Chapter 12 Endophytic Rhizobacteria for Mineral Nutrients Acquisition in Plants: Possible Functions and Ecological Advantages



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Abstract Nutrient-deficiency in agricultural soils is a major problem in many parts of the world, it is, therefore, artificial fertilizers are widely used to boost crop production. Unfortunately, these fertilizers are associated with a myriad of environmental problems hence, there is a need for viable alternatives. The realization that the plant microbiome can improve plant health, soil fertility, and crop productivity is one of the most fascinating scientific discoveries in the world. For several decades, rhizobacteria have been studied due to their various plant growth-promoting (PGP) traits. Endophytic rhizobacteria are unique plant microbiome that establish themselves within plant root tissues and exert beneficial functions to their hosts without harming them. A lot of emphases have been put on these bacteria as viable tools for sustainable agriculture and it is advanced that they could be better plant growth promoters than their external counterparts. However, this theory is not yet clearly understood. This chapter provides the current state of understanding of the putative functions of endophytic rhizobacteria and their future prospects for plant mineral nutrients acquisition. Their advantageous traits that largely advanced to facilitate these PGP functions are also discussed. Such informations can provide better opportunities for improved plant mineral nutrients acquisition and enhance the application of these microbes as viable strategies for sustainable agriculture.

Keywords Endophytes · Rhizobacteria · Sustainable agriculture · Plant growth promotion

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D. K. Maheshwari and S. Dheeman (eds.), *Endophytes: Mineral Nutrient Management, Volume 3*, Sustainable Development and Biodiversity 26, https://doi.org/10.1007/978-3-030-65447-4_12

12.1 Introduction

Agricultural activities are quickly gaining momentum to feed the rapidly growing population across the globe. One of them is excessive use of chemicals established as an effective tool to increase crop productivity of different crops. However, conventional agricultural practices have a lot of undesirable outcomes as the chemical inputs have commonly been linked to land degradation, environmental pollution, global warming, climate change, etc. (Steffen et al. 2015; Di Benedetto et al. 2017). For many decades, researchers all over the world have focused on alternative crop fertilization mechanisms such as the use of plant growth-promoting bacteria (PGPB) to replace the contemporary fertilization practices (Smith et al. 2016). In fact, these are free-living bacteria with unique capabilities of stimulating plant growth, either directly or indirectly through different mechanisms (Archana et al. 2013; Ahemad and Kibret 2014; Kumar et al. 2014). Glick (2014) and later, Baliyan et al. (2018) described the exploitation of such organisms as a viable and environment friendly technology befitting for sustainable crop production in eco-safe ways.

Among them, endophytes are organisms that spend all or part of their lives in plant cells or tissues with different degrees of dependence without harming their hosts (Compant et al. 2010; Hardoim et al. 2015; Brader et al. 2017; Lata et al. 2019) and can be recovered from surface-sterilized plant tissues (Santoyo et al. 2016). As many plant species as exist on earth host bacterial endophytes (Ryan et al. 2008), and several endophytic bacteria like the Proteobacteria, Firmicutes Actinobacteria, and Bacteroidetes have putative PGP functions (Rosenblueth and Martinez-Romero 2006; Bulgarelli et al. 2013; Hardoim et al. 2015; Liu et al. 2017). Endophytic bacteria have been isolated from various plant parts including stems, roots, seeds, leaves, fruits, ovules, tubers, nodules, etc. (Benhizia et al. 2004; Pandey et al. 2018). Nevertheless, below ground potential i.e., plant roots harbor the greatest populations of these bacteria in comparison to aerial parts (Rosenblueth and Martinez-Romero 2006; Taghavi et al. 2010), at approximately 10^4 – 10^6 per g of root tissue (Compant et al. 2010; Bulgarelli et al. 2013).

Depsite occupying different ecological niches, endophytic bacterial populations employ PGP mechnaisms similar to those of free-living rhizosphere bacteria (Compant et al. 2005). The common PGP mechanisms can either be direct such as nitrogen-fixation, solubilization of nutrients, production of siderophores and phytohormones or indirect such as the suppression of plant pathogens and diseases (Suman et al. 2016; Lata et al. 2018). Diverse PGP bacterial endophytes have been explored and applied for crop yield enhancement under nutrient-poor conditions (Rosenblueth and Martinez-Romero 2006; Liu et al. 2017). Several studies demonstrate their positive effects in different food and cash crops such as the banana (*Musa* spp.) (Patel et al. 2017b), maize (*Zea mays*) (Alves et al. 2015), tomato (*Lycopersicon esculentum*) (Upreti and Thomas 2015), groundnut (*Arachis hypogaea*) (Dhole et al. 2016), and many more outlined by various workers (Hardoim et al. 2015; Pandey et al. 2018; Maheshwari 2018). Literature documents that endophyte-elicited PGP activities culminate into increased seed germination rates, biomass, chlorophyll, N and protein contents, root and shoot lengths, yield, and tolerance to abiotic stresses (Verma et al. 2013, 2015). The rhizobia which are the best-understood endophytes are critical for Nitrogen (N) nutrition in leguminous plants (Santoyo et al. 2016).

