

# Chapter 9

## Impact of Arbuscular Mycorrhizal Symbiosis on Plant Response to Biotic Stress: The Role of Plant Defence Mechanisms

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**Abstract** Arbuscular mycorrhizal associations imply a remarkable reprogramming of functions in both plant and fungal symbionts. The consequent alterations on plant physiology have a clear impact on the plant response to biotic stresses. In this chapter we discuss the effects of the mycorrhizal symbiosis on plant susceptibility/resistance to potential deleterious organisms, including root and shoot pathogens, root parasitic plants and phytophagous insects, highlighting the mechanisms that may be operating in each particular case. Special attention is given to the modulation of plant defence responses in mycorrhizal systems, as it may affect all interactions. Finally we focus on the priming of jasmonate regulated plant defence mechanisms that seem to mediate the induction of resistance by arbuscular mycorrhizas.

**Keywords** Biotic stress • Bioprotection • Induced resistance • Priming • Plant defence • Biocontrol • Defence signalling • Jasmonates • Pathogens • Insects

### Abbreviations

AM	Arbuscular mycorrhiza
AMF	Arbuscular mycorrhizal fungi
MIR	mycorrhiza-induced resistance
JA	jasmonate
SA	Salicylic acid
Nm	Non-mycorrhizal plants
Gm	<i>Glomus mosseae</i> colonized plants
Hpi	hours post inoculation

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## 1 Introduction

The establishment of the arbuscular mycorrhizal (AM) symbiosis implies remarkable changes in the physiology of the host plant. The changes span from alterations in the hormonal balance and transcriptional profile to altered primary and secondary metabolism (Hause et al. 2007; Liu et al. 2007; Schliemann et al. 2008; López-Ráez et al. 2010). This global reprogramming of plant functions has an impact on the plant interaction with the environment, modifying its responses to biotic and abiotic stresses. As a result, mycorrhizal plants are generally more tolerant to environmental stresses. The consequences go beyond the individual level as they may influence plant diversity and productivity in terrestrial ecosystems (van der Heijden et al. 2008).

It should be noted that the impact of the symbiosis in terms of resistance/tolerance to biotic stresses differs among AM fungal isolates for a given plant-pathogen interaction. Moreover, such impact can be modulated by environmental conditions. Despite of this variability, general trends emerge from the multiple studies dealing with mycorrhiza in diverse pathosystems. Generally, enhanced resistance to soil-borne pathogens has been reported in AM plants. Furthermore, the symbiosis can also impact plant interactions with above-ground attackers. In this case, the outcome ranges from enhanced resistance to increased susceptibility, largely depending on the attacker life-style (Pozo and Azcón-Aguilar 2007).

Early works on mycorrhizas and biotic stresses were mostly descriptive (for reviews see Schonbeck and Dehne 1989; Sharma et al. 1992; Linderman 2000). Generally, reports have focussed on beneficial effects of the symbiosis, aiming at using AM as potential biocontrol agents in integrated management programmes for disease control (Sharma and Adholeya 2000; Harrier and Watson 2004; Whipps 2004; Mukerji and Ciancio 2007).

A key factor determining the effect of the symbiosis on interactions with other organisms seems to be the extension of root colonization by the AM fungi (AMF). With some exceptions (Caron et al. 1986; García-Garrido and Ocampo 1988; St-Arnaud et al. 1997; Kapoor 2008), reports on mycorrhizal protection against pathogens show the requirement of a well established symbiosis prior to the challenge with the attacker (Rosendahl 1985; Cordier et al. 1998; Slezacek et al. 2000; Khaosaad et al. 2007). The first mechanism proposed to be involved in mycorrhiza-induced protection was the improvement of plant nutrition and the consequent compensation of the damages caused by the pathogen. However, studies including nutrient supplemented controls showed that AM effects cannot be regarded as a mere consequence of improved phosphorus nutrition (Trotta et al. 1996; Fritz 2006; Liu et al. 2007). As we advance in our knowledge on the physiology and regulation of the AM symbiosis, we start to understand the diversity of mechanisms underlying the impact of the symbiosis on plant interactions with other organisms. In addition to the nutritional aspects, changes in the plant architecture, root exudation and in the microbial populations in the rhizosphere, and the activation of plant defence mechanisms may all be relevant. Their individual contribution to the final outcome will depend on the organisms involved and the timing of the interactions

(Azcón-Aguilar and Barea 1996; Whipps 2004). In this chapter we will discuss the possible mechanisms affecting the different types of plant-attacker interactions, with special emphasis in those involving plant defence responses.

