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Unraveling mycorrhiza-induced resistance

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Arbuscular mycorrhizal symbioses have a significant impact on plant interactions with other organisms. Increased resistance to soil-borne pathogens has been widely described in mycorrhizal plants. By contrast, effects on shoot diseases largely rely on the lifestyle and challenge strategy of the attacker. Among the potential mechanisms involved in the resistance of mycorrhizal systems, the induction of plant defenses is the most controversial. During mycorrhiza formation, modulation of plant defense responses occurs, potentially through cross-talk between salicylic acid and jasmonate dependent signaling pathways. This modulation may impact plant responses to potential enemies by priming the tissues for a more efficient activation of defense mechanisms.

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Introduction

For more than 400 million years plants have established a mutualistic association known as arbuscular mycorrhizas (AM) with certain soil fungi. Nowadays, about 80% of all terrestrial plants, including most agricultural, horticultural, and hardwood crop species are able to establish this mutualistic association. Arbuscular mycorrhiza forming fungi (AMF) are obligate biotrophs because they rely on their host plant to proliferate and survive. The establishment of the symbiosis requires a co-ordinated developmental program that has been the focus of several recent reviews [1–3]. The benefits of the AM symbiosis on plant fitness are largely known, including a better mineral nutrition and increased ability to overcome biotic and abiotic stresses.

A growing body of evidence supports the overlap in plant responses to different stresses, regulated through a sophisticated signaling network [4]. Synergism and antagonism between signaling pathways provide a cost-efficient regulatory potential for fine-tuning the appropriate defense mechanism. This review summarizes the data on AM-induced protection against biotic stress and the possible mechanisms involved, with special emphasis on the role of plant defense responses. We try to integrate current models on regulation of plant responses during mutualistic and pathogenic interactions to explain the spectrum of effectiveness of mycorrhiza-induced resistance (MIR).

Impact of mycorrhizal symbiosis on plant resistance to biotic stress

Alleviation of damage caused by soil-borne pathogens has been widely reported in mycorrhizal plants. Most studies on protection by AM deal with the reduction of incidence and/or severity of soil-borne diseases mainly root rot or wilting caused by fungi such as *Rhizoctonia*, *Fusarium*, or *Verticillium*, and root rot caused by oomycetes including *Phytophthora*, *Pythium*, and *Aphanomyces*. These studies have been compiled in a comprehensive review by Whipps [5]. A reduction in the deleterious effects by parasitic nematodes such as *Pratylenchus* and *Meloidogyne* has also been reported [6•,7]. As for any biocontrol agent, it should be noted that (i) the ability to enhance resistance/tolerance differs among AMF isolates, (ii) the protection is not effective for all pathogens, and (iii) the protection is modulated by environmental conditions [5,8].

