Chapter 12
Understanding the Evolution of Plant Growth-Promoting Rhizobacteria

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Abstract Soil is an integral part of the complicated natural environment which is very much alive with complex ecosystem of microbes. Among them, the symbiotic association of rhizobacteria with plants especially on agriculturally important crops is very much advantageous in improving the soil and plant health. These plant growth-promoting rhizobacteria (PGPR) have evolved over the years and involved in many plant functions such as growth promotion, root development, colonization, production of metabolites and in eliciting plant defence mechanism against abiotic and biotic agents. The PGPR's ability to fix the atmospheric nitrogen, solubilize phosphate, potassium and zinc, produce siderophore along with wide variety of phytohormones and secondary metabolites such as antibiotics have attributed to their significance as biocontrol agents. These functions lead to their application as biofertilizers, biopesticides, bioprotectants and phytostimulators. The employment of these PGPR is very much important in agricultural fields as they reduce the burden of chemical fertilizers and pesticides to the farmers and in turn promises an increased crop yield. This chapter discusses the symbiotic association of PGPR with plants in detail including their direct and indirect mechanisms and basis of their induced systemic defence mechanism. It also highlights the use of bioinoculants and nano-formulations of PGPR as an effective tool towards enhanced agricultural production and to combat the plant diseases in an eco-friendly manner.

Keywords Rhizobacteria · PGPR · Symbiosis · Biocontrol · Antifungal · Agriculture

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12.1 Introduction

The plant root system interacts with a large mixture of microorganisms and these interactions define the extent of association between the plant and microbe. This relationship between the soil bacteria i.e. rhizobacteria and plant is very precise and often influences a lot of factors such as plant growth, soil health, microbiome and the environment (Muller et al. 2016). Rhizobacteria such as rhizobia, root nodule bacteria of the many leguminous plants, undergo symbiotic association and facilitate in biological nitrogen fixation (Peix et al. 2015). In the arid and semi-arid regions, this rhizobia-legume symbiosis is extensively investigated and many studies have reported for their significant source of Nitrogen (N) input in the agricultural fields (del Pozo et al. 2000; Buhian and Bensmihen 2018). The bioavailability of nutrients and minerals at a given soil location is highly dependent on the type of residing rhizobacteria. These nutrient transformations occur depending on the variety of plant–microbial symbiosis. The symbiotic association between the plant and microbe is the key driving factor for the plant growth and even affects the local soil ecosystem (van der Heijden et al. 2008; Verbon and Liberman 2016).

With greater demand for sustainable agriculture, the application of PGPR to crops is beneficial and essential. These root-associated bacteria are diverse in nature and colonize a wide variety of agricultural crops. The genera of rhizobacteria that exhibits the plant growth promotion include *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Mycobacterium*, *Mesorhizobium*, *Pseudomonas*, *Rhizobium* and *Streptomyces*. These ecological engineers have an association with many agriculturally important crops namely barley, corn, canola, chickpea, groundnut, oats, maize, wheat, rice, lentils, peas, rye and radicchio (Podile and Kishore 2006). These PGPR directly synthesize compounds and provide them to the plant to assist in their well-being. Sometimes they indirectly also facilitates the plant root system to absorb certain nutrients from the soil environment. In this manner, either directly or indirectly the rhizobacteria symbiotically benefit the plant and also fight-off against disease-causing pathogens (Maksimov et al. 2011).

During recent years, several research studies have reported the significance of rhizosphere microbes in playing an important role in the plant growth promotion, in formation of important microbial consortia and disease resistance in host plants (Bhattacharyya and Jha 2012; Alekhya and Gopalakrishnan 2017; Vijayabharathi et al. 2018; Anusha et al. 2019; Gopalakrishnan and Vadlamudi 2019; Kim et al. 2019). Also, they emerged as a potential alternative for chemical fertilizers and have shown promising crop yield outputs in agricultural fields (Laslo and Mara 2019). These PGPR, with high abundance and low cost could be further exploited for their applicative advantages in sustainable agriculture over conventional practices.

PGPR are mainly known to associate with the agriculturally important cereals and leguminous crops. These cereals and legumes are the vital food source for humans and they were also widely used for the livestock (FAO 2018). Hence, the PGPR role as cereals/leguminous plant growth and yield promoters is very much in need of the hour with ever-increasing global population. In the present chapter, the mechanisms and applications of the rhizobacteria were comprehensively analysed to further exploit them and to understand the pre- and post-colonization strategies with changing times. The underlying cellular and molecular mechanisms of rhizosphere microbiota were also studied for their efficacy as bioinoculants.

