

Chapter 3

Interactions of Rhizobia with Nonleguminous Plants: A Molecular Ecology Perspective for Enhanced Plant Growth



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Abstract Rhizobia are known for its symbiotic association with the leguminous plants, which have role in biological nitrogen fixation in root nodules. However, its association with nonlegumes has received relatively lesser attention. With the progress in technology and research strategies, the molecular ecological perspective of rhizobial interaction with nonlegumes has recently gained much progress. Rhizobia are now known to form symbiosis with nonlegumes without forming true nodules, and yet promote the growth of nonlegumes through direct and indirect mechanisms. Plant growth-promoting traits such as production of phytohormones, siderophore, ACC deaminase activity, phosphate solubilization, and improving the nutrient uptake by modulating the root structure are the PGPR mechanisms described for rhizobia. Recently, rhizobia have also been reported to modulate the rhizospheric bacterial community structure that helps plants to adapt to a new or hostile environment. The rhizobia can also mediate biocontrol through antibiosis, parasitism, or competition which inhibits plant pathogens, induces systemic resistance in the host plant, and also releases exopolysaccharides for improving root adhering soil in the plants. The research on cell-to-cell communication for this unique synergistic interaction with nonlegumes, such as rice and wheat plants, has revealed interesting facts, which may be used for better plant growth. Therefore, the application of rhizobia as PGPR and further use as a biofertilizer, stress regulators, and biocontrol agents for nonleguminous plants need more intervention from the perspective of its interaction with nonlegumes, which has been addressed in this article. Also, the importance of rhizobia with the perspective of molecular ecology,

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genomics attributes of rhizobia colonizing nonlegumes, and possible rhizobial engineering have been included.

Keywords Rhizobia · PGPR · Nonlegumes · OMICS · Nitrogenase · Nitrogen fixation

3.1 Introduction

The demand for food has been increasing at an exaggerating rate worldwide. For such a demanding process, the farmers apply chemical fertilizers, insecticides, herbicides, etc. more than their recommended level for enhancing the production. These applied chemicals, in turn, affect soil health and increase a load of contaminants into the environment, Consequently, affecting the health of humans and other organisms. Therefore, a sustainable approach must be adopted to ensure effective management of all the resources in an agriculture system that reduces the impact of the chemicals while maintaining the fertility of the soil. Presently, the trend in the agricultural sector is to explore the alternatives for the harmful chemicals and focus on organic and inorganic fertilizers (Haggag and Wafaa 2002), which is a daunting task (Ray et al. 2000; Bera et al. 2006). Plant growth-promoting rhizobacteria (PGPR) are a group of beneficial microbes which are involved in symbiotic and nonsymbiotic beneficial traits to improve the growth and yield of legumes as well as nonlegumes (Antoun et al. 1998; García-Fraile et al. 2012; Ahmad et al. 2013; Khaitov et al. 2016; Ziaf et al. 2016). Thus, the use of microbes as biofertilizers for sustainable agriculture is hereby utmost necessary considering their beneficial traits and mode of action (Nosheen et al. 2021).

Rhizobia are soil bacteria belonging to family *Rhizobiaceae* which are gram-negative, chemo-organotroph, or chemolithotroph in nature (Werner 1992), and are capable of fixing atmospheric nitrogen popularly known as biological nitrogen fixation (BNF) (Franche et al. 2009). Some of the well-known genera of rhizobia are *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Azorhizobium*, *Allorhizobium*, etc. (Rao et al. 2018) which possess host-specific ability to establish symbiosis with leguminous plants (Mehboob et al. 2012). However, rhizobia also possess the ability to associate with nonlegumes without forming true nodules which are nonspecific (Reyes and Schmidt 1979). This leads to speculations and further work on the working mechanism of the well-established fact that increases the yield upon their inoculation.

Rhizobia are known to promote the growth of many plants including various crops and grasses (Machado et al. 2016; Borges et al. 2019). Yet various factors govern the successful nature of the inoculants. Rhizobia meditates the growth of nonlegume plants through its direct and indirect mechanisms or a combination of both. These include PGP traits such as IAA production, siderophore activity, and ACC deaminase activity to name a few including biocontrolling property as well as by influencing other beneficial microbes in the vicinity for better growth of the plant (Shakhawat Hossain and Mårtensson 2008).

On the other hand, certainly incompatible rhizobia might have a deleterious effect on certain crops (Perrine et al. 2001). Therefore, it is important to determine the specificity of a particular strain and understand the underlying interaction before selecting it as a PGPR.

3.2 Rhizobia and Nonlegume Interaction

Rhizobia are known for their ability to form root nodules in the leguminous plants, by which they fix atmospheric nitrogen and provide nourishment to the plants (Schloter et al. 1997), there had been early reports for their interaction with the nonlegumes (Reyes and Schmidt 1979; Chabot et al. 1996). The rhizobia possess the ability to survive as well as to colonize the roots of the nonlegume plants (Antoun and Prevost 2000; Bhattacharjee et al. 2008). In fact, bacterial associations with plants are of two types, i.e., close and loose. This may be endophytic, phyllosphere, or rhizospheric (Weyens et al. 2009). This colonizing ability of the bacteria brings about stimulating or inhibiting effects (Höflich et al. 1994; Antoun et al. 1998). The rhizobia enter the nonlegume through cracks present in the root epidermis and colonize the cortex within the xylem (Sabry et al. 1997) and between the root intercellular spaces (Reddy et al. 1997). The roots of a particular plant and rhizobia interact with each other, while this interaction results in enhancement of the growth and yield of the plant (Lemanceau 1992; Yanni et al. 1997). Therefore, those specific and nonspecific interactions make rhizobia a potential endophyte or rhizobacteria for the nonlegumes (Sessitsch et al. 2002). There are various studies which suggests rhizobia as endophytes in nonleguminous plants, e.g., *Rhizobium laguerreae* in spinach (Jiménez-Gómez et al. 2018), *Rhizobium phaseoli*, *Sinorhizobium americanum*, and *Azospirillum brasilense* in maize (Gómez-Godínez et al. 2019), *Rhizobium* species in cotton plant (Qureshi et al. 2019), and *Rhizobium alamii* in *Brassica napus* (Tulumello et al. 2021).

Rhizobial endosymbiosis with other nonlegumes such as *Parasponia* has also been reported (Sytsma et al. 2002). Different *Rhizobium* species are associated with the nodulation process of *Parasponia* (Trinick and Galbraith 1980; Trinick and Hadobas 1989) with diverse genes for Nod factor biosynthesis (Op den Camp et al. 2012). The structure of such nodules is like lateral roots, and is formed following the typical flavonoid-dependent mechanism (Chapman and Muday 2021). It was reported that Nod factors lysin-motif (LysM) domain proteins are important for the symbiosis of nodulation and mycorrhization in *P. andersonii* (Op den Camp et al. 2011).

Rhizobia can flourish in both legumes as well as nonlegumes (Pena-Cabriaes and Alexander 1983). There are reports of the appearance of nodule-like structures in nonlegumes (Ridge et al. 1992; Trinick and Hadobas 1995; Naidu et al. 2004). Rhizobial colonization in rice and wheat seedling has been reported by Shimshick and Hebert (1979), while the effectiveness of rhizobial competence was determined by Wiehe and Höflich (1995) in maize. Many such reports of rhizobial colonization

in nonlegumes were reported by Wiehe et al. (1994), Schlöter et al. (1997), Reddy et al. (1997), and Sabry et al. (1997). Along with endophytic colonization, the ascending migration toward stem, leaves, and leaf sheath has been reported by Chi et al. (2005). The survival and multiplication of rhizobia in the rhizospheric region of wheat, corn, rape, etc. (Wiehe and Höflich 1995), and lettuce (Pena and Reyes 2007) are well studied. Moreover, the presence of rhizobia has been reported from the epidermis of sorghum and millet plants, after inoculation (Matiru et al. 2005). Perrine-Walker et al. (2007) detected the presence of rhizobia and their ability to colonize rice plants.

