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Signalling and Control of Flavonoids in the Biological Nitrogen Fixation Process of Leguminous Plants: A Review

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ABSTRACT

Biological nitrogen fixation in plants gives them a competitive edge by converting atmospheric nitrogen into ammonium. Rhizobia and leguminous plants have symbiotic relationships in which the latter produce nitrogen-fixing nodules in their roots. Rhizobial bacteria infiltrate leguminous plants through signal exchange. Under low nitrogen environments, host plant roots release flavonoids that cause rhizobia to produce Nod factors, which are lipo-chitooligosaccharide signalling molecules. Flavonoids play a crucial role in interactions between plants and microbes, facilitating symbiosis and defensive mechanisms. Flavonoids are a diverse class of phenolic compounds found in all higher plants and act as chemo-attractants, attracting compatible rhizobia, promoting or suppressing expression of rhizobial nod genes, suppressing root pathogens, promoting germination of mycorrhizal spores, quorum sensing and chelating soil nutrients. Flavonoids activate the bacterial regulatory protein NodD, which controls the transcription of *nod* genes required for the synthesis of the bacterial Nod factor. The legume-rhizobium interaction allows rhizobia to enter the host plants and stimulate flavonoids from legume roots.

Key words: Chemo-attractant, Flavonoids, Nitrogen fixation, Nod factors, NodD, Rhizobia.

Biological nitrogen fixation gives plants a competitive edge by converting atmospheric nitrogen into ammonium. Microorganisms that produce the nitrogenase enzyme can carry out this activity (Vessey, 2003). Rhizobium is a crucial element in legumes, as it forms root nodules that facilitate atmospheric nitrogen fixation, which is beneficial for the plant (Arya *et al*., 2024). Rhizobia and leguminous plants have symbiotic relationships in which the latter produce nitrogen-fixing nodules in their roots. Symbiotic interactions between compatible legume host plants and rhizobia involve precise molecular communication between the two partners (Dudeja *et al*., 2025). Only a limited number of plant species exhibit this special relationship (Spaink, 2000). Rhizobial bacteria infiltrate leguminous plants through signal exchange, enabling the bacteria to enter the roots and develop into ammonia-converting forms, the nodules (Jones *et al*., 2007). When rhizobium bacteria and legume crops coexist, the bacteria can infect plant roots and form root nodules, which provide nutrients for crops (Samudin and Kuswantoro, 2017). Various results revealed that plant height (cm), number of effective tillers per m^2 and leaf area index (LAI) are significantly influenced by the combination of nitrogen levels and microbial inoculation treatments (Kumari *et al*., 2025).

According to some estimates, biological nitrogen fixation is responsible for the fixation of up to 200 metric tons of nitrogen annually in the agricultural system, representing a major saving in the cost of crop production both financially and as well as environmentally. It converts atmospheric nitrogen into ammonium, a form that is readily utilized by plants. The ability of some plant species to supply some, if not all, of their requirement for nitrogen in this way gives them a substantial competitive advantage over those that lack this ability. Microorganisms that produce the enzyme nitrogenase can carry out the process of nitrogen fixation. In a very restricted group of plant species, the association between the host plant and the bacterial symbiont is a highly intimate one and the bacteria are housed within nodules, which is a specialized organ that forms in the root (Vessey, 2003).

Under low nitrogen environments, the host roots release particular flavonoids that cause rhizobia to produce particular lipo-chito-oligosaccharide signalling molecules known as Nod factors. The rhizobia perceive flavonoids through NodD, a protein that stimulates the transcription of bacterial Nod genes involved in the production and secretion of Nod factor (Spaink *et al*., 1989; Mulligan and Long, 1985). Many legumes produce specific flavonoids that only induce Nod factor production in homologous rhizobia and therefore act as important determinants of host range (Liu and Murray, 2016). A type of flavonoid called

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isoflavones is primarily found in leguminous plants. It is essential for interactions between plants and microbes, such as symbiosis between rhizobia and legumes and defensive mechanisms (Mazur *et al*., 1998; Sugiyama, 2019). According to Subramanian *et al*. (2006), isoflavones stimulate the nodulation genes in leguminous plants, which helps in the nodulation process.