## 2 Impact of the AM Symbioses on Soil-Borne Pathogens

It is widely accepted that AM symbioses reduce the damage caused by soil-borne pathogens. Many studies revealed a reduction of the incidence and/or severity of diseases as root rot or wilting caused by diverse fungi such as *Fusarium*, *Rhizoctonia*, *Macrophomina* or *Verticillium*, bacteria as *Erwinia carotovora*, and oomycetes as *Phytophthora*, *Pythium* and *Aphanomyces*. A comprehensive review of those studies was compiled by Whipps (2004). Similarly, a reduction of the deleterious effects by parasitic nematodes such as *Pratylenchus* and *Meloidogyne* has been reported in mycorrhizal plants (Pinochet et al. 1996; de la Peña et al. 2006; Li et al. 2006). Additional reports showed protection to other soil pathogens as *Armillaria melea* in grapevine (Nogales et al. 2009), broadening the range of pathosystems in which AM symbioses may have a protective effect. The effectiveness against such diverse range of attackers confirms the broad spectrum character of the induced resistance associated to the AM symbiosis.

Studies comparing different fungal species or isolates highlighted that the degree of protection is highly dependent on the AMF involved (Kobra et al. 2009). Interestingly, many studies point to a higher protector effect of *Glomus mosseae* in comparison to other AMF (Pozo et al. 2002; Utkhede 2006; Ozgonen and Erkilic 2007).

Several mechanisms may operate simultaneously in the enhanced resistance of mycorrhizal plants to soil pathogens. In addition to a possible competition for photosynthates between the AMF and the pathogen, competition for colonization sites has been demonstrated. For example, in tomato roots, full exclusion of *Phytophthora* from arbusculated cells was evidenced (Cordier et al. 1998). Mycorrhizal colonization is also known to induce changes in the root system architecture and morphology (Schellenbaum et al. 1991; Norman et al. 1996). These changes may alter the dynamics of infection by the pathogen, although direct evidences of such correlation are lacking. An altered pattern of root exudation may also impact the development of the pathogen. Mycorrhizal colonization led to modifications in root exudates composition that significantly reduced the sporulation of *Phytophthora fragariae* (Norman and Hooker 2000) and altered the chemotactic response of the zoospores of *Phytophthora nicotianae* (Lioussanne et al. 2008). Since root exudates are key factors in shaping soil microbial communities (Badri and Vivanco 2009), the changes in exudation into the mycorrhizosphere may result in alteration of the microbial communities including possible antagonistic organisms. This may be the reason underlying the biocontrol of pathogens in non-AM species by co-culture with mycorrhizal plants (St-Arnaud et al. 1997).

Because of the root localization of both attacker and AMF, it is difficult to discern the local or systemic character of the protection observed. However, the use

of split-root experimental systems allowing physical separation between AMF and pathogens has confirmed a reduction of disease symptoms in the non-mycorrhizal parts of the mycorrhizal root systems. Systemic protection at the root level has been demonstrated against *Phytophthora* and *Ralstonia* in tomato (Cordier et al. 1998; Pozo et al. 2002; Zhu and Yao 2004), against *Gaeumannomyces* in wheat (Khaosaad et al. 2007), and against parasitic nematodes in banana plants (Elsen et al. 2008). The systemic character of the induced resistance pointed to the involvement of plant defences. Because of its relevance in all kinds of interactions, the implication of plant defence mechanisms will be discussed in Section 7.

### 3 Effects of AM Symbioses on Root Parasitic Plants

Plants of the genera *Striga* and *Orobanche* parasitize different hosts around the world, constituting one of the most damaging agricultural pests. These obligate parasites attach to the roots of many plant species and acquire nutrients and water from their host (Bouwmeester et al. 2003). Studies in African fields infested with the hemiparasite *Striga hermonthica* evidenced that inoculation with AMF significantly reduced the amount of parasitic plants in maize and sorghum cultures. Accordingly, the use of mycorrhizas for integrated management of parasitic weeds was proposed (Lendzemo et al. 2005; López-Ráez et al. 2009a).

