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Plant Immunity Modulation in Arbuscular Mycorrhizal Symbiosis and Its Impact on Pathogens and Pests

V. Fiorilli,[1,*] A. Martínez-Medina,[2,*] Maria J. Pozo,[3] and L. Lanfranco[1]

[1]Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy; email: luisa.lanfranco@unito.it

[2]Department of Plant-Microbe Interactions, Institute of Natural Resources and Agrobiology of Salamanca, CSIC, Salamanca, Spain

[3]Department of Soil and Plant Microbiology, Estación Experimental del Zaidín, CSIC, Granada, Spain; email: mariajose.pozo@eez.csic.es

*These authors equally contributed.

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Abstract

Arbuscular mycorrhizal (AM) symbiosis is the oldest and most widespread mutualistic association on Earth and involves plants and soil fungi belonging to Glomeromycotina. A complex molecular, cellular, and genetic developmental program enables partner recognition, fungal accommodation in plant tissues, and activation of symbiotic functions such as transfer of phosphorus in exchange for carbohydrates and lipids. AM fungi, as ancient obligate biotrophs, have evolved strategies to circumvent plant defense responses to guarantee an intimate and long-lasting mutualism. They are among those root-associated microorganisms able to boost plants' ability to cope with biotic stresses leading to mycorrhiza-induced resistance (MIR), which can be effective across diverse hosts and against different attackers. Here, we examine the molecular mechanisms underlying the modulation of plant immunity during colonization by AM fungi and at the onset and display of MIR against belowground and aboveground pests and pathogens. Understanding the MIR efficiency spectrum and its regulation is of great importance to optimizing the biotechnological application of these beneficial microbes for sustainable crop protection.

1. INTRODUCTION

Following the holobiont concept, higher eukaryotes, including plants, are considered functional units consisting of the sum of the metabolic functions of the host and its entire microbiota (166). Concerning plants, greater attention has been given to root-associated microbiota, as soil, and particularly the area under the influence of root exudates (i.e., rhizosphere), is one of the niches with the highest levels of microbial biodiversity on Earth. Components of the root microbiota can have a positive impact on several aspects of plant biology from an improvement of nutrient uptake to the modulation of developmental processes and increased tolerance to biotic and abiotic stresses (24, 38, 57).

Rhizosphere microbiota display plant immunomodulatory properties (182), and understanding how the plant immune system deals with promoting interaction with beneficials while fending off aggressors has been a major research topic (56). In addition, some beneficial root-associated microbes can stimulate plant immunity, leading to induced systemic resistance (ISR) (119). ISR was classically distinguished from systemic acquired resistance (SAR), which commonly refers to resistance induced by pathogenic microbes (119). Both ISR and SAR define a biologically similar phenomenon—long-lasting, broad-spectrum protection—often share signaling molecules and pathways, and can be also triggered by chemical elicitors and phytohormones. As a consequence, the term induced resistance (IR), which combines ISR and SAR, has been proposed to indicate a reduced disease susceptibility of a plant in response to appropriate stimulation by different biotic or abiotic stimuli, including pathogen and herbivore attacks or wounding, colonization by beneficial microbes, and exogenous application of chemical elicitors (32).

Several soil-inhabiting microorganisms associated with plant roots have been shown to elicit IR in multiple plant species, including agronomically relevant crops. Prominent examples are plant-growth-promoting rhizobacteria, such as strains of *Pseudomonas*, *Bacillus*, and *Serratia* species (7), and plant-growth-promoting fungi, such as *Trichoderma*, nonpathogenic *Fusarium*, *Serendipita indica*, and arbuscular mycorrhizal (AM) fungi (125).

AM fungi, which belong to the subphylum Glomeromycotina, establish an intimate mutualistic association—AM symbiosis—with the majority of land plants, including crops (18). This symbiotic association is one of the oldest on the planet (50), with fossil evidence dating back to the Devonian, when it most likely aided plants in colonizing the harsh terrestrial environment (156). The establishment of a functional AM symbiosis requires several steps, including an initial phase of plant–fungus recognition, the colonization of root tissues, and the activation of symbiotic functions (**Figure 1**; see the sidebar titled Arbuscular Mycorrhizal Symbiosis: The Colonization Process) (27, 146). The mutualistic nature is based on a reciprocal transfer of nutrients: The plant receives mineral nutrients, mainly phosphorus but also nitrogen, sulfur, and trace elements such as manganese, magnesium, and zinc (177), that are efficiently recruited by an extensive network of extraradical hyphae developing in soil. This often results in higher plant biomass and a remarkable growth-promoting effect when plants are grown under conditions of limiting nutrient availability (14, 25, 45). On the other hand, the fungus receives carbohydrates and lipids from the plant. In fact, AM fungi completely rely on the green host for the provision of fatty acids (64, 69, 86), as they lack the fatty acid synthase, a key enzyme for de novo lipid synthesis.

AM root colonization induces systemic effects also evident on epigeous portions of the plant (44, 82), with an impact on plant phenology (i.e., flowering time) and productivity (45, 193). Having a very large host range (18), AM fungi play crucial roles in terrestrial ecosystems by regulating nutrient and carbon cycles and influencing ecosystem multifunctionality (165).

At the organism level, AM symbiosis exerts a beneficial effect on the host plant that goes beyond improving nutritional status and leads to increased tolerance to abiotic and biotic stresses (94, 127,
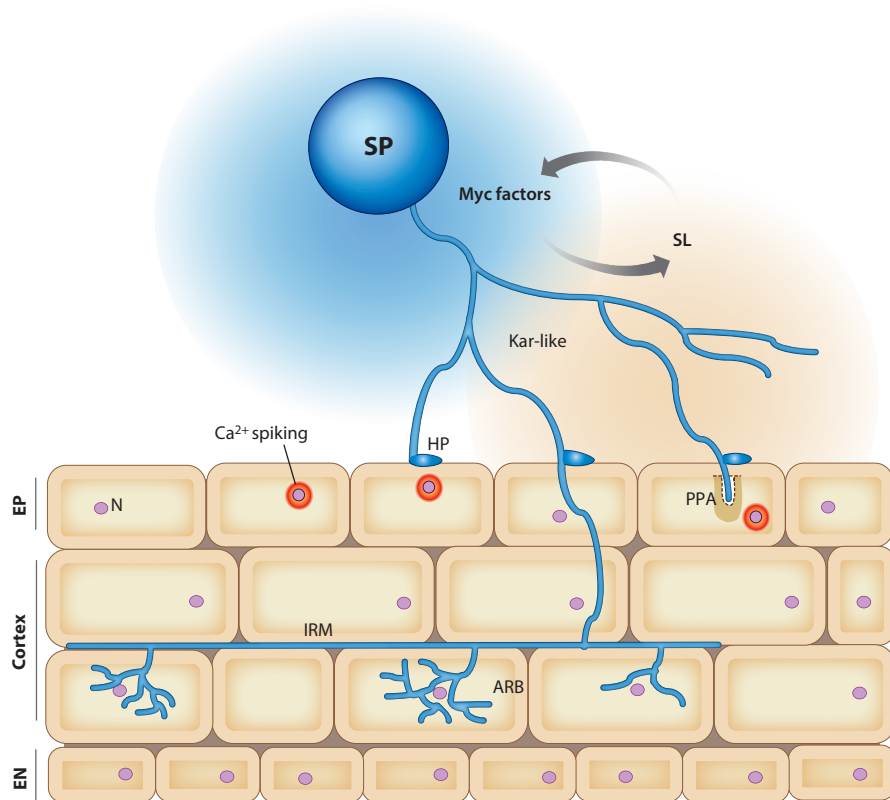
Figure 1

The process of root colonization by arbuscular mycorrhizal (AM) fungi. The roots of the host plant release strigolactones (SL) that induce spore (SP) germination, hyphal branching, and mitochondrial metabolism in AM fungi. The AM fungus produces the Myc factors that activate symbiotic responses in the root epidermis (EP). A positive loop involves SL and Myc factors to favor the early steps of colonization. A still unknown karrikin-like molecule (Kar-like) of fungal or plant origin perceived by the Dwarf 14–like receptor is also involved in the pre-contact phase of the interaction. Myc factor perception induces regular nuclear calcium oscillation (Ca^{2+} spiking) and symbiosis-related gene expression in epidermal cells. On the root surface, the AM fungus develops hyphopodia (HP), and the contacted epidermal cell forms the pre-penetration apparatus (PPA) that guides the entrance of the fungal hypha. In the inner layers of the cortex, the intraradical mycelium (IRM) forms intercellular hyphae and highly branched intracellular structures called arbuscules (ARB), the main site of nutrient exchanges. Abbreviations: EN, endodermis; N, nucleus.

178). In particular, AM symbiosis has been shown to influence the outcome of belowground and aboveground interactions with other organisms (20, 53, 66, 107). It can usually protect plants from biotic stresses through IR that, in this specific case, is known as mycorrhiza-induced resistance (MIR) (66, 123).

