Plant Growth-Promoting Microbes for Sustainable Agriculture

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Suhas P. Wani and S. Gopalakrishnan

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Abstract

Microbes are an integral part of living soil not only in transforming nutrients in the soil but also with multiple functions in influencing soil health. There are specific microbes which help the plant to grow well in their presence by various mechanisms. The direct mechanism may include fixation of atmospheric nitrogen, synthesis of various phytohormones and enzymes, and solubilization of minerals in the soil, while the indirect mechanism includes inhibiting phytopathogens. Hence, such plant growth-promoting rhizobacteria (PGPR) need to be harnessed and exploited for sustainable agriculture. Some of the representative PGPR group includes *Azotobacter*, *Azospirillum*, *Acinetobacter*, *Agrobacterium*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Serratia*, *Streptomyces*, *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Frankia*, and *Thiobacillus*. Demonstrations of these PGPR and their beneficial traits under glasshouse and field conditions are documented for a range of crops including

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S. P. Wani (✉) · S. Gopalakrishnan
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Telangana, India
e-mail: s.wani@cgiar.org; s.gopalakrishnan@cgiar.org

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cereals, legumes, fruits, vegetables, herbs, and ornamentals. Several industries are commercializing the potential PGPR strains as biofertilizers and as biocontrol agents. However, successful commercialization of PGPR in many developing countries is a distant dream largely due to the lack of well-developed technology, quality carrier material, quality control legislation, training programs, and on-farm demonstrations. The development of quality PGPR inoculum and its application will definitely lead to an ideal sustainable agricultural system. Further, PGPR is known for not only reducing the emission of greenhouse gases (GHGs) and carbon footprint but also increasing nutrient-use efficiency.

Keywords

Plant growth-promoting microbes · Secondary metabolites · Biological control · Commercialization · Sustainable agriculture

2.1 Introduction

Food security, agricultural sustainability, energy renewability, and rural livelihoods depend largely on soil fertility. Land degradation and desertification due to anthropogenic activities causes an estimated loss of 24 billion tons of fertile soil around the world's croplands (FAO 2011). It is estimated that, by 2030, the ever-increasing human population and changing food habits would increase the demand for water by 30%, energy by 45%, and food by 50% (IFPRI 2012). These demands cannot be met unless the soil fertility is restored. In addition, environmental pollution, today's biggest public concern, is largely caused by the use of synthetic pesticides, fertilizers, and herbicides. This has led to seek an alternative strategy for synthetic pesticides and fertilizers (Glick et al. 2007). Therefore, a greener and cleaner approach toward crop protection and production is essential. The use of microbes for crop protection and production and soil health had been practiced for centuries. These beneficial microbes are called as "plant growth-promoting rhizobacteria (PGPR)" (Kloepper and Schroth 1978). These heterogeneous bacteria are usually found in the rhizosphere and root surfaces and provide benefits to the crops. In recent years this terminology PGPR has gained a simple expressive term as "plant probiotics" (Maheshwari 2012).

The rhizosphere soil is rich in nutrients due to the accumulation of sugars, vitamins, amino acids, organic acids, fatty acids, phenols, and plant growth promoters released from the roots by secretion, exudation, and deposition. This leads to the enrichment of microbes (10- to100-fold) which include bacteria, actinobacteria, fungi, and algae (Uren 2007). The role of rhizospheric microorganisms in plant growth promotion is widely reported (Vessey 2003; Tilak et al. 2005; Podile and Kishore 2006). Some of the representative rhizospheric microbes/PGPR include the genera *Acinetobacter*, *Agrobacterium*, *Allorhizobium*, *Arthrobacter*, *Azorhizobium*, *Bacillus*, *Bradyrhizobium*, *Brevibacterium*, *Chromobacterium*, *Burkholderia*, *Hyphomicrobium*, *Caulobacter*, *Flavobacterium*, *Erwinia*, *Gluconobacter*, *Mesorhizobium*, *Micrococcus*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Sinorhizobium*, *Sphingomonas*, and *Streptomyces* (Vessey 2003; Vijayabharathi et al. 2016). In recent years, the plant growth-promoting traits of actinobacteria are getting much attention (Jog et al. 2012; Gopalakrishnan et al. 2016b).

2.2 Mechanisms of PGPR

PGPR employs a direct and indirect mechanism to enhance plant growth promotion and protection. The direct mechanisms include the production of growth hormones, solubilization of phosphorous, fixation of atmospheric nitrogen, and acquisition of iron. The indirect mechanisms include minimizing the deleterious effects of biotic stresses through production of low molecular weight compounds such as alcohols, ammonia, aldehydes, cyanogens, ketones, sulfides, cell wall-degrading enzymes, and secondary metabolites with antagonistic traits and competition for nutrients (Glick 2012; Dey et al. 2014).

2.3 Direct Plant Growth Mechanisms

2.3.1 Biological Nitrogen Fixation (BNF)

Nitrogen (N), an essential element for crop growth, is available easily in the air, as 78% of atmosphere is composed of N. However, plants cannot utilize gaseous form of this N. Currently, a variety of synthetic fertilizers are being used for enhancing agricultural productivity. Hence, biological alternatives are preferred as these are addressing economic, environmental, and renewable energy concerns. BNF is a process of converting atmospheric N into plant assailable N (such as ammonia) through a reaction between rhizobia and leguminous plants (such as chickpea, pigeon pea, and groundnut) (Wilson and Burris 1947). Legumes, the major symbionts of BNF, can meet their own N needs. A major portion of N fixed by legumes is harvested in grains. The succeeding crop(s) also get benefitted by N in the form of the root and shoot residues (Bhattacharyya and Jha 2012). Crops such as sugarcane, wheat, and rice have also the capacity to fix atmospheric N using free-living bacteria/diazotrophs such as *Azoarcus*, *Cyanobacteria*, and *Azospirillum*. However, the N fixed by legume-rhizobia symbiosis (13–360 kg N ha^{-1}) is far greater than the N fixed by free-living bacteria or diazotrophic nonsymbiotic systems (10–160 kg N ha^{-1}) (Bohlool et al. 1992). Rhizobia are treated on seeds of legumes for enhanced N fixation (Lindström et al. 1990). They can persist in soil for many years in the absence of their host (Sanginga et al. 1994). Actinobacteria such as *Streptomyces*, *Micromonospora*, *Corynebacterium*, *Agromyces*, *Arthrobacter*, *Propionibacterium*, and *Mycobacterium* also have been shown to exhibit BNF (Sellstedt and Richau 2013). Actinobacteria have also been demonstrated for their BNF capability by acetylene reduction assay (ARA), ^{15}N isotope dilution analysis, ability to grow on nitrogen-free medium, and identification of *Nif* genes via PCR amplification (Ghodhbane-Gtari et al. 2010).

