Mycorrhiza-induced resistance: more than the sum of its parts?

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Plants can develop an enhanced defensive capacity in response to infection by arbuscular mycorrhizal fungi (AMF). This 'mycorrhiza-induced resistance' (MIR) provides systemic protection against a wide range of attackers and shares characteristics with systemic acquired resistance (SAR) after pathogen infection and induced systemic resistance (ISR) following root colonisation by non-pathogenic rhizobacteria. It is commonly assumed that fungal stimulation of the plant immune system is solely responsible for MIR. In this opinion article, we present a novel model of MIR that integrates different aspects of the induced resistance phenomenon. We propose that MIR is a cumulative effect of direct plant responses to mycorrhizal infection and indirect immune responses to ISR-eliciting rhizobacteria in the mycorrhizosphere.

Mycorrhiza-induced resistance (MIR)

Mycorrhizal symbiosis is a mutualism between plants and mycorrhizal fungi during which photosynthetic products are exchanged for soil-derived mineral nutrients [1]. The true age of this relationship and the extent of host–mycorrhiza coevolution has been revealed by fossil evidence and phylogenetic analyses [2,3], dating the emergence of this symbiosis to 450 million years ago. It has been estimated that 80% of plant species retain these ancient arbuscular mycorrhizal associations [1], illustrating the importance of this mutualism to both partners.

Research on plant–mycorrhiza interactions has mostly focussed on the physiology of nutrient-for-carbon exchange and plant signal-transduction pathways controlling the interaction. Comparatively little is known about the mechanisms conferring non-nutritional benefits by mycorrhiza, such as suppression of soil-borne diseases and enhancing plant resistance to pests and diseases [4]. Plants routinely signal to conspecific organisms in the rhizosphere by releasing primary and secondary metabolites from their roots. Some of these metabolites recruit beneficial microbes, including AMF. Furthermore, AMF infection is known to stimulate biological activity in the rhizosphere, a phenomenon commonly referred to as the 'mycorrhizosphere effect' [5] (Box 1). This effect includes the attraction and selection of specific bacterial strains, such as plant growth-promoting rhizobacteria (PGPR) that possess the capacity to enhance plant growth and suppress pests and diseases. Some of these mycorrhizosphere-inhabiting bacteria can act as 'mycorrhiza-helper bacteria' and promote the efficiency of mycorrhizal symbiosis [6] (Box 1). As a consequence of these interactions, it has been suggested that the benefits of AMF on whole-plant physiology are at least partially determined by biological activities in the mycorrhizosphere [6–8].

AMF can suppress plant pests and diseases through induction of systemic resistance [9–11]. Nutrient supply experiments have revealed that MIR cannot be attributed to improved nutritional status [12]. The induced resistance shares characteristics with both pathogen-induced SAR and rhizobacterial ISR; MIR has been associated with SAR-like priming of salicylic acid (SA)-dependent genes, but more often coincides with priming of jasmonic acid (JA)-dependent defences and cell wall defences (Table 1). Accordingly, MIR confers protection against a wide range of attackers, including biotrophic pathogens, necrotrophic pathogens, nematodes, and herbivorous arthropods (Table 1). It has been proposed that MIR is the result of active suppression of components in the SA-dependent defence pathway, causing systemic priming of JA-dependent defences [10]. However, the exact contribution of jasmonates in MIR remains unclear [13] and the long-distance signals controlling MIR remain to be resolved. Most instances of MIR have been reported for non-sterile systems. It is thus possible that MIR is not solely determined by the fungus, but that bacteria in the mycorrhizosphere have a complementary contribution to the full MIR response. Here, we present a four-phase spatiotemporal model explaining MIR as a cumulative outcome of direct plant–AMF interactions and responses to ISR-eliciting bacteria in the mycorrhizosphere (Figure 1).

Phase I: root exudation of mycorrhiza-recruiting chemicals

Plant roots exude a diverse array of biologically active compounds [14]. Estimates suggest plants can exude up to 40% of their photosynthates from roots, representing a rich source of energy for soil microbes [15]. Root exudates typically contain sugars, amino acids, carboxylic acids, phenolics, and other secondary metabolites, which all have the capacity to influence the occurrence, physiology, and behaviour of soil organisms. For the interaction between plants and AMF, strigolactones have been identified as

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Box 1. The mycorrhizosphere effect