12.2 Biology of PGPR

Rhizobacteria are a soil bacterium that infects the host plant root system and help plants in many ways. They form a symbiotic association with the host plants and facilitate its growth and development by the exchange of nutrients and metabolites. The main mechanisms that aid in these host-microbe interactions are symbiosis, nitrogen fixation and growth promotion.

12.2.1 Symbiosis

The symbiosis between the rhizobia and legumes triggers the nodulation process and they are fully functional in 3–4 week old plants. The specificity of these nodules usually depends on the type of microbe associated to it. The plant flavonoids are the important metabolites that are utilized by these soil rhizobia to recognize the host system and initiate the symbiotic nodule association. Especially, the aglycones play a key role in the activation of rhizobial *Nod* genes namely *NodA*, *NodB* and *NodC* (Perret et al. 2000). Apart from the flavonoids, the levels of calcium also alter the plant roots hair structure to develop the nodules (Ehrhardt et al. 1996; Downie and Walker 1999). It is reported that *NIN*, a transposon, is involved in the nodule formation and it is the first cloned gene to successfully develop nodules in the host plant (Schauser et al. 1999). During the formation of these nodules an infection thread is formed between the symbiotic bacteria cell surface and host plant wall. From many studies, it is evident that the root lectins facilitated this attachment of rhizobial infection thread and the nodulation process in the plants (Kijne et al. 1997; Van Rhijn et al. 2001). Galibert et al. (2001) reported higher content of G + C in the nodulating and nitrogen fixation genes.

Rhizobia present in soil usually reside in large colonies and it is very much essential to communicate among them. It is evident from various research studies that rhizobacteria have a complex quorum sensing system to form a symbiotic relationship with the host plant. Some of the rhizobia namely, *Rhizobium fredii*, *Rhizobium leguminosarum* and *Sinorhizobium meliloti* are known to have a well-established quorum sensing signalling for nodulation and nitrogen fixation. Mainly this quorum sensing is mediated by the production of *N*-acyl homoserine lactones (AHLs) by rhizobial strains, which involves the chemical crosstalk (González and Marketon 2003). The purpose of understanding this diverse legume-rhizobial chemical and molecular symbiosis is important because of their ability to fix atmospheric nitrogen and pathogen suppression. By recognizing the evolution of host-rhizobial symbioses in agriculturally important crops, we may have better applicative value towards sustainable agriculture.

The biological nitrogen fixation is a major contribution of soil rhizobia to the plant kingdom. Nitrogen is one of the major atmospheric gases and very much essential for the plant growth and photosynthesis (Wagner 2012). But the available form of nitrogen (NH_3) is only made available by these rhizobacteria through the process of biological nitrogen fixation in the root nodules of the plant. Rhizobia are the best-known group of symbiotic soil bacteria that fix nitrogen in relation with a wide variety of agriculturally important crops (Peoples et al. 1995; Dawson 2008; Lindstrom and Mousavi 2010). Applications of chemical fertilizers have significantly reduced in agriculturally important crops due to rhizobia being an efficient source of nitrogen and nutrients (David and Ian 2000). The process of biological nitrogen fixation is regulated by a group of bacterial *nif* (*nifH*, *nifD* and *nifK*) genes. The structure and function of this *nif* gene are similar in many diazotrophs such as *Azotobacter vinelandii*, *Bradyrhizobium japonicum*, *Herbaspirillum seropedicae* and *Pseudomonas stutzeri* (Fischer 1994). Due to this property of biological nitrogen fixation, many rhizobacterial strains were inoculated in legume plants and a significant increase in nodulation and nitrogen fixation was observed. The size, weight and number of nodules and fixed nitrogen were found to significantly enhance in the PGPR inoculated plants compared to un-inoculated plants (Islam et al. 2013; Kuan et al. 2016; Gopalakrishnan et al. 2017, 2018). Hence, these bacteria are regarded as renewable source of nitrogen in the fields and environment that majorly contribute to the conservation of the soil health.

