Chapter 2
Plant–Microbe Interactions for Sustainable Agriculture: Fundamentals and Recent Advances

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Abstract Coordinated interactions between plants and microbes have supreme importance for improving plant growth as well as maintaining proper soil conditions. Rhizosphere interactions that are based on complex exchange are more complicated than those occurring above soil surface or non-rhizosphere soil. Among diverse microbial population, plant growth promoting rhizobacteria (PGPR) gain special attention owing to their multifarious functional characters like effective root colonization, hormone production, solubilization of nutrients, and production of certain enzymes that are beneficial for sustainable agriculture. An understanding about their ecology, growth-promoting traits, mechanisms of action, and their application for plant growth stimulation has key importance for maximum utilization of this naturally occurring population. The present review highlights the importance of PGPR for enhancing crop production. The mechanisms of plant growth promotions as well as effectiveness of PGPR under different environments have been discussed. The effectiveness of multistrain inocula over single strain has been explained with examples. Also, the limitations related to the use of bacterial inoculants under natural field conditions and some important basics related to their formulation and commercialization have been discussed.

Plant Growth Promoting Rhizobacteria: A Novel Source in Plant Growth Promotion

The zone surrounding the plant roots called as rhizosphere is a region of maximum microbial activity compared to surrounding soil (Hiltner 1904). This environment is a favorable habitat for microbial growth that exerts a potential impact on plant health as well as soil fertility (Podile and Kishore 2006). A number of beneficial microorganisms are associated with the root system of higher plants which depend on the exudates of these roots for their survival (Whipps 1990). In soil environment, particularly in rhizosphere, plants are mostly colonized by microbes (Berg et al. 2005). A variety of compounds present in root exudates including polysaccharides and proteins enable the bacteria to colonize plant roots (Somers et al. 2004; Rodriguez-Navarro et al. 2007). Due to competition for nutrients, those microbial populations having better ability to degrade complex compounds like chitin, cellulose, and seed exudates can survive better in such environment (Baker 1991). Among the diverse microbial population, bacteria are the most abundant microorganisms that competitively and progressively colonize the plant roots. Among this large bacterial population, a number of bacterial strains are considered as very important owing to their metabolically and functionally diverse characteristics. These are free-living plant growth promoting rhizobacteria (PGPR) that promote plant growth by root colonization (Kloepper et al. 1989) and have been studied extensively due to their optimistic effect on plant growth and development. These PGPR belonging to some important genera include *Serratia*, *Bacillus*, *Pseudomonas*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Klebsiella*, *Beijerinckia*, *Flavobacterium*, and *Gluconacetobacter* (Podile and Kishore 2006; Dardanelli et al. 2009; Nadeem et al. 2010b). These PGPR enhance plant growth through various mechanisms like synthesizing a compound essential for plant and facilitating the host in nutrient uptake and also through disease prevention (Glick 1995). The major mechanisms used by PGPR can be divided into two categories, i.e., direct and indirect mechanisms. Phosphate solubilization and phytohormone and siderophore production are some examples of direct growth promotion (Kloepper et al. 1989; Glick et al. 1995; Ayyadurai et al. 2007), while indirect growth promotion occurs by inhibiting the growth of plant pathogens (Glick and Bashan 1997; Persello-Cartieaux et al. 2003; Ravindra Naik et al. 2008). In addition to these general growth promotion mechanisms, PGPR also protect the plant from the deleterious effects of environmental stresses by some particular mechanisms. These include lowering of stress-induced ethylene, production of exopolysaccharides, regulating nutrient uptake, and enhancing the activity of antioxidant enzymes (Sandhya et al. 2009; Glick et al. 2007). There are a number of reports that show outstanding role of this natural microbial population for improving plant growth and development in normal as well as stress environment (Zahir et al. 2004; Glick et al. 2007; Jha et al. 2009; Tank and Saraf 2010; Nadeem et al. 2010b).

Better plant growth promotion depends upon positive plant–microbe interactions. Belowground plant–microbe interactions are more complex than those occurring above the soil surface (Bais et al. 2004), and understanding of these interactions is crucial for maintaining plant growth and health (Barea et al. 2005). The plant–microbe interactions as well as interactions between other rhizosphere microorganisms are still not much clear, and literature shows that most of these interactions are complex in nature. An understanding about microbial ecology, their growth-promoting traits, mechanisms of action, and their application for plant growth stimulation is of pivotal importance for maximum utilization of this naturally occurring population. The diverse study of PGPR is important not only for understanding their ecological role and interactions with plants but also for biotechnological applications (Berg et al. 2002).

Plant Growth Promotion Mechanisms

Plant growth promotion by PGPR is a well-known phenomenon, and this growth enhancement is due to certain traits of rhizobacteria. Some of these traits are very common among certain bacterial species; however, other traits might be specific with some particular species. There are a number of mechanisms used by PGPR for enhancing plant growth and development in diverse environmental conditions (Fig. 2.1). In general, PGPR work as phytostimulators, biofertilizers,

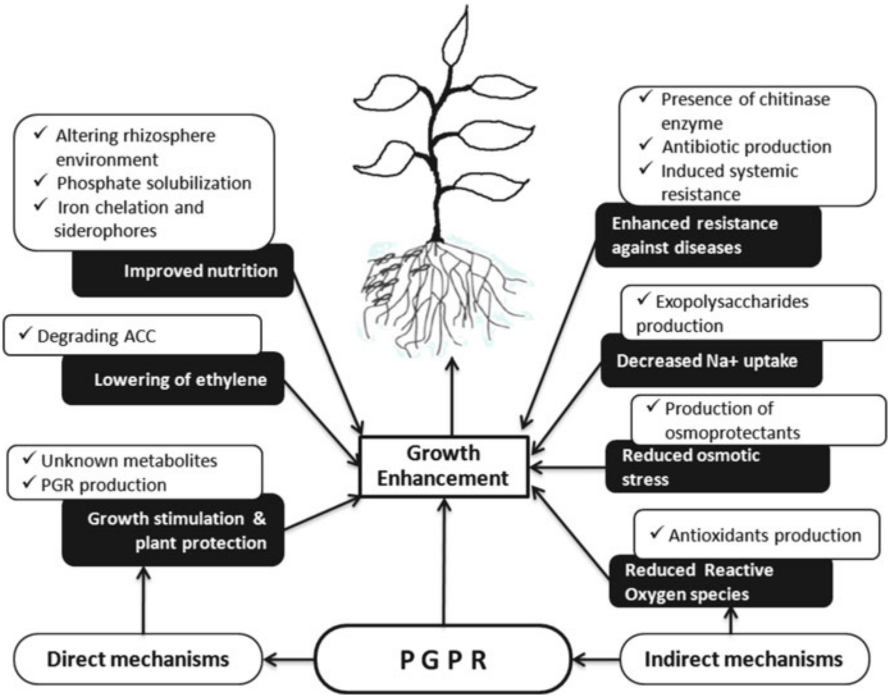

Fig. 2.1 Mechanisms used by PGPR for enhancing plant growth

biocontrol agent, root colonizers, and environmental protectors (Vessey 2003; Zahir et al. 2004). Some of the important and valuable mechanisms are discussed in the following sections.

Phytostimulation

One of the direct growth promotion mechanism used by PGPR is the production of phytohormones including indole acetic acid, abscisic acid, cytokinins, gibberellins, and ethylene. There are a number of reports which advocate the effectiveness of these growth regulators for enhancing plant growth and development (Zahir et al. 2004; Glick et al. 2007). These phytohormones enhance the plant growth by virtue of their positive effect on cell division, cell enlargement, seed germination, root formation, and stem elongation (Taiz and Zeiger 2000; Khalid et al. 2006). Phytohormones influence the physiological processes of plants and facilitate plant growth by altering the hormonal balance (Asghar et al. 2004; Kang et al. 2006). These phytohormones are equally effective in normal and stress conditions. For example, ABA abscisic acid (ABA) helps plant in stress conditions (Zhang et al. 2006) and plays an important role in the photoperiodic induction of flowering

(Wilmowicz et al. 2008). Patten and Glick (2002) observed 35–50 % longer roots in canola inoculated with wild-type GR12-2 compared to IAA-deficient mutant and uninoculated control. Fassler et al. (2010) demonstrated the importance of IAA in stress alleviation of sunflower. Seed inoculation with wild-type GR12-2 induced the formation of tap roots that were 35–50 % longer than the roots from seeds treated with the IAA-deficient mutant and the roots from uninoculated seeds. Similarly, many *Pseudomonas*, *Bacillus*, and *Azospirillum* spp. produce cytokinin and gibberellins (Gamalero and Glick 2011), and positive effects on plant biomass have been reported by these hormones (Gutierrez-Manero et al. 2001; Arkhipova et al. 2005; Spaepen et al. 2009). Steenhoudt and Vanderleyden (2000) demonstrated that the main mechanism used by *Azospirillum* for enhancing plant growth is the production of phytohormones. Although commercially available phytohormones are also used for promoting plant growth, however, microbially produced phytohormones are more effective due to the reason that the threshold between inhibitory and stimulatory levels of chemically produced hormones is low, while microbial hormones are more effective by virtue of their continuous slow release (Khalid et al. 2006).

Biofertilization

The potential of PGPR to enhance plant growth and their participation in carbon, nitrogen, sulfur, and phosphorous cycling increase the effectiveness of PGPR in sustainable agriculture. The application of PGPR for increasing nutrient availability for plants is an important and necessary practice (Freitas et al. 2007) and is very helpful for increasing the nutrient concentration of certain essential elements like N, P, K, Ca, Mg, Zn, Fe, and Mn (Dursun et al. 2010). Inoculation of cotton with PGPR showed enhanced uptake of N, P, K, and Ca (Yue et al. 2007), and similarly PGPR inoculation also enhanced the nutrient content of salinity-stressed maize (Nadeem et al. 2006).