2.3.2 Phosphate Solubilization

Phosphorus (P) plays an important role in cell metabolism and signaling in plants (Vance et al. 2003). P is present in bound form (with inorganic or organic molecules), but plants can take only H_2PO_{4-} and/or HPO_4^{2-}form of P (Smyth 2011). Hence, P is extensively used as a synthetic fertilizer, but their excessive and unmanaged application leads to negative impact on the environment (Correll 1998). The P-solubilizing bacteria mineralize the organic P by several enzymes of microbial origin, such as acid phosphatases, C-P lyase, D-α-glycerophosphate, phosphor hydrolases, phosphonoacetate hydrolase, and phytase which solubilizes the bound form, so that they are available to plants (Gügi et al. 1991; Abd-Alla 1994; Ohtake et al. 1996; McGrath et al. 1998; Skrary and Cameron 1998; Glick 2012). Plant growth-promoting (PGP) microbes such as *Bacillus*, *Pseudomonas*, and *Streptomyces* are widely known for P solubilization. Actinomycetes having high P-solubilizing traits have been reported, for instance, *Streptomyces* sp. mhcr0816 (TCP 1916 mg l^{-1}, RP 990 mg l^{-1}), *Streptomyces* sp. (RP 250 mg l^{-1}), and *Arthrobacter* sp. (RP 519 mg l^{-1}) are comparable to *Pseudomonas* sp. (TCP 1500 mg l^{-1}) or *Bacillus* (TCP 957 mg l^{-1}) strains (Hamdali et al. 2012; Jog et al. 2014). The role of P solubilization by *Mesorhizobium mediterraneum* in enhancing plant growth has been reported in barley and chickpea (Peix et al. 2001).

2.3.3 Phytohormone Production

Plant-associated bacteria are known to produce phytohormones (such as auxins) that regulate plant growth. Phytohormones affect morphological and physiological processes of plants even at lower concentrations (Arshad and Frankenberger 1998). They change growth pattern of the plants and result in branched and lengthier roots with greater surface area enabling the plants to access water and nutrients from deeper depths of soils. Several actinobacteria capable of producing auxins, gibberellins, cytokinins, and abscisic acid are shown in Table 2.1.

2.3.4 Iron Acquisition

In nature, iron exists as insoluble form of hydroxides and oxyhydroxides which are not accessible to plants. Siderophores (high-affinity iron-chelating compounds) can be of both the plant and the microbial origin and trap iron present in the soil (Rajkumar et al. 2010). The mechanism of microbial-origin siderophores in plant growth is not completely understood, but under low iron available conditions, PGP is assumed to involve one of the following mechanisms:

Table 2.1 List of PGP microbes producing growth hormones

Phytohormone/ ACC deaminase	PGP bacteria	References
Auxin /IAA	*Actinomyces* sp., *Bradyrhizobium*, *Bacillus megaterium*, *Frankia* sp., *Micrococcus*, *Methylobacterium oryzae*, *Nocardia* sp., *Rhizobium*, *Streptomyces* spp., *S. atrovirens*, *S. griseoviridis* K61, *S. lydicus* WYEC108, *S. olivaceoviridis*, *S. rimosus*, *S. rochei*, *S. viridis*	Kaunat (1969), Brown (1972), Wheeler et al. (1984), Abd-Alla (1994), Mahadevan and Crawford (1997), Tokala et al. (2002), Tsavkelova et al. (2006), El-Tarabily (2008), Khamna et al. (2010), Verma et al. (2011), Abd-alla (2013), Lin and Xu (2013) and Subramanian et al. (2014)
Gibberellin	*Actinomyces* sp., *Bacillus*, *Arthrobacter*, *Micrococcus*, *Nocardia* sp., *Streptomyces* sp.	Katznelson and Cole (1965), Kaunat (1969), Brown (1972), Merckx et al. (1987) and Tsavkelova et al. (2006)
Cytokinins	*Arthrobacter, Frankia* sp., *Leifsonia soli*, *Rhodococcus fascians*, *Pseudomonas*, *Streptomyces turgidiscabies*	Sang-Mo et al. (2014), Cacciari et al. (1980), Stevens and Berry (1988), Joshi and Loria (2007) and Pertry et al. (2009)
ACC deaminase	*Arthrobacter*, *Microbacterium azadirachtae* sp. nov., *Leifsonia soli* sp. nov., *Micrococcus* spp., *Rhodococcus* sp. R04, *Streptomyces* spp.	El-Tarabily (2008), Dastager et al. (2010), Madhaiyan et al. (2010a, b) and Nascimento et al. (2014)

Source: Swarnalakshmi et al. (2016)

1. Microbial-origin siderophores with high redox potential transfer their ferrous form of iron to a plant's transport system through apoplastic pathway in roots.
2. Iron chelation by microbial-origin siderophores from soil depends on its concentration, pH, and redox potential and does a ligand exchange with plant-origin siderophores. During this process, the iron-free plant-origin siderophores are initially bound to the receptor protein. This complex binds to a receptor, where the ion exchange between the two siderophores occurs (Crowley 2006).

Besides contributing to plant health, microbial-origin siderophores also involved in biocontrol of plant pathogens. It functions by acquiring iron, thereby competing with other pathogenic microbes in the vicinity and supplying it to the plant (Glick 2012). The production of high-affinity siderophores by PGP microbes is perceived as a means of biocontrol, as phytopathogens produce low-affinity siderophores. PGP microbes which produce siderophores with high-affinity colonize efficiently in the rhizosphere (Kloepper et al. 1980). The role of microbial-origin (including actinobacteria) siderophores in phytopathogens suppression are reported widely (Yamanaka et al. 2005; Barona-Gomez et al. 2006; Sontag et al. 2006; Macagnan et al. 2008; D'Onofrio et al. 2010; Johnson et al. 2013).

