

# Signaling in the Arbuscular Mycorrhizal Symbiosis

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## Key Words

endosymbiosis, fungus, mutualistic, phosphate, root

## Abstract

Many microorganisms form symbioses with plants that range, on a continuous scale, from parasitic to mutualistic. Among these, the most widespread mutualistic symbiosis is the arbuscular mycorrhiza, formed between arbuscular mycorrhizal (AM) fungi and vascular flowering plants. These associations occur in terrestrial ecosystems throughout the world and have a global impact on plant phosphorus nutrition. The arbuscular mycorrhiza is an endosymbiosis in which the fungus inhabits the root cortical cells and obtains carbon provided by the plant while it transfers mineral nutrients from the soil to the cortical cells. Development of the symbiosis involves the differentiation of both symbionts to create novel symbiotic interfaces within the root cells. The aim of this review is to explore the current understanding of the signals and signaling pathways used by the symbionts for the development of the AM symbiosis. Although the signal molecules used for initial communication are not yet known, recent studies point to their existence. Within the plant, there is evidence of arbuscular mycorrhiza-specific signals and of systemic signaling that influences phosphate-starvation responses and root development. The landmark cloning of three plant signaling proteins required for the development of the symbiosis has provided the first insights into a signaling pathway that is used by AM fungi and by rhizobia for their symbiotic associations with legumes.

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## INTRODUCTION

### The Arbuscular Mycorrhiza

The AM symbioses, formed between soil fungi and vascular plants, have a long history, with fossils providing evidence of AM fungi in the roots of the earliest land plants more than 400 mya (140). Sequence data and fossils of spores and hyphae point to the existence of AM fungi even earlier, more than 460 mya, and it is suggested that the AM fungi assisted plants in their colonization of land (135, 139, 159). Certainly it is clear that the ability to form an AM symbiosis occurred early in the evolution of plants, and today the capacity to form these associations is distributed widely throughout the plant kingdom

and includes angiosperms, gymnosperms, pteridophytes, and some bryophytes. Within the angiosperms, at least 80% of the species are able to form AM symbioses (72, 122, 163).

AM fungi are obligate symbionts that establish a symbiosis with the plant in order to obtain carbon, which enables them to grow and complete their life cycle. Their main contribution is to assist the plant with the acquisition of mineral nutrients, particularly phosphorus, and recently it was suggested that in an AM symbiosis, plants receive all of their phosphorus via their fungal symbiont (164). Phosphorus is an essential mineral nutrient that constitutes up to 0.2% (dry weight) of each plant cell and is thus required in significant quantities (148). In many soils, the concentration of phosphorus available to plants is limiting for growth (83). Consequently, improvements in phosphorus acquisition have a significant impact on plant growth, health, and subsequently on plant biodiversity and ecosystem productivity (163, 175). While enhanced plant mineral nutrition is of immense significance, other aspects of the AM symbiosis have far-reaching effects (123). The extraradical phase of the arbuscular mycorrhiza includes meters of AM fungal hyphae that impact soil aggregate stability (13, 141, 143). Furthermore, AM fungi receive 100% of their carbon from the plant and this increase in carbon flow to the roots, estimated at up to 20% of the plants photosynthate, translates to a huge amount of carbon worldwide. Thus, the AM symbiosis also plays a significant role in carbon cycling between the atmosphere and biosphere (8, 190).

### The AM Fungi

The AM fungi are obligate biotrophs and depend entirely on the plant to provide them with carbon. Our inability to grow AM fungi in the absence of the plant has impeded the study of these organisms, and in comparison with other groups of fungi, relatively little is known about them. When not in association with a plant, AM fungi exist in the soil as

**AM:** arbuscular mycorrhizal

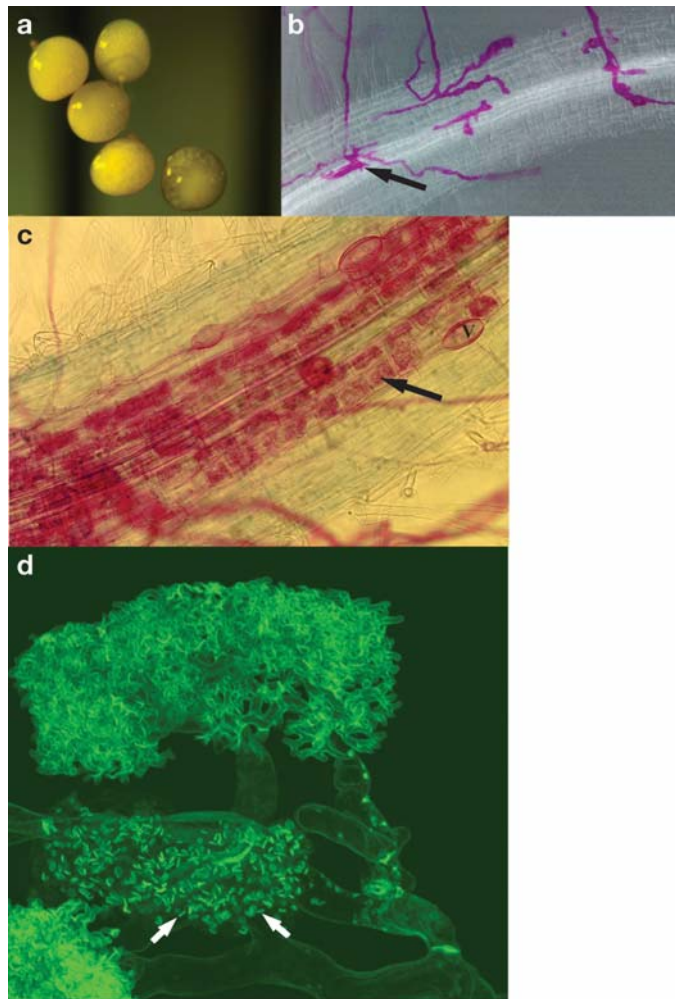
**Mycorrhiza:** The name given to the symbiotic association of plant roots and fungi. The name is derived from the Greek for fungus-root.

resting spores, which in some species are large enough to be visible with the naked eye (**Figure 1a**). Initially, AM fungi were classified as zygomycetes and the morphological characteristics of their spores were used as taxonomic markers (116). Recently, analyses of the small subunit rRNA sequences led to a reclassification and the creation of a new phylum, the Glomeromycota, a sister clade to the Ascomycota and Basidiomycota (153). All AM fungi are members of the Glomeromycota, which is currently subdivided into four orders (153). So far, approximately 150 species of AM fungi have been described and the identification of new species is ongoing (96).

