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Molecular mechanisms modulating beneficial plant root–microbe interactions: What's common?

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SUMMARY

In the current context of climate change, there is a need to develop more sustainable agrifood strategies. As an alternative to the intensive use of chemically synthesized fertilizers and pesticides that pollute water and impact biodiversity, there is a growing interest in using beneficial microbes as biostimulants and/or bioprotection agents. However, their implementation in agriculture remains a challenge due to highly variable outcomes and benefits. Furthermore, there are major knowledge gaps about the molecular mechanisms that regulate different plant–microbe interactions. In the present review, we summarize current knowledge on the molecular mechanisms that control different beneficial plant root–microbe interactions; namely, arbuscular mycorrhiza, the rhizobium–legume symbiosis, ectomycorrhiza, and fungal and bacterial endophytic associations. This includes the signaling pathways required for recognition of microbes as beneficial, the metabolic pathways that provide nutritional benefits to the plant, and the regulatory pathways that modulate the extent of symbiosis establishment depending on soil nutrient availability and plant needs. Our aim is to highlight the main common mechanisms, as well as knowledge gaps, in order to promote the use of microbes, either individually or in consortia, within the framework of a sustainable agriculture that is less dependent on chemicals and more protective of biodiversity and water resources.

Key words: mycorrhiza, nitrogen-fixing nodulation, symbiosis, endophytes, PGPR, biostimulants

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INTRODUCTION

The growing human population requires a large increase in food production, which is leading to an overexploitation of natural resources (Tkacz and Poole, 2015). According to the Food and Agriculture Organization, the food needed to feed a global population projected to be over 9 billion by the year 2050 would require a 60% increase in global agricultural production relative to that in 2005. Furthermore, many indicators suggest that food crises are exacerbated by global warming (Duhamel and Vandenkoornhuyse, 2013; Rhee et al., 2025). Current intensive agriculture relies on the massive use of chemical fertilizers and pesticides to maintain crop production. The negative impact of such agrochemical abuse on the environment, contaminating soils and groundwater, and on farmer safety and consumer health, has led to an urgent need to develop more sustainable and environmentally friendly alternative agricultural practices. One strategy increasingly explored by the agrifood

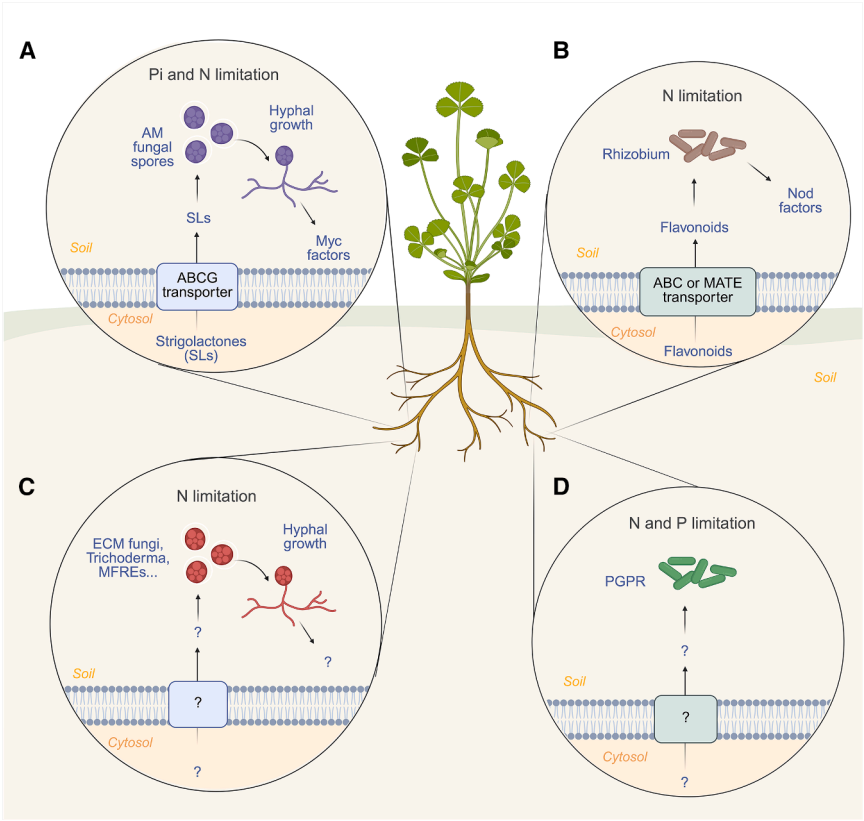

Figure 1. Pre-symbiotic phase of beneficial plant root–microbe interactions in the rhizosphere.

Plants establish beneficial interactions with both fungal and bacterial microbes that they attract from the soil rhizosphere by producing signaling molecules under conditions of nutritional deficiency.

(A) The arbuscular mycorrhizal (AM) symbiosis is promoted by inorganic phosphate (Pi)- and nitrogen (N)-limiting conditions. The host-plant roots trigger the production of strigolactones (SLs), which are exuded into the rhizosphere through ABCG transporters. SLs are recognized by AM fungal spores, stimulating their germination, as well as hyphal growth and branching. SLs also induce the production of AM fungal mycorrhizal factors (Myc factors) that are recognized by the host plant in the root epidermis.

(B) Rhizobial nodulation (RN) is promoted by N deficiency. Legume host-plant roots produce specific flavonoids that are exuded into the rhizosphere through ABC or multidrug and toxic compound extrusion transporters. Flavonoids are recognized by compatible rhizobia, which produce nodulation factors (Nod factors) that are specifically recognized by the host plant in the root epidermis.

(C) Other beneficial plant–fungus interactions, such as the ectomycorrhizal (ECM) symbiosis and associations with *Trichoderma* or Mucoromycotina fine root endophytes (MFREs), are also promoted by N deficiency. Host plants produce unknown signals that may be recognized by the fungal partner to promote hyphal development. Conversely, fungi could produce specific, still-unknown signaling molecules that are recognized by host plants.

(D) Interactions with plant growth-promoting rhizobacteria (PGPRs) are induced by N and Pi deficiency. Signaling molecules that may be involved in the reciprocal recognition of the two partners remain unknown. The figure was generated using BioRender (https://biorender.com/).

sector is the use of soil microbes that are beneficial for plant growth and/or health. Plants can indeed establish beneficial interactions with both fungi and bacterial microbes that they attract from the soil rhizosphere. Through these mutualistic associations, both plants and microbes obtain a benefit. Typically, these benefits come in the form of reciprocal nutritional exchanges and the generation of specific growth niches to reduce microbial competition. On the plant side, these associations can provide additional benefits, such as improved abiotic stress resilience and defense responses (Bakker et al., 2020; Giovannetti et al., 2023). These microbes can then be used as biostimulants and/or bioprotective agents against different abiotic and/or biotic stresses. Plant–microbe associations are as old as land colonization by plants and constitute an ecological unit termed the "holobiont" (Uroz et al., 2019). It can be hypothesized that the molecular mechanisms associated with the most ancient beneficial plant–microbe interactions have been reused during evolution and rewired for more recent interactions. According to the intricacy of their interactions with plant roots, beneficial plant–microbe interactions can be classified as endophytic (within root tissues), epiphytic (on root surfaces), or rhizospheric (enriched in the rhizosphere relative to the bulk soil). Because endophytic microbes colonize plant root tissues, their interaction with the host plant is tighter and more elaborate than that of free-living microbes established in the rhizoplane/rhizosphere (Uroz et al., 2019; Chialva et al., 2022).

Harnessing rhizosphere microbes has been proposed as the keystone of the next-generation agricultural revolution (Bakker et al., 2020; Giovannetti et al., 2023). However, despite their potential, the implementation of complex microbial inoculants in agriculture still remains a challenge due to the inconsistency of their effects, which notably depend on environmental conditions and plant species and genotypes (Buss et al., 2025). A better understanding of the mechanisms that enable optimal establishment of plant–microbe symbioses is thus paramount to promoting the efficient and more stable use of beneficial microbes as biostimulants, with the aim of transitioning toward more environmentally friendly and sustainable agriculture that is less reliant on chemical fertilizers. In the present review, we aim to highlight both common mechanisms and knowledge gaps associated with different beneficial plant–microbe associations, with the goal of promoting their use within the framework of sustainable agriculture.