Although endophytic rhizobacteria have widely been investigated, their significance in improving plant mineral nutrient acquisition has emerged quite recently (Harman and Uphoff 2019), and literature propounds that they could be better plant growth promoters and possess certain advantageous traits that give them an edge over their external counterparts (Coutinho et al. 2015; Asaf et al. 2017). However, this theory is not yet clearly understood as both are similar to their facilitation of plant mineral nutrients acquisition. This chapter reviews the potential functions of endophytic rhizobacteria in the acquisition of certain plant mineral macronutrients such as N, P, K and micronutrients like Zn and Fe. The putative advantageous traits that facilitate these functions and make them suitable candidates for enhancing mineral nutrients acquisition in plants are also discussed. Such information will enrich our knowledge on these important plant endophytic microbiome and possibly pave the way for their complete understanding and utilization as biofertilizers for sustainable crop production.

12.2 Putative Functions of Endophytic PGPR for Mineral Nutrients Acquisition in Plants

Several studies demonstrate the diversity and functions of endophytic rhizobacteria toward plant mineral nutrients acquisition and general PGP activities. In this section, we outline some of these studies and functions to demonstrate the importance of these bacteria in plant mineral nutrition.

12.2.1 Endophytic Rhizobacteria and Nitrogen Acquisition in Plants

Nitrogen is the most important nutrient required for plant growth (Verma et al. 2019). Although the atmosphere contains about 78% N, most of this is present in inert form and inaccessible to plants, making it a major plant-limiting nutrient. Artificial N-fertilizers are commonly applied to supply N to plants. However, out of every 100 Tg of N applied in agricultural fields globally, only about 17 Tg are utilized by plants and the rest is either lost or accumulates in the environment with serious implications to the soil and environment (Erisman et al. 2008; Howarth 2008). The microorganisms can convert excess ammonium or nitrate in the soil into nitrous oxide (N₂O), a potent greenhouse gas (GHG) (Kandel et al. 2017), whose effects are reportedly much worse than that of CO₂ (Ramaswamy et al. 2001).

Endophytic N₂-fixing rhizobacteria are now emerging as one of the most efficient and environmentally sustainable approaches for increasing N acquisition for crops (Suman et al. 2016; Defez et al. 2017). Their potential has been illustrated in many studies, examples of which are provided in Table 12.1. It is proposed that endophytic N₂-fixers can enable plants to survive under N-limiting conditions better than their external rhizobacterial counterparts (Gupta et al. 2013). For instance, the N₂ fixation process requires energy to reduce the bonds in the N₂ molecules and the endophytic N₂-fixers can obtain the required energy from plant host tissues (Olivares et al. 2013). Similarly, their internal plant habitats offer favorable micro-aerobic environments that are more conducive to the nitrogenase enzyme complex that catalyzes the N₂ fixation process (Doty et al. 2016).

Although all diazotrophs are important for providing N to plants and enhancing their growth (Kumar et al. 2017), endophytic rhizobacteria not only provide the fixed N to their plant hosts more directly but also more efficiently (Suman et al. 2016; Lata et al. 2019). This is because the BNF process is largely mediated by the *nif* and *fix* genes whose transcriptions are primarily induced under low-oxygen conditions as in the interior plant tissues parts that host the endophytes (Bhagya and Rajkumar 2017). Literature suggests that the fixed N_2 is converted to NH_4^+ in the bacterial cytoplasm and subsequently excreted into the host cytoplasm (Mia and Shamsuddin 2010), where it is assimilated into glutamate and transported in the xylem from the plant roots to their shoots as the major source of organic N (Nawaz et al. 2017). Thus the endophytic diazotrophs can release NH_4 easily and directly into the plant host cell cytoplasm. Although some N2-fixers can assimilate the produced NH4 into organic compounds, most N₂-fixing strains have unique regulatory mechanisms to secrete the NH₄ outside their cells by diffusion instead of assimilating it (Day et al. 2001). This has a significant implication on the utilization of rhizobacteria as biofertilizers since the absence of this negative feedback mechanism can allow the nitrogenase enzyme complex to produce NH₃ continuously for plant uptake.