All AM fungi are thought to be asexual, which, considering their ancient origins, has ignited interest as to how they have maintained their genomes. Currently, little is known about their genetics or the organization of their genomes. Their resting spores are multinucleate, and analyses of the ribosomal DNA sequences of many species indicated unusually high levels of polymorphism at these loci (38, 97, 104). Some analyses suggested that they are heterokaryotic, whereas other studies predicted that they are homokaryotic (97, 133). Estimates of genome sizes for these fungi vary greatly and most indicated large genomes (84). In contrast, a recent study found that *Glomus intraradices*, a species that has been maintained in coculture with excised roots for many years (14, 168), has a haploid genome of 15 Mb (80). The genome of this species is now being sequenced, which will provide significant insights into this ancient, obligate symbiont.

### Development of an AM Symbiosis

Despite the wide array of plant and fungal species involved, the development of the AM symbiosis progresses, at least at a morphological level, along broadly similar lines. The interaction is accompanied by significant alterations in the cellular morphology of both symbionts to create the novel symbiotic in-



**Figure 1**

(a) Spores of the AM fungus *Gigaspora gigantea*. The dark lines below the spores are the 1-mm markers of a ruler. The diameter of the spores ranges from 0.3 to 0.5 mm. (b) *Glomus versiforme* appressoria (arrow) on the surface of a *Medicago truncatula dmi2* mutant root. (c) *M. truncatula* root colonized with *Glomus intraradices*. The root is stained with acid fuchsin. Arbuscules are visible in the cortical cells (arrow). Vesicles (V) are also visible in the roots. (d) A confocal microscope image showing a fully developed arbuscule (top) and an arbuscule that is in the process of collapse (bottom). In the dying arbuscule, many septa (indicated by arrows) are visible and the individual branches can no longer be distinguished. (The image is of *G. versiforme* in a *M. truncatula* root. The root cells are not visible in this image.)

terfaces of the arbuscular mycorrhiza, over which carbon and phosphate are exchanged. Detailed descriptions of this process can be found in other reviews (24, 25, 62, 73, 75, 162, 163).

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**Arbuscular mycorrhiza:**

The name given to the endosymbiotic association of a plant root and a fungus from the Glomeromycota. This is also called AM symbiosis.

**Arbuscule:**

A branched hypha that develops within the root cortical cell. It is enveloped in a plant-derived membrane called the peri-arbuscular membrane. The arbuscule–cortical cell interface is the site of phosphate transfer to the plant.

**Endosymbiosis:**

A symbiosis in which one organism lives within the cell of another organism.

**Rhizobia:** Bacteria that form nitrogen-fixing endosymbioses with legumes.

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Briefly, AM fungi exist in the soil as spores, and following germination, the hyphal germ tube grows through the soil in search of a host root. Once contact between the symbionts is established, the fungus forms an appressorium on the root surface (**Figure 1b**) via which it enters the root. The pattern of growth within the root varies depending on the species involved, and two morphological types, the *Paris*-type and the *Arum*-type, named after the plant species in which they were first observed, have been described (35, 161). In practice, the divisions may not be so clear-cut and intermediate morphologies are apparent (45). As most molecular studies have featured *Arum*-type AM symbioses, this review focuses on this type as well (**Figure 1c**).

In the *Arum*-type associations the fungus grows intercellularly through the outer cortex, although occasionally a hypha traverses a cell directly, sometimes forming a coil in the cell. Once inside the inner cortex, the fungus forms dichotomously branched hyphae, called arbuscules, within the cortical cells (**Figure 1c**). Arbuscules are terminally differentiated and they develop on side branches that arise from the long intercellular hyphae (**Figure 1d**). These elaborate structures form inside the plant cell but remain separated from the plant cell cytoplasm by an extension of the plant plasma membrane that surrounds the fungus and follows the contours of the hyphal branches (25). Plant cell wall biosynthesis continues from this extended membrane, and the narrow space between the membrane and the fungal cell wall contains extracellular matrix material that has a composition similar to a primary cell wall (9). Phosphate is delivered to the plant across the arbuscule–cortical cell interface, and recently, plant phosphate transporters involved in this process were identified (76, 132, 137). Although not proven directly, it is anticipated that carbon is taken up by the arbuscule. The arbuscule–cortical cell interface shares some structural and functional similarities with the endosymbiotic interfaces of other plant-microbe endosymbioses including the symbiosome, the symbiotic inter-

face of the rhizobium-legume symbiosis, and the haustorial-plant interface formed by the biotrophic fungal pathogens (74, 129, 160). It should be noted that in the latter example the endosymbiosis is parasitic and nutrient flow is unidirectional, in favor of the microbe.

The AM symbiosis is a highly compatible association, and in phosphate-limiting conditions, intraradical development of the fungus can occur in more than 80% of the root length. In addition to the intraradical growth phase, the fungus also maintains an extraradical mycelium that can extend several centimeters from the root. The fungal hyphae within the root are connected to the extraradical mycelium and form a single continuum. The extraradical hyphae acquire phosphate, initiate the colonization of other roots, and, in most species, are also the site of sporulation.