AM-colonized plants often show increased tolerance/resistance to microbial soilborne pathogens such as fungi from the genera *Fusarium*, *Rhizoctonia*, *Macrophomina*, and *Verticillium*; bacteria such as *Erwinia carotovora*; and oomycetes such as *Phytophthora*, *Pythium*, and *Aphanomyces* (reviewed in 66). Protection against infestation by nematodes (144) and root-feeding insects has also been documented (72). AM symbiosis can also alleviate plant damage from aboveground pathogens, including viruses (106), bacteria (45, 48, 82), fungi (22, 37, 43, 104, 126, 137, 140, 149,

ARBUSCULAR MYCORRHIZAL SYMBIOSIS: THE COLONIZATION PROCESS

AM fungi are present in the soil as quiescent spores ready to respond to host signals delivered by root exudates. Under the control of a gene regulatory network activated by the phosphate starvation response (31, 147), plant roots synthetize and release strigolactones that induce spore germination and hyphal branching. The fungus exudes a mixture of different chito-oligosaccharides (tetra- or penta-chito-oligosaccharides) and lipo-chito-oligosaccharides called Myc factors. Their perception activates in the plant the common symbiotic signaling pathway (CSSP), a conserved genetic pathway that controls the formation of arbuscular mycorrhizas and nodulation in legumes (113). A key CSSP component is the high-frequency nuclear calcium (Ca^{2+}) spiking that induces transcription factor expression controlling cellular programs for fungal accommodation and symbiotic functions (27, 146). Another pathway mediated by the plant receptor Dwarf14-like is also necessary for AM symbiosis formation (26, 55). On root surface, fungal hyphae develop hyphopodia. In the hyphopodium-contacted rhizodermal cell, a subcellular structure called pre-penetration apparatus is formed to guide fungal intracellular accommodation. In the inner cortex, fungal hyphae penetrate the cell and form arbuscules, ephemeral highly branched intracellular structures, separated from plant cytoplasm by the peri-arbuscular membrane (27, 146, 187) where reciprocal nutrient transfer occurs.

174), oomycetes (159, 191), and herbivore insects (34, 92, 134, 143, 153). However, the outcomes seem to greatly depend on the pathogen/arthropod lifestyle and environmental conditions (66, 72, 106, 121, 125), and enhanced susceptibility to some aggressors has been also reported (72, 107). Protection has been observed in very diverse plant species from different families, including crops of great economic importance such as tomato, potato, rice, melon, wheat, and even fruit trees (10, 21, 92, 99, 134, 143).

During plant colonization and MIR display, AM fungi interact intimately with the plant immune system, and knowledge of the mechanisms underlying this interaction is of great importance to fully exploit these beneficial organisms in sustainable agriculture and crop protection. In this review, we examine the molecular mechanisms that drive the modulation of plant immunity by AM fungi to clarify how AM fungi circumvent plant defense responses to guarantee an intimate and long-lasting mutualism, what the impact of AM fungi on the plant defensive capacity against pathogens and pests is, how MIR is regulated in plants, and how the biotic and abiotic context affect MIR display.

2. MODULATION OF PLANT IMMUNITY DURING ARBUSCULAR MYCORRHIZAL COLONIZATION

Over the past few years, it has been demonstrated that to develop functional symbiosis, AM fungi are able to overcome plant defenses through the activation and/or modulation of different signaling pathways involving chitin-derived elicitors, effectors, and phytohormones. Below, we explain mechanisms and molecules that are key during the process of the establishment and maintenance of AM symbiosis.

2.1. Myc Factor–Mediated Signaling

Effectors: proteins secreted by plant-colonizing microbes able to manipulate the host defense pathways or mechanisms to favor colonization

Innate immunity allows plants to limit pathogen proliferation through the activation of defense mechanisms upon recognition of microbe-associated molecular patterns (MAMPs), which activate pattern recognition receptors that act as a surveillance system (122). These receptors recognize MAMPs ranging from peptides (e.g., flagellin) to carbohydrates (e.g., microbial cell wall components). Among carbohydrates, chitin is one of the major MAMPs and the most abundant structural

component of the cell wall of pathogenic as well as beneficial fungi, including AM fungi (138). Plants react to chitin-related molecules depending on their length and acetylation degree (29). AM fungi secrete short-chain chito-oligosaccharides [mainly chitotetraose (CO4)] and nonsulfated lipo-chito-oligosaccharides called mycorrhizal factors (Myc factors), which activate accommodation responses in the host root (**Figure 2**), whereas fungal pathogens release long-chain COs [such as chitooctaose (CO8)], which trigger plant defense responses. Perception of Myc factors induces Ca^{2+} influx in the plant cells. In the case of AM symbiosis, a repeated oscillation in nuclear $[Ca^{2+}]$ called Ca^{2+} spiking is observed, whereas during pathogenic interactions the long-chain COs released by the attackers trigger a transient cytosolic $[Ca^{2+}]$ elevation (8). This differential pattern leads to the activation in the first case of a specific symbiotic program. However, evidence shows that subtle boundaries exist in plant immunity responses between symbiotic and root pathogenic fungi. Indeed, the symbiotic signal CO4 induces plant cellular reactive oxygen species (ROS) burst and MAPK cascades, similar to the changes observed upon CO8 and chitin perception (16) (**Figure 2**). In several plant species, cellular and molecular data show that in the early stage of the AM interaction, root cells activate a plethora of defense responses, including the upregulation of pathogenesis-related (PR) genes, that are transient and weak compared to pathogenic interactions (49, 51, 82). The inability of AM fungi to trigger a strong plant defense response has been linked to the limited number of genes encoding plant cell wall–degrading enzymes and the large repertoire of putative effectors in AM fungal genomes (67, 184). In agreement with these data, Binci and colleagues (12) demonstrated in legumes the biphasic nature of Ca^{2+} AM-mediated signals, reporting an early strong and quick cytosolic Ca^{2+} influx, which possibly triggers immunity-related responses also depending on the CO4 concentration, and a later nuclear Ca^{2+} spiking associated with symbiotic responses (**Figure 2**). Regarding the perception of Myc factors, evidence from various plant species has implicated the role of lysin motif (LysM) receptor-like proteins and receptor-like kinases (RLKs) located at the plasma membrane. The chitin receptor responsible for chitin-triggered immunity against fungal pathogens is a LysM-RLK receptor (CERK1), which interacts with a chitin elicitor-binding protein (CEBiP), a plasma membrane glycoprotein with LysM motifs. In 2019, He and colleagues (60) identified a complex of LysM RLKs consisting of OsMYR1 and OsCERK1 that in rice mediates the perception of AM fungi. The recognition of symbiont or pathogen and the coordination of downstream clearcut binary Ca^{2+} responses are strictly controlled by the competition in the assembly of alternative receptor complexes: When the plant perceives CO4, CERK1–CEBiP complex is reduced in favor of CERK1–MYR1 complex, and downstream symbiosis-associated responses are activated (186). Furthermore, Yu et al. (181) recently demonstrated the role of plant extracellular LysM proteins in sequestering long-chain COs and quenching defense responses during AM development. It is interesting to note that, analogous to pathogens, AM fungi also produce LysM extracellular proteins to optimize root colonization (185).

2.2. Arbuscular Mycorrhizal Fungal Effectors

To engage the symbiosis, AM fungi produce effectors, similar to those described in pathogens, known to reprogram plant cells to dampen defense responses and/or interfere with host cellular processes to favor host colonization (83). One common feature of effectors is that they contain a signal peptide that guides proteins toward secretion. Despite the genomes and transcriptomes of AM fungi containing hundreds of candidate effector-secreted proteins (67, 184), only a few have been functionally characterized and shown to interfere with plant immunity (4) (**Figure 2**). As mentioned above, Zeng et al. (185) demonstrated that a secreted LysM-containing effector (RiSLM) from the model AM fungus *Rhizophagus irregularis* is induced by strigolactones (SLs) and,

