J. Plant Growth Regul.* ,1999; **18**, 49–53.
75. Mazurier S, Corberand T, Lemanceau P, Raaijmakers JM, Phenazine antibiotics produced by fluorescent pseudomonads contribute to natural soil suppressiveness to Fusarium wilt. *ISME J,* 2009; **3**: 977–991.
76. Meyer JM, Abdallah MA, The fluorescent pigment of Pseudomonas fluorescens: biosynthesis, purification and physico-chemical properties. *J Gen Microbiol,* 1978; **107**: 319–328.
77. Meyer JM, Gruffaz C, Raharinosy V, Bezverbnaya I, Sch€afer M, Budzikiewicz H. Siderotyping of fluorescent Pseudomonas: molecular mass determination by mass spectrometry as a powerful pyoverdine siderotyping method. *Biometals,* 2008; **21**: 259–271.
78. microorganisms on plant health and productivity. *Soil Biol Biochem* **40**: 1733–1740
79. Mirleau P, Delorme S, Philippot L, Meyer JM, Mazurier S, Lemanceau P, Fitness in soil and rhizosphere of Pseudomonas fluorescens C7R12 compared with a C7R12 mutant affected in pyoverdine synthesis and uptake. *FEMS Microbiol Ecol*, 2000; **34**: 35–44
80. Mirleau P, Philippot L, Corberand T, Lemanceau P, Involvement of nitrate reductase and pyoverdine in competitiveness of Pseudomonas fluorescens strain C7R12 in soil. *Appl Environ Microbiol,* 2001; **67**: 2627–2635.
81. Mirza, M.S., Mehnaz, S., Normand, P., Prigent-Combaret, C., Moënne-Loccoz, Y., Bally, R., Malik, K.A. Molecular characterization and PCR detection of a nitrogen fixing Pseudomonas strain promoting rice growth. *Biol. Fertil. Soils,* 2006; **43**; 163–170.
82. Morgan PW, Drew CD, Ethylene and plant responses to stress. *Physiol Plant*, 1997; **100**: 620–630.
83. Neilands JB, Iron adsorption and transport in microorganisms. *Annu Rev Nutr,* 1981; **1**:27–46.
84. Okon Y, Labandera-Gonzalez C, Agronomic applications of Azospirillum: an evaluation of 20 years of worldwide field inoculation. *Soil Biol Biochem,* 1994; **26**: 1591–1601
85. Okon, Y., Labandera-Gonzalez, C.A. Agronomic applications of Azospirillum: an evaluation of

20 years worldwide field inoculation. *Soil Biol. Biochem.*, 1994; **26**; 1591–1601.

86. Oliveira, C.A., Alves, V.M.C., Marriel, I.E., Gomes, E.A., Scotti, M.R., Carneiro, N.P., Guimarães, C.T., Schaffert, R.E., Sá, N.M.H. Phosphate solubilizing microorganisms isolated from rhizosphere of maize cultivated in an oxisol of the Brazilian Cerrado Biome. *Soil Biol. Biochem*, 2009; **41**, 1782–1787.
87. Ongena M, Jourdan E, Adam A, Paquot M, Brans A, Joris B, Arpigny JL, Thonart P. Surfactin and fengycin lipopeptides of Bacillus subtilis as elicitors of induced systemic resistance in plants. *Environ Microbiol*, 2007; **9**: 1084–1090.
88. Poonguzhali S, Munusamy M, Sa T, Isolation and identification of phosphate solubilizing bacteria from Chinese cabbage and their effect on growth and phosphorus utilization of plants. *J Microbiol Biotechnol*, 2008; **18**:773–777.
89. Raaijmakers, J.M., Bonsall, R.F., Weller, D.M. Effect of population density of *Pseudomonas fluorescens* on production of 2,4-diacetylphloroglucinol in the rhizosphere of wheat. *Phytopathology*, 1999; **89**, 470–475.
90. Ray J, Bagyaraj DJ, Manjunath A, Influence of soil inoculation with versicular arbuscular mycorrhizal (VAM) and a phosphate dissolving bacteria on plant growth and 32P uptake. *Soil Biol Biochem*, 1981; **13**:105–108.