## SIGNALING PRIOR TO PHYSICAL INTERACTION BETWEEN THE SYMBIONTS

In many plant-microbe symbioses, detection or attraction of the partner occurs prior to direct contact, and in some instances a molecular dialog initiates events essential for progression to the physical stages of the interaction. In one plant-oomycete interaction, cociophilin, a flavonoid present in root exudates, triggers the germination and chemotraction of the peronosporomycete zoospores (85, 145). Although not a plant-microbe symbiosis, germination of the seeds of parasitic plants and the induction of haustoria are initiated with phenolic signals released from the host plant roots (51, 91). Probably the best-characterized molecular dialog occurs in the rhizobium-legume symbiosis, in which flavonoid molecules released from the plant signal the biosynthesis of a bacterial signal molecule called Nod factor. Nod factor is released from the bacterium and perceived via receptors on the legume roots, and this triggers many of the initial events required for

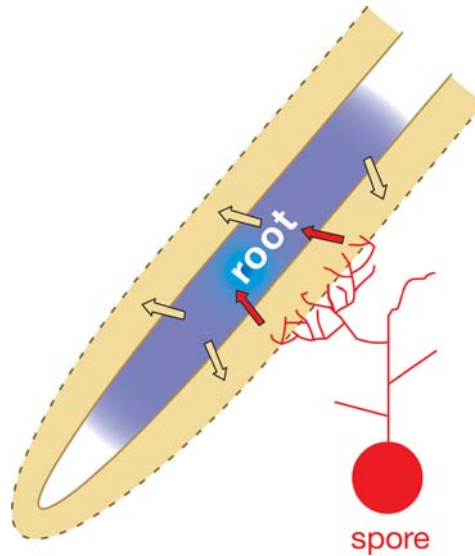
physical interaction and nodule development (43, 44, 54, 106).

## Evidence That AM Fungi Perceive Plant Signals

AM fungal spores can germinate in water, which indicates that they do not require a plant signal for germination; however, plant root exudates and volatiles, including CO<sub>2</sub>, stimulate germination, which suggests that the fungus can sense components of the rhizosphere (16, 60, 120). Following germination, the fungus uses triacylglyceride and glycogen reserves in the spore to support growth and the hyphal germ tube extends a few centimeters from the spore (8). In the absence of a plant root, hyphal growth will cease but this happens before spore reserves are depleted so that the fungus has an opportunity to germinate again and additional chances to find a host root. Some species, with particularly large spores, are capable of germinating up to 10 times (93).

Observations of AM fungi growing on agar or membranes revealed that once the hyphae reach the vicinity of a root, growth increases substantially and the hyphae undergo intense branching, which suggests that they perceive something exuded from the root (31, 67) (**Figure 2**). The extensive branching in the vicinity of the root is assumed to maximize the chance of contact with the root. Branching responses were not observed adjacent to nonhost roots, indicating that discrimination between host and nonhost roots occurs at this stage (31, 67, 69). Consistent with these studies, root exudates applied directly to spores stimulated hyphal growth (16, 17, 60), whereas exudates from nonhost roots were not stimulatory and in some cases showed inhibitory effects (67, 69, 151, 178).

A recent study revealed that the AM fungus *Gigaspora rosea* responds rapidly to partially purified exudates and activates the expression of genes encoding mitochondrial proteins within 60 min of exposure. Significant increases in respiratory activity, includ-



**Figure 2**

Signal exchange between the root and AM fungus prior to their physical interaction. When the fungal germ tube comes into the vicinity of the root, a signal(s) in the plant root exudates (yellow) triggers an increase in respiratory activity in the fungus and intense hyphal branching. A diffusible signal from the fungal hyphae (red arrows) activates gene expression in the plant root (blue shading).

ing oxygen consumption, and reducing activity were detected in *G. rosea* and in a second AM fungus, *Glomus intraradices*, within 2 to 3 h of exposure to exudates. Hyphal branching responses were observed shortly thereafter (171). Together, these data suggest that the fungus perceives a signal in root exudates that triggers an increase in respiration and the onset of active growth. As fungal growth in the presence of exudates is extensive and continues until spore reserves are depleted, it has been proposed that the signal in the exudates initiates a transition to a “presymbiotic growth phase,” at which point the fungus is committed to fully utilize its spore reserves (15). It makes sense then that nonhost root exudates would not trigger this activity.

Currently, the component(s) from root exudates that elicits respiratory activity and branching is not known. In general, exudates

from phosphate-starved plants contain more of the active component than exudates from phosphate-sufficient plants (118, 172). Studies with dialysis membranes indicated that branching factors were smaller than 500 Da (68). From one set of purification experiments, it was concluded that exudates contained multiple compounds of both hydrophilic and hydrophobic nature capable of stimulating branching (117, 118). Another partial purification procedure suggested that the active component was a lipophilic molecule (31). Flavonoid compounds are common components of exudates from phosphate-starved roots, and many of them stimulate fungal growth (2, 60, 177). However, it seems unlikely that the branching factor is a flavonoid, as root exudates from flavonoid-deficient maize mutants stimulated branching at a level comparable to that of wild-type maize root exudates. In the same study the authors tested a range of plant hormones, but these were unable to stimulate branching (31).

Two tomato mutants, *pmi1* and *pmi2*, are unable to form AM symbioses and have exudates that fail to stimulate growth of *G. intraradices* (40, 41). However, additional analyses suggested that *pmi1* does not lack the stimulatory signal but rather actively inhibits hyphal growth (57). It would be interesting to know whether the *pmi1* exudates contain a general inhibitor of fungal growth or whether the effect is specific for AM fungal hyphae. In the latter case the mutant may have the potential to provide insights into specific inhibitors of AM fungal growth and possibly shed light on the individual components that make up the chemical signatures of host and nonhost exudates.

