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Opinion

Mucoromycotina 'fine root endophytes': a new molecular model for plant–fungal mutualisms?

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The most studied plant–fungal symbioses to date are the interactions between plants and arbuscular mycorrhizal (AM) fungi of the Glomeromycotina clade. Advancements in phylogenetics and microbial community profiling have distinguished a group of symbiosis-forming fungi that resemble AM fungi as belonging instead to the Mucoromycotina. These enigmatic fungi are now known as Mucoromycotina 'fine root endophytes' and could provide a means to understand the origins of plant–fungal symbioses. Most of our knowledge of the mechanisms of fungal symbiosis comes from investigations using AM fungi. Here, we argue that inclusion of Mucoromycotina fine root endophytes in future studies will expand our understanding of the mechanisms, evolution, and ecology of plant–fungal symbioses.

Highlights

Mucoromycotina fine root endophytes have similar ecological functions as arbuscular mycorrhizal fungi in assisting plant nutrient uptake. The mechanisms enabling their symbiosis with plants remain largely unexplored.

The mechanisms of Mucoromycotina fine root endophyte symbioses may overlap with those regulating arbuscular mycorrhizal fungal symbioses or the plant endophytes *Colletotrichum tofieldiae* and *Serendipita indica*.

Contrasting colonisation mechanisms between Mucoromycotina fine root endophytes and arbuscular mycorrhiza fungi could provide insights into how ancient fungi facilitated the terrestrialisation of land plants.

Investigations into mechanisms of symbiosis will benefit from inclusion of Mucoromycotina fine root endophytes as these fungi are more culturable than arbuscular mycorrhizal fungi under laboratory conditions and can be grown in the absence of a plant host.

Mucoromycotina: an enigmatic group of plant symbiotic fungi

Mutualistic symbioses between plants and fungi are nearly ubiquitous, with virtually all plants forming symbiotic associations in their roots or rhizoids with certain groups of soil fungi [1]. Of these 'mycorrhizas' [2], **AM** (see Glossary) [3] associations are the most abundant and are formed by Glomeromycotinian fungi, which fall within the fungal phylum Mucoromycota [4]. AM fungi produce fine-branching hyphal structures named arbuscules that develop intracellularly within host tissues, such as root cortex cells in angiosperms [1]. Through AM fungi, plants gain access to otherwise inaccessible soil nutrients, including phosphorus (P) and nitrogen (N), which are assimilated by the extraradical hyphae [1]. In return, photosynthetically-fixed carbon is transferred to the AM fungal partner as fatty acids or sugars [5]. AM fungi may provide several other benefits to their plant partners, including induced disease resistance [6] and improved water acquisition [7]. On a global scale, their ability to transport an estimated 1.07 gigatonnes of host-derived carbon below ground annually [8] plays a critical role in sustaining Earth's ecosystems and regulating global climate [9].

The advancement of new technologies has greatly enhanced our understanding of the mechanisms underpinning AM fungi–plant symbioses. Over the past 30 years, the application of genetic screens, transcriptomics, and phylogenetics has helped to piece together a model of symbiotic establishment that regulates the interactions of plants with AM fungi [10]. Many AM plant models already possess fully annotated genomes, including *Medicago truncatula* and *Lotus japonicus* [11,12], allowing genome-wide studies of the genetic mechanisms driving host recognition and response to AM associations. Advancements in techniques for microbial community profiling have helped improve the detection and identification of diversity within mycorrhiza-forming fungi. In particular, the development and refinement of 18S primers has resulted in the delineation of 'fine root endophytes' (now Mucoromycotina) from AM fungi (Glomeromycotina; Table 1) [13,14]. Mucoromycotina is a distinct fungal clade that encompasses a variety of saprotrophic, pathogenic, and endo- and ectomycorrhizal fungi [15–17]. **Mucoromycotina fine root**

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Table 1. Similarities and differences between MFRE and AM symbioses

	AM fungi	MFRE
Fungal subphyla	Glomeromycotina	Mucoromycotina
Reported host plant taxa	Angiosperms, gymnosperms, liverworts, hornworts, lycopods, ferns	Angiosperms, liverworts, hornworts, lycopods
Known function	N and P for carbon Mycorrhizal-induced resistance water acquisition	N and P for carbon
Reported intracellular structures	Arbuscules, arbusculated coils, vesicles, thick hyphae (>3 μm diameter), distinct spores	Arbuscules in some host plants, hyphal coils, fine hyphae (<2 μm diameter), hyphal swellings/lumps surrounded by mitochondria-rich host cytoplasm
Confirmed site(s) of nutrient exchange	Arbuscules/arbusculated coils	Unknown
Refs	[1,4,18,90]	[4,13,18,23,32,57,79,90]

endophytes (MFRE) were previously assumed to be AM fungi based on their morphological similarity and, frequently cryptic, cocolonisation of plant roots alongside AM counterparts [18,19]. In 2018, the paraphyletic fine root endophyte known as *Glomus tenue* underwent taxonomic revision. Formerly classified as an AM fungus, it was repositioned within the Mucoromycotina and denoted as *Planticonsortium tenue* [20,21].

