Chapter 2
Beneficial Effects of Plant Growth-Promoting Rhizobacteria on Improved Crop Production: Prospects for Developing Economies

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2.1 Introduction

Bacteria that exert beneficial effects on plant development known as plant growth-promoting rhizobacteria (PGPR) have been reported widely. One of the basic requirements for the effectiveness of PGPR is their ability to colonize hosts' rhizosphere, rhizoplane, or the root interior (Glick et al. 2007). Some inoculants enter the root interior to establish endophytic populations with adaptability to the niche and benefits to the host plants (Compant et al. 2005; Kloepper et al. 1999) while some increase root surface area, thus enhancing nutrients uptake, and in turn, induce plant productivity (Adesemoye et al. 2008a, 2009). In a review, Adesemoye and Kloepper (2009) compiled the benefits derivable from plant–PGPR interactions to include the following: improvements in seed germination rate, root development, shoot and root weights, yield, leaf area, chlorophyll content, hydraulic activity, protein content, and nutrient uptake—including phosphorus and nitrogen.

The use of beneficial microbes in agricultural production systems started long time ago, and there is increasing evidence that beneficial microbes can enhance plants' tolerance to adverse environmental stresses, which include salt stress (Egamberdieva 2008), drought stress (Zahir et al. 2008), weed infestation (Babalola 2010), nutrient deficiency, and heavy metal contaminations (Sheng 2005). The term "induced systemic tolerance" has been used to describe the capacity of PGPR to elicit tolerance to salt and drought (Yang et al. 2009). A range of salt-tolerant rhizobacteria identified so far has shown beneficial interactions with plants in

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D.K. Maheshwari et al. (eds.), *Bacteria in Agrobiology: Crop Productivity*,
DOI 10.1007/978-3-642-37241-4_2, © Springer-Verlag Berlin Heidelberg 2013

stressed environments. These PGPR (e.g., *Rhizobium*, *Azospirillum*, *Pseudomonas*, *Flavobacterium*, *Arthrobacter* and *Bacillus*) utilize osmoregulation; oligotrophic, endogenous metabolism; resistance to starvation; and efficient metabolic processes to adapt under dry and saline environments (Lugtenberg et al. 2001; Egamberdiyeva and Islam 2008). The bacteria, with their physiological adaptation and genetic potential for increased tolerance to drought, increasing salt concentration, and high temperatures, could improve plant production in degraded sites (Maheshwari et al. 2012; Yang et al. 2009).

Many mechanisms have been reported for the activities of PGPR (Glick et al. 2007). Some strains produce metabolites such as hydrogen cyanide (HCN), 2, 4-diacetylphloroglucinol (DAPG) (Duffy et al. 2004); antibiotics, e.g., phenazine antibiotics (Chakraborty et al. 2009); and volatile compounds that stimulate plant growth (Ryu et al. 2003). Other strains produce siderophores and play roles in sequestering iron for plants, help in delayed senescence, biological control (Buyer et al. 1993; Kloepper et al. 1991), and produce plant hormones such as gibberellins, cytokinins, abscisic acid, and auxins, which at low concentrations influence plant physiological processes such as host's root respiration rate, metabolism, and root abundance.

Specifically, gibberellins influence seed germination, stem elongation and development, flowering, and fruit setting of plants, and auxins, especially indole acetic acid (IAA) and indole acetamide (IAM), influence root development, tissue differentiation, and responses to light and gravity. Lowering of ethylene (Saleem et al. 2007) levels in plants through the synthesis of the enzyme 1-amino-cyclopropane-1-carboxylate (ACC) deaminase that hydrolyzes the ethylene precursor ACC is another well-reported mechanism for growth promotion by PGPR (Glick et al. 2007; Shaharoona et al. 2007). The role of ACC deaminase-producing PGPR was reviewed extensively by Saraf et al. (2010).

Evidently, PGPR holds enormous prospects in improved and sustainable plant production, including enhanced plant tolerance to stress, better plant nutrient uptake and reduced use of chemical inputs. The roles of PGPR in nutrient uptake and stress management are emerging areas in agriculture that is not yet well understood; consequently, the benefits are yet to be maximized anywhere in the world. It is even less explored in many developing economies and may seem entirely new in some regions. Efforts to better understand the role of inoculants and biofertilizers in nutrient uptake and plant response to environmental stress are more compelling now that the continuous use of high amounts of chemical inputs are generating environmental problems and not sustainable.