12.2.2 Growth Promotion

Many research studies have reported that the treatment of PGPR has enhanced the plant growth and nutrition status. This proves the fact that these PGPR have the ability to increase the soil fertility and microbial diversity through the production of various root exudates namely extracellular metabolites, hormones, signal compounds and antibiotics (Van Loon 2007; Wani and Gopalakrishnan 2019). PGPR have the capacity to synthesize the phytohormones that directly aid in the plant development. Many reports have identified the synthesis of indole acetic acid (IAA) by PGPR which is mainly responsible for the maturation of plant root system (Patten and Glick 2002; Remans et al. 2008). Cytokinins were also observed and regulated the cell division and root–shoot development of the host plants when inoculated with PGPR (Hussain and Hasnain 2009). In addition, ethylene, gibberellic acid and abscisic acid were also emitted by PGPR that aids in the plant development (Dodd et al. 2010).

The importance of these soil bacteria is mainly attributed to their ability to produce siderophores, which greatly assists in the iron uptake of the host plants. In the presence of metal competition these siderophores aid in the solubilization and diffusion of iron into the plant cell walls (Crowley 2006). This siderophore production also assists in the PGPR colonization by evading other microbial and fungal pathogens. In iron-deficient agricultural fields, the siderophore expressing PGPR are promising alternative for the bioavailability of iron to soil and plants (Sayyed et al. 2013). Fertilizer applications will secure enough phosphorous (P) in the agricultural fields but, these PGPR are the main solubilizers that provide soluble form of phosphate to the crops. PGPR such as *Bacillus*, *Pseudomonas*, *Rhizobium* and *Streptomyces* species are known to enhance the phosphate uptake in the inoculated plants (Ramaekers et al. 2010). Apart from the plant growth and development, these PGPR also influence the yield of the crops, by increasing the mineral density of the seeds (Sathya et al. 2016). Enhanced content of Fe, Zn, Mg, Mn, Ca and Cu were reported in the seeds of PGPR inoculated crops such as wheat, rice chickpea and pigeon pea (Rana et al. 2012; Sharma et al. 2013; Gopalakrishnan et al. 2016a). This ability of biofortification by the PGPR in the agricultural inoculated crops will provide greener choices for better nutrition intake in humans.

In evidence, various greenhouse and field research studies conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), based at Patancheru, Hyderabad, India, with different strains of PGPR have shown multiple growth potentials by enhancing the plant growth-promoting and biocontrol traits in the PGPR inoculated host crops (Table 12.1). This emphasizes the significance of PGPR utilization in the future for sustainable agricultural practices in legume crops.

12.3 Role of PGPR as Biocontrol Agents

It is reported that PGPR have antagonistic activities against wide array of bacterial, viral and fungal pathogens. These soil rhizobacteria, within its habitation, exhibit a variety of defence mechanisms to control and fight against the invaders. They trigger the host plant induced systemic resistance i.e. alters the plant cell wall, pathways and metabolites in response to the pathogen infection. Hence, the utilization of PGPR for the management of soil-borne pathogens is highly beneficial in the agriculturally important crops, as it reduces the use of chemical fungicides and eco-friendly in nature (Gopalakrishnan and Vadlamudi 2019). The anti-oxidant enzymes namely, peroxidase, phenylalanine ammonia-lyase, superoxide dismutase and polyphenol oxidase are elicited in the infected host plants by the PGPR to trigger the defence pathways (Gopalakrishnan et al. 2019). This in turn initiates the production of plant defence metabolites such as phenolic compounds, phytoalexins, lytic enzymes and antibiotics (Conrath et al. 2001; Walters et al. 2005). The antibiotics produced by these soil bacteria, especially by *Bacillus* spp. were known to suppress many pathogenic bacteria (Maksimov et al. 2011). Metabolic compounds such as lipids produced by *Bacillus* and *Pseudomonas* are effective biocontrol agents against many bacteria, fungi and protozoans (Raaijmakers et al. 2010). PGPR especially, the

