REVIEW

Arbuscular mycorrhizal associations and the major regulators

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Abstract Plants growing in natural soils encounter diverse biotic and abiotic stresses and have adapted with sophisticated strategies to deal with complex environments such as changing root system structure, evoking biochemical responses and recruiting microbial partners. Under selection pressure, plants and their associated microorganisms assemble into a functional entity known as a holobiont. The commonest cooperative interaction is between plant roots and arbuscular mycorrhizal (AM) fungi. About 80% of terrestrial plants can form AM symbiosis with the ancient phylum Glomeromycota. A very large network of extraradical and intraradical mycelium of AM fungi connects the underground biota and the nearby carbon and nutrient fluxes. Here, we discuss recent progress on the regulators of AM associations with plants, AM fungi and their surrounding environments, and explore further mechanistic insights.

Keywords AM symbiosis, signal, regulators, nutrients, phosphate, microbiota

1 Progression of arbuscular mycorrhizal (AM) symbiosis

AM fungi can develop potentially symbiotic relationships with the majority of land plant species based on bidirectional nutrient transfer between host plants and fungi[1]. AM fungi can supply host plants with essential mineral nutrients such as phosphorus (P) and nitrogen (N)[2], and a large amount of carbon fixed by the plants flows to the fungal symbiont mainly in the form of fatty acids[3–5]. The establishment of AM symbiosis starts from the molecular dialog between plant and mycorrhizal fungi. AM fungi form hyphopodia on the root surface, invade cortical cells through a pre-penetration apparatus (PPA) and develop highly branched structures termed arbuscules

in inner cortical cells[6] (Fig. 1). Arbuscules are mainly responsible for the bidirectional nutrient exchange. This symbiotic process is precisely regulated by the host plant, the mycorrhizal fungi and the surrounding environment.

1.1 Signals from roots

Plant root exudates and phytohormones. Plant root exudates play an important role in the signaling communications between host plant and AM fungi and can stimulate morphological changes in fungal spores and hyphae. The active compounds in root exudates include strigolactones, flavonoids and 2-hydroxy fatty acids (2-OH-FA).

Strigolactones are derived from carotenoid metabolism. Despite their multiple roles as endogenous phytohormones in suppression of shoot branching, regulation of root architecture and acceleration of leaf senescence (reviewed by Waters et al.[7]), their contribution as exogenous signals at different stages of AM formation have also been documented, such as stimulating the germination of AM fungal spores, hyphal branching in the pre-symbiotic phase and promoting hyphopodium formation in the later stages[8–10]. However, it is unclear how strigolactones are recognized by AM fungi. Phosphorus starvation induces strigolactones biosynthesis and the gene expression of the key SL synthesis enzyme D27, which is depending on GIBBERELLIC ACID-INSENSITIVE, REPRESSOR of GAI, and SCARECROW (GRAS) transcription factors NSP1 and NSP2[11], while the direct targets of NSP1/NSP2 and the mechanism of regulation remain unknown. Exogenous GR24, a synthetic and biologically active SL analog, leads to increased release of short-chain chitooligosaccharides (COs) from germinated spores of *Rhizophagus irregularis*[12]. Exposure to COs increases the expression of strigolactones biosynthesis genes in host plants[13], indicating a positive feedback regulation of the signal dialog between host plant and mycorrhizal fungi.

