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Topical Review

A roadmap of plant membrane transporters in arbuscular mycorrhizal and legume–rhizobium symbioses

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Abstract

Most land plants live in close contact with beneficial soil microbes: the majority of land plant species establish symbiosis with arbuscular mycorrhizal fungi, while most legumes, the third largest plant family, can form a symbiosis with nitrogen-fixing rhizobia. These microbes contribute to plant nutrition via endosymbiotic processes that require modulating the expression and function of plant transporter systems. The efficient contribution of these symbionts involves precisely controlled integration of transport, which is enabled by the adaptability and plasticity of their transporters. Advances in our understanding of these systems, driven by functional genomics research, are rapidly filling the gap in knowledge about plant membrane transport involved in these plant–microbe interactions. In this review, we synthesize recent findings associated with different stages of these symbioses, from the pre-symbiotic stage to nutrient exchange, and describe the role of host transport systems in both mycorrhizal and legume–rhizobia symbioses.

Introduction

Nitrogen (N) and phosphorus (P) are limiting nutrients in most natural soils (Du et al., 2020). A high input of N-fertilizers is required for optimal crop yields in conventional agriculture, which leads to contamination of groundwater and contributes markedly to the release of greenhouse gases (Fowler et al., 2013; Chai et al., 2019). Mutualistic fungal and bacterial symbionts are striking examples of soil microorganisms that have successfully coevolved with their hosts, allowing plants to better adapt to terrestrial ecosystems, and promoting their own success by gaining access to photosynthetic carbon (Chen et al., 2018). The most widespread plant–fungal symbiosis is the arbuscular mycorrhizal symbiosis (AMS) and the majority of land–plant species engage in an interaction with fungi of the subphylum Glomeromycotina (Wang and Qiu, 2006; Parniske, 2008;

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ADVANCES

- A cytokinin transporter functions in LRS.
- Transporters participate in the uptake and distribution of iron and other mineral ions in LRS.
- Candidate transporters for plant lipid provision to the AM symbiont have been identified.
- Nitrate plays a role in N-fixation involving NPF transporters.
- A conserved mycorrhizal pathway of nitrogen acquisition in plants, based on nitrate uptake, was recently discovered.

Spatafora et al., 2016), which has origins probably coinciding with the terrestrialization of plants (Pirozynski and Malloch, 1975). Subsequently, around 100 million years ago (MYA), certain angiosperms, the so-called nitrogen-fixing root nodule clade, evolved nodulation, a symbiosis with nitrogen-fixing soil bacteria (Griesmann et al., 2018; van Velzen et al., 2018). Among all nodulating plants, legumes, which are able to establish the extensively studied legume–rhizobium symbiosis (LRS), are most prominent (Huisman and Geurts, 2020). By forming endosymbiotic associations, plants obtain mineral nutrients and in turn supply the symbiont with organic and, in the case of LRS, also inorganic nutrients. LRS and AMS are intricate and finely tuned interactions that use host membrane transporters for the movement of a wide range of metabolites, including phytohormones, secondary metabolites, and nutrients, throughout the entire symbiotic process (Bapaume and Reinhardt, 2012). Specialized plant membrane transporters represent a promising target to increase crop yields and quality, as well as to improve sustainable production of nutritious foods (Schroeder et al., 2013). In this review, we synthesize current knowledge related to the host membrane transporters that participate in subsequent stages of AMS and LRS. We aim to: (1) demonstrate the importance of transporters in the establishment and maintenance of these symbioses; (2) highlight recent discoveries of long-sought-after transporters involved in translocation of crucial symbiotic molecules; and (3) suggest avenues worthy of future research.

Pre-symbiotic and pre-contact stages—host–symbiont "chemical dialog" in the rhizosphere

AMS and LRS can be categorized into several stages: the pre-symbiotic stage, where the plant signals to prospective symbionts that it is a receptive host; the pre-contact stage, where the signals between host and symbiont are first exchanged; and the colonization stage, where the symbiont contacts and penetrates host cells and the nutrient exchange stage.

