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ReviewArticle

The importance of *Rhizobium*, *Agrobacterium*, *Bradyrhizobium*, *Herbaspirillum*, *Sinorhizobium* in sustainable agricultural production

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Abstract

Rhizobia which are soil bacteria capable of symbiosis with legume plants in the root or stem nodules and perform nitrogen fixation. Rhizobial genera include *Agrobacterium*, *Allorhizobium*, *Aminobacter*, *Azorhizobium*, *Bradyrhizobium*, *Devosia*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Ochrobacterum*, *Phyllobacterium*, *Rhizobium*, *Shinella* and *Ensifer* (*Sinorhizobium*). Review of the literature was carried out using the keywords *Rhizobium*, *Agrobacterium*, *Bradyrhizobium*, *Herbaspirillum* and *Sinorhizobium*. Rhizobial nodulation symbioses steps are included flavonoid signaling, Nod factor induction, and Nod factor perception, root hair responses, rhizobial infection, cell division and formation of nitrogen-fixing nodule. *Rhizobium* improves sustainable production by boosting organic nitrogen content.

Keywords: nod; rhizobial genera; rhizobial nodulation; sustainable production

Introduction

The food shortage is expecting in coming year as the population of the world has increased very fast (Khoshkharam *et al.*, 2010; Riaziat *et al.*, 2012; Soleymani *et al.*, 2016; Shahrajabian *et al.*, 2020), while climate change and natural resource depletion has caused many problems in food security (Soleymani *et al.*, 2011a,b; Yazdpour *et al.*, 2012; Abdollahi *et al.*, 2018; Shahrajabian *et al.*, 2019a,b; Sun *et al.*, 2019, 2020). Rhizobia which are soil bacteria capable of symbiosis with legume plants in root or stem nodules and perform nitrogen fixation for the host (De Meyer *et al.*, 2015) are traditionally belong to the genera *Azorhizobium*, *Sinorhizobium*, *Bradyrhizobium*, *Ensifer*, *Mesorhizobium* and *Rhizobium* (Sawada *et al.*, 2003; Nandasena *et al.*, 2004). *Rhizobia* are Proteobacteria (Mousavi *et al.*, 2014) and *Rhizobial* genera include *Agrobacterium*, *Allorhizobium*, *Aminobacter*, *Azorhizobium*, *Bradyrhizobium*, *Devosia*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Ochrobacterum*, *Phyllobacterium*, *Rhizobium*, *Shinella* and *Ensifer* (*Sinorhizobium*) (Lindstrom and Mousavi, 2010; Lindstrom *et al.*, 2013). Root nodulation is interaction of compatible rhizobia which activates an array of genes which result in nodule development (Das *et al.*, 2019). The bacteria reduce dinitrogen to ammonium inside the legume-root nodule in exchange for a carbon and energy source (Prell and

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Poole, 2006). The ability of adaptation of *Rhizobia* in diverse environment namely soil, rhizosphere and grown within legume roots may lead to nitrogen fixation, in a complicated process which contain a coordinated exchange of signal between the symbionts and plants (Ghosh and Maiti, 2016; Jack *et al.*, 2019; Torabian *et al.*, 2019). Nodulation also varied on the basis of the species and site (Rejili *et al.*, 2012). Two distinct types of nodules are formed on legumes, namely determinate which are usually formed on common plants in tropical regions such as *Glycine max*, *Lotus japonicus* or *Vicia faba*, and indeterminate (Gibson *et al.*, 2008; Haag *et al.*, 2013). The most important examples of indeterminate-type nodules are *Medicago*, *Trifolium*, *Pisum*, and *Vicia* spp. (Janczarek *et al.*, 2015; Bahroun *et al.*, 2018). The most notable plant flavonoids are Flavones, Flavonols, Flavanones, Isoflavones, and Chalcones (Janczarek *et al.*, 2015). There are almost 50 nodule-forming bacterial species within the genera (Wang *et al.*, 2006; Hang *et al.*, 2008). Nodule-forming bacteria is shown in Table 1. The most important characteristics of indeterminate and determinate nodules are indicated in Table 2. The list of some important *Rhizobium* species and their corresponding hosts are presented in Table 3. The metabolic diversity of rhizobia on the basis of their large, complex genomes is shown in Table 4.

Table 1. Nodule-forming bacteria

Genera	Type
The alpha-proteobacterial genera	*Agrobacterium*, *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, *Sinorhizobium*, *Devosia*, *Methylobacterium*, *Ochrobactrum*, *Phyllobacterium*
The beta-proteobacterial genera	*Burkholderia*, *Cupriavidus*

Table 2. The most important characteristics of indeterminate and determinate nodules

Characteristic	Determinate	Indeterminate
Host plant	Bean, Soybean, Lotus	Alfalfa, Pea, *Medicago truncatula*
Nodule shape	Spherical	Elongated
Nodule growth	Cell expansion	Cell division. Persistent meristem
Initial cell divisions	Outer cortex	Inner cortex
Flavonoids including nod genes	Flavones, Flavonones	Isoflavones

Table 3. The list of some important *Rhizobium* species and their corresponding hosts

Rhizobium species	Host plants
Bradyrhizobium japanicum	*Glycine max* (soybean)
Rhizobium fredii	*Glycine max* (soybean)
R. phaseoli	*Phaseolus vulgaris* (common bean)
S. meliloti	*Medicago sativa* (alfalfa)
	Melilotus sp. (sweet clovers)
Rhizobium leguminosarum bv. *trifolii*	*Trifolium* sp. (clovers)
R. leguminosarum	*Pisum sativum* (peas)
	Vicia faba (broad bean)
Rhizobium sp. or cowpea rhizobia group	*Vigna unguiculata* (cowpea)
	Arachis hypogaea (peanut)
	Vigna subterranean (Bambara groundnut)
	Leucaena sp., *Albizia* sp.,
Azorhizobium caulinodans	*Sesbania* sp. *Sesbania rostrata* (stem nodulating)

Table 4. The metabolic diversity of rhizobia on the basis of their large, complex genomes

Rhizobia	Range
Rhizobium etli	6.5 Mb
Sinorhizobium meliloti	6.7 Mb (Giraud and Fleischman 2004)
Mesorhizobium loti	7.6 Mb (Kaneko *et al.*, 2000)
Rhizobium leguminosarum	7.8 Mb
Bradyrhizobium japonicum	9.1 Mb (Kaneko *et al.*, 2002)

