

Chapter 14

Plant Growth Promoting Rhizobacteria (PGPR): Microbes in Sustainable Agriculture

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Abstract Plant growth promoting rhizobacteria (PGPR) contain diverse type of plant growth promoting attributes that has many beneficial effects on crop productivity. The PGPR appear to promote the plant growth via – suppression of plant disease (bio-controls), enhanced nutrient achievement, or phytohormone production (bio-fertilizers). The PGPR protect plants from several biotic and abiotic stresses. Co-inoculation of PGPR can ease the adverse effects on crop plants due to various environmental stresses such as soil salinity, droughts, temperature and nutrient deficiency. During the last couple of decades given the negative environmental impact of artificial fertilizers and their increasing costs, the use of PGPR for sustainable environment and safe agriculture has increased globally. Thus, the PGPR offer an environmentally sustainable approach to increase crop production for future generation.

Keywords Agriculture • Biofertilizers • Bio-control • Environment • Rhizobacteria

1 Introduction

The bacteria colonizing the plant rhizosphere are known as plant growth promoting rhizobacteria (PGPR) (Kloepper et al. 1980). Most of the PGPR strains are found to be associated with plant growth indirectly, via alterations in the structure of rhizosphere soil

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(Noel et al. 1996). Direct mechanisms include production of plant growth regulators, solubilization of mineral materials (Son et al. 2006; Chen et al. 2008) or fixation of atmospheric nitrogen. For example, *Bacillus* strains induce plant resistance against stress and produce various plant hormones for growth improvement (Rajendran et al. 2008). In addition it has been demonstrated that inoculation with plant growth promoting improves plant growth under a variety of salinity stress conditions (Han and Lee 2005).

In the last few years, the number of PGPR like *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus* and *Serratia* have been identified and have gained importance because their dominant role in the microcosm of rhizosphere (Kloepper et al. 1989; Joseph et al. 2007). Now many PGPR inoculants are commercialized which apparently promote the plant growth through at least one mechanism; improved nutrient supply, biofertilizers, bio-control agent and phytohormone production. (Rajendran et al. 2008; Singh et al. 2011; Upadhyay et al. 2012).

Environmental stresses are the major constraints, which hampers the crop production, causing loss of significant quantity of yield. Soil salinity is one of the major environmental constrains that significantly reduces plant nutrient uptake, particularly phosphate (P) ions which tends to get precipitated with Ca ions in saline soil (Grattan and Grieve 1999). Phosphate solubilizing bacteria can increase P availability to plants by solubilizing the insoluble P, and thereby improve the availability of nutrients including the phosphate (Gyaneshwar et al. 2002). Application of such beneficial soil microorganisms in agriculture has drawn the attention of scientists all over the world (Berg 2009; Weyens et al. 2009). Inoculation of PGPR strains, well adapted to rhizospheric conditions and exhibiting P solubilizing attributes, are considered more effective for balanced nutrition to plants and crop yields (Galal 2003). The PGPR can stimulate not only plant growth and yield, but can also alleviate the effects of biotic or abiotic stresses on plants (Lugtenberg and Kamilova 2009). An increase in various agronomic yields involving production of growth stimulating phytohormones as well as by improved phosphate nutrition of plants due to PGPR has been reported (Kohler et al. 2006). Therefore, PGPR inoculation to alleviate environmental stress may be considered as an innovative and cost effective alternative to overcome the various plants stresses (Bano and Fatima 2009). Biofertilizer is the most commonly referred term used for the beneficial soil microorganisms such as PGPR which increase the availability and uptake of nutrients for plants (Vessey 2003). Application of such beneficial soil microorganisms in sustainable agriculture has drawn the attention of scientists all over the world (Berg 2009; Weyens et al. 2009). This review describes the future perspectives of PGPR in sustainable agricultural productivity.

2 Perspective of PGPR in Stress Agriculture

The PGPR associated with plant roots play important role in enhancing the plant productivity and disease resistance. Recently several workers have demonstrated that PGPR provide protection to the plants against several biotic and abiotic stresses.

Table 14.1 Inoculation with PGPR containing ACC deaminase and subsequent physiological changes in plants

PGPR	Plant	Physiological changes	References
<i>Pseudomonas cepacia</i>	<i>Glycine max</i>	Rhizobacterium caused an early soybean growth	Cattelana et al. (1999)
<i>Alcaligenes</i> sp. <i>Bacillus pumilus</i> <i>Pseudomonas</i> sp. <i>Variovorax paradoxus</i>	<i>Brassica napus</i>	Inoculated plant demonstrated more vigorous growth than the control	Belimov et al. (2001)
<i>B. circulans</i> DUC1, <i>B. wrmus</i> DUC2, <i>B. globisporus</i> DUC3	<i>Brassica campestris</i>	Bacterial inoculation enhanced root and shoot elongation	Ghosh et al. (2003)
<i>Enterobactersakazakii</i> 8MR5 <i>Pseudomonas</i> sp. MKS8 <i>Klebsiellaoxytoca</i> 10MKR7	<i>Zea mays</i> L.	Inoculation increased agronomic parameters of maize	Babalola et al. (2003)
<i>P. syringae</i> ; Mk20, <i>P. fluorescens</i> Mk25, and <i>P. fluorescens</i> biotype G	Mung bean	Improve seedling growth and nodulation	Ahmad et al. (2011)
<i>Bacillus subtilis</i> SU47 and <i>Arthrobacter</i> sp. SU18	Wheat	Increase in dry biomass, total soluble sugars and proline content	Upadhyay et al. (2012)

The PGPR dependent enhanced stress resistance in plants may be mediated by specific enzymes, inducing alterations at physiological and molecular level. Among these enzymes, bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase is reported to play a well defined role in the regulation of level of ethylene- a plant growth hormone (Glick 2005). Ethylene is a gaseous plant growth hormone produced endogenously by almost all plants and is known to alter the growth and development of plants (Saleem et al. 2007). Apart from the role of ethylene as a plant growth regulator, it is an established stress hormone in plants. These PGPR boost plant growth particularly under stressed conditions by the regulation of accelerated ethylene production in response to a multitude of abiotic and biotic stresses like salinity, drought, waterlogging, temperature, pathogenicity and contaminants. Recently, Ahmad et al. (2011) showed that co-inoculation with PGPR containing ACC deaminase and *Rhizobium* spp. could be a useful approach for inducing salt tolerance and thus improving growth and nodulation in mung bean under salt-affected conditions. Inoculation of PGPR containing ACC deaminase and subsequent physiological changes in plants are given in Table 14.1.