2.3.5 Role in Nutrient Cycles

Soil microbes, plant growth-promoting microbes in particular, are the key propellers of biogeochemical cycles on nutrients including N, C, P, and S (Bloem et al. 1997) and of which C and N cycle are most important.

2.3.5.1 Carbon Cycle

It is well known that microbes transfer the C primarily for their own survival. For instance, under aerobic conditions, i.e., in rhizosphere soil and oxic layers of wetland systems, aerobic methane-oxidizing bacteria (MOB) play the role in C cycle (Chistoserdova et al. 2005), whereas, under waterlogged anaerobic soils, hydrogenotrophic archaea and methanogenic bacteria play the role (Trumbore 2006). Microbial C is found maximum in forest soils compared to any other soils. Typically, microbial C is found a minimum of 100–1000 μg g − 1 in well aerated soils and a maximum of 500–10,000 μg g − 1 in undisturbed forest soils with the intermittent values in ecosystems such as semiarid tropics (SAT) and grasslands (Kandeler et al. 2005). Microbial biomass C is found about 1–6% of total organic C in rhizosphere soil with an indirect relationship for increasing soil depth. Formation of soil organic matter (OM), a major fraction containing soil organic carbon (OC), is aided by the decomposition process through various hydrolytic enzymes such as cellulase, protease, amylase, chitinase, glucosidase, and phenoloxidase. These hydrolytic enzymes convert the macromolecules into low molecular weight micromolecules for the ready assimilation of microbes (Burns and Dick 2002).

2.3.5.2 Nitrogen Cycle

The first step in the N cycle is assimilation, i.e., biological N_2 fixation (BNF). It is aided by a group of diazotrophic bacteria such as rhizobia, *Frankia*, *Azotobacter*, cyanobacteria, and green sulfur bacteria and of which the first two (rhizobia and *Frankia*) occur through the symbiotic process while the last three through the nonsymbiotic process (Thamdrup 2012). The N fixed, in the form of ammonium, during the BNF process, is further dissimilated by two-step microbial process, nitrification (the aerobic oxidation of ammonium to nitrite and nitrate) and denitrification (the anaerobic reduction of nitrate to N_2 through nitrite, nitric oxide, and nitrous oxide) (Simon 2002). Nitrification is done by two different sets of microbial groups: (1) ammonia-oxidizing bacteria (AOB) such as *Nitrosomonas*, *Nitrosospira*, and *Nitrosococcus*, which transform ammonia to nitrite using ammonia monooxygenase, and (2) nitrite-oxidizing bacteria (NOB) such as *Nitrobacter* and *Nitrococcus*, which transform nitrite to nitrate using nitrite oxidoreductase (Vaccari et al. 2006).

2.4 Indirect Plant Growth-Promoting Mechanisms

It refers to the use of PGP agents for managing the deleterious effects of biotic stresses (such as insect pests and pathogens) to improve the overall health of the plant. Such PGP microbes are also referred as biocontrol agents (BCAs) which employ several mechanisms to alleviate the insect pest and pathogen effects. Some of the important mechanisms are as follows.

2.4.1 Competition

Root exudates of plants play an important role in determining the specific group of microorganisms living in its vicinity. For instance, flavonoids and phenolic compounds in the rhizosphere were reported to influence plant symbiosis with beneficial rhizobacteria (Palaniyandi et al. 2013). Amino acids, organic acids, vitamins, and sugars were reported to serve as important nutrients for microbes (Dakora and Phillips 2002). Antagonism through competition for available nutrients is one form of the biocontrol mechanism used by the beneficial microbes to outlive pathogens and suppression of disease (Palaniyandi et al. 2013). The production of hydrolytic enzymes, siderophores, antibiotics, and volatile compounds are some of the other mechanisms exerted by PGP microbes (Agbessi et al. 2003; Macagnan et al. 2008; Wan et al. 2008).

2.4.2 Cell Wall-Degrading Enzymes

The cell wall of insect pests and fungal pathogens of plants contain polymers such as lipids, glucan, chitin, cellulose, and proteins. PGP microbes are known for their ability to produce cell wall-degrading enzymes. These enzymes disrupt the cell wall components of insect pests and pathogens which results in cell lysis. PGP microbes use this as one of the mechanism to manage plant pathogens and insect pests. PGP microbes are widely reported to produce these hydrolytic enzymes such as peroxidase, chitinase, glucanase, and protease (Gupta et al. 1995; Chater et al. 2010).

2.4.3 Antibiosis

It is one the major biocontrol mechanisms of PGP microbes in nature. The diffusible compounds produced by BCA and/or PGP bacteria are known to inhibit the rhizospheric plant pathogens. A broad spectrum of antibiotics such as polyenes, macrolides, aminoglycosides, nucleosides, and benzoquinones were reported to be produced by PGP microbes. Actinobacteria are the leading producer of antibiotics. For instance, the total number of microbial bioactive molecules (as of year 2012) was about 33,500 and of which 13,700 (41%) were produced by actinobacteria (Berdy 2012). Of these, 1800 metabolites showed antibiosis against pathogenic fungi (Berdy 2005). Antibiotics produced by actinobacteria are listed in Table 2.2.