The symbiotic N₂-fixing rhizobia inhabiting in the cortial tissues of roots have been researched for several decades (Santoyo et al. 2016). The inoculation of crops and agricultural fields with such PGPR can help to maintain the N levels (Daman et al. 2016). For instance, about $1-2 \text{ kg N} \text{ ha}^{-1} \text{ day}^{-1}$ can be obtained for all legumes by rhizobial N₂ fixation alone (Lesueur et al. 2016). Apart from legumes, rhizobia have also been found living endophytically with rice, sweet corn, cotton, maize, bean, barley, and wheat among others as outlined in the review by Bhagya and Rajkumar (2017). This shows that there is a great possibility that several rhizobial interactions can similarly enhance N acquisition with non-leguminous crops. For instance, the discovery of N₂-fixing endophytic rhizobacteria in sugarcane (Ohyama et al. 2014; Mus et al. 2016) and cereals (Annapurna et al. 2004; Suman et al. 2016) especially sparked a substantial interest. Rhizobia have also been found to infect Brassica campestris and enhance its growth by increasing its N content (Chandra et al. 2007). Gluconacetobacter diazotrophicus which is the main endophytic diazotroph in sugarcane can fix up to $150 \text{ kg N} \text{ ha}^{-1} \text{ year}^{-1}$ (Muthukumarasamy et al. 2005), and previous in vivo studies on this species also showed that it can promote the growth, germination, height, and nutrient uptake of sugarcane (Suman et al. 2008). Recently, a study

Source	Endophytic rhizobacteria	Reference
Banana (<i>Musa</i> spp.)	Klebsiella sp., Bacillus sp., Microbacterium sp., Enterobacter sp.,	Patel et al. (2017b)
	B. subtilis	Andrade et al. (2014)
Cassava (Manihot esculenta)	Pantoea dispersa	Chen et al. (2014)
Cowpea (Vigna unguiculata)	Bradyrhizobium, Streptomyces griseoflavus	Htwe et al. (2019)
Groundnut	Enterobacter ludwigii	Dhole et al. (2016)
(Arachis hypogaea)	Bradyrhiziobium	Taurian et al. (2013)
Maize (Zea mays)	Pseudomonas aeruginosa, E. asburiae, Acinetobacter brumalii	Sandhya et al. (2017)
	Klebsiella sp., K. pneumoniae, B. pumilus Acinetobacter sp., B. subtilis	Kuan et al. (2016)
	Bacillus sp., Enterobacter sp.	Szilagyi-Zecchin et al. (2014)
	P. pseudoalcaligenes, P. aeruginosa	Jha (2019)
Mungbean (Vigna radiata)	Bradyrhizobium, Streptomyces griseoflavus	Htwe et al. (2019)
Rice (Oryza sativa)	Microbacterium, Bacillus, Klebsiella spp. Paenibacillus kribbensi, B. aryabhattai, K. pneumoniae, B. subtilis, M. trichotecenolyticum	Ji et al. (2014)
	Rhizobium	Patel et al. (2017a)
	Burkholderia, Herbaspirillum, Azospirillum, Rhizobium leguminosarum	Choudhary and Kennedy (2004), Doty (2011)
	P. stutzeri	Pham et al. (2017)
	Lysinibacillus sphaericus	Shabanamol et al. (2018)
	Rhizobium sp., Azospirillum sp.	Sev et al. (2016)
Soybean (<i>Glycine max</i>)	Bradyrhizobium, Streptomyces griseoflavus	Htwe et al. (2019)
Sugarcane (Saccharum	Gluconacetobacter diazotrophicus	Suman et al. (2008)
		Outpains at al
officinarum L)	Pantoea agglomerans	Quecine et al. (2012)

 Table 12.1
 Some important nitrogen-fixing endophytic rhizobacteria and their associated host plants

(continued)

Source	Endophytic rhizobacteria	Reference
	G. diazotrophicus	Ahmed et al. (2016)
	Kosakania sp. ICB117	Kleingesinds et al. (2018)
Wheat (Triticum aestivum)	Achromobacter insolitus, Azospirillum brasisilense	Silveira et al. (2016)
	Stenotrophomonas maltophilia, Chryseobacterium, Flavobacterium, Pseudomonas mexicana	Youseif (2018)

Table 12.1 (continued)

involving other endophytes in a mixed inoculum also showed increased N uptake in sugarcane under N-limiting conditions (Marcos et al. 2016), an implication that there could be other beneficial diazotrophs in this plant. Ngamau et al. (2014), reviewed a number of endophytic banana rhizobacteria with BNF potential. As evidenced by these studies and many others, diazotrophic endophytes hold immense potential for enhancing N acquisition in various non-leguminous plants and further investigations in this regard are necessary.

12.2.2 Endophytic Rhizobacteria and Potassium Acquisition in Plants

Potassium is the third most important quality macronutrient required for plant metabolism and growth (Ahmad et al. 2016; Proença et al. 2017). However, over 90% of K occurs in soil in fixed forms and only about 2% is readily available for plant use (Tsegaye et al. 2017; Meena et al. 2018). The application of K-based/potash fertilizers is a contemporary practice in extensive and intensive agricultural systems worldwide (Dasan 2012; Yagedari et al. 2012; Zhang et al. 2013). However, these synthetic fertilizers decrease agricultural profitability (Mohammadi and Sohrabi 2012; Ahmad et al. 2016) and sustainable crop yield.