The conversion of insoluble form of phosphorus to make them plant-available form is a common mechanism of various PGPR strains and plays important role to fulfill the phosphorus requirement of plant. Phosphate-solubilizing bacteria are common in the rhizosphere (Ravindra Naik et al. 2008; Jha et al. 2009) that solubilize inorganic phosphate by various mechanisms like production of organic and inorganic acids, release of H ions, and production of chelating substances and through enzymes like phosphatase (Rodriguez et al. 2004; Gamalero and Glick 2011). Also, the exopolysaccharides produced by these bacteria have indirect effect on phosphate solubilization by binding free phosphorus (Yi et al. 2008). It was also observed that cold-tolerant species were able to solubilize P at low temperature (Selvakumar et al. 2008). The application of P-solubilizing bacteria can solve the problem of P precipitation in the soil and therefore increase its availability to plants (Lin et al. 2006). The role of PGPR to improve the uptake of other macronutrients has also been established. Inoculation of *Pseudomonas* sp. having the ability to stimulate calcium (Ca) uptake caused significant improvement in tomato growth and also reduced blossom-end rot of tomato fruits that generally occurs due to Ca deficiency (Lee et al. 2010). Similarly, the solubilization of biotite by silicate mineral-solubilizing bacteria like *Bacillus* sp. can enhance the availability of K^+ to plants (Sheng et al. 2008).

The production of low-molecular-weight ferric-chelating compound siderophores directly increases the iron availability for plant (Robin et al. 2008) and indirectly protects the plant from pathogenic organisms (Singh et al. 2010b). Siderophores play important role in iron nutrition of plants (Jin et al. 2006). Vansuyt et al. (2007) reported that Fe–pyoverdine complex synthesized by *Pseudomonas fluorescens* C7 was efficiently taken up by the *Arabidopsis thaliana* that resulted in enhanced iron content in plant tissue and better growth. Similarly, bacterial strains improved maize growth through biofertilization and phytostimulation mechanisms (Marques et al. 2010).

Certain bacteria can fix atmospheric nitrogen and make it available for plant. The symbiotic relationship between legumes and nitrogen-fixing bacteria and nitrogen fixation by free-living bacteria without forming association is a source of nitrogen for plant (Carvalho et al. 2010). Co-inoculation of PGPR with rhizobia caused positive effect on nitrogen fixation, plant biomass, and grain yield in various crops like alfalfa, soybean, and pea (Bolton et al. 1990; Dashti et al. 1998; Tilak et al. 2006). Similarly, *Azospirillum* sp. have the potential to increase nitrogen fixation (Rai and Hunt 1993) which can contribute about 70 % of the total nitrogen requirement of the host plant (Malik et al. 1997). The presence of such bacteria also enhances ability of plant to use nitrogen efficiently and minimizes its leaching and denitrification losses. Some important genera of such bacteria include *Enterobacter*, *Klebsiella*, *Pseudomonas*, and *Rhizobium* (James 2000).

Zinc is also an essential nutrient and in deficient soils the solubilization of Zn near the root zone can alleviate the deficiency for plants. The Zn solubilization by sugarcane-associated *Gluconacetobacter diazotrophicus* has been demonstrated by Saravanan et al. (2008). The inoculation with *Burkholderia cepacia* enhanced Zn uptake, its translocation from root to shoot, and improved plant growth (Li et al. 2007).

Due to high price and certain environmental concerns about the chemical fertilizers, the use of PGPR in the form of biofertilizers is an effective supportive strategy to provide crop nutrition (Cakmakci et al. 2006). The use of PGPR inoculants as biofertilizer provides a promising support to chemical fertilizers. Moreover the use of PGPR with inorganic fertilizer can increase the availability of nutrients to the crops (Kumar et al. 2009) and therefore could be useful for increasing efficiency of these fertilizers in one hand and also reducing their quantity on other.

Root Colonization and Rhizosphere Competence

Rhizosphere is a complex habitat with temporal and spatial changes where plant and microbial populations interact with each other and are affected by a number of biotic and abiotic factors. The success of bacteria to enhance plant growth depends on its potential to colonize the plant root. The significant effects of microbial inoculation cannot be obtained unless the environment supports growth and survival of these introduced microorganisms (Devliegher et al. 1995). The ineffectiveness of PGPR, particularly in field conditions, is due to their inability to colonize plant root properly (Bloemberg and Lugtenberg 2001). One of the aspects of better root colonization is the ability of the bacteria to compete with the indigenous microbial populations. Being the most abundant microorganisms, it is very likely that bacteria can cause great effect on plant physiology owing to their better competitiveness for root colonization (Barriuso et al. 2008). Literature shows that certain PGPR strains have ability to tolerate unfavorable environment (Paul and Nair 2008; Malhotra and Srivastava 2009) and therefore can be considered as the best population for promoting crop production.

The microbes use different strategies for their survival in the environment. The success of these strategies depends upon their ability to adapt to the nutrient-limited conditions, efficient utilization of root exudations, as well as their interaction with plants (Devliegher et al. 1995; Van Overbeek and Van Elsas 1997). In soil environment, the survival of the inoculated bacteria depends on the availability of an empty niche, so that they can compete effectively with better adopted native microbial population (Rekha et al. 2007). It has been observed that PGPR which possess some particular traits like ACC-deaminase activity and the production of antioxidant enzymes, exopolysaccharides, and organic solutes have some selective advantages over other bacteria under stress environment (Mayak et al. 2004a, b; Saravanakumar and Samiyappan 2007; Sandhya et al. 2009). A variety of compounds, like surface proteins and polysaccharides, have a good role in adherence of bacteria to plant root (Dardanelli et al. 2003; Rodriguez-Navarro et al. 2007), and such bacteria have competitive advantages to colonize plant roots because these exopolysaccharides help them to attach and colonize the roots due to fibrillar material that permanently connects the bacteria to root surface (Sandhya et al. 2009).

Enzymatic Activity

Growth enhancement through enzymatic activity is another mechanism used by PGPR. Bacterial strains can produce certain enzymes such as cellulase, ACC-deaminase, and chitinase. Through the activity of these enzymes, bacteria play a very significant role in plant growth promotion particularly to protect them from biotic and abiotic stresses. For example, the reduction of elevated level of ethylene under stress by ACC-deaminase activity and disease suppression by chitinase activity are common mechanisms used by PGPR (Glick et al. 2007; Nadeem et al. 2010b). Similarly, the enhancement of nodule formation by rhizobia might be due to the production of hydrolytic enzymes such as cellulase which could make penetration of rhizobia into root hairs leading to increased numbers of nodules (Sindhu and Dadarwal 2001).

Growth Enhancement Through Vitamins

Vitamins are organic nutritional factors that influence the growth of living organisms. In addition to the vitamins present in root exudates as a source for bacterial growth (Mozafar and Oertli 1993), certain bacterial species also produce vitamins (Dahm et al. 1993). Like other growth promoting traits of PGPR, the production of vitamins also causes positive effect on plant growth and development (Derylo and Skorupska 1993; Azaizeh et al. 1996; Dakora 2003). More root colonization ability of vitamin-producing *Pseudomonas fluorescence* has been observed (Marek-Kozaczuk and Skorupska 2001). Similarly, co-inoculation of vitamin-producing *P. fluorescence* and *Rhizobium* stimulated the growth and symbiotic nitrogen fixation in clover plants (Marek-Kozaczuk et al. 1996).

Biocontrol Activity

Biocontrol mechanisms for diseases suppression are an important strategy against a number of plant pathogens that cause reduction in crop yield. PGPR also act as effective biocontrol agents by suppressing the effect of diseases (Kotan et al. 2009) and provide protection to the plants against harmful pathogens. The PGPR use certain mechanisms including competition, antibiotic production, degradation of fungal cell wall, and sequestering iron by the production of siderophores (Velazhahan et al. 1999; Siddiqui 2006; Ramyasmruthi et al. 2012).

Cell wall degrading enzymes are very important for controlling the phytopathogenic fungi (Picard et al. 2000). Chitinase, cellulase, and lyases are well-known fungal cell wall degrading enzymes (Inbar and Chet 1991; Lorito et al. 1996; Ayyadurai et al. 2007). These enzymes play very important role by suppressing the onset of diseases. The presence of chitinase enzyme in *Pseudomonas* sp. inhibits the growth of *Rhizoctonia solani* by degrading the cell wall (Nielsen et al. 2000). A volatile antibiotic hydrogen cyanide produced by certain bacterial strains also plays role in disease suppression. Suppression of black rot of tobacco by HCN producer *Pseudomonas* strain was observed by Voisard et al. (1981). The production of siderophores by the bacteria reduces the availability of iron to fungi (Sayyed et al. 2008), therefore causing negative impact on its growth (Arora et al. 2001). Matthijs et al. (2007) reported the suppression of disease caused by *Pythium* sp. owing to siderophores that decreased the availability of iron for fungal growth. It is also an evident fact that fungi are unable to absorb the iron–siderophore complex that causes unavailability of iron to pathogenic fungus (Solano et al. 2009). Bacterial siderophores are also suggested to be involved in inducing systemic resistance (ISR) that enhances plant's defensive capacity against pathogens. Enhanced ISR in tomato has been reported by siderophores, pyochelin, and pyocyanin (Audenaert et al. 2002). Similarly, a number of reports have shown the effectiveness of PGPR for enhancing ISR against various fungal and viral diseases (Radjacommare et al. 2002; Saravanakumar et al. 2007). Systemic resistance can also be induced by a mechanism where inducing bacteria and pathogen remain separated without showing any direct interaction (Ryu et al. 2004).

The disease suppression by PGPR also occurs by the production of antibiotics. The antibiotics in addition to suppressing the pathogen also induce systemic resistance in the plant. The synergistic interaction between antibiotics and ISR further increases resistance against pathogens (Jha et al. 2011). The *Bacillus thuringiensis*, having the ability to produce insecticidal protein (Singh et al. 2010a), can be used as biocontrol agent.

In addition to above-discussed mechanisms, certain environmental factors like water, soil pH, temperature, nutrient contents, and competition for root exudates as well as indigenous microbial population affect the ability of an organism to colonize the plant root. The exclusion of pathogenic organisms from the rhizosphere is one of the significant mechanisms to protect the plant from deleterious effect of such disease-causing organisms. Above discussion shows that owing to their number of mechanisms, PGPR have great competitive advantages over pathogens and could be very effective for protecting the plant from their attack by suppressing their growth.

