PLANT MICROBIOLOGY

Symbiotic exceptions

DOI:

10.1038/nrmicro1700

URLs

ORS278

<http://www.ncbi.nlm.nih.gov/sites/entrez?Db=genomeprj&md=ShowDetailView&TermToSearch=19575>

BTai1

<http://www.ncbi.nlm.nih.gov/sites/entrez?Db=genomeprj&md=ShowDetailView&TermToSearch=16137>

Lotus japonicus

<http://www.ncbi.nlm.nih.gov/sites/entrez?Db=genomeprj&md=ShowDetailView&TermToSearch=16147>

The symbiosis between leguminous plants and rhizobia, which involves the formation of root and sometimes shoot nodules within which the bacteria differentiate into nitrogen-fixing bacteroids, is one of the most well-studied microbial symbioses. The accepted dogma in the field has been that bacterial lipochitooligosaccharide nodulation (Nod) factors are required for nodule formation. However, new results reported in *Science* now indicate that two strains of photosynthetic *Bradyrhizobium* might use an alternative strategy.

The molecular details of the initiation of nodule formation are well understood. Plant flavonoid compounds induce the expression of the bacterial *nod* genes, which encode the enzymes required for Nod-factor production. Nod fac-

tors are recognized by receptor kinases in the plant, leading to the induction of a signal-transduction pathway that is necessary for nodule formation. Although the genomes of all rhizobial bacteria examined so far have contained *nod* genes, Eric Giraud, Michael Sadowsky and colleagues now report some exceptions to this rule. *Bradyrhizobium* species form functional nodules on both the roots and stems of aquatic leguminous plants belonging to the genus *Aeschynomene*. Giraud *et al.* sequenced the genomes of two group II photosynthetic *Bradyrhizobium* sp. strains, strains **ORS278** and **BTai1**, which nodulate *Aeschynomene sensitiva* and *Aeschynomene indica*, respectively, and found that neither genome contains *nod* genes.

Although previous work had shown that the root and stem nodules induced by ORS278 are functionally identical to nodules induced by other rhizobial species, researchers have been unable to isolate any Nod factors from ORS278. To confirm that Nod factors were not involved, Giraud *et al.* examined nodulation by a *nod* deletion mutant of a group I *Bradyrhizobium* sp. strain, strain ORS285, which normally nodulates both *A. sensitiva* and *Aeschynomene afraspera*. The *nod* deletion mutant failed to nodulate *A. afraspera* but could still form nodules on *A. sensitiva*. So, it seems that *nod* genes are not required for the interaction between photosynthetic *Bradyrhizobium* and some *Aeschynomene* species.

What is the bacterial signal that initiates nodule formation in this system? To answer this question, Giraud *et al.* screened an ORS278 transposon mutagenesis library for mutants that were unable to initiate nodule formation on *A. sensitiva*. Of the 9,500 mutants that were screened, 27 were severely defective in symbiosis, including 14 purine biosynthesis mutants. Three of these mutants were evaluated for their ability to form nodules on *A. sensitiva* in the presence of purine precursors, and it was found that the addition of the precursors restored nodulation. As *Bradyrhizobium* species are known to produce plant cytokinin hormones, and cytokinins are derived from the purine nucleotide adenine, the authors suggest that a cytokinin might have a key role in nodule formation in this system. This would correlate with other experimental observations, such as the fact that symbiotically defective purine auxotrophs of *Rhizobium* spp. have been previously reported and that in *Lotus japonicus*, constitutive activation of a cytokinin hormone receptor allows the formation of nodules in the absence of bacteria and Nod factors.

More research is required to definitively prove that a cytokinin is the signal molecule that triggers nodulation in the *Bradyrhizobium*–*Aeschynomene* symbiotic system, and to pinpoint where in the nodulation pathway this signal acts. However, these initial findings remind us that in science, the exceptions to a rule can often be fascinating.

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ORIGINAL RESEARCH PAPER Giraud, E. *et al.* Legumes symbioses: absence of *nod* genes in photosynthetic *Bradyrhizobium*. *Science* **316**, 1307–1312 (2007)

Stem nodules on *Aeschynomene indica*. Image courtesy of Eric Giraud and colleagues.