Flavonoids derived from the phenylpropanoid pathway are known active compounds from legume root exudates
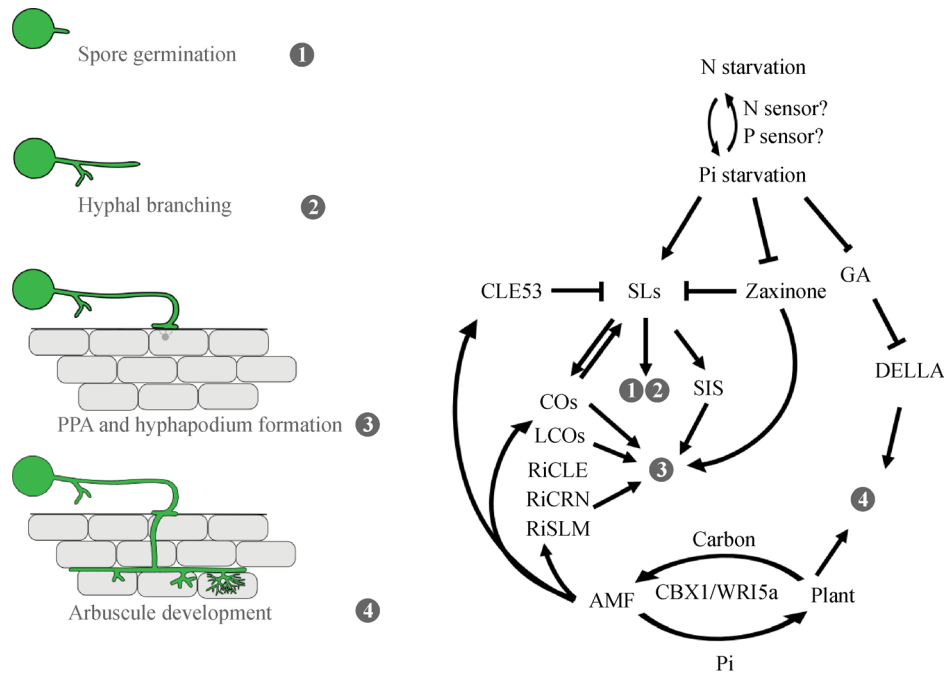
Fig. 1 Schematic of the development of the arbuscular mycorrhizal (AM) symbiosis and the major regulators involved at different stages. AM development is roughly characterized as four steps: (1) spore germination; (2) hyphal branching; (3) PPA and hyphopodium formation; and (4) arbuscule development. AM fungi facilitate nutrient uptake, meanwhile Pi and N starvation also contribute as master regulators in AM development. Strigolactones secreted from host roots induce fungal spore germination and hyphal branching (steps 1 and 2), while the biosynthesis of strigolactones is controlled by inorganic P (Pi) status, chitooligosaccharides (COs), zaxinone and autoregulation of mycorrhizal symbiosis (AOM) feedback signal CLE53. AM fungi produced chitinaceous molecules (COs and LCOs) to promote pre-symbiosis signaling and effectors/peptides (RiCRN, RiSLM, SIS and RiCLE) to increase fungal colonization (step 3). DELLA, the well-known negative regulator in gibberellin acid (GA) signaling, acts as a positive regulator in arbuscule development. CBX1/WRI5a regulate the gene module related to carbon-Pi exchange between plant and fungi in the arbuscule-containing cells (step 4).

that attract potentially symbiotic bacteria[14–16]. It has been shown that flavonoids exhibit stimulatory effects on hyphal tip elongation of AM fungi, especially when CO_2 is present mimicking the situation in the rhizosphere[17]. Moreover, flavonoid biosynthesis is regulated by AM fungi[14], although the type of active flavonoids that act as general signals in AM associations remain uncertain.

2-hydroxy fatty acids (2-OH-FA) were first characterized from carrot root exudates. Exogenous addition of 2-OH-FA promotes lateral branching of AM fungal hyphae[18], suggesting the possible role of 2-OH-FA as signals in the rhizosphere. Another potential fatty acid signal is cutin. Cutin is the main component of cuticle, the waxy coat of the aboveground parts of plants[19]. Addition of cutin monomers directly enhances hyphopodium/appressorium formation of beneficial AM fungi and pathogenic oomycetes, indicating a general role of cutin in fungal development[20].

Zaxinone is a newly identified carotenoid-derived product that is formed by the carotenoid cleavage dioxygenase (OsZAS) in rice[21]. In addition to its growth-regulating activity, exogenous application of zaxinone suppresses strigolactones biosynthesis but increases mycorrhization, indicating a dual role of zaxinone in plant growth and in associations with beneficial fungi[21]. The contribution and crosstalk between zaxinone and strigolactones in plant growth and AM symbiosis merit further study.

