Symbiotic nodule development

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Key message. *The interaction of legumes with rhizobia leads to formation of the symbiotic nodules on their roots, which are specialized plant organs for nitrogen fixation. Considerable progress has been made in deciphering the molecular-genetic and cellular mechanisms of symbiotic nodule development in recent years. However, some aspects of nodule development clearly merit much more attention.*

Keywords: *symbiotic nodule, infection thread, symbiosome, cytoskeleton, phytohormones*

The formation of symbiotic nodule is based on a signaling dialogue between symbionts, which begins with the induction of rhizobial *nod* genes by flavonoids, resulting in the synthesis of lipochitooligosaccharides, called Nod factors. Nod factors trigger a signaling cascade leading to the root hair curling, initiation of the infection thread growth, and induction of cell divisions in the pericycle and root cortex. Currently, many elements of the signaling cascade are identified, including receptor kinases, flotillins, remorin, calcium calmodulin-dependent kinase, ion channels, nucleoporins and transcription factors. In addition to perception of Nod factor, the perception of bacterial exopolysaccharides with the specific receptor is important for successful infection. The development of a symbiotic nodule is accompanied by differentiation of both the cells of the host plant and rhizobia. Rhizobia are changing to forms specialized for nitrogen fixation, called bacteroids. Bacteroids, surrounded by a symbiotic membrane of plant origin, form organelle-like structures, called symbiosomes. Legumes belonging to clade Inverted Repeat-Lacking Clade are characterized by terminal differentiation of bacteroids, which is mediated by the action of nodule-specific cysteine-rich peptides (NCR peptides). NCR peptides are also important for bacteroid survival inside host cells. The differentiation of the infected cell is accompanied by a reorganization of the elements of the tubulin and actin cytoskeleton, aimed at creating conditions for a significant increase in cell size and distribution of cellular organelles and symbiosomes in the cell. There are two types of nodule development, which depend on whether the induced meristem is long-lasting (indeterminate) or transient (determinate). In indeterminate nodules due to prolonged meristem activity different histological zones can be distinguished, including infection zone, nitrogen fixation zone and senescence zone. Some cells remain uninfected and they do not increase in size and are characterized by a dense network of cortical microtubules, which are mainly oriented parallel to each other and perpendicular to the cell axis. An important role in the development of nodules is played by phytohormones. For example, gibberellins and cytokinins play a positive role in the functioning of nodules, and ethylene and abscisic acid are negative regulators, stimulating the termination of the functioning of nodules and their transition to senescence, aimed at the recycling of nutrients. The active antioxidant system in nodule maintains concentrations of reactive oxygen species and reactive nitrogen species in the cell at the certain levels. One of the key components of antioxidant system in nodule is glutathione, which participates at different stages of nodule development. Despite significant progress in studying the mechanisms of development of symbiotic nodules, many questions remain unresolved. It is not known exactly how the signal transduction activated by Nod factors from receptors located on the membrane to the nucleus is carried out. Of great interest is the study of the distribution mechanisms of various organelles, including symbiosomes, in an infected cell. Thus, these aspects of molecular-genetic and cellular mechanisms of nodule development clearly merit much more attention.

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