Potassium solubilizing bacteria (KSB) are an important source of the rhizosphere microbiome where they promote plant growth by solubilizing K-bearing minerals. Recent literature shows that KSB can be used to ameliorate K-deficient soils for crop production (Suman et al. 2016; Dhiman et al. 2019), and are quickly gaining momentum in the wake of calls for sustainable crop production (Ahmad et al. 2016). The burgeoning evidence of the large diversity of KSB associated with different plants shows that they have an immense potential for application in K-deficient soils (Meena et al. 2016; Velázquez et al. 2016). However, K solubilization abilities are less reported among endophytic rhizobacteria (Proença et al. 2017; Dhiman et al. 2019). For instance, in a study by Patel et al. (2017b), none of over 50 endophytic banana rhizobacteria were associated with K solubilization despite them showing

other essential PGP functions including the solubilization abilities for other important plant nutrients. Nevertheless, there are studies that demonstrate the existence of K solubilizing endophytes.

Potassium solubilizing endophytic rhizobacteria have been identified from wheat (Verma et al. 2013, 2015), more recently, from pearl millet (Kushwaha et al. 2019), maize (Jha 2019), and other crops (Dhiman et al. 2019). Rhizobia are the best-studied endophytes and are widely known for symbiotic N_2 fixation in leguminous plants (Santoyo et al. 2016). However, of late, these novel rhizobacteria have also been shown to solubilize K in plant rhizospheres. For instance, K solubilization by rhizobia in rice has recently been reported by Patel et al. (2017a). Thirumal et al. (2017) demonstrated 5 rhizobial cultures associated with K solubilization in vitro. These new discoveries suggest that apart from enhancing N nutrition in plants, rhizobia can also be exploited for their K solubilizing abilities to enhance K availability in plant rhizosphere.

Indigenous KSB are currently in the limelight for sustainable cropping systems and environmental conservation and have emerged as one of the viable technologies for mitigating K-deficiency in soils (Meena et al. 2015). Potassium solubilization indeed holds a lot of potential for PGP and the K solubilizing abilities of endophytic rhizobacteria are worth exploring. According to Meena et al. (2018), KSB are precious bio-resources that can mitigate K-deficiency in agricultural soils but their experimental evidence at the field level is still inadequate. Such processes may need to be exploited in detail so as to increase their usability.

12.2.3 Endophytic Rhizobacteria and Phosphorus Acquisition in Plants

Phosphorus is the second most important plant nutrient after N (Goswami et al. 2016). Although soils contain P reserves, most of this is available in insoluble forms and inaccessible to plants (Verma et al. 2019).

This non-availability is recognized as a major plant growth-limiting factor in agricultural systems (Sharma et al. 2013). The P solubilization potential of soil microorganisms is one of the most essential traits of PGPR for enhancing P-nutrition acquisition in plants (Walia and Shirkot 2012; Ouattara et al. 2019). While P solubilizing rhizobacteria are widely investigated, recent literature maintains that only a few endophytic rhizobacteria possess this ability (Brigido et al. 2019).

Nevertheless, there is mounting evidence on the role of endophytes in P solubilization and mobilization compared to their widely reported rhizospheric counterparts (Ji et al. 2014; Oteino et al. 2015; Walitang et al. 2019). PSB can proliferate both in plant rhizospheres and endosphere (Hui et al. 2011), and according to Suman et al. (2016), P solubilization is a common trait among endophytic bacteria. However, the P solubilizing bacteria (PSB) still tend to be more abundant in plant rhizospheres in comparison to plant cells and tissues (Chen et al. 2006; Mwajita et al. 2013; Mehta et al. 2015; Walia et al. 2017). Generally, the population of endophytic PSB range between 10² and 10⁴ bacteria/g of root tissue (Kumar et al. 2013; Saini et al. 2015). A number of endophytic rhizobacterial populations belonging to *Burkholderia, Enterobacter, Pantoea, Pseudomonas, Citrobacter, Azotobacter* genera from wheat, rice, maize, legumes, and sunflower, respectively, are reported to solubilize mineral P in plate assays, and a vast number of P solubilizing PGPR are documented (Verma et al. 2013, 2015). In a recent study, Patel et al. (2017b), examined that 36% of over 50 endophytic rhizobacterial isolates belonging to genera *Bacillus, Klebsiella, Microbacterium*, and *Enterobacter* showed P solubilization. Further reports on P solubilizing endophytic rhizobacteria are depicted in Table 12.2.