The concept of integrated nutrient management (INM) system as proposed by Adesemoye and Kloepper (2009) relating to the use of biofertilizers in combination with chemical fertilizers to stimulate uptake of nutrients remains very important. The benefits of INM to different cropping systems have been further discussed by other authors (Joshi et al. 2006; Kumar et al. 2009a, b; Maheshwari et al. 2011). Maximizing the impacts of beneficial microbes towards enhancing the response of plants to environmental stress (Egamberdieva 2011; Glick et al. 2007) is also very important. This chapter discusses the benefits of PGPR in broad terms, but attempts were made to present specifics about the use of PGPR to enhance plant nutrient uptake, for better plant response to environmental stress, and unexplored potentials in developing economies.

2.2 Major Crop Production Problems in Developing Regions

The Food and Agriculture Organisation (FAO) report titled "World agriculture: towards 2015/30" among others, discussed global long-term prospects for trade and sustainable development. One of the conclusions in the report was that the development of local food production in low-income countries, which depend highly on agriculture for employment and income, is the one factor that dominates all others in determining progress or failure in improving their food security. The report predicted that without the development of local food production and other related efforts, the target of halving the number of undernourished persons by no later than 2015 is far from being reached and may not be accomplished by 2030.

Socioeconomic, political, cultural, environmental factors, low technological development, bad agricultural methods and policies are major hindrances against agricultural development in many developing economies. There may be limited biological activity in response to environmental stresses such as salt and drought in certain areas resulting in low soil nutrients. In some regions, vast areas of land are highly weathered, very low in macro- and/or micronutrients or limited in arable land resources. Low level of soil fertility is a major hindrance against agriculture in some parts of Africa, South America, and many other regions, which makes productivity very low especially in locations with little or no use of fertilizers. There is continuous need for nitrogen and phosphorus, which are limiting nutrients (Graham and Vance 2000).

In arid regions of low rainfall and high evaporative demand, the causes of soil salinity are (1) cultivation of naturally saline lands, (2) rise in secondary salinity because of inflow of saline groundwater from higher plateau, and (3) increase in soluble salts concentration of water used for irrigation because of the recycling of drainage water for irrigation (Shirokova et al. 2000). Soil salinization is reducing the area that can be used for agriculture by 1–2 % every year (FAO 2002). Salinity causes a disturbance of plant–microbe interaction which is a critical ecological factor to help further plant growth in degraded ecosystems (Requena et al. 2001; Egamberdiyeva et al. 2007). As a result of soil salinization, plants are under saline or water unbalance stress and become more vulnerable to diseases, often caused by pathogenic fungi which can hardly be overcome by conventional methods of pest management (Kurth et al. 1986; Werner and Finkelstein 1995). Gratuitous use of fungicides and type of irrigation creates a strong concern regarding environmental pollution and development of fungicide resistance (Alva et al. 2000).

The benefits of resident soil microbes are hardly explored, and when commercial inoculants are used, they are usually not derived from microbes isolated locally and so may not be effective. Overall, the result is dismal agricultural productivity.

These underscore the urgent need to develop management practices and biotechnological applications that can improve soil productivity, environmental health, reduce erosion, and enhance food security. In fact, attempts to meet food needs in some regions have led to the adoption of agricultural practices capable of degrading the soil, such as high use of chemical inputs, e.g., fertilizers. Low efficiency in the uptake of fertilizer as identified by Adesemoye and Kloepper (2009) is prompting the use of high amounts of fertilizer. Consequent upon ineffective soil management is many environmental maladies, two of which Hungria and Vargas (2000) identified as nutrient depletion and soil acidification. Therefore, improvement in plant nutrient uptake is a requirement for overall reduction in fertilizer use and sustainable crop productivity.

2.3 Reported Use and Prospects of Microbes and PGPR in the African Region

Akanbi et al. (2007) compared the application of manure extract from cassava (*Manihot esculenta*) peel and Mexican sunflower (*Tithonia rotundifolia*) composts as foliar spray or liquid fertilizer with NPK in Nigeria. The authors also tested the extracts as pesticide and reported that the growth of fluted pumpkin (*Telfairia occidentalis*) plants with foliar spray of compost extracts from cassava peel and Mexican sunflower was significantly the same with those that received NPK fertilizer. Depending on the ratio of extract used, there was certain level of protection against five insect pests tested, which included leaf beetle (*Lagria villous* T.), red pumpkin beetle (*Aulacophora* spp.), cotton leaf roller (*Sylepta derogate* F.), cut worms (*Noctuidae* spp.), and green grasshopper (*Zonocerus variegatus*) (Akanbi et al. 2007).

Babalola and coworkers conducted pot experiments in Nigeria and Kenya to determine the growth effect of three different rhizobacteria (*Pseudomonas* sp. 4MKS8, *Klebsiella oxytoca* 10MKR7, and *Enterobacter sakazakii* 8MR5) on maize under *Striga hermonthica* infestation. The three bacteria were selected based on their plant growth-promoting effects (Babalola et al. 2007). Some of the treatments showed statistically significant plant growth promotion and increased agronomic characteristics of maize. The authors studied 1-amino-cyclopropane-1-carboxylic acid (ACC) deaminase gene in *Pseudomonas* sp. 4MKS8 and *Klebsiella oxytoca* 10MKR7, and *Enterobacter sakazakii* 8MR5 and found that not all plant growth-promoting rhizobacteria contain the enzyme ACC deaminase.

