

Host specificity and plant growth promotion by bacterial endophytes

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ABSTRACT

Plant-microbe interactions in the rhizosphere are the determinants of plant health, productivity and soil fertility. Bacterial inoculants can contribute to increase agronomic efficiency by reducing production costs and environmental pollution, as use of chemical fertilizers can be reduced or eliminated. Rhizobia can interact with legumes and establish a symbiotic relationship where it provides the plant with fixed nitrogen (N) and the plants in return provide the photosynthate as carbon source for its growth. Rhizobia influence growth of legumes as well as cereals and show increased persistence in soil even in the absence of their specific host making them suitable candidates for biofertilizer formulation. A recent study suggests that though non rhizobial bacterial endophytes cannot colonize the plant nodules on their own, they can colonize plant tissues by mechanisms of crack entry or by invading the rhizobial infection thread. Crop inoculation with such efficient plant growth promoting rhizobia and endophytes may heal problems of loss of soil fertility, fluctuation in climatic conditions, improved pathogen and pest attacks, etc. For bacterial inoculants to obtain success in improving plant growth and productivity, factors like exudation by plant roots, the bacterial colonization in the roots, and soil health play a pivotal role.

Keywords: rhizobia; endophyte; host specificity; plant growth promotion; breach.

1. INTRODUCTION

Biological nitrogen (N) fixation (BNF) is a mechanism which has directed the interest of researchers for over a century and has been exploited extensively in agricultural practices [1-2] as an alternative to the addition of harmful nitrogenous fertilizers for plant nutrition. Extensive application of N fertilizers have led to an unacceptable level of water pollution and eutrophication of water bodies [3]. N fixing organisms are capable of converting the atmospheric N to plant utilizable form by the enzyme nitrogenase. The process is intensive and the enzyme nitrogenase is inactivated irreversibly by oxygen [1]. The process of BNF is extremely efficient [4] with the mechanism of microbe mediated N fixation representing a renewable source of N for agriculture. The most important N fixing agents in agricultural systems are the symbiotic associations between crop and forage/fodder legumes and rhizobia. Annual inputs of fixed N are calculated to be 2.95Tg for the pulses and 18.5 Tg for the oilseed legumes. Soybean

(*Glycine max*) is the dominant crop legume, representing about 50% of the global crop legume area and 68% of global production. Accurately estimating global N fixation for the symbioses of the forage and fodder legumes is challenging because statistics on the areas and productivity of these legumes are almost impossible to obtain [5]. N fixing bacteria comprises the free living soil bacteria like *Azotobacter*, bacteria forming associative relations with plants like *Azospirillum* along with the bacteria forming symbioses with plants like *Rhizobium* and *Bradyrhizobium* [6]. Rhizobia encompasses members of diverse bacterial genera of α proteobacteria including *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Allorhizobium* and *Azorhizobium* [7]. Some members of β proteobacterial genera like *Burkholderia* and *Cupravidus* have seemed to have acquired *nod* genes from members of α proteobacteria long ago [8-9]. In most soils, naturally occurring N is often present in plant growth limiting

concentrations and hence the symbiotic association of the rhizobia with the legumes is ecologically and economically important. This mutualism culminates in the formation of a new plant organ in the roots, called the root nodule. Within the root nodule, the microsymbionts convert atmospheric nitrogen into ammonia, a biological form that can be directly consumed by the plant [10]. Ability of rhizobia to establish a N fixing symbiosis is limited to legumes, with *Parasponia* genus of *Ulmaceae* family being an exception [11]. Leguminosae family has three subfamilies namely *Caesalpinioideae*, *Mimosoideae* and *Papilionoideae*, with each having the ability to form root nodules [12-13]. By supplying the host with N, rhizobia can enhance host photosynthesis thereby increasing its own access to the photosynthate [14]. This specific and intimate association between bacteria of genus *Rhizobium* and leguminous plants provide most of the fixed N available for agriculture [15]. *fix*, *nif*, *nod* and *hcn* genes are involved directly in symbiotic N fixation [16-19]. *nod* gene products are required for the early steps of nodule formation [20] while *nif* and *fix* genes are indispensable for N fixation. Symbiotic genes may be horizontally transferred among distantly related bacteria, which may be vital for evolution of rhizobia [20-21].

