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# Mycorrhiza-Induced Resistance and Priming of Plant Defenses

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## ABSTRACT

Symbioses between plants and beneficial soil microorganisms like arbuscular-mycorrhizal fungi (AMF) are known to promote plant growth and help plants to cope with biotic and abiotic stresses. Profound physiological changes take place in the host plant upon root colonization by AMF affecting the interactions with a wide range of organisms below- and above-ground. Protective effects of the symbiosis against pathogens, pests, and parasitic plants have been described for many plant species, including agriculturally important crop varieties. Besides mechanisms such as improved plant nutrition and competition, experimental evidence supports a major role of plant defenses in the observed protection. During mycorrhiza establishment, modulation of plant defense responses occurs thus achieving a functional symbiosis. As a consequence of this modulation, a mild, but effective activation of the plant immune responses seems to occur, not only locally but also systemically. This activation leads to a primed state of the plant that allows a more efficient activation of defense mechanisms in response to attack by potential enemies. Here, we give an overview of the impact on interactions between mycorrhizal plants and pathogens, herbivores, and parasitic plants, and we summarize the current knowledge of the underlying mechanisms. We focus on the priming of jasmonate-regulated plant defense mechanisms that play a central role in the induction of resistance by arbuscular mycorrhizas.

## INTRODUCTION

Arbuscular mycorrhizas are mutualistic associations formed between the roots of 80 % of terrestrial plant species and fungi from the small phylum *Glomeromycota* (reviewed by Schüßler et al., 2001). The symbiosis is named after the Greek “*mycos*” and “*rhiza*” meaning “fungus-root,” and it is probably the oldest and most widespread plant symbiosis on Earth. Indeed, fossil records and phylogenetic evidence date their existence back more than 450 million years (Smith and Read 2008), which indicates a considerable selective advantage for both partners. Arbuscular mycorrhiza-forming fungi (AMF) are obligate biotrophs that require the host plant to complete their life cycle. The fungus colonizes the root cortex and forms intracellular structures called arbuscules (from the Latin “*arbusculum*”, meaning bush or little tree) where the exchange of nutrients between the partners takes place. The extracellular hyphal network spreads widely into the surrounding soil, thereby reaching out of the nutrient depletion zone and improving the supply of inorganic nutrients, especially phosphate and nitrate (Smith et al., 2011). In return, the heterotrophic fungal partner receives photosynthates from the host plant (Smith and Smith, 2011). Mutual benefits are the basis of the evolutionary success of the interaction, ensured through a tight bidirectional control of the mutualism (Kiers et al., 2011). From the plant side, this regulation implies important changes in the plant primary and secondary metabolism and regulation of the plant defense mechanisms (Harrison, 1999; Hause and Fester, 2005). These changes usually have a deep impact on plant physiology, altering the plant’s ability to cope with stresses.

Early studies on mycorrhizas showed an improved growth and/or yield of mycorrhizal plants, first attributed exclusively to the improved nutritional status of the plant (reviewed in Linderman, 1994). Later, several authors reported a higher tolerance of mycorrhizal plants to abiotic stresses, such as drought, salinity, or presence of heavy metals (Miransari, 2010; Smith et al., 2010). Evidence also has accumulated on the higher resistance of mycorrhizal plants to a wide range of below-ground attackers such as soil-borne fungal and bacterial pathogens, nematodes, or root-chewing insects (Azcón-Aguilar and Barea, 1997; Whipps, 2004). Only in the last decade, has induced resistance against shoot pathogens also been reported (Pozo and Azcón-Aguilar, 2007; Koricheva et al., 2009; Campos-Soriano et al., 2012, Jung et al. unpublished). The need for assistance in overcoming stressful conditions has been considered one of the explanations for mycorrhizas' persistence during evolution, even in systems where the symbiosis does not confer growth benefits (Newsham et al., 1995). With regard to its biofertilizer and bioprotective properties, the mycorrhizal symbiosis has become a focal point of research as an alternative to chemical fertilizers and pesticides in sustainable agriculture (Harrier and Watson, 2004; Mukerji and Ciancio, 2007; Fester and Sawers, 2011).

Despite the obvious benefits of an improved nutritional status for stress tolerance/resistance, mineral supply experiments have shown that the protective effect observed in mycorrhizal plants cannot be attributed to improved nutritional status alone (Fritz et al., 2006; Liu et al., 2007). AM associations bring about significant changes in the host plant and its environment: at the rhizosphere level, they influence soil structure, carbon deposition in soil, and microbial diversity, in part through changes in root exudation. These shifts in the microbial communities of the rhizosphere may indirectly influence the outcome of plant interactions with other organisms, including pathogens and beneficial microbes (Berta et al., 2002; Barea et al., 2005; Artursson et al., 2006; Lendzemo et al., 2007; see also Cipollini et al., 2012, this issue; Effmert et al., 2012, this issue). Apart from the changes in the rhizosphere, multiple modifications also occur within the host plant. In the roots, changes in architecture, alterations of the metabolic profile, and accumulation of certain defense compounds may occur (García-Garrido and Ocampo, 2002; Strack et al., 2003; Hause et al., 2007; Schliemann et al., 2008; Péret et al., 2009; López-Ráez et al., 2010a, b). For example, the accumulation of apocarotenoids (cyclohexenone and mycorradicin derivatives) can be observed in mycorrhizal roots, which are the main component of the yellow pigment found in many plant species upon colonization by AMF and have been proposed to play a role in control of the degree of colonization and mycorrhizal functionality (Strack et al., 2003; Strack and Fester, 2006; Floß et al., 2008; Schliemann et al., 2008).