Rhizobia are also known to secrete different kinds of metabolites which ensure the development of nonleguminous plants. Such compounds provide stabilizations and protection to the plant. These compounds include cytokinins (Noel et al. 1996), abscisic acid (Minamisawa et al. 1996), indole-3-acetic acid (Pandey and Maheshwari 2007; Venieraki et al. 2011), gibberellic acid (Humphry et al. 2007), ethylene (Boiero et al. 2007), ACC-deaminase (Glick et al. 1994), antibiotics (Bhattacharya et al. 2013), etc. These metabolites are produced through the interaction of rhizobia and the nonlegume which results in better tolerance of stress, growth, and yield (Mehboob et al. 2012). In contrast, sometimes overproduction of certain metabolites may also harm the plant. Production of bacteriocin was reported from *Sinorhizobium meliloti* which inhibits the growth of rice (Perrine-Walker et al. 2009). Similarly, a high concentration of auxin and nitrate by rhizobia was reported to inhibit nonleguminous plants (Perrine-Walker et al. 2007). The PGP of endophytic *Bradyrhizobium* sp. strain SUTN9-2 isolated from rice plants was examined. The expression of genes involved in IAA (*nit*) and ACC deaminase (*acdS*) synthesis was contradictory with the results of quantitative analysis of IAA and ACC deaminase. This inconsistency suggested that IAA and ACC deaminase generated by SUTN9-2 have no direct effect on rice development, but those other components arising from IAA and ACC deaminase activities may have their role. Furthermore, SUTN9-2 enhanced the expression of genes involved in nitrogen-fixing (*nifH* and *nifV*) in rice tissues (Greetatorn et al. 2019). Hara et al. (2019) discovered that the functional N₂-fixing *Bradyrhizobia* (TM122 and TM124) found in sorghum roots were phylogenetically related to photosynthetic *B. oligotrophicum* S58T and non-nodulating *Bradyrhizobium* sp. S23321. In terms of the G+C content of the *nifDK* genes, *nifV*, and possibly *nif* gene regulation, the *nif* genes of “Free-living diazotrophs” TM122, TM124, S58T, and S23321 differ significantly from those on the symbiosis islands of nodule-forming *Bradyrhizobium* sp.

The successful nature of the rhizobial and nonleguminous plant association depends on many factors. Along with the bacterial strain, the type of plant, culture condition, microflora, quality of soil, and various biotic-abiotic factors contribute to the success of the inoculum (Lynch 1990a, b; O’Sullivan and O’Gara 1992; Antoun et al. 1998; Biswas et al. 2000; Hilali et al. 2001; Dobbelaere et al. 2003; Depret et al. 2004; Mehboob et al. 2008; Hussain et al. 2009). Depending upon these factors, rhizobia have been divided into three groups depending upon their growth-promotional, inhibitory ability, and nonassociating nature (Prayitno et al. 1999; Perrine et al. 2001, 2005). The development of competent rhizobial strains by the

plant, soil, and environment is key (Mehboob et al. 2012). On the basis of these reports, it may be concluded that just like the rhizobial-legume interaction, rhizobial and nonlegume interaction is also much important for green and sustainable agriculture.

3.2.1 Molecular Interaction of Rhizobia in Nonlegumes

The molecular aspect of rhizobial inoculation has been extensively explored in *Parasponia andersonii* and rice plants. The recruitment of LysM-Type Mycorrhizal Receptor, which is responsible for the symbiotic association with *Rhizobium*, is the fundamental mechanism of Parasponia-Rhizobia interaction (Op den Camp et al. 2011). A class of LysM-type receptors namely *MtNFP/LjNFR5* is reported from *Parasponia* and the functional analysis of this gene revealed a dual symbiotic function in *P. andersonii* (Streng et al. 2011). Comparative transcriptomics of *P. andersonii* revealed 290 symbiotic genes which are similar to a legume *Medicago truncatula* that is responsible for its nodule-enhanced expression profile. Some important genes are Nodule Inception (Nin) And *Rhizobium*-Directed Polar Growth (RPG), known for their importance for nitrogen-fixing root nodules. These set of genes along with a putative ortholog of the NFP/NFR5-type LysM receptor for *Rhizobium* LCO Signaling molecules namely NFP2 in *Parasponia* are critical in forming the nodules which separate it from other plants of its category (van Velzen et al. 2018; Dupin et al. 2020).

In rice plants, however, rhizobial invasion occurs mostly through pores in the epidermis and fissures formed during the development of lateral roots (Reddy et al. 1997). This infection process is nod-gene independent, nonspecific, and does not include infection thread development. Naringenin, a flavonoid, has been shown to enhance this form of rhizobial colonization in rice plants (Webster et al. 1997). Perrine et al. (2001) reported the involvement of specific plasmids carried by rhizobial strains affecting the growth and development of rice seedlings. Piromyou et al. (2015) investigated the effect of *Bradyrhizobium* inoculation in rice seedlings and reported strong expression of *peces*, *rhcJ*, *virD4*, exopolysaccharide production (*fliP*), and glutathione-S-transferase (*gst* genes). Wu et al. (2018) reported the growth-promotional and signaling potential of *Sinorhizobium meliloti* in rice seedlings, which resulted in increased gene expression, which is responsible for accelerated cell division and cell expansion. Transcriptomic analysis revealed that differentially expressed genes (DEG) are involved in upregulation of phytohormone production, photosynthetic efficiency, glucose metabolism, cell division, and cell-wall expansion. Moreover, the inoculation of *Bradyrhizobium* sp. in rice plants revealed colonization, enlargement of bacterial cells, increased DNA content, and nitrogen fixation. Some factors in rice extract induced the expression of cell cycle and nitrogen fixation genes. The transcriptomic analysis revealed encoding a class of oxidoreductases that act with oxygen atoms and may play a role in maintaining an appropriate level of oxygen for nitrogenase activity, followed by GroESL

chaperonins, which are required for nitrogenase functioning. The expression of the antimicrobial peptide transporter (*sapDF*) was also increased, leading to cell differentiation (Greetatorn et al. 2020).

3.3 Methods to Detect N₂ Fixation by Rhizobia in Nonlegumes

There are methods by which we can identify the activity of nitrogen fixers in nonlegumes. One indirect method is to detect the *nifH* DNA in the tissues having DNA of endophytes, which indicates the occupancy of N₂-fixating bacteria. The expression of *nifH* genes stipulates the probability of active N₂ fixation by diazotrophs. It is done with the help of Rt-PCR where soft stem tissues of plants like sugarcane are being used to detect any signs of *nifH* expression (Thaweenut et al. 2011). RNA is isolated and reverse transcribed into cDNA in this method (Thaweenut et al. 2011). Using the product of RT-PCR as a template, the fragments of *nifH* are amplified through nested PCR with Taq DNA polymerase. The efficiency of the *nifH* PCR primer has been re-examined in different laboratories (Gaby et al. 2018) and a new modified annealing temperature was set at 58 °C to determine the largest diversity of *nifH* templates.

The second way is to detect the diazotrophic rhizobia by metaproteomics. For this, the first step is to obtain the bacterial cell-enriched fraction. The bacterial cells are extracted from the root tissues of rice plants through different centrifugation steps followed by a density gradient centrifugation followed by proteins extraction. A metaproteomic analysis based on metagenome analysis on the roots of rice plant was used to determine the peptide abundances of the proteins involved in methane oxidation (particulate/soluble methane monooxygenase (pMMO/sMMO), methanol dehydrogenase (MxaFI), formaldehyde dehydrogenase (FAD), formate dehydrogenase (FDH)) and N₂ fixation (NifH, NifD, NifK, VnfD). This was followed up by Nanoliquid chromatography (LC)–electrospray ionization–tandem mass spectrometry (MS/MS) analyzed using an LTQ ion-trap MS coupled with a multidimensional high-performance LC Paradigm MS2 chromatograph and a nanospray electrospray ionization device. The tryptic peptide spectra were recorded in an *m/z* range of 450–180. The MS/MS data were explored against the rice root microbiome database that was constructed using metagenome data targeting the same rice root samples (Bao et al. 2014).

3.4 Genomic Attributes of Rhizobia Colonizing Nonlegumes

Genomics is the study of genes and genomes that focuses on the structure, function, evolution, mapping, epigenomic, mutagenomic, and aspects of genome editing (Muthamilarasan et al. 2019). Genomics plays an important role in elucidating genetic variation, which may enhance the performance or the efficiency of the strains resulting in improved crop production. The rhizobial genomes that are studied, largely belong to α and β class of Proteobacteria. The average and median genome sizes of rhizobia were reported to be 3.65 Mb and 3.46 Mb, respectively (Dicenzo et al. 2016) which are nearly two-three times larger than other bacterial groups. The rhizobial genomes reflect their ability to adapt in complex conditions, where limited and diverse types of nutrients are available to the rhizobia (Dicenzo et al. 2016). Mostly, the genomes are multipartite, which are split into two or more large self-replicating fragments (replicons). The replicons vary from 100 to >2000 kb in size (Geddes et al. 2020). Though the majority of the research works have been associated with the rhizobia of legume crops, there are some genomic data available for the rhizobia in the nonleguminous group which enable us to understand the role of molecular machinery other than nodule formation.