Ugoji et al. (2006) examined the impacts of seed coating with *Bacillus* sp. on the storage of seeds of maize (*Zea mays* L.), bean (*Phaseolus vulgaris* L.), lettuce (*Lactuca sativa* L.), and cucumber (*Cucumis sativus* L.) over a 12-month period in South Africa. One important finding was that microbial populations decreased from month 7 to month 12 which, according to the authors, indicated protection of the seed by the applied *Bacillus* sp. against growth of pathogens and saprophytes.

In a study conducted in Nigeria, Adesemoye and Ugoji (2006) examined the effectiveness of plant growth-promotion ability of *Pseudomonas* sp. in three test crops—okra (*Abelmoschus esculentus* L.), tomato (*Lycopersicon esculentum* L.), and African spinach (*Amaranthus* sp.). The aim of the study was to determine whether inoculation method had impacts on PGPR's effectiveness. They found that tested *Pseudomonas* isolates promoted crop growth and had great potentials as PGPR in the region. The test on two methods of bacterial inoculation (soaking and coating) produced statistically similar results of plant growth enhancement. Adesemoye et al. (2008a) compared PGPR properties between *Bacillus subtilis* and *Pseudomonas aeruginosa* as representatives of their two genera. The authors reported similarities but no significant difference at $p < 0.05$ between the overall performances of *B. subtilis* and *P. aeruginosa*. It was suggested that *Bacillus* may be relatively more versatile than *Pseudomonas* as PGPR because of the ability to form endospores, which can make them retain viability for long periods either in storage or in the soil.

Jida and Assefa (2011) reported that Ethiopian soils harbor highly efficient nitrogen-fixing lentil-nodulating rhizobia. They collected 30 isolates of such rhizobia from farmers' field soils in central and northern parts of Ethiopia and selected for symbiotically efficient ones, which possess plant growth-promoting characteristics. Under glasshouse conditions, they found characteristics such as IAA production in 36.7 % and inorganic phosphate solubilization capacity in 16.7 %. Additionally, one or a combination of carbon sources and nitrogen sources utilization, tolerance to acidic or alkaline pH, metal toxicity, and antibiotics production were found in most isolates (Jida and Assefa 2011).

One study in Egypt examined tripartite interactions among bacteria (*Azospirillum brasilense*), mycorrhiza (*Glomus clarum*), and legume (*Vicia faba*) under five saline (NaCl) levels in pot cultures (Rabie and Almadini 2005). Significant effects of inoculation were reported in the plants for salinity tolerance, mycorrhizal dependency, phosphorus level, phosphatase enzymes, nodule number, nitrogen uptake, protein content, and nitrogenase enzymes. Based on the findings, the authors suggested that bacterial–AMF–legume tripartite symbioses could be a new approach to increasing the salinity tolerance of legume plants.

Galal et al. (2001) demonstrated the beneficial influence of co-inoculation of *Azospirillum lipoferum* and *Bacillus megaterium* for providing balanced nitrogen and phosphorus nutrition of wheat plants in Egypt. El-Azouni (2008) observed significant increase of dry matter, N, P uptake and yield of soybean grown in Egyptian soil inoculated with phosphate-solubilizing fungi *A. niger* and *P. italicum*. *Rhizobium leguminosarum* bv. *trifolii* was reported to colonize rice roots endophytically in the fields where rice is grown in rotation with Egyptian berseem clover (*Trifolium alexandrinum*) and can supplement 25–33 % of the recommended rate of N fertilizer for rice (Yanni et al. 1997). All these studies are evidences that PGPR have high potentials in Africa.

2.4 Reported Use and Prospects of Microbes and PGPR in the Asian Region, Including Asia Pacific and Middle East

The reduction of chemical fertilizers by using biological fertilizers based on bacteria involved in nitrogen fixation is one of the effective steps in sustainable agriculture. Owing to population growth and increasing food demand, intensive and environment-friendly agriculture such as biofertilizers and biopesticides have become the ideal model for the Asian region. According to the reports of Jee (2009), a total of 138 companies were producing hundreds of commercial products, and 23 biopesticides are now registered in Korea, and they are based on strains such as *Paenibacillus polymyxa*, *Bacillus subtilis*, *B. amyloliquefaciens*, *Paecilomyces fumosoroseus*, and *Streptomyces goshikiensis*. Quyet-Tien et al. (2010) reported regarding *P. polymyxa* KNUC265 strain, which increased plant growth of pepper and elicited both induced systemic resistance (ISR) and plant growth promotion, suggesting that it could be potentially used in improving the yield of pepper and other crops.

