



Nitrogen Fixation in Leguminous Plants

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Rhizobium is a gram negative free living soil bacteria that fix nitrogen. Martinus Beijerinck was the first who isolate and cultivate microorganisms from the nodules of legumes in 1888. He named it *Bacillus radicicola*. Frank in 1889 named this bacterium *Rhizobium leguminosarum*. *Rhizobium* sp. form symbiotic association with most leguminous plants (e.g. pea, clover, alfalfa, acacia) and convert atmospheric nitrogen into ammonium ions which is then used by plants in formation of amino acids and nucleotides.

There are different phases in the symbiotic interaction between *Rhizobia* and leguminous plants.

Initiation: *Rhizobia* present freely in soil. The root hairs of leguminous plant secrete flavanoids or isoflavonoids. Flavanoids initiate the interaction between bacterium (*Rhizobium*, *Bradyrhizobium*, *Azorhizobium*) and leguminous plant root i.e. this chemical is responsible for chemotactic movement of bacteria towards root hair and it is the inducer of nodulation (nod) and other genes. The first flavanoid to be discovered to act as nod gene inducer was Luteolin that is isolated from *Medicago sativa* (alfalfa plant). The rhicadhesins protein present on surface of *Rhizobium* that help in the attachment of rhizobium with leguminous plant root. Rhicadhesins proteins are calcium binding proteins. When bacteria attach to root hairs, flavanoids promote transcription of regulatory nod D gene in bacteria. This regulatory nod D gene is constitutively expressed in bacteria. After transcription regulatory nod D gene give rise to Nod D proteins. This Nod D protein act as activator for transcription of other nod genes.

Bacteria contain two types of nod genes:

1. Common nod genes: nod A, nod B, nod C genes.
2. Host specific nod genes: nod P, nod Q, nod H and nod E, nod F, nod L genes

There is a promoter region present in common nod gene and host specific nod gene that contain conserve sequence called Nod box. Nod D protein bind to Nod box and simultaneously promote the transcription of nod gene. Enzymes encode from common nod gene (nod A, nod B, nod C) are Nod A, Nod B, Nod C. All these enzyme collectively give rise to Nod factor. Nod factor is lipochito-oligosaccharides that consists of beta-1,4 linked N-acetyl D-glucosamine and non-reducing sugar. At the C-2 terminal of non-reducing sugar, fatty acyl chain is present. Nod A enzyme is N-acyltransferase that help in the addition of fatty acyl chain. Nod B enzyme is chitin oligosaccharide deacetylase that remove acetyl group from terminal non-reducing sugar. Nod C enzyme is chitin oligosaccharide synthase that help in addition of N acetyl-D-glucosamine residue. These all three products of enzyme are collectively help in the formation of backbone of Nod factor. Nod factor derive their name from the fact when they interact with proteins on the surface of root cells, they cause plant to initiate a series of changes of root cells, they cause plant to initiate a series of changes of root cells that ultimately results in a nodule containing bacteria.

Invasion: Nod factor produce by bacteria cause root hair curling. The bacteria become non-motile and trapped in the root hair curl, start degrading root hair cell wall by producing some degradative enzymes and form infection thread. The infection thread is elongated by the vesicles that are secreted by golgi complex. These vesicles fuse to form long infection thread or elongate infection thread. This infection thread is terminating into cortical cells of root. Bacteria enter through infection thread and move toward cortical cells of root.

Maturation: When bacteria pass through infection thread, they start division. The root cells begin to divide and after physiologically to form nodule that will house the bacteria. Meanwhile, the bacteria have changed in shape, from rods to a larger more spherical form and become capable of fixing nitrogen and called bacteroids. Bacteroids start division and derived a membrane from plant called peribacteroid membrane in nodules called symbiosome. It is the site where nitrogen fixation occurs. In the nodules, the plant feeds the bacteroids malate or other citric acid cycle intermediates through peribacteroid membrane. The bacteroids use these compounds together with an electron transport system to make nicotinamide adenine dinucleotide phosphate (NADH) and ATP to support the reduction of nitrogen gas to ammonia. Ammonia is exported to the plant cells which use it to make glutamate and glutamine that are in turn passed to other parts of plants for use in making nitrogen containing cell components. To obtain maximum amount of ATP, the bacteroids use an electron transport system that employs oxygen as an electron acceptor. Yet oxygen poisons nitrogenase enzyme. To reduce oxygen level in bacteroids, leghemoglobin is secreted by both plant and bacteria. In this globin protein is encoded by plant and heme protein is encoded by bacteria. The leghemoglobin binds to oxygen that can be reduced by electron transport system but it is not free to interact with nitrogenase, which is in cytoplasm of bacteroids.

Senescence phase: The space between the peribacteroid membrane and the bacteroid membrane called peribacteroid space (PS), mediate the exchange of metabolites between the symbionts. Plant provide organic acid to the bacteroids through peribacteroid membrane. These organic acids or other metabolite lowers the pH of peribacteroid space. In turn, bacteroids undergo nitrogen fixation and release ammonium ions in peribacteroid space and neutralizes the pH of peribacteroid space. When plant stop provide organic acid to bacteroid through peribacteroid space, bacteroid continuously release small amount of ammonium in peribacteroid space, as a result the pH of peribacteroid space become more alkaline and there is senescence of nodules.

After nodule senescence some rhizobia are released back into the soil, where they can reinitiate the cycle of legume infection.

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