Myc factors:
N-Acetylglucosamine-based molecules (lipo-chito-oligosaccharides and short chitin tetra- and pentamers) released by AM fungi to activate symbiotic responses in the host plant
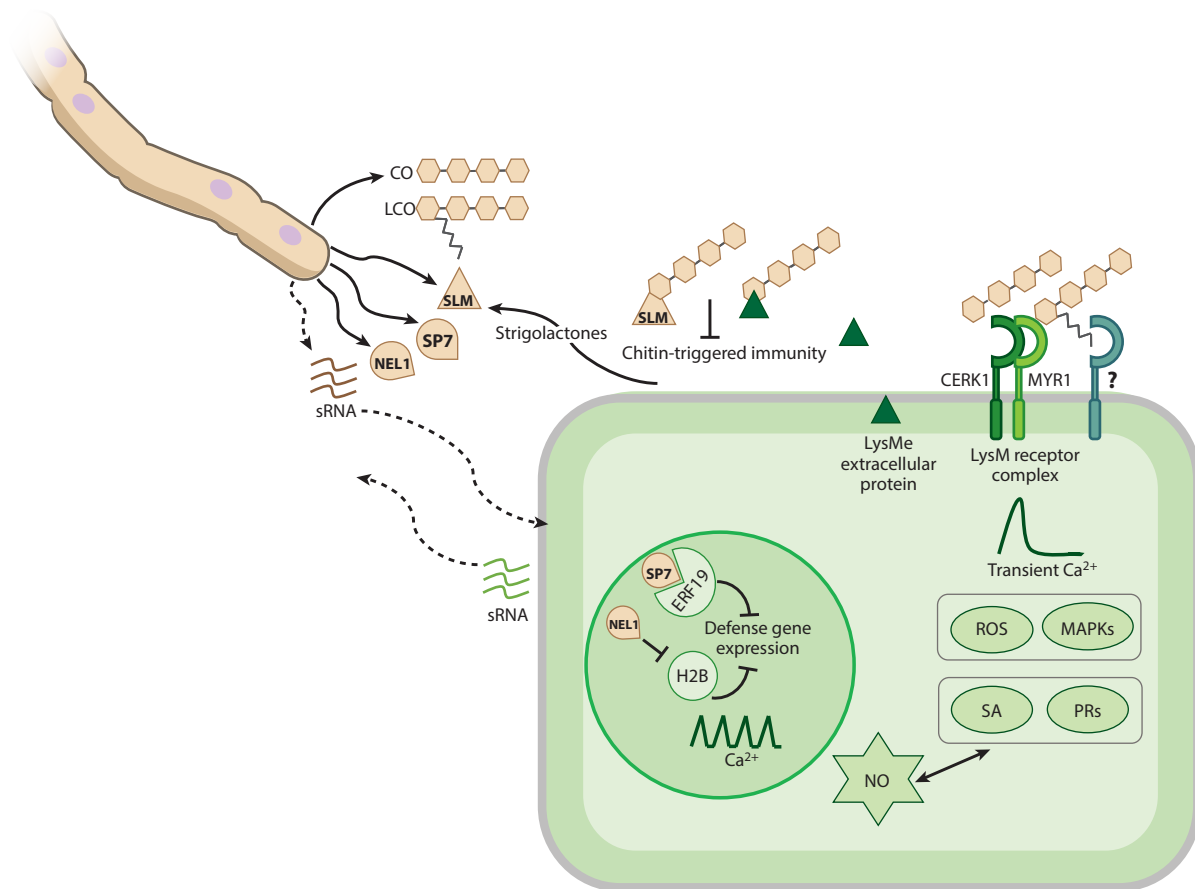
Figure 2

Modulation of plant immunity during arbuscular mycorrhizal (AM) colonization. In response to strigolactones, AM fungal hyphae increase the release of short-chain chito-oligosaccharides (CO; mainly chitotetraose) and nonsulfated lipo-chito-oligosaccharides (LCO) called mycorrhizal factors (Myc factors), which are perceived by the membrane-localized LysM receptors, such as CERK1 and MYR1 described in rice, and possibly other unknown receptors (*indicated with question mark*). Myc factor perception induces a plant cellular ROS burst, MAPK cascades, and Ca^{2+} influx in the plant cells, first as strong and quick cytosolic Ca^{2+} increase (Ca^{2+} transient) and later as nuclear Ca^{2+} spiking associated with symbiotic responses. The AM fungus *Rhizophagus irregularis* produces and releases effectors to engage AM symbiosis: The secreted LysM-containing effector (SLM), which is induced upon treatment with strigolactones, binds chitin-oligomers and, by protecting fungal cell walls from chitinases, modulates plant chitin-triggered immune responses. *R. irregularis* also releases SP7 which counteracts the plant immune response by suppressing the pathogenesis-related transcription factor ethylene response factor ERF19, and NLE1, a nuclear-localized effector that acts via an epigenetic modification, suppressing the expression of plant defense-related genes by interfering with plant histone 2B ubiquitination. Host plants also release extracellular LysMe proteins to sequester long-chain CO and quench defense responses during AM development. It has also been hypothesized that the presence of small RNA effectors that move from AM fungi to plants and vice versa exploit cross-kingdom RNA interference to reduce plant defense during AM fungi colonization. Among phytohormones, a short-lived rise in SA levels was detected in several host plants during the early stages of AM colonization, which was accompanied by activation of defense-responsive genes and nitric oxide (NO) accumulation. Dashed arrows indicate hypothesized processes, blunt-ended lines indicate repression, and dotted arrows indicate still unproved molecular mechanisms. Abbreviations: H2B, histone 2B; MAPKs, mitogen-activated protein kinases; PRs, pathogenesis-related proteins; ROS, reactive oxygen species; SA, salicylic acid; SLM, secreted LysM-containing effector from *Rhizophagus irregularis*.

by binding CO, can protect fungal cell walls from chitinases and modulate plant chitin-triggered immune responses. But the first effector from AM fungi was characterized by Kloppholz and colleagues (71): The *R. irregularis* secreted protein 7 (SP7) counteracts the plant immune response by suppressing the PR transcription factor ethylene response factor ERF19. Notably, SP7 belongs to an effector family conserved across the Glomeromycotina that was recently shown to interact with the plant mRNA processing machinery and modify the alternative splicing of several plant genes (11). Interestingly, alternative splicing is increasingly recognized to play a key role in controlling innate immunity in plant–pathogen interactions (179). Another nuclear-targeted effector from *R. irregularis*, RiNLE1, was shown to act through an epigenetic modification: It suppresses the expression of plant defense-related genes by interfering with plant histone 2B ubiquitination, although the mechanism behind the selection of target genes is not known (175). From these data, it is evident that AM fungal effectors can act through different mechanisms (**Figure 2**), and there is a large knowledge gap on the role in the mycorrhizal symbiotic context of the hundreds of putative protein effectors annotated in AM fungal genomes. Moreover, small RNA effectors that, moving from microbes to plants, exploit cross-kingdom RNA interference to reduce plant defense/microbial virulence also deserve further investigation regarding AM symbiosis (75).

2.3. Phytohormones and Other Signaling Molecules Regulating Arbuscular Mycorrhizal Symbiosis

Phytohormones are key regulators of plant immunity shaping plant responses to invaders, and experimental evidence on different host plants revealed that nearly all phytohormones have a role in the regulation of AM symbiosis formation and/or functioning (61, 80, 124). Because AM symbiosis is a multistep process, diverse phytohormones are engaged differentially during the different steps of the colonization that shape the plant response through complex synergistic and antagonistic cross-talk. In the early steps of the interaction the biosynthesis of some phytohormones has been reported. For instance, SLs and salicylic acid (SA) biosynthesis are transiently induced. The increment of SL levels favors AM hyphal branching and contact with the host and induces the production of fungal CO, which in turn promotes SL biosynthesis (170). A short-lived rise in SA levels was detected in host plants during the early stages of AM colonization, which was accompanied by activation of defense-responsive genes (e.g., phenylalanine ammonia-lyase, PR genes) (13). Elevated SA levels have also been found at later stages of AM symbiosis in different plant species (51, 188), although the changes are dependent on the plant–AM fungus combinations (41). Thus, SA signaling seems to have a biphasic induction during AM symbiosis, with an increase in presymbiotic stages that levels off as the colonization initiates and an induction at later stages that likely controls the extension of root colonization (48, 123). Besides transient activation of these hormones, other hormones, such as jasmonates, appear elevated in mycorrhizal roots along the symbiosis (41); furthermore, fine-tuned regulation of abscisic acid, auxins, and gibberellins plays a key role in regulating mycorrhizal functioning (reviewed in 61, 80).

Systemic signals are also produced by plants to limit over-colonization in a process called autoregulation of mycorrhization (AOM). A prominent role in this phenomenon seems to be played by the plant extracellular signaling peptides—CLE peptides—that act through RLKs to reduce SL content in mycorrhizal roots and limit further colonization (111). Because the expression of some CLE genes is induced by AM colonization or phosphate (Pi), it has been suggested that this regulation might also function through the Pi starvation response, but further studies are needed to confirm this hypothesis and to identify the mobile signals involved (146). It can also be

Jasmonates: fatty acid–derived signaling components involved in the regulation of development and defense response in plants

Autoregulation of mycorrhization (AOM): finely regulated process, including systemic signals, by which the host plant controls mycorrhizal colonization of the roots to prevent excessive colonization and keep the symbiosis at mutualistic levels

MIR display
- Primed accumulation of defense-related proteins
- Primed accumulation of secondary metabolites
- Changes in carbohydrate mobilization
- Improved structural barriers
- Altered volatile blends

c

MIR systemic signaling
- Oxylipins (jasmonic acid and derivatives)
- Other phytohormones
- Changes in primary and secondary metabolites
- Small RNAs

b

MIR onset
- Autoregulation of mycorrhization
- Inmunological memory
  ◦ Epigenetic modifications
  ◦ Alternative splicing
  ◦ Small RNAs

a

Figure 3

Molecular mechanisms regulating mycorrhiza-induced resistance (MIR). Three main phases can be considered when studying the molecular mechanisms underlying MIR. (*a*) The onset of MIR, comprising the changes at the molecular level caused by mycorrhizal symbiosis establishment leading to the primed defensive status. (*b*) Systemic signaling that extends these effects throughout the plant. (*c*) The MIR display, comprising the diverse responses triggered in mycorrhizal plants under attack that contribute to the enhanced resistance phenotype. The main molecular mechanisms proposed to operate in the different phases are listed. The indicated processes that have been proposed but not demonstrated so far are in blue.

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hypothesized that AOM, by modulating the plant immunity to guarantee a long-lasting mutualistic association, may be involved in MIR onset (**Figure 3**).