This review has been done to compile the various factors responsible for BNF (Biological nitrogen fixation) and highlights the role played by flavonoids in the BNF process of leguminous plants. Flavonoids are the key signaling molecules that initiate and regulate the symbiosis between rhizobia and legumes.

This review article is based on literature search and data analysis. Abstracts and full research papers were systematically reviewed; databases like Web of Science, Google Scholar and PubMed were thoroughly searched for research papers and related articles published till 2025.

Legume-rhizobium symbiosis

The effective symbiosis between rhizobia and legumes depends on the Nod factors, flavonoids, bacterial surface polysaccharides and plant lectins (Pindi *et al*., 2020). Nod factors allow the rhizobia to enter the host plants and stimulate flavonoids from legume roots. Once bacteria enter the legume roots, extracellular polysaccharides and proteins are exchanged between symbionts and amplifying the response to inoculation (Broughton, 2003). The specific exudation of flavonoid mixtures from legume hosts and NodD proteins from different rhizobia is partially responsible for the host specificity of symbiosis (Gibson *et al*., 2008; Skorupska *et al*., 2010; Rose *et al*., 2012; Sharma *et al*., 1993).

Flavonoid metabolism in leguminous plants

Flavonoids are a large (≈9000) structurally diverse class of phenolic compounds found in all higher plants and classified into one of the following groups: flavones, isoflavonoids, flavonols, flavandiols, proanthocyanidins and anthocyanins (Ferrer *et al.,* 2007; Kumar *et al.,* 2024). Flavonoids are crucial signalling molecules in the symbiosis between legumes and their nitrogen-fixing symbionts, the rhizobia (Liu and Murray, 2016). Flavonoids, secreted by legume roots, act as chemical messengers, regulating physiological processes and inhibiting cell cycle (Kumari *et al*., 2025). Flavonoids in symbiosis attract rhizobia, induce Nod gene synthesis, determine host specificity and regulate root development. Isoflavonoids attract rhizobia to legume root nodules, establishing symbiotic relationships that enhance plant growth (Abd-Alla *et al*., 2023). There are seven different subclasses of flavonoids based on their structural differences, which are presented in Table 1.

Flavonoids act as chemoattractants

Flavonoids act as chemical signals to attract the rhizobium bacteria. They are frequently exuded into the rhizosphere to attract compatible rhizobia that reside in the rhizosphere, promote or suppress the expression of rhizobial nod genes, suppress root pathogens, promote the germination of mycorrhizal spores and hyphal branching, influence quorum sensing and chelate soil nutrients (Broughton *et al*., 2003; Cooper, 2004; Martens and Mithofer, 2005). The rhizobial membrane absorbs flavonoids, in the form of aglycone, after they are released, potentially *via* porins (Kobayashi *et al*., 2004; Wang *et al*., 2012; Taylor and Grotewold, 2005).

Flavonoids act as a selective agent for compatible symbiotic organisms

The symbiosis between *Rhizobium* spp. and legumes is highly host-specific. Only a certain strain of *Rhizobium* spp. can successfully establish a symbiotic connection with a limited number of host plant species (Gyorgypal *et al.,* 1991; Hassan and Mathesius, 2012*)*. It has been demonstrated that the NodD protein produced by a *Rhizobium* spp., a strain with a wide host range, interacts with more flavonoids than does NodD produced by a strain with a confined host range (Yokoyama, 2008). This affinity between NodD and flavonoids partially dictates the host range. The combination of flavonoids present in the root exudate of legume species acts as a selective agent for compatible symbiotic organisms (Maxwell *et al.,* 1989). Recent studies suggest that production of key “infection” flavonoids is highly localized at infection sites and are phytoalexins that may have a role in the selection of compatible symbionts during infection (Liu and Murray, 2016).