2.4.3.1 Induction of Systemic Resistance

Host plant resistance is the best strategy to manage plant pathogens and insect pests of crops. Induced resistance in plants is elicited by interaction with an external factor

Table 2.2 List of actinobacteria capable of producing antibiotics

Actinobacterial species	Antibiotic	References
Streptomyces sp., *S. alboniger*, *S. padanus*	Alnumycin, coronamycins, fungichromin, goadsporin, kakadumycins, pamamycin-607, rhodomycin	Shockman and Waksman (1951), Kondo et al. (1987), Bieber et al. (1998), Onaka et al. (2001), Castillo et al. (2003), Shih et al. (2003) and Ezra et al. (2004)
Actinoplanes teichomyceticus	Teichomycins, teicoplanin	Parenti et al. (1978) and Somma et al. (1984)
Actinoplanes friuliensis sp. nov. *II.*	Friulimicins	Vertesy et al. (2000)
Actinoplanes ianthinogenes N. sp.	Purpuromycin	Coronelli et al. (1974)
Actinoplanes	Lipiarmycin	Coronelli et al. (1975)
A. utahensis	Echinocandin	Boeck et al. (1989)
Actinomadura sp.	Cationomycin, chandrananimycins, oxanthromicin	Nakamura et al. (1981), Patel et al. (1984) and Maskey et al. (2003)
Actinomadura spiralis	Pyralomicins	Kawamura et al. (1995)
Microbispora sp.	Cochinmicins, glucosylquestiomycin	Igarashi et al. (1998) and Lam et al. (1992)
Microbispora aerata	Microbiaeratin	Ivanova et al. (2007)
Micromonospora lomaivitiensis	Lomaiviticins A and B	He et al. (2001)
Micromonospora inyoensis	Sisomicin	Reimann et al. (1974)
Micromonospora carbonacea	Everninomicin	Weinstein et al. (1964)
Micromonospora echinospora subsp. *armeniaca* subsp. nov.	Clostomicins	Omura et al. (1986)
Nocardiopsis	New thiopeptide antibiotic	Engelhardt et al. (2010)
Nocardia sp. *I.*	Nocathiacins	Li et al. (2003)
Nocardia mediterranei subsp. *kanglensis*	Chemomicin A	Sun et al. (2007)

Source: Swarnalakshmi et al. (2016)

such as PGP microbes or even with a metabolite. In plants, two types of nonspecific defense systems are widely reported. These are PGP microbe-induced systemic resistance (ISR) and pathogen-induced systemic acquired resistance (SAR) (Schuhegger et al. 2006). Hoffland et al. (1995) demonstrated ISR for the first time in radish. In ISR, plants are treated with PGP microbes providing protection from pest and pathogen attack (Alstrom 1991; Walters et al. 2013). ISR is regulated by salicylic acid, ethylene, and jasmonic acid (De Meyer et al. 1999; Verhagen et al.

Table 2.3 List of antagonistic actinomycetes suppressing plant pathogens

Diseases	Pathogen	Antagonistic strain	References
Root rot of lupine	*P. cinnamomi*	*M. carbonacea*	El-Tarabily (2003)
Root rot of turfgrass	*P. infestans*	*S. violaceusniger* strain YCED-9	Trejo-Estrada et al. (1998)
Root rot of wheat	*P. infestans*	*S. olivaceoviridis*	Aldesuquy et al. (1998)
Lupin root rot	*P. tabacinum*	*A. missouriensis*	El-Tarabily (2003)
Lupin root rot	*F. oxysporum*	*S. halstedii*AJ-7	Joo (2005)
Wood rot	*P. chrysosporium*	*S. violaceusniger* XL-2	Shekhar et al. (2006)
Wood rot	*P. placenta*	*S. violaceusniger* XL-2	Shekhar et al. (2006)
Wood rot	*C. versicolor*	*S. violaceusniger* XL-2	Shekhar et al. (2006)
Wood rot	*G. trabeum*	*S. violaceusniger* XL-2	Shekhar et al. (2006)
Damping-off	*P. aphanidermatum*	*A. campanulatus*	El-Tarabily et al. (2009)
Crown rot	*P. aphanidermatum*	*M. chalcea*	El-Tarabily et al. (2009)
Damping off chickpea	*P. aphanidermatum*	*S. rubrolavendulae* S4	Loliam et al. (2013)
Damping off chickpea	*F. oxysporum*	*Streptomyces* sp.	Ashokvardhan et al. (2014)
Lupin root rot	*R. solani*	*S. vinaceusdrappus*	Yandigeri et al. (2015)

Source: Arasu et al. (2016)

2004). Representative reports on microbes inhibiting plant pathogens and insect pests are listed in Tables 2.3 and 2.4.

2.5 PGP Research at ICRISAT

PGP microbial research was at a peak in ICRISAT in the 1980s and 1990s but mostly on BNF. BNF plays an important role in sustaining productivity of soils in the semiarid tropics (Wani et al. 1995). It was reported to benefit succeeding cereal crops, such as wheat, rice, sorghum, and maize with a relative yield increase of up to 350% in different cropping systems. Besides calculating the amount of fixed N by legumes during the determination on legume fixed N in different cropping systems, it was important to consider the overall N balance of the cropping system. ICRISAT had gathered such information using chickpea (CP), pigeon pea (PP), cowpea (C), sorghum (S), safflower (SF), fallow (F), and mung bean (M) on several cropping system involving S/PP-S + SF, S + CP-S + SF, C/PP-S + SF, S + SF-S + SF, F + S-F + S, F + CP-F + S, and M + S-M + S (/ intercrop; + sequential crop; - rotation) (Wani et al. 1994). It was also suggested that significant contributions observed in those cropping systems were not only due to legume fixed N but also due to its N sparing effect, the break-crop effect, and soil microbial activity. It is

Table 2.4 Lists of microbial compounds with insecticidal and larvicidal properties