Owing to their role in plant-pathogenic interactions, ROS and nitric oxide (NO) were also investigated in the context of AM symbiosis. Plant NADPH oxidases (also called RBOH) are the major source of ROS that play key roles as both signal and stressor in defense responses against pathogens. Notably, the upregulation of a specific isoform (*MtRbohE*) was found in arbusculated cells of *M. truncatula* and its silencing generated a strong alteration in root colonization, suggesting a role for MtRbohE in intracellular accommodation of arbuscules (9). However, our knowledge of how ROS regulate AM symbiosis is still limited. NO was detected in roots of different host

Arbuscules:
tree-shaped structures formed by the fungus inside root cortical cells; they are main sites of nutrient exchanges between symbiotic partners

plants after the perception of AM fungal exudates (19, 97) and in cells shortly after contact with fungal hyphae (39, 97), indicating that NO signaling is a component of the early plant responses to diffusible factors in the AM fungal exudates. NO was also detected in the later stages of AM colonization (192). It has been hypothesized that NO might be involved in the control of several processes such as cell wall remodeling, lateral root development, and host defense modulation. In tomato, the establishment of AM symbiosis was associated with a specific NO signature in the host roots. Interestingly, modulating tomato NO levels by silencing or overexpressing a tomato phytoglobine (Phygb1) led to altered AM colonization patterns. It has been hypothesized that NO might contribute to plant regulation of AM colonization levels by modulating plant defenses (97). It is worth noting that NO production in AM symbiosis shows a different profile in terms of amplitude and spatio-temporal distribution compared to that occurring in pathogenic interactions (97), but the precise molecular mechanisms shaping such patterns and their signaling properties are unknown.

3. IMPACT OF MYCORRHIZA ON PLANT INTERACTIONS WITH PATHOGENS AND PESTS

AM fungi can enhance the plant's ability to cope with biotic stresses. Different mechanisms have been shown to mediate this effect, including changes in the nutritional status of the plant, photosynthesis and growth, anatomical and chemical defenses, and priming of plant immunity (53, 66, 90, 103, 139, 140). Thus, the effect of mycorrhiza on plant interaction with pathogens and pests may result from changes in the plant tolerance and/or resistance phenotypes. In this section, we review the experimental evidence of the impact of mycorrhization on both plant tolerance and resistance and the potential underlying mechanisms.

3.1. Mycorrhiza-Enhanced Tolerance

Plant defense phenotype is greatly determined by both resistance (minimize pathogen or herbivore proliferation) and tolerance (minimize damage and the fitness consequences of the attack) (112). Plant tolerance is primarily determined by plant physiological traits and resource availability (115). Given that AM symbiosis can improve plant access to nutrients and influence plant physiology, it seems likely that it contributes to plant tolerance upon herbivore or pathogen attack. For instance, host responses triggered by AM symbiosis, such as enhanced photosynthesis activity, alterations in resource allocation patterns, mobilization of carbohydrates, or alterations in the temporal pattern of plant development, are prominent mechanisms involved in plant compensation for negative effects of attackers (115). However, the specific impact of these responses on AM-induced tolerance to pathogens and pests, and the mechanisms behind these processes, are yet to be investigated. In this regard, several studies have linked the ability of AM symbiosis to provide plant tolerance to herbivory with the enhanced capacity of mycorrhizal plants to take up Pi from the soil (131, 157). For instance, Zeng et al. (183) found that AM symbiosis led to an over-compensatory growth of *Medicago* plants suffering from *Spodoptera exigua* herbivory, thus increasing plant tolerance to herbivory damage, and linked this effect to an AM-triggered boost in Pi uptake. Still, research has found that AM symbiosis can increase, decrease, or have no effect on tolerance-associated mechanisms (47). It is noticeable that the impact of AM on plant tolerance to herbivore or pathogen attack is less well characterized compared to their effects on resistance. This may be in part due to a lagging understanding of the ecology and mechanistic basis of tolerance (47).

Because plant resources available for allocation to defense are limited, commonly accepted theory predicts that there are trade-offs between tolerance and resistance-based defense mechanisms

(77, 88). The question stems from whether, and to what extent, AM symbiosis contributes to trade-offs between both defense strategies (resistance and tolerance) and thus to the overall plant defense phenotype. In this regard, a recent study demonstrated that in *Medicago*, AM symbiosis enhanced plant tolerance to *S. exigua* herbivory by boosting Pi uptake, but, at the same time, AM symbiosis interfered with the resistance-related phenotype by partially counteracting the jasmonate burst triggered upon herbivore attack (183). Along similar lines, Pi availability has been also proposed to contribute to the AM-triggered modulation of resource allocation to either resistance or growth upon herbivory (34). These results support the idea that AM symbiosis can lead to specific shifts in the plant defense strategy and that this phenomenon is modulated by the environment.

In this context, investigations into viral pathogens gave insightful results. Experimental evidence, primarily focused on single-stranded RNA viruses, indicates that AM colonization can boost virus multiplication, increase susceptibility, and intensify symptomatology (105, 107). This response may be attributed to the improved nutritional status of mycorrhizal plants (107). In contrast, other studies pointed to a protective effect of AM colonization on plants against viral infections (89, 106, 155, 158). In these cases, mycorrhizal plants exhibit a reduction in disease symptoms and, in general, a decrease in viral titers compared to nonmycorrhizal plants. Physiological and transcriptomic analyses revealed that AM colonization can alleviate the pronounced downregulation of genes associated with photosynthesis and the decline in the photosynthetic CO_2 assimilation rate induced by Cucumber mosaic virus infection (106). From these data, tripartite interactions between viruses, AM fungi, and plants thus appear to be complex systems in which different factors, including viral pathogen lifestyle, plant–virus combination, plant nutritional status, and timing of interaction, contribute to the final outcome (106).

3.2. Mycorrhiza-Induced Resistance

AM colonization triggers an important transcriptional and metabolic reprogramming in roots (25, 45, 93, 132, 148). The changes extend, although to a lesser extent, to aboveground organs (44, 45, 52, 82, 98, 134, 140). Some of these changes, such as elevated basal levels of certain secondary metabolites, altered hormone levels, or some structural changes in the plant cell wall, may directly contribute to the induced resistance phenotype in MIR. Still, MIR seems to largely rely on an enhanced defensive status in mycorrhizal plants, leading to more efficient activation of defenses upon attack—i.e., defense priming—not only in the colonized tissues but also in distal parts (66, 121, 134, 140). Defense priming is a form of plant immunological memory in which a first stimulus (the priming stimulus) is perceived by the plant as a warning signal, leading to a minor and transient activation of defenses. This first challenge is memorized by the plant and leads to a superactivation of defenses upon subsequent attack by a pest or pathogen (28, 96, 101). Priming is proposed to be an adaptive, low-cost defensive mechanism because defense responses are not, or only slightly and transiently, activated by the priming stimulus. Instead, defense responses are deployed faster and/or stronger upon the perception of a later attacker (96). Priming appears as a common feature in microbe-induced resistance, including MIR (53, 66, 119). Indeed, MIR depends on the plant genotype, confirming that it relies on the plant defensive system, and it is graft transmissible, pointing to root-derived signals being transported to the shoot (110). Although the key signal(s) mediating MIR are yet to be identified, root-derived metabolites being transported to the shoots, including lignans as yatein, have been identified and proposed to have a role in MIR against shoot fungal pathogens (140). Thus, three main aspects can be considered when addressing MIR: the changes that lead to the primed state, or MIR onset (see Section 2); the systemic signaling that allows priming of distal tissues, or MIR systemic signaling; and the MIR display, referring to the

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Defense priming: physiological state in which a plant is conditioned for a faster or enhanced activation of defenses in response to challenges

differential defensive responses to the aggressor attack occurring in mycorrhizal plants that lead to the induced resistance phenotype (**Figure 3**).

3.3. Priming of Plant Defenses During Mycorrhiza-Induced Resistance

Faster and/or stronger activation of a plethora of defensive traits upon pathogen or herbivore attack has been shown in mycorrhizal plants as compared to nonmycorrhizal ones. Such primed responses lead to more efficient direct and indirect defenses and include accumulation of bioactive secondary metabolites, defensive proteins, and physical barriers, as reported in several pathosystems in mycorrhizal plants (63, 134, 137, 139, 143, 149, 150, 153). Although most studies addressing mycorrhizal priming of plant defenses used simplified (or sterile) soils, defense priming and MIR have also been shown in real, microbiologically complex soils. The use of nontargeted 'omic approaches has contributed to elucidating the plasticity of MIR-associated responses, because diverse signaling and biosynthetic pathways are regulated during the display of MIR, depending on the interacting partners—plant and pathogen/pest species and AM fungus—involved (53). Nonetheless, multiple experimental studies and a meta-analysis focused on the key pathways regulating plant–microbe–insect interactions point to phytohormones as major regulators shaping the outcomes, with jasmonate signaling playing a key role in IR triggered by beneficial microbes, including AM fungi (53, 119, 123).