Considering the wide array of plants capable of forming AM symbioses, multiple stimulatory compounds might be predicted. Although the AM symbioses are considered largely nonspecific, differences in functional compatibility are becoming apparent and there may be levels of specificity that are not yet appreciated (134, 165). Multiple stimula-

tory molecules, capable of eliciting differential growth responses in different AM fungal species, would provide a mechanism by which plants could encourage interaction with their preferred symbiont.

### Evidence That Plants Perceive an AM Fungal Signal

It was predicted that AM fungi would produce a signal analogous to Nod factor (4, 34), but direct evidence for a "Myc factor" signal was lacking. Recently, in experiments with *Medicago truncatula*, it was shown that *MtENOD11*, a gene whose expression is induced in the AM symbiosis (36, 86), could be triggered in roots prior to direct contact with the AM fungus (94). In experiments in which the fungus was separated from the plant root by a cellophane membrane, the authors detected expression of an *MtENOD11* promoter-*gusA* transgene in the lateral roots close to the rapidly proliferating fungal hyphae (94). Three species of *Gigaspora* and one *Glomus* species were capable of eliciting expression, indicating that it is not a species-specific effect. In addition, three fungal pathogens did not elicit the same response, which indicates that expression is not activated in response to general by-products of fungal growth and supports the hypothesis of a specific AM fungal signal molecule. By varying the membrane barrier, the authors suggested that the diffusible molecule was less than 3.5 kDa (94). *MtENOD11* encodes a proline-rich cell wall protein that is present in the root tip and some aerial tissues of the plant. *MtENOD11* gene expression is induced significantly during nodulation and in mycorrhizal roots, but its roles in these symbioses are unknown (86). While it remains to be established whether this diffusible fungal signal is critical for development of the symbiosis, it is an exciting finding and, together with work on the branching activity in plant exudates, provides direct evidence for signaling prior to physical contact between the plant and fungal symbionts (**Figure 2**).

## THE ENDOSYMBIOTIC PHASE

### Evidence of Signals for Appressoria Formation

Once in contact with the plant root, the fungus forms an appressorium on the root epidermis through which it enters the root. In contrast to the elaborate, melanized appressoria formed on plant leaves by fungal pathogens, the appressoria formed by AM fungi are simple, nonmelanized structures. For some biotrophic fungal plant pathogens, appressoria formation is triggered by chemical cues from the leaf surface layers and thigmotropic cues such as the ridges on the leaf surface (6, 64, 174). The signals that trigger appressoria formation in AM fungi are not yet known. Attempts to induce appressoria formation on synthetic surfaces were unsuccessful (65), but *Gigaspora margarita* was induced to form appressoria on isolated epidermal cell wall fragments. The fungus would not form appressoria on fragments of vascular or cortical cell walls, which suggests that the signaling molecule is specific to the epidermal cell wall (65, 66, 119). In general, AM fungi do not form appressoria on the surface of nonhost roots, but this may be a consequence of the failure to activate respiration and stimulate hyphal growth rather than the absence of an appressoria-inducing signal.

Interestingly, it was shown recently that the rice pathogen *Magnaporthe grisea*, usually considered a leaf pathogen, also invades rice roots. In the absence of the appressoria-inducing signals of the leaf, *M. grisea* did not form its usual melanized appressorium but instead formed simple hyphal swellings on the surface of rice roots that, at least at a superficial level, appear similar to the appressoria formed by AM fungi (155). Is it possible that pathogenic fungi and AM fungi respond to similar cues on the root surface? Although this is currently unknown, genomics data suggest that some of the molecular events associated with appressoria formation in fun-

gal pathogens and AM fungi might be similar (30).

### Symbiosis Signaling Pathways Identified in Legumes

Growth of the fungal symbiont inside the root and development of the arbuscule–cortical cell interfaces require the alteration of numerous cellular processes, and it is anticipated that the underlying signaling will be complex. In legumes a number of loci required for the development of the AM symbiosis have been defined genetically, and recently three of these have been cloned, providing the first insight into proteins essential for the AM symbiosis (7, 49, 100, 115, 169). All mycorrhizal mutants reported in legumes so far were identified from small populations of nodulation mutants and consequently represent genes required for both symbioses (19, 47, 63, 113, 144, 184). A range of molecular and cell biology data support further commonalities between these symbioses (3, 4, 10, 82, 86, 167, 179), and recent transcriptional profiling experiments indicate significant overlaps in their transcriptomes as well as genes sets unique to each (48, 87, 112). Although the microorganisms involved in these two symbioses are different, their associations with the plant are endosymbioses and the data support the proposal of a common cellular program involved in establishing the microorganisms within the cell (92, 129).

The first symbiosis mutants were identified in pea and two mycorrhizal phenotypes were described (47, 63). In the first class, represented by five mutants, the AM symbiosis progressed normally to the appressoria stage, but the fungus was unable to enter the cortex. In the second class, represented by a single mutant, the AM symbiosis was blocked at a later developmental stage, and the fungus was able to grow in the cortex but unable to develop normal arbuscules (63). Subsequently, mutants impaired in the early stages of the AM symbiosis were reported widely among

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**CCaMK:**  
calcium/calmodulin-  
dependent protein  
kinase