Plant–fungus associations

Fungi live in many different environments, but the majority are found in soils or associated with plants (Nilsson et al., 2019). Plant roots can host a broad taxonomic spectrum of beneficial fungal endophytes that penetrate the roots, among which mycorrhizal fungi are the most studied (Martin and van der Heijden, 2024) (Figure 1). Indeed, about 85% of land plants develop mycorrhizas (Brundrett and Tedersoo, 2018), which is

a clear indication of the ancient evolutionary origin and ecological success of this symbiosis. Through these associations, specialized plant–fungus interfaces are formed for resource exchange (Skiada et al., 2020). Mycorrhizas can be classified into two main types: ectomycorrhiza (ECM) or endomycorrhiza (Martin and van der Heijden, 2024). In ECM, the fungal hyphae remain extracellular, surrounding the roots and forming a sheathing mantle. They also form an intercellular interface of highly branched hyphae in the apoplast of epidermal and cortical cells, known as the Hartig net (Brundrett and Tedersoo, 2018). In endomycorrhizas, fungal hyphae penetrate the root cells to establish an intracellular symbiosis. Endomycorrhizas include arbuscular mycorrhizas (AMs), ericoid mycorrhizas, and orchid mycorrhizas (Martin and van der Heijden, 2024; Perotto and Balestrini, 2024). Because our understanding of the molecular basis of ericoid and orchid mycorrhizas is still very limited, we focus on the AM and ECM symbioses in the present review. AM endosymbioses involve a small group of soil fungi from the Glomeromycotina subphylum (phylum Mucoromycota) that are able to colonize the majority of land plants (Shi et al., 2023). Through this association, AM fungi develop intercellular hyphae and highly branched intracellular structures, called arbuscules, within root cortical cells. These arbuscules generate a larger plant–microbe membrane interface, enabling a greater exchange of water and nutrients between the two symbionts. Indeed, the AM fungus is an obligate symbiont that relies on the host plant for the supply of carbon (C) compounds, in particular fatty acids. In turn, the fungus provides the host plant with mineral nutrients, particularly phosphorus and nitrogen (N), and water (Duan et al., 2024). Recently, there has been increasing interest in the phylogenetically related Mucoromycotina fine root endophytes (MFREs) (Prout et al., 2024). These endophytes often co-colonize plant roots alongside AM fungi to assist with host-plant nutrient uptake. MFREs can form arbuscule-like structures in a few plant species. However, unlike AM fungi, MFREs can grow on minimal medium without a host plant, which facilitates molecular and genetic studies of the mechanisms, evolution, and ecology of these ancient plant–fungus symbioses.

Approximately 6000 plant species from the Pinaceae family and various angiosperm families (e.g., Fabaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, and Salicaceae) form ECM associations with an estimated 20,000 fungal species, including members of the Ascomycota and Basidiomycota phyla (Brundrett and Tedersoo, 2018). ECM symbioses represent the most prevalent symbiotic relationship between trees and soil fungi in boreal and temperate forest ecosystems. They play a vital role in maintaining forest sustainability by facilitating nutrient cycling and promoting C storage in soils (Brundrett and Tedersoo, 2018; Martin and van der Heijden, 2024).

Other root-colonizing fungi with a positive impact on host plants include *Trichoderma* spp. and the generalist root endophytes *Serendipita indica*, *Fusarium solani*, and *Colletotrichum tofieldiae* (Skiada et al., 2019; Díaz-González et al., 2020; Shekhawat et al., 2021; Woo et al., 2023) (Figure 1). *Trichoderma* is a genus of ubiquitous filamentous ascomycete fungi from the Hypocreaceae family that are of interest to agriculture as biocontrol agents, although they also show other plant-beneficial effects, such as growth promotion and increased tolerance to abiotic stresses (Woo et al., 2023). Unlike AM fungi, *Trichoderma* is an opportunistic symbiont, as it can grow as a free-living fungus or associated with plant roots. *S. indica* is a generalist root endophyte that belongs to the Sebacinales order and Serendipitaceae family. It shows some functional similarities to AM fungi with respect to its nutrient and water uptake capacity, C assimilation efficiency, and ability to improve plant stress tolerance and induce local and systemic (long-distance) disease resistance (Shekhawat et al., 2021). *F. solani* is generally considered a pathogenic species; however, some strains, such as *F. solani* strain K, initially isolated from tomato roots and also shown to be beneficial in legumes, can protect plants against stresses such as drought and the pathogen *Nesidiocoris tenuis* (Garantonakis et al., 2018; Kavroulakis et al., 2018). Finally, *C. tofieldiae* was originally isolated from *Arabidopsis thaliana* (Díaz-González et al., 2020) but probably has a broad host range. It colonizes roots and, from there, spreads systemically through the stele, a feature that is reminiscent of pathogenic infection, in line with its phylogenetic relationship with pathogenic *Colletotrichum* species (Fesel and Zuccaro, 2016). It is worth noting that *C. tofieldiae* is a beneficial fungus only in certain circumstances, e.g., phosphate (Pi) deficiency (Hiruma et al., 2016). Overall, these selected examples show that plant roots host highly taxonomically diverse beneficial fungal endophytes.

Plant–bacterium associations

Like fungi, bacteria can live in a variety of environments and associate with plants. They are classified as epiphytes, which live on the plant surface, or endophytes, which colonize healthy plant tissues. In general, epiphytic bacteria contribute to host fitness and are highly exposed to the external environment, whereas endophytes colonize the root niche. Especially among the root endophytes, certain bacteria can more directly improve plant nutrient uptake and defense against pathogens (Kumar et al., 2017). A variety of endophytic diazotrophic bacteria can establish an N-fixing symbiosis with a diverse set of plants within the Rosid I clade, including legume (Fabaceae) plants (Figure 1). These bacteria, collectively known as rhizobia, belong to various families within the alpha- and betaproteobacteria (e.g., Rhizobiaceae and Burkholderiaceae, respectively). They form symbiotic relationships with legumes and the non-legume *Parasponia*. In addition, Gram-positive *Frankia* strains engage with a group of so-called actinorhizal plants, which are mostly non-legume woody shrubs or trees such as *Casuarina*, *Myrica*, and *Alnus* (Hu et al., 2023). A common feature of these symbioses is the formation of unique organs, the nodules, on roots. Within nodules, bacteria find a specialized niche with low oxygen levels that allows their differentiation into bacteroids, which express nitrogenase genes that enable N fixation. Intracellular symbiotic N-fixing bacteria are surrounded by a plant-derived membrane to form symbiosomes, organelle-like structures dedicated to N fixation. In some ancient legumes (Caesalpinioideae subfamily), N-fixing bacteria are retained within so-called ‘‘fixation threads’’ (de Faria et al., 2022). In exchange for the N fixed by symbiotic bacteria, host plants provide C compounds and micronutrients to ensure bacterial proliferation, differentiation, and fixed N assimilation (Ledermann et al., 2021).

In addition to N-fixing rhizobacteria, plants, including agronomically relevant crops, can also be colonized by a diverse array of other bacteria, which may or may not be N-fixing and help plants to grow under adverse conditions (Sun et al., 2024). Such bacteria are termed plant growth-promoting rhizobacteria (PGPRs) (Figure 1) and are ubiquitous in the rhizosphere, at the root surface, in the root endosphere, and in the apoplast between cells. As these bacteria are less tightly associated with plant roots than intracellular microbial symbionts such as rhizobia and *Frankia*, beneficial PGPR interactions are proposed to be less co-evolved than N-fixing symbioses. A huge diversity of PGPRs, including species from the genera *Streptomyces, Pseudomonas, Bacillus, Azospirillum, and Burkholderia,* have been reported in different host plants, where they have been shown to support host growth by increasing plant nutrition, notably in poor soils and under stress conditions, and to improve plant biotic and/or abiotic stress tolerance (He et al., 2024). Notably, a pioneering study in barley showed that plant genes can shape the composition of the rhizosphere microbiota (Escudero-Martinez et al., 2022), and recent studies have shown that co-inoculation of AM fungi with PGPRs (e.g., P-solubilizing bacteria) leads to synergistic effects. Mycorrhizal helper bacteria isolated from the rhizosphere of ECM trees or from the fruiting bodies or hyphal mantles of ECM fungi promote the ECM symbiosis and increase tree biomass (Frey-Klett et al., 1997; Andre et al., 2005). Specific bacterial taxa are selected in ECM root tips to synergistically promote tree growth (Berrios et al., 2023). These studies indicate that the use of tripartite interactions/microbial consortia is an interesting strategy from an applied inoculation perspective (Pandino et al., 2024; Zeng et al., 2024; Severo et al., 2025).

MOLECULAR MECHANISMS ASSOCIATED WITH BENEFICIAL INTERACTION NETWORKS

The widespread use of beneficial microbes as probiotics for agriculture still remains a challenge, although some progress has been made in recent years. This is due in part to the fact that the mechanisms regulating the establishment and maintenance of these beneficial associations are still largely unknown at the molecular level. In this section, we will review the main processes that occur during the early and late stages of these beneficial interactions.

Common features of arbuscular mycorrhiza (AM), rhizobial nodulation (RN), and endophyte associations at early interaction stages

Plant-derived signals involved in AM and RN symbioses: Strigolactones (SLs) and flavonoids

The best-studied beneficial plant–microbe interactions are the AM and rhizobium–legume symbioses. In both cases, the interaction starts with a molecular communication, even before physical contact is established between the two partners (pre-symbiotic phase; Figure 1). The pre-symbiotic molecular dialogue is initiated by nutrient deficiencies and begins with the exudation of plant-derived signaling molecules into the rhizosphere, indicating the presence/receptivity of compatible partners. In the AM symbiosis, carotenoid-derived strigolactones (SLs) are key plant-derived molecular cues produced and secreted mainly under Pi- and/or N-limiting conditions (Figure 1) (Akiyama et al., 2005; López-Ráez et al., 2008; Yoneyama et al., 2012). Accordingly, SL-deficient mutants from different plant species, including crops such as pea, rice, and tomato, show reduced mycorrhization levels (Gomez-Roldan et al., 2008; Vogel et al., 2010; Kohlen et al., 2012; Yoshida et al., 2012). The pleiotropic drug resistance 1 transporter from *Petunia hybrida*, a member of the ATP-binding cassette subfamily G (ABCG), has been shown to participate in SL transport (Kretzschmar et al., 2012). SL perception by currently unknown AM fungal receptors promotes spore germination, activates fungal metabolism, and induces extensive hyphal growth and branching, thereby increasing the probability of finding host roots and establishing the symbiosis (Akiyama et al., 2005; Besserer et al., 2006). In addition to having an ancestral function as signaling molecules in the rhizosphere, SLs are phytohormones that modulate plant development, notably shoot branching, in response to the plant's nutritional status (Al-Babili and Bouwmeester, 2015; López-Ráez et al., 2017). Interestingly, SLs have also been shown to promote the association of the endophytic fungus *Mucor* with *A. thaliana* (Rozpądek et al., 2018). In addition to SLs, certain flavonoids and 2-hydroxy fatty acids may promote AM symbiosis at the pre-contact stage by influencing fungal growth in the rhizosphere, although the underlying molecular mechanisms remain unknown (Scervino et al., 2007; Nagahashi and Douds, 2011; Lidoy et al., 2023).