Rhizobial modulation symbioses consists of flavonoid signaling, Nod factor induction and perception, root hair responses which included calcium flux and spiking, gene expression), rhizoial infection, cell division and nitrogen-fixing nodule formation. The most important alphaproteobacteria are 1) Allorhizobium included, *Aminobacter*, *Azorhizobium*, *Bradyrhizobium*, *Devosia*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Neorhizobium*, *Ochrobactrum*, *Phyloobacterium*, *Rhizobium*, *Shinella*, *Sinorhizobium* (*Ensifer*), 2) Betaproteobacteris, consists of *Cupriavidus*, *Paraburkholderia* and *Trinickia*, and 3) Gamaproteobacteria. In this manuscript, we want to review *Rhizobium*, *Agrobacterium*, *Bradyrhizobium*, *Herbaspirillum*, and *Sinorhizobium*.

Rhizobium

The most important group of nitrogen fixing soil bacteria which can lead to mutualistic symbiotic association (root nodules) with leguminous plants are rhizobia (Gage, 2004: Werner, 2007; van Ham *et al.*, 2016). Rhizobium improves sustainable production by boosting organic nitrogen content (Youseif *et al.*, 2014; Vanlauwe *et al.*, 2019; Karoney*et al.*, 2020). The gram-negative rod-shaped bacteria was first discovered by Frank (1889). Indole acetic acid (IAA) catabolising enzyme in nodule, root, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity have significant important in plant growth promotion and plant-microbes interaction of symbiotic phenomenon (Ghosh *et al.*, 2013). Notable parameters which have been related to successful establishment of the symbiotic interaction are chemotaxis of the bacteria towards the roots, root colonization and its hair deformation, infection thread formation, and rapid division or root cortex cells (Spaink *et al.*, 1998, 1992; Dardanelli *et al.*, 2008; Junier *et al.*, 2014; van Zeijl *et al.*, 2015; Wang *et al.*, 2016). Rhizobia produce Nod factors during the early development of nodules upon perception of flavonoid molecules secreted by legume roots (Servin-Garciduenas *et al.*, 2014; Shamseldin *et al.*, 2014), and Nod factors structure depends on species, chemical substitutions added which may impact legume specificity (D'Haeze and Holsters, 2002; Feng *et al.*, 2002; Geurts and Bisseling, 2002). More than 44-66 million tons of nitrogen biologically fixed per year which provide half of requirements in agriculture (Alberton *et al.*, 2006; Acosta *et al.*, 2011). Nitrogen fixation and legumes yields depends on the *rhizobium* strain, the genotype of the legume, bio-physical environment, and management practices (Giller *et al.*, 2013; Tong *et al.*, 2018; Wolde-meskel *et al.*, 2018; Flores-Felix *et al.*, 2019). The combination of *Rhizobium* and *Arbuscular mycorrhiza* are more effective than individual applications as the highest root colonization, root nodulation and the maximum yield of chickpea (*Cicer arietinum* L.) was related to combined application of these treatments (Erman *et al.*, 2011). Ahmad *et al.* (2013) observed that *Rhizobium* and *Pseudomonas* strains can improve the growth, physiology, and quality of mung bean under salt-affected conditions. Shaping rhizobial species-level taxonomic biogeography maybe under the influence direct or indirect impacts of abiotic and biotic soil factors and legume hosts (Ide Franzini *et al.*, 2010; Uyanoz and Karaca, 2011; Xiong *et al.*, 2017; Gao *et al.*, 2019). Cao *et al.* (2017) found soil factors shaped the rhizobial populations stronger compare to the geographic distance. Moreover, the native rhizobia differed by site (Yadav and Verma, 2014; Mwenda *et al.*, 2018; Stefan *et al.*, 2018). *Rhizobium* and *cyanobacteria* inoculants have positive feedback on plant growth and legumes yields (Babu *et al.*, 2015). Inoculation of *Rhizobium pisi* and *Pseudomonas monteilii* is a promising biofertilization strategy for common bean production (Sanchez *et al.*, 2014). Different rhizobiums and their usages are shown in Table 5.

Table 5. Different *Rhizobium* and their usages

Rhizobium	Application and mechanism	Reference
Rhizobium leguminosarum	It can nodulate *Lathyrus* spp., *Pisum sativum*, *Melilotus indicus*, *Robinia pseudoacacia*, *Securigera varia*, *Trifolium* and *Vicia* plants	Weir *et al.* (2004) Alvarez-Martinez *et al.* (2009) Ramirez-Bahena *et al.* (2009) De Mayer *et al.* (2011) Rogel *et al.* (2011) Marek-Kozaczuk *et al.* (2013)
Chloralla vulgaris-*Rhizobium* sp. mixotrophic co-cultivation	It can be applied for wastewater reclamation in continuous mode at multiple hydraulic retention times (HRT) of 3-7 days	Ferro *et al.* (2019)
Rhizobium sp.	Reduction of lipid accumulation in microalgae	Fei *et al.* (2019)
Rhizobium species	Promote algal growth	Gonzalez and Bashan (2000) Yao *et al.* (2019)
Rhizobium laguerreae	It is the main nitrogen fixing symbiont of lentil (*Lens culinaris*)	Moswad and Beck (1991) Laguerre *et al.* (1992) Tian *et al.* (2010) Riah*et al.* (2014) Taha *et al.* (2018)
Rhizobium meliloti	Alfalfa and *Rhizobium* symbiotic association may stimulate the rhizosphere microflora is a useful method for aged polycyclic aromatic hydrocarbons (PAHs)-contaminated soils	Mehmannavaz *et al.* (2002) Chekol*et al.* (2004) Radwan *et al.* (2007) Teng *et al.* (2011) Sanchez-Pardo and Zornoza (2014) Deepika *et al.* (2016) Cardoso *et al.* (2018) Duan *et al.* (2019) Ju *et al.* (2019)
Rhizobium rhizogenes	Its T-DNA is involved in fasciation of *Nicotiana* leaves. It also contains a highly mosaic genetic organization in tumorigenic strains. The pathogenic strains of *Rhizobium* could be considered as model to analyse bacterial evolution	Velazquez *et al.* (2010)
Rhizobium	There is one alcohol dehydrogenase encoding gene in Rhizobium, and aldo-keto reductases which decrease aldehydes to alcohols	Sadowskyt and Bohloot (1986) Willis and Walker (1998) Pizzimenti*et al.* (2013) Matos *et al.* (2019)
The molecular structure of *rhizobium* exopolysaccharide (REPS)	REPS polysaccharide possesses antitumor activity	Zhao *et al.* (2010)
Rhizobium massiliae	Its water-soluble extracellular polysaccharide (WSP) of *R. massiliae* CA-1 can be used as a new immunomodulatory enhancing the early innate immunity	Kim *et al.* (2017)
Rhizobium radiobacter CAS	Its physic-functional properties make it an important candidate for food processing and also product development sector	Kavitake *et al.* (2019)
Rhizobium	*Rhizobum* strain contained ALK gene which revealed strong Nonylphenol (NP) degradation ability in liquid culture and showed a potential bio-remediating NP-contaminated sediment	Wang *et al.* (2014)
Rhizobium spp.	Pre-treatment of chickpea seedlings with *Rhizobium* spp. isolates activates genes involved in the phenylpropanoid pathway by promoting the accumulation of phenolic compounds	Arfaoui *et al.* (2007)
Rhizobium sp. MRP1	It can be used as bacterial inoculants to boost pea production in fields which are polluted	Ahemad and Khan (2011)