2.1 Salinity Stress

Soil salinity constitutes a serious problem for vegetable as well as for other crops. An alteration in physiology of plants induced by salt stress leads to reduced nutritional uptake and also the plant growth (Singh et al. 2011). Salinity stress boosts

endogenous ethylene production in plants, which in most cases serves as a stress hormone (O'Donnell et al. 1996; Blumwald 2000). It is very likely that reducing salinity-induced ethylene production by any mechanism could reverse the negative impact of salinity onto the plant growth. Since the PGPR is known to colonize the plant roots (Upadhyay et al. 2011), it can be an effective tool in developing the strategies to enhance the wheat production in salinity affected areas (Ashraf et al. 2004). We very recently during an experiment demonstrated that co-inoculation of *B. subtilis* and *Arthrobacter* sp. might ease the unfavorable influence of the soil salinity on wheat plants (Upadhyay et al. 2012). Studies have revealed that plants inoculated with PGPR containing ACC deaminase were better able to thrive through the salinity stress while demonstrating a normal growth pattern. In this direction, Mayak et al. (2004b) during an investigation showed that *Achromobacter piechaudii* having ACC deaminase activity considerably enhanced the tomato seedlings fresh and dry weights when treated with NaCl salt (up to 172 mM). The bacterium *Achromobacter piechaudii* has been found to reduce the generation of ethylene by salt stressed tomato seedlings. However, the sodium content of the plant was not decreased whereas the uptake of phosphorous and potassium were slightly increased, which might have contributed in part, to the activation of processes involved in the alleviation of the adverse effect of salt on plant growth. The bacterium also increased the water use efficiency (WUE) in saline environment and helped in alleviating the salt suppression of photosynthesis. Saravanakumar and Samiyappan (2007) reported that *Pseudomonas fluorescens* strain TDK1 containing ACC deaminase activity enhanced the saline resistance in groundnut plants and increased yield as compared with that inoculated with *Pseudomonas* strains lacking ACC deaminase activity. Cheng et al. (2007) have also confirmed that ACC deaminase bacteria conferred salt tolerance onto plants by lowering the synthesis of salt-induced stress ethylene and promoted the growth of canola in saline environment. Nadeem et al. (2006) have observed almost similar results in the case of maize growth under salt stress in response to inoculation with ACC deaminase PGPR.

2.2 Drought Stress

Drought is one of the major constraints to the yield of crop globally. Since the global population continues to increase and water resources for crop production decline, the development of drought-tolerant cultivars and water-use-efficient crops is a global concern. Drought affects virtually all climatic regions of the world (Wilhite 2000) and more than one half of the earth is susceptible to drought every year (Kogan 1997). Drought is one of the major environmental stresses that limit the growth of plants and the production of crops. Plants respond to drought stress at cellular and molecular levels (Bray 1997; Ingram and Bartels 1996; Shinozaki and Yamaguchi-Shinozaki 1999). Like many other environmental factors, drought also induces accelerated ethylene production in plant tissues which leads to abnormal growth of a plant (Mattoo and Suttle 1991). Mayak et al. (2004a) reported that ACC

deaminase in *Achromobacter piechaudii* ARV8 significantly increased the fresh and dry weights of both tomato and pepper seedlings exposed to transient water stress. In addition, the bacterium also reduced the production of ethylene by tomato seedlings exposed to water stress. During water scarcity, the bacterium did not influence the water content of plants; however, it significantly improved the recovery of plants when watering was resumed. Interestingly, inoculation of tomato plants with the bacterium resulted in continued plant growth both during water stress as well as when watering was resumed. The bacterial effects were more pronounced and more consistent under controlled soil drying (moisture stress conditions). In short term experiments, the ACC deaminase producing bacteria showed positive effects on the root and shoot biomass, leaf area and plant transpiration. In case of long-term experiments, plants inoculated with ACC deaminase producing bacteria gave higher yield (25–41%); greater seed number and seed nitrogen accumulation than that in the uninoculated plants. Moreover, PGPR inoculation of drought affected pea plants restored the level of root nodulation when compared with well-watered uninoculated plants. It has been shown that the inoculation with ACC deaminase producing bacteria partially eliminated the effects of water scarcity on growth and yield of *Pisum sativum* L. both in pot and field conditions (Arshad et al. 2008).

Several investigations have been carried out under greenhouse and field situations by using mixtures of PGPR strains with symbiotic nitrogen-fixing rhizobia (Figueiredo et al. 2008) or with mycorrhizal fungi (Kohler et al. 2008). The co-inoculation of PGPR with *Rhizobium tropici* under low soil water content conditions has been found to show improved plant growth and enhanced number of root nodules in *Phaseolus vulgaris* L. (Figueiredo et al. 2008). Interestingly, the effect of co-inoculation of two strains of *P. polymyxa* strains on nodule number exhibited synergistic effects.