2. Mode of infection by rhizobia

Specific interaction between the two partners performing symbiotic N fixation is initiated by flavonoids or isoflavonoids secreted by the host plant, which induces expression of *nod* genes in the rhizobia. Products of *nod* genes are vital to biosynthesis of species specific *nod* factors [22-23]. *Nod* factors released by the rhizobial cells elicit root hair curling and meristematic cell division leading to formation of root nodules. Rhizobial cells are attracted to plants by chemotaxis, gets attached to root hairs and invades the plant through an infection thread that penetrates the root cortex [24-26]. Rhizobia are then released into the plant cells where they further divide and differentiate morphologically and physiologically into bacteroids. Bacteroids take up atmospheric N and reduce it to ammonia. This fixed N is a nitrogen source for plants which in turn provides photosynthates and amino acids to the bacteroids as carbon (C) and N sources respectively [27]. Formation of an effective N fixing root nodule requires a coordinated temporal and spatial expression of plant *nodulin* genes and the bacterial genes involved in nod factor synthesis, nodule development, synthesis of the N fixing apparatus and bacteroid metabolism [24, 28-30]. Signalling events between rhizobia and host legumes are highly explicit such that certain bacterial species can nodulate only a limited number of legumes. Establishment of a successful symbiotic interaction requires signal recognition between both rhizobia and the legume and the evolution of host specificity involves both rhizobial and host genes [10]. *Nod* factors from different rhizobia share the same chitin like N-acetyl glucosamine oligosaccharide back bone with a fatty acyl chain at the non-reducing end, differing in the length of the back

bone, size and saturation of the fatty acyl chain as well as end modifications like glycosylation and sulfation [31]. These end modifications play a critical role in determining whether the nod factor can be perceived by a specific host [32], which in turn determines the *Rhizobium*- legume host specificity. Even though infection thread formation by rhizobia through root hairs is the most widely studied mode of entry of rhizobia into legumes, they may also enter the plant through cracks in the epidermis as in *Arachis hypogaea* [33] and *Stylosanthes sp* [34]. Once inside, rhizobia induces cell divisions in the cortex of an emerging lateral root, whose growth causes separation of cortical and epidermal cells enabling intracellular entry and spread of rhizobia. No infection thread formation occurs, however, continuous host cell divisions result in the development of a uniformly infected central tissue which resembles the determinant nodule [35]. Stem and root nodules of *Sesbania rostrata* are induced following crack entry by *Azorhizobium caulinodans* [36]. In addition to infection thread formation and crack entry, a third mode of infection also occurs. Here, the rhizobial infection sites are epidermal cell junctions and such a mode of entry is observed in *Mimosa scabrella*. Bacteria penetrates the radial walls, proliferates intracellularly, subepidermal root hairs are formed resulting in penetration of outer root cells towards cortical region. This results in elicitation of plant host defence response, rhizobia are released into developing nodule meristem cells, thereby forming an indeterminate nodule [37]. Mode of infection is a host characteristic as the same bacteria can penetrate different host species by any of the three modes and a specific legume is infected by the same mechanism irrespective of the infecting strain [38-39]. Although rhizobial-legume interactions are overall beneficial to the host in N fixation, the efficiency of N fixation varies with different plant-rhizobia combinations [40]. In certain situations, rhizobial strains are able to nodulate a host genotype but are unable to fix N, whereas with different host genotypes they can nodulate and fix N [41]. Some rhizobial strains like *Rhizobium leguminosarum* bv. *trifolii* have very narrow host range while others like *Rhizobium sp.* NGR234 have a very broad host range as it nodulates atleast 35 different genera of legumes as well as the non legume *Parasponia* [42].

3. Host specificity of rhizobia

The specificity of *Rhizobium*-legume symbiosis is because of the failure of other soil organisms in gaining effective entry into the plant by inducing infection thread formation. In addition to the release of nod factors by rhizobia which determines the host specificity, rhizobia also uses the surface polysaccharides or secreted proteins to modulate host range [43]. Plant lectins have long been speculated as receptors of rhizobial surface polysaccharides, hence determining the host range. Plant lectins bind to the rhizobial polysaccharides, promotes rhizobial attachment to root hairs thereby enhancing the nod factor delivery for root hair infection and nodule

initiation [44-45]. *Rhizobium* which infects and nodulates soyabean cannot nodulate clover and vice versa. It is this specificity which is the operational basis of cross-inoculation grouping [15]. Mechanisms of host selective pressure and lateral gene transfers are vital in the genetic structure of symbiotic microorganisms [46]. Table 1 enlists different rhizobial species and their respective host plants. Studies indicate that this N fixation by rhizobia is not only limited to the legumes but also extends to the cereals like rice, wheat, maize,

etc [47]. Previous studies have shown symbiotic relationship of rhizobia with the non legumes like *Parasponia* sp. [48]. Rhizobia have also been isolated as natural endophytes from rice [49-50], sweet corn, cotton [51], maize, bean [52], barley, wheat, canola [53], etc. Further studies investigating the interaction of rhizobia with non legumes may enhance its use as a replacement to nitrogenous fertilizers, not only for the legumes but also for the non legumes.