	with fungicides	
Rhizobium tropici	Symbiosis of common bean's root and rhizobia can decrease the negative effects made by the allelopathic plant	Perez-Peralta *et al.* (2019)
Rhizobium bangladeshense *Rhizobium aegyptiacum*	Nodulation of these *Rhizobium* with *Trifolium alexandrinum* may increase final yield	Shamseldin *et al.* (2016)
Rhizobium anhuiense	*R. anhuiense* is the main symbiont for beach pea (*Lathyrus maritimus* or *Lathyrus japonicus*) rhizobia on the seashore line of China and Japan	Li *et al.* (2016)
Rhizobium (VR-1 and VA-1)	Inoculation of host-specific fly-ash-tolerant Rhizobium strain with plants ha positive role in improving plant growth	Chaudhary *et al.* (2011)
Rhizobium	Rhizobial bacteria can mitigate the negative impacts of excess arsenic (As) in legume-rhizobium symbiosis	Reichman (2007)
Rhizobium	Rhizobium strains in *Sporobolus robustus* Kunth's rhizosphere has ability to act as a nurse plant to improve seedlings recruitment of *Prosopis juliflora* and *Vachellia seyal in* saline soils	Fall *et al.* (2019)
Rhizobium	Nodulation and nitrogen fixation of guar (*Cyamopsis tetragonolobus* L. Taub.)) significantly, increase with indigenous *Rhizobium* in field conditions. *Rhizobium* inoculation also can have positive effects on productive qualitative traits of guar such as Galactomannan content	Thapa *et al.* (2018) Gresta *et al.* (2019)
Rhizobium PEPV16	Inoculation with *Rhizobium* strains is a promising technique to improve the content of several bioactive compounds of strawberries	Flores-Felix *et al.* (2018)
R. leguminosarum *R. fabae* *R. laguerreae* *R. anhuiense*	Nodulation of *Vicia faba* L. with these Rhizobium increase sustainable crop production	Torres *et al.* (2012) Saidi *et al.* (2014) Youseif *et al.* (2014) Zhang *et al.* (2015) Belhadi *et al.* (2018)
Rhizobium BMBS (Diazotrophic bacterium)	Rhizobium BMBS and Arbuscular mycorrhizal fungi (*Glomus intraradices*) primed suggested as a bioprotectant against *Spodopteralitura* in blackgram	Selvaraj *et al.* (2020)
Rhizobium freirei PRF 81	It has adaptive response to acid pH and this acid tolerance decrease internal acidification show the broad range of metabolic pathways of this *Rhizobium*	Hungria *et al.* (2000) Tullio *et al.* (2019)
Rhizobium	*Rhizobium* inoculation can improve uptake of water, macro and micro nutrients in legumes such as soybean	Gao *et al.* (2010) Nyoki and Ndakidemi (2018)

Table 6. The most important rhizobia nodulated with *Phaseolus vulgaris*

Rhizobium	Reference
Rhizobium etili, *Rhizobium tropici*, *Rhizobium leguminosarum* bv. *phaseoli*, *Rhizobium gallicum*, *Rhizobium azibense*	Mnasri *et al.* (2014)
Rhizobium freirei	Dall'Agnol *et al.* (2013)
Rhizobium mesoamericanum	Lopez-Lopez *et al.* (2012)
Sinorhizobium meliloti	Zurdo-Pineiro *et al.* (2009)
Sinorhizobium americanum	Mnasri *et al.* (2012)
Bradyrhizobium sp.	Han *et al.* (2005)
R. etli in the South and Middle Americas	Amarger (2001)
R. etli in Europe	Garcia-Fraile *et al.* (2010)

R. etli in Jordan	Tamimi and Young (2004)
R. tropici in regions with high temperature and acid soils	Martinez-Romero *et al.* (1991) Anyango *et al.* (1995) Grange and Hungria (2004)
R. phaseoli and *R. etli* in Africa	Aserse *et al.* (2012)
R. leguminosarum, *R. etli* and *Rhizobium* sp. II or IV	Cao *et al.* (2014)