Similar to that of the AM symbiosis, the initiation of molecular dialogue during the rhizobial nodulation (RN) symbiosis is triggered by nutrient shortage; in this case, N deficiency. These conditions stimulate the biosynthesis and release of specific flavonoids, mainly isoflavones (Subramanian et al., 2006). The primary symbiotic function of isoflavones in the RN symbiosis is to induce the expression of RN genes in compatible strains, which leads to the production of host-specific signaling molecules known as Nod factors (Figure 1) (Kosslak et al., 1987; Subramanian et al., 2006). This bidirectional molecular dialogue involving flavonoids and Nod factors ensures the recognition of compatible rhizobium–host plant symbiotic combinations. Notably, a member of the multidrug and toxic compound extrusion family from white lupin has been shown to function in genistein secretion and nodule formation (Biała-Leonhard et al., 2021). In addition, G-type ABC transporters have been proposed to participate in the release of ''pre-infection flavonoids'' from soybean roots (Sugiyama et al., 2007) (Figure 1). Flavonoids are a class of specialized plant secondary metabolites derived from phenylpropanoids. They act as molecular cues in the rhizosphere and are also crucial in plant physiology, acting as pigments and antioxidants and influencing seedling growth, root architecture, and defense responses (Hassan and Mathesius, 2012). The production of such defense compounds may also affect the selection of compatible rhizobia and determine host range. For instance, *Sinorhizobium meliloti*, the symbiont of the legume *Medicago*, unlike *Bradyrhizobium japonicum* and *Mesorhizobium loti*, is unresponsive to the main isoflavonoid-derived phytoalexin medicarpin (Pankhurst and Biggs, 1980).

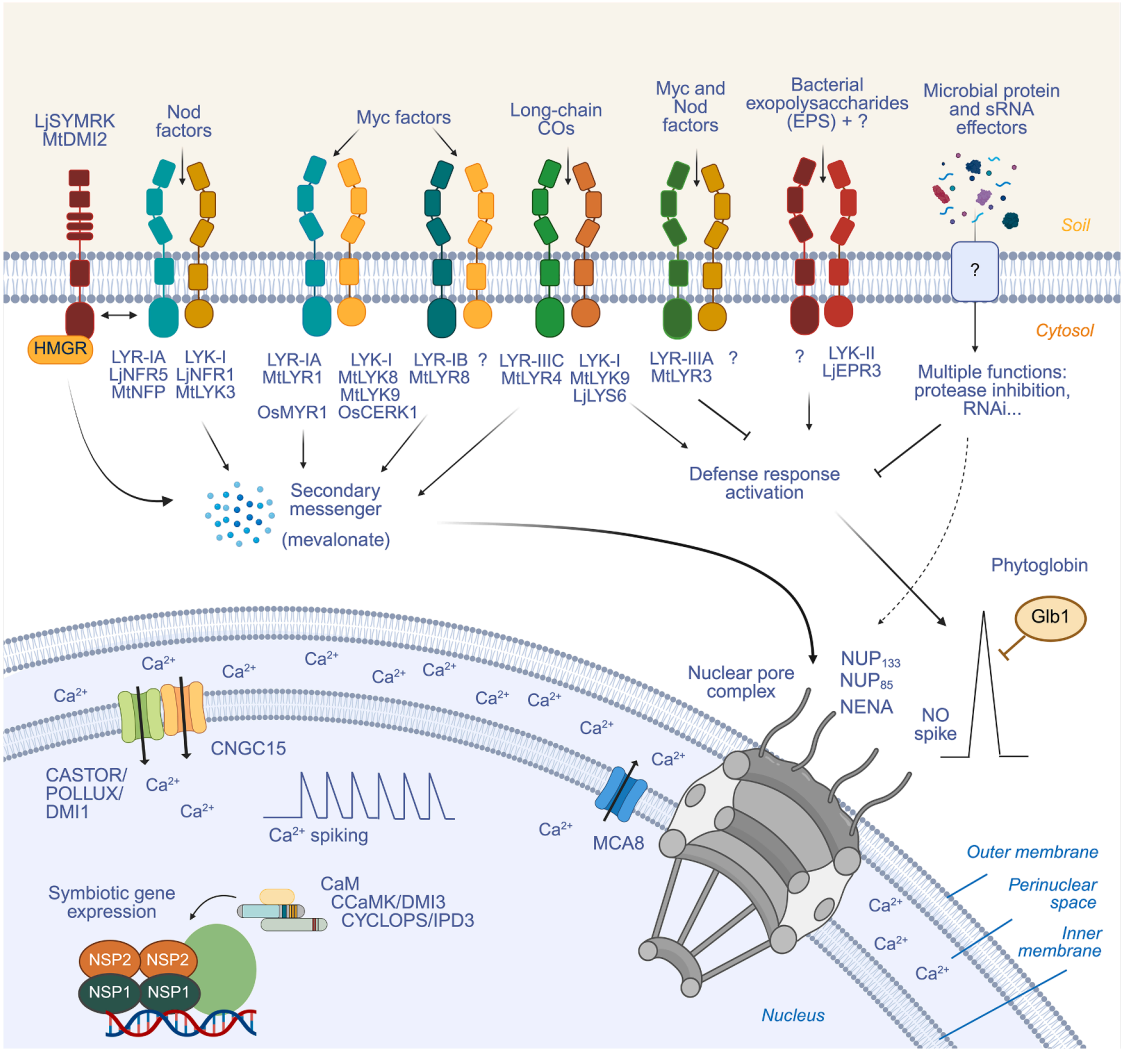

Figure 2. Perception of symbiotic factors and elicitors during the pre-symbiotic phase and common symbiosis signaling pathways associated with the early infection phase.

The perception of Myc (mycorrhizal) and Nod (nodulation) factors and long-chain COs is mediated by heterodimeric Lysin motif receptor-like kinases (LysM-RLKs). The perception of bacterial surface exopolysaccharides (EPSs) involves LjEPR3. The mechanisms by which other microbial effectors remain largely unknown. The recognition of these molecular cues at the plasma membrane triggers different signaling cascades involving nucleocytoplasmic Ca^{2+} spiking, depending on the type of beneficial plant–microbe interaction. Signal transduction involves SYMRK/DMI2, CASTOR/POLLUX/DMI1, CNGC15, NUP85, NUP133, and NENA upstream of the nucleocytoplasmic Ca^{2+} spiking, and CCaMK/DMI3 and CYCLOPS/IPD3 downstream. Several transcription factors, such as NSP1/2, then activate the expression of symbiosis genes and modulate defense responses. The non-symbiotic hemoglobin Glb1 regulates the levels of nitric oxide (NO). LYK, LysM-RLK with a canonical kinase domain; LYR, LYK-related with a pseudo-kinase domain; CO, chitin oligosaccharide; sRNA, small RNA. The figure was generated using BioRender (https://biorender.com/).