A survey on the effect of drought stress in relation to plant hormone revealed that how an increase in the abscisic acid (ABA) content in the plant leaves with simultaneous decrease in the endogenous level of cytokinin elicited a differential response of stomata closure (Cowan et al. 1999; Figueiredo et al. 2008). Earlier the cytokinin – ABA antagonism has been observed as they share a common biosynthetic origin (Cowan et al. 1999). It will be interesting to determine whether cytokinin produced by *P. polymyxa* affects ABA signaling in plants or rhizobia-elicited nodulation (Timmusk and Wagner 1999; Figueiredo et al. 2008) Co-inoculation of lettuce (*Lactuca sativa* L.) with PGPR *Pseudomonas mendocina* and arbuscular mycorrhizal fungi (*Glomus intraradices* or *G. mosseae*) is known to increase the level of antioxidant enzyme catalase under severe drought conditions, suggesting that these can be used as co-inoculants to alleviate the oxidative damage elicited by the drought stress (Kohler et al. 2008).

2.3 Temperature Stress

Changes in the global climate, notably spatial and temporal variations in temperature, are predicted to have important consequences for crop production. Transient or constantly high temperatures may cause an array of morpho-anatomical, physiological

and biochemical changes in plants, which induce changes in the growth and development of plants, and ultimately account for severe decrease in the economic yield. Plants with ACC deaminase expression can successfully cope with the stressful situations by lowering the production of ethylene. Bensalim et al. (1998) reported that a plant growth promoting rhizobacterium *Burkholderia phytofirmans* strain PsJN was able to maintain normal growth of potato plant under heat stress. Barka et al. (2006) reported that ACC deaminase activity of the same bacterium (*Burkholderia phytofirmans* strain PsJN) enhanced plant growth and physiological activity of grapevine (*Vitis vinifera* L.) cv. Chardonnay explants at both ambient (26°C) and low (4°C) temperature conditions. Inoculation of PGPR was able to increase the root growth (11.8- and 10.7-fold at 26 and 4°C, respectively) and plantlet biomass (6- and 2.2-fold at 26 and 4°C, respectively). It was inferred that this bacterium can successfully improve the cold tolerance property of the plantlet when compared with that of the non-bacterized control. Cheng et al. (2007) demonstrated that ACC deaminase producing bacterium *P. putida* UW4 have also promoted the growth of psychrotolerant Canola plant at extremely low temperature under the salt stress. These studies have clearly demonstrated the potential of ACC deaminase enzyme in normalizing the plant growth exposed to temperature extremes by lowering the accelerated production of ethylene.

The various kinds of stresses in fact accentuate the biosynthesis of ethylene, which in the most cases retards the plant growth through several mechanisms at molecular level. In the present scenario, the application of PGPR containing ACC deaminase activity is considered vital in regulation of ethylene production in plants. Thus, application of PGPR containing ACC deaminase in agriculture might prove beneficial and could be a sound step towards sustainable crop production.

2.4 Nutrient Stress

Another crucial abiotic stress faced by the crop plants is supply of inadequate soil nutrients. Although soil fertilization is typically required for better agricultural production. However, external application of nitrate and phosphate fertilizers eventually contaminate the surface and ground waters. Phosphate and nitrate run-off is associated with eutrophication of surface water bodies, resulting in ecological nuisance in aquatic ecosystem. Application of fertilization of soil is attributable to low nutrient level, which is created due to mutual interaction of nutrients such as phosphorous interaction with highly reactive iron, aluminium and calcium minerals in soil, resulting into locking of up to 90% of the soil available phosphorous (Gyaneshwar et al. 2002) and rendering it unavailable to the plants. The PGPR have potential to maintain adequate plant nutrition and also reduce the negative environmental impact of fertilizers. Plant growth promotion by some PGPR has been associated with improved availability of soil nutrients as well as improved uptake of nutrients (Gyaneshwar et al. 2002). PGPR have been known to improve the nitrate uptake by plants (Mantelin and Touraine 2004; Adesemoye et al. 2008). It has been reported that a general

increase in the plant growth and nutrient uptake by PGPR is due to profuse root development (Mantelin and Touraine 2004) and altered root structure due to production of phytohormones like indole acetic acid (IAA) (Adesemoye et al. 2008). An increase in root surface area and numbers of root tips can contribute to improved system tolerance and plant defense against pathogens. An increase in the nutrient uptake efficiency of plants due to PGPR is also suggested to be mediated by stimulated activity of proton pump ATPase (Mantelin and Touraine 2004).

Owing to the ever increasing price of chemical fertilizers and its adverse environmental impact, there is a growing need worldwide to reduce the application of chemical fertilizers. Hence, several studies are now testing the hypothesis that PGPR might enable us to maintain agricultural productivity with reduced application of fertilizers. The preliminary results are found to be promising. The use of PGPR isolates as inoculants is reportedly highly beneficial for rice cultivation as they can enhance the growth of rice by inducing other plant growth promoting traits (Ashrafuzzaman et al. 2009). During a field study with wheat plant (*Triticum aestivum* L.), the total yield of crop plants, given only 75% of the recommended doses of N-P-K fertilizer plus a PGPR strain was comparable to the yield for plants given full dose of fertilizer, but without PGPR (Shaharoon et al. 2008). In another study on tomato (Hernandez and Chailloux 2004), the dry weight of tomato transplants grown with two PGPR strains and 75% fertilizer dose in the greenhouse was significantly higher than that with the full dose of fertilizer and without PGPR. After transplanting the plants in the field, yields with some combinations of PGPR and mycorrhizal fungi at 50% recommended field fertilization were greater than the yield in plants treated with full dose of fertilizer, but without microbes.

Another current hypothesis is that PGPR, used as components of integrated nutrient management systems, can help reduce the build-up of nutrients in fertilized soils. Support for this hypothesis was presented in a report (Adesemoye et al. 2008) of a 3-year field study on maize that evaluated PGPR with and without mycorrhizal fungi, manure and inorganic fertilizer, as well as with and without tillage. Significant increases in grain yield from microbial treatments were accompanied by increased nitrogen content per gram of grain tissue and removal of significantly higher amounts of nitrogen, phosphorous and potassium. Therefore, within the tested nutrient management system, PGPR contributed significantly to reducing nutrient build up in the soil. Many current studies are underway that will further define the utility of PGPR in nutrient management strategies aimed at reducing fertilizer application rates and nutrient runoff from agricultural sources.