MFRE belong to the Endogonales order, located within the Mucoromycotina clade, and comprises the Densosporaceae and Endogonaceae [13,16]. Some Mucoromycotinian fungi of the Endogonaceae have been described as forming ectomycorrhizal associations [15,16], indicating that there may be considerable differences in terms of the types of mycorrhizal associations formed by fungi within the Mucoromycotina clade. Mucoromycotina represents a sister clade to Glomeromycotina, with their divergence having occurred around 620 million years ago (Ma) [16] (Figure 1A). Fungal structures resembling those formed by Mucoromycotinian fungi have been identified in fossilised plant remains from the Rhynie Chert [22], supporting molecular dating analyses [16]. Collectively these lines of evidence suggest that the most recent common ancestor of modern Endogonales emerged approximately 420 Ma during the mid-to-late Silurian period. This aligns with the emergence of the most recent common ancestor of Glomeromycotina (~426 Ma). As such, the possibility that either, or both, of these groups of fungi facilitated the terrestrialisation of plants remains open [13,23].

The frequent cocolonisation of host plants by MFRE and AM fungi makes it challenging to identify the distinct functional advantages that MFRE offer their plant partners. Given the relatively recent phylogenetic differentiation of MFRE from AM fungi [13], the assessment of functional benefits conferred to plants by AM fungi cultivated within natural soils might have inadvertently encompassed MFRE. This could have biased the evidence of distinct functionalities between both fungal groups. For example, the widely studied model plant *Arabidopsis thaliana* is considered a 'non-host' for AM fungi [24–26]. However, an early instance reporting *A. thaliana* as an AM host was based on inoculation with *Endogone* sp. [27]; it is now apparent that this could have been MFRE [4,13].

Since their delineation from AM fungi, research interest in MFRE as nutritionally mutualistic plant symbionts has increased, including characterisation of the natural distribution [28,29], phylogenetics [30,31], and physiological benefits of plant–MFRE symbioses [32,33] (Table 1). The axenic cultivation of MFRE isolated from naturally colonised host plants and the subsequent recolonisations of different host species have facilitated the development of tractable monoxenic

Glossary

Arbuscular mycorrhizal (AM): normally in the form of arbuscular mycorrhizal fungi or arbuscular mycorrhizal fungal. A type of symbiotic fungus belonging to the subphylum Glomeromycotina.
Chitooligosaccharides (COs): chitooligosaccharide(s). A signalling molecule used by fungi and bacteria.
Effector-triggered immunity (ETI): a mechanism for the detection of pathogens in plants where plant immune receptors mediate the recognition of effectors secreted by the pathogen.
Jasmonic acid (JA): a plant hormone involved in plant defence against necrotrophic pathogens and herbivores.
Lipochitooligosaccharides (LCOs): a signalling molecule used by fungi and bacteria.
Lysin motif (LysM): a carbohydrate-binding protein region involved in plant–microbe interactions.
Microbe-associated molecular pattern: a highly conserved pattern produced by microbes but not the host that is recognised by plant cell surface receptors at conserved binding sites.
Mucoromycotina fine root endophytes (MFRE): symbiotic fungi belonging to the subphylum Mucoromycotina.
Reactive oxygen species (ROS): highly reactive chemicals containing oxygen that can act as stress signals during plant immune system operation.
Salicylic acid (SA): a plant hormone involved in plant defence against biotrophic pathogens.
Systemic acquired resistance: an immune response of plants where defences become elevated across the whole plant and not just in the infected cell layers.
Strigolactones (SLs): a group of plant hormones derived from carotenoids.