de Souza et al. (2015) reported the genome of *Rhizobium* sp. UR51a isolated from roots of rice plants which is associated with plant growth-promoting traits such as siderophore, IAA production along with biological nitrogen fixation. The genome analyses revealed the genes for siderophore aerobactin uptake (*fhuABCD*), genes for biosynthesis of auxin, genes for antioxidant enzymes, antibiotic, and toxic compounds resistance genes. Flores-Félix et al. (2021) isolated *Rhizobium laguerreae* PEPV16 strain from root nodules of *Phaseolus vulgaris* and performed genomic analysis. The beneficial traits identified through the analysis have led its application to other vegetables such as carrot and lettuce, subsequently enhancing their growth. The analysis revealed the genomes possess genes related to *N*-acyl-homoserine lactone (AHL) and biosynthesis of cellulose, genes for quorum sensing, and formation of biofilm. Moreover, the genes related to PGP traits such as phosphate solubilization, indole acetic acid production, siderophore biosynthesis, and nitrogen fixation were also reported from the genome. The content of genes related to amino acids and other associated genes were also present. For the production of cellulose, the presence of *bcsA* and *bcsB* genes were reported. Also, a third gene (*celC*) encoding an endonuclease enzyme, CelC2 has been reported to be associated with the biosynthesis of cellulose, and the formation of biofilm. A gene encoding an *N*-acyl-L-homoserine lactone (AHL) synthase has been reported to be associated with quorum sensing. For the colonization which mediates the formation of biofilm and attachment to plant surface, many associated genes for motility, chemotaxis, and biosynthesis of EPS have been reported. Moreover, genes that benefit PGP such as phosphate solubilization-related genes that carry out the phosphate solubilization from organic compounds. A siderophore-producing gene that encodes acetyltransferase that is similar to the *vbsA* gene responsible for the biosynthesis of

vicibactin, a siderophore produced in other rhizobial groups is also reported from the genome.

3.5 Mechanisms of Growth Promotion of Nonlegumes by Rhizobia

Hiltner (1904) termed the soil around the roots as the rhizosphere, where the microbial population is very high (Bodelier et al. 1997). This region is rich in compounds such as amino acids, sugars, vitamins, organic acids, auxins, flavonoids, etc. which are released by the plants. The microbes get attracted by these compounds which are also known as root exudates utilized to the microbial population for their multiplication (Lynch and Whipps 1990; Dakora and Phillips 2002; Somers et al. 2004; Dardanelli et al. 2008, 2010; Raaijmakers et al. 2009). This interaction between plants' roots and bacteria leads all the exchanges between them and governs beneficial, deleterious, and neutral processes. In other words, those compounds act as chemo-attractants and help the microbial population to communicate with the plants, resulting in successful interaction (Bolton et al. 1986; Dardanelli et al. 2008, 2010). As a result, the competent bacteria which multiply and colonize the rhizosphere are known as rhizobacteria (Antoun and Kloepper 2001). These rhizobacteria often possess beneficial traits which enhance the growth of plants, also known as plant growth-promoting rhizobacteria (PGPR) (Kloepper 1978). These groups of bacteria possess different modes of action; some provide direct nourishment by synthesizing beneficial compounds or through indirect mechanisms helping plants to withstand deleterious effects or pathogen crisis (Glick et al. 1995). Rhizobia are also considered as PGPRs (Chandra et al. 2007), which associate themselves with leguminous as well as nonleguminous plants (Höflich et al. 1994; Noel et al. 1996; Yanni et al. 1997; Antoun et al. 1998; Rodríguez and Fraga 1999; Sessitsch et al. 2002). Some of the well-known rhizobial PGPRs belong to genera *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium* (Mehboob et al. 2012). These rhizobia benefit the plants in many ways (Fig. 3.1), some of which are mentioned below.

3.5.1 Direct Mechanisms

The direct mechanism of PGPR shown by various bacterial genera includes phytohormone production, mineral solubilization, nitrogen fixation, siderophore, and HCN production. These mechanisms highly influence the plant growth and result in better crop yield.

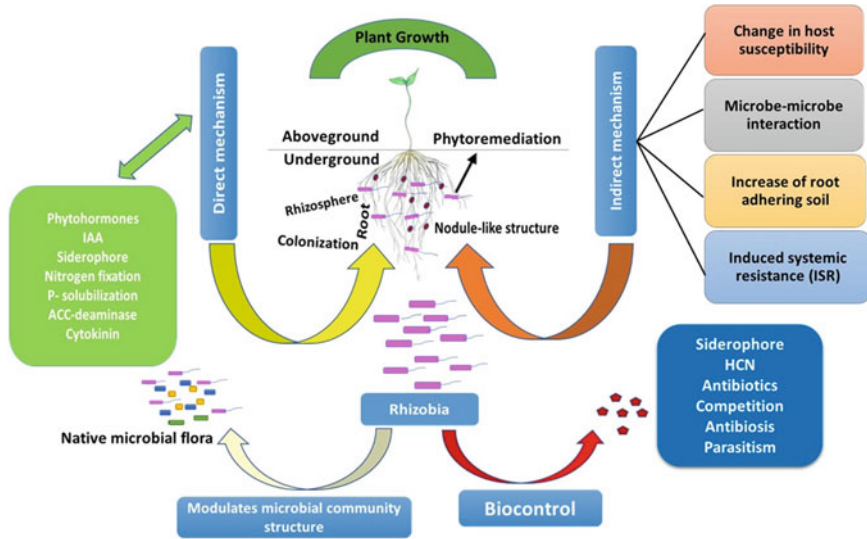


Fig. 3.1 Various mechanisms of rhizobia by which they benefit a nonlegume plant

3.5.1.1 Production of Important Compounds

Rhizobia produces lower molecular weight plant hormones (phytohormones) which are known to regulate important physiological and developmental processes during the growth of the plant (Chiwocha et al. 2003). These compounds affect the process of flowering, aging, root and stem development, fruit coloration, formation and shredding of leaves, and many other processes. Some of the important phytohormones are auxins, cytokinins, gibberellins, abscisic acid, indole-3-acetic acid (IAA), and ethylene (Zahir and Arshad 2004; Khalid et al. 2006). The production of these important compounds is an important characteristic of rhizobia (Phillips and Torrey 1970; Hirsch et al. 1997; Law and Strijdom 1988; Atzorn et al. 1988; Minamisawa et al. 1996), and also benefits the nonleguminous category (Biswas et al. 2000; Yanni et al. 2001; Hafeez et al. 2004; Matiru and Dakora 2005a; Mishra et al. 2006; Chandra et al. 2007; Humphry et al. 2007; Pena and Reyes 2007).

The Nod factors produced by rhizobia which are essential in forming nodules in leguminous plants (Buhian and Bensmihen 2018), also play an important role in nonleguminous crops. These Nod factors help in rapid and transient alkalization of cells of tobacco (Baier et al. 1999), tomato (Staehelin et al. 1994), and restore division of cell and embryonic development in carrot (De Jong et al. 1993), increasing root mass and length (Smith et al. 2002), enhance photosynthate production and yield of grain when sprayed over the surface of leaves (Smith et al. 2001, 2002). It has also been reported to restore cell division and embryogenesis in the plants when auxins and cytokinins are absent (Dyachok et al. 2000). Moreover, in maize and cotton, Nod factors induce the germination of seeds and pitches for early

seedling development, at low temperatures. Nod factors also promote colonization of legumes as well as nonlegumes by AM fungi (Xie et al. 1995).

Besides rhizobia produce some signaling compounds such as lumichrome which stimulates growth of plants (Yang et al. 2002; Beveridge et al. 2003; Dakora 2003; Matiru and Dakora 2005b). This compound is also known to help host plants in surviving the water stress by decreasing the leaf stomatal conductance and reduction of water loss via transpiration through the leaves (Phillips et al. 1999). Rhizobia also produce riboflavin which possesses a significant role in plant-microbe interactions (McCormick 1989). It can be further converted to lumichrome, which promotes plant growth.

3.5.1.2 Production of Enzymes

Ethylene is a hormone that promotes the ripening of fruit, breaks the dormancy of seed, and promotes the formation of root hairs (Dolan 2001). However, its overproduction inhibits the growth of the plant (Li et al. 2018). *Rhizobium* sp. produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which is known to reduce the ethylene levels in plants, by hydrolyzing ACC (the precursor of ethylene) (Walsh et al. 1981; Yang and Hoffman 1984) into ammonia and α -ketobutyrate, then absorbing them as a source of nitrogen and carbon (Honma and Shimomura 1978; Klee et al. 1991). Rhizobia with ACC deaminase activity possess longer roots (Glick et al. 1999) and are known to resist the ethylene stress imposed of heavy metals (Burd et al. 2000), attack of pathogens (Wang et al. 2000), drought stress (Arshad et al. 2008; Zahir et al. 2008), salinity (Mayak et al. 2004; Nadeem et al. 2007; Zahir et al. 2009), and water stress (Grichko and Glick 2001). Thus, impart indirect benefit to the plants.