Agrobacterium

The genus *Agrobacterium* was created by Conn (1943) within the family Rhizobiaceae together with the genus Rhizobium (Frank, 1889). *Agrobacterium tumefaciens* was first isolated from the gall tissue and recognized as the cause of crown gall disease (Smith and Townsend, 1907). Bacteria belong to *Agrobacterium* group are recognized as symbionts and pathogen of specific plants (Long *et al.*, 1989; Goodner *et al.*, 2001), and known as intracellular bacteria in the hyphae of a few endophytic fungal species (Sharma *et al.*, 2008; Baltrus *et al.*, 2017; Guo *et al.*, 2018). It has extraordinary capacity to transfer its genetic material to host cell which makes it evolve from phytopathogen to a powerful transgenic vector (Ziemienowicz 2014; Guo *et al.*, 2019). *Agrobacterium tumefaciens*, is a gram-negative, soil-born phytopathogenic bacterium which is called a nature's engineer because of its ability to genetically transform the host by transferring a DNA fragment (T-DNA) from its Ti plasmid to host-cell genome (Guo *et al.*, 2009; Guo *et al.*, 2011; Nester, 2015; Guo *et al.*, 2017; Sun *et al.*, 2018; Wixom *et al.*, 2018). Agrobacterium tumefaciens-mediated transformation (ATAT) is an effective genetic transformation method in recent 20 years (Gu *et al.*, 206; Moon *et al.*, 2008; Shao *et al.*, 2015; Yang *et al.*, 2018), which is a member of the alpha-Proteobacteria which a resident of the soil and rhizosphere (Hanana *et al.*, 2018; Li *et al.*, 2018; Nathoo *et al.*, 2019; Niazian *et al.*, 2019). ATMT works well with different fungal materials such as spores, mycelia, and gill tissues of mushroom (Chen *et al.*, 2000; Mulllins *et al.*, 2001; Park *et al.*, 2013), which makes it appropriate for fungal genetic manipulation (Xu *et al.*, 2016; Idnurm *et al.*, 2017; Long *et al.*, 2018). In pharmaceutical studies, this technique has been also used to produce various proteins, and general functional studies of plant proteins (O'Neill *et al.*, 2008; Jones, 2016). Several studies introduced ATMT as an initiative bio-transformation system which may provide new insights into fungal pathogenesis, pigmentation, sporulation, and antibiotic resistance (Jeon *et al.*, 2007; Huser *et al.*, 2009; Mischielse *et al.*, 2009; Zhang *et al.*, 2011). Along with *A. tuerfaciens*, *Agrobacterium rhizogenes*, has been used to affect genetic transformation in many plants for several years (Bahramnejad *et al.*, 2017). *Agrobacterium rhizogenes* - mediated transformations has a lot of advantages such as fast growth rates, ease of maintenance, genetic stability, large scale biomass production which does not need external usage of phytohormones and ability to synthesize a broad array of valuable secondary metabolites (Srivastava and Srivastava, 2007; Chandra and Chandra, 2011). Agrobacterium rhizogenes includes a root-inducing (Ri) plasmid (Chen *et al.*, 2018) which contains root locus (rol) genes in the T-DNA region consist of rolA, rolB, rolC, and rolD (Christey and Braun, 2005). Hairy root cultures have been studied for application as pharmaceuticals, nutraceuticals, food additives and cosmetic (Srivastava and Srivastava, 2007; Chandra and Chandra, 2011). Hairy root caused by *Agrobacterium rhizogenes* and cane gall caused by *A. rubi* (Pacurar *et al.*, 2011). The most important characteristics of Agrobacteria is indicated in Table 7. The most important species included in the genus *Agrobacterium* and species causing tumors and hair roots in other genera of family *Rhizobiaceae*are presented in Table 8. Hairy roots benefits in some reported samples are shown in Figure 10. Different *Agrobacterium* for different plants is presented in Table 10.

Table 7. The most important characteristics of *Agrobacteria*

1-	A group of Gram-negative, non-spore-forming soil bacteria, mainly isolated from abnormal proliferating plant tissues
2-	They belong to a large family of plant-associated bacteria, namely Rhizobiaceae, which include *Rhizbonium* and *Sinorhizobium*, which are nitrogen-fixing symbiotic bacteria
3-	They are able to catabolize a large variety of metabolites, and they can show chemotactic behavior for some plant exudates
4-	The genome composition of *Agrobacterium tumefaciens* is circular chromosome secondary linear chromosome
5-	The genome composition of *Agrobacterium radiobacter* is circular chromosome four plasmids
6-	The genome composition of *Agrobacterium vitis* is circular chromosome, chromosome, and five plasmids.
7-	*Agrobacterium*-induced tumors in nature which have been documented on more than 1000 different plant species, belonging to most of the families of the dicotyledonous plants
8-	In researches related to general cell and molecular biology, *Agrobacterium* interactions with its host cells have emerged as an important experimental system
9-	Classification of different species of *Agrobacterium* is predominantly based on their phytopathogenic properties
10-	Under optimal laboratory conditions, *Agrobacteria* are motile (with one to six flagella), aerobic, rod-shaped bacteria, with a slow generation time (1.5 to several hours)
11-	T-DNA and the *virulence* (*vir*) region are two important genetic regions on the Ti plasmid which are essential for *Agrobacterium* to transfer DNA to plant cells
12-	*Agrobacterium* Tiplasmif consider as gene vector for plant genetic engineering
13-	Agrobacterium mediated gene transfer is controlled by different factors such as bacterial factors, host and environmental origin
14-	*Agrobacterium* has been successfully applied for various economically and horticulturally important monocot and dicot species transformation via standard tissue culture and *in planta* transformation techniques
15-	Gene transfer from *Agrobacterium* to plant cells consist of five important steps which are, induction of the bacterial virulence system, generation of T-DNA complex, transfer of T-DNA from *Agrobacterium* to the host cell nucleus, integration of T-DNA into the plant genome, and expression of T-DNA genes
16-	The most important factors which impact *Agrobacterium* mediated plant transformations are explants type, vector plasmid, bacterial strain, composition of culture medium, temperature of co-cultivation, time of co-cultivation, *Agrobacterium* density, pH of co-cultivation medium, antibiotics, chemicals, surfactants and selected markers
17-	The ability of infecting plants is because of the possession of large plasmids by both bacterial species, known as Ti and Ri plasmids for both *A. tumefaciens* and *A. rhizogenes*

Table 8. The most important species included in the genus *Agrobacterium* and species causing tumors and hair roots in other genera of family Rhizobiaceae (Flores-Felix *et al.*, 2020)

Genus	Species
Agrobacterium	*A. radiobacter, A. tumerfaciens, A. rubi, A. larrymoorei, A. albertimagni, A. fabrum, A. pusense, A. nepotum, A. skierniewicense, A. arsenijevicii, A. deltaense, A. salinitolerans, A. bohemicum, A. rosae*
Allorhizobium	*A. vitis*
Rhizobium	*R. rhizogenes, R. tumorigenes*