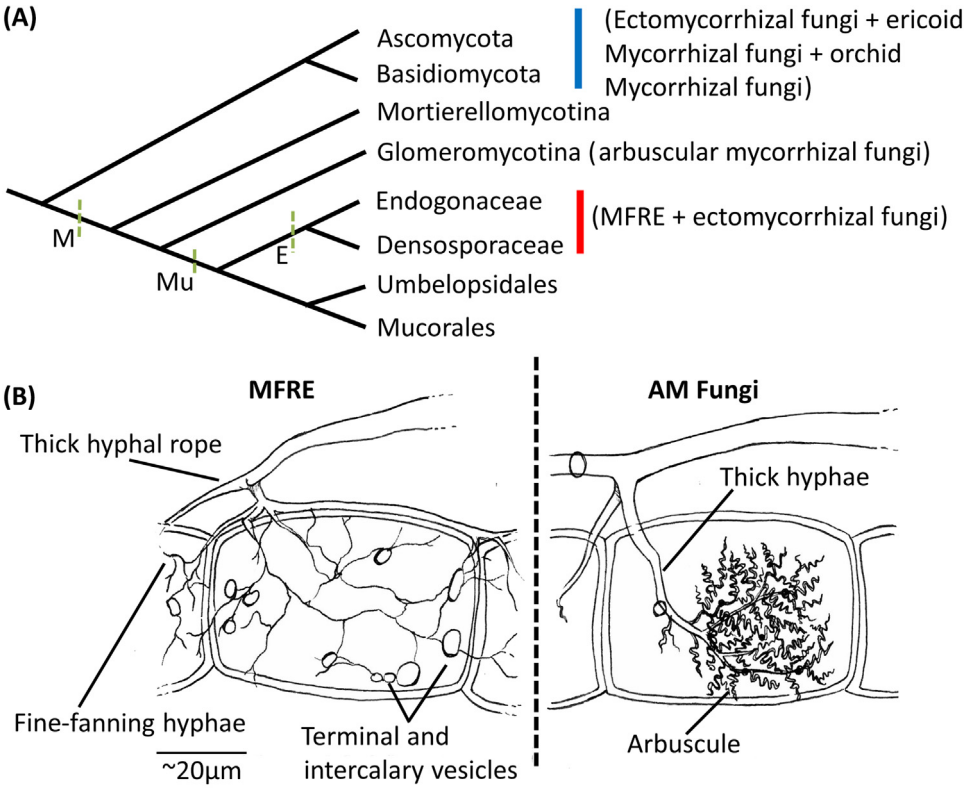

Figure 1. Fungal relationships and morphologies *in planta*. (A) Relationship of selected fungal lineages with and without symbiotic species [4,16]. The phylum Mucoromycota is labelled M and encompasses both Mucoromycotina (Mu) and Glomeromycotina. The order Endogonales is labelled E and is the only order in the Mucoromycotina known to harbour symbiotic fungi [Mucoromycotina fine root endophytes (MFRE) and Ectomycorrhizal fungi]. (B) Illustrations depicting the intracellular morphological differences between MFRE and *Arum*-type arbuscular mycorrhizal (AM) fungal colonisation. The MFRE diagram is based on images [33] where fine hyphae enter the cells at multiple entry points and then diffuse into fine-fanning hyphae. The AM fungi diagram is based on images [91] depicting an arbuscule. The scale bar is approximately 20 µm.

study systems [23,32,33]. This raises the exciting prospect of applying modern molecular methods to this enigmatic group of symbiotic fungi to explore the mechanistic biology underpinning plant–MFRE symbioses. A central question to address is whether the same 'symbiotic toolkit' [34] is used to establish and maintain AM fungal and MFRE symbioses across host plants, despite their independent origins. We argue for more inclusion of the MFRE–plant model system during future molecular investigations into plant–fungal symbiosis and highlight the latest insights from MFRE and AM fungal research to formulate early hypotheses within this budding area.

Initiation of plant–fungal symbioses

The principles of initial mutual detection of partners in AM symbioses are relatively well characterised [35,36] (Figure 2). Plant-secreted **strigolactones (SLs)** play a key role early in the establishment of symbiosis, 'priming' the AM fungus by inducing hyphal branching and elongation [37–39]. AM fungi-derived **lipochitooligosaccharides (LCOs)** and **chitooligosaccharides (COs)** are detected by membrane-bound protein kinase receptors, including **lysin motif (LysM)** domain-containing receptors [40,41]. The binding of LCOs and COs to the LysM domain receptors initiates the common symbiosis signalling pathway and enables transcriptional reprogramming of the host cell to enable intracellular colonisation by AM fungi [35,36]. Nutrient starvation

