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# Mutualism and parasitism: the yin and yang of plant symbioses

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Plants are solar-powered sugar factories that feed a multitude of other organisms. Many of these organisms associate directly with host plants to gain access to the plant's photosynthates. Such symbioses encompass a wide collection of styles ranging from mutualistic to commensal and parasitic. Among these, the mutualistic arbuscular mycorrhizal (AM) symbiosis is one of the evolutionarily oldest symbioses of plants, relying on the formation of an intimate relationship between fungi of the Glomeromycota and roots of the majority of vascular flowering plants. In this symbiosis, the fungus intracellularly colonizes living root cells, implying the existence of an extreme form of compatibility. Interestingly, molecular events that happen in the plant in response to mycorrhizal colonization also occur in other beneficial and, as recently shown, even antagonistic plant symbioses. Thus, basic 'compatibility modules' appear to be partially conserved between mutualism and parasitism.

### Addresses

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**Current Opinion in Plant Biology** 2006, **9**:364–370

This review comes from a themed issue on  
Biotic interactions  
Edited by Anne Osbourn and Sheng Yang He

Available online 19th May 2006

1369-5266/\$ – see front matter  
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DOI [10.1016/j.pbi.2006.05.008](https://doi.org/10.1016/j.pbi.2006.05.008)

### Introduction

All parts of the plant body are continually exposed to an extensive diversity of potential invaders including bacteria, fungi, oomycetes, worms and plants. As plants are equipped with effective pre-formed or inducible mechanisms to protect themselves against undesired visitors, they are resistant to most organisms most of the time [1]. However, some organisms have evolved mechanisms to bypass plant defenses in order to access plant-derived nutrients. These tactics include the destruction of plant cells and feeding on cell content (necrotrophic microbes), intercellular growth and obtaining nutrients from the apoplast (endophytic parasites), fusion of host and parasite root vasculature (parasitic plants), the induction of vascular giant cells (root-knot nematodes), and the intracellular colonization of living cells (biotrophic microbes). Most of these infection patterns require the establishment of

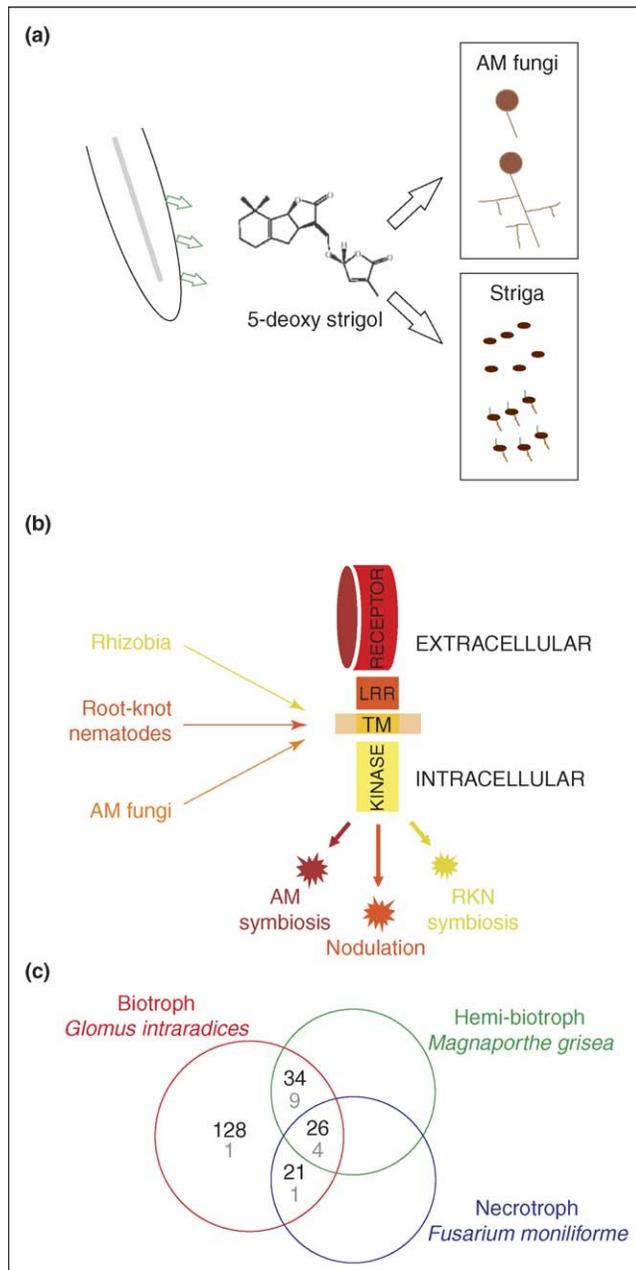
a close relationship. Therefore, a balanced molecular cross-talk between both symbiotic partners must be present that leads to compatibility and, ultimately, to the establishment of such close symbioses. (Throughout this review, the term 'symbiosis' will be used according to its original definition by De Bary 'the living together of differently named organisms' independent on the outcome of the interaction.)