Removal/Detoxification of Organic and Inorganic Pollutants

Plant growth promotion by PGPR inoculation is also due to reduction and improving plant tolerance against heavy metals (Belimov et al. 2005; Sheng et al. 2008). Bacteria use different intra and extra mechanisms to detoxify the adverse effects of heavy metals in their tissues. These mechanisms include production of proteins which absorb heavy metals and detoxification by taking them in vacuoles (Gerhardt et al. 2009; Giller et al. 2009). The mechanisms used by PGPR for tolerating and detoxifying of heavy metals may also vary among bacterial species and also for different metals. For example, microbes can detoxify zinc (Zn) by binding it in the outer membrane, by producing Zn-binding protein, and/or by complexation of organic acids (Appanna and Whitmore 1995; Choudhury and Srivastava 2001). Bacterial inoculation resulted in degradation of chlorobenzoates and pesticides (Crowley et al. 1996; Siciliano and Germida 1997) and the enhancement of plant growth by PGPR inoculation in highly contaminated soils (Gurska et al. 2009).

The production of siderophores by metal-resistant bacteria plays an important role in the successful survival and growth of plants in contaminated soils by alleviating the heavy metal stress-imposed impact on plants (Belimov et al. 2005; Braud et al. 2006; Rajkumar et al. 2010). Also, the production of enzymes and certain hormones which mobilize heavy metals and plant–microbe interactions affects the process of bioremediation (Abbas-Zadeh et al. 2010). For example, the inoculation of *Lupinus luteus* with genetically engineered nickel-resistant *B. cepacia* showed high nickel concentration that was approximately 30 % more than uninoculated control (Lodewyckx et al. 2001). The application of such bacteria could be helpful for the removal of heavy metals from the environment.

Enhancement of Photosynthetic Activity

Photosynthesis is considered as one of the very important reactions in plant growth and development. Under stress environment, reduction in photosynthesis occurs that might be due to decrease in leaf expansion, premature leaf senescence, impaired photosynthetic machinery, and associated reduction in food production (Wahid and Rasul 2005). PGPR enable the plants to maintain their growth by causing positive effect on photosynthesis. Drew et al. (1990) reported that reduction in photosynthetic activity might be due to osmotic stress and closing of stomata; however, the application of PGPR minimized this negative impact and caused significant increase in photosynthesis (Golpayegani and Tilebeni 2011). Heidari and Golpayegani (2011) observed enhancement in chlorophyll contents in drought stress basil (*Ocimum basilicum* L.) by PGPR application. More improvement in chlorophyll content was observed where PGPR were applied in combination than alone. The increase in shoot length, chlorophyll content, and dry weight was observed when banana plants were inoculated with PGPR (Mia et al. 2010a). According to them, this growth enhancement in addition to other factors was likely to be due to the higher accumulation of nitrogen that contributed to chlorophyll formation which consequently increased the photosynthetic activity. While Xie et al. (2009) demonstrated that enhanced photosynthetic activity in *Arabidopsis* by volatile emission from *Bacillus subtilis* might be due to accumulation of iron, because iron is often a limiting ion in photosynthesis. They also observed that when bacterial volatile signal was withdrawn, the photosynthetic capacity and iron content returned to untreated levels. The importance of iron has already been documented by Spiller and Terry (1980) who demonstrated that biogenesis of the photosynthetic apparatus makes heavy demands of iron availability.

Stress Tolerance

Due to sophisticated signaling system, microbes develop high degree of adaptability to environmental stresses. Bacteria are well known for their ability to tolerate the stress conditions due to their exceptional genetic makeup. The PGPR strains have showed tolerance against stress conditions like salinity and drought (Sandhya et al. 2009; Tank and Saraf 2010). Andre's et al. (1998) demonstrated great resistance ability of *Bradyrhizobium japonicum* against high doses of thiram. Although the microbial adaptations to such situations are difficult to understand (Spaepen et al. 2009), however, it might be due to some of their particular traits which enable them to survive under unfavorable conditions. For example, production of exopolysaccharides (EPS) by the bacteria protects them against unfavorable conditions and enhances their survival (Sandhya et al. 2009; Upadhyay et al. 2011b). In an earlier study, Hartel and Alexander (1986) also showed a significant correlation between the amount of EPS produced by the bacteria and their desiccation tolerance. The accumulation of poly-β-hydroxybutyrate during saline conditions and other osmoprotectants like proline and ectoine (1,4,5,6-tetrahydro-2-methyl-4-pyrimidine carboxylic acid) are protective measures taken by bacteria to survive under stress conditions (Bernard et al. 1993; Arora et al. 2006). The occurrence of such stress-tolerant strains could be very effective for improving soil fertility and enhancing plant growth (Mayak et al. 2004a; Egamberdieva and Kucharova 2009), and application of such stress-resistant strains could also be very useful for enhancing plant growth under stress environment (Glick et al. 2007; Nabti et al. 2010). The above-discussed mechanisms not only show the abilities of bacterial strains to withstand in variable soil environmental conditions but also enable them to compete effectively with the other microbial population. These mechanisms could be very useful for maintaining proper soil conditions and promoting sustainable agriculture.

Application of Rhizobacteria for Plant Growth Promotion

Owing to their well-established growth promoting abilities, PGPR are being used effectively for enhancing crop production. The growth promoting abilities of PGPR have been observed in laboratory under control conditions as well as in natural greenhouse and filed conditions. The crop improvement by PGPR inoculation under normal and stress environment has been reviewed by various workers (Zahir et al. 2004; Glick et al. 2007; Nadeem et al. 2010b; Ahemad and Khan 2011).

Growth Promotion Under Normal Conditions

The use of PGPR is an effective biological approach to increase crop yield and is applied to a wide range of agricultural species. Inoculation with PGPR promotes plant growth through phytohormone production, phosphate solubilization, siderophore production, regulation of hormonal level, and certain other mechanisms which have been discussed in the previous section. The root length of canola, lettuce, tomato, barley, wheat, and oats increased when seeds of these crops were treated with PGPR (Hall et al. 1996). Qiaosi et al. (2005) also reported that the roots of inoculated plants were more in number and longer than untreated control. This growth enhancement is due to common and some particular trait of bacteria, as is evident from the work of Cattelan et al. (1999) who tested eight strains of PGPR for their growth-promoting activity in soybean. They examined that six strains promoted growth more as compared to other, and they observed that these strains contained ACC-deaminase activity in addition to other characteristics. The growth enhancement by the PGPR has also been reported under natural field conditions. Inoculation with PGPR increased the dry weight of leaf, stem, and grain of maize (Gholami et al. 2012). They observed that inoculation caused significant effects on leaf area index and crop growth index. A number of other studies have also shown the importance of PGPR for improving plant growth and development, and some selected examples have been mentioned in Table 2.1.

Table 2.1 Plant growth promotion by PGPR inoculation under normal conditions

Test crop	Bacteria	Experimental conditions	Proposed mechanism(s)	Specific comments	Reference
Arabidopsis thaliana	*Burkholderia pyrrocinia* Bcc171, *Chromobacterium violaceum* CV01	Petri plate assay	VOCs production	*B. pyrrocinia* showed growth-promoting effect with low dose (1 drop) on LB media while high dose (3 drops) on MR-VP media over control	Blom et al. (2011)
	Bacillus cereus L254, *Bacillus simplex* L266, *Bacillus* sp. L272a	Petri plate assay	VOCs production	Rhizobacterial inoculation stimulated plant biomass production by twofold compared to control	Gutierrez-Luna et al. (2010)
Medicago truncatula	*Arthrobacter agilis* UMCV2	Glass tube	VOCs production	Plants grown in the presence of UMCV2 also exhibited a 35 % increase in chlorophyll concentration compared to control plants	Orozco-Mosqueda et al. (2012)
Medicago sativa	*A. agilis* UMCV2	Axenic trial	VOCs production	*A. agilis* UMCV2 inoculation promoted plant biomass up to 40 % compared to control	Velazquez-Becerra et al. (2011)
Peppermint	*P. fluorescens*, *Bacillus subtilis*, *Azospirillum brasilense*	Petri dish assay	VOCs production	Production of essential oil (Eos) was increased twofold in *P. fluorescens-treated* plants compared to control	Santoro et al. (2011)

Pearl millet	*Pseudomonas*, *Citrobacter*, *Acinetobacter*, *Serratia*, *Enterobacter* spp.	Pot trial	P-solubilization	All the isolates significantly stimulated plant growth, i.e., increases of 45–75, 5–68, and 64–88 % in root, shoot length, and biomass, respectively, compared to control	Misra et al. (2012)
Wheat	*Bacillus* sp. AW1, *Providencia* sp. AW5, *Brevundimonas* sp. AW7	Pot experiment	N_2 fixation, nutrient solubilization	An enhancement of 14–34 % in plant biometric parameters and 28–60 % in micronutrient content was recorded by bacterial consortia compared to control	Rana et al. (2012)
	Pseudomonas, *Bacillus*, *Azospirillum*	Axenic, pot trials	Indole-3-acetic acid production	Maximum increase in spike length (33 %), number of tillers (71 %), and weight of seeds (39 %) was recorded at final harvest in plants inoculated with *Pseudomonas*	Hussain and Husnain (2011)
Cucumber	*Ochrobactrum haematophilum* H10	Pot trial	IAA production, P-solubilization, and ACC-deaminase	Strain H10 increased the growth of cucumber leaf and root length by 27 and 58 %, respectively, compared to control	Zhao et al. (2012)

(continued)

Table 2.1 (continued)

Test crop	Bacteria	Experimental conditions	Proposed mechanism(s)	Specific comments	Reference
Tomato	*Gluconacetobacter diazotrophicus* PAL 5 and UAP 5541	Greenhouse experiment	N_2 fixation	Inoculation of PAL 5 increased total fruit number and weight up to 18 and 14 % in 2nd year compared to control	Luna et al. (2012)
	Bacillus amyloliquefaciens IN937a and *Bacillus pumilus* T4	Greenhouse	N_2 fixation/uptake	PGPR inoculation led to increased nitrogen uptake compared to uninoculated control	Adesemoye et al. (2010)
Canola	*Achromobacter* sp., *Klebsiella* sp., *Pseudomonas* sp., *Klebsiella* sp., *Pantoea* sp., *Chryseobacterium* sp.	Greenhouse trial	IAA production, P- solubilization, and ACC-deaminase	The inoculation of canola with *Chryseobacterium* sp. increased plant dry matter 55 and 127 %, respectively, compared to N +ve and –ve control	Farina et al. (2012)
	Methylobacterium fujisawaense strains CBMB 20, CBMB 10	Gnotobiotic	ACC-deaminase activity	*M. fujisawaense* strains CBMB 20 inoculation increased root length up to 78 % compared to control	Madhaiyan et al. (2008)
Lentil	PGPR strains LCA-1, LCA-2, LCA-3, LCA-4, and LCA-5	Greenhouse experiment	IAA production and P-solubilization	Application of PGPR significantly increased shoot weight and root weight by 63 and 92 %, compared to control. Increases in root length, fresh weight, and dry weight were 74, 54, and 92 %, respectively, as compared to control	Zafar et al. (2012)