Karrikins are smoke-derived organic compounds that can stimulate the seed germination of many fire-prone plants[22]. Notably, the karrikins signaling pathway is closely related to that of strigolactones. Both karrikins and strigolactones are perceived by the closely-related α/β hydrolase receptors KAI2/DWARF14LIKE (D14L) and DWARF14 (D14), respectively, requiring F-box proteins (KAI1/DWARF3 and MAX2, respectively) and triggering proteasome-mediated degradation of class I Clp-ATPase SMAX/DWARF53 to regulate development[23]. Surprisingly, D14L is required for the initial colonization by AM associations in rice[24], indicating the existence of currently unidentified endogenous karrikins-mimic hormones in plants. Although the functions of KAI2 and D14 signaling pathways have been well dissected in root and root hair development[25] the contribution of and the interplay between D14L and D14 signaling pathways in mycorrhizal plants remain unknown.

Gibberellins (GA) are a large class of cyclic diterpenoid phytohormones and function not merely in various aspects of plant growth but also in symbiosis[26]. Phosphorus starvation leads to a reduction in bioactive GA levels and accumulation of DELLA protein[27]. Addition of GA decreases fungal penetration and arbuscule development, while DELLA, a suppressor of GA signaling, is a positive regulator in AM symbiosis, as arbuscule development is greatly reduced in DELLA mutants including *Medicago della1della2* double mutant and rice *slr1*[28,29]. Importantly, GA also suppress root nodulation and DELLA is required for nodule symbiosis[30]. The CCaMK-CYCLOPS-DELLA complex regulates transcriptional expression of *RAM1* in mycorrhization and *ERN1* in nodulation, respectively[30,31]. Moreover, DELLA interacts with multiple transcription factors/regulators such as MYB1, MIG1, DIP1, NSP2 and RAD1[29,30,32–34], along with the capacity for interactions with GRAS proteins[29,35–37], suggesting a integrator role of DELLA in symbiotic associations and a complicated network in the regulation of downstream genes depending on the context.

1.2 Signals from AM fungi

Chitooligosaccharide and lipochitooligosaccharide signals and LysM receptor-like kinases. Molecular signals from exudates of germinated spores and mycorrhizal carrot roots have been identified playing an essential role in pre-symbiotic communication. Rapid turnover of mycelium in soil may release photo-assimilates into the soil and provide more signals for plant-microbe and microbe-microbe interactions. The fungal cell wall consists mainly of chitin and chitin degradation generates COs which are homopolymers of β-1,4-linked N-acetyl-D-glucosamine (GlcNAc)[38]. Chitinaceous molecules of various fungi serve as microbe-associated molecular patterns (MAMP) monitored by plant immunity[39]. Apart from COs, mycorrhizal fungi also produce lipochitooligosaccharides (LCOs). LCOs possess the COs backbone but with lipid modification and further modifications such as sulfate on the reducing and nonreducing ends, and can stimulate early symbiotic responses[12,40]. Recently, COs (especially CO8) have been reported to activate symbiotic signaling as well. Moreover, the combination of CO8 and LCOs can enhance the symbiotic response but suppress immunity[41]. In addition, Nod-factors from rhizobacteria, acting as nodulation symbiotic signals, also belong to LCOs[42], raising the question of how plants perceive and distinguish these signals to elicit the subsequent divergent downstream responses. Lysin motif receptor-like kinases (LysM-RLKs) are responsible for the recognition of COs from fungal pathogens and Nod-factors from rhizobacteria[43]. Nod-factors are perceived by the LjNFR1/MtLYK3 and LjNFR5/MtNFP complex in *Lotus japonicus* and *M. truncatula*[44,45]. LysM-RLK CERK1 associates with LYK4/LYK5 in *Arabidopsis thaliana* or CEBiP in rice for activation of immune signaling[46,47]. CERK1 is also required for mycorrhizal symbiosis[48,49]. In *Medicago*, MtCERK1 is essential for COs-induced response genes both in defense and in symbiosis[41], and this is in line with the dual function of CERK1 in immunity and mycorrhization[48,49]. MtNFP contributes mainly to LCOs-induced expression of symbiotic response genes, while LCOs-mediated suppression of the CO8-induced defense response depends on MtNFP rather than the common symbiosis signaling pathway (CSSP)[41,50]. Although MtCERK1 binds COs and MtNFP binds LCOs, considering the normal mycorrhization in the *Mtnfp* mutant and the lower colonization still occurring in the *Mtnfp Mtcerk1* double mutant[41], additional COs and LCOs receptors are proposed to exist. Consistently, LysM-RLKs OsMYR/OsLYK2 was reported to act as a Myc-factor receptor, as reduced mycorrhization was observed in an *OsMYR* defective mutant and OsMYR directly binds CO4 so as to enhance the association with OsCERK1[51]. CO4 enhances the phosphorylation of OsMYR and OsCERK1[51]. Notably, the variation in the second LysM of OsCERK1 was found to be important for the mycorrhization[52]. LjNFR5/MtNFP orthologs in petunia and tomato, PhLYK10 and SlLYK10, showed higher binding affinity toward LCOs and are required for mycorrhizal symbiosis. *PhLYK10* and *SlLYK10* can also rescue the nodule formation in the *Mtnfp* mutant[53]. These findings provide novel insights into the signal recognition in pre-symbiosis in natural contexts when AM fungal-secreted COs/LCOs signal cocktail triggers integrated output of immune and symbiotic responses through various LysM-RLKs, some of which are multifunctional.