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the legumes, including the model legumes *M. truncatula* and *Lotus japonicus* (19, 28, 34, 90, 109, 144, 154, 158, 184). *M. truncatula* symbiosis mutants, *dmi1*, *dmi2*, and *dmi3*, and *L. japonicus* mutant *Ljsym2* are similar to the first class of pea mutants and fungal growth arrests at the epidermal cell layer (19, 33, 34, 70, 144, 184) (**Figure 1b**). In response to the appropriate rhizobium species, these mutants perceive Nod factor and show the initial root hair responses but then fail to nodulate (34, 169, 181). Recently, the corresponding genes were cloned via positional cloning. *DMI2* of *M. truncatula* and its ortholog *SYMRK* (*LjSYM2*) of *L. japonicus* encode a receptor-like kinase (49, 169). *DMI1* encodes a novel protein that shares similarities with bacterial ligand-gated channels (7), and *DMI3* resembles a CCaMK (100, 115). The proteins are predicted to be involved in signaling, which suggests the existence of a signaling pathway used in both symbioses. As the AM symbiosis is the older of the two associations, it is proposed that the signaling pathway was developed for the AM symbiosis and later coopted for the rhizobium-legume symbiosis. Phylogenetic analyses of *DMI1* and orthologs in other plant species suggested that this protein arose early in the evolution of land plants, an origin that fits well with the concept of a mycorrhizal signaling pathway (7).

How are these proteins envisaged to transduce symbiotic signals, and where do they fit in a symbiosis signaling pathway? For the AM symbiosis, this is not known, and currently there is little information about the signal molecules or early cellular events with which to interrogate the mutants. In contrast, the signals and early responses of the rhizobium-legume interaction are better defined and provide a framework for models of symbiosis signaling (130, 142). In the rhizobium-legume symbiosis, rhizobial Nod factors induce membrane depolarization, calcium fluxes, and rapid oscillations in cytoplasmic calcium, termed calcium spiking, in the root hairs of their legume hosts (50, 157, 182). These responses occur within minutes

of exposure to Nod factors and are followed by an alteration in the directional growth of the root hair such that it curls, trapping the rhizobia within the curl. The bacteria invade the root hair, traveling in a host-derived infection thread that leads them to the root cortex, where they are released into the developing nodule (44, 106). The initial perception of Nod factor occurs via receptor kinases *NFR1* and *NFR5* of *L. japonicus* and *LYK3* of *M. truncatula* (101, 110, 136). These proteins possess novel extracellular domains with motifs that are implicated in binding Nod factor. *nfr1* and *nfr5* lack all responses to Nod factor but are fully able to establish associations with AM fungi, indicating that these receptors are unique for the rhizobium-legume symbiosis (110, 136). As *DMI1* and *SYMRK/DMI2* respond to Nod factor, but do not show calcium spiking and fail to form infection threads, they are placed just downstream of the Nod factor receptors. Whether *SYMRK/DMI2* interacts directly or indirectly with *NFR1/LYK3* and *NFR5* to transmit the Nod factor signal remains to be determined (136), but analogous to other systems, a direct interaction between these receptors kinases is certainly a feasible proposition (121). *SYMRK* has kinase activity, further supporting the idea that the signal is transduced via a phosphorylation event (189). A popular conceptual model proposes that *SYMRK/DMI2* acts upstream of *DMI1* and regulates channel activity, possibly by phosphorylation (130, 142). *DMI1* is a candidate for mediating one of the early ion fluxes, but currently it is not easy to predict which ions it might transmit. Although *dmi1* does not show calcium spiking, the early calcium flux into the root hairs is intact in the *dmi1* mutant (157). The calcium spiking response occurs in the *dmi3* mutant, and therefore *DMI3* is placed downstream of *DMI1*, *SYMRK/DMI2*, and the calcium spiking response (181). On the basis of the identification of *DMI3* as a CCaMK, it is anticipated that *DMI3* perceives and transduces the calcium spiking signal, leading to the activation of downstream responses including

the expression of early nodulation genes (100, 115).

For the rhizobium-legume interaction, the input signal is defined and activation of the pathway occurs via the Nod factor receptors NFR1/LYK3 and NFR5 (101, 110, 136). For the AM symbiosis, the input and, consequently, the beginning of the pathway are not yet clear. There might be additional receptors, or the pathway might begin with the SYMRK/DMI2 receptor kinase. SYMRK/DMI2 has a large, novel extracellular domain potentially able to perceive a ligand that could be of fungal origin (49, 169). Recently, the extracellular domain of the BRI1 receptor kinase was shown to bind its brassinosteroid ligands (79, 91a, 183).

The identities of the DMI1 and DMI3 proteins suggest that ion fluxes and calcium signaling are also central to the AM symbiosis. Exposure to chitin oligomers from fungal cell walls induces calcium fluxes in a range of plant cells (53, 150), and it is reasonable to expect that AM fungi might elicit a similar response. Whether AM fungi induce calcium spiking remains to be determined, but it is interesting to note that high levels of chitin tetramers can induce calcium spiking in *M. truncatula* and that this is blocked in *dmi1* (126). The DMI3 CCaMK is predicted to have the potential to respond to more than one calcium event and to distinguish subtly different calcium signatures (100, 115). It is tempting to speculate that the fungal and bacterial symbionts might induce different calcium signatures that are perceived by DMI3 and translated to different downstream signaling pathways.

What is downstream of DMI3? Currently, this is not known but there are two *L. japonicus* mutants whose symbiosis phenotypes suggest that they might represent additional components of the shared signaling pathway. Mutants *LjSYM4* and *LjSYM15* show root hair swelling responses to Nod factor, but like *dmi1*, *dmi2/LjSYM2*, and *dmi3* infection threads do not initiate (149). Detailed analyses of the mycorrhizal phenotypes suggested that *LjSYM15* plays a role in the entry of the AM

fungus between the epidermal cells (42). In *LjSYM4* the fungus penetrates the epidermis but membrane envelopment of the hypha does not occur, and death of the epidermal cell and the hyphae follows (23). The position of these two mutants relative to *dmi1*, *dmi2/LjSYM2*, and *dmi3* remains to be determined.