Meunchang et al. (2006) selected effective PGPR strains which increased plant growth and nutrient uptake of rice and indicated the possibility of producing biofertilizer for rice production in Thailand. In another work, Young et al. (2003) studied the effect of a combined treatment of multifunctional biofertilizer (mixture of *Bacillus* sp. *B. subtilis*, *B. erythropolis*, *B. pumilus*, and *P. rubiacearum*) on the growth of lettuce in Taiwan and found 25 % increase of lettuce yield over the control. In Mongolia, it was observed that *Bacillus pumilus* 8N-4 can be used as a bio-inoculant for biofertilizer production to increase the crop yield of wheat variety *Orkhon* (Hafeez et al. 2006).

Rice (*Oryza sativa*) could be described as the major food crop across the world's population, especially in Asian populations, and as noted by Kumar et al. (2011), more than 90 % of rice is produced in Asia. Rice plants require large amounts of N for their growth, development, and grain production (Sahrawat 2000). In Vietnam the application of BioGro based on various PGPR strains resulted in increase in rice growth and yield (Nguyen et al. 2003; Nguyen 2008). Mia and coworkers (2009) observed that *Rhizobium* inoculation significantly initiated more root hairs in rice seedlings. The authors also studied the effects of rhizobacterial inoculation on growth and nutrient accumulation of tissue-cultured banana plantlets under low N-fertilizer regime in Malaysia, and they found an increase in growth and yield of plant after inoculation (Mia et al. 2007). Many diseases that attack rice generate global concerns due to the popularity of the crop. However, PGPR could play very important roles in managing the diseases. For instance, PGPR has been reported exhibiting high potentials in the management of sheath blight of rice caused by *Rhizoctonia solani* AG 1-1A, particularly through combined application of PGPR with chemical fungicides in integrated disease management (IDM) systems (Kumar et al. 2011).

With the developed commercial PGPR (Ecomonas) in India, the rice sheath blight caused by *Rhizoctonia solani* reduction over the control was 37.7 % and grain yields significantly increased (3,901 and 1,938 kg/ha) over control (2,690 and 1,550 kg/ha) (Kumar et al. 2009a). Also in India, inoculation with vesicular arbuscular mycorrhizal fungi (*Glomus mosseae*, *G. fasciculatum*, *Acaulospora laevis*, and *Gigaspora gilmorei*) resulted in increased plant height, dry weight, number of pods, and nutrient content of chickpea (Kumar et al. 2009a).

Beneficial characteristic of PGPR has been reported in Malaysia on potato (Yasmin et al. 2009). The authors screened 15 PGPR strains for indole acetic acid (IAA) production (with and without addition of the precursor L-tryptophan [L-TRP]), phosphate-solubilizing activity, nitrogen synthesis, antagonistic activity against fungal pathogens, siderophore production, and intrinsic antibiotic resistance. All isolates produced IAA and grew in N-free media, which the authors suggested was an indication of N "production."

In Indonesia, Supanjani et al. (2006) conducted experiments to evaluate whether applications of lipochitooligosaccharides (LCOs) and inoculation with rhizobia could improve the uptake of calcium into soybean (*Glycine max* [L.] Merr.) leaves by inoculating with rhizobia or application of Nod factors LCOs. Two strains of *Bradyrhizobium japonicum* reportedly increased the uptake of labeled Ca, while a *nod*C-mutant incapable of producing LCO did not. Also, rhizobia that do not normally nodulate soybean (*Rhizobium leguminosarum* and *Sinorhizobium meliloti*) did not affect calcium uptake, nor did the tetramer or pentamer of chitosan or lumichrome. However, *Rhizobium* sp. NGR234, which can nodulate certain soybean without effective N_2 fixation, did not affect calcium uptake. Based on the findings, Supanjani et al. (2006) suggested that the rhizobial symbiosis can improve early calcium uptake into soybean plants, in addition to nitrogen fixation.

The availability of K and P in arid saline soils of China is limited. In such soils having bacterial strains that are able to solubilize "unavailable" forms of K- and P-bearing minerals to bring the K and P into solution is an important approach (Ullmann et al. 1996). Sheng (2005) observed that *Bacillus edaphicus* NBT strain increased K content of cotton and rape plants by 30 % when the soil was treated with insoluble K sources. In other field experiments in China, the plant biomass, nutrient uptake, and yield of wheat were increased by phosphorus-solubilizing bacteria (PSB) *Bacillus strains* (Chen et al. 2006).