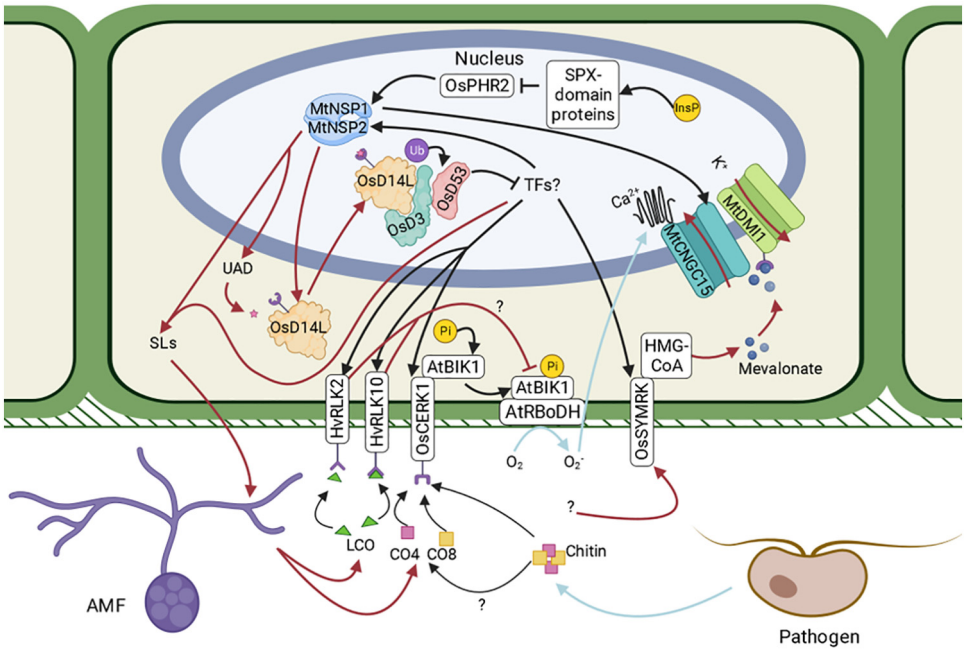

Figure 2. The release of arbuscular mycorrhizal (AM) fungi-recruiting strigolactones (SLs) and the detection of AM fungi are regulated by the phosphate starvation response. Inorganic phosphate (P_i) becomes incorporated into inositol phosphate (InsP), which can bind to SPX domain proteins and enables their repression of PHR2 in rice [46,92]. Under low inorganic phosphate abundance, PHR2 is active and promotes the transcription of *NSP1* and *NSP2* in *Medicago truncatula* [42]. The activity of NSP1 and NSP2 in rice promotes the biosynthesis of strigolactones, which are then exported to the rhizosphere where they have stimulatory effects on AM fungi [37,38,93]. The production of SLs likely also causes the production of an unidentified apocarotenoid derivative (UAD), which acts as a ligand to rice D14L, enabling it to form a Skp, Cullin, F-box (SCF) complex with D3 [43,52]. The D14L–D3 SCF complex ubiquitinates the transcriptional repressor D53/*At*SMAX1 and targets it for proteasomal degradation [52,94–96]. The degradation of D53 or its orthologues causes many cell surface receptors to become upregulated, including CERK1 and SYMRK in rice [43]. The recognition of chitinous elicitors by CERK1 results in the phosphorylation of associated cytosolic protein kinases, leading to transphosphorylation and activation of NADPH oxidases, which release a reactive oxygen species (ROS) burst [68]. In *Medicago*, the binding of lipochitooligosaccharide (LCO) to Nod Factor Perception (NFP; the orthologue to HvRLK2 and HvRLK10) can prevent chitooligosaccharide (CO)-dependant ROS production via an unidentified mechanism [53]. In pathogen interactions, a ROS burst can induce nuclear calcium oscillations via an unknown mechanism [97]. Nuclear calcium oscillations are also induced during AM symbiosis, where mevalonate acts as a secondary messenger released after recognition of the AM fungus and binds to *Mt*DMI1 to activate an efflux of potassium ions from the nucleus, which sustains an influx of calcium ions via the coupled channel protein *Mt*CNGC15 [51]. Predominantly symbiosis-specific processes are shown in red, while predominantly immunity-driven processes are shown in blue, and shared processes are in black; Abbreviations: AM, arbuscular mycorrhizal; TFs, transcription factors; Ub, ubiquitin.

facilitates AM symbiosis via different mechanisms. Apart from indirectly increasing the chances of colonisation by enhancing biosynthesis and release of SLs [42,43], nutrient starvation also directly drives the perception of AM fungi through starvation-induced production of LCO and CO receptors [43]. As MFRE also supply nutrients to their hosts [18,23,32,33,44], it is possible that MFRE recruitment is similarly influenced by the host's nutritional status and could, therefore, involve similar colonisation-promoting mechanisms as AM symbioses.

Plant SL exudation is driven by P starvation

The symbiosis signalling pathway has been directly linked to plant P status through the transcriptional promotion of SL biosynthesis and symbiosis receptors in response to P depletion [42]. *L. japonicus* plants inoculated with the AM fungus *Rhizophagus irregularis* allowed less colonisation and fewer arbuscules and vesicles in the high-P treatment [500 μM inorganic P (P_i)] than in

the low-P treatment (25 μM P_i) [42]. The PHOSPHATE STARVATION RESPONSE (PHR) proteins belong to the MYB transcription factor family and act in the P_i signalling pathway [45]. In rice, the loss-of-function *Oryza sativa PHOSPHATE STARVATION RESPONSE2* mutant (*Osphr2*) showed reduced root colonisation by AM fungi under low-P conditions compared with wild-type plants, while constitutive expression of Os*PHR2* increased total root length colonisation by 20% under high-P conditions compared with wild type [42]. OsPHR2 promotes the transcription of 144 AM symbiosis-related genes through binding to P1BS or P1BS-like DNA motifs [42]. OsPHR2 is controlled by the binding of SPX domain-containing proteins, which sense P depletion and prevent binding of OsPHR2 to P1BS and P1BS-like elements [46]. Furthermore, *O. sativa* NODULATION SIGNALING PROTEIN 1 and 2 (OsNSP1 and OsNSP2), which are essential GRAS domain family transcription factors in the common symbiosis pathway, are both induced by the activity of OsPHR2 [42]. MtNSP1 and MtNSP2 promote the expression of SLs and apocarotenoid biosynthesis genes, such as Mt*DWARF27* [43]. SLs can therefore be produced by the host in response to P starvation and exuded into the rhizosphere where they have stimulatory effects on AM hyphae [37,38]. Given the stimulatory effect of MFRE colonisation on host P supply [23,33], it is plausible that MFRE recruitment occurs via the induction of PHR- and NSP-dependent transcriptional cascades. However, additional quantitative physiological studies will resolve the degree of MFRE-mediated P supply to plants and the effect of environmental P availability on the MFRE–plant symbiosis. If the interaction is dependent on environmental nutrient availability, MFRE recruitment is likely similarly driven by NSP-induced exudation of SLs, although it is equally possible that alternative NSP- or PHR-dependent semiochemicals in root exudates play a role as these transcription factors have multiple gene targets.

SLs may not be the only host exudate involved in MFRE recruitment, as the flavonoids quercetin and its glycosylated derivative rutin can promote AM fungal spore germination and increase root colonisation in *Solanum lycopersicum* L. [47]. It is also possible that coumarins play a role, which are similarly derived from the phenylpropanoid biosynthesis pathway [48]. Indeed, the coumarin scopoletin can enable *A. thaliana* to partially overcome its inability to interact with AM fungi by permitting fungal penetration but not enabling the development of intracellular structures or nutrient exchange [49,50]. It is now critical that functional responses of MFRE are assessed against a gradient of soil nutrient availability before focusing on quantification of the effects of SLs, flavonoids, and coumarins on MFRE morphology, metabolism, and root colonisation.