Microbe-derived signals involved in AM and RN symbioses: Myc and Nod factors

In response to these plant-derived molecules, both AM fungi and rhizobia produce and secrete chitin oligosaccharide (CO)-derived signaling molecules. More specifically, AM fungi produce short-chain COs (Myc-COs) and lipochitooligosaccharides (Myc-LCOs), collectively known as "Myc factors" (Maillet et al., 2011; Genre et al., 2013), whereas rhizobia produce LCOs that are referred to as Nod factors (Figures 1 and 2) (Lerouge et al., 1990). The perception of these Myc and Nod factors by high-affinity plant receptors triggers early symbiotic responses, including nucleocytoplasmic Ca^{2+} spiking in rhizodermal cells, activation of gene transcription, accumulation of starch, and stimulation of lateral root formation. Many downstream signaling components are positioned either upstream (SYMRK/DMI2, CASTOR/POLLUX/DMI1, NUP85, NUP133, and NENA) or downstream (Ca^{2+-} and calmodulin-dependent protein kinase [CCaMK]/does not make infection 3 [DMI3] and CYCLOPS/IPD3) of the Ca^{2+}-spiking response. This leads to the activation of several transcription factor complexes, such as the nodulation signaling pathway 1 (NSP1)/2 complex, which induces the expression of symbiosis-related genes (Singh and Parniske, 2012; Zipfel and Oldroyd, 2017). Myc and Nod factor receptors are located in the plasma membrane and belong to the lysin motif receptor-like kinase (LysM-RLK) family (Figure 2) (Buendia et al., 2018). Heterodimeric complexes, comprising

one LysM-RLK harboring a canonical kinase domain (LYK subfamily) and one LysM-RLK harboring a non-canonical kinase domain (LYR subfamily, for LYK-related), are required for the perception and transduction of symbiotic LCO and/or CO signals. More precisely, for the AM symbiosis in most angiosperms, at least two LYRs with high affinity for Myc factors (LYR-IA type with high affinity for LCOs and LYR-IB type with high affinity for short-chain COs and LCOs), together with one LYK-I type with lower affinity and specificity for Myc factors, are involved in AM establishment (Li et al., 2022; Zhang et al., 2024a; Ding et al., 2025). However, biochemical and genetic evidence, based either on LYR double mutants in legumes and cereals (Li et al., 2022; Ding et al., 2025) or on the unique *LYR* gene of the bryophyte *Marchantia paleacea* (Tan et al., 2025; Teyssier et al., 2025), suggests that additional receptors and/or signals are involved in AM fungal perception and AM establishment. For the RN symbiosis, a similar heterodimeric LysM-RLK complex, comprising the LYR-IA type LjNFR5/MtNFP protein and the LYK-I type LjNFR1/MtLYK3 protein, has been reported to be essential for nodulation in the model plants *Lotus japonicus* and *Medicago truncatula* (Limpens et al., 2003; Madsen et al., 2003; Radutoiu et al., 2003; Arrighi et al., 2006). This indicates that, although these two legumes form determinate and indeterminate nodules, respectively, an evolutionary conservation exists. This also suggests a common origin of the AM and RN symbioses (Genre et al., 2020). Indeed, the LysM-RLKs involved in Myc-LCO perception are proposed to have been recruited for Nod factor perception, leading to gene duplication and sub-functionalization in legume plants (Bozsoki et al., 2020; Gysel et al., 2021; Cullimore et al., 2023). Interestingly, the LysM-RLK LYK10, which is essential for nodulation but not for AM symbiosis in legumes, has been shown to be required for fungal penetration in tomato (Buendia et al., 2016), indicating evolutionary differences between the two symbioses. Myc and Nod factors, in addition to establishing AM and RN symbioses, respectively, inhibit plant defense, in part through the LysM-RLKs mentioned above, as well as through a third class of LysM-RLK, the LYR-IIIA type, which shows a high affinity for LCOs (Malkov et al., 2016; Wang et al., 2023). AM fungi also produce long-chain COs, which are well-known defense elicitors. These long-chain COs are perceived by heterodimeric complexes comprising an LYR-IIIC type and an LYK-I type LysM-RLK (MtLYR4 and MtLYK9 in *M. truncatula*) (Zhang et al., 2024a) or an LYM-II type and an LYK-I type LysM-RLK (Buendia et al., 2018). Interestingly, long-chain COs can induce Ca^{2+} spiking in *M. truncatula* (Feng et al., 2019), suggesting cross-talk between AM and defense signaling. Finally, in some legumes, the RN symbiosis can be established independently of nod factor (NF) LCOs through alternative signals and molecular mechanisms that remain to be fully deciphered (Masson-Boivin et al., 2009).

In addition to Myc and Nod factors, bacterial surface polysaccharides are also relevant determinants of rhizobial infection in host plant roots. Exopolysaccharides (EPSs) are perceived in *L. japonicus* by LjEPR3, an LYK-II-type LysM-RLK (Figure 2) (Kawaharada et al., 2015; Bozsoki et al., 2017), although a different signaling pathway probably exists in *M. truncatula* (Maillet et al., 2020). Interestingly, LjEPR3 binds EPS, and its expression is induced by Nod factors, indicating that a two-stage mechanism involving sequential receptor-mediated recognition of NF and EPS signals is involved in determining plant–rhizobium compatibility and bacterial infection in *L. japonicus*. Unexpectedly, although this LYK-II-type LysM-RLK is conserved in all AM-forming plants and lost in non-AM plants, as is typical for genes functionally associated with the AM symbiosis, mutants of the *M. paleacea* and rice EPR3 orthologs do not show an AM phenotype (Roth et al., 2018; Tan et al., 2025; Teyssier et al., 2025).

Microbe-derived effectors involved in AM, ECM, and RN symbioses

Mycorrhizal fungi and rhizobia also produce and secrete effector proteins, small RNAs (sRNAs), and small peptides to modulate plant defenses and promote root colonization (Figure 2) (Zanetti et al., 2020; Ledford et al., 2024; Wulf et al., 2024). Comparative transcriptomic studies have shown that the AM fungus *Rhizophagus irregularis* can produce at least 220 putative effector proteins, and 163 have been identified in *Funneliformis mosseae* (Toro and Brachmann, 2016; Vasistha et al., 2025). In the case of rhizobia, several effector proteins have been identified through *in silico* predictions, mainly related to the type III secretion system (Miwa and Okazaki, 2017; Teulet et al., 2022). In most cases, however, their function remains unknown. Some of these effector proteins have nevertheless been shown to act in the plant cell apoplast or intracellularly to suppress immunity, thus allowing microbial accommodation within the host root (Miwa and Okazaki, 2017). Other effectors have been shown to participate in accommodation of the symbiont (Teulet et al., 2022; Aparicio Chacón et al., 2023). In the ECM fungi *Laccaria bicolor* and *Pisolithus tinctorius*, protein effectors, such as carbohydrate-active enzymes and small secreted proteins (SSPs), have been identified as key symbiotic regulators. Fungal carbohydrate-active enzymes remodel the plant cell wall (Zhang et al., 2018; Chowdhury et al., 2022), whereas SSPs affect the aggregation of fungal hyphae (Pellegrin et al., 2019) or modulate plant immunity (Plett et al., 2011, 2020). For example, *L. bicolor* MiSSP7 (mycorrhiza-induced SSP7) has been shown to inhibit defense responses triggered by jasmonic acid (Marqués-Gálvez et al., 2024). In terms of small peptide effectors, the AM fungi *R. irregularis* and *Gigaspora rosea* have been shown to produce CLE (CLAVATA3/embryo-surrounding region-related) signaling peptide mimics that are expressed during host-root colonization, but not in fungal spores or hyphae, suggesting a symbiotic role (Le Marquer et al., 2019). Accordingly, exogenous treatment with this fungal CLE peptide enhances root colonization by AM fungi. The related *M. truncatula* gene *MtCLE16* is expressed in AM fungus–colonized root cells, and its overexpression increases arbuscule growth and lifespan (Bashyal et al., 2025). MtCLE16 peptides act through the MtCORYNE pseudo-kinase to suppress the accumulation of reactive oxygen species, thus attenuating immune responses and promoting root colonization by AM fungi. Similarly, RiCLE1 also attenuates the production of reactive oxygen species and promotes AM fungal colonization via MtCORYNE (Bashyal et al., 2025). Interestingly, related CLE peptides have recently been proposed to promote the ECM symbiosis in poplar (Bonnot et al., 2025).

sRNAs are also emerging as important modulators of the establishment of beneficial symbioses (Figure 2), although the specific role of these microbial sRNAs is poorly understood. A recent study reported the silencing of plant target genes through RNAi mediated by the transport of sRNAs between AM/ECM fungi or

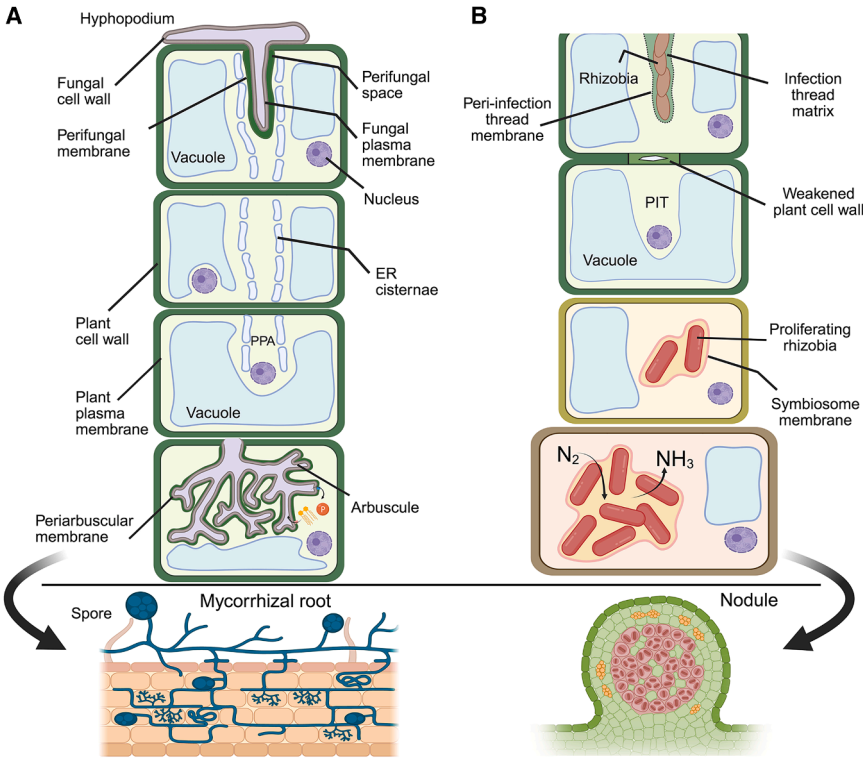

Figure 3. Infection process and intracellular accommodation structures formed within host plants in arbuscular mycorrhizal and legume–rhizobium symbioses.