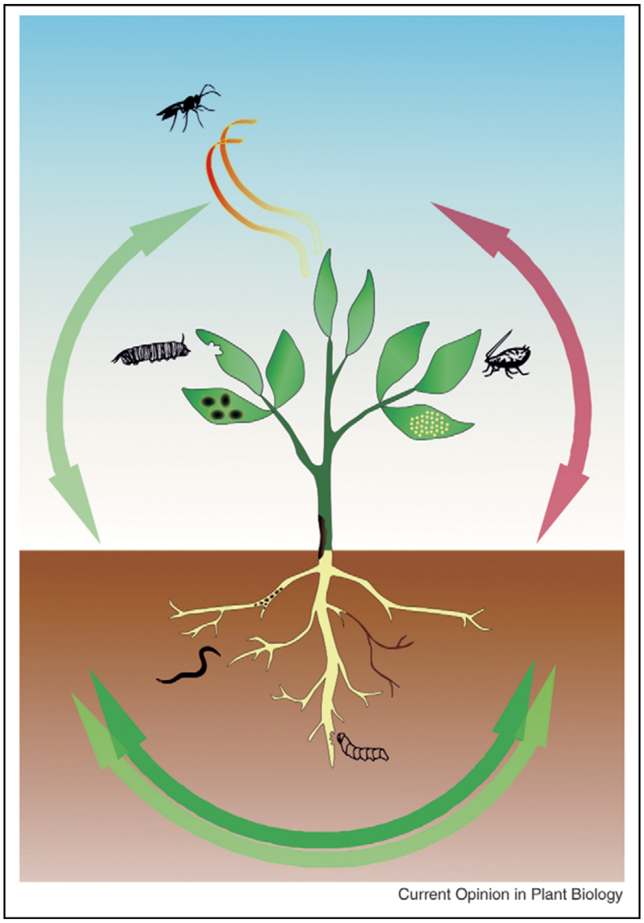
Reports about mycorrhizal effects on aboveground diseases are scarcer and less conclusive. AM symbioses have been associated with enhanced susceptibility to biotrophic pathogens including viruses [9], powdery mildew, and rust fungi (*Blumeria*, *Oidium*, *Uromyces*), although increased tolerance was often observed in terms of plant mass and yield [5,10]. Mycorrhization, however, reduced disease symptoms caused by a phytoplasma, and protection against the necrotroph *Alternaria solani* has been shown in mycorrhizal tomatoes [11,12]. Only recently, the impact of AM on plant interactions with shoot pathogenic bacteria has been assessed: mycorrhizal symbiosis results in enhanced resistance to *Xanthomonas campestris* in *Medicago truncatula* [13••] and to *Pseudomonas syringae* in tomatoes (MJ Pozo *et al.*, unpublished data).

AM have also significant consequences on the growth and/or survival of phytophagous insects. Again, although AM symbioses consistently reduce attacks by root-feeding insects, effects on foliar-feeding insects are more variable. The effect seems to depend on the insect lifestyle and degree of specialism: AM reduce the incidence of generalist chewing insects, whereas sap-feeding or specialist insects show increases in performance on mycorrhizal plants [14••]. Figure 1 summarizes the effects of AM on different plant attackers.

Mechanisms of mycorrhiza-induced resistance

Different mechanisms have been shown to play a role in plant protection by AMF, namely, improved plant nutrition, damage compensation, competition for colonization sites or photosynthates, changes in the root system, changes in rhizosphere microbial populations, and activation of plant defense mechanisms. Several mechanisms can be operative simultaneously, with contributions depending on environmental conditions, timing of the interaction, and partners involved [5,8]. The requirement of a well-established AM symbiosis for induced resistance is generally accepted [15,16•]. In addition to localized effects, split-root experimental systems allowing physical separation between AMF and pathogens have confirmed plant mediated systemic effects [16•–19]. Although an improved nutrient status has been considered a main mechanism in mycorrhiza-induced protection, studies including nutrient-supplemented controls showed that mycorrhizal effects cannot be regarded as a mere consequence of improved phosphorus nutrition [9,12,20].

Figure 1



Spectrum of efficiency of MIR. AM symbioses generally reduce incidence and/or damage caused by soil-borne pathogens, nematodes, and root-chewing insects (bottom). The protection results from the combination of local and systemic mechanisms. In aboveground tissues, MIR is effective against necrotrophic pathogens and generalist chewing insects (left). Indirect defenses are also enhanced: parasitoids are more attracted by volatiles released by AM plants. Viral and fungal biotrophs, as well as phloem-feeding insects, perform better on mycorrhizal plants (right). Green and red arrows indicate increase resistance or susceptibility, respectively, of mycorrhizal plants. Drawing by J. Perez-Tienda.