Arbuscular mycorrhizal (AM) fungi are obligate biotrophs that colonize the roots of more than 80% of terrestrial plants [2]. The AM symbiosis is one of the evolutionarily oldest, yet contemporary, biotrophic interactions. It has been hypothesized that AM fungi might have been instrumental in the transition of plants from water to land, as the origin of the AM symbiosis coincided with the occurrence of the earliest land plants at least 400 million years ago [3]. Compatibility with AM fungi enabled plants to explore and conquer a novel ecosystem and continues to provide a selective advantage because of the nutritional benefit it provides to plants [4]. Furthermore, an increasing number of reports indicate that the AM symbiosis could represent an ancestral form of plant symbioses. In legumes, a signal transduction cascade has been identified that is equally required for the development of AM symbioses and for interaction with nitrogen-fixing *Rhizobia*. This pathway has been the subject of several reviews [5<sup>\*</sup>,6,7,8<sup>\*</sup>]. The identification of commonalities between these two beneficial root symbioses prompted the theory that evolutionarily younger interactions might have hijacked plant programs that were already in place for the primary AM symbiosis [7,9]. In the field of plant interactions, scientific attention has lately shifted from studying plant resistance determinants towards defining compatibility factors [10]. This review considers the beneficial AM symbiosis as an ancient paradigm to highlight the existence of common plant compatibility modules among contrasting types of plant symbioses involving taxonomically distant groups of infecting organisms.

### Development of an AM symbiosis

The soil-borne spores of AM fungi germinate spontaneously, forming a germ tube that grows through the soil in search of a host root. In the absence of a host, hyphal growth is limited. Detection of host signal(s) induces vigorous hyphal branching (Figure 1a; [11–13]). Recently, this plant-released 'branching factor' has been determined to be strigolactone (5-deoxy-strigol) [14<sup>\*\*</sup>]. Plants release strigolactones constitutively but their concentration is higher in the exudates of hosts of AM fungi than in non-hosts, and is further elevated in phosphate-deprived

Figure 1



Conservation in the beneficial AM symbiosis and other plant interactions. **(a)** Plant-released strigolactones (here 5-deoxy strigol) induce hyphal ramification of AM fungi and seed germination of parasitic plants such as *Striga*. **(b)** The *L. japonicus* receptor-like kinase SYMRK is part of a perception machinery for plant interactions with AM fungi, *Rhizobia* and root-knot nematodes. **(c)** Schematic overview of AM-associated rice genes in response to root-infecting fungi. Black numbers represent induced genes; grey numbers represent suppressed genes. LRR, leucine-rich repeat domain; TM, transmembrane domain.

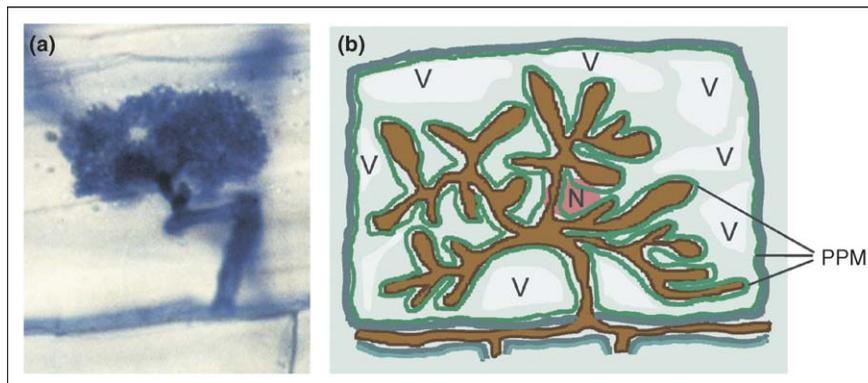
plants [14<sup>••</sup>]. Successful pre-symbiotic signal exchange leads to the formation of fungal appressoria on the root surface [15]. Appressoria are swollen fungal hyphae that mark the first physical contact between plant and fungus,