Qualitative and quantitative changes in flavonoid contents have been observed, the changes depending on the host plant, AMF, and developmental stage of the symbiosis (Vierheilig and Piché, 2002; Akiyama et al., 2002). Changes in phenolic compounds, defense-related phytohormones, and reactive oxygen species also have been reported (Fester and Hause, 2005; López-Ráez et al., 2010a, b). Noteworthy, the symbiosis also has a considerable impact on the aerial parts of mycorrhizal plants, some of the reported changes being related to defense or stress tolerance (Liu et al., 2007; Kaschuk et al., 2009; Fiorilli et al., 2009; Pozo et al., 2009; Fester et al., 2011; Aloui et al., 2011).

As for the higher resistance to pests and pathogens of AMF-colonized plants, observations of systemic protection against pathogens in non-colonized root fragments from mycorrhizal plants and enhanced resistance of the aerial parts to certain attackers have pointed out the involvement of plant defense mechanisms (Cordier et al., 1998; Pozo et al., 2002; Pozo and Azcón-Aguilar, 2007). Defense mechanisms are coordinated by the plant immune system, strikingly similar in some aspects to the innate immune system in animals (Ausubel, 2005). This system allows the plant to distinguish non-self alien organisms by recognizing structurally conserved microbe-associated molecules, such as flagellin, lipopolysaccharides, or peptidoglycans, which are collectively termed microbe-associated molecular patterns (MAMPs, or PAMPs in the case of pathogens). PAMPs are recognized by transmembrane pattern recognition receptors (PRRs), which leads to the induction of the appropriate responses in the host and to PAMP-triggered immunity (PTI) (Ausubel, 2005; Jones and Dangl, 2006; Boller and He, 2009; Thomma et al., 2011). In an evolutionary "arms race," microbes have evolved effector proteins that are secreted into the host and suppress PTI, thus allowing successful host colonization by the pathogen, thus causing effector-triggered susceptibility of the plant to the disease. In some cases, intracellular proteins of the plant recognize pathogen effectors or their

modified target proteins and activate immune responses that are quicker, more pro- longed, and more robust than those in PTI, resulting in effector-triggered immunity (ETI) (Jones and Dangl, 2006; Boller and He, 2009; Thomma et al., 2011).

Plant defense responses are coordinated by small molecules that act as signal transducers and tailor the coordinated expression of genes that code for defense-related proteins and compounds (Ausubel, 2005; Jones and Dangl, 2006). Among these molecules, the phytohormones jasmonic acid (JA), salicylic acid (SA), abscisic acid (ABA), and ethylene (ET) play key roles (Pieterse et al., 2009). According to the challenger life-style, one signaling pathway will prevail over the others. It is generally assumed that the SA-dependent pathway regulates responses such as programmed cell death, effective against biotrophic organisms, and the JA-dependent pathway regulates responses to necrotrophs and chewing insects (Glazebrook 2005). However, these hormone signaling pathways do not act independently, but influence each other through a complex network of regulatory interactions, JA and SA pathways in general being mutually antagonistic (Pieterse et al., 2008). As biotrophs, mycorrhizal fungi share some similarities with biotrophic pathogens, and are able to trigger plant defense responses at initial stages (Paszkowski, 2006). Thus, for a successful colonization, the fungus has to cope with these reactions and actively modulate plant responses. We have proposed that this modulation may result in pre-conditioning of the tissues for efficient activation of plant defenses upon a challenger attack, a phenomenon that is called *priming* (Pozo and Azcón-Aguilar, 2007).