N and P starvation enables the host to detect AM fungi

Recently, both the N and P starvation responses have been linked to LCO perception [43] (Figure 2). The Lys-M motif receptor-like kinases *Hordeum vulgare* RLK10 (HvRLK10) and HvRLK2 are upregulated during N and P starvation and act redundantly to regulate AM fungal colonisation in barley [43]. These receptors contribute to LCO and CO perception, where the double mutant is completely insensitive to LCO perception, ceasing symbiotic nuclear calcium oscillations [43,51] (Figure 2). In barley, Hv*RLK10* is transcriptionally regulated by the combined activity of HvDWARF14-Like, HvNSP1, and HvNSP2 [43]. This conceptually links the P starvation pathway directly to LCO perception via a signalling pathway in which PHR2 (OsPHR2) promotes NSP2 (OsNSP2/HvNSP2) activity, which in turn promotes Hv*RLK10* expression, possibly via proteasomal degradation of the transcriptional repressor SMAX1 (MtSMAX1) [42,43,52] (Figure 2). In rice, SMAX1 acts in the nucleus, where it regulates the transcription of other genes involved in AM symbiosis and SL biosynthesis, including Os*NFR5* (Hv*RLK10*), Os*DXS2* of the methyl-d-erythritol phosphate pathway, and the SL biosynthesis genes Os*D27*, Os*CCD7*, and Os*CCD8* [52].

As CO perception not only regulates symbiotic interactions with AM fungi and rhizobia but also constitutes a major component of the plant's innate immune response to fungal pathogens

[40,53] (Figure 2), there is a strong possibility that the perception of CO and LCO regulates MFRE colonisation. Presentation of only COs elicits a rapid burst of **reactive oxygen species (ROS)** in the host, which is characteristic of a strong immune response, and this early immune response can be averted by the copresentation of LCO alongside COs [53]. The mechanism of LCO and CO production by AM fungi remains unknown but has been postulated to occur either via active exudation or through the constitutive release of plant chitinases, which break down the polymers of the fungal cell wall into these smaller oligomers [53]. Both hypotheses for chitinous elicitor generation could be tested using MFRE in axenic systems. Interestingly, flavonoids and phenolic acids can increase the transcription of genes responsible for LCO and CO production in rhizobia [54]. It will therefore be important to confirm whether MFRE produce LCOs and COs. Since CO production could also occur via the activity of plant chitinases, and activity assays have identified LCOs in a range of fungi with different life cycles, including in Mucoromycotina fungi [55], a regulatory function of CO, LCO, and chitinases during the establishment of MFRE symbiosis seems likely. Future studies should therefore focus on the host ROS response to MFRE colonisation and quantify colonisation in mutants impaired in ROS production.

Overall, the model of mutual exudation that describes initial perception in AM fungi and rhizobia symbioses has a high potential to overlap in several areas with the initial perception of MFRE by host plants, including the potential that the initial induction is driven by plant nutrient starvation responses (Figure 2). For example, in addition to driving AM recruitment, P starvation can increase colonisation of the non-AM host plant *A. thaliana* by its beneficial fungal endophyte *C. tofieldiae* [56]. Future studies should quantify the role of nutrient deficiency on plant–MFRE symbiotic functionality and screen the effects of symbiosis-implicated plant metabolites on MFRE to characterise the initial mechanisms of MFRE recruitment.

Establishment of symbiotic interfaces

Upon recognition by both symbionts, the commencement of symbiosis is preceded by activation of specific signalling pathways that facilitate the transcriptional and biophysical remodelling of the interacting tissue layers. This remodelling enables the morphogenesis of symbiotic structures (Table 1). The stages of symbiosis establishment are well described for AM and rhizobial symbioses [35,36] but have yet to be uncovered for MFRE symbioses. As very little is currently known about MFRE cellular biology and nuclear dynamics, research focus here could expand our understanding of MFRE symbiosis.

Intracellular MFRE hyphae are typically thinner in diameter than AM fungal hyphae by 0.7–5.7 μm [57,58] (Figure 1B) and have been described as smooth (as opposed to coarse) [23,59]. There are two broad types of intracellular AM fungal symbiotic colonisation that represent the extremes of a continuum [60]. *Arum*-type AMs form the classic branched arbuscule morphotype, whereas *Paris*-type AM associations develop as densely wound hyphal coils/pelotons with thick adherent arbuscules [1,61], the formation of which is largely dependent on the combination of AM fungus and host plant [60]. Loss of arbuscules, such as in the REDUCED ARBUSCULAR MYCORRHIZA 1 (*ram1*) mutant in *Petunia hybrida* and the mutant of the *RAM1* regulating transcription factor MtWRI5a (*wri5a*) in *M. truncatula* plants, causes downregulation of genes responsible for nutrient exchange [62,63]. Despite their functional significance in AM symbioses, arbuscules are not always produced by alternative nutritional symbionts, including *C. tofieldiae*, which supplies P to *A. thaliana* [64]. MFRE appear able to form arbuscules or arbuscule-like structures in a few plant species [57], but this is not consistent across all the MFRE–plant symbioses studied to date [32]. Most plant nutrient transporters localise specifically within arbusculated cells [65], while little is known about the localisation and functionality of fungal transporters. For this reason we cannot exclude that nutrient transfer in AM symbioses also occurs outside of arbuscules, possibly through the facilitation of fungal transporters localised to