Strigolactones are germinating stimulants for the seeds of root parasitic plants (Bouwmeester et al. 2007). With the discovery of strigolactones as host detection signals for AMF in the rhizosphere (Akiyama et al. 2005; see chapter by Bécard et al.) a causal connection between AM and its impact on parasitic plants could be established. Indeed, follow up experiments under controlled conditions confirmed that AMF inoculation leads to a reduction of the impact of *Striga*, apparently related to a reduction in strigolactones production (Lendzemo et al. 2007). Similarly, we have observed that extracts from tomatoes colonized by *G. mosseae* induce less germination of *Orobanche ramosa* seeds than those from non-mycorrhizal plants (López-Ráez et al. 2009b). Moreover, a reduced production of strigolactones in a tomato mutant correlated with less susceptibility to *Orobanche* (López-Ráez et al. 2008). All in all, it seems likely that a reduction in strigolactone production underlies the decrease in the incidence of root parasitic plants on mycorrhizal plants.

### 4 Impact of AM Symbioses on Above-Ground Interactions

Studies dealing with AM effects on above-ground diseases are less abundant, and apparently less conclusive. Early reports associated AM symbioses with enhanced susceptibility to viruses (Whipps 2004), and it was generally accepted that AM plants are more susceptible to shoot pathogens. However, recent studies dealing with pathogens of different life styles have evidenced a more complex reality.

Biotrophic pathogens, such as powdery mildew and rust fungi (*Blumeria*, *Oidium*, *Uromyces*) seem to perform better in mycorrhizal plants, although increased tolerance was often observed in terms of plant mass and yield (Gernns et al. 2001; Whipps 2004). Concerning hemibiotrophs, the impact of the symbiosis varies from no effect to reduction of the disease, for example, against *Colletotrichum orbiculare* in cucumber (Lee et al. 2005; Chandanie et al. 2006). Finally, several studies evidenced a positive effect on plant resistance to other shoot pathogens, including the bacteria *Xanthomonas campestris* in *Medicago* (Liu et al. 2007), and the necrotrophic fungus *Alternaria solani* in tomato (Fritz et al. 2006; De La Noval et al. 2007). We have also confirmed that symbiosis with *G. mosseae* in tomato induces systemic resistance to the necrotrophic fungus *Botrytis cinerea* (Jung et al., 2009) (see Section 7). Recently, a positive effect of *G. mosseae* against *Botrytis cinerea* has also been shown in roses, although dependent on environmental factors (Moller et al. 2009).

Phytoplasma are specialized obligate parasites of phloem tissue transmitted by insect vectors. AM establishment in tomato lead to a reduction of the disease symptoms caused by a phytoplasma of the Stolbur group (Lingua et al. 2002). Because they inoculated through grafting with infected scions, potential effects on the insect vector were ruled out. Thus, the protection is related to physiological changes in the mycorrhizal plant. Tolerance to phytoplasma disease was also reported in pear (García-Chapa et al. 2004). Recently, a reduction in the titre of the Chrysanthemum yellows phytoplasma has been shown in mycorrhizal chrysanthemum (D'Amelio et al. 2007), confirming that mycorrhization can confer resistance to this type of pathogens.

In above-ground interactions of mycorrhizal plants, two main mechanisms may be operative. One would be the potential changes in nutrient levels of the host plant and alterations of the source-sink relation within it, that may affect the suitability of the plant for shoot attackers. The other would be the modulation of plant defence mechanisms, as discussed in Section 7.

## 5 Effects of AM Symbioses on Phytophagous Insects

The mycorrhizal status of the host plant can also influence insect herbivore performance, but the magnitude and direction of the effect depend upon the feeding mode and life style of the insect (Hartley and Gange 2009; Koricheva et al. 2009).

Many different studies cover an ample range of mycorrhizal plant-insect interactions under controlled or field conditions. Upon a comprehensive review of the published data, Hartley and Gange (2009) concluded that, generally, mycorrhizas have strong negative effects on rhizophagous insects, but effects on shoot-feeding insects are weaker and more variable. Despite of this variability, some general patterns emerge: generalist insects are usually adversely affected by mycorrhizas, whereas specialist insects may often benefit. Furthermore, aphids usually perform better on AM plants while leaf-chewing insects are usually negatively affected by the symbiosis.