3 Perspective of PGPR as Biofertilizers

The word biofertilizer may be defined as living microorganisms, which can promote growth of plants by increasing the availability of primary nutrients to the host plant. More recent research findings indicated that the treatment of agricultural soils with PGPR inoculation significantly increases agronomic yields when compared with

that of uninoculated soil. There are many mechanisms by which the PGPR can promote the growth of plants. Some of the important mechanisms by which PGPR can enhance the growth and yield of crop plants are listed below:

- (1) PGPR mediated N_2 fixation
- (2) Availability of nutrients in the rhizosphere
- (3) Root surface area enhancement
- (4) Phytohormone synthesis.

3.1 N_2 Fixation

The PGPR as microbial inoculants have been accepted as an alternative source of N-fertilizers and they can promote plant growth and productivity. They are considered environment friendly and can be used to ensure a sustainable crop production. In the biofertilizer technology, efforts are being made to increase biological nitrogen fixation for cereals and other non-legumes, by introducing the N_2 -fixing bacteria in plant roots (Cocking 2000). The plant growth promotion by means of nitrogen fixation is an important criterion used for selection of rhizobacteria as an effective biofertilizer. Application of both symbiotic and free-living N_2 -fixing bacteria (PGPR) has shown a considerable beneficial effect on plant growth (Kloepper et al. 1980; Bashan and Holguin 1998). The bacterial species belonging to genera *Azospirillum*, *Alcaligenes*, *Arthrobacter*, *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* are known to be associated with the plant rhizosphere and are found to show beneficial effect on plant growth (Tilak et al. 2005; Egamberdiyeva 2005). There is an important role played by plant root exudates in selecting and enriching the compatible bacterial strains. Therefore, the type of bacteria colonizing the rhizosphere of plants depends upon the nature and concentrations of organic constituents of root exudates, but also on the ability and efficiency of the microorganism to utilize the organic source present in the root exudates (Curl and Truelove 1986). The rhizospheric bacteria, that have efficient systems for uptake and catabolism of organic constituents of root exudates (Barraquio et al. 2000), can get attached with the root surfaces and derive maximum benefit from root exudates. The associative interactions of plants with microorganisms must have evolved as a result of co evolution. The use of latter group as bio-inoculants, for a long-term successful and sustainable interaction, envisages that microbes must be pre-adapted (Chaiharn et al. 2008). The PGPR application as inoculants offers an attractive and environment friendly technology to replace the chemical fertilizers and pesticides (Ashrafuzzaman et al. 2009). The use of bio-fertilizer and bio-enhancer such as N_2 fixing bacteria would not only reduce the dependence of farmers on the use of chemical fertilizers applications, but also reduce the cost of agricultural production. Utilization of PGPR is a viable alternative to organic fertilizers, which will help in preserving the environment and reducing the pollution (Stefan et al. 2008). Thus, the PGPR or combinations of PGPR and AMF can be exploited for improving the nutrient use efficiency of plants (Adesemoye et al. 2009). Applying the combined

inoculation of PGPR as biofertilizer affects beneficially the yield and growth of chickpea in field conditions (Rokhzadi et al. 2008). Application of PGPR strains, especially *Azospirillum* spp. was reported to fix N_2 in oil palm (*Elaeis guineensis*) and sweet potato (*Ipomoea batatas*). *Bacillus sphaericus* UPMB10 was observed to produce beneficial effects on oil palm (Amir et al. 2001). In sweet potato, PGPR inoculation along with 33% the total N-fertilizer requirement produced a plant biomass comparable to yield obtained with fully fertilized plants, which represents about 67% saving of N-fertilizer (Saad et al. 1999). Halimi et al. (2000) observed that the PGPR can supplement the nutrient requirement of tomato on soilless culture media under protected environment. *Azospirillum* inoculation process has reportedly increased the N_2 fixation, mineral nutrient content (P, K, Ca and Mg) and growth of maize (Rai and Hunt 1993).

3.2 Enhanced Rhizospheric Nutrient Status

There is ample evidence that the primary mode of PGPR action is related with enhanced availability of nutrients to plant rhizosphere (Glick 1995; Rodriguez and Fraga 1999). The method by which availability of nutrients increases involves solubilization of unavailable form of nutrients. The solubilisation of phosphate and production of siderophores help in the availability and transport of certain nutrients (notably ferric iron).

3.2.1 Phosphate Solubilization

Phosphorus (P) is second to nitrogen in mineral nutrients which commonly limits the growth of terrestrial plants. Ironically, there is large reserve of total P in the soil, but the amount of phosphorous available to plants is usually a tiny fraction of the total amount (Stevenson and Cole 1999). The reduced availability of P to plants in the vast majority of soil is due to insoluble form of P and plants can only absorb P in two soluble forms i.e., the monobasic ($H_2PO_4^-$) and the dibasic (HPO_4^{2-}) ions (Glass 1989). P-solubilizing bacteria are commonly present in the rhizosphere secrete organic acids which converts the non-available form of P to soluble form. The phosphatases enzyme present in the P solubilising bacteria facilitates the conversion of insoluble forms of P to soluble form (Kim et al. 1998). The solubilization of P in the rhizosphere is considered as the most common action of PGPR in the direction of improving the P availability to the host plants (Richardson 2001). Few examples of such actions include associations between *Azotobacter chroococcum* with wheat, *Bacillus* sp. and five crop species, *Enterobacter agglomerans* with tomato, *Pseudomonas chlororaphis* and *P. putida* with soybean, *Rhizobium* sp. and *Bradyrhizobium japonicum* with radish, *Rhizobium leguminosarum* with *Phaseolus* (Antoun et al. 1998; Kim et al. 1998; Pal 1998; Chabot et al. 1998; Kumar and Narula 1999; Singh and Kapoor 1999; Cattelana et al. 1999).