The P solubilizing PGPR can greatly impact plant growth by increasing P availability in the rhizospheric soils but must maintain an intimate relationship with the host plants (Walia et al. 2017). Numerous studies have highlighted the importance and mechanisms of P solubilization by PSB (Chhabra and Dowling 2017; Varma et al. 2017; Walia et al. 2017; Shrivastava et al. 2018; Billah et al. 2019; Goswami et al. 2019; Rafi et al. 2019; Dheeman et al. 2020). The solubilization of P is purportedly mediated through acidification, chelation, or exchange reactions (Li et al. 2017). According to Rosenblueth and Martinez-Romero (2006), endophytic PSB are more competitive than free-living rhizobacteria since the plant-endophyte interactions are the result of complex evolutionary processes. Moreover, endophytic rhizobacteria can prevent the adsorption and fixation of P under P-limiting conditions by assimilating the solubilized P (Khan and Joergersen 2009; Shakeela et al. 2017).

12.2.4 Endophytic Rhizobacteria in Zinc Acquisition in Plants

Zinc is an important micronutrient required for primary and secondary metabolism in plants (Goteti et al. 2013; Bhatt and Maheshwari 2020). For instance, Zn is a cofactor in many enzymes (Hafeez et al. 2013) and it is critical for membrane function, photosynthesis, protein synthesis, and auxin metabolism in plants (Tavallali et al. 2010). Reports show that Zn deficiency is a common problem worldwide due to nutrient mining during crop harvesting and increased use of NPK fertilizers containing lesser amounts of Zn micronutrients (Sharifi and Paymozd 2016; Sindhu et al. 2019). Synthetic Zn fertilizers are often applied to overcome these deficiencies at rates of about 25 kg ha⁻¹ ZnSO4 heptahydrate (equivalent to 5 kg ha⁻¹ Zn). Nevertheless, these artificial fertilizers are not cost-effective and quickly get converted into insoluble forms that are inaccessible to plants (Bapiri et al. 2012; Sindhu et al. 2019).

Rhizobacterial Zn solubilization abilities are widely reported phenomenon (Mishra et al. 2013; Shaikh and Saraf 2017). Reports also exist on endophytic Zn solubilization. For instance, Zn solubilizing bacteria (ZSB) have been reported to enhance Zn uptake in soybean up to 21% (Sharma et al. 2014), various *G. diazotrophicus* strains showed solubilization potential for various Zn compounds (Suman et al. 2016)

Source	Endophytic rhizobacteria	Reference
Bananas (Musa spp.)	B. subtilis, Agrobacterium tumefaciens, Streptomyces sp., B. thuringiensis, B. amyloliquefaciens, Micrococcus luteus	Matos et al. (2017)
	B. subtilis, Lysinibacillus sp.	Andrade et al. (2014)
Black pepper (<i>Piper</i> nigrum)	Klebsiella sp., Enterbacter sp.,	Jasim et al. (2013)
Cassava (Manihot esculenta)	Pantoea dispersa	Chen et al. (2014)
Chickpea (Cicer arietinum)	B. subtilis, B. licheniformis	Saini et al. (2015)
	Bacillus sp., Klebsiella sp., Pseudomonas sp.	Chhabra and Sharma (2019)
	P. agglomerans, B. cereus, B. sonorensis	Maheshwari et al. (2019a)
Cocoa (Theobroma cacao)	Not determined	Ouattara et al. (2019)
Common bean (Phaseolus vulgaris)	Pseudomonas sp.	Dinić et al. (2014)
Common pea (Pisum sativum)	P. agglomerans, B. cereus, B. sonorensis	Maheshwari et al. (2019a)
Tumeric (Curcuma longa L.)	B. cereus, B. thuringiensis, B. pumilis, P. putida, Calvibacter michiganensis	Kumar et al. (2016)
Faba bean (Vicia faba L.)	Rhizobium nepotum, R. tibeticum	Rfaki et al. (2015)
Ginseng (Panax ginseng)	Lysinibacillus fusiformis, B. megaterium, B. cereus	Vendan et al. (2010)
Maize (Zea mays)	Bacillus spp., Klebsiella sp., E. ludwigii, Pantoea spp.	de Abreu et al. (2017)
	P. aeruginosa, E. asburiae, Acinetobacter brumalii	Sandhya et al. (2017)
	Klebsiella sp., K. pneumoniae, B. pumilus Acinetobacter sp. and B. subtilis	Kuan et al. (2016)
	Non-identified species	Manzoor et al. (2017)
	P. pseudoalcaligenes, P. aeruginosa	Jha (2019)
Peach (Prunus persica)	Brevundimonas diminuta, Agrobacterium tumefaciens, Stenotrophonomas rhizosphilia	Liaqat and Eltem (2016)
Peanut (Arachis hypogaea)	P. agglomerans	Taurian et al. (2013)

Table 12.2 Studies demonstrating phosphate-solubilization by endophytic rhizobacteria in different crops

(continued)