Table 9. Hairy roots reported in some crops

Benefits of hairy roots	References
Increase the amount of saponin in *Bacopamonnieri*	Majumdar *et al.* (2011)
Enhance the amount of anthroquinones in *Polygonum multiflorum*	Thiruvengadam *et al.* (2014a)
Increase total phenolic content in *Solanum lycopersicum*	Singh *et al.* (2014)
Increase polyphenols in *Momordica charantia*	Thiruvengadam *et al.* (2014b)
Enhance the amount of glucosinolates in *Arabidopsis thaliana*	Kastell *et al.* (2015)
Increase phenolic compounds in *Momordica dioica* Roxb. ex. Willd	Thiruvengadam *et al.* (2016)

Table 10. Different *Agrobacterium* for different plants

Different *Agrobacterium* isolated from nature		Reference
Agrobacterium tumefaciens	*A gram-negative and rod-shaped plant pathogen belonging to the family *Rhizobiacea*. It can transfer transferred DNA (T-DNA), which is located in its tumor-inducing (Ti) plasmid, into the chromosome of the target cells at random sites. *Strain Chry5 is hypervirulent on many plants, especially soybean. Tumors induced by Chry5 contain a novel opine called chrysopine. *Agrobacterium tumefaciens* and its Ti plasmid have been extensively used as a vector to create transgenic plants and fungi. *It is specific for NAD^+ as a cofactor, but accepted both D-galacturonic acid (GalA) and D-glucuronic acid (GlcA) as substrates with similar affinities, and the reaction product is probably the hexaro-lactone, which spontaneously hydrolyzes. *In Soybean, the hypervirulent *Agrobacterium tumefaciens* strains KYRT1 proved to be a better transformer than EHA105 and LBA4404	Van Larebeke *et al.* (1975) Bush and Pueppke (1991) Dessaux *et al.* (1993) Chilton *et al.* (1995) Palanichelvam *et al.* (2000) Satyavathi *et al.* (2002) Dang and Wei (2007) Shao *et al.* (2018) Murugan *et al.* (2019) Xiao *et al.* (2020)
Agrobacterium sp. H13-3 (*Rhizobium lupine* H13-3)	*It is a soil bacterium isolated from the rhizosphere of *Lupiunus luteus*. It is unable to nodulate *Lupinus* under laboratory conditions. Its highly conserved circular chromosome (2.82 Mb) mainly encodes housekeeping functions characteristic for an aerobic, heterotrophic bacterium. It also posses a linear chromosome (2.15 Mb) which is related to its reference replicon and features chromosomal and plasmid-like properties. It has been reported that a tumor-inducing Ti-plasmid is missing in the sequenced strain H13-3 indicating that it is a non-virulent isolate	Balassa (1957) Gabor (1965) Wibberg *et al.* (2011)
Agrobacterium rhizogenes	*Hydroponically-inoculated of *Daturainnoxia* plants with *Agrobacterium rhizogenes* can increase growth and alkaloid metabolism which may be more useful for successful specialized metabolite bioproduction in greenhouses	Vu *et al.* (2018)
Agrobacterium fabrum	*It has evolved a mechanism to deliver genes into cell of wounded plant tissue. It is considered as the suitable model organism, and a widely used vector for plant transformation	Deropp (1951) Klee *et al.* (1987) Zupan *et al.* (2000) Bai *et al.* (2016)
Agrobacterium-mediated transformation	*A common and convenient method to	Kobayashi and Uchimiya (1989)

	integrate gene into plant at higher efficiencies. This method could be providing a regeneration of transgenic plant from leaf and stem segments to increase biomass, chemical components yield and quality of plants. Genetic transformation methods are divided into direct gene transfer and indirect gene transfer methods according to the transferring procedure.	Vardi *et al.* (1990) Hidaka and Omura (1993) Yao *et al.* (1996) Wang *et al.* (1998) Dai *et al.* (2001) Niedz *et al.* (2003) Gao *et al.* (2008) Shewry *et al.* (2008) Ozawa (2009) He *et al.* (2010) Ozawa and Takaiwa (2010) Abdallat *et al.* (2011) Dewir *et al.* (2015) Koetle *et al.* (2015) Nabeshima *et al.* (2016) Huang *et al.* (2017) Shivani and Tiwari (2019) Singh *et al.* (2019)
Agrobacterium tumefaciens	*The Agrobacterium tumefaciens-mediated transformation (ATMT) technique has been used in randomized mutagenesis experiments, which has higher efficiency and percentage of single-copy patterns of T-DNA added into the fungal recipient. ATMT may be used as a molecular tool for different agronomical plants.	Mullins and Kang (2001) Leclerque *et al.* (2004) Sugui *et al.* (2005) Michielse *et al.* (2008) Talhinhas *et al.* (2008) Islam *et al.* (2012) Jiang *et al.* (2013) Li *et al.* (2019)

Bradyrhizobium

Distribution of rhizobial species is significantly influenced by geographical isolation and leguminous hosts (Keller *et al.*, 2018; Ji *et al.*, 2019). Various leguminous woody plants and herbs such as soybean, peanut, and cowpea, nodulated by bacteria belonging to the genus *Bradyrhizobium* (Moulin *et al.*, 2004; Degefu *et al.*, 2017). Slow-growing rhizobia classified within the genus *Bradyrhizobium*, including *B. japonicum*, *B. lupine*, *B. canariense* and *B. elkanii* species have role in nodulating of lupines species (Peix *et al.*, 2015; Shamseldin *et al.*, 2017; Stepkowski *et al.*, 2018; Mellal *et al.*, 2019). *B. japonicum* also recommend as a plant growth-promoting rhizobacterium for various plant species in sites contaminated with heavy metals (Reichman, 2014). The positive role of *Bradyrhizobium* - legume nodulation in maintaining plant community structure and restoration of degraded ecosystems has been reported in Southwest China (Liu *et al.*, 2015). Minimizing deleterious effects of exposing plants to composted tannery sludge because of inoculation with *Bradyrhizobium* is an important way to ensure plant growth and productivity (Moraes *et al.*, 2016). Improving growth and symbiotic performance of lupin under drought stress is reported by HTC-based *Bradyrhizobium* sp. (Egamberdieva *et al.*, 2017). Li *et al.* (2019) proposed isolated *Bradyrhizobium nanningense* sp. nov., *Bradyrhizobium guangzhouense* sp. nov. and *Bradyrhizobium zhanjiangense* sp. nov. of peanut in Southeast China. *B. japonicum*, *B. elkanii* and *B. liaoningense* are famous isolated *Bradyrhizobium* from Glycine max nodules in Japan, the USA and China, respectively (Jordan, 1982; Kuykendall *et al.*, 1992; Xu *et al.*, 1995). *B. pachyrhizi* and *B. jicamae* are isolated *Bradyrhizoium* from *Pachyrhizuserosus* nodules in Costa Rica and Honduras, respectively (Ramirez-Bahena *et al.*, 2009), and *B. Cytisi* and *B. rifense* are isolated *Bradyrhizobium* from *Cytisusvillosus* nodules in Morocco (Chahboune *et al.*, 2011; Chahboune *et al.*, 2012). Inoculation with nodulatin *B. japonicum* is important agricultural practice which can increase the content of bioactive metabolites in *Glycine Max* seeds (Silva *et al.*, 2013). Various benefits and advantages of *Bradyrhizobium* are shown in Table 11.