Cluster bean	*Bacillus coagulans*	Pot trial	P-solubilization	A significant improvement in plant biomass (25 %), root length (28 %), plant P concentration (22 %), and seed yield (19 %) resulted from inoculation when compared with control	Yadav and Tarafdar (2012)
Mammillaria fraileana	*Azotobacter vinelandii* M2Per, *Pseudomonas putida* M5TSA, *Enterobacter sakazakii* M2PFe	Greenhouse trial	Nutrient mobilization	Promotion of plant growth, manifested as an increase in dry weight, was greater in cacti inoculated with *Enterobacter sakazakii* M2PFe compared to control	Lopez et al. (2012)
Strawberry	*Paenibacillus polymyxa* RC05, *Bacillus* spp. RC23	Field trial	IAA production	Root inoculation increased yield, average fruit weight, and quality fruit ratio up to 21, 19, and 32 %, respectively, compared to control	Erturk et al. (2012)
Neem plant	*Streptomyces* strains AzR-010, 049, 051	Controlled	Indole-3-acetic acid	Bacterization improved germination %, root and shoot length by 39, 30, and 31 %, respectively, compared to control	Verma et al. (2011)
Black pepper	*Bacillus tequilensis* NII-0943	Pot trial	IAA production, P- solubilization, and ACC-deaminase	Black pepper cuttings showed 77 and 112.5 % more root and shoot length, respectively, compared to control	Dastager et al. (2011)

(continued)

Table 2.1 (continued)

Test crop	Bacteria	Experimental conditions	Proposed mechanism(s)	Specific comments	Reference
Sugar beet	*Acinetobacter johnsonii* strain 3-1	Pot trial	IAA production and P-solubilization	Inoculation increased plant dry weight and yield of beet by 69 and 37 %, respectively, compared with controls	Shi et al. (2011)
Muskmelon	*B. subtilis* Y-IVI	Pot trial	IAA production, siderophore production	The inoculation of *B. subtilis* significantly increased the shoot dry weight and length by 100 and 34 %, respectively, over control	Zhao et al. (2011)
Walnut	*Pseudomonas chlororaphis* W24, *P. fluorescens* W12, *B. cereus* W9	Pot trial	P-solubilization	Application of W24 or W12 remarkably improved plant height, shoot and root dry weight, and P and N uptake of walnut seedlings compared to control	Yu et al. (2011)
Groundnut	*Pseudomonas* spp. strains PGPR1, PGPR2, PGPR4, PGPR7	Axenic/pot/field trials	ACC-deaminase	Seed inoculation with PGPR containing ACC-deaminase significantly enhanced pod yield, haulm yield, and nodule dry weight (23–26, 24–28, and 18–24 %, respectively) over the control under field conditions	Dey et al. (2004)
Tobacco	*Pantoea agglomerans* strain PVM	Axenic trial	Indole-3-acetic acid production	In vitro root induction in *Nicotiana tobacum* was observed by inoculation over control	Apine and Jadhav (2011)

Rice	*Enterobacter cloacae* GS1	Hydroponics trial	IAA production and P-solubilization	Bacterization significantly improved the fresh weight, root length, shoot length, and nitrogen content as compared to control	Shankar et al. (2011)
	Pseudomonas sp. PAC, *Serratia* sp. CMR165, *A. brasilense* FT326	Glass tube assay	P-solubilization	Inoculation with PAC increased plant height and shoot P content compared to control	Nico et al. (2012)
	Bacillus sp. SVPR30, *P. polymyxa* ATCC 10343	Greenhouse	Indole-3-acetic acid production	*Inoculation with Bacillus* sp. SVPR30 produced 39 % increase in plant dry biomass compared to control	Beneduzia et al. (2008)
Maize	*Acinetobacter* CR 1.8, *Klebsiella* SN 1.1	Pot trials	IAA production and P-solubilization	The inoculation of maize seeds with the *Klebsiella* SN 1.1 showed nonsignificant response compared to control	Chaiharn and Lumyong (2011)
	Acinetobacter rhizosphaerae strain BIHB 723	Pot trial	P-solubilization	Inoculation increased shoot height, shoot biomass, and P uptake by 19, 32, and 83 %, respectively, compared to control	Gulati et al. (2010)
Banana	*A. brasilense* Sp7, *Bacillus sphaericus* UPMB10	Hydroponics	N_2 fixation/uptake	The PGPR inoculation increased the bunch yield up to 51 % compared to control	Mia et al. (2010b)

(continued)

Table 2.1 (continued)

Test crop	Bacteria	Experimental conditions	Proposed mechanism(s)	Specific comments	Reference
Sorghum	*A. brasilense* SM	Axenic	Indole-3-acetic acid production	Seed bacterization with *A. brasilense* improved shoot length and seedling dry weight up to 28 and 62 %, respectively, compared to control	Malhotra and Srivastava (2009)
Mung bean	*Acinetobacter* CR 1.8, *Klebsiella* SN 1.1	Pot trials	IAA production and P-solubilization	The inoculation of bean seeds with the *Klebsiella* SN 1.1 significantly increased the adventitious root length (7.6–7.8 cm^3) over control	Chaiharn and Lumyong (2011)
	Pseudomonas, *Escherichia*, *Micrococcus*, *Staphylococcus* sp.	Axenic conditions	Indole-3-acetic acid production	Bacterization of *V. radiata* seeds significantly enhanced shoot length and biomass up to 48 and 44 %, compared to control	Ali et al. (2010)
Apple	*Bacillus* OSU-142, *Bacillus* M-3, *Burkholderia* OSU-7, *Pseudomonas* BA-8	Field trial	IAA production, cytokinin production	Bacterial inoculation increased average shoot length by 59.2, 18.3, 7.0, and 14.3 % and fruit yield by 116.4, 88.2, 137.5, and 73.7 %, respectively, compared to control	Aslantas et al. (2007)

Considerable work conducted by different researchers shows that PGPR can be used as biofertilizers, and, thus, the use of chemical fertilizer can be reduced (De Freitas et al. 1997; Rabouille et al. 2006). Work of Godinho et al. (2010) showed that application of four PGPR strains having various growth-promoting traits enhanced biomass of eggplant due to balanced nutrient availability and uptake. This growth promotion was also associated with other growth-promoting traits especially indole acetic acid and siderophores. Similarly in a greenhouse study, the application of six bacterial strains on maize plant promoted root and shoot growth and the nutrient status of plant particularly nitrogen and phosphorus (Marques et al. 2010). Such findings have confirmed the perspectives of PGPR as phytostimulators and biofertilizer for agricultural crops. These microbes are also equally effective for promoting growth of fruit trees like apple, apricot, strawberry, plum, and mulberry (Sudhakar et al. 2000; Esitken et al. 2006, 2010; Karakurt and Aslantas 2010; Erturk et al. 2012). Early studies conducted by most of the workers show growth-promoting activity of the PGPR by some common direct and indirect mechanism; however, the production of volatile compound by the bacteria is another growth-promoting mechanism. Zou et al. (2010) found that volatile compounds produced by *Bacillus megaterium* had great growth promotion activity in *A. thaliana*. The fresh weight of inoculated plants was twofold more than uninoculated. They suggested that 2-pentylfuran is a compound that plays an important role in the plant growth promotion activity of this bacterial strain. Prior to this work, Ryu et al. (2003) showed the growth promotion of *A. thaliana* by the volatile compounds 2,3-butanediol and acetoin.

Effectiveness in Stress Agriculture

Environmental stresses are the most limiting factors for crop productivity. Both biotic and abiotic stresses including salinity, drought, extreme temperature, chilling, heavy metals, and insect and pathogen attack are the most detrimental and common stresses plants face in the natural environments. These stresses affect the normal plant processes in one or other way and therefore cause significant reduction in crop yield. PGPR inoculation also proved effective for alleviating the negative impact of these stresses. In addition to improved plant growth under normal conditions, PGPR have great potential for enhancing plant growth under adverse conditions. PGPR use various mechanisms to combat these stresses and enable the plant to maintain their growth under stress environment (Fig. 2.2). There are a number of reports elaborating the effectiveness of PGPR for improving plant growth under stress environment (Glick et al. 2007; Nadeem et al. 2010b; Nabti et al. 2010). The PGPR strains were found equally effective for this growth promotion in variable stress environment like salinity, drought, heavy metal, nutrient stress, and pathogen. Some of the selected examples have been discussed in this section and also listed in Table 2.2.