Phosphate-solubilizing bacteria are common in rhizospheres (Nautiyal et al. 2000; Vazquez et al. 2000). However, their ability to solubilize P with no extra input suggested that a rhizospheric P solubilizing bacterium can be considered as PGPR. Cattelana et al. (1999) found only two out of five rhizospheric isolates positive for P solubilisation, which registered a positive impact on soybean seedling growth. Thus, not all P solubilizing PGPR are able to increase the plant growth by increasing the P availability to the hosts. de Freitas et al. (1997) isolated number of P-solubilizing *Bacillus* sp. and a *Xanthomonas maltophilia* isolate from canola (*Brassica napus* L.) rhizosphere, which had positive effects on plant growth, but no effects on P content of the host plants.

3.2.2 Iron Absorption by Siderophore Production

The PGPR are reported to secrete some extracellular metabolites called siderophores. For the first time, Kloepper et al. (1980) reported the significance of siderophores in plant growth promotion produced by certain genera of PGPR. Siderophores are commonly referred to as microbial chelating agent of Fe. The presence of siderophore producing PGPR in rhizosphere can enhance the Fe supply to plants and thereby, improve the plant growth and yield. Further, this compound after chelating Fe^{3+} make the soil Fe^{3+} deficient for other soil microbes and consequently inhibits the activity of other competing microbes.

Iron (Fe) is an essential nutrient of plants, but it is relatively insoluble in soil solutions. Plant roots prefer absorption of iron in its reduced form i.e., ferrous (Fe^{2+}) ion. The ferric (Fe^{3+}) ion is more common in well aerated soil and tends to get precipitated in the form of iron-oxide (Salisbury and Ross 1992). Plants normally excrete various soluble organic compounds (chelators and phytosiderophores) which tend to bind with Fe^{3+} form and prevent its precipitation. Chelators help in the transport the Fe^{3+} to the root surface where it is reduced to Fe^{2+} and is ready for absorption. Phytosiderophores, excreted by grasses, are absorbed with the Fe^{3+} across the plasmalemma (von Wieren et al. 2000).

There is evidence that a number of plant species can absorb bacterial Fe^{3+} siderophore complexes (Bar-Ness et al. 1992; Wang et al. 1993). However, the significance of bacterial Fe^{3+} siderophore being taken up by plants important mode of iron nutrition in plants (Duijff et al. 1994), it is more vital process especially in calcareous soils (Masalha et al. 2000). There is another school of thought which subscribes to the theory that contribution of bacterial siderophores to the overall iron requirements of plants is small (Glick 1995). Bar-Ness et al. (1992) had earlier supported the concept of bacterial siderophore uptake by plants (Bar-Ness et al. 1992), concluded that two bacterial siderophores (pseudobactin and ferrioxamine B) were inefficient as iron sources for plants and that rhizospheric siderophore-producing bacteria can be in competition with the plant for iron. A vast majority of the researchers believe that the microbial siderophores in the rhizosphere are closely associated with the bio-control activities in the region due to their ability to create an iron deficient condition for competing plant pathogens (Hiifte et al. 1994).

3.3 *Root Surface Area Improvement*

Despite wide ranging impact of PGPR on the solubility and availability of soil nutrients, they are known to affect the root density, surface area and morphoanatomy of the plant. More specifically, enhanced root surface area can have a huge influence on the nutrient uptake efficiency (Vessey 2003). The plant growth promoting attribute of the PGPR is mainly associated with morphological and physiological changes in the inoculated plant roots and which sufficiently improve the water and mineral intake (Sarig et al. 1988).

So far the accumulated evidences on the positive effects of biofertilizing-PGPR points to bacteria-mediated changes in root growth and morphology. Bacterial mediated increases in root weight are commonly reported in response to PGPR inoculations (Vessey and Buss 2002), particularly an increase in the root length and surface area (Galleguillos et al. 2000; German et al. 2000; Holguin and Glick 2001). Fallik et al. (1994) reported that maize plants inoculated with *Azospirillum brasilense* resulted in a proliferation of root hairs and exhibited profound impact on the root surface area. The root length and root surface area are considered important parameters more effective evaluation of PGPR potential, just mention of increase in the root weight i. e. not sufficient. For instance, the clipped soybean roots in the presence of *A. brasilense* Sp7 showed about 63% increase in the root dry weight, but there was about sixfold increase in specific root length (root length per unit root dry weight), and more than tenfold increase in total root length (Molla et al. 2001).

3.4 *Production of Phytohormone by PGPR*

Accumulating evidences indicated that PGPR influence the plant growth and development by bringing about changes in the level of phytohormones such as auxins, gibberellins, and cytokinins. The effects of auxins on plant growth are found to be concentration dependent, where lower concentrations stimulate the growth and higher concentrations reduce the overall growth (Arshad and Frankenberger 1991). However, different plant seedlings respond differently to variable level of auxin concentrations (Sarwar and Frankenberger 1994). The microorganisms (Ahmad et al. 2005) which produce the highest amount of auxins i.e. indole acetic acid (IAA) and indole acetamide (IAM) in non-sterilized soil, cause maximum increase in growth and yield of the wheat crop (Khalid et al. 2004). Even few strains showing low rate IAA production, if secreted continuously, also exhibit improved plant growth (Tsavkelova et al. 2007). It has been observed that addition of IAA to soil not only improves the root and shoot weight, but also ensures better survival of rhizosphere bacteria (Narula et al. 2006). The *Dendrobium moschatum*-originally isolated from the roots of the epiphytic orchid and the strains of *Rhizobium*, *Microbacterium*, *Sphingomonas*, and *Mycobacterium* genera are among the most active IAA producers (Tsavkelova et al. 2007). The species of *Pseudomonas* and *Bacillus* are also considered to promote the growth of plants, but the production of