Table 11. Various benefits and advantages of *Bradyrhizobium*

Bradyrhizobium	Benefits and advantages	References
Bradyrhizobium	Peanut (*Arachis hypogeae* L.) nodulated by the genus *Bradyrhizobium*.	Fabra *et al.* (2010)
Bradyrhizobium and fungal endophyte *Phomopsis liquidambari*	*P. liquidambari* inoculation may increase flavonoids synthesis-related enzymes activities and its contribution enhances peanut-bradyrhizobium interaction, yield and nodulation.	Zhang *et al.* (2016)
Bradyrhizobium japonicum E109 and *Azospirillum brasilense*Az39	*B. japonicum* E109 and *A. brasilense*Az39 inoculation is the useful practice to improve both growth and yield of soybean exposed to As	Armendariz *et al.* (2019)
Bradyrhizobium japonicum E109	It is able to produce indole acetic acid (IAA), gibberellins (GA_3) and zeatin (Z) which can lead to significant morphological and physiological changes in maize and soybean young seed tissues	Cassan *et al.* (2009) Garcia *et al.* (2017)
Bradyrhizobium japonicum	*B. japonicum* can be considered as an attractive selection for remediation of fungicide polluted soils and to concurrently increase greengram production especially in stressed environment.	Shahid and Saghir Khan (2019)
Bradyrhizobium japonicum USDA119	It can be considered as a model organism for screening pollutants for toxicity against a soil microbial community	Shah and Subramaniam (2018)
Bradyrhizobium	It has been used for eco-toxicity studies such as measuring toxicity include chlorimuron-ethyl, heavy metals, metal-rich sewage sludge, acidity, phospate, herbicides, osmotic stress, nanoparticles and etc.	Keyser and Munns (1979) Moorman (1986) Kinkle *et al.* (1987) Zawoznik and Tomaro (2005) Soria *et al.* (2006) Reichman (2014)
Bradyrhizobium yuanmingense	It is a potent rhizobium for the development of groundnut inoculants in Ghana.	Osei *et al.* (2018)
Bradyrhizobium canariense and *Bradyrhizobium japonicum*	These two *Bradyrhizobium* are dominant rhizobium species in root nodules of lupin and serradella plants in Europe	Stepkowski *et al.* (2011)
Bradyrhizobium algeriense	*B. algeriense* is able to establish effective symbioses with *Retama raetam*, *Lupinus micranthus*, *Lupinus albus*, and *Genista numidica*	Ahnia *et al.* (2018)
Brazilian *Bradyrhizobium*	The Brazilian *Bradyrhizobium*	Bellini *et al.* (2019)

japonicum	*japonicum* strain CPAC-15 (=SEMIA 5079) is an important intermediate for semi-synthesis of β-lactam antibiotics such as penicillins, cephalosporins and amoxicillin.	
Bradyrhizobium diazoefficiens	*B. diazoefficiens* strain USDA110 has XoxF, a lanthanides-dependent MDH, which has the ability of methanol oxidation and is induced by methanol/lanthanaides. Lanthanide consider as the key factors in methanol utilization by the strain.	Liu *et al.* (2018) Wang *et al.* (2019)
Bradyrhizobium cytisi and *Bradyrhizobium rifense*	The strains isolated from *Astragalus algarbiensis* clustered with *B. cytisi* and *B. rifense*	Alami *et al.* (2019)
Bradyrhizobium canariense	The Mimosid tree *Leucaena Leucocephala* can be nodulated by symbiovargenistearum of *Bradyrhizobiumcanariense*	Ramirez-Bahena *et al.* (2020)

Herbaspirillum

Herbaspirillum seropedicae which can colonize a variety of higher plants, are diazotrophic endophytes; moreover, they have role in carbon catabolism by utilizing diverse carbon substrates and employ the Entner-Doudoroff route (Baldani *et al.*, 1986; Falk *et al.*, 1986; Catalan *et al.*, 2007). This endophytic diazotrophic *β*-Proteobacterium nitrogen-fixing bacterium has association with important agricultural plants such as rice, maize, sorghum, sugarcane and wheat for nitrogen fixation (Galvao *et al.*, 2004; Chaves *et al.*, 2009; Serrato *et al.*, 2012; Govarthanan *et al.*, 2014; Dos Santos *et al.*, 2017). Its capacity of convert N_2 to NH_3 through biological nitrogen fixation has made it a plant growth-promoting bacterium (Pessoa *et al.*, 2016). NifA protein regulates nitrogen fixation in *H. seropedicae* at the transcriptional level (Oliveira *et al.*, 2012), NifA itself is a member of the enhancer binding protein family with three structural domains (Studholme and Dixon, 2003). Ammonium ions through a mechanism involving its N-terminal domain control the activity of NifA, and N-terminal domain inhibits NifA-dependent transcriptional activation by an inter-domain cross-talk between the catalytic domain of the NifA protein and its regulatory N-terminal domain in response to fixed nitrogen (Monteiro *et al.*, 2001). The activity of NifA is negatively influenced by oxygen (Monteiro *et al.*, 1999; Souza *et al.*, 1999; Oliveira *et al.*, 2009), but interaction with Glnk positively influence it, and binding of 2-OG and MgATP to Glnk are very important for NifA activation (Stefanello *et al.*, 2020). Its oxygen sensitivity may attribute to a conserved motif of cysteine residues in NifA which spans the central AAA+ domain and the interdomain linker which connects the AAA+ domain to the C-terminal DNA binding domain (Oliveira *et al.*, 2009). GlnK, a PII signaling protein which monitors intracellular levels of key metabolite 2-oxoglutrate (2-OG) and works as an indirect sensor of the intracellular nitrogen status (Monteiro *et al.*, 1999; Monteiro *et al.*, 2003; Dixon and Khan, 2004; Noindorf *et al.*, 2011; Oliveira *et al.*, 2012). In the Betaproteobacterium *H. seropedicae*, the sensing of environmental signals is performed by the NifA protein itself, and the NifL protein is absent (Dixon and Kahn, 2004). Colonization sites detected for *Herbaspirillum seropedicae* (β), and *Herbaspirillum rubrishubalbicans* (β) are indicated in Table 12.