Priming sets the plant in an “alert” state in which defenses are not actively expressed but in which the response to an attack occurs faster and/ or stronger compared to plants not previously exposed to the priming stimulus, efficiently increasing plant resistance. Thus, priming confers important fitness benefits (Conrath et al., 2006; Van Hulst et al., 2006; Walters and Heil, 2007). In the past decade, many priming-causing agents have been identified. It has been observed that some chemicals that induce stress responses in plants also induce priming when applied at lower doses, and several fungicides have been shown to prime defenses in treated plants in addition to their primary antifungal activity (reviewed in Conrath et al., 2006; Beckers and Conrath, 2007). Other well-studied examples of priming by chemicals include increased resistance to downy mildew in *Arabidopsis thaliana* after treatment with the non-protein amino acid  $\beta$ -aminobutyric acid (BABA), as well as primed defense responses in tomato and *Arabidopsis* pre-treated with hexanoic acid and subsequently infected with grey mold (Ton et al., 2005; Vicedo et al., 2009; Kravchuk et al., 2011). Remarkably, priming events occur as a result of inter- individual or even inter-species communication. For example, green leaf volatiles released by wounded or infested plants are also able to induce a more efficient activation of defenses in neighboring plants upon subsequent attacks (Kessler et al., 2006; Ton et al., 2007; Yi et al., 2009). In *Arabidopsis* seedlings exposed to volatile blends from two *Bacillus* species, the disease severity caused by a bacterial pathogen was significantly reduced (Ryu et al., 2004). Moreover, priming seems to be the mechanism underlying the Induced Systemic Resistance (ISR) observed in plants interacting with beneficial microorganisms (Conrath et al., 2006; Goellner and Conrath, 2008; Van Wees et al., 2008). Interestingly, priming of the plant immune responses by beneficial microbes is often dependent on a functional JA signaling pathway, as has been described for rhizobacteria and AMF (Verhagen et al., 2004; Pozo et al. 2004, 2010; van der Ent et al., 2009a). The molecular mechanisms behind priming of plant defenses and its biological relevance in plant resistance are now being uncovered (reviewed in Pastor et al., 2012), and evidence for trans-generational effects of priming have been a major advance in plant research (Luna et al., 2012; Rasmann et al., 2012; Slaughter et al., 2012). Here, we give a summary of the impact of the arbuscular mycorrhizal symbiosis on plant interactions with other organisms. We give special emphasis to the spectrum of protection against deleterious organisms (Mycorrhiza-Induced Resistance, MIR) and provide an overview of the underlying mechanisms, focusing on the priming of plant defenses associated with mycorrhization.

## MYCORRHIZAL ASSOCIATIONS ALTERS THE HOST PLANT'S INTERACTIONS WITH OTHER ORGANISMS

As stated above, mycorrhization impacts plant interactions with other organisms. Due to potential practical applications, special attention has been devoted to the interaction with microbial pathogens or other deleterious organisms. In this section, we summarize the main effects of mycorrhization on biotic stress

resistance (summarized in Fig. 1).

### **Mycorrhiza Effects on Below-Ground Interactions**

Many studies show the protective effect of colonization by mycorrhizal fungi against infections by microbial pathogens in different plant systems. The majority of these reports focus on soil-borne pathogens such as fungi from the genera *Fusarium*, *Rhizoctonia*, *Macrophomina*, or *Verticillium*; bacteria such as *Erwinia carotovora*; or oomycetes like *Phytophthora*, *Pythium*, and *Aphanomyces*. In most cases, the protective effect is not only related to damage compensation or tolerance, but frequently the reduced damage also correlates with a decrease of the pathogen content within plant tissues (reviewed by Whipps, 2004). Similarly, there are many studies that show a clear reduction of the detrimental effects by endoparasitic nematodes such as *Pratylenchus* and *Meloidogyne* in mycorrhizal plants (Pinochet et al., 1996; DeLa Peña et al., 2006; Li et al., 2006; Elsen et al., 2008; Vos et al., 2011). Recently, a decrease on the development of ectoparasitic nematodes also has been described (Hao et al., 2012).

In contrast to the well-known effect on nematodes, there are relatively few studies on the impact of AMF on root-feeding insects, and they mostly focus on members of the genus *Otiiorhynchus*, or weevils (Koricheva et al., 2009). The larvae of these insects are rhizophagous, whereas the adults feed on the foliage of the same plant. A clear protective effect of AMF is reported on the black vine weevil (*Otiiorhynchus sulcatus*) that has a wide range of possible hosts (generalist). Experiments with strawberry showed that larval growth and survival was halved when the roots were colonized by several *Glomus* species (Gange, 1996, 2001). In contrast, AMF colonization had no adverse effects on the growth of the specialist clover root weevil larvae (*Sitona lepidus*) that reached similar sizes independently of the mycorrhizal state of the host plant (Currie et al., 2011). Beneficial organisms also are influenced by the presence of mycorrhiza. A positive effect of mycorrhization on beneficial plant-microbe interactions has been noted. For example, promotion of the interaction or synergistic effects have been described with regard to plant associations with nitrogen-fixing bacteria (Jia et al., 2004; Niranjana et al., 2007; Ferrari and Wall, 2008; Larimer et al., 2010); phosphate-solubilizing bacteria (Toro et al., 1996; Belimov et al., 1999; Kohler et al., 2007); biocontrol agents (Haggag and Abd-ElLatif, 2001; Martínez-Medina et al., 2009; Martínez-Medina et al., 2010; Saldajeno and Hyakumachi, 2011); and plant growth-promoting microorganisms (Meyer and Linderman, 1986; Chandanie et al., 2005, 2006, 2009).

These effects on below-ground interactions may result from a combination of diverse mechanisms. Mycorrhizas compete for colonization sites with other microbes, and for example, full exclusion of the pathogenic oomycete *Phytophthora* from arbusculated cells has been described for tomato roots (Cordier et al., 1998). A competition for photosynthates also is possible between AMF and other microbes, especially with microbial symbionts, which require plant resources such as photosynthetically assimilated carbon. Colonization by AMF can lead to alterations in the quality and quantity of root exudates (Bansal and Mukerji, 1994; Azaizah et al., 1995; Marschner et al., 1997; Sood, 2003; Pivato et al., 2008). These changes impact the microbial community of the mycorrhizosphere and, among other effects, may lead to a shift in its composition favoring certain components of the microbiota with the capacity to antagonize possible root pathogens (Barea et al., 2005; Badri and Vivanco, 2009). Altered root exudation also may directly impact microbial pathogens and nematodes. For example, exudates from mycorrhizal tomatoes transiently paralyzed nematodes, and generally their penetration into mycorrhizal tomato roots was decreased (Vos et al., 2011). Similarly, sporulation of the oomycete *Phytophthora fragariae* was severely reduced in the presence of mycorrhizal strawberry root exudates (Norman and Hooker, 2000), and concentrated exudates from mycorrhizal tomato roots were repulsive to *Phytophthora nicotianae* zoospores (Lioussanne et al., 2008). Besides these repellent-like molecules, thus far, no antimicrobial compounds have been isolated from the exudates of mycorrhizal roots.