and are also the site of fungal entrance into the root. The fungus either directly traverses rhizodermal cells or enters the root tissue through a cleft between two adjacent rhizodermal cells, from where it penetrates the bordering cells [5<sup>•</sup>,16<sup>••</sup>]. The cell in contact with the appressorium prepares for the anticipated penetration by developing a pre-penetration apparatus, directing fungal growth through the cell (Figure 3; [16<sup>••</sup>]). This tunnel formation is linked to the production of an interface compartment between the invading hypha and the plant membrane that surrounds the passing fungus [16<sup>••</sup>]. Passage through the outer cell layers therefore appears to be a well-coordinated process that relies on synchronized activities of both symbionts, which is also reflected by the large number of plant mutants in which this step of the interaction is affected [17]. The fungus continues its route towards the inner cortex by a combination of symplastic and apoplastic growth. Once the fungus has reached the inner cortex, it rapidly spreads longitudinally within the intercellular space, thereby colonizing large parts of the root [5<sup>•</sup>]. The fungus then invaginates individual inner cortex cells to form determinate, highly-branched haustoria called arbuscules. Arbuscules can nearly fill the cell and their formation is accompanied by dramatic changes in cell architecture: the nucleus shifts from a peripheral to a central location, the vacuole becomes fragmented and an extensive plant-derived periarbuscular membrane is synthesized. This membrane is continuous with the plant plasma membrane, confining an apoplastic interface matrix (Figure 2; [18]). The development of arbuscules must involve a harmonically arranged molecular cross-talk between plant and fungus. Furthermore, arbuscules are predicted to be the site of symbiotic phosphate acquisition: a plant-encoded phosphate transporter protein has been localized to the periarbuscular membrane [19]. Interestingly, despite the major efforts that the plant and fungus must expend to assemble an arbusculated cell, arbuscules collapse after several days. When the fungus 'leaves' the cell, the cell structure returns to that of a non-colonized cell.

### Conserved host-recognition compounds for AM fungi and parasitic plants

Mutual recognition by potential symbionts is required for the commencement of a coordinated infection process. A landmark in mycorrhizal research has been the identification of strigolactones as a host-recognition compound for AM fungi [14<sup>••</sup>]. It is intriguing that the very same molecule stimulates seed germination of parasitic plants such as *Striga* (Figure 1a; [20]). The establishment of this antagonistic symbiosis involves host-induced seed germination followed by the directional growth of the radicle towards the host root and the formation of a so-called haustorium, which provides a morphological and physiological link to the host root and its vascular system [20]. For both parasitic plants and AM fungi, recognition of a

Figure 2



Fully developed arbuscule. **(a)** Trypan blue stained arbuscule of *Glomus mosseae* in roots of *Zea mays* (400 $\times$ ). **(b)** Schematic representation of an arbuscule inside a cortical cell. The nucleus (N) is at a central position, the vacuole (V) has become fragmented and the plant plasma membrane (PPM) is enveloping the fungus.

proximate host and its rapid colonization are crucial events in their life cycle. Parasitic plants produce tiny dust-like seeds with virtually no storage capacity, and thus the appropriate timing of germination is critical for survival [20]. For AM fungi, the perception of strigolactones characterizes the switch from an asymbiotic 'energy-saving' to a pre-symbiotic 'energy-burning' growth pattern [13,21]. Strigol was the first strigolactone to have its chemical structure determined, initially from root exudates of the false host cotton [22] and later from the true *Striga* hosts maize, sorghum and millet [20]. To date, the chemical structures of six strigolactones have been identified from hosts of *Striga* and *Orobanchae*: strigol, strigyl-acetate, sorgolactone, alectrol, orobanchol and 5-deoxy-strigol [14<sup>••</sup>,20]. These natural seed stimulants, as well as the synthetic analog GR24, are recognized by AM fungi and induce hyphal ramification [14<sup>••</sup>].

The pathway of strigolactone biosynthesis is not currently clear. Strigolactones have been described as sesquiterpenes [14<sup>••</sup>,23], but the recent use of maize mutants that are deficient in carotenoid biosynthesis suggests that they might be carotenoid derivatives [24]. Strigolactones are highly unstable and very short-lived under natural soil conditions. Their presence therefore provides positional information about the distribution of host roots within the soil [14<sup>••</sup>]. Until the discovery of strigolactones as host-recognition factors of AM fungi, their natural role as seed stimulants was not understood. It seemed counterintuitive that plants constitutively exude compounds that serve as essential signaling molecules for their parasites. Now, a plausible explanation could be that the release of strigolactone 'announces' the presence and position of host plants to their beneficial fungal symbionts. This view is corroborated by the observations that phosphate-starved plants release higher levels of strigolactones in their root exudates [25] whereas mycorrhizal plants exude

lower amounts of strigolactones [24]. As the evolutionary origin of AM fungi [3] predates the occurrence of parasitic angiosperms [23,26], it can be assumed that the latter have acquired detection systems that enable them to exploit the existing mutualistic communication system to locate their prey.