3.5.1.3 Production of Siderophore

Siderophores are chelating compounds that are produced by bacteria and supply iron to the plants which is necessary for the synthesis of chlorophyll and also present as co-factors (Rout and Sahoo 2005). It solubilizes ferric iron from the soil and transports it readily into the cells (Neilands 1993). Siderophores contribute the majority of the available iron supply to the plants from the rhizospheric soil (Masalha et al. 2000). Different strains of rhizobia are known to possess siderophore activity in nonlegumes. *Rhizobium meliloti* (Schwyn and Neilands 1987; Arora et al. 2001), *S. meliloti*, *R. leguminosarum* bv. *viciae*, *R. leguminosarum* bv. *trifolii*, *R. leguminosarum* bv. *phaseoli*, *R. tropici* (Chabot et al. 1993; Carson et al. 2000), *Rhizobium* sp. (Derylo et al. 1994; Antoun et al. 1998), and *Bradyrhizobium* (Plessner et al. 1993; Jadhav et al. 1994; Dudeja et al. 1997; Antoun et al. 1998) to name a few which produce siderophore for the acquisition of Fe^{3+} chelation in the iron-deficient environment (Guerinot 1991; Carson et al. 1992; Reigh and O'Connell 1993; Guerinot 1994; Arora et al. 2001).

3.5.1.4 Solubilization and Uptake of Nutrients

Phosphorus is an important nutrient for plants which is available in soil in two forms, organic and inorganic. Organic phosphates are phosphomonoesters, phosphodiester (phospholipids and nucleic acids), and phosphotriesters (Rodríguez and Fraga 1999). Inorganic forms are apatite, hydroxapatite, and oxyapatite (Rodríguez and Fraga 1999; Fernández et al. 2007) which are insoluble. Its deficiency can lead to limited plant growth and low yield (Fernández et al. 2007). Phosphorous remains unavailable for plants due to their immovable nature and depends on soil type as well as pH. Some rhizobia possess the phosphate solubilization ability (both organic and inorganic) which in turn supplies phosphate to the plant (Abd-Alla 1994; Antoun et al. 1998; Dazzo et al. 2000; Alikhani et al. 2007; Afzal and Bano 2008). It was reported that *R. meliloti* possesses phosphate solubilization activity in nonlegumes to enhance their growth (Egamberdiyeva et al. 2004).

Similarly, supply of other important nutrients such as N, P, K, Ca, Mg, Zn, Na, Mo, and Fe by *Rhizobium*, *R. leguminosarum* bv. *trifolii*, *Bradyrhizobium* (Khokhar and Qureshi 1998; Biswas et al. 2000; Yanni et al. 2001), K^+ and Ca^+ in cotton by *R. leguminosarum* bv. *Trifolii* (Hafeez et al. 2004), and N, K, Na, Zn, Fe, and Cu in wheat by *Rhizobium* (Amara and Dahdoh 1995) are some important examples of nutrient supply by rhizobia in nonlegumes.

3.5.1.5 Amelioration of Different Plant-Stress Conditions

Rhizobial inoculation to nonleguminous plants has yielded promising results in stress amelioration (Silva et al. 2020) as rhizobia help in combating different types of biotic and abiotic stresses. Rhizobial inoculation has resulted in countering water stress in the host plant as reported by several workers (Figueiredo et al. 1999; Alami et al. 2000; Tulumello et al. 2021). Rhizobial inoculation alters the stomatal conductance and transpiration (Matiru and Dakora 2005b), improving photosynthetic capacity (Chi et al. 2005), and also known to alter the morphology of roots which helps in absorbing the nutrients from the soil and also resists drought conditions. Pesticides affects the growth of the plant by disturbing the normal root functioning altering root architecture, sites of rhizobial infection, ammonia transformation, and exchange of compounds between plants and microbes, and also by affecting the microbial population and diversity (al-ani et al. 2019). Kanade et al. (2010) reported the use of rhizobia from the fenugreek plant for the degrading of malathion. Though in other reports, the field results were not found to be very satisfactory and require more research (Gopalakrishnan et al. 2015).

3.5.2 Indirect Mechanism

This involved the functional role of rhizobacteria in inhibiting the phytopathogens causing disease in plants.

3.5.2.1 Biocontrol

Biocontrol is the phenomenon by which microbes play an important role to eliminate or reducing the effect of pathogens by secreting various kinds of compounds such as antibiotics, HCN, cell-wall lytic enzymes such as chitinase and glucanase (Chakraborty and Purkayastha 1984; Deshwal et al. 2003; Chandra et al. 2007). Rhizobia possess antagonistic activity against pathogens and also change the level of host susceptibility against a particular pathogen. Different mechanisms are being exhibited by the rhizobia such as competition, antibiosis, or parasitism to eliminate the pathogen. The competition of nutrients between the bacteria and pathogen may also result in the elimination of the pathogen. *Rhizobium* spp. suppress the disease-causing pathogen by the production of lytic enzymes, antibiotics, and ISR (Volpiano et al. 2019). Siderophore activity plays an important role in starving the pathogen from acquiring iron (Carrillo and Vazquez 1992; Arora et al. 2001). Arora et al. (2001) reported the action of siderophore-producing rhizobia against *Macrophomina phaseolina*, a disease-causal fungus in more than 500 angiosperm plants. In antibiosis, the rhizobia produce compounds called antibiotics which act as an eliminator to the pathogen. *R. leguminosarum* bv. *trifolii* produces trifoliotoxin (Schwinghamer and Belkengren 1968; Breil et al. 1993) which is potent enough against many plant and animal pathogens (Triplett et al. 1994). Parasitism includes the elimination of the pathogen with the help of enzymes. For instance, chitinase and glucanase break the cell wall of pathogenic fungi. *R. leguminosarum*, *S. meliloti*, and *B. japonicum* are known to be used against genera *Macrophomina*, *Rhizoctonia*, and *Fusarium* (Ehteshamul-Haque and Ghaffar 1993; Özkoç and Deliveli 2001). *S. meliloti* and *R. trifolii* are reported to inhibit *F. oxysporum*, and rot/knot disease of the root of sunflower and tomato plants (Antoun et al. 1978; Siddiqui et al. 2000; Shaukat and Siddiqui 2003), *R. leguminosarum* bv. *viciae* is known to control *Pythium* that causes damping-off of sugar beet (Bardin et al. 2004), *M. loti* inhibits the growth of *Sclerotinia sclerotiorum* (Chandra et al. 2007), *B. japonicum* controls root rot of mustard and sunflower and may decrease the sporulation of *Phytophthora megasperma*, *Pythium ultimum*, *Fusarium oxysporum*, and *Ascochyta imperfecta* (Tu 1978, 1979; Ehteshamul-Haque and Ghaffar 1992, 1993; Siddiqui et al. 2000). Long back, *R. meliloti* was reported to control root-knot phytoparasitic nematode in okra (Parveen and Ghaffar 1991; Parveen et al. 1993; Ehteshamul-Haque et al. 1996).

3.5.2.2 Change in Host Susceptibility

The microbes often induce resistance in plants (Van Loon 2007), and the process by which resistance is incurred in the plants is known as induced systemic resistance (ISR). Rhizobia can limit the effect of the pathogen through the induction of plant defense mechanisms (Abdel-Aziz et al. 1996). ISR system is adopted by rhizobia for controlling many fungal pathogens of nonlegumes such as sunflower, okra, and soybean (Ehteshamul-Haque and Ghaffar 1993; Nautiyal 1997). Rhizobia have been reported to produce several biostimulatory agents (Yanni et al. 2001; Peng et al. 2002; Mishra et al. 2006; Singh et al. 2006), eliciting ISR in the plants. *Rhizobium etli* was reported to induce ISR in the roots of potato through a special transduction pathway that protects against *Globodera pallida* (Reitz et al. 2000). *R. leguminosarum* bv. *phaseoli* and *R. leguminosarum* bv. *trifolii* inoculations induce increased synthesis of phenolic compounds in rice plants which mediates ISR and provides bioprotection to the plants against pathogens (Mishra et al. 2006). *Mesorhizobium* sp. Showed increased growth and defense against *Sclerotium rolfsii* infection (Singh et al. 2014).