Flavonoids activate the bacterial regulatory protein NodD and nod gene expression

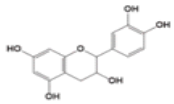
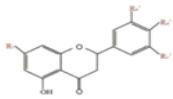
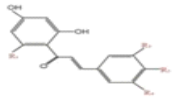
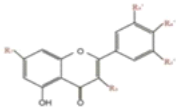
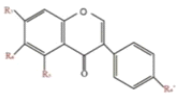
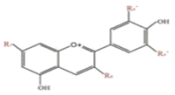
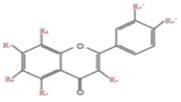
Flavonoids from roots and seeds induce bacterial nodulation genes in legume-rhizobia symbioses, controlling lipo-chitooligosaccharide signals to host plants. However, successful symbiotic development requires the transmission of a variety of other signals from rhizobia to plant roots and flavonoids initiate the production of most of them (Cooper, 2004). Flavonoids activate the bacterial regulatory protein NodD in nitrogen-fixing symbiosis. This protein functions as a plant morphogen that can initiate nodule formation by controlling the nod regulation required for the synthesis of the bacterial Nod factor (Dénarié and Roche, 1992; Schultze *et al*., 1994; Fisher and Long, 1992). The binding of a flavonoid to NodD protein enhances transcription of nod genes by facilitating RNA polymerase access, forming a nod box with target DNA sequences (Long, 1996; Spaink *et al*., 1989; Mulligan and Long, 1985). NodD recognizes a specific promoter sequence, the Nod box and NodD binds to this promoter element, resulting in transcriptional activation of the downstream genes (Stacey, 2007). The produced NodD is recognized by plant LysM receptor-like kinases, which causes root tip curl and encloses symbiotic cells and thereby fixing nitrogen.

Nodulation strategies in legume symbionts

The legume family (Fabaceae) is the third largest family of flowering plants, with members of more than 650 genera,

18,000 species spread around the globe (Frankow-Lindberg and Dahlin, 2013). Their evolutionary success is due to their symbiosis with the *Rhizobium* spp., which enables the plants to tolerate nitrogen-deficient soils. In natural ecosystems, the quantity of nitrogen fixed by legumes is estimated to be 28-84 kg per hectare per year, while during a cropping environment, this can rise to several hundred kilograms per hectare (Catherine and Joel, 2018). Rhizobia follow three nodulation strategies during the process of nodulation: Nod, T3SS and non-Nod/non-T3SS. In the Nod strategy, strain-specific lipochitin oligosaccharides (LCOs) called Nod factors (NFs) are

Table 1: Subclasses of flavonoids based on their structural differences.

Name of flavonoids	Chemical structure	Associated legumes	Signaling effect
Flavanol		Beans	Induce the expression of nod genes
Flavanone		Beans	Attracts rhizobia to the plant roots through chemotaxis
Chalcone		Beans	Triggers nodulation
Flavonol		Beans, peas, common beans	Triggers nodulation
Isoflavone		Soybean	Triggering the expression of genes that helps in nodulation
Anthocyanin		Black and red beans	Helps in nitrogen fixation
Flavones		Beans, peas, soybean	Induce nodule formation and infection threads