Table 1: Rhizobia and their respective plant hosts.

Rhizobial species	Host plants	References
<i>R. leguminosarum</i> bv. <i>phaseoli</i>	<i>Phaseolus vulgaris</i>	[102]
<i>R. haultense</i>	<i>Sesbania herbacea</i>	[103]
<i>R. galegae</i>	<i>Galega</i>	[104]
<i>Rhizobium meliloti</i>	Alfalfa <i>Medicago truncatula</i> <i>Medicago albus</i>	[32]
<i>R. leguminosarum</i> bv. <i>viciae</i>	<i>Pisum</i> <i>Vicia</i>	[105]
R. NGR234	Broad host range; 18 genera including <i>Vigna</i> , <i>Macroptilium</i> , <i>Parasponia</i>	[106]
<i>Bradyrhizobium japonicum</i>	<i>Glycine max</i> <i>Glycine soja</i>	[107] [108]
<i>Azorhizobium caulinodans</i>	<i>Sesbania</i>	[109]
<i>R. tropici</i>	Broad host range; <i>Phaseolus</i> , <i>Leucaena</i> , <i>Medicago</i> , <i>Macroptilium</i>	[110] [111]
<i>R. fredii</i>	Soyabean (<i>Glycine max</i>)	[112]
<i>M. ciceri</i>	<i>Cicer arietinum</i>	[113]
<i>R. leguminosarum</i> bv. <i>trifolii</i>	<i>Trifolium</i>	[114]
<i>R. etli</i>	<i>Phaseolus</i>	[115]
<i>M. loti</i>	<i>Lotus</i>	[116]
<i>E. medicae</i>	<i>Medicago truncatula</i> , <i>Melilotus</i>	[117]
<i>R. gallicum</i>	<i>Phaseolus vulgaris</i>	[118]
<i>R. giardinii</i>	<i>Phaseolus vulgaris</i>	[118]
<i>R. mongolense</i>	<i>Medicago ruthenica</i> , <i>Phaseolus</i>	[119]
<i>R. undicola</i>	<i>Neptunia natans</i>	[120]
<i>R. oryzae</i>	<i>Oryza alta</i>	[78]
<i>R. fabae</i>	<i>Vicia faba</i>	[89]
<i>R. endophyticum</i>	<i>Phaseolus vulgaris</i>	[121]
<i>R. phaseoli</i>	<i>Phaseolus</i>	[121]

4. Rhizobial genes involved in nitrogen fixation and nodulation

nif and *fix* genes are vital for N fixation in rhizobia. Transcription of nitrogen fixation genes is induced primarily by low-oxygen conditions. Low-oxygen sensing and transmission of this signal to the level of *nif* and *fix* gene expression involve at least five regulatory proteins, FixL, FixJ, FixK, NifA, and RpoN (sigma 54). *nif* gene cluster includes *nifD* and *nifK* which encodes the α and β subunit of MoFe protein of nitrogenase, *nifH* which encodes Fe protein of nitrogenase, *nifE*, *nifN* and *nifB* genes are involved in FeMo cofactor biosynthesis and *nifS* which encodes a cysteine desulfurylase. *fix* genes like *fixABCX* are required for nitrogenase activity,

fixNOQP encodes a microaerobically induced membrane bound cytochrome oxidase, *fixGHIS* encodes a redox process coupled cation pump, *fixK* encodes for a positive regulator of *fixNOQP* and *fixLJ* encodes for an oxygen responsive two component regulatory system involved in positive control of *fixK* (a subgroup of the Crp-Fnr family of bacterial regulators) and *nifA.nfrA* is also involved in regulation of *nifA* [54]. In *S. meliloti*, the expression of *nifA* gene under microaerobic conditions which requires the FixLJ two component system is negatively regulated by NH_4^+ through a FixL protein mediated process [55-56]. Table 2 indicates a brief list of all the rhizobial genes known to be involved in N fixation.