### Conserved signaling components between beneficial and harmful invaders

*Lotus japonicus SYMRK* encodes a receptor-like kinase that is required for both the successful establishment of AM symbioses and the nitrogen-fixing symbiosis with *Rhizobia* [27]. The gene was isolated by map-based cloning using mutants in which penetration of the root by AM fungi beyond the rhizodermal cell layer was compromised and that did not support root-hair curling in response to *Rhizobia*. Surprisingly, the *symRK* mutation also affects the early stages of infection by root-knot nematodes (RKN) [28<sup>••</sup>]. Entrance of RKN into root tissue is typically accomplished by mechanical penetration. RKN then grow intercellularly through the cortex and induce specific giant cells only upon reaching the vasculature. During the pre-symbiotic phase, however, root-hairs of wildtype plants respond to the perception of a RKN-released signal by enhanced branching [28<sup>••</sup>]. On *symRK* roots, RKN-induced root-hair branching was reduced to half the wildtype levels, indicating that signal perception is affected. Therefore, the signal-detection machinery for interaction with beneficial AM fungi and *Rhizobia* employs common components that are also implicated in the detrimental symbiosis with RKN (Figure 1b). These findings indicate that the evolution of RKN parasitism involved the partial recruitment of more ancient symbiotic pathways [28<sup>••</sup>]. Furthermore, it can be predicted that, as RKN have a large host range, analogous proteins might participate in RKN symbioses in non-legumes.

### Conserved host transcriptional responses to infection by beneficial and pathogenic fungi

A recent study revealed that 43% of rice genes that respond transcriptionally to root colonization by AM fungi also respond to root infection by pathogenic fungi (Figure 1c; [29\*\*]). The root pathogens used were the hemi-biotroph *Magnaporthe grisea* and the necrotroph *Fusarium moniliforme*. It had previously been shown that the early stages of rice root infection by *M. grisea* involve hyphopodia formation and intracellular growth while traversing the root cortex. The fungus then enters the vascular system of the root from where it can spread systemically [30\*]. Thus, the initial infection pattern of *M. grisea* resembles that of AM fungi. By contrast, the invasion strategy of the necrotrophic fungus *F. moniliforme* is fundamentally different: the root tissue is disintegrated during the infection process [31]. Similar invasion practices trigger related expression profiles in rice: the number of genes that responded similarly in the biotroph and the hemi-biotroph infections was twice that in the biotroph and necrotroph infections [29\*\*]. The same study showed overlapping expression patterns for 13% of the genes in all three types of interactions (Figure 1c). Among these was a putative WRKY transcription factor, which was suggested to play a role in modulating the expression of genes that were involved in the plant's response to fungal invaders. Some of the described genes might be involved in determining the compatibility of rice to fungal infection, but this remains to be investigated.

It has been a general observation that biotrophic microbes circumvent plant defense responses. Results of the rice transcriptome analysis are in agreement with these observations and reflect the absence of plant defense responses when monitoring the transcriptional activity of the complete rice genome at the stage of a fully established AM symbiosis [29\*\*]. The absence of plant defense could be due either to active suppression or to avoidance of defense induction. Several studies of the AM symbiosis show that plant defense becomes weakly induced during early stages of the AM symbiosis but is subsequently downregulated as development of the symbiosis progresses [8\*]. The existence of a suppression mechanism is consistent with these findings, and it has been suggested that activation of this mechanism might be linked to the formation of haustoria [8\*]. Haustoria-associated absence of pathogenesis-related transcripts has been reported in individual barley leaf cells that were infected with powdery mildew [32\*\*]. Furthermore, haustoria-containing cells display an increased susceptibility to subsequent infections [33]. It is currently not clear, however, whether suppression is directly fungus-mediated or indirectly plant-induced. These data collectively suggest that suppression of plant defense responses in plant-biotroph interactions might involve mechanisms that are conserved between mutualism and parasitism.