the intraradical hyphae, such as PT7 in *R. irregularis* [66]. A feature of MFRE symbioses may also be that arbuscules are not necessary for MFRE–plant interactions to be considered nutritionally mutualistic. Resource exchange may alternatively occur via other symbiotic MFRE structures, such as swellings, coiled hyphae, or thick-walled fungal structures (Box 1) [32].

Given that genes involved in lipid biosynthesis and the transport of lipids, ammonium, and phosphate are commonly upregulated in both *Paris*- and *Arum*-type AM fungal colonised roots [67], the structures of symbiosis can be divergent while the transporters responsible for functionality of the symbiosis remain the same. This supports that MFRE may not have to form arbuscules for functional symbiosis. Transcriptomics and functional genomics analyses could be used to compare the presence of genes related to arbuscule function between known MFRE hosts, followed by functional studies of the activity and localisation of plant nutrient transporters during MFRE colonisation. More research is needed to determine the extent and frequency with which MFRE may form arbuscules and the conditions conducive for their formation [59] as well as their functional significance in plant–fungal symbiosis.

Despite frequent lack of observed arbuscules, the extensive endophytic colonisation by MFRE means that it is able to suppress plant innate immune responses. During pathogenic interactions with fungi, COs from the fungal cell wall are recognised by cell surface receptors (e.g., CERK1 orthologues in different species), which results in an early ROS burst through transphosphorylation-based activation of NADPH oxidases [68] (Figure 2). A transient ROS burst may result in **systemic acquired resistance**-related defence priming in distal plant parts, meaning that MFRE must significantly dampen a transient ROS burst in the first instance or overcome systemic acquired resistance responses [68] (Figure 3). The rice and *Medicago* orthologues of CERK1 (*Os*CERK1 and *Mt*CERK1) and the rice CERK1 homologue CERK2 also function during symbiosis signalling where their activity produces a ROS burst alongside nuclear Ca^{2+} oscillations [40,41,53] (Figure 2). The Ca^{2+} oscillations persist while the ROS burst is attenuated when the plant is also presented with *Sinorhizobium meliloti* lipochitooligosaccharide (smLCO) [53,69] (Figure 2). The LysM domain receptor gene family should therefore be investigated for their involvement in plant–MFRE symbioses, as their conserved function in plant–pathogen and plant–AM fungi interactions suggests that these components may be integral to plant–fungal interactions. If CERK1 or calcium transporters (e.g., cyclic nucleotide-gated channels) are required for successful root colonisation by MFRE or the exchange of carbon for nutrients, then this would highlight the relevance of calcium signalling in MFRE–plant symbioses (Figure 3).

Box 1. Ecology, structures, and function of MFRE

MFRE are globally distributed and prevalent within unmanaged and agricultural environments where they appear to have a preference for wet and acidic soils [28,29,87]. They form mutualistic relationships with liverworts, hornworts, lycophytes, and angiosperms, gaining photosynthates in return for supply of nitrogen and phosphorus (see Table 1 in main text) [23,32,33]. Unlike AM fungi, MFRE are able to grow on minimal media without a plant host. This provides evidence for saprotrophic capabilities [23,33], while AM fungi are fatty acid auxotrophs and therefore dependent on the host lipid machinery [5,88]. It would be interesting for future work to quantify the intactness of lipid metabolic machinery within the genomes of MFRE species and investigate whether differences between MFRE and AM fungi in this trait may explain observed differences in saprotrophic capability. During symbiosis with *Haplomitrium gibbsiae*, *Lycopodiella inundata*, and *Trifolium repens*, MFRE appear to share broadly conserved physiological functions with AM fungi, facilitating plant acquisition of N and P in return for host-fixed carbon [23,32,33]. Comparison between symbioses of the liverworts *H. gibbsiae* (with MFRE) and *Marchantia paleacea* (with AM fungi) indicates that MFRE may be more specialised than AM fungi in the supply of N and less in the supply of P to their host liverwort [89]. Similar to AM fungal arbuscules, distinct structures formed by MFRE, such as intracellular hyphae, fine-fanning hyphae, hyphal coils, swollen fungal 'lumps', or sparsely observed arbuscule-like structures, may also have a role in nutrient transfer [19,57,90] (see Figure 1B in main text). MFRE may additionally improve the stress tolerance of their host plants, with MFRE diversity and abundance being favoured over AM fungi in soils of nitrogen eutrophication, low pH, primary successional diversity, metal contamination, and waterlogging, according to a meta-analysis [87].