3.5.2.3 Microbe-Microbe Interaction

The qualities of rhizobia as PGPR can further be enhanced with the addition of one or more bacterial cultures, thus a consortium with other PGPR can prove much beneficial. It was reported that using multiple cultures of PGPR promote the yield of nonlegumes like sorghum (Alagawadi and Gaur 1988), rice barley (Belimov et al. 1995; Höflich et al. 1994), rice (Yanni et al. 1997), maize (Chabot et al. 1993), and wheat (Galal 2003). Nitrogen-fixing bacteria like rhizobia along with other PGPRs are highly beneficial to the crop (Şahin et al. 2004). Sheikh et al. (2006) studied the beneficial traits of using *R. meliloti* and *B. thuringiensis* in okra plants which resulted in better plant growth and performance against fungal pathogens. Han and Lee (2005) reported better growth of lettuce while using co-inoculation of *Serratia* sp. And *Rhizobium* together. Moreover, in degrading soil environments, use of AM fungi, rhizobia, and other PGP strains have been very successful in uplifting the quality of soil (Requena et al. 1997). Also, inoculation of rhizobia can modulate the rhizospheric microbial community, thus improving the soil health and thus growth of the plant (Xu et al. 2020).

3.5.2.4 Increase of Root Adhering Soil

Root adhering soil (RAS) is very important to plants as this region provides water and other nutrients. Two types of such soil exist namely loosely adhering and closely adhering. The soil around the root is much important to the plant as it supports the plant (Dobbelaere et al. 2003). This is the region where the microbial activity is

much higher, results in an exchange of several beneficial compounds. Rhizobia-producing exopolysaccharides (EPS) are of great importance which increase soil aggregation (Martens and Frankenberger 1993), and also trap moisture, and other essential nutrients (Alami et al. 2000). Thus, EPS improves RAS and contributes to soil aggregation (Kaci et al. 2005).

3.6 Nitrogen Fixation in Nonlegumes

BNF in the nonleguminous plants by symbiotic rhizobia has been relatively less studied. Fixation of nitrogen by different rhizobia which form exogenous or endogenous symbiosis in nonleguminous plants has been reported by some of the scientists. Werner (1992) reported *Rhizobium* genus to form nodule-like structures in *Parasponia* and similarly fix N_2 as in leguminous plants. *Rhizobium parasponium* and *Bradyrhizobium* were reported to form nodules in oilseed plants (Cocking et al. 1992). Structures like nodules, galls, or root outgrowths have been observed in many nonleguminous plants such as rice, oilseed, *Arabidopsis thaliana* (Al-Mallah et al. 1989, 1990; Bender et al. 1990; Rolfe and Bender 1990; Jing et al. 1990, 1992; Li et al. 1991; Ridge et al. 1992; Spencer et al. 1994; De Bruijn et al. 1995; Trinick and Hadobas 1995). Velázquez et al. (2005) reported the presence of both symbiosis and pathogenicity-related genes *Rhizobium rhizogenesi*, which help to form nodule-like structures in different plants. *Rhizobium* inoculation enables nitrogen fixation in wheat was reported by Chen et al. (1991), Yu and Kennedy (1995), and Cocking et al. (1995). *Azorhizobium caulinodans* was reported to increase dry weight and nitrogen content resulting from nitrogenase activity when inoculated in wheat, further validating BNF in nonlegumes (Sabry et al. 1997). Nitrogenase activity was observed after inoculation of *A. caulinodans* in rice plants (Naidu et al. 2004). It was suggested that the endophytic nature of particular rhizobia should be active for effective nitrogen fixation with nonlegumes. Diverse genera like *Azoarcus* sp., *Burkholderia* sp., *Gluconacetobacter diazotrophicus*, and *Herbaspirillum* sp. Were reported to have the nitrogen-fixing ability as endophytes (Vessey 2003). Verma et al. (2004) reported higher nitrogen fixation in rice plants inoculated with *Ochrobactrum* sp. Moreover, various attempts have been made by using the latest techniques to incorporate the BNF by rhizobia in nonleguminous plants through genetic engineering but with limited success (Saikia and Jain 2007).

3.7 Application of Rhizobia with Nonlegumes

Rhizobia as a PGPR have multiple practical applications associated with it. Rhizobia are mostly known for its biofertilizer property, biocontrol ability, phytoremediation, and stress regulating properties (Kumari et al. 2019). Biofertilizer increases the growth of the plant through multiple mechanisms such as nitrogen fixation, releasing

compound which helps in the growth of the plant, by increasing the availability of nutrients (Cocking 2003). The biofertilizer supplies or mobilizes the important compounds with minimal resources. These properties were reported from rhizobia while using it as a biofertilizer (Bardin et al. 2004; Chi et al. 2005). These biofertilizers are cost-effective and environment-friendly alternative to chemical fertilizers. Rhizobia are used as commercial biofertilizers in various nonlegumes for enhancing their growth and yield (Perrine et al. 2001; Hussain et al. 2009). Such rhizobial biofertilizer strains have been known to compete with the pathogen (Arora et al. 2001), secrete metabolites such as antibiotics (Deshwal et al. 2003), produce enzymes for cell wall lysis (Özkoç and Deliveli 2001), siderophore activity (Deshwal et al. 2003), HCN production (Chandra et al. 2007), and also reported inducing ISR (Singh et al. 2006). Many PGPR strains including rhizobia are reported for their biocontrol ability (Reitz et al. 2000; Bardin et al. 2004; Chandra et al. 2007). *B. japonicum*, *R. meliloti*, and *R. leguminosarum* are used against *M. phaseolina*, *R. solani*, *Fusarium solani*, and *F. solani* (Ehteshamul-Haque and Ghaffar 1993); *M. loti* against white rot disease of *Brassica campestris* (Chandra et al. 2007); *R. leguminosarum* bv. *Phaseoli* and *R. leguminosarum* bv. *Trifolii* against *R. solani* in rice plants (Mishra et al. 2006).

PGPR are also known for its usefulness in phytoremediation (Khan et al. 2009; Glick 2010). Apart from plant-microbe interactions, phytoremediation largely depends on several abiotic and biotic factors such as soil physicochemical properties, nutrient availability, water content, type, and concentration of contaminants (Thijs et al. 2017). Efficient phytoremediation depends on the growth and survival of both plant and active rhizospheric microbiome in polluted soil. Heavy contamination restricts the microbial population due to its toxic nature (Cook and Hesterberg 2013). It becomes more potent when used in conjunction with a plant, increasing the availability and mobility of pollutants, and also acidifies the targeted contaminants, along with phosphate solubilization and release of chelating agents in addition to enhancing plant growth (Abou-Shanab et al. 2003; Höflich et al. 1994; Noel et al. 1996; Yanni et al. 1997; Dazzo et al. 2000; Arora et al. 2001; Özkoç and Deliveli 2001; Dakora 2003; Matiru et al. 2005; Van loon 2007). Fagorzi et al. (2018) emphasized the advantage of using rhizobia in phytoremediation techniques of heavy metals.

Drought stress is one of the most important limiting factors for plant growth which can ultimately affect agricultural crop yields (García et al. 2017; Khan et al. 2018). Drought tolerance can be regulated by the production of ethylene, ACC deaminase, IAA, cytokinin, EPS, and antioxidant production (Joshi et al. 2019). Due to high salt concentration, soil become dry and thus plants are unable to uptake the water and also a high level of salt toxicity for plant cell (Kumar et al. 2019). Salt-resistant rhizobial strains can survive under osmotic stress (Irshad et al. 2021). Recent research on PGPR suggested that some of the strains can produce heat-/cold-resistant proteins which can enhance the thermal tolerance in plants (Ali et al. 2009). Alexandre and Oliveira (2013) discussed the physiology of rhizobia under thermal stress. There are several reports on ACC-deaminase producing root-nodulating rhizobia such as *Rhizobium leguminosarum* and *Mesorhizobium loti*

(Belimov et al. 2001, 2005; Ma et al. 2003; Sullivan et al. 2002) helping the plant to cope stress. These beneficial rhizobia are being used in different nonlegume crops as mentioned in Table 3.1.

Currently, various rhizobial biofertilizers are commercially available in the Indian as well as global market. The formulation of biofertilizers can be solid carrier-based (organic and inorganic), liquid-based (with or without additives), synthetic polymer-based, and metabolite-based formulations. The solid carrier materials are coal, coconut shell, wheat straw, cellulose, charcoal, etc. Using solid carrier-based formulation provides easy storage, application, and handling of the biofertilizers. Whereas liquid-based formulations are more useful for the legume plants during their sowing in large fields (Arora et al. 2017). A brief summary on crops like rice, wheat, and maize is further discussed.