Source	Compound	Activity	References
Streptomyces nanchangensisNS3226	Nanchangmycin	Insecticidal	Sun et al. (2002)
Streptomyces sp. CP1130	Tartrolone C	Insecticidal	Lewer et al. (2003)
Streptomyces galbus	Ethyl acetate extract	Pesticidal	Jo et al. (2003)
Streptomyces sp.173	Fermented broth	Insecticidal	Xiong et al. (2004)
Metarrhizium sp. FKI-1079	Hydroxyfungerins A & B	Insecticidal	Uchida et al. (2005)
Streptomyces qinlingensis sp. nov.	Fermented broth	Insecticidal	Zhi-Qin et al. (2007)
Streptomyces sp.4138	Staurosporine	Insecticidal	Xiao-Ming et al. (2008)
Streptomyces sp. KN-0647	Quinomycin A	Insecticidal	Liu et al. (2008)
Streptomyces sp. ERI-04	Curde extract	Antifeedant	Valanarasu et al. (2010)
Streptomyces microflavus	Crude extract	Larvicidal	El-Bendary et al. (2010)
Saccharomonospora sp. (LK-1), *Streptomyces roseiscleroticus* (LK-2), &*Streptomyces gedanensis* (LK-3)	Crude extract	Larvicidal	Karthik et al. (2011)
Streptomyces sp. CMU-MH021	Fervenulin	Nematocidal	Ruanpanun et al. (2011)
Streptomyces microflavus neau3	Macrocyclic lactone	Insecticidal	Wang et al. (2011a)
Serratia marcescens NMCC46	Prodiogisin	Larvicidal	Patil et al. (2011)
Streptomyces avermitilis NEAU1069	Doramectin congeners, 1–4	Acaricidal & insecticidal	Wang et al. (2011b)
Streptomyces sp.	2-Hydroxy-3,5,6-trimethyloctan-4-one	Larvicidal	Deepika et al. (2011)
Chromobacterium violaceum ESBV 4400	Violacein	Larvicidal & pupicidal	Baskar and Ignacimuthu (2012)
Streptomyces sp.,VITSVK5	5-(2,4-Dimethylbenzyl) pyrrolidin-2-one (DMBPO)	Larvicidal	Saurav et al. (2011)
Saccharopolyspora pogona	Butenylspinosyn	Insecticides	Lewer et al. (2009)

Source: Vijayabharathi et al. (2014b)

important to identify high nodulating genotypes for developing an efficient variety. ICRISAT had done series of research in identifying high nodulating genotypes in all of its mandate legumes including chickpea, pigeon pea, and groundnut (Nigam et al. 1985; Rupela et al. 1995; Rupela and Johansen 1995). On the other hand, identifying non-nodulating legumes as a reference for quantifying BNF is a key feature in BNF research, and ICRISAT had also identified non-nodulating variants in all of its mandate crops including chickpea (Rupela 1992), pigeon pea (Rupela and Johansen 1995), and groundnut (Nambiar et al. 1986). Such selection, when developed, should be used not only in crossing programs as sources of high BNF genes but should also be developed as cultivars after evaluation.

ICRISAT had also contributed significantly to identifying effective rhizobial strains from chickpea, pigeon pea, and groundnut (Rupela et al. 1991). It also observed the effect of soil depth, cropping pattern, and season in influencing the soil rhizobial counts and identified that chickpea rhizobial counts have maintained even after cropping with pigeon pea, groundnut, and maize but not on rice where the 100-fold decrease was noticed (Rupela et al. 1987). ICRISAT always shared its rhizobial germplasm to researchers around the world. One set of the rhizobial collection at ICRISAT was transferred to Indian Agricultural Research Institute (IARI), New Delhi, India, and another set to University of Queensland, Australia, and CSIRO, Australia. The collection comprises 800 rhizobia strains nodulating chickpea, groundnut, and pigeon pea (Rupela 1997).

In addition to the legume-rhizobia symbiosis, nonsymbiotic N fixation has also been studied mainly on pearl millet and sorghum. Wani (1986) reported genotypic variation in germplasm lines of sorghum and pearl millet for rhizospheric nitrogenase activity. In these studies, of the 184 pearl millet germplasm tested, 18 lines enhanced nitrogenase activity (> 460 nmol C_2H_4 h^{-1} 15 cm diam $core^{-1}$) in the 0–15 cm rhizosphere soils, while 2 lines, J1407 and Gam 73, were reported be to consistently active over several seasons. Similarly, of the 334 sorghum germplasm, 28 lines enhanced nitrogenase activity (>460 nmol C_2H_4 h^{-1} 15 cm diam $core^{-1}$) (Wani 1986). Dart and Wani (1982) observed the effects of inoculation of *Azotobacter* and *Azospirillum* on the grain weight (increased up to 22%) and dry matter (increased up to 29%) of sorghum. Besides all these significant contributions on BNF research, ICRISAT had to freeze BNF research in the mid-1990s due to lack of policy support and funding opportunities. In later years, ICRISAT research focus has been diverted toward the use of low-cost biological inputs in influencing crop sustainability. Long-term experiments were conducted for a period of 9 years in ICRISAT with a new approach in calculating sustainability index with the consideration of nutrient, biological, microbial, and crop indices and demonstrated that the low-cost biological inputs obtained the highest sustainability index than the conventional systems (Hameeda et al. 2006).

ICRISAT and a few private sector biopesticide manufacturing companies initiated the ICRISAT-Private Sector Biopesticide Research Consortium (BRC) in January 2005, which was later renamed as Bio-products Research Consortium to include PGPR and biofertilizers (Rupela et al. 2005). Eleven biopesticide/biofertilizer companies joined the consortium as its founding members. The overall goal of BRC was to make quality biopesticides and other bio-products to the farming community at an affordable price. ICRISAT had a collection of >1500 microbial germplasm (many with PGPR and biopesticidal properties), a few on-the-shelf technologies [such as *Helicoverpa* nuclear polyhedrosis virus (HNPV) and a few proven biopesticidal microbial strains], fermentation technologies, small-scale fermenters, and expertise in policy issues related to biopesticide testing and registration. On the other hand, the biopesticide/biofertilizer companies had medium- to large-scale capacity factories to manufacture bio-products and also the needed market linkages with a network of agro-dealers. The BRC Phase I was implemented with good success (2005–2007), and Phase II was started in 2008. Unfortunately, only 3 out of 11 companies continued their membership.

In recent times, ICRISAT research is focused more toward the usage of PGP microbes and their secondary metabolites for crop production and protection of our mandate crops. ICRISAT has isolated and identified more than 1500 PGP microorganisms including bacteria and actinobacteria, isolated from vermicompost and rhizospheric soils of rice and chickpea. Of the 1500, 59 PGP bacteria (mostly *Bacillus* spp. and *Pseudomonas* spp.) and actinobacteria (mostly *Streptomyces* spp.) were documented for their PGP traits, evaluated under field conditions (Gopalakrishnan et al. 2014a). Some of the promising PGP bacteria including *Pseudomonas monteilii*, *P. plecoglossicida*, *Brevibacterium altitudinis*, *B. antiquum*, *Enterobacter ludwigii*, and *Acinetobacter tandoii*, isolated from system of rice intensification fields, were documented for their PGP traits under field conditions on rice. These bacteria enhanced root weight, root length and volume, tiller numbers, panicle numbers, stover yield, and grain yield (Gopalakrishnan et al. 2012). Actinobacteria such as *Streptomyces* sp., *S. caviscabies*, *S. globisporus* subsp. *caucasicus*, and *S. griseorubens* were also demonstrated for their PGP performance on rice (Gopalakrishnan et al. 2014b). A PGP diazotrophic bacterium *P. geniculata* IC-76, isolated from chickpea nodules, enhanced plant growth and agronomic traits including nodule weight, pod weight, and seed weight (Gopalakrishnan et al. 2015) under field conditions on chickpea.