Altered root exudation also gives rise to the effect of mycorrhizas on plant interactions with parasitic plants: Mycorrhiza have been shown to reduce the incidence of root parasitic plants of the *Orobanchaceae*, including the genera *Striga*, *Orobanche*, and *Phelipanche* (López-Ráez et al., 2011b). These parasitic weeds are ubiquitous obligate parasites that cause immense yield losses in agriculture (Bouwmeester et al., 2003). It is known that seeds of these weeds germinate upon perception of strigolactones (SLs), a group of carotenoid-

derived signaling molecules that are exuded by the roots of the host plant under conditions of phosphate starvation and promote AM hyphal branching and mycorrhiza establishment (Akiyama et al., 2005; Bouwmeester et al., 2007). The *Orobanchaceae* utilize this signal for the detection of an appropriate host plant that will be colonized and parasited. Interestingly, once the mycorrhizal symbiosis is well established, the SL production in the host plant goes down (Fig. 2; Lendzemo et al., 2007; López-Ráez et al., 2011a). This opens the possibility of using AMF in the control of parasitic weeds where conventional strategies have failed. Apart from their role as signaling molecules in the rhizosphere, SLs also play roles in signaling within the plant by acting in the regulation of shoot and root architecture. It is proposed that SLs, together with auxins, favor lateral root development that enables the root system to reach new areas in the soil where phosphate might be available (Stepanova and Alonso, 2009). The SL-mediated changes in root architecture may alter the dynamics of some pathogen infections, although direct evidence of such a correlation are lacking.

The use of experimental split-root systems has confirmed that the protection by mycorrhiza is manifested in non-colonized areas of the root system. For example, systemic protection in the root has been confirmed against oomycetes and bacterial pathogens in tomato (Cordier et al., 1998; Pozo et al., 2002; Zhu and Yao, 2004; Khaosaad et al., 2007), against fungal pathogens in barley (Khaosaad et al., 2007), and in banana and grapevine against nematodes (Hao et al., 2012). These experiments allow physical separation of the AMF and the aggressor, and they highlight the involvement of plant-mediated responses in the enhanced resistance, pointing out a major role for plant defense mechanisms.

### **Mycorrhiza Effects on Above-Ground Interactions**

Systemic protection by a mycorrhizal association can even be observed in the aerial parts of a colonized plant, but in contrast to below-ground interactions, reports on AM effects on pests and pathogens attacking shoots are less studied, and the outcome of the interaction is more variable. Early studies described a higher susceptibility of AM plants to viruses, and biotrophic pathogens appear to thrive better on mycorrhizal plants, although an increased tolerance has been observed in terms of plant mass and yield (Gernnset 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). However, pathogens with a necrotrophic lifestyle are hampered in their proliferation, and symptom development is less severe on mycorrhizal plants. Examples are the fungi *Alternaria solani* in tomato (Fritz et al., 2006; de la Noval et al., 2007), *Magnaporthe grisea* in rice (Campos-Soriano et al., 2012), and *Botrytis cinerea* in roses and tomato (Møller et al., 2009; Pozo et al., 2010).

In relation to phytoplasmas, specialized obligate parasites of phloem tissue that are transmitted by insect vectors, most reports show a reduction of disease incidence (Kamińska et al., 2010a, 2010b; Batlle et al., 2011; D'Amelio et al., 2011). However, it should be noted that the analysis of mycorrhizal effects on phytoplasmas and viruses is difficult because of the potential impact of mycorrhization on the insect vector and the complexity of studies on multi-trophic interactions.

Because of the multiple roles of insects in plant biology and their ecological relevance, the impact of mycorrhization on plant interactions with insects deserves special attention. Insects may be deleterious to plants by directly damaging them through herbivory or by acting as vectors for pathogens such as viruses and phytoplasmas, but they also can have positive effects on plant health by acting as natural enemies of pests or as pollinators. The outcome of the mycorrhiza-plant-herbivore interaction depends on many factors, such as the AM fungus, host and insect species involved, and environmental factors (Gange, 2007; Pineda et al., 2010). Several reviews have tried to compile the published studies dealing with these multitrophic interactions, most of them from an ecological point of view (Gehring and Bennett, 2009; Hartley and Gange, 2009). As a general pattern, the positive roles of insects on plants are favored by mycorrhization. For example, mycorrhization positively influence visitation rates of pollinating insects (Gange and Smith, 2005; Wolfe et al., 2005). This effect may be partly due to mycorrhizal effects on plant biomass, flower number and size, and amount of pollen produced (Gange and Smith, 2005). Similarly, the changes in the volatile profile of mycorrhizal plants under attack by herbivores result in a higher attraction of parasitoids that may help the plant to control the pest (Guerrieri et al., 2004; Leitner et al., 2010; Schausberger et al., 2011).