Signal release during nutrient stress

Nutrient shortage in the host plant results in the production of specific metabolites that serve as signals to facilitate symbiotic interactions. This process occurs in the absence of symbionts but is nonetheless essential for symbiotic interactions, as it signals host receptivity and, in the case of LRS, host–symbiont specificity. Among these signals, carotenoid-based phytohormones, strigolactones (SLs), serve as primary pre-colonization signals that affect arbuscular mycorrhizal (AM) fungi through stimulation of fungal metabolism and the induction of extensive hyphal branching (Akiyama et al., 2005; Besserer et al., 2006, 2008). The first report of active SL secretion came from research on *Petunia hybrida*. In this species, the release of SLs into the rhizosphere occurs through suberin-free hypodermal passage cells (HPCs) located in the root exodermis and is a consequence of Pleiotropic Drug Resistance 1 (PDR1) exporter action (Kretzschmar et al., 2012; Figure 1). PDR1 is a member of the ancient and omnipresent ATP-binding cassette (ABC) protein family, and belongs to the G-type ABC (ABCG) subfamily (reviewed in Kang et al., 2011; Hwang et al., 2016). *Pdr1* mutants secrete less SL (orobanchol) and exhibit reduced mycorrhizal colonization compared with wild-type (WT) plants (Kretzschmar et al., 2012). Further studies have revealed that the orthologous protein from *Petunia axillaris*, PaPDR1, has an asymmetric cellular localization and is present in the outer–lateral membrane of HPCs, facing the external environment (Sasse et al., 2015). Thus, it has been proposed that PDR1 is responsible for SL release into the rhizosphere and participates in the formation of a steep concentration gradient of SLs in the soil (Kretzschmar et al., 2012; Sasse et al., 2015). The latter, also being a result of SL instability, likely indicates the presence and proximity of a host, and serves to attract fungal hyphae to the HPCs, which accordingly act as gates for the entry of mycorrhizal fungi (Sbrana and Giovannetti, 2005; Akiyama and Hayashi, 2006; Sharda and Koide, 2008; Nadal and Paszkowski, 2013). PDR-mediated SL secretion appears to be conserved across species regardless of root anatomy. ABCG59 (also called PDR23) from the non-exodermal legume plant *Medicago truncatula* has recently been described as a potential SL exporter that promotes AMS. Notably, given the absence of an apoplastic hydrophobic diffusion barrier in *M. truncatula* roots, SLs can likely passively enter the rhizosphere and are not dependent solely on MtABCG59 action (Banasiak et al., 2020; Supplemental Table S1).

SLs may not be the only signal molecules affecting the pre-contact stage of AMS. Characterization of the rice (*Oryza sativa*) and maize (*Zea mays*) *no perception 1* (*nope1*) mutants, which do not form AMS, has allowed the identification of the Major Facilitator Superfamily (MFS) protein, NOPE1. It has been proposed that NOPE1 mediates the secretion of *N*-acetylglucosamine (GlcNAc)-like compounds, thereby affecting presymbiotic AM fungal transcriptional reprogramming associated with signaling functions, most notably kinases. However, the actual nature of the NOPE1 substrate and the precise function of this protein