phytohormones or growth regulators is not characterized. But they are known to induce the greater amounts of fine roots which have the effect on the absorptive surface of plant roots and uptake of water and nutrients. Rhizobia were the first group of bacteria characterized for production of IAA which helps and promotes the growth and pathogen resistance in plants (Mandal et al. 2007; Basu and Ghosh 2001; Ghosh and Basu 2002; Roy and Basu 2004). Sridevi and Mallaiah (2007) also showed that all the strains of *Rhizobium* isolated from root nodules of *Sesbania sesban* (L) Merr. were able to produce IAA. The *Rhizobium* sp. isolated from the root nodules of plant *Vigna mungo* (L) Hepper showed high levels of IAA and was made available to young and healthy root nodules (Mandal et al. 2007). All the *Rhizobium* spp. isolated from *Crotalaria* sp. showed IAA production, but the isolates differ significantly in the level of auxin production, perhaps depends upon the cultural conditions. The studies conducted so far indicated that Rhizobia can be effectively used as both bioenhancer and biofertilizer for increasing the crop production as it can easily improve the nutrient uptake (N, P and K) by producing IAA and subsequently increases the plant root system (Etesami et al. 2009). Among all the isolates maximum amount of IAA is produced by isolate from *C. retusa* (Sridevi et al. 2008). Independent of the origin (rhizosphere vs. phyllosphere), the isolated bacterial strains produced IAA, which had positive impact on the growth of pea and wheat plants. Among them, the highest concentration of IAA was particularly produced by the bacterial strain *P. fluorescens* and *Kocuria varians* (Ahmad et al. 2005; Egamberdieva 2008). While working on chickpea, Joseph et al. (2007) observed that all the isolates of genus *Bacillus*, *Pseudomonas* and *Azotobacter* were able to produce IAA. On the other hand, about 85.7% isolates of genus *Rhizobium* exhibited IAA production. Choi et al. (2008) have reported that *Pseudomonas fluorescens* B16 is a plant growth-promoting rhizobacterium and it produces Pyrroloquinoline Quinone which is a plant growth promotion factor. Even the plant growth promoting attribute of nitrogen fixing *Azotobacter* strain is associated with production of phytohormone rather than to its diazotrophic activity. *Pseudomonas* bacteria, especially *P. fluorescens* and *P. putida* are the most important PGPR strains known to produce auxin and promote the plant yield.

In fact, a variety of auxin like substances such as indole-3-acetic acid (IAA), indole-3-pyruvic acid, indole-3-butyric acid and indole lactic acid (Costacurta et al. 1994; Martinez-Morales et al. 2003); cytokinins (Horemans et al. 1986; Cacciari et al. 1989) and gibberellins (Bottini et al. 1989) are known as growth promoters. But the production of auxin is comparatively and quantitatively most important for plants (Barassi et al. 2007). Khakipour et al. (2008) tried to evaluate the auxin production potential of *Pseudomonas* strains through chromatography, using HPLC devise; compared the methods of IAA synthesis in *Azospirillum brasilense* strain SM which has potential to trigger the IAA accumulation in Sorghum plants under nutrient stresses. Further, it also exhibited ability to promote the growth of number of other plants like Mung bean, Wheat and Maize (Malhotra and Srivastava 2008). Some of the P-solubilizing bacteria (PSB) and fungi (PSF) are also known as plant growth promoters due to their ability to produce IAA but there is a differential rate of IAA production among different PSB and PSF isolates

(Souchie et al. 2007). *Bacillus megaterium* isolated from tea plant rhizosphere was found to contribute positively to the plant growth due to its ability to produce IAA (Chakraborty et al. 2006). It has been suggested that the cytokinin receptors in *B. megaterium* also play a complimentary role in plant growth promotion (Ortiz-Castro et al. 2008).

4 PGPR as Bio-control Agents

The plant growth promoting bacteria colonizing the rhizosphere of plants produce substances, which not only increase the growth of plants, but also protect them against various diseases. They are known to suppress a broad spectrum of bacterial, viral, fungal and nematode diseases. The PGPR provide protection to the plants against pathogens by direct antagonistic interactions with pathogens and work as bio-control agents. As the PGPR are indigenous to soil and the plant rhizosphere, it is easier for them to play the role of bio-control agents against plant pathogens. On the other side, they can also induce the host resistance against plant disease. Most of the studies demonstrating the plant protection by PGPR have been carried out in laboratory and greenhouse. The results obtained so far under the field condition have been inconsistent. Recent progress in our understanding of their diversity, colonizing ability, and mechanism of action, formulation and application should be fully utilized to facilitate and devise the cost effective plant protection technology against plant pathogens. Some of these rhizobacteria may also be tried as a part of integrated pest management programmes. Greater the application of PGPR be encouraged in plant protection and biofertilization (Siddiqui 2006). The isolation of bacterial strains from the rhizosphere of *Lolium perenne* rhizosphere are found to be effective as plant growth promoters and as bio-control agents and subsequently resulting into enhanced yield (Shoebitz et al. 2007). The *Pseudomonades* – a major group of rhizobacteria with potential for biological control (Kremer and Kennedy 1996), are ubiquitous and are present in agricultural soils. A great deal of information is available regarding the process of root colonization by *pseudomonads* and also the biotic/abiotic factors regulating the colonization, bacterial traits and genes, which confer the special attributes to this soil bacteria for rhizosphere competence and suppression of pathogen (Weller 2007). *Pseudomonads* possess many more traits that make them well suited as bio-control and growth-promoting agents (Weller 1988). These include the ability to (i) grow rapidly *in vitro* and produce larger biomass; (ii) efficient utilization of seed and root exudates; (iii) ability to colonize and multiply in the rhizosphere environments and within the plant tissue; (iv) ability to produce a wide spectrum of bioactive metabolites (i.e., antibiotics, siderophores, volatiles, and growth-promoting substances); (v) compete aggressively with other microorganisms; and (vi) adapt to environmental stresses. In addition, *pseudomonads* are responsible for the natural suppression of growth of some soil borne pathogens (Weller et al. 2002). The major weakness of *pseudomonads* as

