

Induction of Actinorhizal Nodules by *Frankia*

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Abstract Actinomycetous soil bacteria of the genus *Frankia* can induce the formation of nitrogen-fixing root nodules on a diverse group of host plants from eight angiosperm families, collectively called actinorhizal plants. Nodule induction involves the colonization of the root surface, followed by the elicitation of changes in the plant that lead to nodule primordium formation and to the entry of bacteria into the root. Like in legume-rhizobia symbioses, bacteria can enter the plant root either intracellularly through a curled root hair, or intercellularly without root hair involvement, and the entry mechanism is determined by the host plant species. Mature actinorhizal nodules are coralloid structures consisting of multiple nodule lobes each of which represents a modified lateral root without root cap, a superficial periderm, and infected cells in the expanded cortex. In this review, an overview of infection mechanisms and nodule structure is given; comparisons with the corresponding mechanisms in legume symbioses are presented. Recent results on the perception of bacterial signal factors are described.

1 Introduction

Nitrogen-fixing root nodule symbioses evolved 50–100 million years ago (Kistner and Parniske 2002). Phylogenetic analysis has shown that all plants able to enter a root nodule symbiosis belong to a single clade (Eurosidi I; see chapter by Normand and Fernandez, in this volume), i.e., they go back to

a common ancestor (Soltis et al. 1995). Within the Eurosoid I clade, rhizobial symbioses are supposed to have evolved four times independently, namely three times within the legume family and once for *Parasponia* (Doyle 1998; Fig. 1). Similarly, three or four independent origins have been suggested for actinorhizal symbioses (Swensen 1996; Benson et al. 2004; Fig. 1). Altogether, the phylogenetic data suggest that the common ancestor of the Eurosoid I clade had acquired a unique property based on which a root nodule symbiosis could develop, and that such a development occurred seven times, four times for rhizobia and three times for *Frankia* symbioses. The symbiosis of the Betulaceae, Casuarinaceae, and Myricaceae (Fagales; genera *Alnus*, *Casuarina*, *Allocasuarina*, *Gymnostoma*, *Myrica*, and *Comptonia*) is supposed to have a common origin; similarly, the symbiosis of the Datisceae and Coriariaceae (Cucurbitales; genera *Datisca* and *Coriaria*) and the symbiosis of the Rosaceae, Rhamnaceae, and Elaeagnaceae (Rosales; genera *Cercocarpus*, *Chamaebatia*, *Cowania*, *Dryas*, *Purshia*, *Ceanothus*, *Colletia*, *Discaria*, *Kentrothamnus*, *Retanilla*, *Talguenea*, *Trevoa*, *Elaeagnus*, *Hippophae*, *Shepherdia*).

Phylogenetically, nitrogen-fixing *Frankia* strains fall into three major clusters (Fig. 1; Benson et al. 2004; see chapter by Normand and Fernandez, in this volume). Cluster 1 strains have been isolated from nodules of *Alnus* (Betulaceae), *Casuarina*, *Allocasuarina* (Casuarinaceae) as well as *Myrica*, *Comptonia*, and *Morella* (Myricaceae; Huguet et al. 2004, 2005) species. Cluster 2 strains have been isolated from nodules of *Hippophae*, *Elaeagnus*, and *Shepherdia* (Elaeagnaceae; Clawson et al. 1998), *Discaria* and *Trevoa* (Rhamnaceae; Clawson et al. 1998), as well as *Gymnostoma* (Casuarinaceae; Navarro et al. 1997) and *Myrica* (Myricaceae; Huguet et al. 2004, 2005). Very rarely, cluster 2 strains have been shown to be able to induce nodules on *Alnus* (Betulaceae; Baker 1987; Bosco et al. 1992; Lumini et al. 1996) and *Casuarina* (Casuarinaceae; Gauthier et al. 1999) and clade 1 strains to induce nodules of *Gymnostoma* (Casuarinaceae; Zhang et al. 1984; Zhang and Torrey 1985). Cluster 3 strains have been found in nodules of actinorhizal Rosaceae, *Datisca*, *Coriaria*, and *Ceanothus* (Vanden Heuvel et al. 2004). Strains of clusters 1 and 2 can be isolated and used for reinfection experiments and thus have been studied primarily. Cluster 3 strains capable of reinfecting the host plants cannot be isolated (see, e.g., Mirza et al. 1992).