Chitin is the second most abundant polysaccharide in nature after cellulose and is rich in nitrogen. In addition to serving as an elicitor in defense and symbiosis in the form of oligomers, the monomer for chitin may also act as an alternative source of nutrients for AM fungi or as potential signals exuded by plants in symbiotic associations. The GlcNAc transporter RiGNT from *R. irregularis* is able to take up GlcNAc from yeast and the *RiGNT* gene is highly expressed in intraradical hyphae together with GlcNAc metabolic genes, suggesting that *R. irregularis* may recycle COs as N nutrients in degenerated arbuscules[54]. The plant GlcNAc transporter NOPE1 was first identified in rice and maize and is required for initiation of AM symbiosis[55]. The distinct transcriptional responses in *R. irregularis* spores treated with exudates from the wild type or *Osnope1* rice mutant support the proposition that *NOPE1* is essential for priming AM fungi at the pre-symbiotic stage through the release of unknown bioactive components (GlcNAc derivatives) as early signals[55].

1.3 Proteins and effectors secreted by AM fungi

A genome-wide survey reveals that *R. irregularis* and *Gigaspora rosea* possess a large set of putative secreted proteins (SPs). Some of these SPs are commonly upregulated during the colonization of different hosts and might be important in establishing and maintaining the AM symbiosis[56]. Most of the SPs are small proteins of unknown function and may serve as effectors regulating plant-AM fungal interactions. Numerous SPs in *R. irregularis* have been predicted to be cleaved by KEX2, the conserved endoprotease in fungi that recognizes specific motifs and produces small peptides that are released into the extracellular spaces[57]. Through AM fungal genome sequencing in combination with bioinformatic analysis, a total of 220 effector candidates were identified in *R. irregularis* and about 95% of these showed homologs in *Rhizophagus clarus*[58]. It appears that AM fungi can provide the potential candidates of secreted effectors in a host- and stage-dependent manner[59]. Although effectors are known to counter MAMP-triggered immunity and facilitate colonization in pathogenesis, very few effectors have been well investigated in AM symbiosis.