Source	Endophytic rhizobacteria	Reference
Pearl millet (Pennisetum glaucum)	Bacillus spp.	Ribeiro et al. (2018), Kushwaha et al. (2019)
Potato (Solanum tuberosum L.)	Bacillus spp., Pseudomonas spp., Serratia spp.	Abd El-Moaty et al. (2018)
Rice (Oryza sativa)	Paenibacillus kribbensi, B. aryabhattai, K. pneumoniae, B. subtilis, Microbacterium trichotecenolyticum	Ji et al. (2014)
	Serratia sp., Pseudomonas sp.	Yasmin et al. (2016)
Strawberry (Fragaria ananassa)	B. subtilis, B. megaterium	Dias et al. (2009)
Soybean (Glycine max)	E. sakazakii, P. straminae, Acinetobacter calcoaceticus	Kuklinsky-Sobral et al. (2004)
Sugarcane (Saccharum	Herbaspirillum spp., Bacillus spp.	Silva et al. (2015)
officinarum L)	Burkholderia mallei, B. cepacia, Proteus vulgaris, Pasteurella multocida, K. pneumoniae, K. oxytoca, E. cloacae, C. freundii	Awais et al. (2019)
	Gluconacetobacter diazotrophicus	Crespo et al. (2011)
Tea (<i>Camellia sinensis</i> L.)	Bacillus, Brevibacterium, Paenibacillus, Lysinibacter	Borah et al. (2019)
Tomato (Solanum lycopersicum)	Lysinibacillus spp.	Sahu et al. (2018)
Wheat (Triticum aestivum)	Stenotrophomonas maltophilia, Chryseobacterium, Flavobacterium, P. mexicana	Youseif (2018)
	Non-identified strains	Batool and Iqbal (2018)
Wild mint (Mentha arvensis)	Bacillus sp.	Prakash and Arora (2019)

Table 12.2 (continued)

and the endophytic *G. diazotrophicus* inhabiting sugarcane have shown to possess Zn solubilization abilities alongside other multifarious PGP activities (Saravanan et al. 2007; Natheer and Muthukkaruppan 2012).

Yaish et al. (2015), isolated endophytic bacteria from the date palm tree (*Phoenix dactylifera* L.), identified as *P. aeruginosa*, *P. monteilii*, *P. putida*, *Acitenobacter brumalii*, *E. asburiae*, *Sinorhizobium meliloti*, *P. thivervalensis*, *P. fulva*, and *P. lini* were capable of solubilizing Zn oxide (ZnO). The Gram-positive *B. aryabhattai* was also shown to improve the growth of soybean and wheat due to Zn solubilizing processes (Ramesh et al. 2014). Investigations on rhizobial and *Pseudomonas* cultures demonstrated the in vitro solubilization of different forms of insoluble Zn (Thirumal et al. 2017). The ability to solubilize various sources of insoluble Zn

has been emphasized in the selection of potential endophytes for enhancement of Zn uptake in plants (Singh et al. 2018). Other endophytic ZSB include species of *Bacillus, Chryseobacterium, Paenibacillus, Rhodococcus, Staphylococcus, Achromobacter, Acinetobacter, Enterobacter, and Klebsiella* (Suman et al. 2016). Recently, Kushwaha et al. (2019) also observed that endophytic *Bacillus* strains from pearl millet exhibited Zn solubilization potential and had multiple roles in stress tolerance of the plant. The use of such ZSB can increase Zn uptake by filed crops, which would in turn lead to their improved growth and yield (Suman et al. 2016).

12.2.5 Endophytic Rhizobacteria and Iron Acquisition in Plants

Iron is the fourth most abundant element in soil and is an important micronutrient required by plants for many physiological processes (Saha et al. 2016). However, most agricultural soils are Fe-deficient because the element occurs in the insoluble ferric (Fe³⁺) form that is unavailable for plant uptake (Rajkumar et al. 2010; Arora and Verma 2017; Singh et al. 2019). Some microorganisms have developed a special Fe acquisition mechanism under these Fe-limiting conditions by producing certain special metabolites known as siderophores (Maheshwari et al. 2019b).

Siderophores are secondary metabolites with high affinity for Fe³⁺ (Goswami et al. 2016; Arora and Verma 2017), and under Fe-limiting conditions, siderophores complex with Fe³⁺⁻, a phenomenon which is important for enhancing Fe availability in the rhizosphere (Ferna ndez-Scavino and Pedraza 2013; Boiteau et al. 2016; Chhabra and Dowling 2017). It is proposed that once the siderophores bind onto Fe^{3+} , the acquisition of the bound Fe by plants can occur by the degradation of the chelates or complexes (Rajkumar et al. 2009). According to Loaces et al. (2011), siderophore production is a common trait among the free-living PGPR (Souza et al. 2015) and is rarely reported for the endophytic rhizobacteria. Recent literature suggests that only a few endophytic bacterial isolates possess this trait (Brigido et al. 2019), investigated mainly as a bio-control agent against plant pathogens (Suman et al. 2016). In such cases, the siderophores chelate most of the Fe present in the rhizosphere and prevent the proliferation of pathogens due to its non-availability in the rhizosphere soil (Mitter et al. 2013; Olanrewaju et al. 2017). Nevertheless, endophytic rhizobacteria can also produce these metabolites under Fe-stress and aid in plant Fe acquisition (Ghavami et al. 2017; Perez-Rosales et al. 2017), and endophytic genera like *Pantoea, Bacillus*, Burkholderia, and Pseudomonas can increase the concentration of bioavailable Fe in plant tissues (Maheshwari et al. 2019a).