91. Reed MLE, Glick BR, Applications of free living plant growth-promoting rhizobacteria. *Antonie Van Leeuwenhoek*, 2004; **86**: 1–25
92. Reed, M.L.E., Glick, B.R. Growth of canola (*Brassica napus*) in the presence of plant growth-promoting bacteria and either copper or polycyclic aromatic hydrocarbons. *Can. J. Microbiol.*, 2005; **51**; 1061–1969.
93. Reinhold-Hurek, B., Hurek, T., Gillis, M., Hoste, B., Vancanneyt, M., Kersters, K., De Ley, J. Azoarcus gen. nov., nitrogen-fixing Proteobacteria associated with roots of Kallar grass (Leptochloa fusca (L.) Kunth), and description of two species, Azoarcus indigens sp. nov. and Azoarcus communis sp. nov. *Int. J. Syst. Bacteriol.*, 1993; **43**; 574–584.
94. Rezzonico, F., Zala, M., Keel, C., Duffy, B., Moënne-Loccoz, Y., Défago, G. Is the ability of biocontrol fluorescent pseudomonads to produce the antifungal metabolite 2,4-diacetylphloroglucinol really synonymous with higher plant protection? *New Phytol.*, 2007; **173**; 861–872.
95. Richardson, A.E., Hadobas, P.A. Soil isolates of *Pseudomonas* spp. that utilize inositol phosphates. *Can. J. Microbiol*, 1997; **43**, 509–516.
96. Robin A, Vansuyt G, Hinsinger P, Meyer JM, Briat JF, Lemanceau P, Iron dynamics in the rhizosphere: consequences for plant health and nutrition. *Adv Agron*, 2008; **99**: 183–225.
97. Rodriguez H, Fraga R, Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnol Adv*, 1999; **17**: 319–339
98. Rodriguez H, Gonzalez T, Goire I, Bashan Y, Gluconic acid production and phosphate solubilization by the plant growth-promoting bacterium Azospirillum spp. *Naturwissenschaften*, 2004; **91**: 552–555
99. Rojas A, Holguin G, Glick BR, Bashan Y, Synergism between Phyllobacterium sp. (N2-fixer) and Bacillus licheniformis (P-solubilizer), both from a semiarid mangrove rhizosphere. *FEMS Microbiol Ecol*, 2001; **35**: 181–187.
100. Roy, N., Chakrabartty, P.K. Effect of aluminum on the production of siderophore by *Rhizobium* sp. (*Cicer arietinum*).*Curr.Microbiol.*, 2000; **41**; 5–10.
101. Salamone GIE, Hynes RK, Nelson LM , Cytokinin production by plant growth promoting rhizobacteria and selected mutants. *Can J Microbiol*, 2001; **47**: 404–411.
102. Salisbury F B, The role of plant hormones. *In* Plant– Environment Interactions.Ed. R EWilkinson., 1994 ; 39–81. Marcel Dekker, New York, USA.
103. Salisbury FB, Ross CW (1992) Plant physiology. Wadsworth, Belmont, CA
104. Salisbury FB, Ross CW (1992) Plant physiology. Wadsworth, Belmont, CA
105. Schippers, B., Bakker, A.W., Bakker, P.A.H.M., Van Peer, R. Beneficial and deleterious effects of HCN-producing pseudomonads on rhizosphere interactions. *Plant Soil*, 1990; **129**; 75–83.
106. Sharma, A., Johri, B.N. Growth promoting influence of siderophore-producing *Pseudomonas* strains GRP3A and PRS9 in maize (*Zea mays* L.) under iron limiting conditions. *Microbiol. Res.*, 2003; **158**, 243–248.
107. Shedova, E., Lipasova, V., Velikodvorskaya, G., Ovadis, M., Chernin, L., Khmel, I. Phytase activity and its regulation in a rhizospheric strain of *Serratia plymuthica*.*Folia Microbiol*, 2008; **53**; 110–114.