The SP7 effector from *R. irregularis* interacts with the pathogenesis-related transcription factor MtERF19 in *M. truncatula* and constitutive expression of SP7 in roots leads to increased mycorrhization and reduced expression of plant defense genes[60]. A group of Crinkler effectors present in *R. irregularis* and silencing of RiCRN1 by host-induced gene silence (HIGS) lead to reduced mycorrhization in *M. truncatula*[61]. SL-induced putative SP SIS1 is required for mycorrhizal symbiosis, as knockdown of *SIS1* by HIGS results in a reduced mycorrhization rate and stunted arbuscules in *M. truncatula*[62]. The LysM effector RiSLM is one of the highest expressed effectors from *R. irregularis* and is able to sequester fungal cell wall-derived COs to protect hyphae from plant chitinases so as to evade chitin-triggered immunity[63,64]. Silencing *RiSLM* by HIGS shows that *RiSLM* is positively required for AM fungal colonization and arbuscule development[63]. Although RiSLM also binds LCOs, the LCO-triggered symbiotic transcriptional response was not inhibited by excessive RiSLM[63]. It is therefore conceivable that AM fungi might use a suite of effectors to block plant immunity and develop a successful association.

AM and root nodule symbiosis and actinobacteria symbiosis share the common symbiotic signaling pathway (CSSP) and, even if few signal molecules and cognate receptors are reported, several interesting questions remain. How do plant cells discriminate the signals from different microbes to trigger divergent downstream networks of transcriptomic and metabolic responses? How are the host spectrum and distribution of the divergent AM fungi determined? What are the roles of secreted proteins/effectors in determining host specificity?

2 Regulation of AM symbiosis

2.1 Nutrients as regulators of AM symbiosis

Nitrogen, phosphorus and potassium (K) are the major macronutrients limiting plant growth despite the fact that they are the most abundant elements in soils, as a result of their availability being low due to strong adsorption on mineral surfaces. Plants have adapted to assimilate mineral nutrients from their surroundings directly or through beneficial microbes such as *Frankia*, *Rhizobium* and mycorrhizal fungi, especially when the hydromineral resources are scarce[65–67]. The characteristic effect of AM symbiosis is to increase nutrient uptake, especially N, P and K uptake. Plants take up inorganic phosphate (Pi) from soils via direct Pi uptake (DPU) and mycorrhizal Pi uptake (MPU) pathways, but MPU suppresses DPU and may contribute up to 100% of the total Pi uptake by host plants[68,69]. The plant phosphate transporter 1 (Pht1) family has a pivotal role in phosphate uptake, translocation and remobilization[70,71]. Numerous studies over the past two decades have found mycorrhiza-inducible and mycorrhiza-specific Pi transporters in different plant species and these transporters are clustered into two clades of the Pht1 family according to their protein sequences[72–78], while the transcriptional regulation mechanism of the mycorrhiza-specific Pi transporters has been recently reported. AP2 transcription factors CBX1 in *Lotus japonicus* and WRI5a in *Medicago truncatula* regulate the transcription of the mycorrhiza-specific Pi transporter gene *PT4* in the CTTC/AW-dependent manner and transient expression of CBX1 may also activate the mycorrhiza-specific Pi transporter genes from different host species, suggesting a conserved mechanism in dicotyledon species[79,80]. Moreover, the genes involved in *de novo* biosynthesis and transport of fatty acids in response to AM fungi were upregulated by CBX1 and WRI5a, indicating that the gene module related to carbon and Pi exchange in AM symbiosis is regulated by CBX1/WRI5a. As the periarbuscular membrane localized Pi transporters are Pi:H symporters, H^+-ATPase was supposed to generate the proton gradient to counteract the proton influx in cytoplasm via Pi transporters[71]. The co-regulated H^+-ATPase is essential for AM symbiosis[81,82] and over-expression of H^+-ATPase simultaneously enhanced phosphate and nitrogen uptake[83], supporting the linked P and N uptake in AM symbiosis. Increasing evidence indicates that AM fungi take up and transfer organic (amino acids and peptides) and inorganic N (nitrate, NO_3^- and ammonium, NH_4^+) to their hosts, and about one-third of the root protein N may be provided by AM fungi[84]. Several mycorrhiza-inducible N transporters have been reported in plants (reviewed by Wipf et al.[85]), while their function and regulation mechanisms in AM symbiosis are not yet characterized. Genome-wide gene expression

