CHAPTER 16

GENOMICS OF ROOT NODULATION IN SOYBEAN

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Abstract: Soybean is a suitable crop material for studying root nodulation and full genome sequencing because of its economic value. This review introduces the "nodulation" phenomenon that occurs in legume root systems such as the soybean. In addition, the paper identifies and discusses nodulation mutants (e.g., non-nodulation, ineffective nodulation, and super-/hypernodulation) and the genetic loci that control nodulation. The advent of genomics, proteomics, metabolomics, etc., has greatly contributed in improving our understanding of the symbiotic interactions between legume plants and Rhizobia, particularly for the identification of nodulation-related genes. Furthermore, molecular gene identification should be combined with biochemical pathways for nodulation in order to better understand the symbiotic interactions between legume and Rhizobia.

1. INTRODUCTION

The Leguminosae plant family is the third largest of the angiosperms, has spread to every continent, adapted to the tropics and the Arctic and comes in different varieties ranging from annual herbs to trees (Long 1989). \textit{Rhizobium} and \textit{Bradyrhizobium} are unique among microorganisms in their ability to develop nitrogen-fixing nodules on the roots of leguminous plants, which may be the most highly-evolved system for fixing nitrogen from the atmosphere.

Legume plants have two main sources of nitrogen including combined nitrate or ammonia nitrogen and biologically-fixed nitrogen from the atmosphere in the root nodule. As biological nitrogen fixation is of agronomic importance reducing the need for chemical nitrogen fertilizer for agriculturally-important crops such as

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soybean and alfalfa (Stacey et al. 2006), the utilization of nitrogen fixation in the root nodule is given considerable emphasis. Legume plants show a wide range of nodulation response: non-nodulation, ineffective nodulation, normal nodulation and super-/hypernodulation. In addition to the biological importance of these mutants for characterizing the molecular basis of symbiotic association, non-nodulating mutants can be used as a control to estimate the biological N\textsubscript{2} fixation. Furthermore, super-/hypernodulating mutants can reduce the nitrogen fertilizer requirements for crops, thereby reducing the impact of agricultural practices on the environment.

This paper deals with the genetic and molecular analysis of soybean symbiotic mutants. Emphasis is placed on the genetic and genomic components of the nodulating soybean mutant loci and the methods used in identifying the genes involved in nodulation.

2. NODULATION IN LEGUME AND SOYBEAN: PLANT-RHIZOBIUM INTERACTION

Many recent studies have focused on legumes rather than the model plant *Arabidopsis thaliana* because legumes show symbiotic relationships between plants and soil-borne bacteria and they have *Rhizobia* for nitrogen fixation (Sato and Tabata 2006; Shoemaker et al. 2006; Town 2006). In terms of genome full sequencing, the soybean draws more attention than other leguminous plants because of its economic importance in the symbiotic interactions between plants and *Bradyrhizobium* (Sutton 1983). During this symbiotic relationship, *Rhizobia* provide the host plant with nitrogen in the form of ammonia (as do the amides in the alfalfa and pea nodules and the ureides allantoin and allantoic acid in the soybean and cowpea nodules) inside the N\textsubscript{2} -fixing nodules on roots of leguminous plants; in turn, they receive carbohydrates and other compounds from the plant (Long 2001; Riely et al. 2004). This symbiotic nitrogen fixation is beneficial to the farmers because it leads to a significant decrease in the use of N-containing fertilizers (Riely et al. 2004; Stacey et al. 2006). External factors, such as light intensity, temperature, pH, soil moisture, etc., closely regulate the symbiotic formation of nodules (Lie 1974; Lee et al. 1998); in legume plants, the amount of nitrogen fertilizer also controls nodulation and nitrogen fixation. Externally-supplied nitrogen in the form of nitrate prevents symbiosis by inhibiting the infection process of the nitrogen-fixing bacteria (Carroll and Mathew 1990; Lee et al. 1998). Internally, this symbiosis is regulated by ‘autoregulation’ (Delves et al. 1986; Van et al. 2005; Lestari et al. 2005, 2006b), the primary functions of which are to control the number and growth of the nodules on the root; it functions by initiating the nodule primordial signal to the leaf, which produces a shoot-derived inhibitor for to restrict the progress of younger nodule primordia (Lee et al. 1991; Gresshoff 2003; Van et al. 2005).

The symbiosis between the soil bacteria and leguminous plants is characterized by a specific multi-step signal cascade (Israel et al. 1986); the first step is the release of flavonoids from the plant root to attract compatible *Rhizobia* (Schultze and Kondorosi 1998; Riely et al. 2004; Geurts et al. 2005; Stacey et al. 2006). Flavonoids