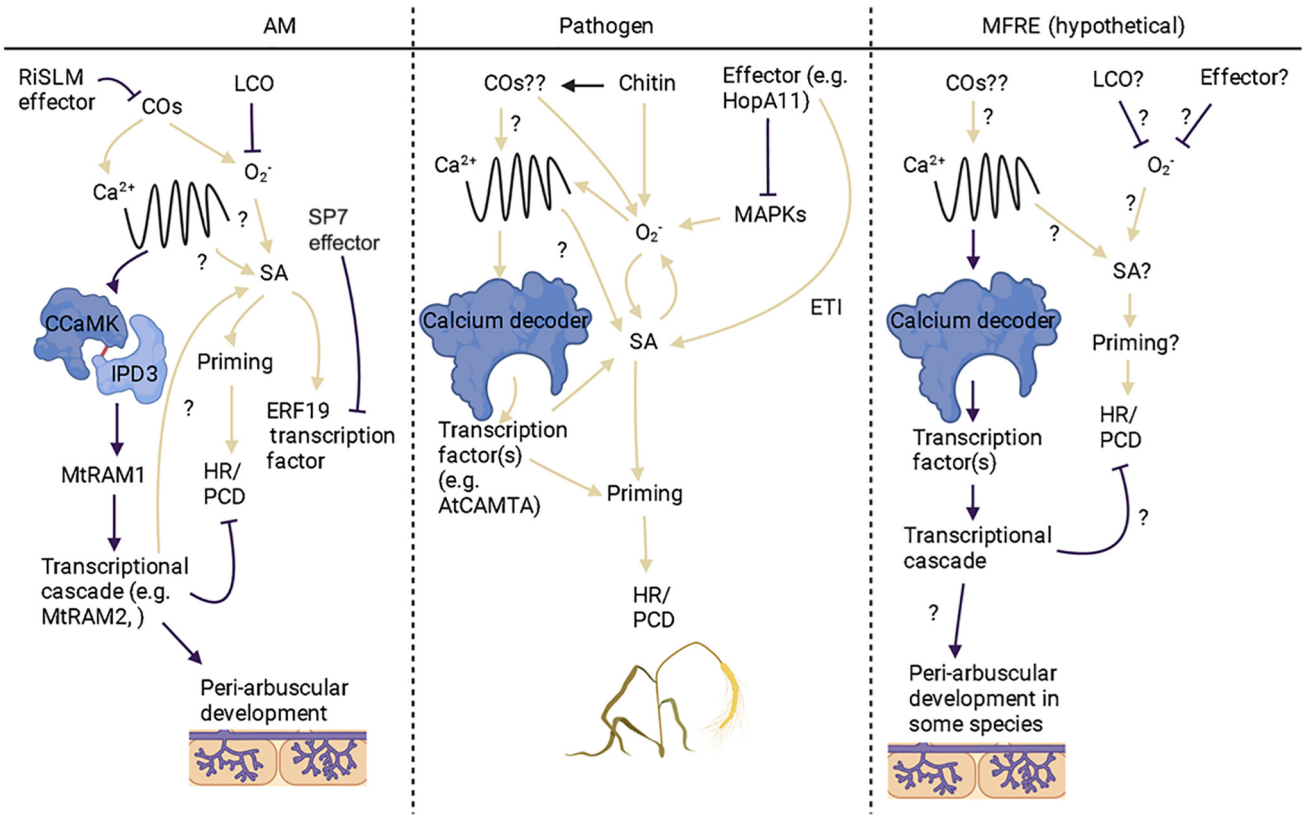

Figure 3. Pathways of plant immune activation (cream) and potential subversion (purple) in response to stimulus from arbuscular mycorrhizal (AM) fungi and plant pathogens compared with the hypothesised pathways during plant–Mucoromycotina fine root endophytes (MFRE) interactions. Drivers/elicitors of processes or components are shown as arrows, while inhibitors of processes or components are shown as junctions. Abbreviations: CCaMK, calcium- and calmodulin-dependent protein kinase; COs, chitooligosaccharides; ETI, effector-triggered immunity; HR, hypersensitive response; LCO, lipochitooligosaccharide; MAPKs, mitogen-activated protein kinases; PCD, programmed cell death; RiSLM, *Rhizophagus irregularis* secreted lysin motif; SA, salicylic acid.

The flow of the common symbiosis signalling pathway makes a useful scaffold on which to build a prediction for how symbiosis signalling operates when MFRE interacts with plant root cells. CO or LCO recognition could similarly be an initial detection event of MFRE, which is then conducted to the cell nucleus to induce nuclear Ca^{2+} oscillations, leading to a transcriptional reprogramming of the cell and suppression of immune pathways (Figure 3). The **microbe-associated molecular patterns** produced by MFRE may overlap with those produced by fungal pathogens and AM fungi (e.g., COs) but have the potential to also include unique identifiers that are specific to MFRE. Local immune repression could occur as a result of transcriptional reprogramming during establishment of the symbiosis. For example, the *MtRAM1*-dependent activation of *MtKIN3* during AM symbiosis directly suppresses the ethylene biosynthesis enzymes ACS and ACO as well as ROS-producing RBOH family members and additionally indirectly modulates **salicylic acid (SA)** accumulation by promoting the accumulation of the SA antagonist **jasmonic acid (JA)** [70].