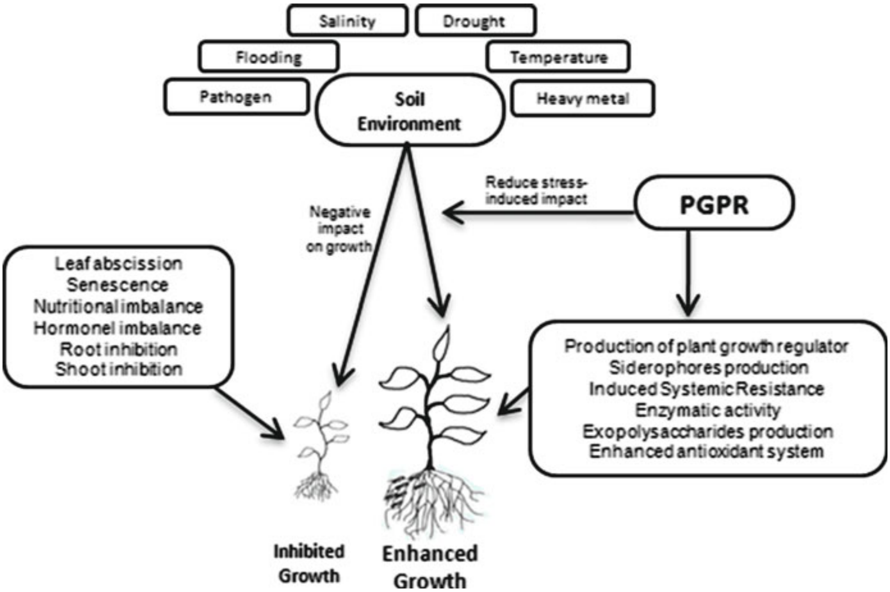

Fig. 2.2 Impact of environmental stresses on plant growth and effectiveness of PGPR for mitigating this negative impact

Abiotic Stress Tolerance

Among various stresses, salinity and drought are the most common that cause adverse effects on crop production in most of the arid and semiarid regions of the world. Salinity limits the production of nearly over 6 % of the world's land and 20 % of the irrigated land (Rhoades et al. 1992; Munns 2005). The changes in environmental scenario result in increasing aridity due to decrease in annual rainfall and because of agriculture under sustained pressure to feed an ever-increasing population. Water limitation in the growing medium reduces diffusion, nutrient uptake by roots, and transport of nutrients from roots to shoots due to restricted transpiration rate, impaired active transport, and altered membrane permeability (Sardans et al. 2008a, b). Similarly, under salinity stress, increasing Na^+ contents cause an increase in Na^+ uptake and, in general, decrease in K^+ and Ca^{2+} contents of plant. Moreover, under stress conditions, plants produce significant quantity of ethylene which can damage them due to negative impact on roots, and it can also cause epinasty, premature senescence, and abscission (Nadeem et al. 2010b). Many efforts have been made to understand the adaptive mechanisms of stress tolerance. These include the reduction of stress ethylene, reduction of toxic ion uptake such as Na^+, and formation of stress-specific protein in plants. Microbial inoculation to alleviate stresses in plants could be a more cost-effective and environment-friendly option which could be available in a shorter time frame.

Table 2.2 Plant growth promotion by PGPR inoculation under biotic and abiotic stress conditions

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
Drought stress/waterlogging				
Ocimum sanctum	*Achromobacter xylosoxidans* Fd2, *Serratia ureilytica* Bac5, *Herbaspirillum seropedicae* Oci9, *Ochrobactrum rhizosphaerae* Oci13	ACC-deaminase activity	The Fd2 induced maximum waterlogging tolerance as treated waterlogged plants recorded maximum growth and herb yield (46.5 % higher) and stress ethylene levels (53 % lower ACC) compared to uninoculated waterlogged plants	Barnawal et al. (2012)
Capsicum annuum	*Achromobacter*, *Klebsiella*, *Citrobacter* sp.	ACC-deaminase	Root length and fresh weight in the inoculated plants showed up to 20 and 60 % increase depending on the bacterial strain, compared to the noninoculated stressed control plants	Marasco et al. (2012)
Vigna unguiculata	*Bacillus* sp. RM-2	ACC-deaminase, IAA production, P-solubilization	Seeds coated with RM-2 showed a significant increase in seed germination, shoot length and biomass, and pod yield over control	Minaxi et al. (2012)
Triticum aestivum	*Streptomyces coelicolor* DE07, *S. olivaceus* DE10, *S. geysiriensis* DE27	Production of phytohormones	The DE10 culture treatment improved seedling vigor and yield (up to 88 %), compared to control	Yandigeri et al. (2012)
Helianthus annuus	*Azospirillum lipoferum* 21, *Azospirillum brasilense* OF, *Azotobacter chroccoccum* 5	Not described	Inoculation increased grain yield up to 24, 29, and 27 %, respectively, under normal H_2O, mild, and severe stress	Jalilian et al. (2012)
	Pseudomonas sp. strain GAP-P45	Exopolysaccharide production	An increase in total dry biomass by 64.6 and 23 % due to strain GAP-P45 inoculation was observed under drought stress and no stress conditions, respectively	Sandhya et al. (2009)

(continued)

Table 2.2 (continued)

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
Vigna radiata	*P. fluorescens* Pf1, *B. subtilis* strains EPB5, EPB 22, EPB 31	Catalase/peroxidase enzyme	The greater activity of catalase and peroxidase was observed in green gram plants bacterized with *P. fluorescens* against water stress compared to untreated plants	Saravanakumar et al. (2012)
Cicer arietinum	*Paenibacillus lentimorbus* B-30488	Biofilm formation	The chickpea seed bacterization with B-30488 along with sodium alginate and $CaCl_2$ caused an increase of 30, 9, and 20 %, in shoot length, 100-seed weight, and plant dry weight, respectively, as compared to control	Khan et al. (2011)
Ornamental species	*Variovorax paradoxus* 5C-2	ACC-deaminase activity	Inoculation of growth media with *V. paradoxus* lowered ethylene emission from mature leaves of *Cytisus praecox* and consequently reduced abscission of the leaves under drought treatment	Sharp et al. (2011)
Saccharum officinarum cv. M 1176/77 and R 570	*Azospirillum* isolates, Azo 195, Azo 249, Azo 274	Auxin production	Inoculation increased shoot height and root dry mass by 15 and 75 % in cv. M 1176/77 when subjected to drought stress, whereas cv. R 570 responded negatively particularly in the absence of drought stress	Moutia et al. (2010)
Zea mays L.	*P. entomophila* BV-P13, *P. stutzeri* GRFHAP-P14, *P. putida* GAP-P45, *P. syringae* GRFHYTP52, *P. monteilli* WAPP53	Not described	Seed bacterization with *Pseudomonas* spp. strains improved plant biomass, proline, sugars, and free amino acids under drought stress. However, protein and starch content was reduced under drought stress conditions	Sandhya et al. (2010)
Trifolium repens	*Pseudomonas* sp., *P. putida*, *B. megaterium*	Indole-3-acetic acid production	Inoculation increased shoot and root biomass and water content under drought conditions	Marulanda et al. (2009)

Pisum sativum	*P. fluorescens* biotype G (ACC-5), *P. fluorescens* (ACC-14), *P. putida biotype* A (Q-7)	ACC-deaminase activity	Bacterization of ACC5 increased dry weight, root length, shoot length, number of leaves per plant, and water use efficiency on fresh and dry weight basis by 150, 92, 45, 140, 46, and 147 %, respectively, compared to respective controls	Zahir et al. (2008)
Catharanthus roseus	*P. fluorescens*	IAA/gibberellin production	*P. fluorescens* enhanced the growth parameters and partially ameliorated the drought-induced growth inhibition by increasing the fresh and dry weights significantly	Abdul Jaleel et al. (2007)
Salinity stress				
C. roseus	*A. xylosoxidans* strains AUM54, AUENR9, AUENRL3, AUENRL7	ACC-deaminase activity	*A. xylosoxidans* AUM54 inoculated plants increased germination % age (7 %), vigor index (48 %), plant height (14 %), root dry weight (13 %), and ajmalicine content (30 %) compared to uninoculated plants grown without NaCl	Karthikeyan et al. (2012)
Lactuca sativa L.	*A. brasilense* Sp245	Hormone (IAA) production	Inoculation increased leaf area, chlorophyll content, and dry weight up to 63, 24, and 102 %, respectively, at higher salinity. At 40 mol m^{--3}NaCl, 60 % and 73 % of plants remained alive in noninoculated and *Azospirillum*-inoculated plants, respectively	Fasciglione et al. (2012)
Oryza sativa L./*Abelmoschus esculentus* L.	*Agrobacterium* sp. SUND BDU1, *Bacillus* sp. strains SUND LM2, Can4, Can6	N_2 fixation, IAA production	The *Bacillus* sp. Can6 inoculation increased yield and N uptake by 7, 16, and 35, 42 % of rice and okra, respectively, compared to control	Barua et al. (2012)

(continued)

Table 2.2 (continued)

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
O. sativa L.	*A. brasilense* Az39	Cadaverine production	*A. brasilense* Az39 produced cadaverine in chemically defined medium and inoculated plants; this capacity correlated with root growth promotion or osmotic stress mitigation in hydroponics conditions	Cassan et al. (2009)
Gossypium hirsutum L.	*Raoultella planticola* Rs-2	ACC-deaminase activity, IAA production	Inoculation of Rs-2 increased germination % age, plant height, and dry biomass by 30, 15, and 33 %, respectively, compared to control	Wu et al. (2012)
	P. putida Rs-198	IAA production	The inoculation of Rs-198 increased the germination rate, plant height, and dry weight by 24, 13, and 10 %, respectively, as compared to control	Yao et al. (2010)
Z. mays L.	*Azotobacter* sp. C5, C7, C8, and C9	N_2 fixation, IAA production	*Azotobacter* sp. C9 increased shoot biomass and polyphenol content up to 122 and 27 %, respectively, at highest salinity level compared to respective control	Rojas-Tapias et al. (2012)
	Bacillus megaterium	Regulation of aquaporins	Inoculated plants showed higher root hydraulic conductance values; correlated with higher plasma membrane type two (PIP2) aquaporin amount in their roots under stressed conditions	Marulanda et al. (2010)

