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Mechanistic action of gibberellins in legume nodulation

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Minireview

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Abstract Legume plants are capable of entering into a symbiotic relationship with rhizobia bacteria. This results in the formation of novel organs on their roots, called nodules, in which the bacteria capture atmospheric nitrogen and provide it as ammonium to the host plant. Complex molecular and physiological changes are involved in the formation and establishment of such nodules. Several phytohormones are known to play key roles in this process. Gibberellins (gibberellic acids; GAs), a class of phytohormones known to be involved in a wide range of biological processes (i.e., cell elongation, germination) are reported to be involved in the formation and maturation of legume nodules, highlighted by recent transcriptional analyses of early soybean symbiotic steps. Here, we summarize what is currently known about GAs in legume nodulation and propose a model of GA action during nodule development. Results from a wide range of studies, including GA application, mutant phenotyping, and gene expression studies, indicate that GAs are required at different stages, with an optimum, tightly regulated level being key to achieve successful nodulation. Gibberellic acids appear to be required at two distinct stages of nodulation: (i) early stages of rhizobia infection and nodule primordium establishment; and (ii) later stages of nodule maturation.

Keywords: Gibberellic acid; legume; nodulation; phytohormone; plant development; rhizobia; symbiosis
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INTRODUCTION

Nitrogen is one of the key macro-nutrient elements essential for plant growth and development. Unlike most plant species, legume plants are able to acquire nitrogen by forming a symbiotic relationship with soil-living bacteria collectively known as the rhizobia (Ferguson et al. 2010; Oldroyd 2013). Only compatible species of rhizobia are able to successfully communicate and establish a symbiotic relationship with their specific legume host plants (Pueppke and Broughton 1999). A compatible relationship results in a novel organ on the host root, called a nodule, where the rhizobia are internally housed and supply the plant with fixed nitrogen in exchange for carbohydrates, such as malate (reviewed in Udvardi and Day 1997; Terpolilli et al. 2012).

Nodule formation is initiated by signal exchanges that occur between the two symbionts in the rhizosphere (Ferguson and Mathesius 2003; Oldroyd 2013). Legume roots exude flavonoid compounds into the rhizosphere that act as a chemo-attractant for the rhizobia (Caetano-Anollés et al. 1988). The flavonoid compounds, such as the isoflavones daidzein and genistein from soybean roots, or the flavone 7, 4′-dihydroxyflavone, also induce the expression of rhizobia genes that are responsible for the production and secretion of a lipo-chito-oligosaccharide called Nod factor (Dénarié et al. 1996). LysM type receptors, termed NFR1 and NFR5 in soybean and *Lotus japonicus*, located at the periphery of the plant root, act to recognize Nod factor from compatible rhizobia (Limpens et al. 2003; Madsen et al. 2003; Radutoiu et al. 2003; Indrasumunar et al. 2010, 2011; Broghammer et al. 2012). Host plants also recognize chemical rhizobia characteristics, including lipo- and exo-polysaccharides (Leigh et al. 1985; Jones et al. 2008). The recognition of compatible rhizobia leads to the activation of a series of signaling cascades, resulting in cortical cell divisions that give rise to nodule primordia and enabling bacterial entry (Gage 2004; Ferguson et al. 2010). These two processes are critical for the formation of a fully functional legume nodule.

The interaction between compatible rhizobia and the host plant can be physically observed as early as 1 min after inoculation, with the rhizobia attaching to the root surface and the young root hairs being induced to deform (Turgeon and Bauer 1982, 1985). Within 12 h, (depending on the legume species), the root hairs curl, entrapping the rhizobia (Napoli and Hubbell 1975; Newcomb et al. 1979; Turgeon and Bauer 1982, 1985; Perrine-Walker et al. 2014). While the rhizobia are still at the surface of the root, initial cell divisions for the majority of legumes are seen to be activated in the root pericycle and the root cortex (Turgeon and Bauer 1982, 1985). The rhizobia gain entry into the plant via tube-like structures called infection threads (reviewed in Gage and Margolin 2000;