A relatively small volume of soil around plant roots is under the direct influence of root exudates, termed the 'rhizosphere'. This zone is characterised by increased levels of microbial activity. However, 80% of all plant species form symbiotic relationships with AMF [1]. Consequently, the volume of soil influenced by plant-derived carbon via AMF can be extended to encompass the 'mycorrhizosphere'. AMF have a selective influence on microbial communities in the mycorrhizosphere. The enhanced microbial activity surrounding mycorrhizal roots compared with non-mycorrhizal roots is called the 'mycorrhizosphere effect' [5]. Having resolved that extramatrical hyphae from AMF have access to resources from a vast volume of soil, it was discovered that some mycorrhizosphere-inhabiting bacteria, called 'mycorrhiza helper bacteria' (MHB), can stimulate mycorrhizal symbioses [6]. The concept of mutualism between AMF and soil bacteria is not new. In 1962, Mosse first proposed the idea that AMF and bacteria interact directly in the soil, showing that mycorrhizal roots can enhance the survival of *P. fluorescens* bacteria [74]. Since then, multiple studies have demonstrated that MHB can promote mycorrhizal infection and symbiosis through stimulation of mycelial extension and reducing the impact of adverse environmental conditions [6]. Whether increased AMF growth and survival by MHB are due to production of growth factors, detoxification of soil allelochemicals, or antagonism of competitors and/or parasites remains unresolved [6]. With the development of metagenomics technologies and DNA-sequencing methods, the true extent of quantitative and qualitative changes in the microbial community due to AMF is beginning to emerge. The chemical basis driving mycorrhizosphere development is less well resolved, although there are indications that carbon exudation by AMF in the form of the glycoprotein glomalin plays a role [75]. This is an attractive hypothesis, given that up to 5% of active soil organic carbon pools comprise glomalin, which is recalcitrant in the soil and thus represents a 'slow-release' carbon substrate [75]. The consequences of the mycorrhizosphere effect, including recruitment of PGPRs, may not only boost nutrient mobilisation by AMF but could also provide non-nutritional benefits, such as disease suppression via antibiosis and/or competitive exclusion. Crucially, increased densities of selected rhizobacteria in the mycorrhizosphere have the potential to suppress pests and diseases in systemic plant tissues through priming of inducible defences.

important AMF-recruiting signals (Box 2). This class of terpenoid lactones, long known as germination signals for parasitic plants, stimulates hyphal branching in AMF, thereby helping the fungus to localise host roots and so facilitate infection [5,6]. Involvement of root signals in the attraction of both pathogenic and mutualistic soil organisms is not rare. For instance, root-borne isoflavones secreted by soybean can attract the endosymbiotic N-fixing bacterium *Bradyrhizobium japonicum* [16], but can simultaneously attract the pathogenic oomycete *Phytophthora sojae* [17]. Similarly, benzoxazinoid metabolites in root exudates of maize (*Zea mays*) can attract both beneficial *Pseudomonas putida* bacteria [18] and western corn rootworm [19]. From an evolutionary perspective, common attraction of mutualistic and parasitic organisms is unsurprising given the strong selection pressure on parasites to adopt the same plant signals as beneficial mutualists (Box 2).

Phase II: the plant immune system responding to AMF infection

The initial stages of root colonisation by AMF are accompanied by transient induction of selected plant defences, followed by localised suppression at later stages of the interaction [20]. It is plausible that initial induction of plant immunity is based on host recognition of microbe-associated molecular patterns (MAMPs) from the AMF. Recognition of MAMPs by pattern-recognition receptors elicits a series of signalling cascades resulting in enhanced production of the plant defence hormone SA and expression of MAMP-triggered immunity [21]. For instance, infection by *Funneliformis mosseae* (syn. *Glomus mosseae*) induces transient accumulation of SA in pea [22], whereas this response was more pronounced and permanent in symbiosis-resistant P2 pea genotypes. Hence, the initial SA response is suppressed during successive stages of AMF infection. Localised MAMP recognition and SA production can lead to production of long-distance SAR signals and cause systemic priming of SA-dependent defences [23–25]. Because most SAR studies have been conducted with AMF-incompatible *Arabidopsis*, it is difficult to draw direct comparisons between SAR and MIR. However, like SAR, MIR has been associated with systemic priming of SA-dependent defences and protection against (hemi)biotrophic pathogens (Table 1). Furthermore, the primed defence state of SAR is long lasting [26,27] and can act additively on other forms of systemic disease resistance [28]. We therefore propose that SAR-related signals during the early stages of plant–AMF interactions contribute to MIR (Figure 1).

Phase III: immune suppression by AMF and recruitment of mycorrhizosphere bacteria

The transient nature of MAMP-triggered immune responses during the early stages of mycorrhization suggest that AMF employ strategies similar to those of pathogenic fungi, which secrete specific effector molecules to suppress plant immunity and establish a successful infection [29]. A comparative transcriptome study in rice revealed striking similarities between responses to AMF and pathogenic fungi [30]. Additional evidence for active immune suppression by AMF came from the discovery that the calcium/calmodulin kinase DMI3, a central regulator in the symbiotic pathway, represses early-acting defence genes [31]. Kloppholz *et al.* [32] were the first to identify an effector protein (SP7) from *Rhizophagus irregularis* (syn. *Glomus intraradices*). This secreted protein is expressed during the initial stages of contact between the mycorrhizal fungus and roots and is translocated to the plant nucleus, where it inhibits the transcription factor ERF19 to suppress plant defence and promote infection by biotrophic fungi like *R. irregularis* [32]. AMF induce species-specific changes in defence hormones in their hosts [13,33]. Some of these hormonal changes can restrict AMF colonisation, whereas others function to promote biotrophic AMF infection. For instance, AMF promote production of the plant hormone abscisic acid (ABA) [34]. Experiments with the ABA-deficient tomato (*Solanum lycopersicum*) mutant *sitiens* have revealed that arbuscular development and functionality in tomato are dependent on ABA [35]. Because ABA can suppress SA-dependent defences against biotrophic pathogens [36,37], it is plausible that AMF stimulate ABA production in the roots to promote their