(A) The root colonization process of arbuscular mycorrhizal fungi and arbuscule formation. Formation of the pre-penetration apparatus (PPA), a channel formed across the vacuole, involves a reorganization of the endoplasmic reticulum (ER) and cytoskeleton and an invagination of the plasma membrane. Growth of the PPA within the colonized cell is guided by the nucleus, and only when the PPA has formed can the fungal hypha penetrate the cell. Hyphae then elongate intracellularly through PPAs to reach the root inner cortex, where arbuscules (interfaces for plant–AM fungus exchange) are formed.

(B) Rhizobial root colonization and nodule formation. A channel-like pre-infection thread (PIT) structure is initially formed across the vacuole in the infected root hair, involving reorganization of the ER and cytoskeleton. PITs then also form in cortical cells, connecting cells as transcellular passage clefts to allow the intracellular progression of infection threads within the root cortex. Inside nodules, N-fixing rhizobia are surrounded by a plant-derived symbiosome membrane, which prevents direct contact of the bacteria with the plant cytoplasm, and differentiate into N-fixing bacteroids. The figure was generated using BioRender (https://biorender.com/).

rhizobia and their host plant, a process termed cross- or *trans*-kingdom RNAi. In this way, microbes hijack host genes that are important for regulating AM colonization (Silvestri et al., 2025) or nodule development (Ren et al., 2019). Recently, the microRNA (miRNA) *Pmic_miR-8* from the ECM fungus *Pisolithus microcarpus* was shown to be transferred into its host plant, *Eucalyptus grandis*, probably to target host immune receptors (Wong-Bajracharya et al., 2022). Evidence of cross-kingdom RNAi was also recently found in the interaction of the beneficial endophyte *S. indica* with *A. thaliana*, targeting host genes related to hormonal regulation and immunity (Nasfi et al., 2025).

Common features of AM, RN, and endophyte associations during root colonization

The AM/RN common symbiosis signaling pathway (CSSP)

Upon reciprocal recognition as symbiotic partners, the host plant actively promotes root colonization by the microsymbiont, controlling its proliferation, progression toward the root cortex, and formation of symbiosomes (symbiotic phase; Figure 3). The recognition of Myc and Nod factors by host plants triggers a shared intracellular signaling cascade in root epidermal cells, referred to as the common symbiosis signaling pathway (CSSP). This involves oscillations in nucleocytoplasmic Ca^{2+} concentrations that are pivotal for the onset of both AM and rhizobial symbioses (Singh and Parniske, 2012). Ca^{2+} spiking is decoded by a CCaMK, called DMI3 in *M. truncatula*, that phosphorylates the transcription factor LjCYCLOPS/MtIPD3 (interactor of DMI3) (Lévy et al., 2004; Tirichine et al., 2006; Yano et al., 2008). This activates a set of downstream transcriptional regulators (NSP1, NSP2, nodule inception [NIN], and required for arbuscular mycorrhization 1 [RAM1]), which promote the expression of AM and/or nodulation genes (Zipfel and Oldroyd, 2017; Pimprikar and Gutjahr, 2018). Decoding Ca^{2+} spiking promotes cytoskeletal rearrangement and nuclear migration toward the cell surface prior to symbiont penetration. Upon physical contact between the two partners at atrichoblast cells, the fungal hyphae differentiate into attachment structures called hyphopodia (Genre et al., 2005), whereas rhizobia, in most cases, penetrate root hairs (Brewin, 2004). To accommodate symbionts intracellularly, root host cells undergo drastic subcellular changes. In the case of the AM symbiosis, a pre-penetration apparatus (PPA) is formed. The PPA consists of a channel across the vacuole, surrounded by the endoplasmic reticulum and cytoskeleton, through which the plasma membrane invaginates through massive and targeted vesicular trafficking. Fungal hyphae further elongate through this thread, growing intracellularly toward the inner cortex (Figure 3A) (Genre et al., 2005). A similar process is initiated during intracellular rhizobial colonization. In general, upon successful recognition, a rhizobial microcolony becomes entrapped in a curling root hair. Subsequently, local cell-wall hydrolysis and invagination of the cellular membrane lead to the formation of an infection thread. This thread grows inward through continuous cell membrane deposition and rhizobial cell division. The infection thread progresses along the root hair epidermal cell to reach a group of cortical cells that has followed a stereotyped cell division pattern to form a nodule primordium, where bacteria will be released (Figure 3B) (de Carvalho-Niebel et al., 2024). Similar to that of AM fungi, the growth of infection threads is guided by pre-infection threads (PITs), which are cytoplasm-dense, endoplasmic-reticulum-rich, tube-like regions that cross the vacuole in root hairs and

cortical cells, as well as by structures that connect cells, designated transcellular passage clefts (Zhang and Ott, 2024).

Conservation of the CSSP across the land plant phylogeny suggests that it may play a role in other plant–microbe interactions beyond AM and RN symbioses. In the ECM symbiosis, because this trait evolved independently in different gymnosperm and angiosperm lineages, involvement of the CSSP seems to occur in some but not all ECM associations (Garcia et al., 2015). It has indeed been suggested that evolution of the ECM symbiosis in the Fagales order involved co-option of the CSSP from the more ancient AM symbiosis because (1) Fagales ECM-only hosts have maintained 64% of the AM-conserved gene homologs, whereas all previously studied non-AM hosts have lost all of them (Radhakrishnan et al., 2020), and (2) *Populus, which hosts both* AM and ECM symbioses, requires AM-conserved genes to enable Ca^{2+} spiking and development of the ECM symbiosis (Cope et al., 2019). In addition, a potential convergent evolutionary co-option of some CSSP genes for the ECM symbiosis, including *DMI2/SYMRK and CCaMK,* has been identified in the Rosid clade (van Beveren et al., 2025). Finally, the ECM fungus *L. bicolor* produces LCOs in pure culture that are able to trigger Ca^{2+} spiking in *Populus* roots (Cope et al., 2019), in analogy with the AM symbiosis.

CSSP-dependent nuclear Ca^{2+} is triggered during the beneficial endophytic interaction with *F. solani* strain K, and CSSP mutant/RNAi lines showed reduced intraradical fungal colonization (Skiada et al., 2020). Accordingly, LCOs are produced in different non-AM fungal species (Rush et al., 2020). Regarding MFRE associations, although plants defective in DMI2/SYMRK or RAM1—which participate in the CSSP and the AM-specific symbiotic signaling pathway, respectively—were not impaired in formation of the beneficial association, mutants affecting the central CSSP component DMI3 showed lower colonization and reduced C transfer toward the MFRE fungi (Williams et al., 2025). In the case of *Trichoderma*, sucrose within root exudates has been reported to attract the fungus to the host root surface (Mendoza-Mendoza et al., 2018), although this probably does not provide any specificity for recruiting this specific beneficial microbe. Fungi then colonize not only the root surface but also the apoplastic space between the epidermal and first outer cortical cell layers. At this stage, *Trichoderma* behaves as a pathogen, but subsequent events, including the secretion of effector proteins and the build-up of an oxidative burst, differentiate it from pathogenic fungi (Mendoza-Mendoza et al., 2018). However, no detailed and comprehensive molecular mechanisms explaining this differential behavior are available. Finally, although *S. indica* root colonization shows some similarity to AM fungal root colonization, the molecular mechanisms involved do not seem to rely on the CSSP and remain unknown (Dunken et al., 2024).

Role of nitric oxide (NO) in symbiotic and endophytic interactions

The colonization of plants by AM fungi also triggers a rapid and transient burst of nitric oxide (NO), a free radical gaseous molecule with multiple functions in plants, as well as the induction of a non-symbiotic hemoglobin or phytoglobin of class 1 in tomato (Martínez-Medina et al., 2019). Phytoglobins can be grouped into three classes according to their phylogeny and biochemical properties, and those in class 1 regulate NO levels by converting NO into nitrate through their dioxygenase activity. Overexpression of *Glb1* in *L. japonicus* reduces root NO levels and enhances AM fungal colonization. Conversely, a *glb1* knockout mutant accumulates NO and shows reduced fungal colonization (Fukudome and Uchiumi, 2024). A transient burst of NO and *Glb1* expression in legume host roots also occurs within the first hours of infection with compatible rhizobia (Berger et al., 2020; Fukudome and Uchiumi, 2024). Remarkably, legume roots in contact with incompatible rhizobia do not show an NO burst, whereas roots challenged with pathogenic bacteria such as *Pseudomonas syringae* experience a prolonged accumulation of NO (Nagata et al., 2008). Overall, similar spatiotemporal regulation of NO accumulation occurs in host plants at the initial stages of interaction with AM fungi or rhizobium, and this transient ''NO signature'' differs from that which occurs in response to pathogens.