T. aestivum	*Streptomyces* isolates C	IAA production, siderophores	Inoculation increased germination % age and biomass up to 33 % compared to respective NaCl stressed control	Sadeghi et al. (2012)
	Bacillus sp. (SKU-13), *Paenibacillus* sp. (SKU11)	Exopolysaccharide production	Under saline condition, inoculation with SKU13 resulted in an increase of shoot weight by 34 % compared to stressed control	Upadhyay et al. (2011b)
	B. pumilus, *Pseudomonas mendocina*, *Arthrobacter* sp., *Halomonas* sp., *Nitrinicola lacisaponensis*	IAA production, siderophores, P-solubilization	Maximum shoot and root length (33.8 and 13.6 cm) and shoot and root biomass (2.73 and 4.48 g dry weight) were recorded in plants inoculated with *B. pumilus* compared to control	Tiwari et al. (2010)
	P. putida (N21), *P. aeruginosa* (N39), *Serratia proteamaculans* (M35)	ACC-deaminase activity	Inoculation increased the plant height, root length, grain yield, 100-grain weight, and straw yield up to 52, 60, 76, 19, and 67 %, respectively, over uninoculated control at 15 dS m^{-1}	Zahir et al. (2009)
Lycopersicon esculentum/*Cucumis sativus*	*P. chlororaphis* isolate TSAU13	Not described	The bacterial strain stimulated shoot growth (up to 32 %), dry matter (up to 43 %), and the fruit yield of tomato and cucumber (up to 16 %) compared to the uninoculated control plants under saline conditions	Egamberdieva (2012)
L. esculentum	*B. subtilis* FZB24 and FZB41	Peptides, auxin production	The application of *Bacillus* sp. metabolites increased root length and plant dry mass up to 23 and 36 %, respectively, compared to stressed control	Stavropoulou (2011)
	P. fluorescens NT1, *P. aeruginosa* T15, *P. stutzeri* C4	ACC-deaminase, siderophores	Inoculation with C4 strain increased plant height and biomass up to 25 % compared to control under stressed condition	Tank and Saraf (2010)

(continued)

Table 2.2 (continued)

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
H. annuus	*P. fluorescens* biotype F and *P. fluorescens* CECT 378^{T}	IAA production, siderophores	The isolate CECT 378T produced 66 % increment in leaves, 34 % in stems, and 16 % in roots, while the effect of isolate inoculation was (only) more evident in leaves and stems with 30 and 26 %, respectively	Shilev et al. (2012)
C. arietinum	*P. putida* MSC1, *P. pseudoalcaligenes* MSC4	IAA production, siderophores, P-solubilization	Plants inoculated with MSC1 or MSC4 isolates showed an increase in the parameters that evaluate plant growth when compared to uninoculated controls	Patel et al. (2012)
C. annuum L.	*Brevibacterium iodinum* RS656, *Bacillus licheniformis* RS111, *Zhihengliuela alba* RS16	ACC-deaminase activity	Inoculation of *B. licheniformis* RS656, *Z. alba* RS111, and *Br. iodinum* RS16 reduced ethylene production by 44, 53, and 57 %, respectively	Siddikee et al. (2011)
Temperature stress (heat and cold stress)				
Vitis vinifera L.	*Burkholderia phytofirmans* strain PsJN	Colonization/ metabolite production	The endophytic colonization of PsJN improved plant photosynthetic parameters and regulated carbohydrate metabolism compared to control	Fernandez et al. (2012a)
	B. phytofirmans strain PsJN	Metabolite production	At 4 °C, both stress-related gene transcripts and metabolite levels increased earlier and faster and reached higher levels in PsJN-bacterized plantlets than in nonbacterized counterparts	Theocharis et al. (2012)
	B. phytofirmans strain PsJN	Trehalose and trehalose 6-phosphate	Plants colonized by *B. phytofirmans* and cultivated at 26 °C accumulated T6P and trehalose in stems and leaves at concentrations similar to nonbacterized plants exposed to chilling temperatures	Fernandez et al. (2012b)

T. aestivum L.	*Pseudomonas* sp.	IAA production, siderophores, P-solubilization	Bacterization significantly improved the root/shoot length, biomass, and the level of cellular metabolites compared to control	Mishra et al. (2011)
	Pseudomonas lurida strain M2RH3	IAA production, siderophores, P-solubilization	Seed bacterization with the isolate positively influenced the growth and nutrient uptake parameters of wheat seedlings cv. VL 804 at controlled cold growing temperature	Selvakumar et al. (2011)
	Exiguobacterium acetylicum strain 1P (MTCC 8707)	IAA production, siderophores, P-solubilization	Seed bacterization with the isolate positively influenced the growth and nutrient uptake parameters of wheat seedlings at suboptimal cold growing temperatures	Selvakumar et al. (2010)
Sorghum bicolor L.	*Pseudomonas* sp. strain AKM-P6	IAA production, P-solubilization	Inoculation induced the biosynthesis of high-molecular-weight proteins in leaves under elevated temperature, reduced membrane injury, and improved the levels of cellular metabolites	Ali et al. (2009)
Cucurbita pepo	*S. marcescens* strain SRM (MTCC 8708)	IAA production, siderophores, P-solubilization	Seed bacterization with the isolate significantly enhanced plant biomass and nutrient uptake of wheat seedlings grown in cold temperatures	Selvakumar et al. (2007)

(continued)

Table 2.2 (continued)

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
Heavy metal stress				
Z. mays/*H. annuus*	*Pseudomonas* sp. DGS6	ACC-deaminase, IAA production/ phytoextraction	Inoculation with DGS6 increased the root–shoot dry weight of maize by 85, 49 % and sunflower by 45, 34 %, respectively, in Cu contamination	Yang et al. (2013)
	Pseudomonas strains 3–3.5-1, TLC 6–6.5-1, TLC 6–6.5	IAA production, P-solubilization/ metal solubilization	*Pseudomonas* sp. TLC 6–6.5-4 resulted in a significant increase in copper accumulation in maize and sunflower, and an increase in the total biomass of maize	Li and Ramakrishna (2011)
Solanum nigrum L.	*Serratia nematodiphila* LRE07	Endophytic coloniza-tion/ phytoimmobiliza-tion	The inoculation of bacterium alleviated the Cd-induced changes, resulting in more biomass production and higher photosynthetic pigments content of leaves compared with nonsymbiotic ones	Wan et al. (2012)
T. aestivum L.	*Staphylococcus arlettae* Strain Cr11	ACC-deaminase, IAA production/ phytoextraction	Bacterial inoculation in controlled Petri dish and soil environments showed significant increase in percent germination, root and shoot length, as well as dry and wet weight in Cr(VI)-treated and Cr(VI)-untreated samples	Sagar et al. (2012)
S. bicolor L.	*Bacillus* sp. SLS18	IAA production, ACC-deaminase, siderophores/ phytoextraction	Inoculation increased the dry weights of aerial part and root for sweet sorghum by 45.5, 81 % and 38.0, 80.3 % in Mn/ Cd-contaminated soil compared to noninoculated control, respectively	Luo et al. (2012)

Pteris vittata L.	*Rhodococcus* sp.TS1, *Delftia* sp.TS33, *Comamonas* sp.TS37, *Delftia* sp.TS41, *Streptomyces lividans* sp. PSQ22	Phytoaccumulation	Inoculation increased plant biomass by 53 % and As uptake by 44 % over control. Leaching was reduced by 29–71 % depending on the As-reducing bacterium	Yang et al. (2012)
Brassica napus	*Ralstonia* sp. J1-22-2, *P. agglomerans* Jp3-3, *Pseudomonas thivervalensis* Y1-3-9	ACC-deaminase activity/ phytoaccumulation	The aboveground tissue Cu contents of rape cultivated in 2.5 and 5 mg kg^{-1} of Cu-contaminated substrates varied from 9 to 31 % and from three- to four-fold, respectively, in inoculated rape plants compared to the uninoculated control	Zhang et al. (2011)
Brassica juncea	*A. xylosoxidans*Ax10	ACC-deaminase, IAA production/ phytoextraction	Inoculation of *A. xylosoxidans* Ax10 increased the root length, shoot length, fresh weight, and dry weight of *B. juncea* plants compared to the control	Ma et al. (2009)
Eucalyptus camaldulensis	*Microbacterium paraoxydans* BN-2, *Ochrobactrum intermedium* BN-3, *Bacillus fusiformis* BN-4	Fatty acid/ phytoextraction	Inoculation of *O. intermedium* BN-3 significantly increased the biomass and Pb accumulation by *E. camaldulensis* compared to the uninoculated control	Waranusantigul et al. (2011)
Sedum alfredii	*Burkholderia* sp.D54	IAA production, ACC-deaminase, siderophores/ phytoextraction	Bacterial inoculation significantly enhanced *S. alfredii* biomass production and increased both shoot and root Cd concentration, compared to control	Guo et al. (2011)
Pathogen stress				
A. thaliana	*P. fluorescens* strains Pf-5, Q2-87, Q8r1-96, HT5-1	ISR/2,4-diacetylphloroglucinol	Root colonization by 2,4-DAPG-producing *P. fluorescence* induced systemic resistance (ISR) against bacterial speck caused by *P. syringae* pv. tomato	Weller et al. (2012)

(continued)

Table 2.2 (continued)

Test crop	Beneficial bacteria	Proposed mechanism(s)	Plant response	Reference
Camellia sinensis	*Ochrobactrum anthropi* BMO-111	Antifungal metabolites	Foliar application of 36-h-old culture of BMO-111 significantly reduced the blister blight disease incidence compared to control	Sowndhararajan et al. (2012)
N. tobacum L.	*P. polymyxa* strain C5	Biofilm formation	In comparison with the control, the disease incidence was significantly reduced by 50 % with the application of *P. polymyxa* C5	Ren et al. (2012)
L. esculentum	*Bacillus amyloliquefacien* CM-2, T-5	IAA production, siderophore production	Both CM-2 and T-5 strains showed strong biocontrol and growth promotion effects on tomato seedlings. In comparison to the control, the disease incidence was reduced by 70 and 79 % for CM-2 and T-5, respectively	Tan et al. (2013)
	Pseudomonas strain, PCI2	Fungal cell wall-degrading enzymes (Protease)	In *Sclerotium rolfsii*, infested mixture, inoculation of tomato seeds with strain PCI2 improved seedling stand by 29 % and increased shoot and root dry weight of plants over the untreated pathogen controls	Pastor et al. (2012)
	B. cereus AR156	Induced systemic resistance (ISR)/ colonization	The AR156 inoculation elicited induced systemic resistance against *P. syringae*, reduced bacterial speck disease severity 1.6-fold. The tomato biomass increased up to 48 % by AR156 application over control	Niu et al. (2012)
G. hirsutum L.	*Streptomyces cyaneofuscatus* ZY-153, *S. kanamyceticus* B-49, *S. rochei*X-4, *S. flavotricini* Z-13	Production of fungal cell wall-degrading enzymes	The biocontrol efficacy of the four isolates against *Verticillium* wilt of cotton ranged from 18.7 to 65.8 % compared to uninoculated control	Xue et al. (2013)