Table 12.1 In vitro evaluation of PGPR strains for PGP and biocontrol traits

PGPR	NCBI no.	PGP properties			Biocontrol properties						Crops evaluated (greenhouse/ field)	References
		IAA	*Sid.*	*HCN*	*Cel.*	*Lip.*	*Pro.*	*Chi.*	$\beta - 1,3$	P Sol		
Acinetobacter tandoii (SRI-305)	JQ247013	–	+	–	+	+	+	+	–	+	Chickpea; Rice	Gopalakrishnan et al. (2012), Sreevidya and Gopalakrishnan (2015), Anusha et al. (2019)
Bacillus sp. (VBI-4)	KM250376	+	+	+	+	+	+	+	+	–		
Bacillus sp. (VBI-19)	KM250377	+	+	+	+	+	+	+	+	–		
Bacillus sp. (VBI-23)	KM250378	+	+	+	+	+	+	+	+	–		
Bacillus sp. (SBI-23)	KM250375	+	+	+	+	+	+	+	+	–		
Bacillus altitudinis (SRI-178)	JQ247010	+	+	+	+	+	+	+	–	+		
Bacillus xiamenensis (BS-10)	MF359733	+	–	–	+	+	–	–	+	–		
Bacillus safensis (BS-15)	MF359733	+	+	+	+	+	+	+	+	–		
Bacillus subtilis (BS-17)	MF359737	+	–	+	+	+	+	+	+	–		
Bacillus altitudinis (BS-19)	MF370070	+	–	+	+	+	+	+	+	–		
Bacillus altitudinis (BS-20)	MF370069	+	+	+	+	–	+	+	+	–		
Brevibacterium antiquum (SRI-158)	JQ247009	+	+	–	+	–	+	+	–	+		

Chryseobacterium indologenes (ICKM-4)	KX583496	+	+	+	+	+	+	–	+	–	Chickpea	Gopalakrishnan et al. (2017)
Chryseobacterium sp. (ICKM-17)	KX611375	+	+	–	+	+	+	+	+	–		
Chryseobacterium indologenes (ICS-31)	KY800376	+	–	–	+	+	+	+	–	+		
Enterobacter ludwigii (SRI-211)	JQ247011	+	+	+	+	–	+	+	–	+	Rice	Gopalakrishnan et al. (2012)
E. ludwigii (SRI-229)	JQ247012	+	+	+	+	+	+	+	–	+		
Pseudomonas plecoglossicida (SRI-156)	JQ247008	+	+	+	+	+	+	+	–	+	Rice; chickpea	Gopalakrishnan et al. (2017, 2018)
Pseudomonas monteilii (SRI-360)	JQ247014	+	+	+	+	+	+	+	–	–		
Paraburkholderia kururiensis (IC-76A)	MF373465	+	+	+	+	–	+	–	+	–		
Pantoea dispersa (ICKM-1)	KX583493	+	+	+	+	+	+	–	+	–		
Pseudomonas geniculata (ICKM-7)	KX583495	+	+	+	+	+	+	+	+	+		
Pseudomonas geniculata (ICKM-12)	KX583492	+	+	+	+	+	+	+	+	+		

(continued)

Table 12.1 (continued)

PGPR	NCBI no.	PGP properties			Biocontrol properties						Crops evaluated (greenhouse/ field)	References
		IAA	*Sid.*	*HCN*	*Cel.*	*Lip.*	*Pro.*	*Chi.*	$\beta - 1,3$	P Sol		
P. geniculata (ICKM-14)	KX611373	+	+	+	+	+	+	+	+	–		
Pseudomonas geniculata (ICS-30)	KX611376	+	+	+	+	+	+	+	–	+		
Rhizobium pusense (IC-59)	MF372582	+	+	+	+	+	+	–	+	–		
Stenotrophomonas maltophilia (IC-2002)	MF372584	+	+	+	+	–	+	–	+	–		
Stenotrophomonas pavanii (ICKM-9)	KX583494	+	+	+	+	+	+	+	+	+		
Stenotrophomonas maltophilia (ICKM-15)	KX611374	+	+	+	+	+	+	+	–	+		
Stenotrophomonas acidaminiphila (ICS-32)	KX611377	+	+	+	+	+	+	+	+	–		

IAA Indole Acetic Acid (μg/ml); *β, 1–3* β-1,3-glucanase (mg/ml); *Sid* siderophore; *HCN* hydrocyanic acid; *Cel* cellulase; *Lip* lipase; *Pro* protease; *Chi* chitinase. For HCN production, the following rating scale was used: 0 = no colour change; 1 = light reddish brown; 2 = medium reddish brown; and 3 = dark reddish brown

Streptomyces spp. produce various hydrolytic enzymes and acids that show antifungal ability against different agriculturally important fungal pathogens (Alekhya and Gopalakrishnan 2017; Vijayabharathi et al. 2018; Kim et al. 2019; Gopalakrishnan et al. 2019). This PGPR-plant interaction also enhances the jasmonic acid, salicylic acid and ethylene production, which in turn activates the induced and systemic acquired resistance to subdue the disease (Vleesschauwer and Höfte 2009). As the agriculturally important crops namely chickpea, pigeon pea, groundnut and soybean are more prone to the soil-borne pathogens, it is essential to utilize these rhizobacteria for their broad spectrum of biocontrol and plant growth-promoting activities.