Concerning mycorrhizal effects on herbivorous insects, different outcomes have been reported. The improved growth and nutritional status of a mycorrhizal plant can compensate for feeding damage, whereas improved nutrient and water uptake facilitate the regrowth of tissues; all of which can increase host tolerance to herbivory (Kula et al., 2005; Bennett and Bever, 2007; Hoffmann et al., 2011).

Besides tolerance, direct effects on the insect also can occur. These effects largely vary depending on the type of the attacking insect. Generalist insects, able to feed on diverse plants and sensible to the plant defense mechanisms, are usually negatively affected by the presence of mycorrhizas (Rabin and Pacovsky, 1985; Gange and West, 1994; Vicari et al., 2002; Fontana et al., 2009). However, the outcome of the mycorrhiza-plant-herbivore interaction is not always favorable for the plant. Specialist insects, which feed from one or only a small number of hosts and show a high degree of adaptation to their hosts' defense responses, usually perform better on mycorrhizal plants, probably because of the improved nutritional quality of the host (Gehring and Bennett, 2009; Hartley and Gange, 2009). This general pattern, i.e., protection by mycorrhiza mostly against insect species sensitive to plant defense mechanisms, again supports the key role of the defense mechanisms on plant protection by mycorrhiza.

The degree of protection also depends on the feeding guild of the attacking herbivore. Phloem-sucking insects produce minimal damage to the plant while feeding and thereby avoid detection by the host's immune system (Walling, 2008). Thus, it is unlikely that potentiation of plant defense mechanisms in mycorrhizal plants may have a significant impact on them. Moreover, they may profit from its higher nutritional value. In fact, higher incidence of phloem-sucking insects in mycorrhizal plants has been reported (Gange et al., 1999; Goverde et al., 2000). In contrast, leaf chewers and miners usually are negatively affected by mycorrhization (Gange and West, 1994; Vicari et al., 2002). These insects feed on the leaf tissue and cause massive damage, which activates defenses that depend on the plant hormone JA (Howe and Jander 2008).

Taking into account the degree of specialization of the herbivore and its feeding guild, it can be summarized that mycorrhization negatively affects generalist leaf chewers, while having a positive or neutral effect on phloem feeders and specialist chewers (Gehring and Bennett, 2009; Hartley and Gange, 2009; Koricheva et al., 2009; Pineda et al., 2010). This spectrum of action strongly suggests that the effect of mycorrhization is related to priming of the plant defense mechanisms, and points out a prominent role of jasmonate signaling in the plant protection achieved by mycorrhization.

## **MECHANISMS UNDERLYING MYCORRHIZAS' IMPACT ON PLANT-INTERACTIONS WITH PATHOGENS AND PESTS**

The effects of the AM symbiosis on plant interactions with other organisms, and, in particular, the induction of resistance against deleterious organisms seem to result from the combination of multiple mechanisms that may operate simultaneously. In the previous section, the possible role of competition for colonization sites and photoassimilates, and the contribution of the modifications in the microbial populations in the rhizosphere were discussed. Apart from that, a major transcriptional reprogramming takes place upon mycorrhizal colonization of the roots (Liu et al., 2003, 2007; Güimil et al., 2005; López-Ráez et al., 2010b). This reprogramming originates alterations in the primary and secondary metabolism in mycorrhizal plants (Hause et al., 2007; Toussaint, 2007; Schliemann et al., 2008). The majority of the changes affect the host's secondary metabolism, and have far-reaching consequences for the plant. One example is the alteration in root exudates, composed of various secondary metabolites such as phenolic compounds, strigolactones, and allelopathic compounds that regulate multiple interactions in the rhizosphere (Zeng, 2006; López-Ráez et al., 2010a, 2011b; Cipollini et al., 2012, this issue). Accordingly, all those changes may have special relevance to mycorrhizal effects on plant interactions below-ground. The symbiosis also increases the rate of photosynthesis and influences the carbon assimilation and allocation, thereby possibly affecting the source-sink relations that may influence the suitability of the plant for shoot attackers (Wright et al., 1998a, b). Obviously, improved nutrition in the plant also may account for damage compensation phenomena, and may, therefore, contribute to plant tolerance to diseases and herbivory. However, those mechanisms do not explain, for example, protection by AM under conditions where there are no nutritional benefits, and they do not

explain the spectrum of action of mycorrhiza-induced resistance. These and other evidence discussed in the former section support the idea that the regulation of plant defenses during mycorrhization plays a major role in mycorrhiza induced resistance.