There is evidence for the accumulation of defensive plant compounds related to mycorrhization, although to a much lower extent than in plant–pathogen interactions. Accumulation of reactive oxygen species, activation of phenylpropanoid metabolism, and accumulation of specific isoforms of hydrolytic enzymes such as chitinases and glucanases has been reported in mycorrhizal roots. These reactions, however, are generally localized, suggesting a role in AM establishment or control of the symbiosis [18,21,22]. Concerning aboveground effects, accumulation of insect antifeedant compounds [14••] and transcriptional regulation of defense-related genes [13••] (MJ Pozo *et al.*, unpublished data) have been described in the shoots of mycorrhizal plants. Furthermore, the volatile blends released by AM plants can be more attractive to aphid parasitoids than those from non-mycorrhizas [23]. Nevertheless, accumulation of PR proteins, salicylic acid, or expression of marker genes associated with systemic acquired resistance has not been reported in systemic tissues.

Mycorrhiza-induced priming for defense

Defense responses are vital but costly for the plant. A rapid and strong activation of defense mechanisms is crucial for success in controlling attackers. Accordingly, preconditioning of plant tissues for a more effective activation of defenses is a plausible strategy [24••]. This phenomenon, known as priming, is the focus of the review by Uwe Conrath in this issue.

Priming seems to be the main mechanism operating in MIR. The lack of systemic activation of cellular or biochemical defense mechanisms in mycorrhizas and the stronger defense reactions observed upon pathogen challenge support this hypothesis. Root colonization by AMF systemically protected tomato plants against *Phytophthora parasitica* infection. Only mycorrhizal plants formed papilla-like structures around the sites of pathogen infection through deposition of non-sterified pectins and callose, preventing the pathogen from spreading further, and they accumulated significantly more PR-1a and basic β-1,3 glucanases than non-mycorrhizal plants upon *Phytophthora* infection [17,18,25]. Similarly, mycorrhizal transformed carrot roots displayed stronger defense reactions at challenge sites with *Fusarium* [26]. Mycorrhization also amplified the accumulation of the phytoalexins rishitin and solavetivone in *Rhizoctonia*-infected potato plantlets, whereas AMF itself did not alter the levels of these compounds [27]. Protection of mycorrhizal grapevine roots against *Meloidogyne incognita* has been also associated with primed expression of a chitinase gene, *VCH3*, in response to the nematode [6•]. These results illustrate that primed responses are not restricted to AMF-colonized areas, but they occur in the whole root system. We have recently confirmed primed expression of defense genes in shoots of mycorrhizal plants upon treatment with the defense related signals methyl jasmonate and ethylene (MJ Pozo *et al.*, unpublished data). On the whole, experimental evidences strongly support that mycorrhizal symbiosis triggers a primed state that is effective throughout the whole plant.

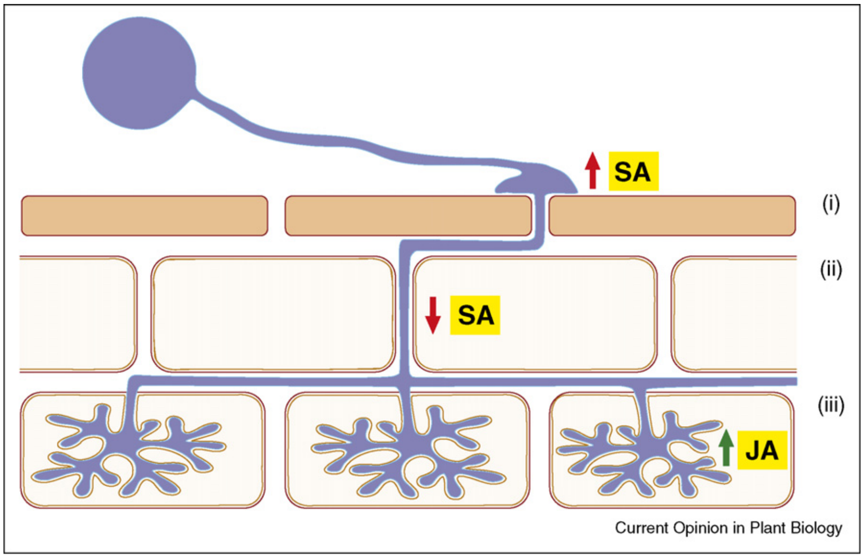
Signaling pathways involved

The establishment of mutualistic associations involves mutual recognition and a high degree of co-ordination based on a continuous molecular dialogue between both symbionts [1,2]. Advances in our knowledge about plant–microbe signaling are unraveling mechanisms regulating biotic interactions. For example, the identification of strigolactones, known to stimulate seed germination of parasitic plants, as host recognition compounds for AMF [28] has uncovered a possible mechanism mediating the protector effect of AM against parasitic plants. Mycorrhizal plants by exudating lower amounts of strigolactones are unfavorable to parasitic plant seed germination [29].