Table 2: Rhizobial genes involved in nitrogen fixation

Genes	Predicted function
<i>nifA</i>	Nif- specific regulatory protein, transcriptional activator
<i>nifB</i>	Fe - Mo cofactor biosynthesis protein
<i>nifD</i>	Nitrogenase molybdenum -iron protein, alpha chain
<i>nifE</i>	Nitrogenase molybdenum cofactor synthesis protein
<i>nifH</i>	Nitrogenase protein
<i>nifK</i>	Nitrogenase molybdenum - iron protein, beta chain
<i>nifN</i>	Nitrogenase Fe - Mo molybdenum cofactor biosynthesis protein
<i>nifQ</i>	Nitrogen fixation protein, molybdenum - iron binding
<i>nifR</i>	Nitrogen regulation protein
<i>nifS</i>	Nitrogenase metallocluster biosynthesis protein, Cysteine desulfurase
<i>nifU</i>	Iron - sulphur cluster scaffold protein
<i>nifW</i>	Nitrogenase stabilizer
<i>nifV</i>	Homocitrate synthase
<i>nifX</i>	Iron - molybdenum cluster binding protein protein
<i>nifZ</i>	Nitrogen fixation protein
<i>fixA</i>	Nitrogen fixation protein, electron transfer flavo protein beta chain
<i>fixB</i>	Nitrogen fixation protein, electron transfer flavoprotein alpha chain
<i>fixC</i>	Nitrogen fixation protein, oxidoreductase
<i>fixG</i>	Iron sulphur binding domain
<i>fixH</i>	Nitrogen fixation cation transport protein
<i>fixI</i>	Transmembrane copper transport ATPase protein
<i>fixJ</i>	Two component nitrogen fixation regulatory protein
<i>fixK</i>	Ferredoxin like protein, FNR/CRP transcriptional regulator
<i>fixL</i>	Two component nitrogen fixation oxygen regulated sensory histidine kinase
<i>fixN</i>	Cytochrome c oxidase
<i>fixO</i>	Cytochrome c oxidase
<i>fixP</i>	Cytochrome c oxidase membrane anchored subunit
<i>fixQ</i>	Cbb3 Cytochrome oxidase
<i>fixR</i>	Short chain dehydrogenase, oxidoreductase
<i>fixS</i>	Nitrogen fixation protein
<i>fixU</i>	Nitrogen fixation protein
<i>fixX</i>	Ferredoxin like protein

Rhizobial genes involved in legume root infection and nodulation can be divided into two classes. First class includes genes vital for the bacterial cell surface formation like *exo* genes for exopolysaccharide synthesis [57], *lps* genes for lipopolysaccharide or K antigen synthesis [58] and *ndv* genes responsible for glucan synthesis [59]. If these genes get mutated, it may result in formation of ineffective root nodules [60-61]. *exo* and *lps* genes determine the host specificity [57,62]. Second class comprises of *nod* or *nol* genes whose mutation can lead to absence of nodulation, delayed but effective nodulation or changes in the host range. Some *nod* genes are interchangeable for nodulation function, hence called as common *nod* genes while some are responsible for nodulation in a particular host termed as *hsn* (host specific *nod*) genes [63]. Most *nod* genes of rhizobia are not expressed in cultured cells but are induced in the presence of plant flavonoids [64-65]. Expression of *nod* genes is controlled by an activator, NodD [66], in response to the presence of certain plant flavonoid inducers like luteolin, methoxychalcone, naringenin and diadzein, in addition to non flavonoid inducers like trigonelline and stachydrine [65].

Resistance (R) genes may have a role in rhizobial symbioses [67]. Ability to nodulate depends on the release of rhizobial nod factors, secreted in response to plant flavonoids [68]. The production of these glycolipids (lipooligochitosaccharides) is specified by rhizobial *nod*, *nol*, and *noe* genes (collectively referred to as *nod* genes) [69]. Genes *nodA*, *nodB*, and *nodC* specify the nod factor basic structure – the N-acetylglucosamine oligomer (*nodC*) and the fatty acyl adduct (*nodA* and *nodB*). *nodJ* genes are generally found in nod clusters as well; they are presumed to affect transport of the nod factors out of the rhizobial cell. Transcription of the common and accessory nod genes is controlled by *nodD* [70]. NodD proteins bind to nucleotide sequences called ‘Nod boxes’ upstream of the transcription start site of the various nod operons. In the presence of the flavonoids of the rhizobial host, NodD activates transcription. Certain other exuded plant compounds, aside from flavonoids, also have been shown to trigger nod induction [71]. Table 3 indicates a brief list of all the rhizobial genes known to be involved in nodulation.

Table 3: Rhizobial genes involved in nodulation.