Such patterns may arise from the differential impact of nutritional and defence aspects in the insect. While generalist insects are sensitive to plant defence mechanisms, specialist herbivores are likely to be able to circumvent the defences of their host and remain undetected. As a result, generalists may be affected by the enhanced defence capacity of AM plants, while specialists will circumvent the defences and may benefit from the improved nutritional status of the plant. The negative effect on leaf-chewers is likely related to their susceptibility to jasmonate-dependent defences (Peña-Cortés et al. 2004) potentiated in mycorrhizal plants (see Section 8). In addition, AM can also have an impact on herbivores by affecting the performance of their predators and parasitoids: in tomato, the volatile blends released by AM plants can be more attractive to aphid parasitoids than those from non-mycorrhizal ones (Guerrieri et al. 2004).

## 6 AM Symbiosis Modulate Host Defence Responses

As discussed earlier in this book and reviewed elsewhere (Gianinazzi-Pearson 1996; Harrison 2005; Parniske 2008) the establishment of a successful mutualistic interaction requires a high degree of coordination between both partners. Plant and fungus actively engage in the process of colonization, and a tight control of plant defence mechanisms is necessary. Interestingly, the plant is able to restrict AMF colonization once plants are already mycorrhizal, a phenomenon known as *autoregulation* (Vierheilig et al. 2008). The mechanisms operating in such autoregulation may also impact plant interactions with pathogens.

The levels of several phytohormones (mainly salicylic acid (SA), jasmonates (JAs), ethylene (ET) and abscisic acid (ABA)) fine-tune the defence responses in plants through an intricate regulatory network (Pieterse et al. 2009). Remarkably, the levels of these hormones seem to be altered in mycorrhizal plants (Hause et al. 2007; López-Ráez et al. 2010), probably affecting plant defence mechanisms. There is evidence for the accumulation of defensive plant compounds in mycorrhizal roots, although to a much lower extent than in plant-pathogen interactions. Activation of phenylpropanoid and oxylipin metabolism, accumulation of reactive oxygen species and of specific isoforms of defence-related enzymes has been reported in mycorrhizal roots (García-Garrido and Ocampo 2002; De Deyn et al. 2009; López-Ráez et al. 2010). These reactions, generally localized, may control the development of the fungus inside the roots (Pozo et al. 2002; Dumas-Gaudot et al. 2000; García-Garrido and Ocampo 2002). Indeed, as obligate biotrophs, AMF share similarities with biotrophic pathogens (Paszowski 2006) and transcriptional profiling of plant responses to AMF revealed some overlap with responses to biotrophic pathogens (Güimil et al. 2005). Coherently, SA, a key regulator of plant defences against biotrophs (Glazebrook 2005), seems to have a negative effect on AM colonization (García-Garrido and Ocampo 2002; López-Ráez et al. 2010). Thus, it is plausible that AMF repress SA-dependent responses in the host in order to achieve a compatible interaction. Indeed, a delay in the accumulation of PR-1 proteins, common markers of SA-dependent responses, has been observed in mycorrhizal

roots (Dumas-Gaudot et al. 2000). Even repression of defence responses triggered upon pathogen attack has been reported when *G. intraradices* was co-inoculated with *Rhizoctonia solani* (Guenoune et al. 2001). Although AMF are able to trigger plant defence responses as evidenced in *myc* mutants, only weak and transient defence responses are activated during compatible AM interactions (Liu et al. 2003). Thus, AM establishment seems to require inhibition of certain SA-regulated defence responses. Remarkably, inhibition of SA responses is also necessary for the *Rhizobium*–legume symbiosis (Stacey et al. 2006).

Modulation of plant defences during AM formation does not only occur in the roots, but also in the shoots. Accumulation of insect anti-feedant compounds (Gange 2006; Pozo et al. 2009) and transcriptional up-regulation of defence-related genes (Liu et al. 2007; Pozo et al. 2009) have been described in leaves of mycorrhizal plants. Also a repression of certain defences may take place: a delay in the systemic accumulation of PR1 upon treatment with SA or analogs has been reported in mycorrhizal tobacco shoots (Shaul et al. 1999) and suppression of certain chemical defences has also been reported (Bennett et al. 2009). This modulation may affect the interaction with shoot attackers. To this regard, the reciprocal influence of below-ground and above-ground interactions through their impact on plant defences is receiving increasing interest (Bezemer and van Dam 2005; Erb et al. 2009). An additional level of complexity is related to the altered volatile profile released by AM plants (Guerrieri et al. 2004; Rapparini et al. 2008). Volatiles may play key roles in defence, for example, by attracting natural enemies of potentially harmful insects, or by priming distal parts of the plant for a more efficient activation of defences (Heil and Ton 2008).