Endophytic siderophore producers that include *Brevundimonas diminuta, Leif-sonia shinshuensis, Sphingomonas parapaucimobilis, Brevundimonas vesicularis,* and *Agrobacterium tumefaciens* have been identified from pear and peach roots (Liaqat and Eltem 2016). *Bacillus* sp., *Pseudomonas* sp., and *Stenotrophomonas* sp. are also recognized among the effective siderophore-producing endophytes (Jasim

et al. 2014). Serratia sp. and Pseudomonas sp. from rice have been recently reported to produce siderophores by Yasmin et al. (2016). Siderophore-producing endophytic *P. agglomerans* from peanuts (Taurian et al. 2013), and in turmeric (Kumar et al. 2016) have also been reported. The endophytic Bacillus sp. and P. putida were also associated with siderophore production. Similar studies on pepper endophytic Paenibacillis polymyxa by Phi et al. (2010) also exhibited such abilities by Vendan et al. (2010). The endophytic bacteria such as B. cereus, B. flexus, B. megaterium, Lysinibacillus fusiformis, L. sphaericus, Microbacterium phyllosphaerae, Micrococcus luteus isolated from maize also showed excellent siderophore production. Investigations by Youseif (2018) also demonstrated siderophore production capabilities by wheat-root endophytic Stenotrophomonas maltophilia, Chryseobacterium sp, Falvobacterium sp., and Pseudoxanthomonas mexicana. In another study, Maheshwari et al. (2019b), characterized siderophore-producing endophytic bacteria from chickpea (Cicer arietinum) and pea (Pisum sativum). Earlier, Wani and Khan (2010) stated that chickpea endophytic *Pseudomonas sp.* was one of the dominant siderophore-producing genera of the plant. Patel et al. (2017b), observed endophytic rhizobacterial isolates identified as Bacillus, Klebsiella, Microbacterium, and Enter*obacter* species which showed excellent siderophore production abilities. Similarly, siderophore-producing endophytes have also been isolated from maize and canola (Ghavami et al. 2017), corn (Szilagyi-Zecchin et al. 2014), banana, etc. (Ouma et al. 2014).

Siderophore-producing endophytes are important to crops not only directly by improving Fe availability for plant uptake but also indirectly by depriving Fe required to plant pathogens (Chhabra and Dowling 2017; Aloo et al. 2019b). The completed genome analyses of endophytic microbes like *Enterobacter* species have shown that they contain a large number of genes that code for siderophore transporter proteins (Taghavi et al. 2010). The production of siderophores is a classic example of how rhizobacteria can improve Fe availability in the plant rhizosphere and due to its indisputable role in plant nutrition, further investigations on siderophore-producing rhizobacteria are necessary (Aloo et al. 2019a).

12.3 Ecological Significance of Endophytes in Mineral Nutrients Acquisition by Plants

Endophytic rhizobacteria are considered as sub-sets of rhizosphere microbiome that have acquired the ability to colonize plant root tissues and exhibit specialized and unique lifestyles (Compant et al. 2010; Dheeman et al. 2017). Despite their special interaction with plants, endophytes share all the important PGP traits with other rhizobacteria (Compant et al. 2005). However, they possess characteristics that are distinct from rhizospheric bacteria, suggesting that not all rhizospheric bacteria can enter plants, and/or that once inside their hosts, they change their lifestyles to adapt to internal habitats within plants (Monteiro et al. 2012; Sessitsch et al.

2012). For instance, a study on plant colonization and the establishment of symbionts by Hardoim et al. (2015) showed the presence of significant putative properties in endophytes compared to other types of bacteria interacting with plants.

There is an increasing interest in harnessing the potential of endophytic microbes to develop sustainable crop production systems. Although endophytic rhizobacteria are considered a subset of the rhizospheric microflora, their endophytic lifestyle offers them a myriad of advantages over rhizospheric growth (Compant et al. 2010). For instance, they establish themselves in sheltered micro-environments within the plant root tissues (Castanheira et al. 2017), which are protective ecological niches that provide them with safe, consistent, and undisturbed environments as opposed to external rhizobacteria (Senthilkumar et al. 2011). Literature advances that endophytic microbes are relatively protected from external biotic and biotic environmental stresses, unlike their external counterparts whose survivability and colonizability are largely dependent on extrinsic soil factors (Rajkumar et al. 2009; Suman et al. 2016; Waghunde et al. 2017; Lata et al. 2019; Dubey et al. 2020).