bio-control agents is their inability to produce resting spores like many other *Bacillus* spp. which restricts the wide application of the bacteria for commercial use. *Fluorescent pseudomonas* spp. has been studied for decades for their plant growth-promoting effects through effective suppression of soil borne plant diseases. Among various bio-control agents, *Fluorescent pseudomonads*, are well equipped with multiple mechanisms of bio-control as well as plant growth promotion (Banasco et al. 1998; Dileep et al. 1998). They produce a wide spectrum of compounds like antibiotics, chitinolytic enzymes, P solubilising enzymes, growth promoting hormones, siderophores, HCN and catalase enzyme (Kraus and Loper 1995). *Pseudomonas fluorescens* MSP-393 has been tried as plant growth-promoting rhizobacterium as well as bio-control agent for rice crop grown in saline soils of coastal areas (Paul et al. 2006). Cold-tolerant fluorescent *Pseudomonas* isolated from Garhwal district of Uttarakhand has shown its potential both as plant growth promoter and bio-control agents for pea (Negi et al. 2005).

Bacillus subtilis, an endospore forming bacterium predominantly an inhabitant of soil, has been widely recognized as a powerful bio-control agent as it produces different biologically active compounds with a broad spectrum of activity (Nagorska et al. 2007). *Bacillus megaterium* – an isolate from tea plant rhizosphere can solubilize phosphate, produce IAA, siderophore and antifungal metabolites and thereby, it helps in the plant growth promotion and protection of plant diseases (Chakraborty et al. 2006). Two strains *Bacillus thuringiensis* (*kurstaki*) and *B. sphaericus* have also been reported to have the ability to solubilise phosphates and help in the control of the lepidopteron pests (Seshadri et al. 2007).

In recent years, role of siderophore producing PGPR have been implicated in bio-control of soil-borne plant pathogens. Now the Microbiologists have developed the techniques for introduction of siderophore producing PGPR in soil system through seed, soil or root system. The suppression of plant pathogens by PGPR, can indirectly contribute to enhancement in the plant growth/ yield via a variety of mechanisms. These include:

- The ability to produce siderophores (as discussed above) that chelate iron, making it unavailable to pathogens.
- The capacity to synthesize anti-fungal metabolites such as antibiotics, fungal cell wall-lysing enzymes, or hydrogen cyanide, which suppress the growth of fungal pathogens.
- The ability to successfully compete with pathogens for nutrients or specific niches on the root; and the ability to induce systemic resistance.

Among the various PGPRs identified, *Pseudomonas fluorescens* is considered as one of the most extensively used rhizobacterium because of its antagonistic action against several plant pathogens. Banana bunchy top virus (BBTV) is one of the deadly viruses which severely affects the yield of banana (*Musa* spp.) crop in Western Ghats, Tamil Nadu, India. It has been demonstrated that application of *P. fluorescens* strain significantly reduces the incidence of BBTV disease incidence in the banana under both greenhouse and field conditions. Different PGPR spp. as bio-control agents against various plant diseases has been given in Table 14.2.

Table 14.2 Bio-control behaviour of PGPR against various plant diseases

PGPR	Pathogens	Plant diseases	References
<i>Fluorescent pseudomonas</i>	Under gnotobiotic conditions	Black root-rot of tobacco	Voisard et al. (1989)
<i>P. fluorescens</i> CHA0	<i>Thielaviopsis basicola</i>	Black root rot of tobacco	Voisard et al. (1989)
<i>F. pseudomonas</i> EM85	<i>Rhizoctonia solani</i>	Damping-off of cotton	Pal et al. (2000)
<i>P. oryzihabitans</i> and <i>Xanthomonas nematophila</i> strains	<i>Pythium</i> and <i>Rhizoctonia</i> sp.	Damping-off of cotton	Kapsalis et al. (2008)
<i>F. pseudomonads</i>	<i>Rhizoctonia bataticola</i> and <i>Fusarium oxysporum</i>	Rice and sugarcane rhizosphere	Kumar et al. (2002)
<i>Pseudomonas</i> strains	<i>Xanthomonas oryzae</i> pv. <i>Oryzae</i> and <i>Rhizoctonia solani</i>	Bacterial leaf blight and sheathblight pathogens of rice (<i>Oryzasativa</i>)	Rangarajan et al. (2001)
<i>F. pseudomonads</i>	<i>Helminthosporium sativum</i>	Endo-rhizosphere of wheat	Gaur et al. (2004)
<i>P. fluorescens</i> CHA0	<i>Meloidogyne javanica</i>	Root-knot nematode	Siddiqui et al. (2005)
<i>P. putida</i>	<i>Macrophomina phaseolina</i>	Root-rot disease complex of chickpea	Saraf et al. (2008)
<i>P. aeruginosa</i> Sha8	<i>F.oxysporium</i> and <i>Helmithosporium</i> sp.	Antagonistic activities	Hassanein et al. (2009)
<i>P. fluorescens</i> CHA0	<i>Tetrahymena pyriformis</i>	Pathogenic against the ciliated protozoa	Jousset et al. (2009)

4.1 PGPR as Biological Fungicides

The PGPR and bacterial endophytes are known to play a vital role in the management of various fungal diseases. But one of the major hurdles experienced with bio-control agents is the lack of appropriate delivery system. Some PGPR can synthesize antifungal compounds, viz. synthesis of 2, 4-diacetyl phloroglucinol by *P. fluorescens* which inhibits the growth of pathogenic fungi (Nowak-Thompson et al. 1994). Certain PGPR can degrade fusaric acid produced by the fungi *Fusarium* sp. – a causative agent of wilt (Toyoda and Utsumi 1991). There are few PGPR strains which can produce enzymes that hydrolyses the fungal cell wall, for instance secretion of chitinase and laminarinase enzymes by the *Pseudomonas stutzeri* which can lyse the mycelia of *Fusarium solani* (Mauch et al. 1988). *Pseudomonas fluorescent* has been suggested not only as a plant growth promoter, but also as potential bio-control agent due to its ability to