### **Modulation of the Host Plant's Immune System by AMF**

A functional mycorrhizal association requires a high degree of coordination between both partners. The fungus has to deal with the plant's immune system, contend with the defense mechanisms and overcome them for successful colonization of the host (Kloppholz et al., 2011; Zamioudis and Pieterse, 2012). Once established, the plant has to regulate the level of fungal proliferation within the roots to prevent excessive colonization and carbon drainage, thus maintaining the interaction at mutualistic levels. For example, under conditions of high exogenous phosphate supply, the plant actively inhibits proliferation of the fungus within the roots (Breuillin et al., 2010). Similarly, plants possess a feedback system that prevents excessive colonization over a critical threshold, a phenomenon termed auto-regulation of the symbiosis, described initially in the rhizobium-legume symbioses (Vierheilig, 2004; Vierheilig et al., 2008). Mechanistic similarities between the auto-regulation of mycorrhization and nodulation and the induction of systemic resistance by beneficial microbes have been pointed out (Vierheilig et al., 2008; Zamioudis and Pieterse, 2012). In summary, from presymbiotic stages and throughout a well-established AM association, plant defense mechanisms are tightly regulated to control the symbiosis. As a side effect, this regulation may directly impact root pathogens.

During the early stages of the interaction, the plant reacts to the presence of AM fungi by activating some defense-related responses that are subsequently suppressed (García-Garrido and Ocampo, 2002; Liu et al., 2003). Before penetration of the roots, the fungus seems to trigger the plant's immune system as a biotrophic pathogen would (Güimil et al., 2005; Paszkowski, 2006). In response to colonization by AMF, a quick but transient increase of endogenous salicylic acid (SA) occurs in the roots (Fig. 2) with a concurrent accumulation of defensive compounds, such as reactive oxygen species, specific isoforms of hydrolytic enzymes, and the activation of the phenylpropanoid pathway (Pozo et al., 1998; Blilou et al., 1999; Dumas-Gaudot 2000; Fester and Hause, 2005; de Román et al., 2011). These reactions are temporally and spatially limited compared to the reaction during plant-pathogen-interactions, suggesting a role in the establishment or control of the symbiosis (Dumas-Gaudot et al., 1996; García-Garrido and Ocampo, 2002). Indeed, SA signaling seems to have a negative effect on AM colonization (de Román et al., 2011; Herrera-Medina et al., 2003), and AM establishment requires inhibition of certain SA-regulated responses (Dumas-Gaudot 2000) as described for other mutualistic symbiosis (Soto et al., 2009). Despite our lack of knowledge on how the AM fungi evade and manipulate the host's innate immune system, recent studies support that AM fungi can actively suppress SA-dependent defense reactions by secreting effector proteins that interfere with the host's immune system (Campos-Soriano et al., 2010; Kloppholz et al., 2011). Not only SA, but also the level of other phytohormones related to defense, such as JA, ABA, and ET, is altered during the plant interaction with the AM fungus (Hause et al., 2007; López-Ráez et al., 2010b; Ludwig-Müller, 2010). Indeed, as the colonization progresses, the regulation of JA levels gains a central role in the correct functioning of the AM symbiosis (Hause et al., 2002, 2007; Hause and Schaarschmidt, 2009). Since induced resistance is generally manifested only when the AM symbiosis is well established, the changes in signaling associated with a well-established mycorrhiza are likely mediating MIR (Cordier et al., 1998; Slezacek et al., 2000; Pozo et al., 2002, Jung et al., unpublished). It should be noted here that the extent of the hormonal changes associated with the symbiosis depends on the AM fungus involved (López-Ráez et al. 2010b; Fernandez and Pozo, unpublished). The differences may correlate with the differential ability of various AMF to induce resistance. The level of protection conferred by the mycorrhization is highly dependent on the fungus engaged in the symbiosis (Pozo et al., 2002; Garmendia et al., 2004; Kobra et al., 2009; Sikes et al., 2009).

The dependence of successful mycorrhization on the control of JA and SA signaling would explain the range of protection conferred by this symbiosis (Pozo and Azcón-Aguilar, 2007). As summarized, AMF plants are more resistant to necrotrophs and chewing insects, aggressors targeted by JA-dependent defense responses, and they are more susceptible to biotrophs, targeted by SA-regulated defenses. This pattern correlates with an activation of JA-dependent defenses and repression of SA-dependent ones in a well-established

mycorrhiza. JA signaling leads to the synthesis of toxins and defensive proteins that target physiological processes in the insect, thus reducing insect growth and survival (Howe and Jander 2008). Similarly, JA regulates defense response genes that are effective against necrotrophic microbial pathogens (Poza et al., 2009). Moreover, JA triggers indirect plant defenses upon herbivory, regulating the emission of volatile blends that attract predators or parasitoids, which then prey on the herbivores (Dicke et al., 2009; Snoeren et al., 2009). Together with altered JA responses, the volatile profile changes in mycorrhizal plants under attack, and they become more attractive to natural enemies like parasitoids (Guerrieri et al., 2004; Rapparini et al., 2008; Fontana et al., 2009; Leitner et al., 2010; Schausberger et al., 2011).