3.7.1 Rice (*Oryza sativa*)

Rhizobia are known to improve the growth and yield of rice plants. There are several reports of rhizobial inoculation enhancing the growth of rice plants (Peng et al. 2002; Yanni et al. 2001; Chaintreuil et al. 2000; Matiru and Dakora 2004; Singh et al. 2005; Bhattacharjee et al. 2008; Senthilkumar et al. 2008). Naidu et al. (2004) reported the increased growth and yield of rice after rhizobial inoculation. Colonization of rice was checked by Chi et al. (2005), who reported increased root and shoot biomass followed by a rate of photosynthesis, stomatal conductance, transpiration rate, efficiency in water utilization, and increased area of flag leaves when inoculated with rhizobia. Singh et al. (2005) reported increased biomass and grain yield of rice due to the application of three rhizobial strains. These rhizobial strains are potent enough to colonize the rice plants and exhibit different PGP characteristics (Yanni et al. 1997). Biswas et al. (2000) studied rhizobial isolates from different legumes and their application in rice plants, resulting increased grain (8–22%), the yield of straw (4–19%), nutrients N, P, K (10–28%), and Fe uptake (15–64%). Rhizobial strains significantly contributed to the increased vigor of rice seedlings, growth physiology, and modulate root morphology (Mehboob et al. 2012).

3.7.2 Wheat (*Triticum aestivum*)

Rhizobia colonize endophytically in wheat and result in various growth and yield promotion (Sabry et al. 1997; Biederbeck et al. 2000). Webster et al. (1997) reported *A. caulinodans* inoculation elicits lateral roots in the wheat plants. *R. leguminosarum* bv. *Trifolii* is reported to increase shoot length in the wheat (Höflich 2000). Anyia et al. (2004) observed inoculation of *A. caulinodans* enhances increased grain yield and total biomass by 34% and 49%, respectively and also larger leaf surface area. Amara and Dahdoh (1995) discussed *Rhizobium* inoculation resulted in a high yield

Table 3.1 Some of the rhizobia and their mode of action in nonleguminous crops

Host plant	Rhizobia	Mechanism	References
Rice	<i>Bradyrhizobium</i> sp.	Plant growth	Chaintreuil et al. (2000)
	<i>R. leguminosarum</i>	IAA production	Biswas et al. (2000), Dazzo et al. (2000)
	<i>Rhizobium leguminosarum</i>	Auxin and nitrate production, and root colonization	Perrine et al. (2001)
	<i>Bradyrhizobium</i> sp.	Plant growth promotion	Peng et al. (2002)
	<i>Rhizobium</i> sp.	Indole-3-acetic acid, gibberellin production, and root colonization	Chi et al. (2005)
	<i>Rhizobium leguminosarum</i>	Biocontrol/phenolics production	Mishra et al. (2006)
	<i>Rhizobium</i> sp.	N ₂ -fixation and root colonization	Singh et al. (2006)
	<i>Rhizobium leguminosarum</i> bv. <i>trifolii</i>	N ₂ -fixation	Perrine-Walker et al. (2007)
	<i>Rhizobium phaseoli</i> , <i>Mesorhizobium cicer</i>	Plant growth promotion	Hussain et al. (2009)
	<i>Bradyrhizobium</i>	Plant growth promotion	Mia and Shamsuddin (2009)
	<i>Rhizobium</i> sp.	Rhizosphere, root colonization, and N ₂ -fixation	Vargas et al. (2009)
	<i>Sinorhizobium meliloti</i>	Nutrient uptake and indole-3-acetic acid production	Chi et al. (2010)
	<i>Azorhizobium caulinodans</i>	Indole-3-acetic acid, cytokinins production, and nitrogenase activity	Senthilkumar et al. (2009)
Wheat	<i>Rhizobium leguminosarum</i>	Plant growth promotion	Hilali et al. (2001)
	<i>Rhizobium</i> sp.	EPS production	Kaci et al. (2005)
	<i>Rhizobium leguminosarum</i>	Phosphate solubilization	Afzal and Bano (2008)
	<i>Rhizobium leguminosarum</i>	Production of indole-3-acetic acid and nutrient solubilization	Etesami et al. (2009)
Maize	<i>Bradyrhizobium japonicum</i>	Plant growth promotion	Prévost et al. (2000)
	<i>Rhizobium</i>	Low nutrient solubilization	El-Tarabily et al. (2006)
	<i>Mesorhizobium ciceri</i> , <i>Rhizobium leguminosarum</i> , <i>Rhizobium phaseoli</i>	Plant growth promotion	Mehboob et al. (2008)

(continued)

Table 3.1 (continued)

Host plant	Rhizobia	Mechanism	References
	<i>Bradyrhizobium</i>	Plant growth promotion	Roesch et al. (2008)
Barley	<i>Mesorhizobium mediterraneum</i>	Phosphate solubilization	Peix et al. (2001)
	<i>Rhizobium radiobacter</i>	Indole-3-acetic acid and gibberellic acid production	Humphry et al. (2007)
	<i>Bradyrhizobium japonicum</i>	Lipo-chitooligosaccharides and gibberellin production	Miransari and Smith (2009)
Brassica campestris/napus	<i>Rhizobium leguminosarum</i>	Indole-3-acetic acid and cytokinin production	Noel et al. (1996)
	<i>Rhizobium alarii</i>	Plant growth	Tulumello et al. (2021)
Sunflower	<i>Rhizobium sp.</i>	EPS production	Alami et al. (2000)
	<i>Mesorhizobium loti</i>	Biocontrol, production of hydrocyanic acid, indole-3-acetic acid, and phosphate solubilization	Chandra et al. (2007)
Sorghum	<i>Bradyrhizobium japonicum</i> , <i>Sinorhizobium meliloti</i>	Indole-3-acetic acid production and nutrient solubilization	Matiru et al. (2005)
Cotton	<i>Rhizobium leguminosarum</i>	Indole-3-acetic acid production	Hafeez et al. (2004)
	<i>Rhizobium sp.</i>	Plant growth and yield	Qureshi et al. 2019
Raddish	<i>Rhizobium</i> , <i>Bradyrhizobium</i>	Plant growth	Antoun et al. (1998)
Canola	<i>R. leguminosarum</i>	Plant growth	Noel et al. (1996)
Potato	<i>Rhizobium etli</i>	Biocontrol	Reitz et al. (2000)
Tomato	<i>Bradyrhizobium japonicum</i>	Plant growth	Carletti et al. (1994)
Lettuce	<i>Rhizobium sp.</i>	Phosphate solubilization, siderophores and auxins production	Chabot et al. (1993)
	<i>Rhizobium sp.</i>	Indole-3-acetic acid production and P-solubilization	Pena and Reyes (2007)
Switchgrass	<i>Bradyrhizobium spp.</i> , <i>Rhizobium helanshanense</i>	Plant growth promotion	Bahulikar et al. (2014)
Sugarcane	<i>Rhizobium daejonense</i> , <i>Sinorhizobium fredii</i>	Plant growth promotion	Thaweenut et al. (2011)
Sweet potato	<i>Bradyrhizobium</i>	Plant growth promotion	Reiter et al. (2003)
	<i>Sinorhizobium meliloti</i> , <i>Bradyrhizobium japonicum</i> , <i>Rhizobium leguminosarum</i>	Plant growth promotion	Terakado-Tonooka et al. (2008)

of grains as compared to control. Kaci et al. (2005) studied the inoculation of *Rhizobium* in wheat, increased shoot dry mass (85%), root dry mass (56%), root adhering soil (RAS) dry mass (dm) per root dm (RAS/RT) up to 137%, and aggregate water stability in RAS with its EPS-producing property. Similarly, Afzal and Bano (2008) reported rhizobia along with other PGPR considerably enhance the grain yield of wheat.

3.7.3 Maize (*Zea mays L.*)

Rhizobia are also reported to increase the yield of maize. Though they do not contribute to the nitrogen-fixing element (Höflich et al. 1994), inoculation of *R. etli* has resulted in increased dry matter (Martínez-Romero et al. 2000). Chabot et al. (1998) reported rhizobial inoculation under P-deficient and P-rich soils has resulted in better growth of maize. Höflich (2000) reported *R. leguminosarum* bv. *Trifolii* strain promotes the growth of maize in both greenhouse and field trials. Shakhawat Hossain and Mårtensson (2008) reported rhizobial inoculation enhanced shoot and root dry weight of maize plants. Mehboob et al. (2008) reported inoculation of *Rhizobium phaseoli* has resulted in increased root length, shoot length, and seedling biomass as compared to uninoculated control. Rhizobia with multiple PGP traits have to increase the dry matter of shoots after inoculation (Chabot et al. 1993).