Besides increasing plant growth and yield traits, they also significantly enhanced rhizospheric available phosphorus (13–44%), total nitrogen (8–82%), and organic carbon (OC; 17–39%). Production of hydrolytic enzymes, including chitinase, cellulase, protease, and lipase, by these bacteria and actinobacteria (Table 2.5), is an additional evidence for the increased soil OC and total nitrogen contents (Gopalakrishnan et al. 2014a, b). Soil health indicators such as microbial biomass nitrogen (MBN; 7–321%), microbial biomass carbon (MBC; 23–48%), and dehydrogenase activity (14–278%) were also found to enhance on inoculated plots over the uninoculated control plots on chickpea (Gopalakrishnan et al. 2015), rice (Gopalakrishnan et al. 2012, 2013, 2014b), and sorghum (unpublished). Figures 2.1, 2.2, and 2.3 illustrate the results of field trials of PGP bacteria/actinobacteria on enhancing soil health traits.

Apart from their plant growth and yield promotion and soil health traits, PGP bacteria were also found to have antagonistic traits and act as biocontrol agents. PGP bacteria including *B. antiquum*, *P. plecoglossicida*, *E. ludwigii*, *B. altitudinis*,

Table 2.5 Extracellular enzyme profile identified for PGP bacteria and actinomycetes

Isolates	Cellulase	Chitinase	Lipase	Protease
PGP bacteria				
SRI-156	+	+	+	+
SRI-158	+	+	+	+
SRI-178	+	+	+	+
SRI-211	+	+	+	+
SRI-229	+	+	+	+
SRI-305	+	+	+	+
SRI-360	+	+	+	+
SBI-23	+	–	–	+
SBI-27	+	–	–	+
PGP actinomycetes				
KAI-26	+	+	+	+
KAI-27	+	+	+	+
KAI-32	+	+	+	+
KAI-90	+	+	+	+
KAI-180	+	+	+	+
SAI-13	+	+	–	+
SAI-25	+	+	+	+
SAI-29	+	+	–	+

Source: Gopalakrishnan et al. (2014a)

A. tandoii, and *P. monteilii* and actinobacteria including *S. setonii*, *Streptomyces* sp., *S. tsusimaensis*, *S. africanus*, and *S. caviscabies* were found to have antagonistic activity against soilborne plant pathogens including *Macrophomina phaseolina* (causes charcoal rot in sorghum) and *Fusarium oxysporum* f. sp. *ciceri* (causes wilt in chickpea) under both greenhouse and field conditions (Gopalakrishnan et al. 2011a, b). These PGP bacteria/actinobacteria were also found to produce hydrolytic enzymes (in the context of biocontrol) including chitinase and β-1,3-glucanase (Gopalakrishnan et al. 2014a). In another study, 15 *Streptomyces* spp. were found to have broad-spectrum insecticidal activities against lepidopteran insect pests including *Spodoptera litura*, *Helicoverpa armigera*, and *Chilo partellus* (Vijayabharathi et al. 2014a). Two insecticidal metabolites, N-(1-(2,2-dimethyl-5-undecyl-1,3-dioxolan-4-yr)-2-hydroxyethyl)stearamide and cyclo(Trp-Phe), have been isolated and purified from *Streptomyces* sp. (Sathya et al. 2016a; Gopalakrishnan et al. 2016a).

In the context of formulations, ICRISAT is using peat-based formulation for groundnut, pigeon pea, and chickpea rhizobial inoculants. Quality of microbial inoculants can be improved only if good carrier is used for maintaining and multiplying. In order to find whether peat can be used as suitable carrier material for rhizobial inoculant, a total of 16 rhizobia (six rhizobia specific for chickpea and five each rhizobia specific for pigeon pea and groundnut) were inoculated on sterilized peat and allowed to multiply at 28 ± 2 °C for 15 days. At the end

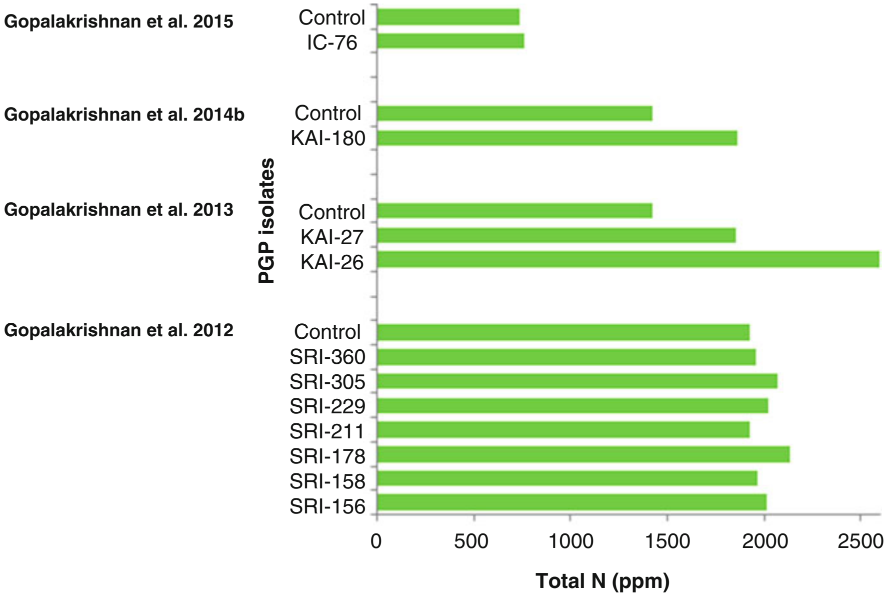

Fig. 2.1 Effect of PGP bacteria and actinomycetes on soil total N under field conditions of chickpea and rice cultivation. Control indicates the treatment groups without any PGP bacterial inoculation. (Source: Sathya et al. 2016b)

incubation and at 1-month interval for 10 months, peat-based inoculants were tested for survival and longevity of rhizobia. The rhizobia were enumerated as colony-forming units (CFU). The results indicated that all 16 rhizobia survived and maintained purity (at least 10^8 CFU/ml) up to 9 months in peat-based carrier materials (Table 2.6).