3.3.1. Priming of direct defenses.
Large-scale analysis of MIR transcriptomes and metabolomes of different plant species confirms that MIR display is commonly associated with primed activation of broad-spectrum defense responses (45, 92, 106, 134, 140). Upon pathogen or herbivore attack, mycorrhizal plants display a stronger transcriptional upregulation of defense-related proteins (22, 34, 137, 149, 153), primed accumulation of defensive secondary metabolites (92, 116, 134, 140), and improved structural barriers such as callose deposition (30, 117, 139). For instance, papilla formation prevented *Phytophthora parasitica* infection in roots of mycorrhizal tomato plants, reducing pathogen spread and disease development (30). This papilla formation was observed in non-AM-colonized parts of mycorrhizal plants, confirming the systemic character of this priming effect for more efficient activation of physical barriers. Recently, analysis of the plant responses to the necrotrophic pathogen *Botrytis cinerea* revealed enhanced callose accumulation in leaves of mycorrhizal tomato plants at the pathogen penetration points. The use of the callose inhibitor 2-deoxy-D-glucose abolished MIR, supporting the relevance of this mechanism in preventing pathogen proliferation in plant tissues (139). Remarkably, the primed callose deposition was associated with enhanced starch degradation rate in mycorrhizal plants and increased transcription of genes coding for sugar transporters and invertases, the vesicular trafficking proteins ATL31 and SYP121, and the callose synthase PMR4. These results highlight the importance of sugar mobilization and vesicular trafficking in the priming of callose deposition in MIR. Indeed, carbohydrate content and distribution are altered in roots and shoots of mycorrhizal plants (91, 135). As sugar transport is relevant in plant–pathogen interactions (17), additional functions of AM-mediated changes in carbohydrate levels and distribution in MIR are plausible. Besides changes in sugar mobilization, a wide modulation of plant primary metabolism has also been reported in mycorrhizal plants (25, 52), including changes in amino acid content (25, 176). In some cases, the changes have been related to enhanced pathogen or pest resistance (92).

The impact of mycorrhizal colonization on plant secondary metabolism has been amply described. First, important changes occur in colonized roots and include enhanced accumulation of oxylipin-related compounds, cell wall–bound phenolics, lignans, alkaloids, and phenylpropanoids, which can also be of biotechnological interest (190). Primed accumulation of defensive compounds

has also been shown in aboveground tissues of mycorrhizal plants upon challenge with pathogens and pests. For example, mycorrhizal tomato showed primed accumulation of alkaloids such as physostigmine (eserine), huperzine A, and cotinine; phenylpropanoid poliamine conjugates such as feruloylputrescine and feruloylagmatine; and fatty acid derivatives such as 4-oxo dodecanedioic acid and azelaic acid upon challenge with the herbivore pest *S. exigua* (134), or lignans such as yatein in *B. cinerea*–attacked plants (140). Similarly, primed accumulation of malic acid and flavonoids, such as coumaric acid and diconiferyl alcohol, was observed in mycorrhizal citrus challenged by the spider mite *Tetranychus urticae* (91). The antimicrobial/antiherbivore properties of some of the identified compounds have been functionally confirmed: Yatein inhibited *B. cinerea* growth (140), and physostigmine and 4-oxo dodecanedioic acid inhibited *S. exigua* survival and development (134), whereas malic acid or a blend including malic acid, coumaric acid, and diconiferyl alcohol reduced *T. urticae* damage on citrus leaves (92). These functional analyses of primed compounds confirm that primed responses related to MIR are efficiently controlling the different aggressors. These results further illustrate the plasticity of defense priming associated with MIR: Different compounds may be primed in different systems.

It is worth mentioning that changes in root exudate composition induced by AM symbiosis can reduce infestation by parasitic plants (42, 79). In particular, it has been shown that root exudates of mycorrhizal plants have a lower content of SL compared to nonmycorrhizal plants (84), possibly as a mechanism related to AOM (111). As SL are potent germination stimulants for seeds of root-parasitic plants, mycorrhizal plants are likely less susceptible to parasitic plant infestation.

3.3.2. Priming of indirect defenses.
Indirect defense in plants occurs when plants promote/increase the attraction of the natural enemies of the attacking herbivore. For instance, following herbivore attack, plants emit volatile blends that attract natural enemies of herbivores (35). The AM symbiosis can alter plant traits involved in indirect defenses, contributing to enhanced resistance to insect herbivores. Among those, one of the most widely studied is the release of herbivore-induced plant volatiles (HIPVs), which serve as cues for foraging herbivore predators or parasitoids. Several studies have shown mycorrhizal-triggered alterations in HIPV profiles in different plant species, including changes in the emission of leaf green volatiles, monoterpenes, and sesquiterpenes (5, 78, 102, 116, 142). Some of these changes were concomitant with a higher attraction to herbivore enemies. For example, mycorrhizal colonization enhanced the production of the sesquiterpenes β-ocimene and β-caryophyllene induced by the two-spotted spider mite *T. urticae*, resulting in an enhanced attraction of the predatory mite *Phytoseiulus persimilis* (142). Along similar lines, mycorrhizal colonization of tomato plants enhanced the emission of the monoterpene α-terpinene, resulting in an enhanced attraction of the omnivorous predator *Macrolophus pygmaeus* (116). Notably, in these cases, mycorrhizal colonization did not increase the emission of these volatiles in the absence of herbivory but boosted their release upon herbivore attack, supporting a possible role of priming indirect defenses in MIR. This is not surprising, as the oxylipin pathway, which can be primed by mycorrhizal colonization (see Section 4.2), is involved in volatile biosynthesis (36). It is worth mentioning that although there are some examples in which AM fungi increase the attractiveness of their host plants to herbivore natural enemies, their effects on HIPV release are not always consistent and are highly context-dependent (78, 102, 171).

Although less explored, AM colonization can affect other plant traits related to indirect defenses. Enhanced levels of secondary metabolites may increase larval developmental time and, hence, the time available for successful attack by natural enemies, or may change herbivore quality for natural enemy consumption or parasitism (130). Moreover, AM symbiosis can alter extrafloral nectar composition, which is an effective indirect defense attracting carnivorous arthropods, particularly ants (73).

4. REGULATION OF PLANT IMMUNITY DURING MYCORRHIZA-INDUCED RESISTANCE

Multiple experimental pieces of evidence illustrate the prevalence of MIR in different plant species and the relevance of priming cellular and biochemical defenses in MIR. However, our knowledge of the underlying regulatory mechanisms is still very limited. IR mechanistic studies have greatly benefitted the tools of the pioneer model system involving *Arabidopsis thaliana* and the rhizobacteria *Pseudomonas simiae* WCS417, which has allowed the uncovering of molecular mechanisms regulating microbe-triggered IR (119, 120, 163). Some of them were shown to be conserved across diverse IR biological systems. A prominent example is the discovery of the central role of jasmonic acid (JA) signaling (119) and the root transcription factor MYB72 (164) in the regulation of IR by WCS417 in *Arabidopsis*, which was later demonstrated in a wide diversity of biological systems, including other IR-triggering beneficial bacteria and fungi (53, 100, 118, 145). However, the fact that *Arabidopsis* is a nonmycorrhizal plant species limited the potential for translating the mechanistic discoveries on IR from this model to MIR. Particularly, the challenges for conducting genetic approaches required for disentangling IR regulation in plants other than *Arabidopsis* have hampered advances in MIR regulation. Also, the difficulties associated with the obligate biotrophy of AM fungi, challenges in their in vitro cultivation, and the lack of genetic transformation protocols (74, 125) have limited the identification of specific fungal molecules and metabolites involved in the onset of MIR. An additional obstacle is the difficulty of dissecting mechanisms exclusively regulating MIR, as several plant signaling mutants have altered mycorrhizal establishment (61). VIGS (virus-induced gene silencing) has been used to explore the role of some genes in MIR (191). Grafting experiments combining wild-type rootstocks and mutant scions would be useful to uncover the role of the mutated trait in the MIR phenotype aboveground while allowing fully functional AM symbiosis establishment in roots. Despite the technical challenges, a significant effort has been made over the past decade to uncover the main plant genetic pathways that regulate MIR, and we are now just starting to understand the mechanisms underlying MIR and the main factors influencing its output.

4.1. Role of Small Signaling Molecules in Mycorrhiza-Induced Resistance Regulation

Although the hormonal regulation of MIR and MIR-related priming is being elucidated (see Section 4.2), other regulatory aspects remain obscure. In fact, the molecular mechanisms responsible for the stress memories and defense priming in plants are now being described mostly in model plants: the establishment and maintenance of immunological memory in plants upon perception of the priming stimulus have been associated with elevated levels of certain transcription factors and pattern recognition receptors, differential accumulation of mitogen-activated protein kinases (MAPKs), and epigenetic changes in DNA methylation and histone modifications (28, 58). Interestingly, mycorrhizal colonization induced transcriptional changes in diverse defense-related *WRKY*, *MYB*, *bHLH*, *bZIP*, and *AP2/EREB* transcription factors (44, 81, 82) and led to a significant upregulation of *MAPKs*, along with a concomitant enhanced response to pathogens (174). Moreover, it has been observed that root colonization by AM fungi triggers changes in DNA methylation levels in roots and shoots of the host plant (167, 168).