By contrast, very little information is available regarding the potential function of NO in ECM and PGPR interactions, although some studies have suggested that it could play a positive role. Indeed, increased root colonization by the ECM fungus *Tuber indicum* was observed when an NO donor was used for soil amendment (Rosenkranz et al., 2023). Similarly, a positive effect of NO on colonization of cucumber roots by the PGPR *Bacillus velezensis* SQR9 has been shown (Kang et al., 2022).

Common and different features of AM, RN, and other endophytic associations at late stages

Nutrient exchange between symbionts is a central aspect of both the AM and RN symbioses (Table 1). During the intracellular symbiotic stage of these interactions, AM fungi develop highly branched structures called arbuscules within the inner cortex of the root, whereas rhizobia differentiate into N-fixing bacteroids in root nodules. Arbuscules and bacteroids are enveloped by host-derived membranes—the periarbuscular membrane (PAM) and the symbiosome membrane (SM), respectively—to form specialized symbiotic interfaces (Figure 3). Whereas the PAM is physically continuous with the plasma membrane, the SM exhibits an intermediate identity between the PM and the prevacuolar membrane, reflecting the organelle-like characteristics of the symbiosomes (De La Peña et al., 2018). Notably, the PAM and SM possess distinct sets of membrane proteins, primarily transporters, which are crucial for nutrient exchange (Hogekamp and Küster, 2013; Limpens et al., 2013). Plants deliver C sources, such as hexoses and lipids, to AM fungi in exchange for a range of macro- and micronutrients, primarily Pi (Pfeffer et al., 1999; Bago et al., 2000). In the RN symbiosis, plants supply dicarboxylates and metal ions and receive fixed N in the form of ammonia (NH_3)/ammonium (NH_4^+) (Rosendahl et al., 1992).

Nutrient transporters in the AM and RN symbioses

In the context of the AM symbiosis, the transport of nutrients through the PAM requires energy provided by the proton electrochemical gradient generated by H^+-ATPases. These enzymes also lead to an acidification of the periarbuscular space that favors the development and maintenance of arbuscules (Wang et al., 2017). The H^+ gradient is used by members of the proton-coupled phosphate transporter 1 (PHT1) family that belong to the mycorrhiza-specific clade I (e.g., PT4 from *M. truncatula* and tomato and PT11 from *Oryza sativa*) and are

Beneficial interaction	Nutrients exchanged	Main transporters	Infection and structures formed
AM symbiosis	● fungus to plant: mainly Pi and N (NO_3^- and NH_4^+) ● plant to fungus: C (hexoses, lipids)	● Pi: PHT1 family (MtPT4/OsPT11) ● NH_4^+: AMT family; NO_3^-: NPF ● carbohydrates: SWEET family ● lipids: ABCG subfamily (STR/STR2)	● arbuscule ● PAM
RN symbiosis	● bacteria to plant: fixed N (NH_4^+) ● plant to bacteria: C (dicarboxylates), Pi, metal ions, and sulfate (S)	● Pi: MtPHO1 ● NH_4^+: AMT family; NO_3^-: NPF ● carbohydrates: SWEET family (?) ● iron: GmVTL1a, MtVTL4/8, MtFPN2 ● sulfate: LjSST	● nodule ● SM
ECM symbiosis	● fungus to plant: N (NH_4^+) and Pi ● plant to fungus: C	● Pi: HcPT2, PiPT1 ● NH_4^+: AMT family ● C transfer: SWEET family	● mantle ● Hartig net
Fungal endophytes	● fungus to plant: N (NO_3^- and NH_4^+) and Pi ● plant to fungus: C	● Pi: high-affinity transporters ● NO_3^-: NPF ● C transfer: SWEET family	● intercellular colonization with occasional intracellular penetration
PGPRs	● bacteria to plant: in some cases, N fixation (NH_4^+) and Pi ● plant to bacteria: C	● difficult to demonstrate direct nutrient exchange ● transporters unknown	● intercellular colonization

Table 1. Characteristics of the main beneficial plant root–microbe interactions at late stages.
PHT1, phosphate transporter 1; AMT, ammonium/methylammonium transporter; NPF, nitrate transporter 1/peptide transporter family; SWEET, sugars will eventually be exported transporter; VTL1, vacuolar iron transporter-like; FPN2, ferroportin 2; SST1, symbiotic sulfate transporter 1.

essential for symbiotic Pi uptake (Table 1) (Harrison et al., 2002; Paszkowski et al., 2002). In addition to Pi, the fungal partner provides host plants with various forms of soil-derived N and other mineral nutrients. PAM-localized members of the ammonium transporter (AMT) and nitrate transporter 1/peptide transporter (NPF) families mediate the uptake of NH_4^+ and NO_3^-, respectively (Koegel et al., 2013; Wang et al., 2020). In turn, AM fungi obtain C in the form of monosaccharides and lipids, most likely sn-2 monoacylglycerols. Transporters from the half-size ABCG family STR/STR2 (stunted arbuscule/stunted arbuscule 2) are proposed to mediate the transfer of C16:0 sn-2 monoacylglycerol compounds or their derivatives through the PAM (Keymer and Gutjahr, 2018; Zhang et al., 2023). These transporters, together with the transcription factor RAM1, FatM (an acyl-ACP thioesterase-like protein), and RAM2/GPAT (glycerol-3-phosphate acyl-transferase), are likely part of the AM-specific functional unit that enables lipid biosynthesis and transport in arbuscule-containing cells (Keymer and Gutjahr, 2018; Zhang et al., 2023). In addition, members of the "sugars will eventually be exported transporter" (SWEET) family are involved in carbohydrate transfer across the PAM (An et al., 2019).

During the RN symbiosis, nutrient transport through the SM also requires energy provided by H^+-ATPases, which, in addition, facilitate the conversion of NH_3 to NH_4^+ (Pierre et al., 2013). Remarkably, although the translocation of fixed N (NH_3/NH_4^+) across the SM is a critical process, it remains poorly documented. It has been proposed that the aquaporin Nodulin 26 facilitates the diffusion of NH_3 (Hwang et al., 2010). In turn, rhizobia receive C in the form of dicarboxylates, which are transported across the SM by SWEETs (Table 1) (Kryvoruchko et al., 2016). In addition to photoassimilates, N-fixing bacteroids also rely on plant-derived metal ions, especially iron, which is a key cofactor of the bacterial nitrogenase enzyme. Ferrous iron (Fe^{2+}) is the major form transported from plant cells toward bacteroids through the SM. Vacuolar iron transporter-like (GmVTL1a) from soybean (*Glycine max*) and *M. truncatula* MtVTL4/8 and ferroportin 2 (MtFPN2) have been described as Fe^{2+} SM-localized transporters crucial for nodulation (Table 1) (Brear et al., 2020; Escudero et al., 2020; Walton et al., 2020). Symbiotic N fixation also relies on sulfate, transported by the *L. japonicus* nodule-specific symbiotic sulfate transporter 1, and on Pi, transported by members of the PHO1 phosphate permease superfamily into the peribacteroid space (Krusell et al., 2005; Nguyen et al., 2021).

Hemoglobins, NO, and O_2 in the AM and RN symbioses

Regarding the role of NO and hemoglobins in the AM symbiosis, AM fungi induce expression of the phytoglobin Glb1 in root cortical cells containing arbuscules, vesicles, and hyphae, suggesting that NO may be involved not only in early infection but also in late symbiotic stages (Table 1) (Martínez-Medina et al., 2019). The enzymes that produce NO in this AM symbiotic context remain unknown, although it has been suggested that reductive pathways, including nitrate and NO/NO_2^- reductases, may be involved under low-O_2 conditions (Kumari et al., 2019). Because fungal genomes encode flavohemoglobins and/or single-domain hemoglobins, they may also contribute to the control of NO concentrations, as shown in the case of pathogenic fungi (Vinogradov et al., 2013; Cánovas et al., 2016). This NO regulation could facilitate the AM symbiotic interaction by inhibiting defense responses and nitro-oxidative stress.

In the RN symbiosis, tight regulation of O_2 concentration within nodules is critical for N_2 fixation. This is achieved by the combination of an O_2 diffusion barrier located within the peripheral nodule parenchyma and symbiotic hemoglobins that accumulate in the central nodule region colonized by the rhizobia (Becana et al., 2020). These include the leghemoglobins (Lbs) of legume plants and the symbiotic hemoglobins of actinorhizal plants. All of these hemoglobins deliver O_2 to the bacterial symbiont at a low but steady concentration that is compatible with both bacterial

respiration and nitrogenase activity. Nodules, like other plant organs, also express Glbs. These include class 1 Glbs, which regulate NO metabolism and are critical for hypoxia tolerance, and class 2 and class 3 Glbs, whose functions are unknown. Interestingly, *L. japonicus* mutant nodules that lack all three Lbs (*lb123*) accumulate NO, which suggests that not only Glb1 but also Lbs are involved in NO homeostasis (Minguillón et al., 2024). Rhizobial genomes may encode flavohemoglobins (Hmp in *S. meliloti* and *M. loti*), single-domain hemoglobins (Bjgb in *B. japonicum*), and truncated hemoglobins (Meilhoc et al., 2011; Becana et al., 2020). Interestingly, nodules formed by *S. meliloti* mutants deficient in Hmp accumulate NO, whereas nodules formed with strains that overexpress Hmp show lower NO levels (Cam et al., 2012). Likewise, the respiratory NO reductase NorB of *S. meliloti* contributes to NO degradation (Meilhoc et al., 2013). In addition, host plant nitrate and *S*-nitrosoglutathione reductase enzymes contribute to NO metabolism (Table 1), with nitrate reductase potentially reducing NO_3^- to NO under these hypoxic conditions.