Genes	Predicted functions
<i>nodA</i>	Acyltransferase, nodulation protein
<i>nodB</i>	Nodulation chitoooligosaccharide deacetylase
<i>nodC</i>	N-acetylglucosaminyltransferase
<i>nodD</i>	Transcriptional regulator, nodulation protein
<i>nodE</i>	Nodulation beta keto acyl ACP synthase
<i>nodF</i>	Nodulation acyl carrier protein
<i>nodG</i>	Nodulation protein, 3-ketoacyl-(acyl carrier protein) reductase
<i>nodH</i>	Sulfotransferase
<i>nodI</i>	Nodulation ATP binding protein
<i>nodJ</i>	Membrane transport nodulation protein
<i>nodL</i>	Putative nodulation protein
<i>nodM</i>	Glutamine-fructose-6 phosphate trasnaminase nodulation protein
<i>nodO</i>	Calcium ion binding nodulation protein
<i>nodP</i>	Nodulation protein, sulfate adenylate transferase, subunit 2
<i>nodQ</i>	Nodulation protein, sulfate adenylate transferase, subunit 1
<i>nodS</i>	Methyltransferase involved in Nod factor biosynthesis, nodulation protein
<i>nodT</i>	Putative exported nodulation protein
<i>nodX</i>	Putative nodulation protein, probable sugar acetylase
<i>nodZ</i>	Nodulation protein, fucosyltransferase
<i>nodK</i>	GDP-L- Fucose synthetase
<i>nodL</i>	Acetyltransferase
<i>nodO</i>	Nodulation protein
<i>nodR</i>	Transcriptional regulator
<i>nodT</i>	Nodulation protein
<i>nodU</i>	Nodulation protein
<i>nodV</i>	Nodulation protein
<i>nodW</i>	Nodulation protein
<i>nodX</i>	Nodulation protein
<i>noeA</i>	Host specific nodulation protein
<i>noeB</i>	Host specific nodulation protein
<i>noeC</i>	Nodulation protein
<i>noeK</i>	Phosphomannomutase
<i>noeL</i>	GDP-D-Mannose dehydratse
<i>nopC</i>	Nodulation outer protein C
<i>nopA</i>	Nodulation outerprotein A

5. Rhizobia as plant growth promoting rhizobacteria

Rhizobia are an important class of plant growth promoting rhizobacteria which exerts positive effect on plant growth by direct as well as indirect mechanisms. Rhizobia can be used as inoculants for enhanced N fixation and studies have demonstrated their predominance in nodules for 5-15 years after initial inoculation [72]. They are effective colonizers persisting in the soil for many years even in the absence of their host [73]. Rhizobia have long been studied for their ability to colonize legumes and promote N fixation. However, recent studies on

rhizobia are focused on rhizobial cereal association as it has been found that rhizobia can make an association with graminaceous plants such as rice, wheat, maize, barley, millet, etc. Several reports have studied the ability of rhizobia to solubilize P, production of siderophore production, IAA, GA, HCN, ammonia, cytokinin, exopolysaccharides, antifungal metabolites, organic acids, ACC deaminase, etc. as shown in Table 4. Accumulation of plant nutrients like P, K, Ca, Mg and Fe have been obtained with rhizobial inoculation [74]. In addition to plant inoculation with rhizobia, co-inoculation of rhizobia with other PGP bacteria have proved to be more efficient and cost effective [75-76].

Table 4: Rhizobia and their plant growth promotion traits.

Rhizobia	Plant growth promotion activity	References
<i>Rhizobium</i> , <i>Bradyrhizobium</i>	Siderophores, P solubilization, IAA, HCN	[122] [123-127]
<i>Rhizobium</i> sp.	IAA, Siderophore, HCN, ammonia, exopolysaccharides	[128-138]
<i>R. phaseoli</i>	IAA	[139]
<i>R. ciceri</i>	Siderophores	[140]
<i>R. meliloti</i>	Siderophores	[141-142]
<i>R. leguminosarum</i>	Cytokinin	[143]
<i>Bradyrhizobium</i>	Siderophores, IAA, HCN, P solubilization	[122-125]
<i>Bradyrhizobium</i> sp.	IAA, HCN, ammonia, siderophore, exopolysaccharide	[126, 144-146]
<i>B. japonicum</i>	IAA, siderophores	[147-148]
<i>Mesorhizobium</i> sp.	IAA, siderophores, HCN, ammonia, exopolysaccharides, antifungal activity	[126, 149-153]
<i>Mesorhizobium ciceri</i>	IAA, siderophores	[154]
<i>Azotobacter chroococcum</i>		
<i>Rhizobium</i> sp.	P solubilization	[155-158]
<i>Bradyrhizobium</i> sp.	P solubilization	[156]
<i>R. leguminosarum</i>	2 ketogluconic acid mediated P solubilization	[156]

<i>R. meliloti</i>	2 ketogluconic acid mediated P solubilization	[157]
<i>Bradyrhizobium sp.</i>	Heavy metal mobilization	[159]
<i>R. phaseoli</i>	IAA production	[143]
<i>Azospirillum amazonense</i>	IAA, nitrogenase activity	[160]
<i>Burkholderia</i>	ACC deaminase, IAA, siderophore, heavy metal solubilization, phosphate solubilization	[161]
<i>Azotobacter sp. Mesorhizobium sp.</i>	IAA, siderophore, antifungal activity, Ammonia production, HCN	[162]
<i>Azospirillum brasilense, Azospirillum amazonense</i>	IAA, P solubilization, nitrogenase activity, antibiotic resistance	[163]
<i>Azotobacter chroococcum</i>	Gibberellin, kinetin, IAA	[164]