2.6 Commercialization

Voluminous data and information on better understanding of commercialization are available for various formulation technologies and longevity and efficacy of the PGP bacteria and/or rhizobia. However, still the quality of PGP bacteria/rhizobia available in the market worldwide is of suboptimal or poor quality. Development of rhizobia as inoculants for leguminous crops is the most valuable contributions ever made by science to agriculture, as BNF has been demonstrated to reduce N fertilizer use (Fred et al. 1932). Good quality PGP bacteria/rhizobia are available in the European Union market for a range of crop species (Guthrie 1896; Perret et al. 2000). However, in Asian countries, still the PGP bacteria/rhizobia inoculant technology is underdeveloped/slowly developing, and the major reasons are discussed here.

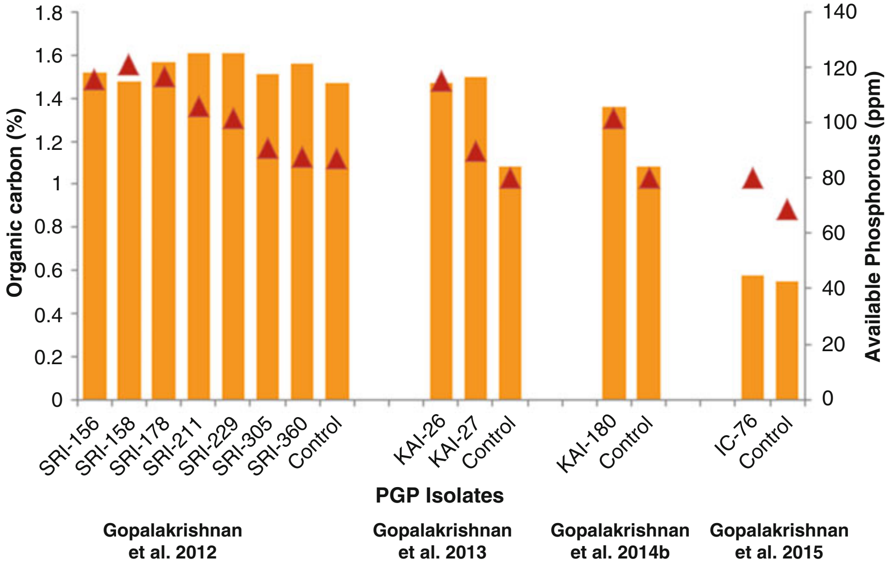

Fig. 2.2 Effect of PGP bacteria and actinomycetes on soil organic carbon and available phosphorous under field conditions of chickpea and rice cultivation. Solid bars (🟧) are the % organic carbon on the left axis, and solid triangles (▲) are the available phosphorous (ppm) on the right axis. Control indicates the treatment groups without any PGP bacterial inoculation. (Source: Sathya et al. 2016b)

2.7 Inoculant Selection and Development

The effective PGP microbial strain selection is the core for developing an inoculant. A set of must-have desirable and essential traits required for selection of inoculant strains including competence with native microbial flora, host specificity, and genetic stability are available (Brockwell et al. 1995). Asian countries including China, India, Myanmar, and Nepal have been reported with a vast diversity of nodulating rhizobia for many leguminous crops including chickpea, pigeon pea, and groundnut (Adhikari et al. 2012; Ansari et al. 2014; Htwe et al. 2015; Jiao et al. 2015). Diversity analysis of rhizobia under hostile environments such as soils with alkalinity, acidity, and micronutrient deficiency was also reported (Biate et al. 2014; Mishra et al. 2014; Unno et al. 2015; Singh et al. 2016). Biogeographic and phylogenetic diversity of rhizobia across the world are available through two genome sequencing reports (Reeve et al. 2015). According to this report, among the 107 rhizobial strains, only 7 were from Asian origin. This suggests that further exploration and characterization of rhizobial biodiversity in Asian countries needs to be done in order to get good quality inoculant.

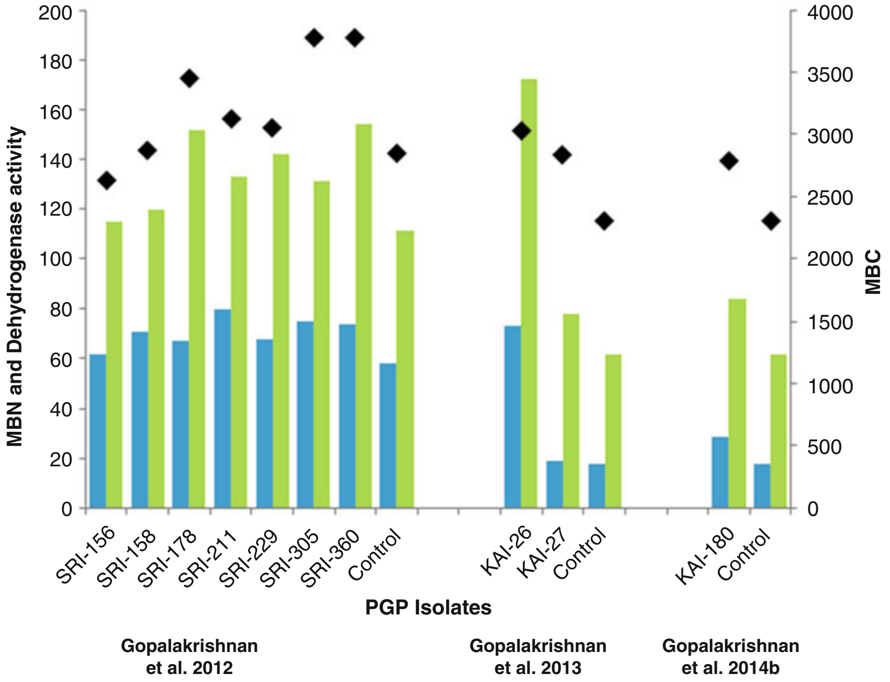

Fig. 2.3 Effect of PGP bacteria and actinomycetes on soil health indicators during field trials of rice cultivation. Solid bars (🟦; 🟩) are the microbial biomass nitrogen (μg g^{-1} soil) and dehydrogenase activity (μg TPF g^{-1} soil 24 h^{-}) on the left axis, and solid diamond (◆) is the microbial biomass carbon (μg g^{-1} soil) on the right axis. Control indicates the treatment groups without any PGP bacterial inoculation. (Source: Sathya et al. 2016b)