If the *DMI/SYM* genes represent part of a pathway developed originally for the AM symbiosis, then nonlegume species might be expected to contain orthologs of the *DMI/SYM* genes. On the basis of sequence similarity, possible orthologs of *DMI1* and *DMI3* in rice were noted (7, 100). The only mycorrhizal mutant identified in a nonlegume species is *rmc*, a tomato mutant (11). *rmc* has a mycorrhizal phenotype similar to that of the *dmi* mutants, and it will be interesting to determine if *RMC* is an ortholog of any of the *DMI* genes. In *rmc*, the mycorrhizal phenotype varied depending on the fungal symbiont, and with one fungal species, a full symbiosis was established (58). This suggests that interactions with AM fungi may not all occur via the same signaling pathways. The study by Kosuta et al. (94) also provides support for the idea of multiple signaling pathways. The diffusible fungal signal activates *MtENOD11* expression in wild-type and *dmi* mutant backgrounds, suggesting that this particular signal is perceived and transduced by a pathway separate from the *DMI/SYM* signaling pathway (94).

### Cell Autonomous and Cell Nonautonomous Signaling Associated with Development of Arbuscules

Significant changes to both symbionts occur with the formation of arbuscules. These highly branched hyphae develop in the inner cortical cells, and as this cell layer is closest to the vascular tissue, the source of carbon delivery to the root, it has been suggested that a carbon gradient may be involved in signaling their development (20). Currently, nothing is known about the signaling pathways in the fungus that induce the repeated

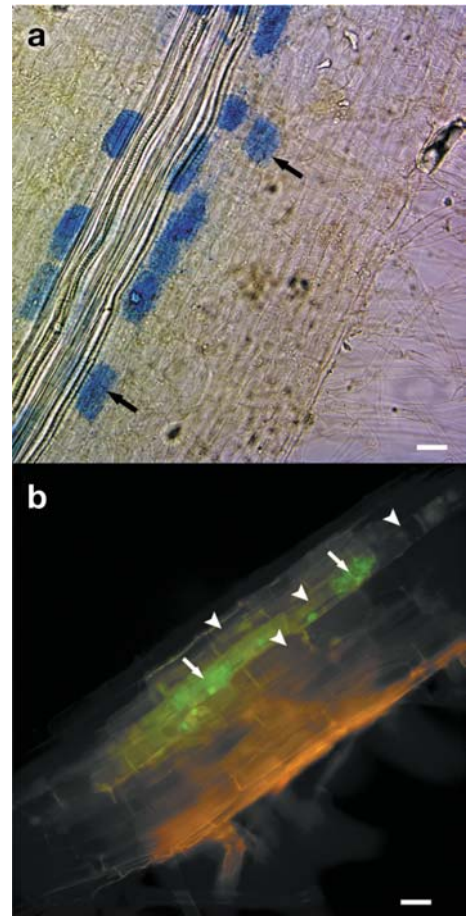
**SCP:** serine carboxypeptidase

**GST:** glutathione-S-transferase

dichotomous branching that results in arbuscule formation. Likewise, it is unknown what factors signal the development of septa in the hypha and the collapse of the arbuscule (**Figure 1d**), and whether this occurs in response to signals from the plant or whether it is triggered by an endogenous fungal program. The observation that the dynamics of arbuscule development and collapse were similar in six plant species supports the latter suggestion (5).

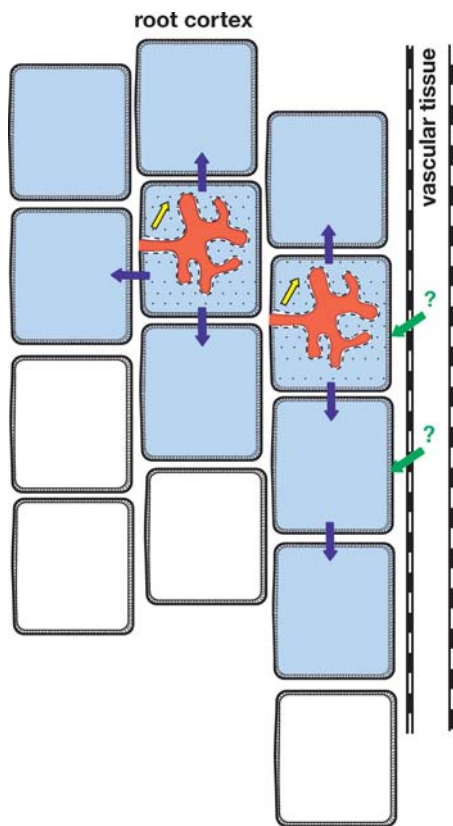
So far, only one plant mutant impaired in arbuscule development has been reported. In pea *sym36* arbuscules are stunted and contain a few short hyphal branches (59, 63). In response to rhizobia, *sym36* develops Fix<sup>-</sup> nodules, which suggests that the missing protein is required for the development of both endosymbiotic interfaces. Weak alleles of the *LjSym4* and *LjSym15* show reduced arbuscule development, pointing to an additional role for these common symbiosis proteins in arbuscule development (42, 124).