Table 12. Colonization sites detected for *Herbaspirillum seropedicae* (β), and *Herbaspirillum rubrishub albicans* (β)

Herbaspirillum seropedicae (β)	Sugar cane	Roots: Intercellular, Intracellular in cortex, Xylem vessels Shoots: Intracellular in xylem vessels
	Sorghum	Shoots: Intracellular, Confined to xylem vessels at point of injection
Herbaspirillum rubrishub albicans (β)	Sugar cane	Shoots: In leaves, Intercellular, Intracellular in substomatal cavities, Mesophyll, Xylem vessels
	Sorghum	Shoots: In leaves, Intracellular in xylem vessels

Pedrosa *et al.* (2001) found that nitrogen fixation in *H. seropedicae* (of the *β*-subgroup of Proteobacteria), has regulatory features in common with Klebsiella pneumonia (of the γ-subgroup and with rhizobia and *Azospirillum brasilense* (of the α-subgroup), at the level of NifA expression, and at the level of control of NifA by oxygen, respectively. Hu *et al.* (2020) found observed that *nirS* denitrifying bacteria *Herbaspirillum* and *Pseudomonas* were the dominant species in declined *P. crispus* sediment. NtrC regulates several operons involved in nitrogen assimilation in *Herbaspirillum seropedicae* (Twerdochlib *et al.*, 2003). Lubambo *et al.* (2013) found that *Herbaspirillum seropedicae* GlnB (Glnb-Hs) is a signal transduction protein which has role in controlling of nitrogen, carbon, and energetic metabolism.

Sinorhizobium

Sinorhizobium meliloti is a Gram-negative soil bacterium which accumulate *N*-acetylglutaminyl glutamine amide and trehalose in hyperosmolarity (Brique *et al.*, 2010; Ferroni *et al.*, 2012), and it survive needs developing active adaptive mechanisms quite different in humidity and aridity (Miller and Wood, 1996). Two famous phylogenetically closely-related species are *Sinorhizobium* (Ensifer) *meliloti* and *S. medicae* (Rome *et al.*, 1996; Roumiantseva *et al.*, 1999; Young *et al.*, 2001), live free in soil or in symbiosis with leguminous plants and perform nitrogen fixation (Ferri *et al.*, 2010; Wibberg *et al.*, 2013; Dohlemann *et al.*, 2016). Their genomes show multipartite architecture (Roumiantseva *et al.*, 1999), and high genetic similarity (Rome *et al.*, 1996). The endogenous compatible solutes in *S. meliloti* are the amino acid glutamate, the dipeptide *N*-acetylglutaminyl glutamine amide (NAGGN) and the disaccharide trehalose (αGlucose-(1↔1)-αGlucose) (Smith and Smith, 1989; Breedveld *et al.*, 1990; Botsford and Lewis, 1990). The *S. meliloti* genome is composed of a chromosome (3.65 Mb), and the megaplasmidspSyma (1.35 mb) and pSymB (1.68 Mb) (Galibert *et al.*, 2001). It produces sizable quantities of synthesize polyhydroxyalkanoates (PHA) and exopolysaccharides (EPS) (Tombolini and Nuti, 1989; Reinhold *et al.*, 1994; Saranya Devi *et al.*, 2012). Shamala *et al.* (2014) found that free living cells of *S. meliloti* influenced by fermentation conditions like pH, dissolved oxygen level, amount of carbon and nitrogen. It has been reported that all strains of *Sinorhizobium meliloti* do not stimulate plant growth of alfalfa cultivar in a similar extent (Zeng *et al.*, 2007). Tu *et al.* (2011) suggests that *S. meliloti* is promising in biodegradation capability and metabolic intermediate of polychlorinated biphenyls. The survival and persistence of *S. meliloti* was increased by alfalfa cultivation and enhanced soil fertility (Bhattacharya and Das, 2003; Da and Deng, 2003). This nitrogen-fixing α-proteobacterium is able to biosynthesize osmoprotectant glycine betaine from choline sulfate via a metabolic pathway which starts with the enzyme choline-*O*-sulfatase (Sanchez-Romero and Olguin, 2015). The nifA gene of *S. meliloti* is the most important regulator which activates the expression of fix genes and a bunch of nif (Better *et al.*, 1984; Szeto *et al.*, 1984; Earl *et al.*, 1987). NifA plays a regulatory role in multiple cellular process, and it may nifA null mutant may induce small white invalid nodules in the roots of host plant (Gong *et al.*, 2007). The rhizobia which nodulate the tropical leguminous trees *Acacia Senegal* and *Prosopis chilensis* are *Sinorhizobium arboris* and *S. kostiense* (Zhang *et al.*, 1991; Nick *et al.*, 1999; Nowak *et al.*, 2004). The first strains of the species described as nodulating Lotus was *S. meliloti* symbiovar lancerottense (Leon-Barrios *et al.*, 2017). Nodulation and mycorrhizal dependency (MD) in each plant genotype vary on the basis of *Sinorhizobium* strain and arbuscular mycorrhizal (AM) fungi involved (Vazquez *et al.*, 2001). Several studies recognized *Sinorhizobium meliloti* 1021 as a model organism for the study of symbiotic nitrogen fixation with legume plant hosts such as alfalfa, barrel medic, and some other plants of the *Medicago* and *Melilotus* genera (Jones *et al.*, 2007b; Gibson *et al.*, 2008). Its important transducing phage ΦM12 (Brewer *et al.*, 2014) was originally isolated from a commercial rhizobial seed inoculants prepared for field crop use on alfalfa (Finan *et al.*, 1984). Carbohydrate cycling in *S. meliloti* is independent of the gluconate bypass and also observed on fructose which makes this bacterium different from those of alginate-synthesizing species (Gosselin *et al.*, 2001).

