

Review

Identification and expression regulation of symbiotically activated legume genes

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Abstract

Legume plants are able to enter two different endosymbioses with soil prokaryotes and soil fungi, leading to nitrogen-fixing root nodules and to arbuscular mycorrhiza (AM), respectively. We applied *in silico* and microarray-based transcriptome profiling approaches to uncover the transcriptome of developing root nodules and AM roots of the model legume *Medicago truncatula*. Several hundred genes were found to be activated in different stages of either symbiosis, with almost 100 genes being co-induced during nodulation and in arbuscular mycorrhiza. These co-induced genes can be associated with different cellular functions required for symbiotic efficiency, such as the facilitation of transport processes across the perisymbiotic membranes that surround the endosymbiotic bacteroids in root nodules and the arbuscules in AM roots. To specify promoter elements required for gene expression in arbuscule-containing cells, reporter gene fusions of the promoter of the *Vicia faba* leghemoglobin gene *VfLb29* were studied by loss-of-function and gain-of-function approaches in transgenic hairy roots. These analyses specified a 85-bp fragment that was necessary for gene expression in arbuscule-containing cells but was dispensable for gene activation in root nodules. In contrast to promoters mediating gene expression in the infected cells of root nodules, the activation of genes in AM appears to be governed by more complex regulatory systems requiring different promoter modules.

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1. Introduction

Legume plants establish two different endosymbioses with soil microorganisms: the nitrogen-fixing root nodule symbiosis and the arbuscular mycorrhiza (AM). Whereas nodulation is almost exclusively restricted to legumes and requires the organogenesis of a root nodule that houses the rhizobial prokaryotes capable of symbiotic nitrogen fixation (Brewin, 1991; Schultze and Kondorosi, 1998; Vessey et al., 2005), more than 80% of terrestrial plants enter an AM with fungi of the phylum *Glomeromycota* (Schüssler et al., 2001).

Arbuscular mycorrhizae support plant development under nutrient-limiting and various stress conditions (Smith and Read, 1997; Graham and Miller, 2005). In AM, fungal hyphae from an extraradical mycelium penetrate the root epidermis via an appressorium and subsequently proliferate in the inner cortex (Harrison, 1997; Strack et al., 2003). In the Arum-type of arbuscular mycorrhiza (Smith and Read, 1997), these intraradical, intercellular hyphae terminate in highly branched, intracellular structures designated arbuscules (Bonfante and Perotto, 1995). Comparable to root nodules, where nutrient exchange takes place across the perisymbiotic membrane surrounding the nitrogen-fixing bacteroids (Day et al., 2001), solute exchange during AM occurs at the perisymbiotic membranes that surround the arbuscules (Gianinazzi-Pearson, 1996; Harrison, 1999; Parniske, 2000). In addition, it is assumed that the intraradical hyphae are a major site for the transfer of nutrients, most importantly for an allocation of carbohydrates to the fungus (Bago et al., 2000). In return for the supply with carbohydrates, fungal microsymbionts transfer minerals, in particular phosphorus, from the soil to the plant (Shachar-Hill et al., 1995; Smith et al., 2001). With respect to phosphorus, arbuscules are the major site of nutrient exchange, and mycorrhiza-specific plant phosphate transporters are exclusively localized at the arbuscular interface (Harrison et al., 2002). It has to be emphasized that although symbiotic microbes colonize root tissues intracellularly during nodule and AM endosymbioses, they stay separated from the plant cytoplasm by the highly specialized perisymbiotic membranes (Provorov et al., 2002).

Considering the apparent analogies in the infection process (Parniske, 2000), including the only recently discovered establishment of an epidermal pre-penetration apparatus during AM that resembles the cortical pre-infection threads formed during nodulation (Genre et al., 2005), an overlap in the activation of gene expression can be expected (Lum and Hirsch, 2002). This overlap is particularly evident for the signal perception and signal transduction cascades that initiate nodulation and mycorrhization (Parniske, 2004). The recent developments in this area are summarized by Limpens and Bisseling (2003), Geurts et al. (2005), and Stacey et al. (2006). Interestingly, studies on legume mutants defective in early stages of both endosymbioses suggest the existence of a Myc-factor that, similar to the action of Nod-factors triggering nodulation,

initiates AM formation (Cullimore and Dénarié, 2003). Based on the observation of common signaling cascades, it is tempting to speculate that the root nodule symbiosis where fossil records date back to the late Cretaceous adopted and subsequently modified more ancient signal transduction pathways leading to AM formation, having been in place already 400 million years ago (Kistner and Parniske, 2002).

In the past few years, different expression profiling strategies were pursued to identify symbiotically induced (symbiosin) genes co-activated during early and late stages of nodulation and mycorrhization. In general, these strategies relied on high-throughput EST sequencing, the construction and analysis of suppressive subtractive (SSH) cDNA libraries, *in silico* profiling of symbiosis-related gene expression by mining comprehensive EST collections, and experimental microarray-based transcriptome profiling (cf. also the reviews by Küster et al. and Krajinski et al. in the present issue). These approaches were facilitated by the selection of two model legumes: *Medicago truncatula* (Barker et al., 1990) and *Lotus japonicus* (Handberg and Stougaard, 1992). In these models and additionally in soybean (Lee et al., 2004), genome and high-throughput EST-sequencing was performed, and different expression profiling tools have been developed to study nodulation and mycorrhization (Colebatch et al., 2002, 2004; Kouchi et al., 2004; Küster et al., 2004; Hohnjec et al., 2005; Lohar et al., 2005).

In this review, we summarize our work on the identification of legume genes transcriptionally activated during nodulation and mycorrhization. Based on *in silico* and experimental transcriptome profiling approaches, novel genes with a symbiosis-enhanced expression were found, and these can be connected to cellular processes relevant for the establishment of either root endosymbiosis. For selected genes, promoter activities have been studied in transgenic roots and minimal promoter regions mediating reporter gene activity in arbuscule-containing cells were specified.

2. *In silico* and experimental expression profiling of different legumes uncover the root nodule transcriptome

To identify genes differentially expressed during the symbiotic interaction of *Sinorhizobium meliloti* and *M. truncatula* leading to nitrogen-fixing root nodules (Fig. 1), both wild-type and mutant plant materials were used to allow not only an identification of genes expressed in developing and mature nodules, but also to detect differential expression of those genes that are regulated by the Nod-factor signaling pathway or require a successful infection for their activation. In case of wild-type tissues, young and mature nitrogen-fixing *S. meliloti*-induced root nodules were taken (El Yahyaoui et al., 2004; Küster et al., 2004; Manthey et al., 2004), whereas whole root systems harvested 3 and 6 days post inoculation (dpi) with *S. meliloti* were chosen from a hypernodulating *M. truncatula* mutant

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