In Russian region, there are several commercially available biofertilizers and plant protectors against plant diseases caused by *Fusarium graminearum*, *F. culmorum*, and *F. avenaceum*. Effectiveness of biofertilizers based on strains *Azotobacter chroococcum, Bacillus mucilaginosus*, and *Pseudomonas fluorescence* P 469 has been tested in field trials with winter and spring wheat, spring barley, potato, and sugar beet in different soils in Central Russia (Zhigletsova et al. 2010; Kutyova et al. 2002). In early studies, Belimov et al. (1995) reported positive effect of mixed cultures of nitrogen fixers *Azospirillum lipoferum*, *Arthrobacter mysorens*, and *Agrobacterium radiobacter* on grain yield and N uptake of barley in Russia.

Hasnain and Sabri (1996) showed that inoculation of wheat with *Pseudomonas* spp. stimulated plant growth by reducing plant uptake of toxic ions and increasing the auxin content of wheat grown in Pakistan. Similar results were observed by Afzal et al. (2005) where combined inoculation of nitrogen-fixing bacteria

(*Rhizobium leguminosarum*) with PSB *Pseudomonas* sp. strain 54RB increased dry matter and yield of wheat. In 2008, Kang and coworkers showed the capacity of *Aspergillus* spp. PS 104 to solubilize rock phosphate in soil-amended medium (Kang et al. 2008). Shaharoona et al. (2007) tested several *Pseudomonas* spp. strains in the field to determine their efficacy to increase growth and yield of wheat. Nosheen et al. (2011) reported that PGPR inoculation of *A. brasilense* and *P. stutzeri* either alone or in combination with half dose of chemical fertilizers was highly effective in improving root morphology and growth in safflower.

Naveed et al. (2008) reported that application of organic fertilizer and *Pseudomonas* strains significantly improved the growth (up to 39 %) and yield of maize. They found that *P. fluorescens* significantly increased plant height (16 %), the number of grains per spike (11.7 %), and grain yield (39 %) compared to non-inoculated control. Hafeez et al. (2006) showed that biofertilizer (BioPower) gave 50–70 % savings in nitrogen fertilizer and 20 % increase in rice in Pakistan. The bacterial-based fertilizer increased the yield of wheat and maize and protected plants from fungal disease. It was reported that the PSB-plant inoculations resulted in 10–15 % increases in crop yields and P uptake in 10 out of 37 experiments in India. In another study, Tomar et al. (1996) reported the efficiency of a PSB (*Pseudomonas* sp.) on the growth and yield of gram (*Cicer arietinum*).

Similar results were observed where combined inoculation of *Rhizobium* and PSB (*Pseudomonas striata* and *Bacillus polymyxa*) led to increase in nodulation, growth, and yield of chickpea under greenhouse conditions. This was associated with increase in nitrogenase activity in nodules and phosphorous content in plants (Khurana and Sharma 2000). In other works, Verma et al. (2010) observed that chickpea inoculated with *Rhizobium leguminosarum* subsp. *ciceri* annually produced up to 176 kg N/ha as a result of significant stimulation of plant growth. Hameeda et al. (2006) reported that two P-solubilizing bacteria (*Serratia marcescens* EB-67 and *Pseudomonas* spp. CDB-35) increased the biomass of maize by 99 % and 96 %, respectively, under greenhouse conditions.

Egamberdiyeva et al. (2002) reported on the effect of a *Pseudomonas fluorescens* PsIA12 and *Pantoea agglomerans* on the growth of maize in the field, and bacterial strains were found to significantly increase root development, shoot growth, and K uptake of maize. The application of *Bradyrhizobium japonicum* enhanced the number of nodules, dry weight of plant, grain yield, and protein content in soybean grown in salinated soils of Uzbekistan (Egamberdiyeva et al. 2004). Seed inoculation of common bean (*Phaseolus vulgaris*) by *Pseudomonas chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 resulted in improved root and shoot biomass in nutrient-deficient soil of Uzbekistan (Egamberdieva 2011).

Priming of seedlings with selected PGPR strains reduced *Fusarium* root rot of cucumber to as low as 10 % and showed a significant stimulatory effect on plant growth, increasing the dry weight of whole cucumber plants up to 62 % and fruit yield up to 32 % in comparison to the nonbacterized control (Egamberdieva et al. 2010). The inoculation of cotton seeds with salt-tolerant phosphate-solubilizing bacteria *Rhizobium meliloti* URM1 combined with phosphate had a significant

Table 2.1 Effects of PGPR strains on tomato cv. *Belle*) shoot length and fruit yield in salinated soil