Small RNAs have also been deemed important regulators in the gene networks orchestrating AM development, and systemic responses to mycorrhization may also be linked to small RNA-regulated processes (75). Differentially expressed small RNAs were identified in leaves of AM-colonized plants; in silico analysis predicts that some of them target genes related to the biosynthesis or modification of cell wall components (103). It was thus hypothesized that plant

cell wall remodeling contributes to the induction by AM symbiosis of a priming state that leads to increased resistance to foliar pathogens (103). Recently, a plant miRNA, upregulated in mycorrhizal tomato leaves infected by *Phytophthora infestans*, was shown to target a TCP transcription factor controlling SA-mediated defense and resistance (191).

The onset of defense priming triggered in plants by different stimuli, such as wounding, PAMPs, insect feeding, chemical treatments, and root colonization by other beneficial microbes, has also been associated with specific alterations in the levels of Ca^{2+}, ROS, and NO (28, 101). Noticeably, alterations in Ca^{2+} fluxes and ROS and NO levels are also triggered in roots by mycorrhizal colonization (see Sections 2.1 and 2.3). This might hint at a possible role of these signaling molecules in the establishment of the priming state upon mycorrhizal colonization, but experimental evidence is still lacking. To what extent this immune modulation leading to MIR lasts along the plant life and whether it can be transmitted to the progeny is still an open question. These aspects deserve further investigation, as they are of fundamental relevance in the exploitation of MIR for crop protection.

4.2. Hormonal Regulation of Mycorrhiza-Induced Resistance

Hormonal signaling networks connect perception and early signaling to broad transcriptional reorganization and defense induction in plants. Among hormonal pathways, JA signaling is well established as the core pathway that regulates IR triggered by beneficial bacteria and fungi, including AM fungi (53, 65, 119). Several studies have reported a higher accumulation of jasmonates in mycorrhizal roots, including JA, its precursor 12-oxophytodienoic acid (OPDA), and its bioactive molecule jasmonoyl-isoleucine (JA-Ile), and enhanced transcriptional activation of the 13-lipoxygenase branch of the oxylipin (13-LOX) pathway, which leads to the production of JA (85, 133). Moreover, upon pathogen or herbivore attack, mycorrhizal plants frequently display higher accumulation of jasmonates, higher expression levels of JA biosynthesis genes, and JA-regulated defense marker genes (80, 137, 140, 143, 149, 153). It is noteworthy that JA signaling also regulates plant secondary metabolism (141); therefore, primed JA signaling may mediate the stronger accumulation of defensive compounds observed in mycorrhizal plants upon challenge. For example, mycorrhizal tomato challenged by *S. exigua* displayed primed accumulation of certain alkaloids, fatty acid derivatives, and phenylpropanoid-polyamine conjugates with antiherbivore properties (134), and there is evidence of a positive role of JA signaling in the regulation of their biosynthesis (23). Moreover, the 13-LOX pathway is involved in volatile biosynthesis (36), so primed regulation of this pathway may underlie the boosted indirect defense responses reported in mycorrhizal plants.

Genetic approaches have further demonstrated the key role of JA signaling in the regulation of MIR against pathogens and pests. For instance, the tomato mutant line *jai1* (*jasmonic acid–insensitive1*), defective of the homolog of *Arabidopsis* CORONATINE-INSENSITIVE1 (COI1), is ineffective in MIR against the herbivore *Helicoverpa armigera* (153). Along similar lines, *spr2* (*suppressor of prosystemin-mediated responses2*) and *spr8* (*suppressor of prosystemin-mediated responses8*), which are impaired in wound-induced JA biosynthesis, failed in mounting MIR against the pathogens *Alternaria solani* (149) and *F. oxysporum* (173), and against the herbivore *H. armigera* (153). Accordingly, *jai1*, *spr2*, and *spr8* tomato lines are impaired in the deployment of MIR-triggered immune responses, including the expression of JA-regulated defense-related genes and overaccumulation of JA-regulated secondary metabolites (149, 153, 173). Besides the model plant tomato, silencing of the lipoxygenase gene *LOX2* in *Phaseolus vulgaris* L. blocked MIR expression against the pathogen *Sclerotinia sclerotiorum* (110).

Although all this evidence supports the role of mycorrhiza-related elevated JA levels in promoting MIR, its role may be more complex. The tomato mutant line *def-1*, which is impaired in

wound-induced JA biosynthesis, displayed MIR against the herbivore *S. exigua* (46). The authors hypothesized that residual JA levels or other oxylipins accumulating in this line can be sufficient for MIR expression. Strikingly, lower activation of JA signaling has also been reported in some mycorrhizal plants (183). JA signaling seems to play a pivotal role in prioritizing the mycorrhizal effects on the host plant according to its needs. For example, in mycorrhizal tomato, boosted expression of JA-regulated defense genes and MIR against the pathogen *B. cinerea* and the herbivore *S. exigua* was dependent on Pi availability (34). The study suggested that phosphorus availability controls the activation of JA-dependent priming in tomato by regulating the JA transcriptional repressors *JAZ1* and *JAZ2*, key regulators of JA-dependent growth/defense responses (34, 108). These results illustrate that the plant genotype and nutrient availability might exert a strong influence on the specific role of JA signaling in MIR (see Section 5).

Beyond JA signaling, other phytohormones shape plant immune responses and modulate JA-triggered responses through cross-talk. Indeed, the salicylic acid (SA), ethylene (ET), and abscisic acid (ABA) pathways are known regulators that fine-tune the JA-dependent responses activated upon specific challenges (1). As described above, not only JA but also SA, ET, and ABA levels are modulated in plants by mycorrhizal colonization, mostly in roots, and hormone homeostasis may also be altered in shoots (41, 95, 98, 124, 132). Thus, other phytohormonal pathways are likely to contribute to MIR, directly or indirectly, by interacting with the JA pathway, but empirical evidence is scarce. A recent study demonstrated that ET signaling is essential for MIR against herbivores in tomato (81). Mycorrhizal colonization primed JA and ET biosynthesis and signaling upon herbivory by *S. exigua* or *Manduca sexta*. Tomato lines deficient in ET synthesis or perception failed to display mycorrhiza-associated primed JA accumulation and were unable to develop MIR against the herbivores. Thus, genetic analysis confirmed the role of ET signaling in MIR, likely acting as a positive regulator of JA biosynthesis.

Multiple studies also report altered ABA levels in mycorrhizal plants, and this has been related mostly to improved tolerance to abiotic stress, but the role of ABA in modulating MIR is mostly unexplored. The role of ABA in disease resistance is complex (160). Nonetheless, altered ABA levels in shoots of mycorrhizal plants have been suggested to be related to MIR against *B. cinerea* in tomato (43), and differential regulation of ABA signaling has also been observed in mycorrhizal tomato plants upon herbivory (81). Moreover, ABA is also a key regulator of callose deposition. Because evidence supports a key role of primed callose accumulation during MIR in roots and shoots (30, 139), a positive role of ABA in regulating differential callose deposition is plausible. A pivotal role for hormonal cross-talk, particularly the interplay between SA, JA, and ABA, has also been proposed in regulating plant–AM fungi–virus interactions (106).

5. INTERPLANT COMMUNICATION VIA COMMON MYCORRHIZAL NETWORKS CAN PROMOTE MYCORRHIZA-INDUCED RESISTANCE IN NEIGHBORING PLANTS

A feature of many mycorrhizal fungi, including AM fungi, is their ability to develop a large extraradical mycelium in the soil that can simultaneously colonize adjacent plants of the same or different species, leading to common mycorrhizal networks (CMNs). This feature in AM fungi is favored by the lack of specificity in the interactions between plants and fungi. CMNs are suggested to play important roles in ecosystems, from capture and distribution of nutrient resources to transmission of defense signals (3, 177). However, the structure and function of CMNs, especially in nature, are still poorly characterized, and their role in ecosystems may have been overestimated (3, 68). Under controlled conditions, CMNs of AM fungi can convey defense signals from a pathogen-infected or pest-infested plant (usually referred to as a donor plant) to a neighboring uninfected plant (referred to as the receiver) (**Figure 4**). This phenomenon was