### Priming of JA-dependent Defenses in Mycorrhiza-Induced Resistance

The induction of resistance (IR), does not necessarily require direct activation of defense mechanisms, but can result from a sensitization of the tissue upon appropriate stimulation to express basal defense mechanisms more efficiently after subsequent pathogen attack. This priming of the plant's innate immune system is common upon interaction with beneficial microorganisms, and has important fitness benefits compared to direct activation of defenses (Conrath et al., 2006; Van Hulten et al., 2006; Van Wees et al., 2008). Induction of the primed state usually is associated with a moderate accumulation of defense-related regulatory molecules, such as transcription factors or MAP kinases (Poza et al., 2008; Beckers et al., 2009; Van Der Ent et al., 2009b). For example, rhizobacteria-induced systemic resistance in *Arabidopsis* is related to priming of JA-dependent responses through the accumulation of MYC2, a transcription factor with a key role in the regulation of JA responses (Poza et al., 2008).

Examples of primed defense responses in mycorrhizal plants were first observed in root tissues. Mycorrhizal transformed carrot roots displayed stronger defense reactions at sites challenged by *Fusarium* (Benhamou et al., 1994). In tomato, AMF colonization systemically protected roots 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  $\beta$ -1,3 glucanases than non-mycorrhizal plants upon *Phytophthora* attack (Cordier et al., 1998; Poza et al., 1999, 2002). Priming for callose deposition also was reported to underlie protection against *Colletotrichum* in cucumber (Lee et al., 2005). Similarly, mycorrhizal potato showed amplified accumulation of the phytoalexins rishitin and solavetivone upon *Rhizoctonia* infection, whereas AMF alone did not affect the levels of these compounds (Yao et al., 2003). Recently, primed accumulation of phenolic compounds in AM date palm trees also has been related to protection against *F. oxysporum* (Jaiti et al., 2007), and priming has been involved in mycorrhizal induction of resistance against nematodes (Li et al., 2006; Hao et al., 2012). However, the primed response is not restricted to the root system. Recently, we have shown priming of defenses also in shoots of mycorrhizal plants (Poza et al., 2010). AM symbiosis induced systemic resistance in tomato plants against the necrotrophic foliar pathogen *Botrytis cinerea*.

While the amount of pathogen in leaves of mycorrhizal plants was significantly lower, the expression of some jasmonate-regulated, defense-related genes was higher in those plants (Poza et al., 2010, Jung et al., unpublished). A primed response of JA-dependent defenses was confirmed by transcript profiling of leaves after exogenous application of JA, since JA-responsive genes were induced earlier and to a higher extent in mycorrhizal plants, particularly in those colonized by *G. mosseae* (Poza et al., 2009). A similar primed response was observed in mycorrhizal tomato leaves upon mechanical wounding or caterpillar feeding, both responses known to be regulated by JA, thus underscoring the importance of the JA signaling pathway in MIR (Fig. 3). The use of tomato mutants impaired in JA signaling has confirmed that JA is required for mycorrhiza induced resistance against *Botrytis* (Martinez-Medina et al., unpublished), confirming that MIR is similar to the well-studied rhizobacteria-induced systemic resistance (ISR) in *Arabidopsis* and requires a functional JA signaling pathway for the efficient induction of resistance (Pieterse et al., 1998). The JA signaling pathway also is required for rhizobacteria-mediated 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). Recently, MIR against the rice blast fungus *Magnaporthe grisea* has been demonstrated, and the resistance seems to rely on both the systemic activation of genes with a regulatory role in host immunity, and the priming for stronger



expression of defense effector genes during pathogen infection (Campos- Soriano et al., 2012).

In addition to this priming effect on above-ground tissues, the AMF hyphal network may even extend the induction of resistance to neighboring plants, acting as a plant-plant underground communication system (Song et al., 2010). Song and co-authors showed that healthy “receiver” plants activate JA-regulated, defense-related genes when neighboring “donor” plants, connected via a common mycorrhizal network in the soil, were infected by the foliar pathogen *Alternaria solani*. According to this finding, plants can ‘eavesdrop’ on signals from the pathogen-challenged neighbors to activate defenses before being attacked themselves (Song et al., 2010). With regard to this, since mycorrhizal establishment alters the volatile emission, and volatiles have been shown to prime distal plant parts or even neighboring plants for a faster induction of defense responses (Heil and Ton, 2008), it remains to be determined if changes in volatiles in mycorrhizal plants also prime neighboring plants for efficient activation of defense against attackers.

## SUMMARY AND OUTLOOK

Arbuscular mycorrhizas significantly impact the host plant interaction with multiple organisms. Even though the individual outcome always depends on the AMF-plant-attacker combination, protective effects against deleterious organisms have been described for many interactions (Fig. 1). Experimental evidence confirms that this protection is based not only on improved nutrition or local changes within the roots and rhizosphere, but that priming of plant immunity plays a major role in Mycorrhiza-Induced Resistance. Although the molecular basis for the regulation of plant defenses and the priming of the plant immune system during mycorrhization remains mostly unknown, a prominent role of jasmonate signaling has been confirmed. The great majority of land plants form arbuscular mycorrhizas, thus, unveiling the principles behind a successful symbiosis and the functional interplay between plant and fungus is of major interest. The identification of defense regulatory elements that may operate in priming of plant defenses in mycorrhizal plants may have important practical implications regarding the effectiveness of AMF in the biological control and integrated management of pests and diseases.