6. Breach of host specificity in legume-rhizobium symbiosis

Endophytes are microorganisms living within the tissue of a plant, without causing disease [77]. Despite the high specificity of legume- *Rhizobium* interaction and the selective nodule environment, presence of non-rhizobial nodule rhizobacteria within the root nodules or plant root, termed as endophytes have been reported. Rhizobacterial endophytes cannot nodulate the host plant as they can neither trigger plant flavonoid release nor release nod factors. But when co-inoculated along with nodulating rhizobial strains which release nod factors specific to plant flavonoids, rhizobacteria can enter the plant along the rhizobial infection thread and survive as an endophyte in the root nodule as shown in Fig 1. Legumes like maize and

soya bean along with non legumes like sweet potato, banana, sugarcane, wheat and carrot have been shown to harbour variety of rhizobacterial endophytes as indicated in Table 5. In our previous report, we have reported with the help of confocal microscopy, that rhizobacteria migrate along the length of the infection thread formed by the host nodulating rhizobial strain and become localized in root nodules [78]. Presence of rhizobacteria does not alter the nodulating ability of the rhizobia [79]. Some endophytes may enter independent of other bacteria through cracks formed at the emergence of lateral roots or at the zone of elongation and differentiation of the root [80]. Entry of only the host specific rhizobia is facilitated through nod factor release in response to plant flavonoids.

Table 5: Nonrhizobial endophytes and their respective host plants.

Plant species	Endophytes	References
Maize	<i>Burkholderia pickettii</i>	[165]
	<i>Klebsiella variicola</i>	[166]
	<i>Bacillus megaterium</i>	[165, 167]
	<i>Arthrobacter globiformis</i>	[168]
	<i>Microbacterium testaceum</i>	[169]
Soyabean	<i>Enterobacter sakazakii</i>	[170]
	<i>Enterobacter agglomerans</i>	
	<i>Klebsiella pneumoniae</i>	
	<i>Klebsiella oxytoca</i>	
	<i>Pseudomonas citronellolis</i>	
Sweet potato	<i>Pantoea sp.</i>	[171]
	<i>Enterobacter asburiae</i>	[51]
	<i>Klebsiella sp.</i>	[172-173]
	<i>Pantoea agglomerans</i>	[51, 174]
	<i>Paenibacillus odorifer</i>	
Banana	<i>Klebsiella variicola</i>	[166]
Sugarcane	<i>Klebsiella variicola</i>	[166]
Wheat	<i>Klebsiella sp.</i>	[172-173]
	<i>Mycobacterium sp.</i>	[175-176]
	<i>Streptomyces</i>	[177]
Carrot	<i>Klebsiella terrigena</i>	[167]
	<i>Pseudomonas putida</i>	
	<i>Pseudomonas fluorescens</i>	
	<i>Staphylococcus saprophyticus</i>	
	<i>Salmonella enterica</i>	[178-179]
Rice	<i>Azospirillum caulinodans</i>	[178]
	<i>Sphingomonas paucimobilis</i>	
	<i>Burkholderia sp.</i>	
	<i>Herbaspirillum seropedicae</i>	
	<i>Klebsiella variicola</i>	[172]
	<i>Serratia sp.</i>	[180]
	<i>Serratia marcescens</i>	[181]
<i>Sphingobacterium sp.</i>	[182]	
Citrus plants	<i>Methylobacterium mesophilicum</i>	[80]
	<i>Burkholderia cepacia</i>	[183]
	<i>Enterobacter cloacae</i>	
	<i>Pantoea agglomerans</i>	[80,183]
	<i>Bacillus sp.</i>	[80, 183]
	<i>Curtobacterium flaccufaciens</i>	[183]
	<i>Nocardia sp.</i>	[183]