108. Shoebitz, M., Ribaudo, C.M., Pardo, M.A., Cantore, M.L., Ciampi, L., Curá, J.A. Plant growth promoting properties of a strain of *Enterobacter ludwigii* isolated from *Lolium perenne* rhizosphere. *Soil Biol. Biochem*, 2009; **41**: 1768–1774.
109. Siddiqui IA, Shoukat SS, Suppression of root-knot disease by Pseudomonas fluorescens CHA0

in tomato: importance of bacterial secondary metabolite, 2,4-diacetylphloroglucinol. *Soil Biol Biochem*, 2003; **35**:1615–1623.

110. Siddiqui, I.A., Shaukat, S.S., Hussain Sheikh, I., Khan, A. Role of cyanide production by *Pseudomonas fluorescens* CHA0 in the suppression of root-knot nematode, *Meloidogyne javanica* in tomato.*World J. Microb.Biot*, 2006; **22**; 641–650.
111. Siddiqui, Z.A. PGPR: Prospective biocontrol agents of plant pathogens. In: Z.A. Siddiqui (ed). PGPR: Biocontrol and Biocontrol. Springer, Netherlands, pp: 112–142; 2006.
112. Spaepen S, Vanderleyden J, Remans R, Indole-3-acetic acid in microbial and microorganism plant signaling. *FEMS Microbiol Rev*, 2007; **31**: 425–448
113. Spaepen, S., Vanderleyden, J., Remans, R. Indole-3-acetic acid inmicrobial and microorganism-plant signaling. *FEMS Microbiol. Rev.*, 2007; **31**, 425–448.
114. Sperber JI, The incidence of apatite-solubilizing organisms in the rhizosphere and soil. *Aust J Aric Res*, 1958; **9**: 778–781
115. Sperber JI, The incidence of apatite-solubilizing organisms in the rhizosphere and soil. *Aust J Aric Res*, 1958; **9**: 778–781.
116. Stintzi A, Evans K, Meyer JM, Poole K, Quorum-sensing and siderophore biosynthesis in Pseudomonas aeruginosa: lasR/lasI mutants exhibit reduced pyoverdine biosynthesis. *FEMS Microbiol Lett*, 1998; **166**: 341–345.
117. Swain, M.R., Naskar, S.K., Ray, R.C. Indole-3-acetic acid production and effect on sprouting of Yam (*Dioscorea rotundata* L.) minisetts by *Bacillus subtilis* isolated from culturable cowdung microflora. *Pol. J. Microbiol.*2007; **56**; 103–110.
118. Tao GC, Tian SJ, Cai MY, Xie GH, Phosphate-solubilizing and -mineralizing abilities of bacteria isolated from soils. *Pedosphere*, 2008; **18**: 515–523.
119. Tien T, Gaskin M, Hubbel D, Plant growth substances produced by Azospirillum brasilense and their effect on the growth of pearl millet (Pennisetum americanum L.). *Appl Environ Microbiol*, 1979*;* **37**:1016–1024.
120. Tilak, K.V.B.R., Ranganayaki, N., Pal, K.K., De, R., Saxena, A.K., Nautiyal, C.S., Mittal, S., Tripathi, A.K., Johri, B.N. Diversity of plant growth and soil health supporting bacteria.*Curr. Sci. India*, 2005; **89**; 136–150.
121. Timmusk S, Nicander B, Granhall U, Tillberg E, Cytokinin production by Paenobacillus polymyxa. *Soil Biol Biochem* , 1999; **31**:1847–1852.
122. Toro M, Azcon R, Barea J, Improvement of arbuscular mycorrhiza development by inoculation of soil with phosphate solubilizing rhizobacteria to improve rock phosphate bioavailability (32P) and nutrient cycling. *Appl Environ Microbiol*, 1997; **63**:4408–4412.
123. Tran H, Ficke A, Asiimwe T, H€ofte M, Raaijmakers JM, Role of the cyclic lipopeptide massetolide A in biological control of Phytophthora infestans and in colonization of tomato plants by Pseudomonas fluorescens. *New Phytol*, 2007; **175**: 731–742.