Upon perception of any 'foreign' organism, different signaling pathways operate within the plant to co-ordinate the appropriate response. These pathways are orchestrated by 'alarm signals' that regulate differential sets of defense-related genes [30•]. Salicylic acid (SA) co-ordinates defense mechanisms that are generally effective against biotrophic pathogens, whereas jasmonates (JA) regulate wounding responses and resistance against necrotrophs [31,32•]. Nevertheless, there is some overlap in their spectrum of efficiency, especially on pathogens with intermediate lifestyles [33,34]. Insect feeding guilds also determine the response they trigger in the plant. Generalist chewing insects, but not phloem-feeding ones, cause wounding and trigger JA-regulated responses [30•,35]. Intensive efforts have been devoted over the past years to determine interactions within the defense regulation network, and trade-offs between SA and JA signaling pathways are well documented [36,37].

As obligate biotrophs, AMF share similarities with biotrophic pathogens [38,39•]. Thus, their sensitivity to SA-regulated defenses is likely. Indeed, exogenous SA application delays mycorrhizal colonization. In mycorrhiza defective *myc*$^-$ mutants, SA levels are enhanced in response to AMF, whereas the accumulation is low and transient in mycotrophic plants [22] (Figure 2). Only local, weak, and transient defense responses are activated during early steps of compatible AM interactions [20], whereas stronger defense responses occur in *myc*$^-$ mutants [40]. These data argue that modulation of plant defenses is required for the establishment of the symbiosis. Accordingly, it is plausible that AMF repress SA-dependent defense responses in the host in order to achieve a compatible interaction. A suppression of SA responses is also necessary for the establishment of the symbiotic *Rhizobium*–legume association [41]. In the case of mycorrhizal

Figure 2

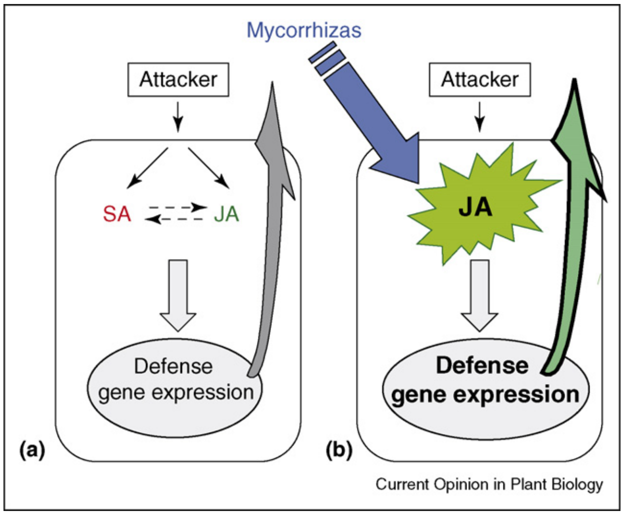


Modulation of plant defense signaling during mycorrhiza establishment. **(i)** Upon germination, AM fungi grow toward the root and form appresoria at the root surface. At this stage, the plant reacts with an increase in SA levels. **(ii)** In a compatible interaction, SA levels decrease as the fungus colonizes the cortex. **(iii)** JA biosynthesis occurs in arbuscule containing cells. Drawing by J. Perez-Tienda.

plants, such attenuation could explain the delay in systemic accumulation of PR proteins upon treatment with SA or analogs [9,21].