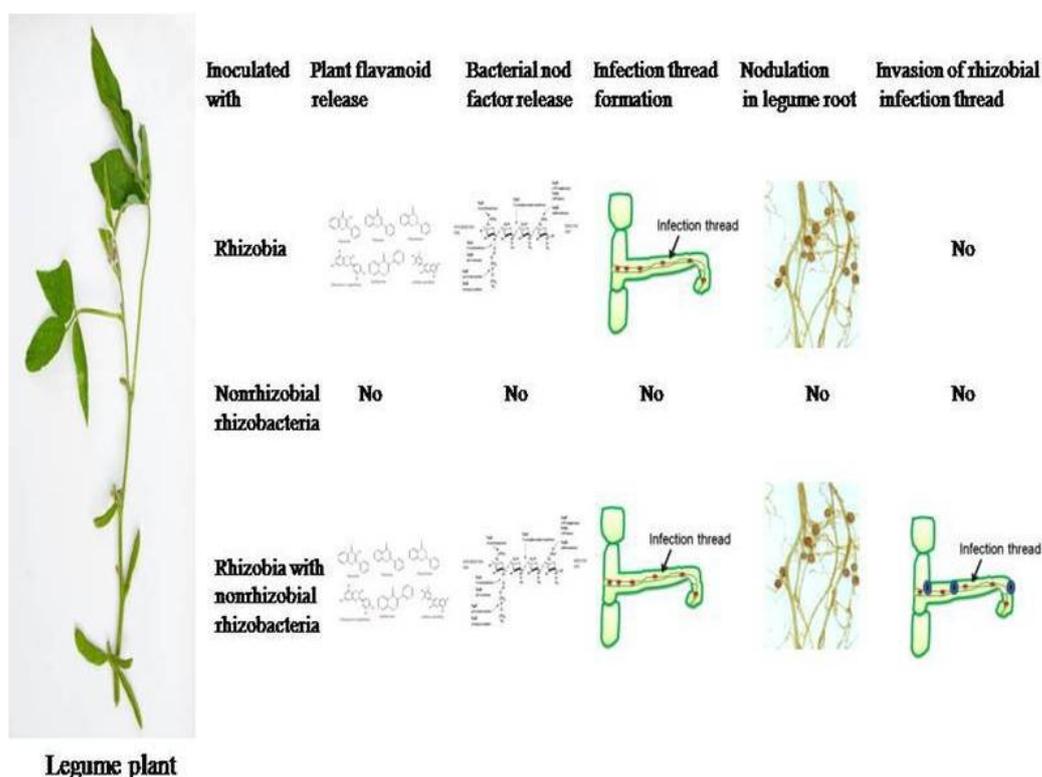


Figure 1: Rhizobia nodule formation and invasion of rhizobial infection thread by rhizobacteria: Plants in the presence of specific rhizobia will release flavonoids which trigger nod factor release by rhizobia, leading to infection thread formation and nodulation. Nonrhizobial rhizobacteria cannot nodulate the host plant as they lack the ability to release nod factors. However, when rhizobacteria are co-inoculated with the host nodulating rhizobia, nod factors released by the rhizobia leads to infection thread formation which is then invaded by the rhizobacteria to localize within the plant tissues.

7. Nonrhizobial endophytes as plant growth promoting rhizobacteria

Plant endophytes have been defined as organisms that colonize internal plant tissues without causing apparent harm to the host [81]. Endophytic populations, like rhizospheric populations, are conditioned by multiple biotic and abiotic factors [82-84], but endophytic bacteria could be better protected from biotic and abiotic stresses than rhizospheric bacteria [82]. Endophytic bacteria in a single plant host are not restricted to a single species but comprise several genera and species. Endophytic bacteria are found in legume nodules as well. In red clover nodules, some species of rhizobia were found, including *Rhizobium (Agrobacterium) rhizogenes*, in addition to *R. leguminosarum* bv. *trifolii*, which is the normal clover symbiont [54]. Some γ - proteobacteria are cooccupants with the specific rhizobia in *Hedysarum* plant nodules [85]. In most cases, the endophytic bacteria are unable to form nodules. In rhizosphere, there is a selection of microorganisms which are able to survive in root exudates and compete with others [86]. Some rhizospheric bacteria can colonize the internal roots and stems, showing that these bacteria are a source for endophytes [87], but also phyllosphere bacteria may be a source of endophytes. Changes in plant physiology can lead to the development of a distinct endophytic population [82]. They are found in roots, stems, leaves, seeds, fruits, tubers, ovules and also inside legume nodules [54, 82, 85]. In most plants, roots have higher

number of endophytes compared to above ground tissues [86]. In plant endophyte interactions, plant host provides protective niche for the endophytes while the endophytes in return produce useful metabolites and signals [88,89] which increases plant nutrient uptake [90], modify plant growth, development and biomass [91], induce resistance to pathogens [92-94] and insects [95] and increase resistance to osmotic stress [96], heavy metals [97], contaminated chemicals [98] and other abiotic factors. Majority of studies on endophytes are focused on root endophytic associations [99-100] while studies on the environmental factors and farming practices that affect endophyte community diversity and the mechanisms in which plant-endophyte associations occur in agrosystems are not well studied [89].

Endophytes can be classified into three main categories of plant inhabiting life strategies. Obligate endophytes which are unable to proliferate outside of plants and are likely transmitted via seed rather than originating from rhizosphere; facultative endophytes are free living in soil but will colonize plants when opportunity arises through coordinated infection and passive endophytes which do not actively seek to colonize the plants but do so as a result of stochastic events like open wounds along the root hairs [101]. Various PGP traits shown by non rhizobial bacterial endophytes are depicted in Table 6.