Common mycorrhizal networks (CMNs): underground networks created by mycorrhizal fungal hyphae that connect the roots of multiple plants of the same or different species
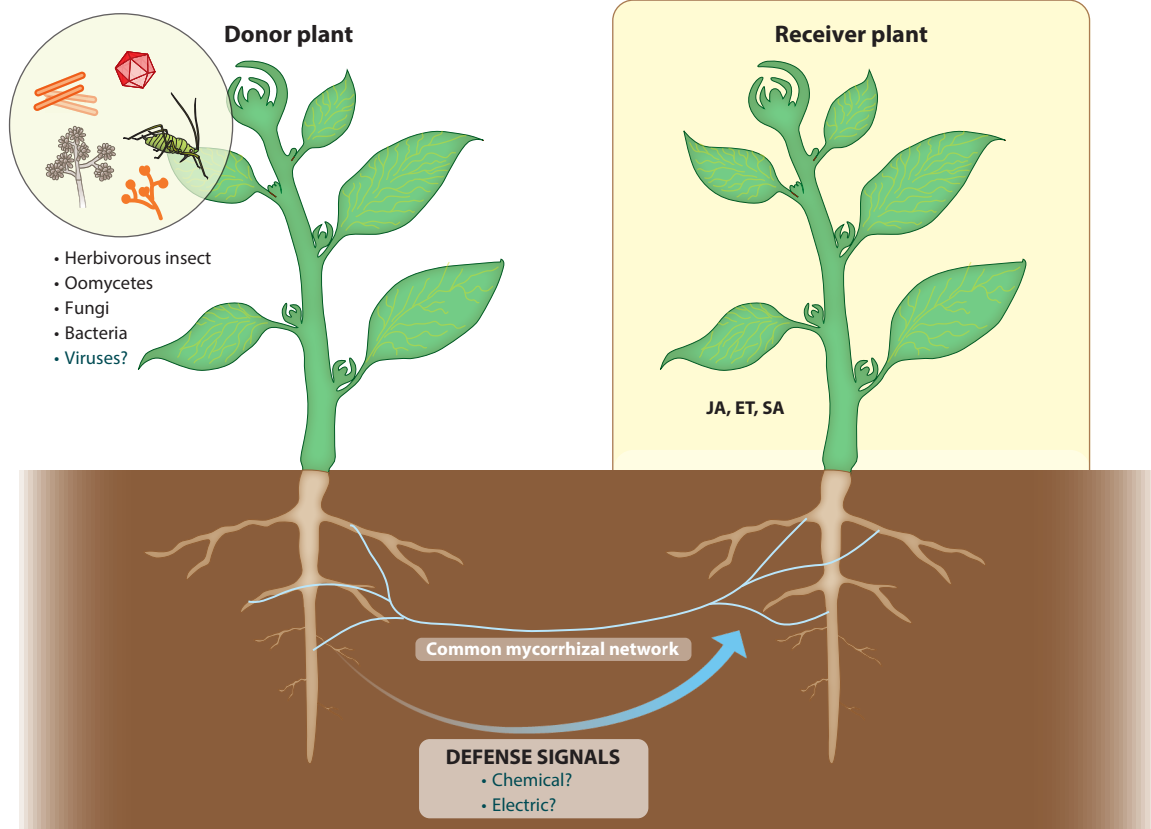
Figure 4

Modulation of plant defenses mediated by common mycorrhizal networks. Defense signals can be transmitted from an infected/infested plant (donor) to an adjacent plant (receiver) through the common mycorrhizal networks. This phenomenon has been observed in donor plants infected by bacteria, fungi, and oomycetes or infested with herbivorous insects. Jasmonate (JA), ethylene (ET) (2, 150, 152), and salicylic acid (SA) (154, 189) have been shown to contribute to plant responses in the receiver plants.

observed in different plant species (tomato, potato, tobacco) and in cases of different foliar biotic stresses, such as herbivorous insects (6, 152), elicitors (150), pathogenic fungi (154), oomycetes (2), and bacteria (189). No data are currently available for plant viruses. Interestingly, the transmission of defense signals between plants through a shared mycelial network might not be exclusive to AM fungi, as it was also observed in the ectomycorrhizal fungus *Wilcoxina rehmii* (151) and the endophytic fungus *Serendipita indica* (162).

These findings raised several questions, mainly about the specificity of the signals regarding the species of plants among which the warning signal can be transferred or the pathogens/pests toward which the defense is activated. Also, we have limited knowledge of the efficacy of the alert signal: Are receiver plants less susceptible to pathogens/pests, and how long does this protection last? Another black box is the nature of the mobile signals transferred (65). Depending on the system, the time of defense activation in neighboring plants occurred from 6 h to 100 h after the donor plant was challenged by the attacker (2, 6, 150). So far, investigations have explored the molecular responses in the receiver plants in terms of expression of genes—but no genome-wide transcriptomic data are available—and quantification of hormones and metabolites related to

defense. In a few cases, mutant lines, impaired in pathways related to hormone metabolism, were considered. Indeed, JA, ET (2, 150, 152), and SA (154, 189) have been shown to contribute to plant responses in the receiver plants (**Figure 4**). Although experimental setups to establish and properly test the biological functions of CMNs are extremely challenging, especially in field conditions (68), further investigations are needed to solve the many open questions and understand whether CMNs can be exploited in sustainable agricultural practices to reduce plant diseases. In this context, it will also be important to consider that soil management practices such as tilling negatively interfere with the ability of AM fungi to develop extraradical hyphae and then extend CMNs (177).

# 6. THE CONTEXT DEPENDENCY OF MYCORRHIZA-INDUCED RESISTANCE

A common feature of microbe IR is its high context dependency, with variable effects depending on factors such as soil nutrient availability, plant and microbe identities and diversity, and environmental conditions, among others (76). Accordingly, MIR display seems to be modulated by the fungal and plant genotypes and the biotic and abiotic environments (**Figure 5**). Thus, the triggering of MIR is not only an inherent fungal trait by itself but depends on the fungal interaction with the host plant and the environment. We describe below several relevant biotic and abiotic factors that can modulate MIR onset and display.

6.1. Impact of the Abiotic Context on Mycorrhiza-Induced Resistance Functioning

Among abiotic factors, phosphorus is the most influencing nutrient that drives the establishment of AM symbiosis (see the sidebar titled Arbuscular Mycorrhizal Symbiosis: The Colonization Process). Moreover, phosphorus availability can also affect plant immune signaling during MIR display. Specifically, Pi availability and the phosphorus status of the plant play relevant regulatory roles in the activation of JA-dependent defenses in mycorrhizal plants (34, 128, 183). This is not surprising, as a link has been established between JA and phosphorus starvation signaling pathways during the activation of plant immunity (70). Interestingly, it has been hypothesized that the mycorrhizal Pi uptake pathway can regulate the activation of JA-dependent defenses against herbivory in *Medicago* (183).

Nitrogen availability can also have a strong impact on the expression of MIR. A transient nitrogen starvation of AM tomato plants led to a partial impairment of MIR against *B. cinerea* (137). Indeed, defense-related responses that were activated by MIR such as enhanced callose deposition, NRT2 transcript induction, and OPDA and indolic derivative accumulation were repressed or reduced when tomato plants were subjected to nitrogen starvation. Along similar lines, MIR triggered in maize against the herbivore *S. exigua* was abolished when plants were grown under nitrogen-deficiency conditions (129). In this case, this effect has been attributed to AM-triggered alterations in carbon/nitrogen leaf concentrations.

Besides nutrient availability, further abiotic factors that can strongly affect MIR functioning are water regime and light intensity (114, 126, 128) (**Figure 5**). For example, MIR to *Spodoptera littoralis* was found to be more efficient under drought conditions in tomato plants (114). Volpe and colleagues (171) showed that under drought stress, increased methyl salicylate levels in volatiles of mycorrhizal tomato plants led to greater attraction of the aphid parasitoid *Aphidius ervi* than in nonmycorrhizal ones. Finally, higher light intensity boosted MIR in lettuce against *B. cinerea* (126). These data emphasize the need to conduct research that considers multiple stresses/conditions, bringing experimentation closer to field and real production conditions.
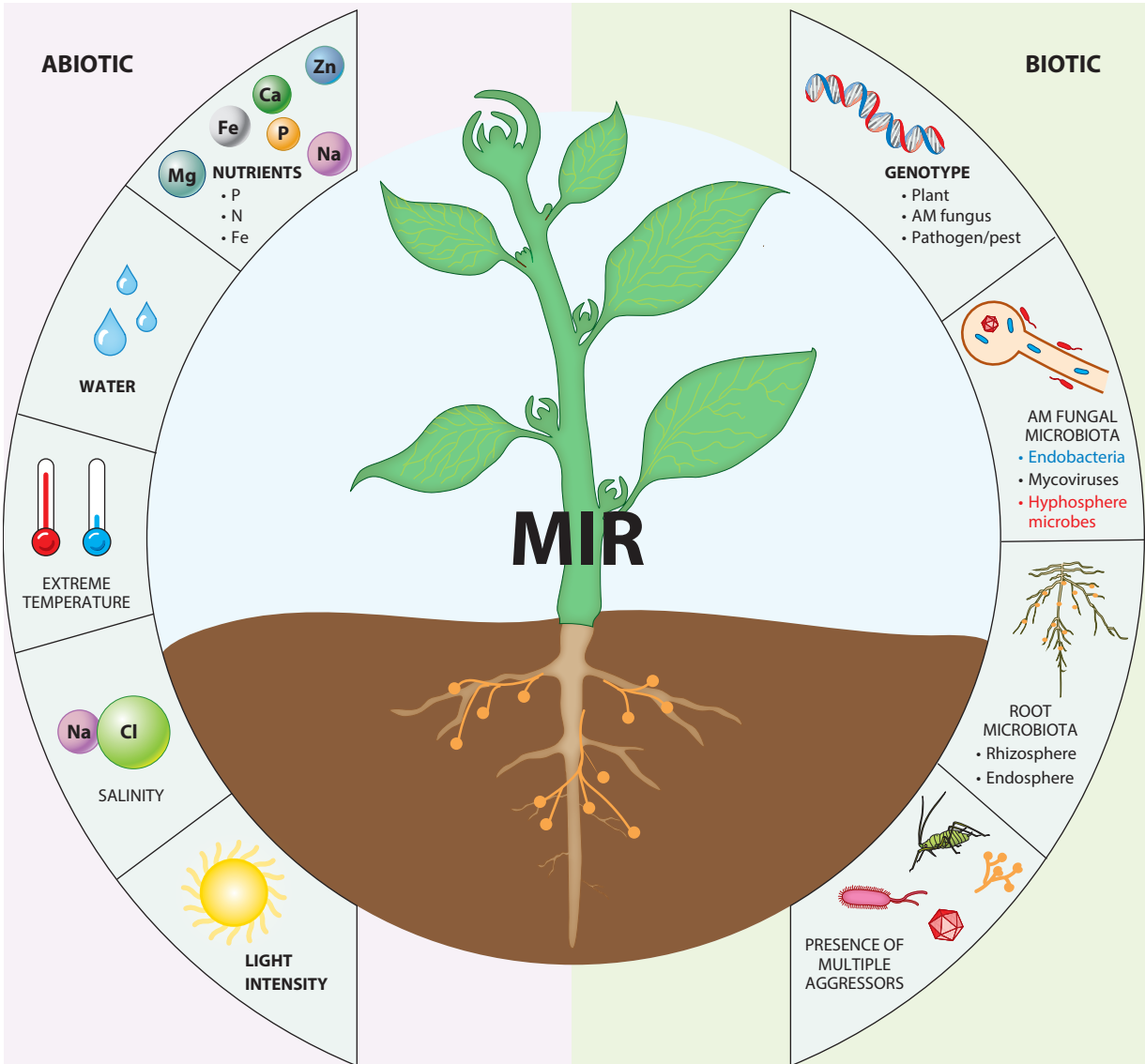
Figure 5