What about ECM and endophytic interactions?

Compared with those of the AM and RN symbioses, much less is known about the mechanisms that govern nutrient exchange in ECM, at least on the plant (tree) side, and in endophytic interactions. MFRE fungi, which often co-exist with AM fungi, can use plant-derived C for their own metabolic needs and transfer N to the plant, although the transporters involved remain unknown (Howard et al., 2024). ECM fungi can metabolize both organic N, the predominant form in soils of temperate and boreal forests, and inorganic N, with a preference for NH_4^+ when available. NH_4^+ is probably the main N form exported by the ECM fungus to plant root cells (Sebastiana et al., 2023), and several fungal and host plant AMT NH_4^+ importers have been characterized (Table 1) (Nehls and Plassard, 2018). Interestingly, the expression of these transporters is induced by low-N conditions and during symbiosis. The N taken up by the ECM fungus is then metabolized and transferred to the plant, a process that requires the coordinated action of fungal exporters and plant importers from the AMT family. Regarding Pi, it has been suggested that the HcPT2 transporter from the fungus *Hebeloma cylindrosporum* has a dual role in Pi influx from soil and efflux toward roots (Becquer et al., 2018). Similarly, the Pi transporter PiPT1 from *Paxillus involutus* is upregulated by Pi deficiency, showing that activation of the Pi signal transduction pathway also occurs in ECM (Paparokidou et al., 2021). In exchange, the fungus receives photoassimilates from the plant. Inactivation of the *Populus PtaSWEET1c* gene notably reduces C translocation to ECM roots, suggesting that it facilitates glucose and sucrose transport at the *Populus–L. bicolor* symbiotic interface (Li et al., 2024). Overall, the specific transporters and mechanisms involved in nutrient transport in the ECM symbiosis are poorly characterized (Stuart and Plett, 2020; Zhang et al., 2024b).

Among the beneficial fungal endophytes, *Trichoderma* improves N use efficiency. Inoculation of tobacco plants with *T. asperellum* T42 induces higher expression of NO_3^- transporters from the Nod Factor Perception (NFP) family (also previously termed NO_3^- transporter) and increases total N content and plant growth (Table 1) (Singh et al., 2018). *S. indica* mediates growth promotion in plants by boosting mineral nutrition. However, very little is known about the host plant molecular machinery involved in the transfer of nutrients (Kundu and Vadassery, 2022). Interestingly, *S. indica* seems to primarily influence Pi distribution and metabolism in *A. thaliana* under Pi limitation rather than promoting Pi uptake from soil (Bakshi et al., 2017). Conversely, phylogenetically unrelated fungal endophytes can promote growth by transferring Pi in non-AM hosts (e.g., *C. tofieldiae* in *A. thaliana* or the *Helotiales* taxon in *Arabis alpina*) in a process analogous to that which occurs in the AM symbiosis (Table 1) (Hiruma et al., 2016; Almario et al., 2017). The growth promotion mediated by *C. tofieldiae* notably relies on Pi starvation transcriptional regulators, indicating that the Pi starvation-induced Pi uptake machinery was also recruited for at least some beneficial fungal interactions, even in non-mycorrhizal plants.

For the more loosely interacting PGPRs, demonstrating a reciprocal nutrient exchange is far more challenging. As an example, although many PGPRs with the potential to fix N_2 when free living have been isolated, it is significantly more difficult to identify this activity when bacteria are in close association with plants, as well as to prove that this N-fixing activity is directed toward the plants' benefit. The interactions of *Azoarcus* spp. and *Azospirillum brasilense* with grasses are the clearest examples to date (Hurek et al., 2002; Pankievicz et al., 2015). Notably, known free-living diazotrophs could be engineered to become more efficient N fixers in non-legume crops, thereby helping to reduce the use of N chemical fertilizers (Martinez-Feria et al., 2024). Similar to N fixation, Pi solubilization under laboratory conditions has also been reported for numerous free-living PGPRs, including representatives from the genera *Bacillus*, *Burkholderia*, and *Pseudomonas* (He et al., 2024). Nonetheless, proving the *in vivo* relevance of this Pi solubilization and subsequent Pi transfer to the plant is far more challenging.

The role of NO metabolism in plant interactions with fungal or bacterial endophytes is also poorly understood. This is especially true for fungi because their NO biosynthesis pathways are largely unknown. NO production has been detected in the fungus *Preussia (Sporormiaceae family)*, along with other potential signals such as gibberellins, polyamines, and other secondary metabolites (Al-Hosni et al., 2018). Cucumber plants pre-treated with the beneficial *T. atroviride* TRS25 fungus accumulate NO in their leaves, which activates systemic plant defense upon attack by the pathogenic fungus *Rhizoctonia* (Nawrocka et al., 2019). In the case of the PGPR *A. brasilense*, the aerobic production of NO, which is dependent on a periplasmic nitrate reductase, is correlated with the development of lateral and adventitious roots in tomato (Cohen et al., 2009). However, in most, if not all, of these cases, it is unclear whether the beneficial effects of the endophytes on plant growth are indeed related to NO metabolism.

IMPACT OF PLANT NUTRITION ON SYMBIOSES

Beneficial plant–microbe associations not only provide benefits to the host plant but also come with an energetic cost associated with the formation and activity of symbiotic organs, as well as the feeding of fungal or bacterial partners. Symbioses must therefore be tightly regulated both in relation to whole-plant nutrient needs

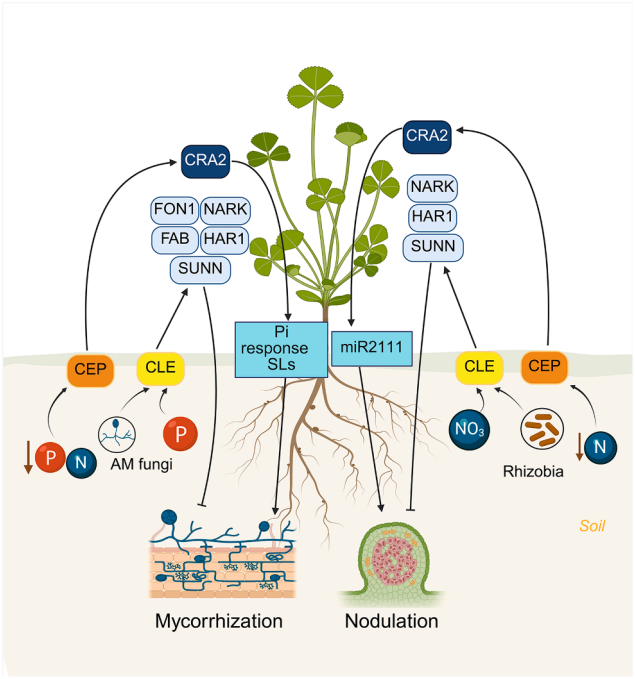

Figure 4. Impact of plant nutrition on the establishment and maintenance of beneficial plant–microbe symbioses

Left: regulation of the AM symbiosis by Pi-related signaling peptide regulatory pathways. In the legume *M. truncatula*, low Pi promotes mycorrhization through induction of C-terminally encoded peptide (CEP)-encoding genes and the compact root architecture 2 (CRA2) receptor-like kinase. This induction activates a Pi starvation response and the biosynthesis of SLs, which are required to attract AM fungi and trigger the AM symbiotic interaction. High Pi levels or extended root colonization by AM fungi induce the production of CLAVATA3/embryo surrounding region-like (CLE) signaling peptides, which act through a receptor complex involving, notably, the SUNN (super numeric nodule) receptor-like kinase. Related receptor-like kinases identified in other legumes include nodule autoregulation receptor kinase (NARK) in soybean and hypernodulation and aberrant root (HAR1) in *L. japonicus*. In non-legume plants, CLE peptides act through the FLORAL ORGAN NUMBER 1 (FON1) receptor in *B. distachyon* or FASCIATED AND BRANCHED (FAB) in tomato. In all cases, the interaction of CLE peptides with these receptor-like kinases represses mycorrhization. Right: regulation of nitrogen (N) fixation by N-related systemic signaling pathways. Under low-N conditions, CEP signaling peptides are produced in roots and perceived in shoots by the CRA2 receptor, promoting systemic root nodulation. Under high-N conditions, or when an optimal number of nodules have already formed, CLE signaling peptides are produced in roots and/or nodules and then perceived in shoots by the receptor-like kinase SUNN, NARK, or HAR1 to systemically inhibit root nodulation. The CEP/CRA2 and CLE/SUNN systemic signaling pathways induce and repress expression of the mobile miRNA miR2111, a downstream shoot-to-root signal that promotes root nodulation. The figure was generated using BioRender (https://biorender.com/).