As occurs in plant mutualisms with AM fungi, rhizobia, and *S. indica*, fungal effector secretion could enable the suppression of host immune responses by MFRE [71–73] (Figure 3). **Effector-triggered immunity (ETI)** responses could lead to termination of the symbiosis unless ETI is suppressed or MFRE effectors are not recognised by host R proteins (e.g., NLRs). The functions of many AM fungi effectors remain largely uncharacterised, but some have been

reported to intersect with plant immune pathways, including small protein 7, which represses the activity of the ETHYLENE RESPONSE FACTOR19 transcription factor upon production of ethylene, JA, and SA [71] (Figure 3). Effector roles within AM symbioses indicate specialisation, for instance the inducibility by SLs or restricted production at the arbuscular interface [71,74,75]. Accordingly, potential MFRE effectors will include those specific to MFRE symbioses and related structures. Future work should focus on the identification of MFRE effectors during the critical stages of symbiotic establishment and characterise their immune-repressing functions. Particular attention should also be given to cross-kingdom RNA transfer as a mechanism to exploit host immunity, as this has now been demonstrated in AM and rhizobia symbioses [76] and may therefore occur during MFRE interactions.

Maintenance of symbiotic interface

In AM symbioses, arbuscules are determinate and senesce over 2–7 days [77,78]. What exactly constitutes the MFRE symbiotic interface remains an open question (see Box 1); thus, predicting the life cycle of an MFRE interface is challenging. There is evidence of degradation of fungal structures within the rhizoids of liverworts [23], and the association of fungal 'lumps' with mitochondria at an interfacial matrix suggests that they may well be metabolically active [23,79,80] (Table 1). The relationship between the degradation of MFRE symbiotic structures [80] and time remains to be determined, but evidence suggests that the abundance of quality fungal structures rather than purely hyphal colonisation may relate to the level of carbon-for-nutrient exchange [44]. Despite fungal colonisation not correlating with the transfer of nutrients in juvenile sporophytes of *Lycopodiella inundata* in symbiosis with MFRE, there was a poor abundance and quality of MFRE symbiotic structures in this example, with the swellings and hyphae present being described as collapsed [44]. This may have affected carbon-for-nutrient exchange in addition to the temporal dynamics of alternating life strategies. Research is now needed to assess to what extent symbiotic structures may influence nutrient exchange within MFRE systems.

As the lifespan of an MFRE symbiotic structure (either hyphae or swellings) appears to be finite, both partners in the symbiosis may need to agree to 'resubscribe' and thus direct the development of new interfaces to maintain the association. As with AM fungi [81], MFRE are likely to provide non-nutritional benefits to host plants. Mycorrhiza-induced resistance occurs in some AM fungal–host interactions, including *Triticum aestivum–R. irregularis* and *S. lycopersicum–Funneliformis mosseae*, via immune priming of systemic plant parts [81,82]. This could be triggered by the initial pattern-triggered immunity responses elicited during the early stages of the interaction but could also be a consequence of a systemic compensation response to localised immune suppression by fungal effectors. Apart from spatial differences in immune responses, induced resistance via priming is typically long lasting, involving modification of the innate immune system via dedicated epigenetic pathways that are not necessarily involved in immediate (short-term) pattern-triggered immunity responses [83,84]. Whether colonisation of a host drives MFRE-induced systemic resistance via priming remains to be tested; future work should seek to quantify this by measuring defence-related changes in RNA transcript accumulation within the host over the course of symbiosis and subsequent challenge by pathogens.

Concluding remarks: MFRE as a potential model for fungal-plant symbioses

The development of axenic and monoxenic plate-based experimental systems has enabled the screening of several plant species for their ability to form associations with MFRE by assessing colonisation status and tracing the flow of nutrients directly between symbionts [23,33,44]. This opens exciting new directions for plant–fungal research. One of the most critical knowledge gaps concerns the level of conservation of symbiotic signalling mechanisms between

Outstanding questions

What chemicals are involved in preparatory signalling during MFRE symbiosis?

How analogous, morphologically and metabolically, are the symbiotic structures and interfaces formed in MFRE and AM fungal symbioses?

What is the extent of overlap in the genetic regulation of MFRE and AM fungal symbioses?

What mechanism(s) do MFRE use to bypass plant host immune responses?

Do MFRE fungi have different strategies to engage in nutritional mutualism depending on the respective host and prevailing environmental conditions?

MFRE and AM symbioses (see Outstanding questions). Given the widespread global occurrence of MFRE and their advantages over AM fungi in laboratory experiments, studies need to explore the functionality of plant–MFRE symbiosis and define their host range. A genetic understanding of the regulation of the symbiosis could help to identify hosts through genomic screening for conserved elements and consequently may aid identification of targets for crop breeding programs similarly to approaches in AM fungal symbioses [85,86]. It is essential to distinguish the impact of MFRE from AM fungi by exploring how MFRE colonisation and its symbiotic functions relate to our understanding of the ecological role of MFRE. Investigating the molecular and evolutionary aspects of this symbiosis may reveal explanations for the significant ecological differences between MFRE and AM fungi. Studies into the regulation of MFRE colonisation can help predict the influence of MFRE and broader fungal communities on shaping above-ground plant communities. A molecular-level understanding of the widespread MFRE interaction has strong potential to yield discoveries with profound implications for application of symbiotic fungi in agriculture and enhancing our knowledge of the evolution and natural ecologies of plant-interacting fungi.

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