Solanum tuberosum	*B. amyloliquefaciens* BAC03	Production of antimicrobial metabolites	The BAC03 applied in potting mix significantly reduced potato common scab severity and potentially increased the growth of potato plants compared to control	Meng et al. (2012)
C. sativus	*P. aeruginosa* PW09	Induced systemic resistance (ISR)/colonization	The PW09 inoculation reduced seedling mortality by 60 % and increased biomass accumulation by 7 % under *Sclerotium rolfsii* stress	Pandey et al. (2012)
Pennisetum glaucum	*P. fluorescens* UOM ISR 17, *P. fluorescens*, UOM ISR 20, *P. fluorescens* UOM ISR 23, *Acetobacter* UOM Ab 9, *Acetobacter* UOM Ab 11, *Azospirillum* UOM Az 3	Induced systemic resistance (ISR)	*Pseudomonas* spp. UOM ISR 17 inoculation improved plant height, dry mass, leaf area, and plant protection of 44, 42, 47, and 73 %, respectively, against downy mildew disease stress compared to control	Jogaiah et al. (2010)
Citrullus lanatus	*P. aeruginosa* 231-1	Antibiosis and induced systemic resistance (ISR)	*P. aeruginosa* 231–1 treatment inhibited pathogen penetration and significantly reduced disease infection in plants against *Didymella bryoniae*	Nga et al. (2010)

Stress environment can also make physicochemical and biological properties of soil unsuitable for microbial and plant growth. However, particular characteristics of certain bacteria enable them to survive under such harsh environments. For example, certain bacterial strains have the ability to tolerate high salinity, and, similarly, the production of exopolysaccharides by the bacteria protects them from water stress. Besides developing mechanisms for stress tolerance, microorganisms can also impart some degree of tolerance to plants toward abiotic stresses like drought, salinity, metal toxicity, and high temperature (Grover et al. 2011). The exopolysaccharides released into soil can be adsorbed by clay particles and form a protective layer around soil aggregates (Tisdall and Oades 1982) and, therefore, protect the plant from desiccation. Moreover, exopolysaccharide production increases root colonization of microbes (Santaella et al. 2008), improves soil aggregation (Sandhya et al. 2009), channelizes water and nutrients to plant roots (Tisdall and Oades 1982; Roberson and Firestone 1992), and forms biofilm (Seneviratne et al. 2011) which is beneficial to plant growth and development. Alami et al. (2000) observed a significant increase in root-adhering soil per root tissue (RAS/RT) ratio in sunflower rhizosphere inoculated with the EPS-producing rhizobial strain YAS34 under drought conditions. The inoculation with ACC (1-aminocyclopropane-1-1carboxylic acid)-deaminase-containing bacteria can reduce negative impact of stress-induced ethylene (Mayak et al. 2004a, b). The elevated level of ethylene caused negative impact on plant growth by inhibiting the root growth particularly. These microorganisms secrete enzyme ACC-deaminase that hydrolyses ACC into ammonia and a-ketobutyrate. The rhizobacteria bound to plant roots act as sink for ACC (immediate precursor of ethylene) and thereby lower the level of ethylene in a developing seedling or stressed plant. Therefore, the inoculation of seeds with such strains containing ACC-deaminase would be very useful for enhancing plant growth under stress conditions by diluting the negative impact of stress-induced ethylene on root growth (Glick et al. 2007). As is evident from one of our greenhouse study conducted under salinity-stressed conditions, that application of PGPR strains having ACC-deaminase activity significantly enhanced the root length of maize compared to uninoculated control (Fig. 2.3). The work of Mayak et al. (2004a) shows that bacterial strain (*Achromobacter piechaudii*) containing ACC-deaminase conferred tolerance to water deficit in tomato and pepper. Ethylene production was reduced in inoculated plants, resulting in significant increase in fresh and dry weights compared to uninoculated controls. *Pseudomonas* spp. also improved the growth of pea (*Pisum sativum*) under drought stress in axenic conditions as well as in potted soil (Zahir et al. 2008). They concluded that inoculation might have reduced the ethylene synthesis, which resulted in better plant growth under drought stress. Similar results were also obtained by Arshad et al. (2008) while studying the effectiveness of *Pseudomonas* spp. for eliminating the drought effect on growth, yield, and ripening of pea. It has been observed that the presence of elevated levels of ethylene in the vicinity inhibits the nitrogen fixation by rhizobia. However, the co-inoculation of *Rhizobium* with PGPR having ACC-deaminase activity can minimize this negative impact of ethylene and enhance nodulation

Fig. 2.3 Effect of PGPR containing ACC-deaminase on root growth of maize in a pot trial at 12 dS m^{-1} salinity level

(Ahmad et al. 2011). Stimulation of root elongation and biomass production of different plant species by inoculation with PGPR having ACC-deaminase activity has been repeatedly documented, particularly when the plants were subjected to stressful growth conditions (Nadeem et al. 2007, 2010a; Saravanakumar and Samiyappan 2007; Tank and Saraf 2010; Siddikee et al. 2012). Similarly, the presence of other growth-promoting characteristics like indole acetic acid (IAA), siderophore production, phosphate solubilization, and phytohormone production may provide extra benefits for stress tolerance in plants and improve their growth. The production of antioxidant enzymes protects the plant from the harmful impact of reactive oxygen species. The reactive oxygen species (ROS) as singlet oxygen (O^-), hydrogen peroxide (H_2O_2), and hydroxide ions (OH^-) are developed in the photosystem of plants. These ROS denature cell membranes, proteins, and DNA through oxidation reaction. To combat/reduce the impact of these ROS, plant's immune system generates antioxidant enzymes such as superoxide dismutase, peroxide dismutase, catalase, and glutathione reductase (Arora et al. 2002). The PGPR inoculation also enhances the activity of these enzymes and helps them to reduce the negative impact of stress (Fu et al. 2010). Similarly, enhanced production of osmoprotectants by bacterial inoculation under stress enables the plant to maintain their internal water potential for better uptake of water and nutrients.

Rhizobacteria as Biocontrol Agent

In soil environment, there are a number of plant pathogens that reduce crop yield. Although these plant pathogens can be controlled by the application of chemicals and growing disease-resistant varieties, however, there are certain environmental concerns about the use of such chemicals like their persistent nature in the soil as well as accumulation of toxic residues of these chemicals in the food parts. Some of these toxic chemicals have been banned due to their persistent nature. Similarly in certain cases, the resistance of genetically resistant crops is often broken by the pathogen that results in reduction in crop yield (Fry 2008). An alternative strategy to overcome this problem is the use of PGPR that act as biocontrol agent by virtue of their certain biocontrol mechanisms like production of antibiotics, production of antifungal metabolites, decreasing availability of iron for pathogenic organisms, production of fungal cell wall-degrading enzymes, and through induced systemic resistance. Number of reports have shown the effectiveness of PGPR for enhancing plant growth by protecting them from pathogens (Siddiqui et al. 2005; Ayyadurai et al. 2007; Ravindra Naik et al. 2008; Srinivasan and Mathivanan 2009). PGPR have competitive advantage over fungi for iron uptake due to production of siderophores. These siderophores have very high affinity for iron, and bacteria can take up iron–siderophore complex. By using this mechanism, PGPR retard the pathogen growth by reducing the availability of iron and therefore providing protection to the plant against diseases (Penyalver et al. 2001).

The above-discussed review and number of examples mentioned in Tables 2.1 and 2.2 show the effectiveness of PGPR for enhancing plant growth and development under normal as well as stress environment. Such growth promotion was due to certain direct and indirect mechanisms used by PGPR. It was also evident from discussion that inoculation of plant seed or seedlings with most promising strains having best growth-promoting traits not only enables the plant to maintain their proper growth but also causes positive impact on soil health.

Role of Bacterial Consortium in Advance Agriculture: Effectiveness and Challenges

Although above-discussed review highlights the effectiveness of rhizobacteria for enhancing plant growth under stress environment, however, under certain cases, the results obtained in the laboratory could not be reproduced in the field (Zhender et al. 1999; Smyth et al. 2011). This might be due to the low quality of the inocula and/or the inability of the bacteria to compete with the indigenous population under adverse environmental conditions (Brockwell and Bottomley 1995; Catroux et al. 2001). Great variations in the plant response to PGPR in laboratory and field assays demonstrate that the full potential of rhizobacteria to promote plant growth should be more extensively investigated. It is necessary to develop efficient inocula that can perform better under field conditions (Ahmad et al. 2008). The application of multistrain

PGPR in combination could be more beneficial than a single strain. It has been reported that co-inoculation and coculture of microbes have better ability to fulfill the task in an efficient way than single-strain inoculation (Guetsky et al. 2002). Each strain in the multistrain consortium can compete effectively with the indigenous rhizosphere population and also enhance plant growth with its partners (Shenoy and Kalagudi 2003). The two strains used in a consortium showed that each strain not only competed successfully for rhizospheric establishment but also promoted plant growth (Shenoy and Kalagudi 2003). The co-inoculation of *Rhizobium* with PGPR proved useful for promoting growth and increasing nodulation (Tilak et al. 2006). The use of multistrain inoculants could be a good strategy that enables organisms to successfully survive and maintain themselves in communities (Andrews et al. 1991). Van Veen and others (1997) critically reviewed the reasons for the poor performance of agricultural bioinocula in natural environments and in the rhizosphere of host plants and suggested that instead of using a single strain for a single trait, multiple microbial consortia could be used for multiple benefits. Microbial studies performed without plants indicated that some combinations allow the bacteria to interact with each other synergistically, provide nutrients, remove inhibitory products, and stimulate growth of each other through physical and biochemical activities that may have beneficial impacts on their physiology (Bashan 1998). Rajasekar and Elango (2011) studied the effectiveness of *Azospirillum*, *Azotobacter*, *Pseudomonas*, and *Bacillus* sp. separately and in combination on *Withania somnifera* for two consecutive years. They observed that PGPR consortia significantly increased plant height, root length, and alkaloid content in *W. somnifera* when compared to the uninoculated control and single inoculation. Similarly, dual inoculation with *Azotobacter* and *Azospirillum* significantly increased total dry weight, leaf area index, and crop growth index (Gholami et al. 2012). Jha and Saraf (2012) observed that growth of Jatropha (*Jatropha curcas*) plant improved maximally in greenhouse and field experiments when three strains were applied together. Co-inoculation provided the largest and most consistent increases in shoot weight, root weight, total biomass, shoot and root length, total chlorophyll, shoot width, and grain yield. Similarly, the consortia of three strains gave the best performance in terms of growth parameters of *Lycopersicum esculentum* (Ibiene et al. 2012). They demonstrated that the use of combined biofertilizers containing consortia of bacteria is an excellent inoculant for growth performance of plants.