2.8 Conclusions

PGP microbe possesses a broad spectrum of benefits including plant growth and yield, defense against diseases, and survival under stress conditions. This chapter illustrates the potential of PGP bacteria and highlights its importance in plant growth induction, defense pathways, and resistance spectrum available against various stresses on many crops. However, the extent of success in realizing the benefits of PGP tends to diminish as it moves from laboratory to greenhouse and to fields, which reflects the scarcity of research on the beneficial effects of PGP microbes under field conditions. Therefore, the generation of comprehensive knowledge on screening strategies and intense selection of best strain for rhizosphere competence and survival is the need of the hour to enhance the field-level successes.

Table 2.6 Viability and longevity of 16 rhizobia in peat formulations over 10 months

Rhizobial isolates	Colony-forming units (CFU/ml) at different months (values are mean of 3 replications)										
	0	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th
Chickpea rhizobia											
IC-53	8.5×10^{9}	8×10^{9}	6.5×10^{9}	2.7×10^{9}	1.2×10^{9}	2.9×10^{8}	2.8×10^{8}	2.8×10^{8}	2.5×10^{8}	2×10^{8}	1.1×10^{8}
IC-59	3.3×10^{9}	2.3×10^{9}	2.2×10^{9}	1.7×10^{9}	2.3×10^{8}	1.5×10^{8}	1.3×10^{8}	1.2×10^{8}	1×10^{8}	3×10^{7}	2.0×10^{7}
IC-76	4.6×10^{9}	3.5×10^{9}	2.3×10^{9}	2×10^{9}	1.7×10^{9}	4.2×10^{8}	4×10^{8}	3.9×10^{8}	3.7×10^{8}	2.65×10^{8}	1.2×10^{8}
IC-2002	16×10^{9}	12×10^{9}	6.6×10^{9}	4.3×10^{9}	1.5×10^{9}	2.5×10^{8}	2.2×10^{8}	2×10^{8}	1.7×10^{8}	0.9×10^{8}	2.3×10^{7}
IC-2018	7.5×10^{9}	7.2×10^{9}	5.6×10^{9}	4.2×10^{9}	16×10^{8}	4.7×10^{8}	4.2×10^{8}	3.6×10^{8}	3.2×10^{8}	1.8×10^{8}	1.3×10^{8}
IC-2099	4.4×10^{9}	3.8×10^{9}	2.4×10^{9}	2.1×10^{9}	7×10^{8}	2.1×10^{8}	2×10^{8}	1.7×10^{8}	1.5×10^{8}	9×10^{7}	7.0×10^{7}
Pigeon pea rhizobia											
IC-3195	16×10^{9}	8.7×10^{9}	3.4×10^{9}	2.5×10^{9}	1.9×10^{8}	1.1×10^{8}	9×10^{7}	8×10^{7}	4×10^{7}	1×10^{7}	4×10^{6}
IC-4059	8.6×10^{9}	7.5×10^{9}	5.8×10^{9}	3.6×10^{9}	1×10^{9}	5.2×10^{8}	4.9×10^{8}	3.4×10^{8}	2.3×10^{8}	1.1×10^{8}	4.1×10^{7}
IC-4060	18×10^{9}	17×10^{9}	7.6×10^{9}	4.1×10^{9}	1×10^{9}	4.5×10^{8}	4.3×10^{8}	4.1×10^{8}	3.1×10^{8}	1.3×10^{8}	7×10^{7}
IC-4061	15×10^{9}	11×10^{9}	9.7×10^{9}	4.2×10^{9}	1.7×10^{9}	4.4×10^{8}	4.2×10^{8}	4.1×10^{8}	3.6×10^{8}	2.2×10^{8}	1.1×10^{8}
IC-4062	7.7×10^{9}	6.3×10^{9}	2.2×10^{9}	1.9×10^{9}	2.3×10^{8}	3.4×10^{8}	2.6×10^{8}	2.1×10^{8}	1.4×10^{8}	1×10^{8}	6×10^{7}
Groundnut rhizobia											
IC-7001	5.2×10^{9}	4.8×10^{9}	4×10^{9}	2×10^{9}	1.9×10^{8}	1.2×10^{8}	2.3×10^{8}	2.210^{8}	2×10^{8}	1×10^{8}	2.4×10^{7}
IC-7017	7.6×10^{9}	6.6×10^{9}	3×10^{9}	2.1×10^{9}	2.2×10^{8}	1.7×10^{8}	1.6×10^{8}	1.3×10^{8}	1.1×10^{8}	7×10^{8}	3.3×10^{7}
IC-7029	8.2×10^{9}	6.8×10^{9}	5.2×10^{9}	3.6×10^{9}	2.0×10^{9}	5.8×10^{8}	5.5×10^{8}	5.2×10^{8}	4.8×10^{8}	1.3×10^{8}	1.5×10^{7}
IC-7100	6.1×10^{9}	8.2×10^{9}	6.3×10^{9}	3.6×10^{9}	1.7×10^{9}	3.7×10^{8}	3.2×10^{8}	3×10^{8}	2.7×10^{8}	1.3×10^{8}	7×10^{7}
IC-7113	8.1×10^{9}	7.5×10^{9}	5.4×10^{9}	4.5×10^{9}	2.1×10^{9}	5.5×10^{8}	5.1×10^{8}	4.5×10^{8}	3.7×10^{8}	1.9×10^{8}	1.2×10^{8}

Source: Gopalakrishnan et al. (2016b)

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