profiles in different mycorrhizal species have been described, including mycorrhiza-induced K transporter genes[86–88]. In tomato, the mycorrhiza-specific K transporter *SlHAK10* is involved in mycorrhizal K uptake, as *Slhak10* mutants showed decreased mycorrhizal K uptake and overexpression of *SlHAK10* enhanced mycorrhization only under low K conditions[89].

In addition, P and N status are major regulators of AM symbiotic associations rather than other major nutrients such as K, S, Mg, Ca and Fe[90]. Pi deficiency promotes AM symbiosis and Pi sufficiency suppresses AM symbiosis[91]. Addition of N also decreases mycorrhization[92]. The suppression of AM symbiosis by high Pi may lead to starvation of other nutrients due to reduction of functional fungal structures. However, N starvation forces the plant to bypass the high Pi suppression on AM formation in plants, suggesting a complicated regulation by N and P status[90]. Mature arbuscules and periarbuscular membrane are responsible for nutrient exchange during AM symbiosis. The degenerated arbuscule phenotype in the phosphate transporter *Mtpt4* mutant was suppressed by deprivation of N simultaneously, which is dependent on the ammonium transporter gene *AMT2.3*, but with unchanged shoot N transport[93]. It is therefore reasonable to speculate that the transporters may also act as P and N sensors in AM symbiosis and interaction between P and N signaling may exist. In the AM nonhost *A. thaliana*, inositol pyrophosphate InsP8 ligand binds the Pi sensor SPX domain-containing protein 1 (SPX1) to regulate the Pi-dependent response[94], and the nitrate transceptor NRT1.1 (CHL1/NPF6.3) functions as a dual-affinity transporter and nitrate sensor in nitrate signaling[95–97]. Further investigations are therefore required to obtain insights into the P and N sensing and crosstalk between P and N signaling in mycorrhizal symbiosis. In addition, the impact of K on AM symbiosis has been little studied. When long-term K deprivation was induced in *M. truncatula*, K availability did not affect AM colonization, but mycorrhizal plants showed increased root biomass and shoot K$^+$ contents compared with nonmycorrhizal plants under K-limited conditions, and the genome-wide transcriptional profile indicates that AM fungi might modulate the plant responses to K starvation[98]. In addition, cross-talks between macronutrients and micronutrients have been recognized[99]. The complicated tripartite interactions among the nutrients Pi, Zn and Fe in mycorrhizal and non-mycorrhizal plants have been discussed in detail[100].

2.2 Systemic regulation of AM symbiosis

CLAVATA3/Endosperm surrounding region-related (CLE) peptides comprise 12–13 amino acid glycosylated peptides and work in a similar manner to phytohormones regulating developmental processes and stress responses locally and systemically[101]. Several CLEs are responsive to the macronutrients N, P and S or AM fungi in *M. truncatula* and *L. japonicus*[87,102]. CLE peptides are involved in local and systemic control of the extent of symbionts[103]. Root nodule formation is controlled by a systemic feedback loop called autoregulation of nodulation (AON), involving nodule-induced CLE peptides and CLV1-like leucine-rich repeat (LRR) RLKs LjHAR1/MtSUNN/GmNARK in the shoots, leading to a shoot-derived suppression of nodule numbers in the roots[104,105]. Similarly, defects in *LjHAR1/MtSUNN/GmNARK* led to increased AM fungal colonization, implicating a role for these LRR-RLKs in autoregulation of mycorrhizal symbiosis (AOM)[106–108]. *MtCLE53* was induced by both *Glomus versiforme* and *R. irregularis* in *M. truncatula* roots and *MtCLE33* was induced in response to high Pi[109]. Overexpression of either *MtCLE53* or *MtCLE33* resulted in reduced fungal entry and colonization, while knockdown of *MtCLE53* by RNA interference showed enhanced mycorrhization. Overexpression of *MtCLE53* or *MtCLE33* also led to downregulation of SL biosynthesis genes and upregulation of the cognate receptor gene *MtSUNN*[109]. This evidence provides a new avenue toward the AOM in roots by CLEs-SUNN through strigolactones, integrating P status and mycorrhization. Interestingly, a RiCLE from *R. irregularis* was identified that can promote mycorrhizal colonization[110]. A large set of AM-induced and AM-suppressed RLKs was identified *in silico*[87]. Only a few LysM-RLKs and LRR-RLKs have been well studied, while the functions of other RLKs such as L-type lectin RLKs, malectin RLKs, pollen RLKs and wall-associated kinases in AM symbiosis remain unknown, and the cognate ligands of these potential receptors are also unknown.