Treatments	Plant height (cm)	%	Fruit yield (kg/m^2)	%
None	118.2 ± 3.9	100	13.9 ± 1.5	100
P. putida TSAU1	154.4 ± 4.9*	130	16.4 ± 1.6*	117
P. chlororaphis TSAU13	149.8 ± 7.1*	126	15.6 ± 1.2*	112
P. extremorientalis TSAU20	152.5 ± 7.5*	128	17.0 ± 1.2*	122

The temperature range was day 28–32 °C and night 16–18 °C
*Significantly different from the control at $P < 0.05$

Table 2.2 Effects of biological control agents on wheat growth and yield in salinated soil

Treatments	Grain yield (g/plant)	%	Biological yield (g/plant)	%
Control	19.8	100	62.2	100
TSAU20	24.0*	121	78.7*	126
TSAU1	22.4*	113	80.1*	128

Bacterial strains were *P. extremorientalis* TSAU20 and *P. putida* TSAU1
*Significantly different from the control at $P < 0.05$

stimulatory effect on total dry matter, shoot and root dry weight, yield, and P content (Egamberdiyeva et al. 2004).

The data below were obtained in recent experiments with tomato grown in salinated soil and inoculated with *P. putida* TSAU1, *P. chlororaphis* TSAU13, and *P. extremorientalis* TSAU20. The inoculants increased the growth and yield of tomato (Table 2.1).

The plant height were stimulated from 26 to 28 % after inoculation of tomato seeds with bacterial strains *P. putida* TSAU1, *P. putida* TSAU13, and *P. extremorientalis* TSAU20 compared to those in the control treatment. The yield of tomato increased up to 22 % after bacterial treatment. In wheat, traits such as grain yield and biological yield were also significantly increased by inoculation with PGPR *P. extremorientalis* TSAU20 and *P. putida* TSAU1 (Table 2.2).

As evidenced in the table, the grain yield increased after inoculation with *P. extremorientalis* TSAU20 and *P. putida* TSAU1 up to 21 % compared to non-inoculated control plants. The inoculation also increased biological yield by 28 % compared to control plants.

In Iran, *Azotobacter* in combination with PSB had been shown to increase the plant height, dry weight, and yield of maize up to 30 % over the control (Gholami et al. 2009). In another study, Khorshidi et al. (2011) showed that application of fertilizers with *Pseudomonas fluorescens* and *Azospirillum lipoferum* had a significant effect on rice yield in Iran. Rokhzadi et al. (2008) reported that combined inoculation of *Azotobacter*, *Azospirillum*, *Pseudomonas*, and *Mesorhizobium* resulted in promotion of grain yield and biomass in chickpea in Iran. In Turkey, seed inoculation of barley with N_2-fixing bacteria *P. polymyxa* RC05, *P. putida* RC06, and *R. capsulatus* RC04 increased root and shoot weight by 54 % and N uptake. *Pseudomonas* strains also increased the yield of sugar beet (Çakmakçi et al. 2001). Evidently, PGPR and biofertilizers have great potentials in agricultural productions in Asia, at least in the specific regions of isolation.

Table 2.3 Control of cotton root rot by antagonistic bacteria in two different soils

Treatments[a]	Diseased plants	
	Cambisol	Sierozem
Control, *F. oxysporum*	69 ± 5.8	76 ± 9.8
P. alcaligenes PsA15	43 ± 11.2	26 ± 10.2*
B. amyloliquefaciens BcA12	50 ± 8.2	31 ± 9.1*
B. polymyxa BcP26	48 ± 6.8	37 ± 7.2
M. phlei MbP18	39 ± 9.1*	30 ± 6.9*

*Significantly different from the negative control at $P < 0.05$

[a]Bacteria were coated on pre-germinated cotton seeds, and plants were grown under open natural conditions in pots infested with *F. oxysporum* spores (3.0×10^7 spores/kg)

2.5 Biological and Edaphic Factors That May Affect PGPR Effectiveness in Different Regions

Many countries in the world have been using bacterial fertilizers in agriculture (Dashti et al. 1997), and it is envisaged that the usage will increase but also expand to other regions. This optimism is predicated on the fact that the apathy against PGPR and biofertilizers which arose mainly from the reported variability in performance on the field is beginning to fade out. This makes it important to discuss possible factors/conditions that can affect the performance and effectiveness of PGPR and how the issues can be handled. Some of the important factors perceived to be hindering wide acceptance and use of PGPR are variability in colonization efficiency, rhizosphere competence, and field performance. Arguably, the most important factor that affects PGPR performance is colonization of the host. For instance, a strain with biological control potentials in vitro may be unable to exhibit the trait in the field if it is incapable of successful colonization of the host.