Figure 1 shows that some so-called promiscuous genera, *Myrica* and *Gymnostoma*, can be infected by a broader range of strains than the other genera in the Myricaceae and Casuarinaceae, respectively. Phylogenetic studies and fossil analysis indicate that the promiscuous genera represent more ancient symbiosis than those of more recently derived genera, such as *Casuarina*, *Allocasuarina* or *Alnus*, which are infected by a narrower range of strains. Consequently, it has been proposed that actinorhizal symbioses proceed evolutionarily toward more specialization, leading to a greater probability of losing the symbiosis in more recently derived lineages (Maggia and Bousquet

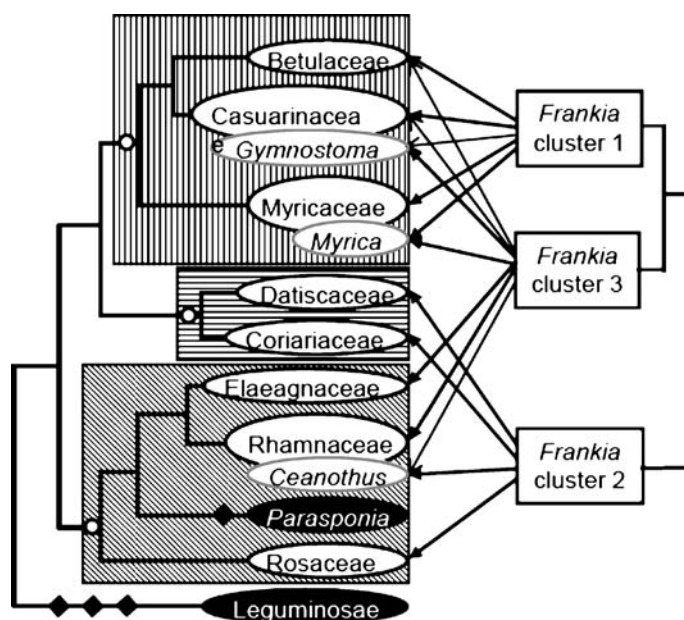


Fig. 1 Simplified scheme of the phylogenetic relationship between actinorhizal plants based on Benson and Clawson (2000). Groups of plants infected by rhizobia are labeled by inverse print. Boxes indicate the three main groups of actinorhizal plants: Fagales (vertical stripes), Cucurbitales (horizontal stripes), and Rosales (diagonal stripes). The phylogenetic relationship between the three clades of symbiotic *Frankia* is included. Some actinorhizal genera (*Gymnostoma*, *Myrica*, *Ceanothus*) that differ in microsymbiont specificity from the rest of the family are indicated. Thick arrows connect *Frankia* clades with the plant group members that the clades are commonly associated with. Thin arrows indicate that members of that clade have been isolated from, or detected in, an effective or ineffective nodule of a member of the plant group at least once. Host specificity exists within the *Frankia* clades, i.e., not all members of a *Frankia* clade can nodulate all plants associated with that clade. Circles indicate the three putative origins of the ability to enter an actinorhizal symbiosis (Swensen 1996; Benson et al. 2004); black rhombs indicate the four putative origins of the ability to enter a symbiosis with rhizobia (Doyle 1998)

1994). However, it should be pointed out that this promiscuity is mostly restricted to greenhouse experiments and not commonly observed in the field (Huang et al. 1985; Clawson and Benson 1999; Navarro et al. 1999).

Bacterial nitrogen fixation is catalyzed by the nitrogenase enzyme complex which is irreversibly denatured by oxygen. However, nitrogen fixation has a high energy demand requiring oxygen for respiratory processes in the nodules. This leads to the so-called oxygen dilemma of nitrogen fixation, necessitating a tight control of oxygen distribution in nodules. In legumes, this control is achieved by the host plant. However, in contrast with rhizobia, *Frankia* can fix N_2 ex planta under aerobic conditions, providing oxygen protection for nitrogenase by forming specialized cell types, vesicle, surrounded

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