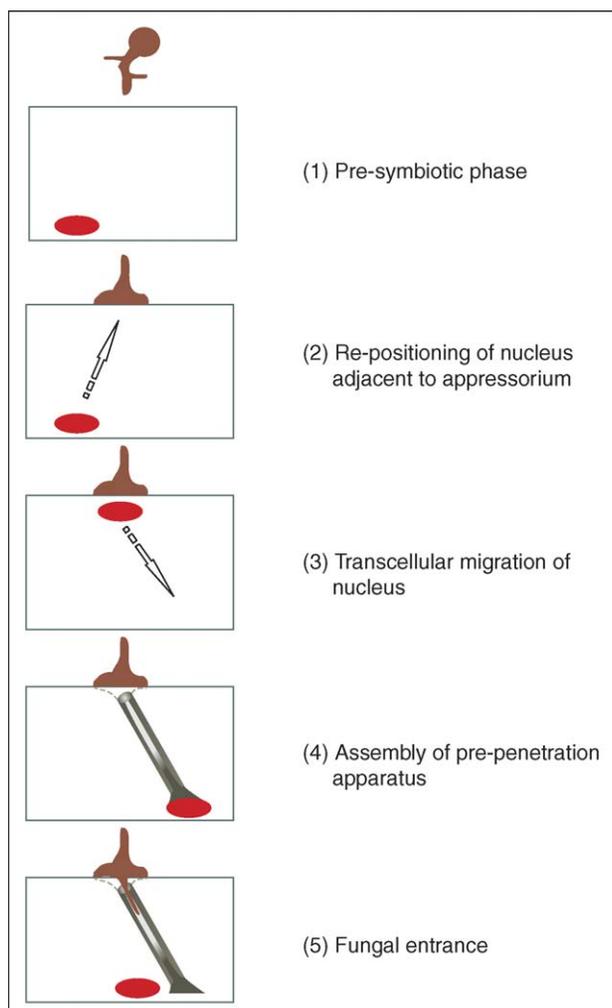
However, the absence of host defense responses in plant interactions that do not include the formation of haustoria, such as that between grasses and *Epichloë* endophytes [34], suggests that additional, haustoria-independent mechanisms exist.

### Conserved cellular response to penetration by beneficial and pathogenic biotrophs

Cellular responses to contact with plant-invading organisms are highly dynamic but largely similar whatever the outcome of the association [35]. The plant cytoskeleton plays an important role during plant-microbial interactions [35,36]. The infection process that leads to compatible interactions between plants and biotrophic pathogens is broadly conserved and similar to the development of an AM symbiosis. It involves adhesion of the spores (or conidia) to the leaf surface, appressoria formation and penetration [37\*\*]. Specialized infection structures, such as haustoria, are typical of biotrophs whereas intracellular hyphae are formed by hemi-biotrophs and biotrophs [38\*]. The morphological similarities between haustoria and the perihyphal interface of pathogens and of AM fungi are considerable and have been previously reviewed [9]. The focus here is on cellular responses to intracellular hyphal growth during the early biotrophic period.

Using green fluorescent labeled markers of the plant cytoskeleton and the endoplasmic reticulum (ER), it has been shown that rhizodermal cells of *Medicago truncatula* that are in contact with the appressorium of the AM fungus *Gigaspora gigantea* prepare for cell penetration by development of a pre-penetration apparatus, which subsequently directs fungal growth through the cell lumen (Figure 3; [16\*\*]). Upon appressorium formation and prior to fungal ingress, the nucleus becomes repositioned next to the appressorium. From here, the nucleus migrates transcellularly but remains linked to its earlier position below the appressorium by microtubules, microfilaments and ER cisternae, thereby producing a hollow column. Once the column completely spans the cellular lumen, the fungus enters and trespasses the rhizodermal cell. Thus, the movement of the nucleus across the cell lumen defines the route that the fungus takes during penetration. Re-positioning of the plant cell nucleus to underneath the appressorium of biotrophic pathogens has been frequently reported [39]. This nuclear movement occurs in both compatible and incompatible interactions as a result of cytoskeleton re-arrangements [40,41]. The process spanning the period from appressoria development to the arrival of the nucleus below the appressorium leads to cell polarization, which can result in resistant or susceptible outcomes and is therefore an important decisive step for the interaction [37\*\*,39]. Interestingly, during the compatible interaction with pathogens, a subsequent transcellular nuclear movement takes place that is comparable to the nuclear migration in cells being infected by

Figure 3



Preparation of the host cell for penetration by AM fungi. The individual stages are indicated (modified after Genre *et al.* [16\*\*]).

beneficial AM fungi [40,41]. Furthermore, in incompatible interactions that include fungal penetration, the nucleus performs a similar movement across the cell lumen prior to cell death [40,41]. It is not known whether the transcellular movement during pathogen infections also results in the formation of a tunnel-like structure.