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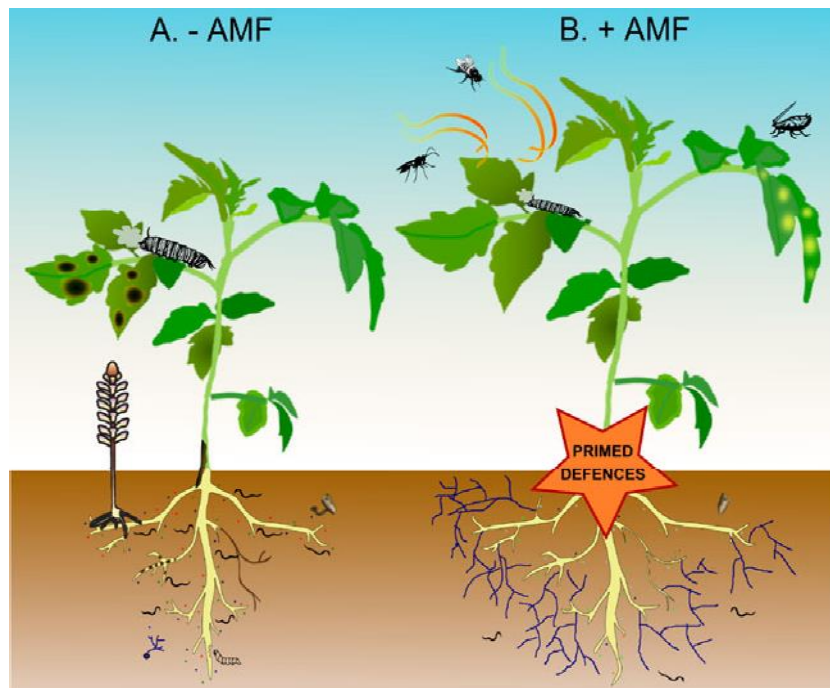
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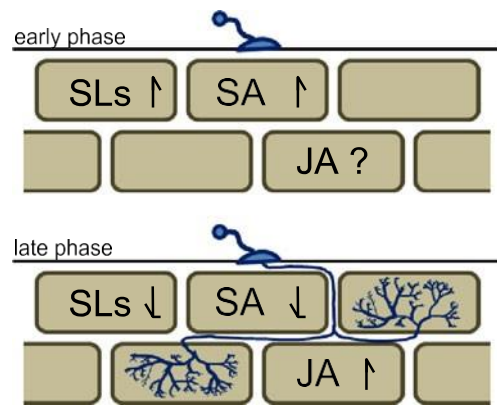
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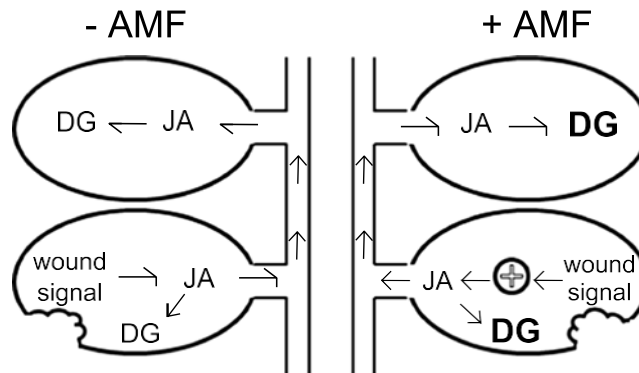
FIGURES



**Fig. 1** a Non-mycorrhizal plant (– AMF). Absence of root colonization by AMF leads to stronger development of symptoms in response to necrotrophic pathogens and more damage upon feeding by chewing insects in roots and shoots when compared to mycorrhizal plants. Release of strigolactones (SLs) as part of the root exudates induces branching of AMF hyphae to promote mycorrhization but also induces germination of *Orobanchaceae* seeds which then parasitize the host plants' root system. b Mycorrhizal plant (+AMF). Growth promotion is often observed due to improved acquisition of mineral nutrients through the AM fungal hyphal network (represented in blue). Changes in the root exudate patterns repel nematodes and induce changes in the soil microbial community, possibly attracting antagonists of pathogens and a reduced release of SLs minimizes the risk of infection by root parasitic plants. Priming of plant defenses leads to a general reduction of the incidence and/ or damage caused by soil-borne pathogens, nematodes and chewing insects. In above-ground plant parts, viral and fungal biotrophs, as well as phloem-feeding insects, perform better on mycorrhizal plants. In contrast, the primed jasmonate-regulated plant defense mechanisms restrict the development of necrotrophic pathogens and the performance of phytophagous insects. Indirect defenses, such as the release of volatiles, are boosted and parasitoids are efficiently attracted



**Fig. 2** Model for hormonal changes in the roots associated to the arbuscular mycorrhizal symbiosis. In the early phase of colonization strigolactone (SL) production is still high. Initially the AMF is perceived as an alien organism and as a consequence salicylic acid (SA) levels increased. In a well-established mycorrhiza both SL and SA production are repressed while biosynthesis of jasmonates (JA) increases



**Fig. 3** Priming of jasmonate-dependent wound signaling in the shoots. In non-mycorrhizal plants (- AMF) the initial wound signal activates the JA-dependent pathway that leads to the activation of defense genes (DG) in local and systemic tissue. In mycorrhizal plants (+ AMF) the response to the wound signal is amplified leading to a primed defense response.