3.7.4 Other Crops

Other than above crops, the application of rhizobia as PGPR has also been tested in cotton plants with *R. meliloti*, which resulted in increased yield (Egamberdiyeva et al. 2004). Hafeez et al. (2004) reported increased seedling emergence, shoot dry weight, biomass, and nitrogen uptake after inoculation with various rhizobia strains. *B. japonicum*, *A. caulinodan*, *Rhizobium*, *Rhizobium*, *S. meliloti*, *R. leguminosarum* bv. *Viceae*, and *R. leguminosarum* bv. *Viceae* have been reported to promote the growth and yield of sorghum, millet, and sudangrass (Matiru et al. 2005). Chabot et al. (1993) examined increased growth of lettuce after application of rhizobial strains. Noel et al. (1996) observed inoculation of *R. leguminosarum* resulted in increased growth of lettuce. Along with growth promotion, biocontrol activity of rhizobia has also been reported from *B. japonicum* and *R. leguminosarum* against *M. phaseolina*, *R. solani*, and *Fusarium* spp. Causing disease in sunflower and okra plants (Ehteshamul-Haque and Ghaffar 1993). Sheikh et al. (2006) used *R. meliloti* and *B. thuringiensis* against *M. phaseolina*, *R. solani*, and *Fusarium* spp. In okra plants. Moreover, EPS-producing *Rhizobium* strain plays a role in PGP, mediates water stress, and also supplies water in sunflower plants (Alami et al. 2000). Peix et al. (2001) reported *Mesorhizobium mediterraneum* enhances the growth of barley, while Humphry et al. (2007) observed the effect of *R. radiobacter* strain in barley

plants. Application of *B. japonicum* in radish induces plant dry matter (Antoun et al. 1998). Chandra et al. (2007) reported enhanced seed germination, early vegetative growth, and yield of Indian mustard (*Brassica campestris*) by *M. loti*. It was also reported that the use of multiple strains of PGPR is more beneficial than using single culture of rhizobia for growth promotion (Akintokun and Taiwo 2016).

3.8 Rhizobial Bioengineering

The competitiveness of rhizobia in various types of soil can be by increasing their multiplication in the specific environment or through modifying the signal mechanism of the competitive microbes which in turn disrupts the normal functioning of the introduced microbes (Savka et al. 2002). As we know for a successful interaction, the soil of a particular environment, associated microbes, and the plant are interlinked. Altering, one of them can be beneficial for the colonization of the target rhizobia. The genetic aspect is always important which governs the competitive nature of the target bacteria. Several studies have underlined the causative genes, their deficit leads to limited or less competitiveness. However, the study of genes that might increase the competitive nature is yet to be determined (Geetha and Joshi 2013). Some successful techniques for manipulating the genes are to construct chimeric *Nif HDK* operon under *NifHc* promoter and expression in PHB negative mutants of *R. etli* (Peralta et al. 2004), to develop an acid-tolerant *R. leguminosarum* bv. *Trifolii* strain (Chen et al. 1991), to express the ACC deaminase gene in *S. meliloti* (Ma et al. 2004), overexpression of *putA* gene (Van Dillewijn et al. 2001), overexpression of trehalose 6-phosphate synthase gene (Suárez et al. 2008), overexpression of *rosR* and *pssR* genes (Janczarek et al. 2009), heterologous expression of ferrichrome siderophore receptor *fegA* and *fhuA* genes (Joshi et al. 2008; Geetha et al. 2009; Joshi et al. 2009), and overproduction of the adhesion rap1 (Mongiardini et al. 2009). Also introducing the property to utilize diverse nature of siderophore into the bacterial inoculants further enhances the root colonization ability and biofilm formation. Though the *nifH* genes are critical for competitiveness, the genes of iron up-taking are equally important. Through genome analysis, it was established that TonB-dependent siderophore receptors are important in iron uptake and are not adequately present naturally in the rhizobia (Joshi et al. 2009). Among rhizobia, *Bradyrhizobium* possesses the most TonB receptor and hence their accumulation and competitive nature are higher than other rhizobia groups (Hume and Shelp 1990). Also, some FhuA homologs are present in the inner membrane, possess similar functioning to FhuE (rhodotorulic acid and coprogen receptor) and IutA (aerobactin receptor) (Streeter 1994). The receptors work in combination with FhuBCD (ferrichrome system), suggest the transport of ferric siderophores through the inner membrane is more specific than the outer membrane, resulting in a lesser number of periplasmic and cytoplasmic membrane proteins present in the inner membrane (Stevens et al. 1999). Thus, the increase of repertoire of outer membrane siderophore receptors could enable rhizobial isolates to enhance iron uptake and

colonization in different environments (Geetha and Joshi 2013). The BNF can be made more efficient by accelerating the delivery of electrons required for catalyzing the biochemical reaction performed by nitrogenase enzyme. This is by overexpressing the set of *nif* and *fix* groups of genes (Goyal et al. 2021). Moreover, the structurally similar genes such as *Nod* and *Myc* factors are responsible for activating the signaling pathway during mycorrhizal symbiosis in various crops (Maillet et al. 2011). The modulation of nod factors for activating the mycorrhizal symbiosis signaling pathway which activates the modified nodulation-related genes has been reviewed in nonlegumes (Rogers and Oldroyd 2014). As such, a transgenic rice plant exhibiting root deformation similar to initial nodule formation in legumes through expressing legume-specific nodulation (*Nod*) factor receptor protein genes suitably responded to the rhizobial Nod factors (Altúzar-Molina et al. 2020) but more alteration is to be paid in carrying out the similar work on the crops.

3.9 Challenges and Limitations

Though in many instances, rhizobia act as a potential PGPR and enhance the quality of applied crops, sometimes it also turns harmful to the plant. Though such phenomenon may be caused due to noncompatibility of the plant with an interacting microbe or the applied inoculant may lead to overproduction of certain harmful compounds. This phenomenon leads to deleterious effects on the plant (Alström 1991). Some PGP traits such as IAA, HCN, etc. are proved better for the plants when released in low concentration, but are harmful to the plant at supra-optimal concentration (Antoun et al. 1998; Alström and Burns 1989; O’Sullivan and O’Gara 1992). Perrine et al. (2001) reported the harmful nature of auxin and nitrate when available in high concentrations. Further, the growth inhibitors produced by the rhizobial strain proved harmful to the plant (El-Tarabily et al. 2006). Other factors, such as the plant-microbe or microbe-microbe interaction, where the inoculated PGPR may not be competent enough to bend with the native microbial flora led to undesired results (Antoun et al. 1998). It is also stated that the soil, pH, and environmental factors also play multifarious role in the plant-microbe interaction (Lynch 1990a, b; O’Sullivan and O’Gara 1992; Hilali et al. 2001).

To evaluate rhizobia as PGPR, and to develop it on a mass scale, requires a considerable amount of time and require various steps. To develop an effective biofertilizer, we must aim to evaluate the developmental processes, the policymakers, associated industries, research, and tie-ups with educational institutions. All should work collaboratively and must be implemented as per guidelines. The field-oriented research carried out must be readily made available to the public domain. The commercialization of the outcome of the conducted work should be more encouraged and technology be transferred to the industries. There are some limitations and associated disadvantages which are suggested below.

3.9.1 Limitation in Field Application

Rhizobial application as PGPR in greenhouse or laboratory trials showed optimistic outcomes. But the growth conditions in greenhouses can be controlled and adjustable to the favorable growing requirement of the crop throughout the season (Paulitz and Bélanger 2001). Thus, achieving such controlled field trials is not possible as several biotic and abiotic factors influence crop developments. Also, the abundance of indigenous microorganisms is more pronounced in field soil which can alter or affect the proliferation of applied PGPR strains. Knowledge and research are required for the successful application of rhizobia in the field. The proper timing of inoculation, types of crops, mutual interactions between host plant and microbes, bioformulation of rhizobial strains, the concentration of inoculum applied, and management of crops can ensure the growth support, augmentation, and bioactivity of PGPR in field practices (Bowen and Rovira 1999; Gardener and Fravel 2002; Mansouri et al. 2002). However, recent approaches such as rhizosphere engineering and improved carrier techniques can overcome the limitations of rhizobial field applications (Date 2001; Yardin et al. 2000).

3.9.2 Selection and Characterization

Major challenges in rhizobial product application are the screening of potential microbial strains and its bioformulation process (Kumari et al. 2019). For the selection and screening of the most promising strains, plant adaptations to particular soil types, root exudates, and surrounding ecological environmental status play a vital role (Bowen and Rovira 1999). Various approaches include the use of enrichment medium for the selection of need-based indigenous N-fixing bacteria from the rhizosphere. Another application of the spermosphere model is where plant root exudates use as a sole nutrient source for the proliferation of rhizosphere bacteria (Joshi et al. 2019). The selection of microbial populations based on their phosphate solubilizing, siderophore, and antibiotic production abilities (Weller et al. 2002; Silva et al. 2003) with other beneficial traits are most desirable.

3.9.3 Limitations in Commercialization

Slow growth in commercialization is due to a lack of knowledge among farmers. The field trainers and farmers must be educated about the beneficial role of rhizobial inoculants, its bioformulation, and its economical acceptability to the diverse genera (Kumari et al. 2019). Several factors are to be considered before the commercialization of the PGPR. These include large-scale production of strains, shelf-life compatibility, temperature tolerance, eco-friendly economic which does not impart

toxicity or pathogenicity to human and animal should be measured before marketing (Joshi et al. 2019).