3 AM symbiosis and root microbiota in natural soils

Plants grow in a microbe-rich environment and different plant species harbor diverse microbiome in their roots and the rhizosphere. Plants recruit functional conserved core microbial consortia from soil[111]. A beneficial association with AM fungi can affect the root fungal community. Based on the relative microbiota profiling (RMP) of bacterial 16S *rRNA* genes and fungal internal transcribed spacers (ITSs), it has been shown that wildtype *L. japonicus* plants host a wide spectrum of Glomeromycota, while defective mutants in AM symbiosis disturbed the assemblage of microbes especially in the endosphere, characterized by depletion of Glomeromycota and concomitant enrichment of Ascomycota including fungi from Helotiales and Nectriaceae[112,113]. AM fungi may inhibit root colonization by other endophytic fungi through direct interactions such as antagonism via the release of antimicrobial substances or competition for resources, and by indirect effects associated with plant

mycorrhization and/or primed plant immunity[113]. It has been hypothesized that non-symbiotic microorganisms can highjack components of AM signaling pathways to effectively colonize plant tissues, but experimental evidence is insufficient to provide a clear conclusion[114–117]. Few fungal taxa were consistently depleted in all tested symbiotic mutant plants other than Glomeromycota taxa, suggesting that this might be true for some but not all microbes[113]. Further investigations on isolation of the fungi which require CSSP genes for colonization will help to answer this question. Recently, based on a quantitative microbiota profiling (QMP) method to absolutely quantify the bacterial 16S *rRNA* gene in bulk soil and rhizocompartments, a novel feature of rhizosphere bacterial microbiota assembly compared to the RMP method was proposed[118]. It will be important to revisit the impact of AM fungi on the root community based on quantitative microbiota profiling.

Plant species and environmental factors contribute significantly to the assemblage of the microbial community. Indeed, *L. japonicus* and *A. thaliana* possess distinguishable fungal communities, even though the soil was taken from the same site[113,119]. Phosphorus status and active compounds in root exudates (strigolactones and cutin monomers) do have effects on other biotic interactions[20,120–122]. Other beneficial endophytes were reported to be functional under P deficiency conditions. In non-mycorrhizal Brassicaceae species, beneficial fungi (ascomycetes *Collectotrichum tofieldiae* and *Helotiales* F229) can alleviate phosphate starvation in *A. thaliana* and *Arabis alpina*, respectively; the basidiomycete *Serendipita indica* (syn. *Piriformospora indica*) was isolated and reintroduced, and this significantly increased plant growth and P uptake in *A. thaliana* and maize[119,123–125]. On the other hand, mycorrhiza helper bacteria were isolated from various plant-mycorrhizal fungal symbioses or the rhizosphere with significant effects on mycorrhiza formation or positive impacts on the function of mycorrhizal symbiosis[126]. Some AM fungi from Gigasporaceae harbor endobacteria which are not essential for AM fungal survival but can enhance fungal fitness[127]. Further studies on the endobacteria in AM fungi and beneficial microbes in nonmycorrhizal species are needed to understand and exploit beneficial associations in and beyond legume species in natural soils.

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