protect the plants against the incidence of a wide range of important fungal diseases such as black root-rot of tobacco (Voisard et al. 1989), root-rot of pea (Papavizas and Ayers 1974), root-rot of wheat (Garagulia et al. 1974), damping-off of sugar beet (Kumar et al. 2002). There is ample scope for genetic manipulation of these organisms to improve their efficacy as bio-control agents (Dowling and O’Gara 1994). A number of fluorescent *Pseudomonads* exhibit strong antifungal activity (Reddy and Rao 2009). *Pseudomonas fluorescens* spp. EM85 and *P. oryzae* exhibit strong antagonistic interaction with *Rhizoctonia solani* – a causal agent of damping-off of cotton (Pal et al. 2000). The *X. nematophila* strain also produce secondary metabolites which can suppress the growth of *Pythium* and *Rhizoctonia* species causing damping-off in cotton (Kapsalis et al. 2008). The fluorescent *Pseudomonads* also exhibit strong antagonistic effect against *Rhizoctonia bataticola* and *Fusarium oxysporum* associated with the rhizosphere of rice and sugarcane plants (Kumar et al. 2002). *Xanthomonas oryzae* pv. *oryzae* and *Rhizoctonia solani* – the bacterial leaf blight (BB) and sheath blight (ShB) pathogens of rice (*Oryza sativa*) are suppressed by indigenously present *Pseudomonas* strains isolated from rice cultivated coastal agricultural fields, having saline soils (Rangarajan et al. 2001). *Pseudomonas fluorescens* isolated from rice plant rhizosphere are found to have strong antifungal activity against *P. oryzae* and *R. solani* mainly due to excess production of antifungal metabolites (Reddy et al. 2008). About 50–60% of several fluorescent pseudomonads isolated from the rhizosphere and endorhizosphere of wheat plant growing Indo-Gangetic plains exhibit antagonistic interactions with *Helminthosporium sativum* (Gaur et al. 2004). Zadeh et al. (2008) reported antagonistic potential of non-pathogenic rhizosphere isolates of fluorescent *Pseudomonas* in the bio-control of *Pseudomonas savastanoi* – a causative agent of Olive knot disease. The *P. corrugata*, which grows at 4°C under laboratory conditions (Pandey and Palni 1998), also produces antifungal compounds like diacetylphloroglucinol and/or phenazine. *Pseudomonas fluorescens* CHA0 is reported to suppresses the black root rot of tobacco plant caused by the fungus *Thielaviopsis basicola* (Voisard et al. 1989) and it also contributes to biological control of root-knot nematode disease caused by *Meloidogyne javanica* (Siddiqui et al. 2005). In addition, certain soils from Morens, Switzerland, were found to be natural suppressive agent for *Thielaviopsis basicola*-mediated black root rot of tobacco due to presence of fluorescent *Pseudomonads* populations (Pal et al. 2000). *P. putida* has potential for the bio-control of root-rot disease complex of chickpea due to its antagonistic interaction against *Macrophomina phaseolina* (Saraf et al. 2008). It has also been shown that anaerobic regulator ANR-mediated cyanogenesis has important role in the suppression of black root rot (Laville et al. 1998). The suppression of *Phytophthora capsici* by fluorescent *Pseudomonads* in all seasons of plant growth helps in control of foot rot disease (Paul and Sarma 2006). Some metabolites produced by *Pseudomonas aeruginosa* Sha8 include toxic volatile compound which reduces the growth of both *F. oxysporium* and *Helminthosporium* sp. but not the growth of *A. niger* (Hassanein et al. 2009). *B. luciferensis* strain KJ2C12 controls the *Phytophthora blight* of

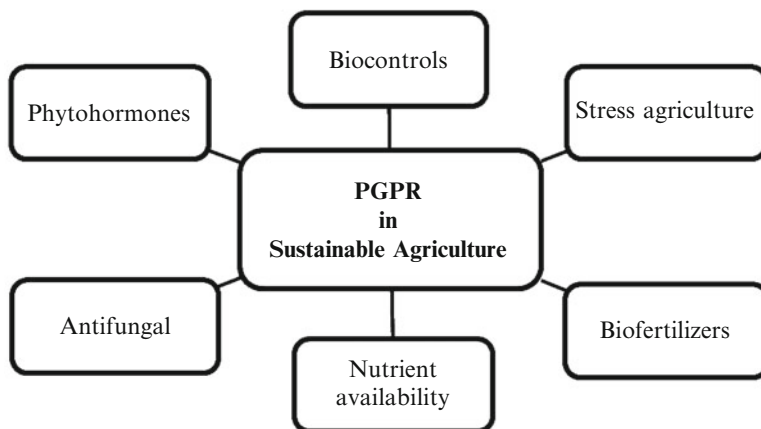


Fig. 14.1 A schematic diagram showing perspectives of PGPR in sustainable agriculture development

pepper by effective root colonization and enhanced production of protease enzyme and, also by increasing the soil microbial activity (Kim et al. 2009).

5 Conclusions

It has been demonstrated and proven that PGPR can be the very effective and potential microorganisms for enriching the soil fertility and enhancing the productivity in various agriculture yields. In the present scenario, application of PGPR is vital to overcome the problems of various environmental stresses such as soil salinity, drought, water logging, temperature and nutritional stresses to crop plants. Inoculation of plants under salinity stress with PGPR having ACC-deaminase activity is expected to mitigate the inhibitory effects of salinity on root growth by lowering the ethylene concentration in the plant. The PGPR is the most commonly used as biofertilizer which increase the availability and uptake of nutrients in plants. Current and future progress in our understanding of PGPR diversity, colonization ability, mechanisms of action, formulation, and application could facilitate their development as reliable components in the management of sustainable agricultural systems. On a commercial scale, application of PGPR in agriculture might prove beneficial and could be a sound step towards sustainable crop production and conservation. A schematic diagram showing role of PGPR in sustainable agriculture productivity is presented in Fig. 14.1.

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