Regulation of the Soybean-*Rhizobium* Nodule Symbiosis by Shoot and Root Factors—Commentary

Delves AC, Mathews A, Day DA, Carter AS, Carroll BJ, Gresshoff PM (1986) Regulation of the soybean-*Rhizobium* nodule symbiosis by shoot and root factors. Plant Physiol **82:** 588–590

In 1986, Delves et al. demonstrated the existence of two critical factors involved in legume nodulation. The first is required for nodule initiation and functions in the root. The second is required for regulating nodule numbers and functions in the shoot.

These discoveries were the first to conclusively demonstrate that different plant organs influence the nodulation phenotype, significantly predating discoveries in other legumes such as *Medicago* and *Lotus*. Furthermore, they have been monumental in shaping the fields of legume nodule development and autoregulation.

Legume nodules form as a result of a symbiotic relationship between the host plant and soil bacteria termed rhizobia. Within such nodules, rhizobia fix atmospheric nitrogen gas for the plant in exchange for carbohydrates. Because plant growth is typically limited by nitrogen availability, this relationship provides legumes with a tremendous competitive advantage.

The findings of Delves et al. were achieved using novel soybean mutants coupled with an elegant grafting technique. Using the nonnodulating mutant *nod49*, the authors demonstrated that the nodulation phenotype was controlled by the genotype of the rootstock. The *nod49* gene was recently identified as a LysM receptor kinase called *Nod Factor Receptor1* and is likely involved in perceiving the rhizobia-produced Nod factor molecule that initiates legume nodule development.

Using reciprocal grafting and the supernodulation soybean mutant *nts382*, Delves et al. were also the first to unequivocally demonstrate that the shoot controls legume root nodule numbers. This finding strongly influenced the entire field of legume nodulation. In fact, the work of Delves et al. helped establish the long-distance signaling model of autoregulation of nodulation (AON) that still holds true today (e.g. Ferguson et al., 2010). According to the model, AON commences during early nodule development with the synthesis of a root-derived signal named Q. Q is transported to the shoot, where its perception leads to the production of a novel shoot-derived molecule named SDI, which subsequently travels from the shoot down to the roots, where it acts to inhibit further nodulation events. The *nts382* gene of the supernodulating mutant used in the studies of Delves et al. was later identified as a Leu-rich repeat receptor kinase called Nodulation Autoregulation Receptor Kinase (NARK; Searle et al., 2003). NARK is predominantly expressed in the phloem parenchyma of the leaf (Nontachaiyapoom et al., 2007), where it acts to perceive Q and relay its activity via inducing the production of SDI.

Thus, the findings of Delves et al. were tremendously influential to the legume nodulation discipline and the concept of long-distance regulation and signaling of plant developmental processes. Indeed, by being the first to identify the location of NARK activity, Delves et al. helped establish the field of AON research. As a result, their article has been cited more than 175 times (Web of Science, March 3, 2010) and continues to be cited steadily, with an average of more than seven citations per year, 24 years after first being published. One notes that the article was accepted without revision.

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Submitted by Brett Ferguson
Australian Research Council Centre of Excellence for Integrative Legume Research,
The University of Queensland, St Lucia, Brisbane, Queensland 4072, Australia

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