Plant gene expression associated with arbuscule development provides evidence for at least two signaling events that are unique to the AM symbiosis. A number of genes, including mycorrhiza-specific phosphate transporters, a cellulase, a chitinase, and a proton ATPase, are expressed only in mycorrhizal roots and expression occurs exclusively in the cortical cells containing arbuscules (22, 76, 95, 103, 138, 170) (**Figure 3a**). This spatial expression pattern suggests that a mycorrhiza-specific signal, operating in cell autonomous fashion, activates expression of these genes. In contrast, expression of an SCP and a GST occurs only in mycorrhizal roots also, but expression is triggered in cells containing arbuscules and cortical cells in the vicinity of the invaded cell, particularly those in the same cell file or the adjacent cell file (**Figure 3b**). This suggests the presence of a second signal acting in a local, cell nonautonomous fashion in the colonized region of the root (103, 187) (**Figure 4**). Further evidence of this type of signal is provided by studies of the cytoskeleton, in which alterations in microtubule arrays



**Figure 3**

Gene expression patterns in mycorrhizal roots associated with arbuscule formation. (a) *M. truncatula* root expressing the *gusA* reporter gene under the control of the MtPT4 promoter. Roots are colonized with *Glomus versiforme*. Histochemical staining reveals GUS expression exclusively in cells containing arbuscules (indicated by black arrows) (76). (b) *M. truncatula* root expressing the green fluorescent protein (GFP) gene under the control of the MtSCP1 promoter. Roots are colonized with *G. versiforme*. Two cells containing arbuscules (indicated by white arrows) show GFP expression. Adjacent cells that do not contain arbuscules (white arrowheads) also show GFP expression. Note, GFP is visible in the cytoplasm but also diffuses into the nucleus, and this is visible as an intense fluorescent sphere within the cells (103).



**Figure 4**

Signaling associated with arbuscule development in the cortex of a mycorrhizal root. Arbuscules (red) develop in the cortical cells but remain separate from the plant cell cytoplasm by an extension of the plasma membrane, called the peri-arbuscular membrane (dashed black line), that surrounds the hyphal branches. Gene expression patterns and cytoskeletal rearrangement supports the existence of two signals operating in the cortex of mycorrhizal roots. A signal (yellow arrows) that acts in a cell autonomous fashion induces expression of a set of genes (e.g., MtPT4) exclusively in cells with arbuscules (black spots). A second signal that acts in a cell nonautonomous fashion (blue arrows) induces expression of a second set of genes (e.g., MtSCP1) in cells with arbuscules and in adjacent cells (blue shading). It has been proposed that arbuscule formation is triggered in response to a signal, possibly carbon-based, from the vascular tissue (green arrows and question marks).

were observed not only in the cells in which arbuscule development was occurring, but also in adjacent cells that had not been invaded (18).

The nature of these signals and signaling pathways are unknown. Recent transcriptional profiling experiments have identified signaling proteins whose expression is associated only with the AM symbiosis and these are possible candidates for mediating arbuscular mycorrhiza-specific signaling (29, 48, 87, 98, 103, 112, 187).

### Defense Response Signaling in the AM Symbiosis

AM fungi possess many of the same surface molecules as plant pathogenic fungi, including chitin and glucans, oligomers of which act as general elicitors of plant defense responses (21). These general elicitors are conceptually equivalent to PAMPs (125, 128), and recently some of the receptors responsible for their recognition have been identified (71). If AM fungi have fungal PAMPs, how do they avoid triggering plant defense responses? One possibility is that the molecules that act as PAMPs in fungi are subtly different in AM fungi. This is the case for rhizobial flagellin. Flagellin is a bacterial PAMP (71); however, the rhizobial flagellin molecule fails to trigger plant defenses because the molecule is marginally different in the elicitor active part (52). Alternatively, AM fungi may induce alterations in their host cells that lead to the destruction of the elicitor molecule. Spruce cells secrete a chitinase that acts on chitin molecules released from the cell walls of an ectomycorrhizal fungus, cleaving them to a size that renders them inactive and incapable of inducing defenses (146, 147). The induction of chitinase activity in mycorrhizal roots has been reported widely (22, 166), and in *M. truncatula*, specific chitinase genes are induced in mycorrhizal roots, whereas pathogen-induced chitinases are not expressed (145a). In the fine branches of the arbuscules, the fungal cell wall is thin and the chitin is not highly

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**PAMPs:**  
pathogen-associated  
molecular patterns

**IFR:** isoflavone  
reductase

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polymerized (26, 27). Consequently, the concentration of chitin oligomers, the elicitor-active molecules, could be particularly high at this location. As chitinase gene expression occurs specifically in cells with arbuscules (22), it is possible that the enzyme plays a role similar to that of the chitinases in the spruce interaction and inactivates the elicitor signal molecule.

A number of studies have reported the induction of defense responses during the initial stages of the development of the AM symbiosis, and these were noted to decline, or were subsequently downregulated, as the symbiosis developed (39, 61, 77, 88, 99, 180). Cell death responses were not reported, which is consistent with the general defenses triggered by PAMPs. How do AM fungi avoid or limit plant defense responses, and is there evidence for active suppression? The biotrophic fungal pathogens face similar problems, and in the barley–*Blumeria graminis* interaction the haustoria play a role in suppression of plant defenses (152). There is some evidence for localized suppression of defenses in mycorrhizal roots, which, analogous to the barley–*B. graminis* interaction, might be mediated via the arbuscule. In *M. truncatula* roots, IFR, a gene whose product is involved in the biosynthesis of an antimicrobial phytoalexin, medicarpin (127), is expressed at basal levels in the cortical cells of the root. Transcript levels increase in the initial stages of AM symbiosis but subsequently decline as the symbiosis develops. *In situ* hybridization revealed that the decrease in IFR transcripts occurred in cells containing arbuscules and adjacent cells but not in noncolonized regions of the root (77, 78). This spatial expression pattern is consistent with suppression mediated via the arbuscules. In most studies the timing of downregulation of defenses correlates well with the initial onset of arbuscule development, and as arbuscule formation is ongoing throughout the symbiosis, potential defense suppression mediated by arbuscules would be continuous (39, 77, 99, 180). Whether this occurs remains to be determined. In terms of a mechanism, there is

evidence that the haustoria of the biotrophic fungal pathogens express small, secreted proteins that act within their host plant cell (46). Many of the so-called avirulence proteins produced by pathogens trigger suppression of defense responses (1), and it is possible that the arbuscules of AM fungi secrete proteins with a similar function.