Living endophytically allows these bacteria to maintain close contact with plant root tissues for the direct and constant supply of nutrients and their beneficial effects can be exerted onto the host plants more directly (Lata et al. 2019). The plant endosphere niche presents a unique habitat, and bacterial endophytes possibly have differential functions, specializations, adaptations, and competence (Compant et al. 2010). The diversity of endophytic communities also varies depending on host plant species and genotypes, location, developmental stages, and local environmental conditions (Shi et al. 2014). Nevertheless, the direct and intimate interactions that endophytic rhizobacteria form with plant root tissues makes them highly valuable tools and suitable candidates for improving mineral nutrient acquisition in plants more directly and efficiently (Sreejith et al. 2019).

12.4 Conclusions and Future Prospects

The need for eco-friendly crop fertilization alternatives is increasingly becoming urgent. However, endophytic rhizobacteria have not been fully understood and the prospects of finding unique and interesting bacteria are great. Identifying endophytic rhizobacterial strains with multiple PGP functions for specific plants can definitely pave way for more benefits in terms of plant mineral nutrients acquisition. As such, present and future research work should focus on the largely unexplored rhizobacterial endophytes and their potential uses for mineral nutrients acquisition in plants (Turner et al. 2013). Most plant-endophyte interactions have involved rhizobia and legumes and future research should explore fresh alternatives on their application for other agronomically important crops (Suman et al. 2016).

Although there is a wealth of information on culture-dependent and independent characterization of endophytic rhizobacterial diversity and their associated in vitro PGP mechanisms, reports on their practical applications as plant inoculants under field conditions are extremely scarce (Liu et al. 2017). Several endophytic rhizobacteria have been identified in laboratory studies but generally fail to give consistent results under field conditions and there is need to understand the complex dynamics that control plant-endophyte associations probably by identifying genes that govern these relationships at the molecular level. Although some studies have been conducted in this area, they remain limited and genomic analyses can decipher into the capabilities of endophytes and their roles in plant mineral acquisition. Our knowledge about the plant-microbe interactions can greatly be enhanced using metabolomic, genomic, and transcriptomic methods (Dubey et al. 2020). At the moment, only a limited number of genes that contribute to endophytic invasion and colonization have been identified. Perhaps whole-genome sequencing of these organisms will facilitate the identification of novel isolates and their successful exploitation for plant mineral nutrients acquisition. Further analysis of the sequenced genomes and characterization of the involved genes can also help to improve our understanding of their interaction with plants (Compant et al. 2010) for full exploitation. These efforts can also lead to the identification of some new genes required for endophytic lifestyle but there would be a need to separate the common genes for rhizosphere colonization from those involved in the endophytic lifestyle. Additionally, a more comprehensive understanding of whether these organisms are likely to establish themselves in plants if applied as biofertilizers is needed (Compant et al. 2010).

Numerous reports have revealed a range of beneficial features of the endophytic rhizobacteria for plant mineral nutrients acquisition. Nevertheless, there is still a great scope of further exploration and identification of more novel functions. For instance, research on N₂ fixation and P solubilization abilities by endophytic plant rhizobacteria continues to expand, but very little strides have been made regarding K solubilization yet K is the third major essential macronutrient for plant growth. Similarly, limited work has been carried out on S-oxidation (Dhiman et al. 2019). A combination of both traditional and modern biotechnological methods will help in advancements toward improved plant mineral nutrients acquisition and sustainable agriculture (Waghunde et al. 2017). Although a broad range of endophytes with traits for enhancing mineral nutrient acquisition in different plants have been described, only a few of these have conclusively been studied to demonstrate their significance in plants (Chhabra and Dowling 2017). Furthermore, the impact of endophytic colonization and enhanced nutrient uptake in plants can be varied depending on plant host species/cultivars, endophyte strains, and environmental conditions (Shi et al. 2014).

The successful manipulation of the plant microbiome can substantially contribute to sustainable agricultural production (Bakker et al. 2012; Tkacz et al. 2015), by reducing the need for chemical inputs (Adesemoye et al. 2009; Kandel et al. 2017) and GHG emissions (Singh et al. 2010). This chapter provides a comprehensive review of the putatie functions and ecological significance of endophytic PGPR for mineral nutrient acquisition in plants. Taking into consideration the intimate relationships they form with their plant hosts, these rhizobacteria present special tools for improving plant mineral nutrients acquisition and could be better plant growth promoters than their external counterparts (Lata et al. 2019). Endophytes are

indeed fascinating life forms and there is no doubt that their intricate lifestyles and plant interactions still require better understanding to facilitate their application as viable alternatives to artificial fertilizers for agricultural sustainability.

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