The *M. truncatula* penetration mutants *doesn't make infections2 (dmi2)* and *dmi3* carry a defect in a receptor-like kinase and a calcium- and calmodulin-dependent kinase, respectively [42–44]. They were shown to support nuclear repositioning next to the appressorium but failed to build the pre-penetration apparatus [16\*\*]. This phenotype is consistent with a vital function of the pre-penetration apparatus in compatibility with AM fungi and, moreover, indicates that a sequence of signals is required at individual steps for the formation of this structure. In pathogenic associations, the pathogen-induced microfilament

assembly was recently shown to be required for the establishment of compatibility between barley and powdery mildew [45\*\*]. This evidence supports the notion that components of the cytoskeleton not only assist defense mechanisms but also play a role during susceptibility [37\*\*]. In future, it will be interesting to use the available cytological and genetic tools to examine how far conservation extends beyond transcellular nuclear movement among different types of plant symbioses.

### Concluding remarks

We are witnessing a fascinating period of growing awareness towards the existence of commonalities in the continuum between mutualistic and parasitic plant symbioses. The mutualistic AM symbiosis occupies a somewhat peculiar position as it is increasingly considered to be an antique reference for plant symbioses. The currently known commonalities are involved in determining compatibility at early stages of plant interactions that include, often surprisingly, unrelated organisms (e.g. AM fungi and parasitic plants). What is the extent of conservation? Is there a hierarchical principle from general (broadly required) to specific (distinctively required) compatibility factors? The future perspective is exciting as novel technologies, such as laser-capture microdissection combined with global expression profiling, can be applied to focus analyses on individual cell types and thus stages of infection. Moreover, the availability of forward or reverse genetics resources in plants that enter into several types of interactions allows for the identification of compatibility factors that are relevant to each of those interactions.

### Acknowledgements

I apologize to all those researchers whose work I have overlooked or could not include because of page limitations. I am grateful to Jane Glazebrook and Ruairidh Sawers for critical reading of the manuscript and to the University of Geneva and the Swiss National Science Foundation (grant 3100A0-104132) for funding.

### References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
  - of outstanding interest
1. Huckelhoven R: **Powdery mildew susceptibility and biotrophic infection strategies**. *FEMS Microbiol Lett* 2005, **245**:9-17.
  2. Smith SE, Read DJ (Eds): *Mycorrhizal Symbiosis*. Academic Press; 1997.
  3. Remy W, Taylor TN, Hass H, Kerp H: **Four hundred-million-year-old vesicular arbuscular mycorrhizae**. *Proc Natl Acad Sci USA* 1994, **91**:11841-11843.
  4. Karandashov V, Bucher M: **Symbiotic phosphate transport in arbuscular mycorrhizas**. *Trends Plant Sci* 2005, **10**:22-29.
  5. Parniske M: **Molecular genetics of the arbuscular mycorrhizal symbiosis**. *Curr Opin Plant Biol* 2004, **7**:414-421.
- This review provides a comprehensive overview of the signal transduction pathway that is shared between nodulation and mycorrhiza formation, and summarizes the stages of development of the AM symbiosis at which the mutants are affected.