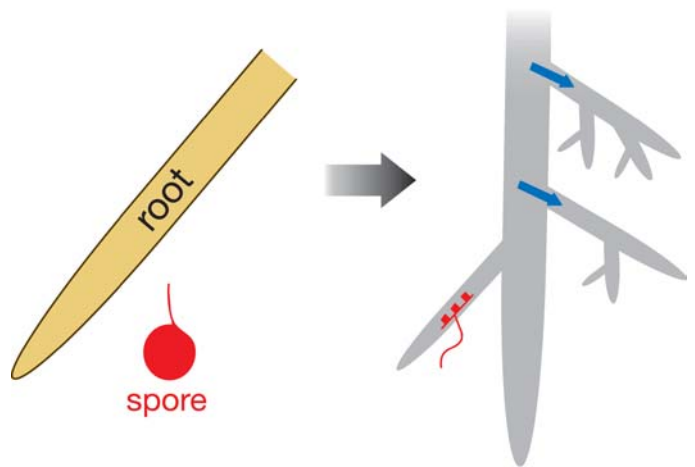
### Evidence of Systemic Signaling: Lateral Root Formation and Phosphate-Starvation Responses

In addition to the changes within the cortical cells, the AM symbiosis also results in alterations to the overall architecture of the root (55). An increase in lateral root development, particularly increases in the number of higher order laterals and in some cases an increase in their length, has been reported for a number of species (188). Alterations in lateral root development were particularly apparent in a maize mutant, *lrt1*, which lacks lateral roots. *lrt1* is impaired in the formation of lateral roots on the primary and seminal roots, although it can form laterals on the crown roots. Following colonization with the AM fungus *Glomus mosseae*, the root system of *lrt1* showed extensive lateral root development including “lateral bushes” containing first-, second-, third-, and fourth-order lateral roots (131). As lateral roots are generally the most highly colonized roots, it appears that the symbionts trigger alterations in root architecture to create the most favored sites of interaction (Figure 5).

Phosphate is a key regulator of root architecture, and one of the responses to low phosphate is a reduction in the growth of the primary root and an increase in lateral root number and length, an architecture that is favorable for the development of the AM symbiosis (107, 173, 186). In general, the AM symbiosis develops most readily under low-phosphate conditions. As the symbiosis becomes established the plants’ phosphate-deprivation responses, such as phosphate-starvation-induced gene expression, are

downregulated (32, 37, 89, 102, 132), and split root experiments demonstrate that this is mediated via a systemic signal (32). As increased lateral root initiation is one of the phosphate-deprivation-induced responses, it might be predicted that this would decrease in the AM symbiosis also. In contrast, in mycorrhizal roots it appears that the lateral root response is uncoupled from the other phosphate-starvation-regulated responses, and lateral root formation is stimulated. This was also apparent in the maize *lrt1* mutant, in which the mycorrhiza-induced lateral root phenotype occurred even at higher levels of phosphate nutrition (131).

Currently, little is known about the signaling pathways that control these responses in mycorrhizal roots. Analysis of lateral roots in *Arabidopsis* indicates that their development is controlled via auxin signaling pathways (111), but cytokinin is implicated in this process also (105). Cytokinins are also involved in the regulation of phosphate-starvation-induced gene expression (56, 107, 114). Increases in auxin and cytokinin levels in mycorrhizal roots have been reported, but hormone signaling in the AM symbiosis has not yet been explored extensively (12, 108, 156, 176). Although the large resource of *Arabidopsis* hormone signaling mutants cannot be used directly for analyzing the AM symbiosis, the information



**Figure 5**

Systemic signaling in mycorrhizal roots. Prior to development of the symbiosis, plants growing in low-phosphate conditions express phosphate-starvation-induced genes (*yellow shading*). The development of the AM symbiosis leads to the downregulation of phosphate-starvation-induced gene expression. This is controlled by a systemic signal (*blue arrows*). The development of the AM symbiosis also results in an increase in lateral root formation. It is likely that this also is controlled systemically.

can be translated to a mycorrhizal host plant species, and hormone signaling genes can be targeted for mutation by reverse genetics approaches (81, 185). With the judicious choice of a few key regulators it may be possible to accelerate our understanding of hormone signaling in the AM symbiosis.

## SUMMARY POINTS

1. Recent evidence indicates that the plant and AM fungus perceive each other prior to their physical interaction. The identities of the diffusible signals are currently unknown, but the plant signal is most abundant in the root exudates of phosphate-deprived plants.
2. Legumes possess a signaling pathway that is used for the development of the AM symbiosis and for the nitrogen-fixing symbiosis formed with rhizobia. Three components of the pathway, a receptor kinase, a putative ion channel, and CCaMK, were identified recently. The identity of the latter protein implicates calcium as a signal in the AM symbiosis. For the AM symbiosis, the input signals to this pathway and the downstream events under its control remain to be determined.

3. Within the plant, development of the arbuscule–cortical cell interface is accompanied by arbuscular mycorrhiza-specific gene expression in the root cortical cells. The expression patterns suggest the presence of cell autonomous signals and mobile signals operating in the root cortex.
4. Development of the AM symbiosis leads to an increase in lateral root formation and a decrease in phosphate-starvation-induced gene expression. There is evidence that the latter occurs via a systemic signal.

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## NOTE ADDED IN PROOF

A recent publication reveals that *L. japonicus LjSYM4* is an ortholog of *M. truncatula DMI1* (Imaizumi-Anraku H, Takeda N, Charpentier M, Perry J, Miwa H, et al. 2005. Plastid proteins crucial for symbiotic fungal and bacterial entry into plant roots. *Nature* 433:527–31).

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