and the soil availability of mineral nutrients. Integration of signals from roots and shoots requires a combination of local and systemic pathways that involve peptide and non-peptide hormonal cues. The N-fixing symbiosis is one of the best-understood examples of the regulation of a symbiotic interaction by nutrient availability and demand. This is because the environmental nutritional conditions that promote nodulation are very clearly identified, i.e., a lack of available mineral N in the soil (Figure 4). First, C-terminally encoded peptides (CEPs) are produced in roots of *M. truncatula* experiencing N deficiency (Imin et al., 2013). These CEPs move through the xylem from roots to shoots, where they act through the *M. truncatula* COMPACT ROOT ARCHITECTURE 2 receptor to promote root competence to form symbiotic nodules (Huault et al., 2014; Mohd-Radzman et al., 2016). This involves CEP/CRA2-dependent upregulation of the miRNA miR2111 in shoots, which acts as a shoot-to-root signal through the phloem. In roots, miR2111 downregulates transcript accumulation of TOO MUCH LOVE (*TML*) genes, which are inhibitors of nodulation, and thus promotes nodulation (Takahara et al., 2013; Tsikou et al., 2018; Gautrat et al., 2020). By contrast, when a sufficient number of symbiotic nodules have formed, the plant activates a systemic inhibitory pathway to block *de novo* formation of additional symbiotic nodules. This "autoregulation of nodulation" pathway involves CLE signaling peptides, whose expression is induced in roots in response to rhizobium or high N levels (Figure 4) (Okamoto et al., 2009; Mortier et al., 2010). CLE peptides move toward the shoots through the xylem sap and are perceived by CLAVATA1-like (CLV1-like) receptors named SUPER NUMERIC NODULES (MtSUNN) in *M. truncatula*, GLYCINE MAX NODULE AUTOREGULATION RECEPTOR KINASE (GmNARK) in soybean, and HYPERNODULATION AND ABERRANT ROOT (LjHAR1) in *L. japonicus* (Searle et al., 2003; Schnabel et al., 2005; Okamoto et al., 2013). This leads to inhibition of miR2111, increasing TML transcript levels in roots and inhibiting nodule formation (Tsikou et al., 2018; Gautrat et al., 2020; Moreau et al., 2021).

In the AM symbiosis, similar CEP/CRA2 and CLE/SUNN regulation has been reported, indicating evolutionary conservation between the two symbioses (Figure 4) (Müller et al., 2019; Karlo et al., 2020; Hsieh et al., 2022; Pedinotti et al., 2024). Pi and N deficiency promote the AM symbiosis (Breuillin et al., 2010; Balzergue et al., 2011; Nouri et al., 2014) through the induction of *CEP* gene expression in *M. truncatula* (Imin et al., 2013; Pedinotti et al., 2024). Consistent with this scenario, *MtCEP*-overexpressing roots have an increased mycorrhization rate, whereas roots of *cra2* receptor mutants show reduced fungal colonization (Pedinotti et al., 2024). This indicates that the CEP/CRA2 pathway promotes root competence for mycorrhization, as observed previously for nodulation. Accordingly, the induction of key genes associated with Pi transport, Pi homeostasis, and SL biosynthesis and transport upon AM fungal colonization is strongly reduced in *cra2* mutant roots. In addition, an "autoregulation of mycorrhization" negative regulatory pathway involves CLE signaling peptides in response to AM fungal colonization or high Pi levels (Figure 4) (Müller et al., 2019; Karlo et al., 2020). These host plant–produced CLE peptides act through the CLV1-type receptors MtSUNN, GmNARK, and LjHAR1 in legumes; FLORAL ORGAN NUMBER1 in *Brachypodium distachyon*; and FASCIATED AND BRANCHED in tomato (Morandi et al., 2000; Meixner et al., 2005; Müller et al., 2019; Wang et al., 2021). Inhibition of SL biosynthesis was observed in roots of *M. truncatula* overexpressing CLE peptide (Müller et al., 2019), although no significant changes in SL level were detected in CLV1-like receptor mutants (Foo et al., 2014; Karlo et al., 2020; Wang et al., 2021). To coordinate the two antagonistic systemic pathways that regulate nodulation, the specific symbiotic *CEP* gene *MtCEP7*, whose expression is induced by rhizobium instead of low-N conditions, controls the

temporal window of root nodulation competence depending on the N fixation capacity of the rhizobial strain (Laffont et al., 2020; Ivanovici et al., 2023; Laffont and Frugier, 2024). Interestingly, *MtCEP7* expression is induced by high Pi (Pedinotti et al., 2024), suggesting a mechanism that would promote nodulation under this condition but not the AM symbiosis.

Regarding the regulation of the ECM symbiosis and/or endophytic associations in response to plant nutrient status and requirements, it remains to be determined whether CEP and/or CLE peptides are involved. Similar to the AM symbiosis, *C. tofieldiae* improves Pi nutrition, and thus *A. thaliana* growth, only when soil Pi is limiting (Hiruma et al., 2016). By contrast, under high Pi, the colonization of *A. thaliana* roots by *C. tofieldiae* induces defense-response genes (Hacquard et al., 2016). This finding indicates that plants unable to form AM symbioses can cope with low nutrient availability by interacting with endophytic fungi. In addition, it suggests that this interaction needs to be regulated depending on soil nutrient availability to avoid a detrimental association for the host plant. Activation of defense-related genes, which led to alterations in the root-inhabiting fungal community, was also observed in maize plants grown at high Pi concentrations (Yu et al., 2018). Similarly, the interaction of plants with *S. indica* is promoted by Pi deficiency, improving plant Pi uptake and production of acid phosphatases, thus enabling the host plant to access insoluble Pi reservoirs in soils (Gill et al., 2016). Interestingly, the growth of fungal hyphae in *A. thaliana* roots is restricted by the activation of plant immune pathways to maintain a well-balanced endophytic interaction (Fesel and Zuccaro, 2016). Overall, lowering plant defense responses under low Pi availability appears to be a shared strategy to promote the recruitment of different beneficial soil microbes and thus overcome nutritional deficiency. Regarding plant associations with PGPRs, several species of *Bacillus*, *Enterobacter*, *Streptomyces*, *Pseudomonas*, *Azospirillum*, and *Burkholderia* have been shown to provide the host plant with N and Pi by N fixation and/or Pi solubilization, respectively, thus promoting plant growth (Hayat et al., 2010; Mohammed and Dakora, 2024). However, very little is known about the molecular mechanisms and signaling pathways that may promote these beneficial plant–bacterium associations under specific nutrient-deficient conditions.

FUTURE PERSPECTIVES

This review highlights the significant knowledge gap between our molecular understanding of AM and RN symbioses and that of ECM and other endophytic beneficial interactions. Indeed, the fact that ECM mostly involves trees rather than economically relevant crops has led to a more limited research effort compared with that directed toward the AM and RN symbioses. Similarly, the *Frankia*-induced nodulation symbiosis, which does not affect major agronomic crops, is much less studied than the RN symbiosis. In the case of beneficial PGPR/endophytic interactions, their characterization has only recently begun. On the basis of our current knowledge, some shared mechanisms between different beneficial plant–microbe interactions were highlighted, such as the involvement of a pre-symbiotic LysM-RLK perception step, the CSSP, NO signaling, and signaling peptide–mediated regulation of symbioses by nutrients. However, further efforts are needed to determine the extent of these commonalities.

Although endophytic interactions can potentially benefit a wider diversity of plants, including all major agronomic crops, their positive impact seems to be more limited than that of the AM and RN symbioses. Moreover, the outcome is variable, depending on environmental, nutritional and stress conditions as well as plant species and genotypes. This context-dependent variability makes it difficult to generalize the beneficial effects of these interactions and limits characterization of the molecular mechanisms that regulate them, as well as the cause(s) of their beneficial effects. In addition, most molecular mechanistic studies have been performed in model plants under controlled laboratory conditions; only a few studies have been carried out in crops. Such knowledge gaps represent a critical issue for current agricultural and forestry practices, as inoculation strategies are increasingly proposed to farmers/foresters without a complete understanding of the main factors that control the establishment and beneficial outputs of these plant–microbe interactions. Therefore, future research should aim to reduce this gap by systematically evaluating whether our understanding of the shared mechanisms that regulate AM and RN symbioses can be extended to ECM and endophytic bacterial and fungal interactions, particularly in agronomically relevant crops or forestry trees. Furthermore, ECM fungi can also endophytically colonize the roots of non-host plant species, such as grasses (Schneider-Maunoury et al., 2020). Understanding the molecular responses of these types of interactions can provide insight into how the switch between mutualistic and endophytic ways of life is regulated by the fungus and/or the plant. From the plant perspective, understanding how non-ECM plants, such as grasses, can be simultaneously colonized by AM and ECM fungi would likely modify our current view of mutualism. Research should also focus on the identification of novel molecular determinants specific to these beneficial interactions relative to the AM and RN symbioses. Finally, most of this molecular knowledge was obtained under experimental conditions in which a single microbe and a single host plant were used, whereas in agricultural or forest ecosystems, different microbes and different plants coexist. Validating, under more realistic environmental conditions, the relevance of knowledge acquired under such simplified conditions is therefore also essential. Overall, a better understanding of the mechanisms that modulate beneficial plant–microbe associations will pave the way for developing more efficient and reliable biotechnological strategies. This will encourage the use of microbes as biostimulants in agriculture and forestry, either individually or in consortia, thereby contributing to the United Nations Sustainable Development Goals.

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