6. Oldroyd GE, Harrison MJ, Udvardi M: **Peace talks and trade deals. Keys to long-term harmony in legume-microbe symbioses.** *Plant Physiol* 2005, **137**:1205-1210.
7. Kistner C, Parniske M: **Evolution of signal transduction in intracellular symbiosis.** *Trends Plant Sci* 2002, **7**:511-518.
8. Harrison M: **Signaling in the arbuscular mycorrhizal symbiosis.** • *Annu Rev Microbiol* 2005, **59**:19-42.  
This review provides a broad update on the current understanding of signaling in the AM symbiosis, covering the plant and the fungal sides and including developmental as well as nutritional aspects.
9. Parniske M: **Intracellular accommodation of microbes by plants: a common developmental program for symbiosis and disease?** *Curr Opin Plant Biol* 2000, **3**:320-328.
10. Panstruga R: **Establishing compatibility between plants and obligate biotrophic pathogens.** *Curr Opin Plant Biol* 2003, **6**:320-326.
11. Giovanetti M, Sbrana C, Avio L, Citernesi A, Logi C: **Differential hyphal morphogenesis in arbuscular mycorrhizal fungi during pre-infection stages.** *New Phytol* 1993, **125**:587-593.
12. Buee M, Rossignol M, Jauneau A, Ranjeva R, Becard G: **The pre-symbiotic growth of arbuscular mycorrhizal fungi is induced by a branching factor partially purified from plant root exudates.** *Mol Plant Microbe Interact* 2000, **13**:693-698.
13. Bécard G, Kosuta S, Tamasloukht M, Séjalon-Delmas N, Roux C: **Partner communication in the arbuscular mycorrhizal interaction.** *Can J Bot* 2004, **82**:1186-1197.
14. Akiyama K, Matsuzaki K, Hayashi H: **Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi.** • *Nature* 2005, **435**:824-827.  
The work described in this report constitutes a major scientific breakthrough: the identification of the chemical structure of the branching factor, a host recognition signal for AM fungi.
15. Giovanetti M, Avio L, Sbrana C, Citernesi A: **Factors affecting appressoria development in the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae* (nicol. & gerd.) gerd. & trappe.** *New Phytol* 1993, **123**:114-122.
16. Genre A, Chabaud M, Timmers T, Bonfante P, Barker DG: **Arbuscular mycorrhizal fungi elicit a novel intracellular apparatus in *Medicago truncatula* root epidermal cells before infection.** *Plant Cell* 2005, **17**:3489-3499.  
This paper describes the discovery of a novel intracellular structure: the pre-penetration apparatus, a hollow column built by the nucleus-directed assembly of cytoskeletal and ER proteins.
17. Marsh J, Schultze M: **Analysis of arbuscular mycorrhizas using symbiosis-defective plant mutants.** *New Phytol* 2001, **150**:525-532.
18. Harrison MJ: **Molecular and cellular aspects of the arbuscular mycorrhizal symbiosis.** *Annu Rev Plant Physiol Plant Mol Biol* 1999, **50**:361-389.
19. Harrison MJ, Dewbre GR, Liu J: **A phosphate transporter from *Medicago truncatula* involved in the acquisition of phosphate released by arbuscular mycorrhizal fungi.** *Plant Cell* 2002, **14**:2413-2429.
20. Bouwmeester HJ, Matusova R, Zhongkui S, Beale MH: **Secondary metabolite signalling in host-parasitic plant interactions.** *Curr Opin Plant Biol* 2003, **6**:358-364.
21. Tamasloukht M, Sejalon-Delmas N, Kluever A, Jauneau A, Roux C, Becard G, Franken P: **Root factors induce mitochondrial-related gene expression and fungal respiration during the developmental switch from asymbiosis to presymbiosis in the arbuscular mycorrhizal fungus *Gigaspora rosea*.** *Plant Physiol* 2003, **131**:1468-1478.
22. Cook C, Whichard L, Wall M, Egley G, Coggon P, Luhan P, McPhail A: **Germination stimulants. 2. The structure of strigol — a potent seed germination stimulant of witchweed (*Striga lutea* Lour.).** *J Am Chem Soc* 1972, **94**:6198-6199.
23. Yoder JI: **Host-plant recognition by parasitic scrophulariaceae.** *Curr Opin Plant Biol* 2001, **4**:359-365.
24. Matusova R, Rani K, Verstappen FW, Franssen MC, Beale MH, Bouwmeester HJ: **The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobancha* spp. are derived from the carotenoid pathway.** *Plant Physiol* 2005, **139**:920-934.
25. Yoneyama K, Takeuchi Y, Yokota T: **Production of clover broomrape seed germination stimulants by red clover requires nitrate but is inhibited by phosphate and ammonium.** *Physiol Plant* 2001, **112**:25-30.
26. Wolfe KH, Gouy M, Yang YW, Sharp PM, Li WH: **Date of the monocot-dicot divergence estimated from chloroplast DNA sequence data.** *Proc Natl Acad Sci USA* 1989, **86**:6201-6205.
27. Stracke S, Kistner C, Yoshida S, Mulder L, Sato S, Kaneko T, Tabata S, Sandal N, Stougaard J, Szczyglowski K et al.: **A plant receptor-like kinase required for both bacterial and fungal symbiosis.** *Nature* 2002, **417**:959-962.
28. Weerasinghe RR, Bird DM, Allen NS: **Root-knot nematodes and bacterial Nod factors elicit common signal transduction events in *Lotus japonicus*.** *Proc Natl Acad Sci USA* 2005, **102**:3147-3152.  
This is the first report to indicate conservation between the AM symbiosis and the root-knot nematode symbiosis. Mutation of the *L. japonicus* receptor-like kinase SYMRK leads to defects in signaling during early stages of the AM symbiosis, nodulation and the RKN symbiosis.
29. Guimil S, Chang HS, Zhu T, Sesma A, Osbourn A, Roux C, Ioannidis V, Oakeley EJ, Docquier M, Descombes P et al.: **Comparative transcriptomics of rice reveals an ancient pattern of response to microbial colonization.** • *Proc Natl Acad Sci USA* 2005, **102**:8066-8070.  
This is the first report comparing the transcriptional responses of a plant to beneficial and harmful fungal infections. The results of this work suggest considerable similarities in the plant's answer to fungal invasion, which are more extensive if the infection strategies are related.
30. Sesma A, Osbourn AE: **The rice leaf blast pathogen undergoes developmental processes typical of root-infecting fungi.** • *Nature* 2004, **431**:582-586.  
This work shows that *M. grisea* is not only a devastating foliar pathogen but also efficiently infects rice and barley roots. These infections are associated with alterations of the fungal morphology that resemble the typical infection structures of root-infecting pathogens.
31. Paszkowski U, Kroken S, Roux C, Briggs SP: **Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis.** *Proc Natl Acad Sci USA* 2002, **99**:13324-13329.
32. Gjetting T, Carver TL, Skot L, Lyngkjaer MF: **Differential gene expression in individual papilla-resistant and powdery mildew-infected barley epidermal cells.** • *Mol Plant Microbe Interact* 2004, **17**:729-738.  
These authors established a protocol that allowed the single-cell analysis of transcript levels of a selected set of pathogenesis-related genes. Resistant cells have a profile of gene expression that is different from that in infected cells.
33. Schulze-Lefert P, Panstruga R: **Establishment of biotrophy by parasitic fungi and reprogramming of host cells for disease resistance.** *Annu Rev Phytopathol* 2003, **41**:641-667.
34. Scott B: ***Epichloe* endophytes: fungal symbionts of grasses.** *Curr Opin Microbiol* 2001, **4**:393-398.
35. Mendgen K, Hahn M: **Plant infection and the establishment of fungal biotrophy.** *Trends Plant Sci* 2002, **7**:352-356.
36. Perfect S, Green J: **Infection structures of biotrophic and hemibiotrophic fungal plant pathogens.** *Mol Plant Pathol* 2001, **2**:101-108.
37. Lipka V, Panstruga R: **Dynamic cellular responses in plant-microbe interactions.** • *Curr Opin Plant Biol* 2005, **8**:625-631.  
This review summarizes all of the available information about plant cellular responses during pathogen attack, emphasizing the participation of the plant cytoskeleton. The authors introduce the 'Janus-faced' role of the plant cytoskeleton, which possibly assists in plant defense and in compatibility.
38. Takemoto D, Hardham AR: **The cytoskeleton as a regulator and target of biotic interactions in plants.** • *Plant Physiol* 2004, **136**:3864-3876.