We have recently shown that mycorrhizal colonization in tomato leads to increases in the expression of defence related genes known to be regulated by JA (Pozo et al. 2009). JA is a key regulator of plant defences against insects and necrotrophic pathogens (Peña-Cortés et al. 2004; Pozo et al. 2005). Because of SA and JA signalling pathways are interconnected, mostly in an antagonistic way (Pieterse et al. 2009) their interplay may explain the pattern of enhanced resistance/susceptibility of AM plants. If AM inhibits SA-regulated responses, the plant would be more susceptible to pathogens resisted through these responses, i.e. biotrophic pathogens. On the contrary, an induction of the JA signalling pathway would make mycorrhizal plants more resistant to necrotrophic pathogens and JA-sensitive insects (Pozo and Azcón-Aguilar 2007). Such pattern is more obvious in shoot interactions, where modulation of plant defences seems to be the main mechanism. In roots, the relevance of this altered balance will be lower since other mechanisms are operating simultaneously (see Section 3), and a reduction of the disease is the most general outcome.

## 7 AM Symbiosis Primes JA-Dependent Responses

Upon detection of a potential attacker, a rapid and strong activation of the defence mechanisms is crucial for resistance. Accordingly, pre-conditioning of plant tissues for a quick and more effective activation of defences upon attack has important



ecological fitness benefits, and seems to be a common feature of the plant's immune system. This boost of basal defences is known as *priming* (Conrath et al. 2006; Goellner and Conrath 2008). Priming seems to be the strategy followed by several beneficial micro-organisms to enhance resistance in plants, avoiding a direct activation of defences which would be too expensive for the host in the absence of challenging attackers (Pozo et al. 2005; Van Wees et al. 2008).

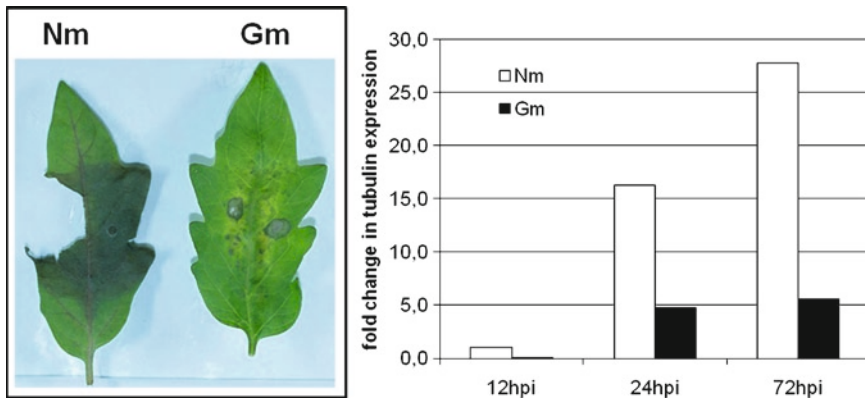
Evidences for primed defence responses in mycorrhizas were first reported in root tissues. Mycorrhizal transformed carrot roots displayed stronger defence reactions at challenge sites by *Fusarium* (Benhamou et al. 1994). Similarly, mycorrhizal potatoes showed amplified accumulation of phytoalexins upon *Rhizoctonia* infection (Yao et al. 2003). Priming for callose deposition seems to be responsible for the protection achieved by *G. intraradices* against *Colletotrichum* in cucumber (Lee et al. 2005). Recently, primed accumulation of phenolic compounds in AM date palm trees has also been related to protection against *F. oxysporum* (Jaiti et al. 2008). Remarkably, priming is not restricted to AMF colonized areas of the roots, but to the whole root system. This was first illustrated in tomato plants during *P. parasitica* infection (Cordier et al. 1998; Pozo et al. 2002). Only AM plants, even in non-mycorrhizal parts of the root system, formed papilla-like structures around the sites of pathogen infection, preventing further spreading of the pathogen. They also accumulated more PR-proteins than non-mycorrhizal plants upon challenge (Cordier et al. 1998; Pozo et al. 1999). Mycorrhizal protection of grapevine against *Meloidogyne incognita* has also been associated with primed systemic expression of a chitinase gene in response to the nematode (Li et al. 2006). But the primed response is not restricted to the root system. Recently, we have shown priming of defences also in shoots of mycorrhizal plants (Pozo et al. 2009).