124. Tsavkelova, E.A., Cherdyntseva, T.A., Klimova. S.Y., Shestakov, A.I., Botina, S.G., Netrusov, A.I. Orchid-associated bacteria produce indole-3-acetic acid, promote seed germination, and increase their microbial yield in response to exogenous auxin. *Arch. Microbiol*, 2007; **188**: 655–664.
125. Tsavkelova, E.A., Klimova, S.Y., Cherdyntseva, T.A., Netrusov, A.I. Microbial producers of plant growth stimulators and their practical use: a review. *Appl. Biochem. Micro*, 2006; **42**; 117–126 .
126. Valverde A, Burgos A, Fiscella T, Rivas R, Velazquez E, Rodrý'guez-Barrueco C, Cervantes E, Chamber M, Igual JM, Differential effects of coinoculations with Pseudomonas jessenii PS06 (a phosphate-solubilizing bacterium) and Mesorhizobium ciceri C-2/2 strains on the growth and seed yield of chickpea under greenhouse and field conditions. *Plant Soil*, 2006; **287**: 43–50.
127. Van Loon LC, Bakker PAHM, Pieterse CMJ, Systemic resistance induced by rhizosphere bacteria. *Annu Rev Phytopathol*, 1998; **36**:453–483.
128. Van Loon LC, Glick BR, Increased plant fitness by rhizobacteria. In: Sandermann H (ed) Molecular ecotoxicology of plants, ecological studies, vol 170. Springer, Berlin, 2004; 177–205.
129. van Loon, L.C. Plant responses to plant growth-promoting rhizobacteria. *Eur. J. Plant Pathol.*, 2007; **119**, 243–254.
130. Velusamy, P., Immanuel, J.E., Gnanamanickam, S.S., Thomashow, L. Biological control of rice bacterial blight by plant-associated bacteria producing 2,4- diacetylphloroglucinol. *Can. J. Microbiol.*, 2006; **52**: 56–65.
131. Voisard, C., Keel, C., Haas, D., Défago, G. Cyanide production by *Pseudomonas fluorescens* helps suppress black root rot of tobacco under gnotobiotic conditions. *EMBO J.*,1989; **8**; 351–358.
132. Wang Y, Brown H N, Crowley D E and Szaniszlo P J, Evidence for direct utilization of a

siderophore, ferrioxamine B, in axenically grown cucumber. *Plant Cell Environ,* 1993; **16**; 579–585.

133. Weller DM, Biological control of soilborne pathogens in the rhizosphere with bacteria. *Annu Rev Phytopathol,* 1988; **26**:379–407.
134. Werner T, Motyka V, Laucou V, Smets R, Onckelen HV, Schmℓulling TH, Cytokinin deficient transgenic Arabidopsis plants show multiple developmental alterations indicating opposite functions of cytokinins in the regulation of shoot and root meristem activity. *Plant Cell* , 2003; **15**: 2532–2550.
135. Whipps JM, Microbial interactions and biocontrol in the rhizosphere. *J Exp Bot*, 2001; **52**: 487–511
136. Williams PM, Sicardi de Mallorca M, Abscisic acid and gibberellin-like substances in roots and root nodules of Glycine max. *Plant Soil* **,** 1982; **65**: 19–26.
137. Yi Y, Huang W, Ge Y, Exopolysaccharide: a novel important factor in the microbial dissolution of tricalcium phosphate. *World J Microbiol Biotechnol*, 2008; **24**:1059–1065.
138. Zahir, A.A., Arshad, M., Frankenberger, W.T. Plant growth promoting rhizobacteria: applications and perspectives in agriculture. *Adv. Agron*. 2004; **81**; 97–168.
139. Zahran, H.H. Rhizobia from wild legumes: diversity, taxonomy, ecology, nitrogen fixation and biotechnology. *J. Biotechnol.*, 2001; **91**: 143–153.
140. Zehnder G W, Murphy J F, Sikora E J and Kloepper J W, Application to rhizobacteria for induced resistance. *Eur. J. Plant Pathol.*, 2001;**107**, 39–50.
141. Zipfel C, Robatzek S, Navarro L, Oakeley EJ, Jones JDG, Felix G, Boller T, Bacterial disease resistance in Arabidopsis through flagellin perception. *Nature*, 2004; **428**: 764–767.