These authors, in addition to those of [37\*\*], include a detailed summary of the contribution of the plant cytoskeleton during the establishment of symbiotic interactions.

39. Schmelzer E: **Cell polarization, a crucial process in fungal defence.** *Trends Plant Sci* 2002, **7**:411-415.
40. Skalamera D, Heath M: **Changes in the cytoskeleton accompanying infection-induced nuclear movements and the hypersensitive response in plant cells invaded by rust fungi.** *Plant J* 1998, **16**:191-200.
41. Heath M, Nimchuk Z, Xu H: **Plant nuclear migration as indicators of critical interactions between resistant or susceptible cowpea epidermal cells and invasion hyphae of the cowpea rust fungus.** *New Phytol* 1997, **135**:689-700.
42. Endre G, Kereszt A, Kevei Z, Mihacea S, Kalo P, Kiss GB: **A receptor kinase gene regulating symbiotic nodule development.** *Nature* 2002, **417**:962-966.
43. Levy J, Bres C, Geurts R, Chalhoub B, Kulikova O, Duc G, Journet EP, Ane JM, Lauber E, Bisseling T *et al.*: **A putative Ca<sup>2+</sup> and calmodulin-dependent protein kinase required for bacterial and fungal symbioses.** *Science* 2004, **303**:1361-1364.
44. Mitra RM, Gleason CA, Edwards A, Hadfield J, Downie JA, Oldroyd GE, Long SR: **A Ca<sup>2+</sup>/calmodulin-dependent protein kinase required for symbiotic nodule development: gene identification by transcript-based cloning.** *Proc Natl Acad Sci USA* 2004, **101**:4701-4705.
45. Opalski KS, Schultheiss H, Kogel KH, Huckelhoven R: **The receptor-like MLO protein and the RAC/ROP family G-protein RACB modulate actin reorganization in barley attacked by the biotrophic powdery mildew fungus *Blumeria graminis* f. sp. *hordei*.** *Plant J* 2005, **41**:291-303.

This work shows that fungal pathogens might target small RAC/ROP G-proteins to modulate barley microfilaments, thereby assisting in the establishment of compatibility against powdery mildew.

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