Evidence is accumulating that priming associated to systemic resistance induced by beneficial organisms is regulated by similar jasmonate signalling pathways (Van Wees et al. 2008). Indeed, studies on rhizobacteria induced systemic resistance (ISR) in *Arabidopsis* revealed the requirement of a functional JA signalling pathway for the efficient induction of resistance (Pieterse et al. 1998; Pozo et al. 2008). The JA signalling pathway is also required for rhizobacteria ISR in tomato (Yan et al. 2002) and for the induction of resistance by the beneficial fungi *Trichoderma* and *Piriformospora* (Shoresh et al. 2005; Stein et al. 2008). Interestingly, JA accumulation have been proposed to mediate plant "memory" of previous challenges (Galis et al. 2009), a possible basis for the primed state.

Jasmonates are key regulators in the AM symbiosis, and elevated endogenous levels of JA have been confirmed in mycorrhizal roots (reviewed in Hause et al. 2007 and Hause and Schaarschmidt, 2009). We have found a significant increase in JAs in mycorrhizal tomato roots (López-Ráez et al. 2010), but the levels were not altered in the shoots (López-Ráez and Pozo, unpublished). However, we found small, yet significant, increases in the expression of marker genes for JA responses, a result that may indicate an enhanced sensitivity to the hormone.

To confirm whether AM leads to priming of JA-dependent responses in the shoots, we compared the response of non-mycorrhizal and AM plants to foliar application of different defence-related stimuli. Transcript profiling of leaves 24 h





**Fig. 1** Mycorrhizal tomato plants are more resistant to the necrotrophic foliar pathogen *Botrytis cinerea*. *Left* – Photograph of necrotic lesions developed 6 days after drop inoculation of tomato leaves with *Botrytis cinerea*. *Right* – Quantification of *Botrytis cinerea* in infected leaves by real time PCR analysis of expression of its tubuline gene. Nm: Non mycorrhizal plants, Gm: *Glomus mosseae*-colonized plants

after treatment with JA revealed a stronger induction of JA-regulated genes in mycorrhizal plants, particularly in *G. mosseae*-colonized plants, confirming a primed response in those plants (Pozo et al. 2009). To address the biological relevance of such primed response, we tested whether priming occurs during interactions with pathogens. AM and non-mycorrhizal plants were challenged with *B. cinerea*, and the expansion of necrotic lesions was markedly lower in the leaves of AM plants (Fig. 1a). The levels of pathogen in the tissues were also lower in mycorrhizal plants at all time points tested (Fig. 1b), confirming induced systemic resistance. Remarkably, this pattern inversely correlated with the expression of the defence-related, JA-marker gene *Pin II*. *Pin II* expression was induced in response to *B. cinerea* in all plants, but this induction was markedly higher in AM plants (Jung et al. 2009). The results support that Mycorrhiza Induced Resistance (MIR) to *Botrytis* is associated to priming of JA-dependent defences.

## 8 Conclusions and Outlook

AM symbiosis affect the outcome of the host plant interaction with other organisms. Although the effect is influenced by plant, AMF and environmental factors, generally there is a clear protector effect of the symbiosis over soil-borne deleterious organisms. However, the impact on shoot interactions is more variable and relies largely on the attacker lifestyle. Besides nutritional effects and local changes in the plant (affecting mainly soil-borne pathogens), modulation of plant defences associated to AM seems to play a crucial role. Instead of constitutive activation of defences, MIR is mediated by priming for an efficient activation of defences.

Experimental evidences and the general spectrum of protection by mycorrhiza point to a central role of jasmonates in MIR. Despite of the relevance of this process, its precise regulation awaits elucidation. Increasing our knowledge on the modifications of plant physiology in AM, as well as in the biology of the potential attackers is essential in order to define markers of induced resistance and to generate predictive models for the outcome of particular mycorrhiza-pathogen interactions. Another challenge ahead is to decipher the connections in plant responses to biotic and abiotic stresses. Experimental evidences point to common regulatory nodes in the signalling pathways governing responses to both types of stresses, and those nodes may be the target of biotechnological strategies for optimization of plant protection by arbuscular mycorrhizas. Finally, it is important to consider mycorrhiza in a multitrophic context, as the impact of the symbiosis on plant interactions can be modified by other organisms in the system.

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