Attenuation of plant defenses, however, is not enough for a successful mutualistic interaction with AMF. Upon mutual recognition, a symbiotic program has to be activated [3]. This program should allow a redistribution of nutrients and active physical accommodation of the fungal symbiont inside root cells [42•]. Both aspects may be regulated by jasmonates [43•]. JA-responsive genes and genes involved in JA biosynthesis are expressed in arbuscule-containing cells, and mycorrhizal roots are associated with increased levels of endogenous JA (Figure 2). This increase occurs after the onset of mycorrhization, likely associated with fully established mycorrhizas [44]. Elevated levels of basal JA production could be related to the increased resistance of mycorrhizal plants to pathogens and insects. In line with this hypothesis, experimental evidences linking the JA pathway with primed deposition of callose and enhanced resistance to oomycetes [45] argue for a role of JA signaling in the primed papillae formation observed in mycorrhizal tomatoes upon infection with *Phytophthora* [17]. Recently, a central role for JA in systemic immunity has been proposed in *Arabidopsis* [46••]. It is tempting to speculate that JA also serves as endogenous signal in MIR. Other hormones such as abscisic acid show altered levels in AM [43•] and may also affect plant resistance to challengers [47].

Figure 3



Model illustrating priming of JA-dependent responses in mycorrhizal plants. **(a)** Upon attacker recognition, the plant produces the defense-related signals JA, ET, and SA in different proportions. Cross-talk among the pathways they co-ordinate fine-tunes the appropriate response. **(b)** Mycorrhiza formation primes the tissues for a quicker and more effective activation of JA-dependent defense responses upon attack, resulting in enhanced resistance. Model modified from [33] with kind permission of Springer Science and Business Media.

We propose that a functional mycorrhiza implies partial suppression of SA-dependent responses in the plant, compensated by an enhancement of JA-regulated responses. This would result in priming of JA-dependent defense mechanisms (Figure 3). This model would explain the spectrum of effectiveness described for MIR: increased susceptibility to biotrophs and increased resistance to necrotrophs and generalist chewing insects (Figure 1).

It is noteworthy that parallels exist between rhizobacteria-induced resistance and MIR. Like MIR, rhizobacteria-mediated ISR is mainly effective against necrotrophic pathogens and is based on priming of JA-regulated responses [24••,48]. ISR by other beneficial organisms seems to be also associated with priming for JA-inducible responses [49]. Thus, modulation of plant defense mechanisms may be a common feature of beneficial interactions.

Conclusions

Aboveground and belowground communities can be powerful mutual drivers, with both positive and negative feedbacks affecting biodiversity and functioning of the ecosystem [50,51]. Mycorrhizal symbioses have an important impact on plant interactions with pathogens and insects. The association leads generally to a reduction of damage caused by soil-borne pathogens, but effects on shoot-targeting organisms depend greatly on the attacker lifestyle. MIR in aboveground tissues seems effective against necrotrophic pathogens and generalist chewing insects but not against biotrophs.

Recent advances regarding signaling processes in mutualistic and pathogenic associations are expanding our understanding of plant interactions with their environment. The spectrum of MIR efficiency correlates with a potentiation of JA-dependent plant defenses. Instead of constitutive activation of defenses, MIR is associated with priming for an efficient activation of defense mechanisms upon attack. This low-cost type of induced resistance may be among the reasons to explain why root associations with AMF have been conserved during evolution and are widespread among plant species worldwide.

We are witnessing important advances in AM research. The identification of new *myc*$^-$ mutants in different plant species [52,53] will uncover key steps in symbiosis regulation. Comprehensive analysis of metabolomic changes coupled to transcript profiling in roots and shoots will help to understand plant–AMF–pathogen interactions. Exciting challenges remain ahead, such as the identification of key regulators in defense modulation during mutualistic symbioses. Future advances should allow identification of marker genes or metabolites associated with induced resistance, as well as generation of predictive models concerning the outcome of particular interactions. These tools will provide a basis for the development of new strategies for crop protection.

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