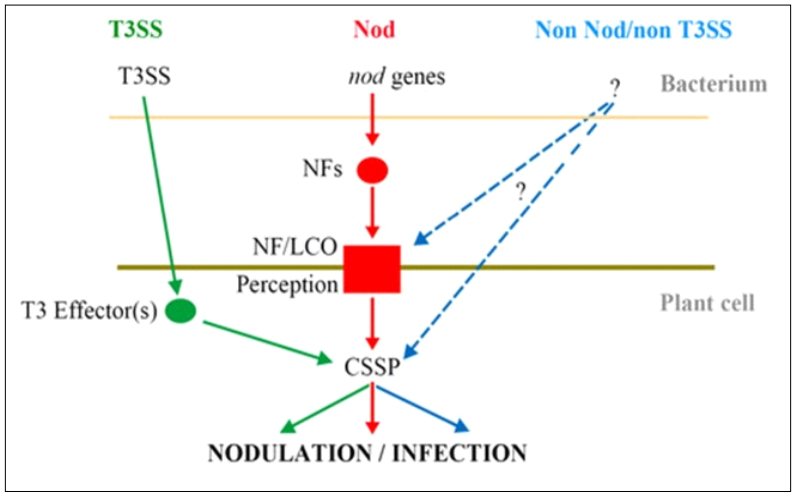


Fig 1: Nodulation strategies in legume symbionts (Catherine and Joel, 2018).

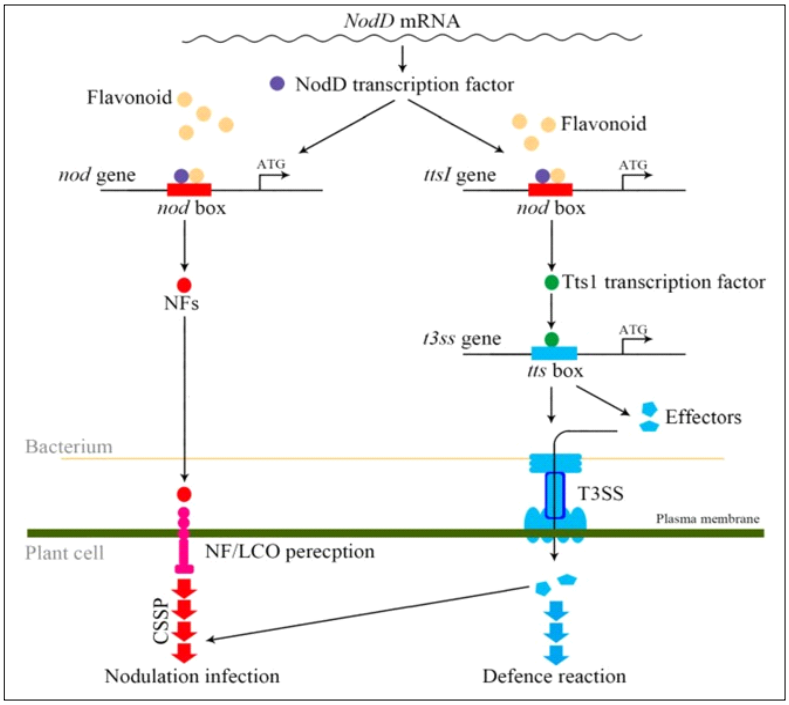


Fig 2: Contrasting cascades for the Nod and T3SS mechanisms (Dong and Song, 2020).

produced under the control of *nod* genes. NFs are perceived by LysM-receptor-like kinases that activate the common symbiotic signalling pathway (CSSP). In the second strategy, the T3SS strategy, T3SS effectors activate CSSP components by bypassing NF recognition. The third nodulation strategy is still unknown, but it involves neither *Nod* nor T3SS functions and occurs *via* CSSP activation (Fig 1). CSSP activation is thus the primary nodulation strategy. Nod-independent and T3SS-independent nodulation (the third strategy) occurs *via* CSSP activation, since most CSSP components have been identified in *Aeschynomene evenia,* which is only nodulated *via* this strategy. It is well established that flavonoids released by the roots of legume species regulate the Nod strategy (Abdel-Lateif *et al*., 2012).