Table 6: Nonrhizobial endophytes and their plant growth promotion traits.

PGPR	PGP traits	References
<i>Pseudomonas putida</i>	IAA, siderophores, HCN, ammonia, exopolysaccharides, P solubilization	[132, 134, 135]
<i>Pseudomonas aeruginosa</i>	IAA, siderophores, HCN, ammonia, exopolysaccharides, P solubilization	[132, 150, 184]
<i>Klebsiella sp.</i>	IAA, siderophores, HCN, ammonia, exopolysaccharides, P solubilization	[133, 185]
<i>Enterobacter asburiae</i>	IAA, siderophores, HCN, ammonia, exopolysaccharides, P solubilization	[129, 130]
<i>Acinetobacter sp.</i>	IAA, P solubilization, siderophores	[186]
<i>Pseudomonas sp.</i> A3R3	IAA, siderophores	[187]
<i>Psychrobacter sp.</i> SRS8	Heavy metal mobilization	[188]
<i>Pseudomonas aeruginosa</i> 4EA	Siderophores	[189]
<i>Pseudomonas sp.</i> <i>Ochrobactrum cytisi</i> , <i>Bacillus sp.</i> PSB10	IAA, Siderophores, HCN, Ammonia	[190]
<i>Paenibacillus polymyxa</i>	IAA, siderophores	[191]
<i>Rahnella aquatilis</i>	P solubilization, IAA, ACC deaminase	[192]
<i>Pseudomonas aeruginosa</i> , <i>Pseudomonas fluorescens</i> , <i>Ralstonia metallidurans</i>	Siderophores	[193]
<i>Proteus vulgaris</i>	Siderophores	[194]
<i>Pseudomonas sp.</i>	P solubilization, IAA, siderophores, HCN, Biocontrol activity	[127]
<i>Pseudomonas sp.</i>	ACC deaminase, IAA, Siderophore	[195]
<i>Serratia marcescens</i>	IAA, siderophore, HCN	[196]
<i>Pseudomonas fluorescens</i>	ACC deaminase, P solubilization	[197]
<i>Acinetobacter sp.</i> , <i>Pseudomonas sp.</i>	ACC deaminase, IAA, antifungal activity, N fixation, P solubilization	[198]
<i>Enterobacter sp.</i>	ACC deaminase, IAA, siderophore, P solubilization	[199]
<i>Pseudomonas jessenii</i>	ACC deaminase, IAA, siderophore, heavy metal solubilization, P solubilization	[200]
<i>Pseudomonas aeruginosa</i>	ACC deaminase, IAA, siderophore, P solubilization	[201]
<i>Pseudomonas sp.</i>	ACC deaminase, IAA, siderophore, heavy metal solubilization, P solubilization	[200]
<i>Pseudomonas sp.</i> <i>Bacillus sp.</i>	P solubilization, IAA, siderophores	[154]
<i>Klebsiella oxytoca</i>	IAA, P solubilization, nitrogenase activity	[202]
<i>Pseudomonas florescens</i>	Induced systemic resistance, antifungal activity	[203]
<i>Pseudomonas chloraphis</i>	Antifungal activity	[204]
<i>B. subtilis</i>	Antifungal activity	[205]
<i>Gluconacetobacter diazotrophicus</i>	Zn solubilization	[206]
<i>Brevibacillus sp.</i>	Zn resistance, IAA	[207]

8. CONCLUSION

N fixation and nodulation ability of rhizobia have made it a very powerful candidate for biofertilizer formulation. Recent studies show rhizobia to be an efficient plant growth promoter not only for legumes but also for cereals. Even though rhizobia have been studied for multiple direct and indirect plant growth promotion traits, development of a robust technology to explore their use by farmers is still in its infancy. One of the most distinctive features of the *Rhizobium*-legume symbiosis is its host specificity. Though earlier studies shows that only the rhizobial strains could inhabit the root and root nodules, subsequent research has led to the understanding that even the non rhizobial rhizobacteria may enter the root nodule along with the rhizobial infection thread. As the indispensable purpose of rhizobia in colonizing the plant is to fix N for the plant, breach of this specificity and the subsequent entrance of other rhizobacteria may lead to alterations in the efficiency of N fixation within the legume root nodules. Further investigations may be inevitable in understanding the presence of non rhizobial rhizobacteria within the root nodules and their effect on BNF. Additional research to exploit the potential of rhizobia and other endophytes along with the knowledge of intensive selection and screening strategies and their rhizospheric competencies may

provide expansion of this research, thereby paving a way for its commercialization and improved sustainability in agricultural production.

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