It has been discussed earlier in this chapter that plant growth stimulation and biological control of plant diseases by rhizobacteria involve one or more mechanisms which include production of phytohormones, antibiosis, parasitism, competition for nutrients and niches, and induced host resistance (Lugtenberg and Kamilova 2004; Adesemoye et al. 2009). Notably, abiotic and biotic factors may influence the different mechanisms and limit the interactions between plant and beneficial bacteria, resulting in less than acceptable performance in plant growth promotion and management of diseases (Egamberdiyeva and Hoflich 2002, 2003).

The data below exemplifies how abiotic factor (soil type) can affect the activities of PGPR. The biological control of cotton root rot caused by *F. oxysporum* using different antagonistic bacteria species showed that soil types have effects on bacterial abilities to control this root pathogen of cotton (Table 2.3).

Infestation of the soil with *F. oxysporum* resulted in an increase of the percentage of diseased plants from 69 to 76 in two different soils. Priming of seedlings with the five selected bacterial strains *P. alcaligenes* PsA15, *B. amyloliquefaciens* BcA12, *B. polymyxa* BcP26 and *M. phlei* MbP18 reduced this proportion to as low as 26 % in sierozem soil but 39 % in cambisol soil in comparison to the non-inoculated control. Overall, the bacterial strains were more effective in sierozem soil than in cambisol soil. It is probable that the physiological adaptation of bacterial strains supported their beneficial activity much better in soil from where they were isolated.

Also, the availability level of macro- and micronutrients in soil has high effects on the performance of PGPR. According to Choudhury and Kennedy (2004), the efficiency of plant-associated N_2 fixation by diazotrophic bacteria may be hampered by a limited supply of energy and substrate. Other factors that could affect inocula success include temperature, soil type, N content, salt concentration, and moisture content. Numerous studies have shown that soil salinity decreases nodulation and dramatically reduces N_2 fixation and nitrogenase activity of nodulated legumes, as reviewed by Zahran (1999). It has been demonstrated that the performance of PGPR after inoculation into the rhizosphere is affected significantly by competition for nutrient and niches with indigenous microflora (Kamilova et al. 2006; Strigul and Kravchenko 2006).

Rashid et al. (1997) reported that response of wheat to bacterial inoculation was variable in different ecological zones of Punjab, Pakistan, ranging from 10 to 35 % increase in yield over control. The inconsistency in results might be due to many factors such as the complex interactions among hosts, rhizobacteria, pathogens, climate, and soil environment. Crop cultivars is another important factor as demonstrated in a study where inoculation of wheat with *Pseudomonas* strains improved plant growth in salinated soil of Uzbekistan at a rate that varied depending upon the wheat cultivars used (Egamberdieva 2010). It is recommended that selection for cultivars should consider bacterial inoculants so that the selected cultivar is the one that carries the trait of successful association with such bacteria. Understanding the mechanisms of growth stimulation and plant disease control by rhizobacteria and impact of abiotic factors on their interactions and beneficial effects are useful in the application of PGPR in countries with varied climatic conditions, enabling a prediction of the success of a PGPR inoculation with the specific variety of crops to be cultivated.

2.6 Unexplored Possibilities of PGPR in Developing Economies: Biofertilization and Biocontrol

It was suggested by Adesemoye and Kloepper (2009) that PGPR as biofertilizers or microbial inoculants can be important components of an integrated nutrient management system. However, the interactions among PGPR and plants are still not well understood, especially in field applications and different environments (Niranjan et al. 2005). Therefore, there is need for more studies on plant–microbe interactions and their activities in different regions and ecologies, including stressed environments, for instance, in arid and tropical regions. Availability of more information will enable the development and widespread acceptance of new agricultural technologies, which can improve soil ecology, plant development, and resistance against diseases and pests. Akanbi et al. (2007) believed that if compost were available in nutrient-rich liquid formulations that involve the use of less quantity, and easier application, it will be more popular among farmers in Nigeria.

Cereals are major crops in many developing economies, and it has been shown by Kennedy and Tchan (1992) that biofertilizers can enhance growth, disease control and yield of cereals, but this is yet to be well explored in many parts of the developing regions of the world. Frequent rhizosphere colonizers of cereal crops and grasses include N-fixing bacteria such as *Azospirillum*, *Acetobacter*, *Azoarcus*, *Herbaspirillum* spp., and *Aeromonas* (Dobbelaere et al. 2001; Mehnaz et al. 2001). Bacteria reportedly have greater adaptability to rice ecosystems compared to fungal antagonists, and PGPR have been used vigorously in controlling rice diseases (Kumar et al. 2011). Possible benefits of PGPR on rice include biological control of diseases (especially through induced systemic resistance); better nutrient uptake—nitrogen, phosphorus, and ferric iron; enhanced seedling growth; increased yield; and sustainable use of agricultural products.