A well-studied effect of root-exuded flavonoids is their regulation of *Rhizobium* spp. *nod* genes (Cooper, 2007). Luteolin in *Medicago sativa* and 7,4' dihydroxyflavone in *T. repens* were found to act as nod genes inducers (Redmond *et al*., 1986). Typically, nanomolar to low micromolar range concentration of flavonoids is required for this induction and mixtures of different flavonoids are more effective than a single compound (Moscatiello *et al*., 2010). Nod factors required for nodule formation are produced by the cooperative action of several *nod* gene products. These *nod* genes are regulated by NodD, a LysR family transcription factor. Binding of an appropriate flavonoid to NodD facilitates the access of RNA polymerase and thereby enhances the transcription of the *nod* genes (Fig 2). The NodD-flavonoid complex binds to its target DNA sequences, known as a *nod* box. The utilization of flavonoids by *Rhizobium* spp. is associated with a rise in the concentration of cellular calcium level, which acts to induce the expression of NodD (Wang *et al*., 2011). The secreted *nod* factors are recognized by the plant's LysM receptor-like kinases, which triggers the characteristic curling of the root hair tip back on itself, thereby trapping the symbiont cells within a particular area, from which they are taken up into the root proper *via* an infection thread (Horvath *et al*., 1993). Once the inner root is reached, they are endocytosed into nodule cells and consequently initiate the process of nitrogen fixation. The cell division process is also induced by Nod factor, as well as gene expression in the root cortex and pericycle, which initiates the development of the nodule (Cullimore *et al*., 2001; Okazaki *et al*., 2013).

Flavonoids in root nodule development

Nodule development involves pre-infection, initiation and differentiation stages, with legume roots' flavonoids activating rhizobial nod genes and host plant flavonoids affecting nodule formation (Hirsch, 1992). Flavonoids play a significant role in modulating auxin transport during the initiation of nodule primordia in plants. Genetic studies in *Arabidopsis* show that flavonoid-null mutants have increased root auxin transport, which can be complemented by external application of flavonols. Flavonoids interact with auxin transporters through Pin-formed gene homologs and *in vitro* studies show that they affect polar auxin transport similarly to synthetic chemical inhibitors (Peer *et al*., 2004; Taylor and Grotewold, 2005).

The first indirect evidence for an involvement of auxin in nodulation came from experiments showing that external manipulation of auxin transport with synthetic auxin transport inhibitors can result in the formation of nodule-like structures (Hirsch *et al*., 1989). Auxin, synthesized in the shoot, is transported to roots *via* polar auxin transport, where levels can be regulated through breakdown, conjugation, or transport (Bandurski *et al*., 1995; Lomax *et al*., 1995). Flavonoids control nodule development and differentiation by inhibiting auxin transport and promoting localized accumulation at the nodule initiation site, potentially influenced by nod factor perception.

Flavonoids may regulate nodule number in symbioses, as evidenced by reduced isoflavonoid formononetin and its glycoside ononin in *Rhizobium* spp.-induced and AM-induced symbioses. Flavonoids actively control symbiosis, with higher accumulation of isoflavonoids in wild-type common bean roots. Exogenous supply of daidzein or coumestrol increases nodule number (Abd-Alla, 2011; Noorden *et al*., 2006; Hayashi, 2012).

CONCLUSION

Flavonoids act as chemoattractants, attracting compatible rhizobia and activating the bacterial regulatory protein NodD. They play a significant role in auxin transport during the formation of plant nodule primordia. They may influence polar auxin transport by interacting with auxin transporters via Pin-formed gene homologs. They may control the number of nodules in symbioses. The successful formation of a symbiotic relationship between *Rhizobium* spp. and legumes is determined by the combination of host flavonoids and NodD protein, which also serve as a selecting agent for compatible symbiotic organisms.

But the exact molecular mechanisms that regulate flavonoid synthesis in plants during nodulation remain unclear. Limited knowledge on flavonoid transport mechanisms, unforeseen effects of flavonoid synthesis pathway changes, spatial heterogeneity of exudation along roots and soil microorganisms altering flavonoid products pose potential obstacles. Flavonoids are essential for biological nitrogen fixation, so further research is needed to understand their biosynthetic pathway, their functions, maximize their application and develop long-term strategies for improving nitrogen fixation in plant-microbe symbioses.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

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