Mycorrhiza-induced resistance (MIR) display and efficiency are under the influence of biotic and abiotic factors. Factors already shown to have an impact on MIR are indicated in bold. Abbreviation: AM, arbuscular mycorrhizal.

6.2. Impact of the Biotic Context on Mycorrhiza-Induced Resistance Functioning

Several studies have shown how the outcomes of MIR also vary with different AM fungal and plant genotypes (21, 33, 54, 109, 129). However, the mechanistic basis of such differences has been only partially addressed. Studies comparing different AM fungal species evidenced their differential impact on phytohormonal signaling and transcriptomic and metabolomic profiles (41, 132, 133). This could underpin the greater ability of some species to trigger MIR; for example, *Funneliformis*

mosseae triggered a stronger modulation than *R. irregularis* in the host root metabolome (41, 132, 133) and usually led to enhanced protection (98, 128). However, this is not a general pattern and may also depend on the fungal strains and plant genotypes (37, 54). Noticeably, the high intraspecific genetic variability of AM fungi (180) could also be reflected in a different ability to induce MIR; however, this aspect has not yet been properly addressed. Genome sequencing data and functional studies will be instrumental in revealing the AM fungal genetic determinants controlling MIR.

A further level of genomic complexity is shown via the fact that many AM fungi contain endobacteria (15) as well as mycoviruses (40, 161), which are emerging as hidden players in AM symbiosis. Almost no functional data are currently available for mycoviruses, but a virus-free strain of *Glomus* sp. produced a greater number of spores and promoted plant growth more efficiently than the strain containing the virus, indicating that viruses may be biologically active components in the symbiosis (62). Investigations on the AM fungus *Gigaspora margarita* showed that its endobacteria have a relevant impact on fungal physiology (136) and trigger molecular changes in host plants (169). Notably, transcriptomic and proteomic profiles revealed that some plant genes related to disease resistance seem to be exclusively elicited by the endobacteria-containing fungus (162), suggesting that the endobacteria could contribute to plant defenses and MIR.

It is worth mentioning that in nature, AM fungi are not the only ones colonizing plant roots, and, in particular, they have been shown to play a key role in determining the composition of the root microbiome (59). Also, extraradical hyphae of AM fungi are able to recruit, thanks to fungal exudates, specific microbial communities in a narrow zone called the hyphosphere that can have an impact on symbiotic functions such as Pi uptake (172). Whether and to what extent the onset of MIR induced by AM fungi depends on associated bacteria or other microbes, including those present within plant tissues, deserves further investigation. A recent study revealed that soil microbiome indicators, rather than other soil parameters such as nutrient availability, can predict plant growth response to inoculation with AM fungi (87). It is noteworthy that the abundance of fungal pathogens in the soil best explained the success of AM fungal inoculation (87). These findings link the benefits of mycorrhizal inoculation to soil pathogen protection and provide cues for the development of diagnostic tools to predict the success of mycorrhizal inoculation under field conditions.

Studies addressing compatibility and complementarity between AM fungi and other well-characterized biocontrol bacteria and fungi are essential to develop multifunctional and versatile biological control products based on microbial consortia for plant protection against a wider range of diseases (104).

7. CONCLUDING REMARKS

There is an urgent need for the development of sustainable alternatives to chemical pesticides in food production. In response, understanding the impact of plant-associated microbiota on plant health and the biotechnological application of beneficial microbes for crop protection is a blooming field of research.

Within the plant microbiota, AM fungi and their intimate association with plants represent a unique, fascinating, but also challenging, system for the dissection of plant–microbe interactions, in particular, the study of how beneficial microbes modulate plant immunity to reach and maintain a stable mutualism while enhancing host resistance to biotic aggressors.

The availability of complete, and now even high-quality, chromosome-level genomes of AM fungi already offers opportunities to better understand AM fungal biology and its complex interaction with host plants. Specifically, we envisage that these genomic data will be exploited to

Hyphosphere: narrow region of soil influenced by hyphal exudates; it hosts distinct microbes that could significantly contribute to nutrient mobilization and possibly other functions

unravel major factors involved in overcoming plant immunity during colonization, for example, through the characterization of the large number of putative effectors that have been identified. These genomic resources will pave the way for a more comprehensive and holistic view of how the AM symbiotic system works.

We are now just starting to uncover the molecular mechanisms underlying MIR regulation. MIR seems to largely rely on an enhanced alert status in AM-colonized plants, leading to a stronger activation of defenses upon attack at both local and systemic levels. The primed defense responses in mycorrhizal plants include accumulation of bioactive secondary metabolites, defensive proteins, and physical barriers such as callose. However, the molecular mechanisms that regulate the onset of MIR-related priming remain to be uncovered. Omics, genetic, and biochemical approaches on both plants and fungal symbionts will help decipher the intriguing alliance between AM symbiosis and plant immunity, but we anticipate that other factors, not yet sufficiently addressed, may be important; for example, epigenetic changes are likely to be involved, and these changes could also provide means to transmit MIR over generations, a feature of large interest in crop protection yet to be explored.

MIR can be sensibly exploited in agriculture by using specific plant–fungal combinations and considering the environmental (biotic and abiotic) conditions that maximize MIR effects. AM fungi–associated bacteria as well as endobacteria and mycoviruses infecting AM fungi, which are emerging as hidden players in AM symbiosis, should also be considered for their potential in influencing the mutualistic association and MIR. Increasing our knowledge of the molecular mechanisms that regulate MIR functioning and its context dependency will be instrumental in the application of MIR as a biotechnological tool for controlling pests and diseases in sustainable agriculture.

SUMMARY POINTS

1. AM fungi overcome plant defenses through the modulation of different signaling pathways involving chitin oligomers, plant receptors, fungal effectors, and phytohormones.

2. The impact of AM symbiosis on plant interaction with pathogens and pests may result from changes in plant tolerance and/or resistance phenotypes.

3. MIR is commonly associated with primed activation of broad-spectrum immune responses leading to enhanced accumulation of defense-related proteins, defensive secondary metabolites, callose deposition, and altered profiles of volatile compounds.

4. Biochemical, molecular, and genetic approaches have demonstrated the key role of JA signaling in the regulation of MIR against pathogens and pests, and evidence is emerging for other hormones such as ET and ABA.

5. The plant and fungal mechanisms involved in MIR onset and display remain obscure. Systems biology approaches, including untargeted and functional analyses, are instrumental for in-depth insight into MIR functioning.

6. MIR can be strongly modulated by the abiotic context, including nutrient availability and environmental conditions. Biotic factors, such as fungal and plant genotypes, and AM fungi–associated microbiota can also influence MIR outcomes.

7. MIR is a highly promising biotechnological tool for controlling pests and diseases in the frame of sustainable agriculture.

FUTURE ISSUES

1. To better understand the regulation of plant immunity during root colonization by AM fungi, extensive characterization of the many candidate effectors identified in AM fungal genomes is needed; in this context, the role of small RNAs by both plant and fungus, including their possible involvement in cross-kingdom RNA interference, must also be elucidated.

2. Further investigations are needed to identify the determinants of AM fungi leading to the elicitation of MIR and to identify mobile signals that contribute to the activation of systemic defenses in MIR.

3. It would also be important to determine how long-lasting MIR is over the plant life and whether it persists over generations.

4. The extent and manner in which MIR is transmissible from plant to plant through common mycorrhizal networks also merit further study.

5. Outstanding questions are whether and how the regulation of MIR differs from that operating in other IR models, or whether the MIR phenotypes have adaptive and/or evolutionary consequences for pathogens and insects that interact with MIR-presenting plants.

6. The complexity of the microbiota associated with AM fungi, from that living within the fungus to that living on the hyphal surface, and its contribution to symbiotic functions and MIR should be explored.

7. There is also a need to expand translational research to define how to exploit the use of MIR as a biotechnological tool for crop protection in sustainable agriculture.

DISCLOSURE STATEMENT

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