3.10 Rhizobia and Omics Technologies

Didier Raoult and Jean-Christophe Lagier coined the word *culturomics* to describe an approach for bringing more bacterial isolates from environmental microbiomes into laboratory culturing (Lagier et al. 2018). PCR amplification of the ubiquitous 16S ribosomal RNA (rRNA) has been used to identify bacterial isolates in conjunction with these culture techniques (Turner et al. 2013). Despite its significance, "culturomics" has many limitations, the most notable of which is the still limited ability for cultivating some bacterial taxa. Now a days, the *culturome* (strains that can be cultured in the laboratory) does not represent the entire microbiome (Martiny 2019; Steen et al. 2019). The genus *Rhizobium* is found in the core microbiome of many plants (Oberholster et al. 2018; Pérez-Jaramillo et al. 2019). Besides next-generation sequencing (NGS), the classification, platforms like Illumina and PacBio are essential for analyzing the genomes of *Rhizobium* species (Ormeno-Orrillo et al. 2015; González et al. 2019). Some studies have already used PacBio to generate genomes of novel species, such as *Rhizobium jaguaris* CCGE525T isolated from *Calliandra grandiflora* nodules (Servín-Garcidueñas et al. 2019), or to complete genome sequences, such as *Rhizobium* sp. strain 11515TR from tomato rhizosphere (Montecillo et al. 2018). Irar et al. (2014), on the other hand, described a proteomic approach to the nodule response to drought in *Pisum sativum*. Plants were inoculated with *R. leguminosarum* strains and cultivated in "normal well-irrigated" conditions and the other was impacted by a drought. The results showed a total of 18 proteins expressed during a period of drought: *Rhizobium leguminosarum* encodes 11 genes, and *Pisum sativum* encodes seven nodule proteins. These proteins have such a relation to RNA-binding proteins, flavonoid metabolism, and sulfur metabolism. All of the data gave a new goal for improving legume drought tolerance. Despite the relevance of these techniques, the scientists used model organisms such as *Sinorhizobium* or *Bradyrhizobium* species for their research. By using nuclear magnetic resonance, researchers were able to detect the exo-metabolomes generated by *Rhizobium etli* CFN42T, *Rhizobium leucaenae* CFN299T, *Rhizobium tropici* CIAT899T, and *Rhizobium phaseoli* Ch24-10 from free-living culture (Montes-Grajales et al. 2019), except the culture supernatant of *R. tropici* CIAT 899T none of them contained ornithine. This chemical has been linked to symbiotic efficiency as well as resilience to stress conditions like acidity (Rojas-Jiménez et al. 2005; Vences-Guzmán et al. 2011).

3.11 *Rhizobium* in Microbiome of Nonlegumes

The omics-based research revealed that the order is a keystone taxon in a variety of settings, including forests, agricultural land, Arctic and Antarctic ecosystems, polluted soils, and plant-associated microbiota (Banerjee et al. 2018; LeBlanc and Crouch 2019). These habitats identify *Rhizobium* as a keystone taxon in the core microbiomes of several plant crops rhizospheres, including tropical crops, e.g., sunflower and sorghum (Bulgarelli et al. 2015; Yeoh et al. 2017; Oberholster et al. 2018), as well as their well-known presence and functions in the legume nodule microbiome (Velázquez et al. 2019; Zheng et al. 2020). In long-term experiments, several genera from the order Rhizobiales that are closely related to *Rhizobium*, such as *Agrobacterium*, *Bradyrhizobium*, and *Devosia* have been identified to be part of the maize rhizospheric core microbiome (Walters et al. 2018). Members of the Rhizobiaceae family and certain other Rhizobiales members appeared to be part of the heritable component of the maize rhizosphere microbiome. Several reports have been published in recent years about the occurrence of *Rhizobium* and related taxa in the rhizosphere, endosphere, and phyllosphere of nonleguminous crops. This is due to the interest in the investigation of agricultural microbiomes with the goal of discovering native rhizobial and nonrhizobial bacteria that may be endophytes to create benefits in nonlegume crops, being friendly with the indigenous microbiomes (Menéndez and Paço 2020).

Further, nonleguminous crops inhabit *Rhizobium*, also fix nitrogen within legume nodules, and other endophytic diazotrophs (Yoneyama et al. 2017, 2019). Using *nifH* gene amplification and cloning from various sources, some studies reported the presence of *Rhizobium* sp. in the roots and stems of maize plants grown in fields (Roesch et al. 2008), *R. etli* in the roots of one cultivar of sorghum grown with low and high nitrogen fertilizer doses (Rodrigues Coelho et al. 2008), while, *R. leguminosarum* applied in sweet potato tubers (Terakado-Tonooka et al. 2008), *R. helanshanense* in switchgrass roots and shoots (Bahulikar et al. 2014), and *R. daejeonense* in sugarcane stems and roots in Japan and Brazil (Thaweenut et al. 2011). Lay et al. (2018) used NGS approaches to compare the rhizosphere and endosphere of canola, pea, and wheat grown on the Canadian prairies. On the other hand, *R. leguminosarum* was detected in varying degrees of abundance in the endospheres and rhizospheres of the three crops; however, similar members of the Rhizobiaceae family, such as *Agrobacterium* sp., were associated with the endospheres of canola and wheat, but not in case of pea (Lay et al. 2018). Essel et al. (2019) investigated the selection of appropriate agronomic procedures for isolation of rhizobia from rhizospheric soils of rotationally farmed wheat and pea. This indicates that *Rhizobium* is more prevalent in soils that are closely linked to the roots, revealing the specialized functioning of genus *Rhizobium* with crops. *Rhizobium* was identified as a prominent OTU among other diazotrophs in rice fields (Jha et al. 2020). Other related OTUs, such as unclassified *Rhizobiales* and unclassified Rhizobiaceae, as well as other rhizobia OTUs, were also detected with a lower prevalence. The inclusion of a *R. leguminosarum* strain as an inoculant with or

without a low dosage of urea fertilizers lowered the OTU richness; *Rhizobium* remained a relevant OTU, but other α -Proteobacteria OTUs were less prevalent. Nonetheless, the beneficial effects of inoculation and inoculation + low dose of N showed enhanced rice growth and yield, implying that the communities are not negatively affected by selective dosage of chemical fertilizers and adaptive fertilizer adaptive nature of rhizobia explored.

The majority of the nonlegume researched are cereals, although, work also conducted on the microbiomes of vegetable plants, trees, and shrubs. Member of genus *Rhizobium* and related genera were reported from those microbiomes which indicates their relevance in plant growth promotion and biocontrol measures. *Rhizobium* spp. were found in bulk and rhizospheric soils of cucumber plants (Jia et al. 2019). Marasco et al. (2013) identified several *Rhizobium* species in grapevine roots, both in the rhizosphere and in the interior tissues, using DGGE rather than amplicon sequencing or metagenomics. Members of the *Allorhizobium–Rhizobium/ParaRhizobium–Rhizobium* complex were only discovered in *Xylella*-infected and *Xylella*-uninfected olive trees of the variety "Leccino" (tolerant to *Xylella* infection). This was relevant after using NGS in the phyllosphere and endosphere of leaves and branches (Vergine et al. 2019). *Rhizobium* was detected in the resistant cultivar but not in the susceptible cultivar, implying that this taxon may have a role in this cultivar's resistance to infections. Recently, Wang et al. (2020) identified *Rhizobium* as a key bacterial genus in the microbiome of rice root and shoot.

3.12 Conclusion and Future Aspect

The rhizobia can benefit the nonlegumes as well as the legume plants. The compounds released or secreted by rhizobia are beneficial to both the category of plants alter their environment with the help of these compounds. With the advent of new technology, the plant-microbe interaction is better understood and more research allows us to predict the exact requirement of both the plant and microbe. With the positive interaction, the microbe may fix atmospheric N₂, release phytohormones, increasing the immunity of the plant against different stress. It also allows the plant to blend in a new environment, altering rhizospheric microflora. The goal is to achieve and identify beneficial communities which not only save time but are also cost-effective. Therefore, with the new technologies, more research has to be done emphasizing the genetic aspect, molecular biology, and ecology of the rhizobia and better understanding of nonleguminous plants for improving the productivity, to attain useful rhizobia for sustainable agriculture. The futuristic focus should be to understand the signaling mechanisms between rhizobia and nonlegume plants and the process of colonization, to exhibit synergistic effect between host plant and rhizobia, to genetically modify the partners for better co-operation, the use of crop-specific promoters per the environment or soil type, selecting mutant types with better growth traits. Also focus should be there to use of multiple beneficial

nitrogen-fixing strains benefited to diverse germ plasm of nonlegume crops so as to achieve sustainable goal in agroecological practices.

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