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Understanding Mechanism behind Plant-Rhizobacterial Symbiotic Interaction

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Rhizobium is rod shaped, motile, gram-negative bacteria belonging to family Rhizobiaceae, order Rhizobiales and class Alphaproteobacteria. The other rhizobial species includes *Bradyrhizobium, Sinorhizobium, Azorhizobium* and *Mesorhizobium* (Willems and Collins, 1993). They live in the soil; infect roots of leguminous plants leading to the formation of lumps or nodules on roots, where nitrogen fixation takes place. Biological nitrogen fixation is the process of reduction of nitrogen gas to ammonia, which is done by nitrogen fixing bacteria both symbiotic (e.g. *Rhizobium*, *Bradyrhizobium*, *Frankia)* and free-living organisms (e.g. *Azotobacter*, *Beijerinckia*, *Clostridium*, *Bacillus*, *Klebsiella*, *Chromatium*, *Rhodospirillum*). Several groups of rhizobial species (biovars) specifically nodulate and form a symbiotic relationship with specific leguminous host plants. Symbiotic interaction is defined as the process of living together in close association of two or more different organisms. It includes mutualistic associations in which all the organisms involved in the association derive benefit, as well as parasitic associations in which one organism benefits to the detriment of other members of the association. The symbiosis between plant, microbe and soil can be of various types; such as Rhizobial and Mycorrhizal symbiotic interaction.

Mechanism of rhizobial symbiotic interaction

The mechanism of rhizobial symbiotic interaction between nitrogen fixing bacteria and roots of leguminous plants includes plant invasion and infection and nodule organogenesis (Plate 1). It is based on several steps:

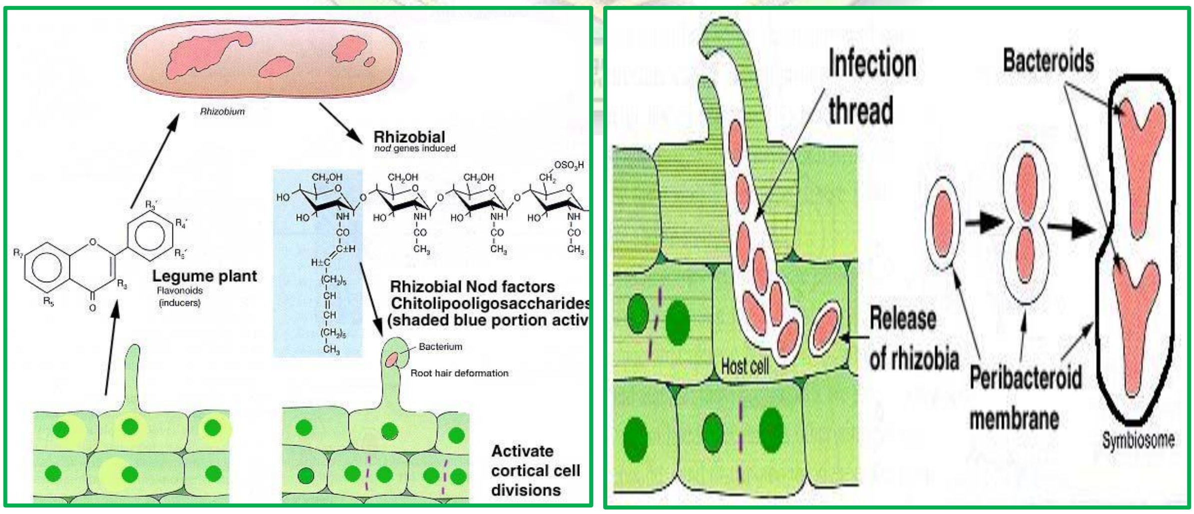

Plate 1: Mechanism of rhizobial symbiotic association in legume crops

Detection of host-released signals by rhizobial bacteria

Bacterial chemotaxis towards the root exudates of plants namely sugars, amino acids, various dicarboxylic acids such as succinate, malate, fumarate, and aromatic compounds which acts as chemoattractants for binding of rhizobial bacteria to specific host plant surfaces (Bergman et al., 1991). The specificity of plant *Rhizobium*- legume symbiosis is mediated by lectins. Nitrogen fixation occurs by invasion of rhizobia into root or stem cortex and generation of signals which would lead altered patterns of gene expression that culminate in specific and adaptive changes in bacterial physiology that are required for such symbiotic associations (Brencic and Winans, 2005). Their main role in the initiation of a rhizobial symbiosis is an interaction with the constitutively expressed *nodD* gene product(s) of the microsymbiont to form a protein-phenolic complex which is a transcriptional regulator of other rhizobial nodulation (*nod*) genes that are responsible for synthesis of reciprocal signals to the plant root. The combination of Nod D proteins with appropriate plant flavonoids triggers the production of highly specific reverse signal molecules by rhizobia – the chitolipooligosaccharide (CLOS) Nod factors.

Reverse signalling from rhizobal bacteria to legume roots

The rhizobial bacteria releases small molecules *i.e.*, Nod factors, which are detected by a specific legume host triggering the formation of the nodule, thus, facilitating the entry of rhizobia into the host (Geuts and Bisseling, 2002). The tip of a root hair to which binding of rhizobial bacteria has taken place would curl back on itself to trap the bacteria within the pocket from which they are taken upto plant made intercellular infection thread. Nod factors comprise of several host specific modifications such as sulphuryl, methyl, carbamoyl, fucosyl, arabinosyl in addition to its β-1-4-linked N-acetyl glucosamine residues with a long acyl chain (Perret *et al.,* 2000). Nod factors also induce cell division and gene expression in the root cortex and pericycle, where they initiate development of the nodule (Cullimore et al., 2001). Rhizobial species consists of many *nod* genes coding for *nod* proteins as transcriptional regulators of *nod* genes which are responsible for detection of plant released flavonoids by rhizobial and its entry into legume roots by chitolipooligosaccharides nod factors (Relic *et al.*, 1994). Nod factors are responsible for inducing plant genes *viz.*, nodulins that expresses preinfection, infection, nodule development and nodule phases of symbiotic interaction.

Signalling of Nod factors (NF) in root epidermis

LysM-receptor-like kinase are excellent candidates for nod-factor receptors as LysM domains are chemically identical to the Nod factor N-acetylglucosamine backbone which binds to chitin (Steen *et al.,* 2003; Pointing *et al.*, 1999; Walker *et al.,* 2000). NF- factors induces changes in gene expression by oscillations of cystolic active upstream and downstream NF-induced Ca2+ (Ca2+ flux followed by depolarization) spiking in the perinuclear region of epidermal cells leading to the development of root nodule formation in the legume host (Ehrhardt *et al.*, 1996; Mitra *et al.*, 2004). Nod factor induces Ca2+ flux in the cystol region that is associated with nucleus (Ehrhardt *et al.*, 1996). Ca2+ triggers the activation of an anion channel that allows Cl− efflux and K+ might serve as a charge balance, which eventually stops the depolarization and initiates repolarization. Increased Ca2+ concentrations at the tip of growing root hairs establishes a gradient of Ca2+ down the root hair which induces a wave of Ca2+ that migrates down the root hairs to nucleus. Rhizobial induced genes *i.e.,* early nodulins and late nodulins leads to the initiation of nodule formation directly from nod factor signal transduction pathway both in symbiotic and non-symbiotic zone.

Infection and nodule organogenesis

The symbiotic interaction due to rhizobial bacterial colonization of root surface induces curling of root hairs in the root zone susceptible to rhizobacteria leading to root hair deformation. Root hair curling induced due to gradual and constant reorientation of the growth direction of root hairs when bacteria gets entrapped within the pocket of curl at the degradation of plant cell wall, invagination of cell membrane and deposition of plant and bacteria. Percycle and cortical cells gets activated and divide to form the nodule primordium with the accumulation of large amout of amyloplasts. The infection thread penetrates to reach nodule primordium cells traversing their walls and enters cortical cells initiating the process of cell differentiation and cell enlargement. The rhizobial bacteria multiply within the infection thread and are released from the tip of infection by endocytosis at the time of development of nodules from primordial cells, which further differentiates into bacteroids surrounded by peribacteroid membrane.

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