As far as growth under stress environment is concerned, Annapurna et al. (2011) studied the effectiveness of PGPR separately and in combination for reducing the impact of salinity on wheat growth. They found that single and dual inoculations of PGPR strains showed variations in their effect to enhance the crop tolerance to salts. The bacterial consortium was more effective for inducing salinity tolerance in wheat plants. They considered it as an acceptable and environment-friendly technology to improve plant performance and development under stress environment. In another study, Upadhyay et al. (2011a) evaluated the growth-enhancing potential of single and dual inoculation of *B. subtilis* SU47 and *Arthrobacter* sp. SU18 on wheat under saline conditions. They observed that in addition to enhancing dry biomass, soluble sugars, and proline content, wheat sodium content was reduced under co-inoculated conditions but not after single inoculation with either strain or in the control. The results indicate that co-inoculation with *B. subtilis* and *Arthrobacter* sp. could alleviate the adverse effects of soil salinity on wheat growth. The bacterial consortium is also effective for protecting the plant from disease under field condition. It is evident from the work of Srinivasan and Mathivanan (2009) that effective control of necrosis virus in sunflower can be obtained by the application of powder and liquid formulations of PGPR consortia. They applied two bacterial consortia consisting of *Pseudomonas*, *Bacillus*, and *Streptomyces* spp. along with farmer's practice, i.e., imidacloprid + mancozeb. They observed a significant reduction in disease with an increase in seed germination, plant height, and crop yield. They demonstrated that PGPR consortia show high benefit–cost ratio compared to farmer's practice and untreated control.

Inoculant Technology: Formulation and Commercialization

The application of PGPR for improving crop production is becoming an emerging technology owing to their environmental friendly traits. For that purpose various microbial inoculants have been formulated and are being marketed. A number of strains having ability to protect plant from pathogens belonging to genera *Bacillus*, *Pseudomonas*, and *Agrobacterium* are being used as biopesticides (Fravel 2005).

Formulation of Microbial Inoculants

A number of PGPR strains have great potential to be formulated as biofertilizer for improving plant growth and development under normal and stress environment. Successful inoculation of PGPR can result in better plant growth and therefore higher economic return to the farmers. For effective transfer of research findings from laboratory to field, an excellent formulation technology has great advantages. Various microbial inoculants have been formulated, marketed, and applied successfully (Reed and Glick 2004). Commercial bioinoculants prepared from *Bacillus* spp. are used widely as biocontrol agents (Ongena and Jacques 2007). *B. thuringiensis*, which is used to control insect pest, is estimated having sale of >70 % (Ongena and Jacques 2007; Sanchis and Bourguet 2008). *Pseudomonas putida*, *Paenibacillus*, and *Bacillus* sp. are formulated and have successfully enhanced the growth and yield of wheat (Cakmakci et al. 2007). Similarly, field application of salt-tolerant bioformulation of certain bacteria enhanced plant growth under salinity stress (Paul et al. 2006).

The major bottleneck to the commercial use of PGPR as biofertilizers is their inconsistent performance in the field. In certain cases, plant growth promotion due to microbial inoculation is not so effective in terms of investment applied and net return when compared with chemical fertilizers (Lucy et al. 2004). The development of valuable formulation is a challenging task for improving the efficacy of microbial inoculants. Actually, formulation is one of the crucial steps that determines the success or failure of a PGPR strain. However, this important step is generally neglected which results in less efficient outcome. The reason of this failure is the preparation of microbial formulation under lack of quality control and proper guidelines (Paau 1988; Berg 2009). The active ingredient in a microbial formulation is its viable culture. Regardless of the organism used, the success of bioagent depends upon the preparation of such inoculum having high level of viability and vigor (Jones and Burges 1998). In microbial formulation, the maintenance of bacterium in metabolically and physiologically active state is an important aspect for gaining maximum advantage (Paau 1998). In certain environmental conditions, where single-strain inoculum is unable to perform better, the development of multi-strain inoculum can be very effective (Domenech et al. 2006). Such multistrain inoculum would be more effective for enhancing plant growth and development due to the presence of more growth-promoting traits which might not be possible in single strain.

Another important aspect regarding formulation is carrier material, which plays active role in shelf life of formulation. It aids in the stabilization and protection of the microbial cells during storage and transport (Xavier et al. 2004). It also protects the active ingredient, i.e., microbe from environmental conditions, and enhances its activity in field (Deaker et al. 2004). Various organic and inorganic carrier materials are used for formulation development (Bashan and Levanony 1990; Bashan 1998). Organic carriers like peat have some advantages due to their higher nutrient content, and, however, complete sterilization by steam is difficult, and also during sterilization, toxic by-products are produced that may cause decrease in bacterial population (Weiss et al. 1987). Therefore, the use of inorganic carrier may be a good strategy for enhancing the effectiveness of the microbial formulation. However, the effectiveness of these inorganic carrier materials may also be different, as it is evident from the work of Saharan et al. (2010) who used talc and aluminum silicate powders to develop inorganic carrier-based formulation. They observed that the shelf life of talc powder-based formulation was higher compared to aluminum silicate-based formulation. It was also observed that both sterile and nonsterile carrier formulations significantly enhanced the growth of *Vigna mungo* and *Triticum aestivum*. The application of microbial inoculants in the form of granular or liquid form is also attaining much attention nowadays. For optimizing nodulation, granular inoculants particularly rhizobia can be placed below or at the side of seeds with appropriate equipment according to seeding depth and moisture availability (Stephens and Rask 2000). On the other hand, due to easy application of liquid inoculants, liquid formulation has also achieved much popularity (Xavier et al. 2004). However, both types of formulations have shown their effectiveness for enhancing the biomass yield of soybean (Atieno et al. 2012). They have also demonstrated that formulation of rhizobia and PGPR gave better response.

Bacterial Characters for Formulation Development

Although a good number of microbial strains are used for formulation development and also their performance is observed, however, there are various constraints for commercialization of microbial inocula. One of the challenges for developing PGPR inoculants on commercial basis is the selection of such strains which could have competitive advantage over indigenous population and also have the ability to maintain their growth under unfavorable environment. The most important aspect in this regard is the selection of such strains which have host plant specificity as well as adaptation to soil and climatic conditions (Bowen and Rovira 1999). An organism with properties like phosphate solubilization, phytohormone production, root colonization, siderophore, and indole acetic acid production is thought to be an ideal bioinoculant.

To develop a successful PGPR formulation, in addition to above-mentioned growth-promoting traits, bacteria should have the ability to tolerate harsh environmental conditions like drought, heat, salinity, and toxic metals. It should have high rhizosphere competence and compatibility with other rhizobacteria. Such bacteria should also have capability of multiplication and broad spectrum of action. In addition to possessing a number of other characteristics, a PGPR should also have great viability and good shelf life (Lianski 1985). Cost-effectiveness, shelf life, and delivery systems are very important aspects that should be kept in mind while preparing the microbial formulation.

Concluding Remarks and Future Prospects

The above discussion showed the effectiveness of PGPR for enhancing the growth and development of plants. These beneficial effects are obtained owing to a number of direct and indirect mechanisms including phosphate solubilization, production of plant growth regulators, iron sequestration by siderophores, production of antibiotics, synthesis of antifungal metabolites, production of fungal cell wall degrading enzymes, inducing systemic resistance, reducing deleterious effects of stress-induced ethylene by ACC-deaminase activity, and production of vitamins. These plant growth promoting abilities of microbes under normal as well as stress conditions have certified their role in sustainable agriculture. For better performance, the PGPR strain must be rhizosphere competent that should be able to survive and colonize (Cattelan et al. 1999). In addition to rhizosphere competency, the compatibility between the rhizodeposition of compounds by the plant host and the ability of the inoculated bacteria to utilize them are also very important (Strigul and Kravchenko 2006). However, there is still lack of evidence about the consistent performance of these microbes, particularly under field conditions. In certain cases, the results obtained in laboratory are not reproduced in the field (Zhender et al. 1999; Smyth et al. 2011). This may occur due to the low quality of the inoculum and/or the inability of the bacteria to compete with the indigenous population (Brockwell and Bottomley 1995; Catroux et al. 2001). Therefore, the use of such technologies that enhance the agriculture production is indispensable to feed the burgeoning population. The application of multistrain bacterial consortium over single inoculation could be an effective approach for reducing the harmful impact of stress on plant growth. Strains that have the ability to protect the plant from diseases through biocontrol mechanisms may also be included in the formulation. The efficacy of such strains may be enhanced by ACC-deaminase gene (Hao et al. 2007). Therefore, the application of such strains which have multitraits for growth promotion should be preferred for inoculant formulation. It is also necessary to understand the interactions between microbial consortium and plant system. Understanding of such interactions could be very effective for improving plant growth (Raja et al. 2006).

It has been seen that certain growth-promoting traits may interact with each other and have influence on plant growth. For example, in one of our studies (submitted for publication), the strain having high ACC-deaminase activity and low IAA and/or high ACC-deaminase and high IAA performed better compared to a strain having high IAA and low ACC-deaminase. Therefore, such aspects need further research so that most effective strains or combinations of strains can be selected. Other beneficial aspects of bacterial inoculation also need special attention. For example, the addition of ice-nucleating bacteria to agriculture has potential benefits of protecting crops from frosts dropping below freezing, which might contribute to a solution of the worldwide problem of starvation and chronic hunger. Therefore, the application of these bacteria could be an effective technology for enhancing plant growth at low temperature. Similarly, cyanide-producing bacteria can be used effectively for disease suppression. Certain *Pseudomonas* strains produce allelochemicals that can be used as bioherbicides to minimize the use of chemicals and therefore eliminate environmental hazards.

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