Sinorhizobium meliloti belongs to the alpha class of the Gram-negative proteobacteria (Alphaproteobacteria). For a long time, it has been studied to infect roots of leguminous plants especially the genus *Medicago* (*M. sativa* and *M. truncatula*) (Xue and Biondi, 2019). Nod factors produced by bacteria and the flavonoids secreted into the rhizophere by the plants after the first contact between bacteria and plants (Cooper, 2007; Liu and Murray, 2016). Nod factors modulate the entry of the bacteria into the plant tissue which occurs following the formation of a modified radical root hair (Shaw and Long, 2003; Sieberer *et al.*, 2005). Then, the root hair traps a few *S. meliloti* cells, which penetrate inside the root tissue and induce the formation of an infection thread which is sealed after the entrance of few bacteria (Jones and Walker, 2008). After that, bacteria divides, reach the internal tissue which will host the future bacteroids. Then, bacteria are introduced into the plant cell by invagination of the plant cell membrane, which may lead to bacterium being surrounded by a plant derived membrane. This prokaryotic cell called a symbiosome (Jones *et al.*, 2007). Even without the presence of legumes, *S. meliloti* lives in the soil are free-living organism (Carelli *et al.*, 2000). *S. meliloti* is able to colonize the whole plant and the plant may have evolved a way to induce a terminal differentiation which may lead to blocking bacteria duplication and preventing uncontrolled colonization of the plant (Xue and Biondi, 2019). A *S. meliloti* bacteroid has two important features: a) Nitrogen fixation, b) Generating new cells once the nodule enters a senescent state (Kereszt *et al.*, 2011). Specific regulators of Fix and Nif control the bacteroid metabolism (Jones *et al.*, 2007). The activity of CtrA which has role in cell cycle regulation across alphaproteobacterial species, may regulate coordinates DNA replication, cell division and presumably bacteroid differentiation (Brilli *et al.*, 2010). Ctr A is essential for viability and controlling essential functions such as cell division, DNA replication and DNA methylation in *S. meliloti* (Xue and Biondi, 2019). Ctr A has can also considered as a crucial factor during bacteroid differentiation (Xue and Biondi, 2019). Peptides, such as NCR247, may be targeting directly or indirectly CtrA with its complex regulatory apparatus (Xue and Biondi, 2019).

Conclusions

Soil bacteria which are known as rhizobia (in roots and rarely stems) can associate with some plants (especially from the Leguminosae) and trees, forming specialized organs known as nodules. The ability of adaptation of *Rhizobia* in diverse environment namely soil, rhizosphere and grown within legume roots may lead to nitrogen fixation, in a complicated process which contain a coordinated exchange of signal between the symbionts and plants. Nodulation also varied on the basis of the species and site. There are almost 50 nodule-forming bacterial species within the genera. The most important alphaproteobacteria are 1) Allorhizobium included, *Aminobacter*, *Azorhizobium*, *Bradyrhizobium*, *Devosia*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Neorhizobium*, *Ochrobactrum*, *Phyloobacterium*, *Rhizobium*, *Shinella*, *Sinorhizobium* (*Ensifer*), 2) Betaproteobacteris, consists of *Cupriavidus*, *Paraburkholderia* and *Trinickia*, and 3) Gamaproteobacteria. Rhizobium improves sustainable production by boosting organic nitrogen content. Notable parameters which have been related to successful establishment of the symbiotic interaction are chemotaxis of the bacteria towards the roots, root colonization and its hair deformation, infection thread formation, and rapid division or root cortex cells. Rhizobia produce Nod factors during the early development of nodules upon perception of flavonoid molecules secreted by legume roots, and Nod factor's structure depends on species, chemical substitutions added which may impact legume specificity. Nitrogen fixation and legumes yields depends on the *rhizobium* strain, the genotype of the legume, bio-physical environment, and management practices. *Rhizobium* and *cyanobacteria* inoculants have positive feedback on plant growth and legumes yields. Inoculation of *Rhizobium pisi* and *Pseudomonas monteilii* is a promising biofertilization strategy for common bean production. The genus *Agrobacterium* is within the family *Rhizobiaceae* together with the genus *Rhizobium*. *Agrobacterium tumefaciens*, is a gram-negative, soil-born phytopathogenic bacterium which is called a nature's engineer because of its ability to genetically transform the host by transferring a DNA fragment (T-DNA) from its Ti plasmid to host-cell genome. *Agrobacterium rhizogenes*-mediated transformations has a lot of advantages such as fast growth rates, ease of maintenance, genetic stability, large scale biomas production which does not need external usage of phytohormones and ability to synthesize a broad array of valuable secondary metabolites. Hairy root cultures have been studied for application as pharmaceuticals, nutraceuticals, food additives and cosmetic. Hairy root caused by *Agrobacterium rhizogenes* and cane gall caused by *A. rubi*. Slow-growing rhizobia classified within the genus *Bradyrhizobium*, including *B. japonicum*, *B. lupine*, *B. canariense* and *B. elkanii* species have role in nodulating of lupines species. *B. japonicum* also recommend as a plant growth-promoting rhizobacterium for various plant species in sites contaminated with heavy metals. *Herbaspirillumseropedicae* which can colonize a variety of higher plants, are diazotrophic endophytes. This endophytic diazotrophic *β*-Proteobacterium nitrogen-fixing bacterium has association with important agricultural plants such as rice, maize, sorghum, sugarcane and wheat for nitrogen fixation. Stages of H. seropedicae actions with crops are bacteria attachment to root surface, colonization of the emergence points in secondary roots, penetration through discontinuities of the epidemic tissue, colonization of root xylem, aerenchyma end aerial parts along with intercellular spaces occupation, and lipopolysaccharies is involved in the communication between bacteria and their hosts like the genus of *Agrobacterium*, *Pseudomonas*, and *Azospirillum*. *Sinorhizobium meliloti* is a Gram-negative soil bacterium which accumulates *N*-acetylglutaminyl glutamine amide and trehalose in hyperosmolarity and its survival needs developing active adaptive mechanisms quite different in humidity and aridity. The nifA gene of *S. meliloti* is the most important regulator which activates the expression of fix genes and a bunch of nif.

Authors' Contributions

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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