Salinity being one of the major problems in many developing countries in Asia; the use of salt-tolerant bacterial inoculants is a possible solution that can increase plant growth, induce seed germination, improve seedling emergence, and protect plants from the deleterious effects of some environmental stresses. Velagaleti and Marsh (1989) showed that the development of salt-tolerant symbioses is an absolute necessity to enable cultivation of leguminous crops in salt-affected soils. Egamberdieva and Kucharova (2009) suggested that screening and application of the enhanced potential root-colonising rhizobacteria is essential for developing sound strategies to manage the rhizosphere in such a way that it becomes more difficult for pathogens to colonise the rhizosphere; thus, these beneficial bacteria can engineer positive interactions in the rhizosphere and stimulate plant growth under saline conditions. In some locations, soils are poorly aerated and waterlogged, or well aerated but calcareous. The impact of microbial activity in the rhizosphere on roots directly on mobilization and/or immobilization or indirect effect on root morphology and/or physiology (Babalola 2010) can be utilized to manipulate nutrients uptake.

Pathogens, especially soil-borne, cause inestimable crop losses in many developing regions with more noticeable consequences in Africa. Soil suppressiveness of plant diseases (Weller and Thomshow 1993) is an important consideration that should be continuously studied for possibility of identifying and exploiting the benefits from the specific resident organisms involved. Additionally, the manipulation of the plant–microbe interactions to control quorum sensing (QS) systems in microbes to the benefit of crop production is another focus area with possible benefits awaiting exploitation. Quorum sensing (QS) in which acyl homoserine lactones are utilized is important in many plant–microbe interactions, as in *Pseudomonas aureofaciens* (Babalola 2010; Boyer et al. 2008).

Root exudates, a fraction of rhizodeposition, are rich in carbon and energy sources that affect microbial growth and development in the rhizosphere. Other fractions of rhizodeposition—lysates, mucilage, secretions, and dead cell materials—may play some roles (Dardanelli et al. 2010; Sommers et al. 2004). These dynamics especially interactions of root exudates and PGPR activity which lead to better root growth have been previously explained by Adesemoye et al. (2009). However, more study and better understanding of the dynamics may help in better use of PGPR in crop production in developing regions, and the knowledge may have universal applications across all regions of the world—developing and developed alike.

2.7 Conclusion

One of the immediate reasoning to improve agricultural productivity and development is the use of more chemical fertilizers. However, with the resultant effects of heavy fertilizer use in many regions of the world, it is compelling to look for alternatives. Based on current events, the argument of Adesemoye et al. (2009) that the goal of reducing fertilizer usage will be to this century as what the goal of reducing pesticides was to the last century remains valid. Therefore, the integrated nutrient management (INM) system proposed in that paper, i.e., integration of microbial inoculants with less fertilizer, should be considered in many situations as it promises high crop productivity and agricultural sustainability.

The use of fungicides, bactericides, and pesticides generally continue to generate concerns, so biological control is still as relevant as it was many decades ago. The reason for the inconsistencies reported in some regions with biological control of diseases is not yet well understood though its relevance as a major limitation to widespread acceptance of biofertilizers and commercial PGPR products has been reducing as compared to almost two decades ago when an observation of inconsistencies was made by Weller and Thomshow (1993).

The complex nature of the natural soil environment is a possible explanation for the variation in effectiveness of PGPR strains or products, particularly when such products were used far away from where the microbial inoculants were originally isolated. This implies that there is high chance that commercial PGPR products made from isolates collected in a region may perform better in that region than if it was from strains collected in another region continent or country. Research should focus on identifying effective PGPR strains in each region.

In agreement with Dardanelli et al. (2010), the presence of microorganisms in the soil is critical to the maintenance of soil function, in both natural and managed agricultural soils. The microbes are involved in key processes such as soil structure formation, decomposition of organic matter, toxin removal, and the cycling of elements—carbon, nitrogen, phosphorus, potassium, and sulfur. It is also clear that beneficial microorganisms play key roles in suppressing soil-borne plant diseases and in promoting plant growth and changing the vegetation (Doran et al. 1996).

Efforts should be directed towards maximizing the identified benefits of PGPR or biofertilizers in all developing economies. If the benefits of PGPR in crop production can be maximized, this will certainly help in the fight against hunger. Importantly, regions in developing economies may have to use more of products that are based on local isolates because as emphasized by Adesemoye et al. (2009), no microbial inoculant can be universal for all ecosystems. Rather, biofertilizers' performances may be specific as effectiveness is dependent upon factors like plant type, soil type, and many other factors.

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http://www.springer.com/978-3-642-37240-7

Bacteria in Agrobiology: Crop Productivity
Maheshwari, D.K.; Saraf, M.; Aeron, A. (Eds.)
2013, VIII, 507 p., Hardcover
ISBN: 978-3-642-37240-7