12.4 Application of PGPR in Agriculture

As these soil rhizobacteria are advantageous in many ways and confer multiple benefits to the agriculture, application of these beneficial microbes led to their exploitation as biofertilizers and biopesticides. Nowadays many PGPR based bioproducts with high competence are prevailing in the agri-market. *Actinorhizobium* spp., *Azotobacter* spp., *Azospirillum* spp. and *Rhizobium* spp. based biofertilizers are the promising nitrogen suppliers in the agriculture fields (Marketsandmarkets 2014). The *Bacillus* spp. and *Pseudomonas* spp. were also widely used as biopesticides to increase the plant growth and suppress the pathogen (Sallam et al. 2013). Due to their unique specificity and less toxicity, PGPR are further formulated with inoculants to enhance their shelf life. Inoculants such as peat, compost, talc, alginate and chitosan are widely used to entrap these beneficial microbes (Vijayabharathi et al. 2016). PGPR bioinoculants, especially *Rhizobium* spp. could increase the bioavailability and shelf life of the bacteria in the field conditions and also protects against the adverse climate conditions and native microbial flora (Gopalakrishnan et al. 2016b).

In recent years, with the development of nanotechnology, techniques like micro and nano-encapsulation are also being utilized for the efficient delivery of these rhizobacteria. Nanoparticles such as silver, silica and chitosan, which are known to enhance the plant growth are used to encapsulate these rhizobacteria and their metabolites. This will aid in the improved efficacy and better management of plant growth and yield (Nayana et al. 2020). Nowadays, nanofibers are also being used to immobilize these microbial cells for targeted delivery (John et al. 2011). In order to maintain the viability of these beneficial PGPR, the inoculum will be coated over the seeds using spun nanofibers (De Gregorio et al. 2017). Apart from these, new applicative approaches must be identified in the future to explore these PGPR for more innovative bioproducts.

12.5 Commercialization

Various research studies have confirmed the potential of PGPR such as *Azospirillum*, *Bacillus*, *Pseudomonas*, *Serratia* and *Streptomyces* as growth-promoting and biocontrol agents in many horticultural and agricultural crops (Reddy 2014; Wani and Gopalakrishnan 2019). These strategies have led to their successful commercialization as bioproducts in the agri-market. From strain discovery, lab to field, formulations and mass production many steps are to be undertaken to successfully commercialize a PGPR product. Procedures such as documentation, regulations and registrations of the PGPR bioproduct are the main challenges during commercialization. Over the years, the manufacturing industry of these rhizobial inoculants has increased steadily in many countries. They are successfully applied either as single inoculants or co-inoculants to various crops namely legumes, maize, wheat, rice and sugarcane (Santos et al. 2019). But, factors such as long term efficacy, viability and expenditure act as the limiting factors in their commercialization (Hungria et al. 2005). Apart from that, the global market of PGPR products is also influenced by the different patenting policies and legislations in each continent of EU, US and Asia (Backer et al. 2018). But, measures are being undertaken to establish new legislations, alternative technologies, educating farmers and to provide financial support for successful product commercialization, as these PGPR reduce the cost of synthetic agrochemicals for the farmers and lead towards low-cost agricultural practices.

12.6 Conclusion

It is a well-established fact that these soil rhizobacteria are evolving day-by-day in their plant–microbe association. Hence, for sustainable agricultural practices, the researchers and entrepreneurs are attracted to these symbiotic microbes for their plant growth and development, biofertilization, rhizo-remediation, biofortification and disease resistance properties. The bioproducts of these PGPR are successfully enhancing the agricultural yields but are often discouraged by their inefficacy and less viability over a long time. Environmental factors also affect the growth and proliferation of these rhizobacteria in the field conditions. Hence, these limitations should be addressed by multidisciplinary research team for better PGPR formulations and crop protection.

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Conflict of Interest None.

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