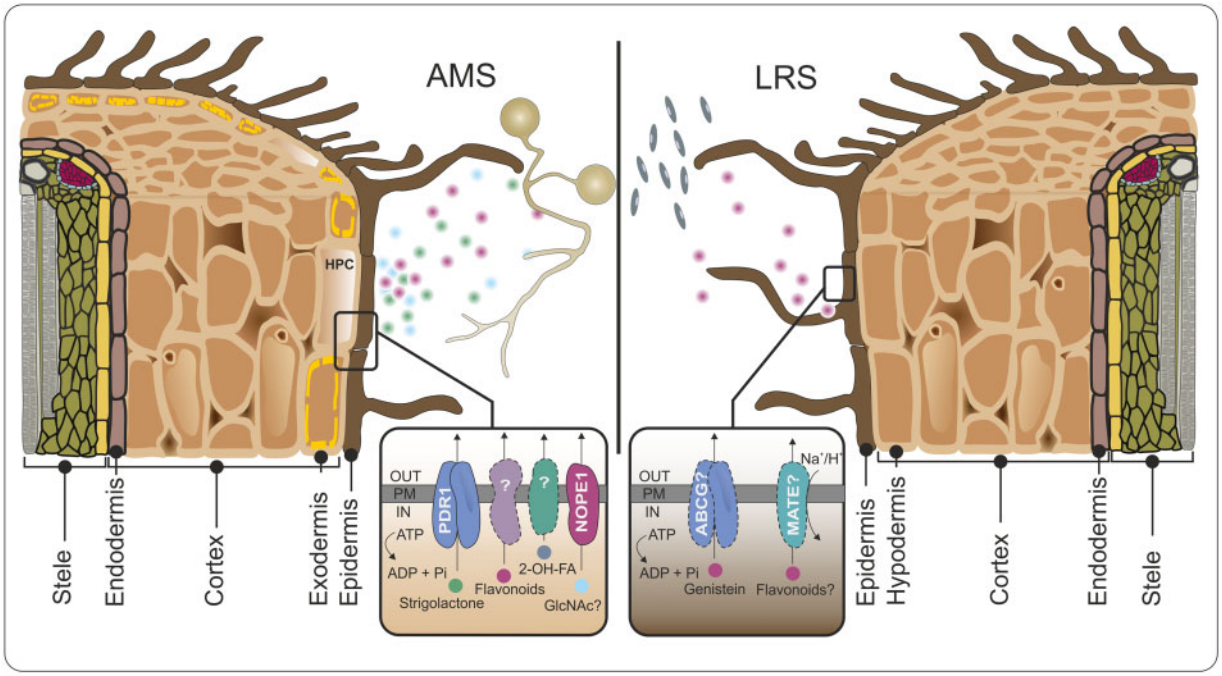

Figure 1 Schematic representation of plant membrane transporters involved in the secretion of signaling molecules during the pre-symbiotic stage of AM symbiosis and LRS. The SL exporter PDR1 specifically localizes to the outer–lateral membrane of HPCs, while other transporters responsible for translocation of signaling molecules are found on the PM of root epidermal cells. NOPE1 secretes GlcNAc-like compounds that affect presymbiotic AM fungal transcriptional reprogramming. No transporters that are involved in the extrusion of flavonoids and 2-OH fatty acids during AM have yet been identified. It has been proposed that release of flavonoids (e.g. genistein) into the rhizosphere during LRS is driven by members of ABCG and MATE families. (AM, arbuscular mycorrhiza; PM, plasma membrane, NOPE1, No Perception 1; GlcNAc, *N*-acetylglucosamine, ABCG, G-type ABC transporter; and MATE, MATE transporter). Orange structures around the exodermis cell perimeters represent suberin lamellae, maroon cells in the stele indicate phloem. Dashed lines and questions marks indicate inferred/proposed subcellular localization or substrate/transporter, respectively.

remain open questions (Nadal et al., 2017; Figure 1 and Supplemental Table S1).

The AM fungal hyphal growth pattern in the rhizosphere can be also altered by the presence of 2-hydroxy fatty acids (2-OH-FAs) and some flavonoids present in root exudates, which promote hyphal tip elongation and hyphal branching (Scervino et al., 2007; Nagahashi and Douds, 2011). Additionally, flavonoids extend asymbiotic fungal growth, increasing the chance of contact between AM fungi and the host (Becard et al., 1992). The transporters responsible for flavonoid secretion during AMS have not yet been identified.

Legume–rhizobia signal exchange

While the importance of flavonoids in AMS establishment is debated (Becard et al., 1992, 1995; Scervino et al., 2007; Steinkellner et al., 2007), these secondary metabolites are undoubtedly the main pre-colonization signals, and ensure specific partner recognition during LRS (reviewed in Liu and Murray, 2016; Wang et al., 2018). It is thought that a flavonoid transporter must be present in the plasma membrane of root cells to release these compounds into the rhizosphere in order to induce the expression of nodulation genes of rhizobia, thus initiating LRS (Redmond et al., 1986). The production of nodulation factor (NF) signals derived from the bacteria, as a consequence of host flavonoid secretion, is subsequently required throughout root hair and nodule infection (Sharma and Signer, 1990; Liu and Murray, 2016), but it is not known whether different flavonoids are important at different stages of nodulation. Surprisingly, despite the importance of this very initial step, the identity of the flavonoid transporters remains unknown. In soybean (*Glycine max*), the isoflavones daidzein and genistein were identified as being required for LRS (Subramanian et al., 2006), while in *M. truncatula*, the flavone (7,4′-dihydroxyflavone) was shown to be essential for nodulation (Zhang et al., 2009). Interestingly, a full-size ABCG transporter from *M. truncatula* was found to be involved in the translocation of liquiritigenin, a precursor of both daidzein and 7,4′-dihydroxyflavone (Biala et al., 2017). Additionally, biochemical studies have suggested that ABCG transporters mediate genistein secretion from *G. max* roots, but the specific proteins have not been confirmed (Sugiyama et al., 2007, 2008). It has been proposed that members of the Multidrug and Toxic Compound Extrusion (MATE) family are involved in the exudation of signaling flavonoids; however, this remains to be validated (Chen et al., 2015; Figure 1). The biosynthesis and secretion of flavonoids are stimulated by nitrogen (N) deprivation, analogous to the elevated exudation of SLs preceding AMS formation under phosphate limiting conditions

(Yoneyama et al., 2007; Sugiyama et al., 2016). Thus, the identity of transporters of "pre-infection flavonoids" may be revealed based on their root-specific expression and induction under nitrogen starvation. A body of evidence, discussed by Liu and Murray (2016), suggests that different legumes use different flavonoids for nodulation, raising the interesting possibility of variations in transporter specificity or expression across legumes. Additionally, transport of phenylpropanoid intermediates was proposed to have an influence on plant–microbe interactions (Banasiak et al., 2013; Biala et al., 2017; Bassard and Halkier, 2018; Biala and Jasinski, 2018). More information concerning this issue can be found in Box 1.

BOX 1. PHENYLPROPANOID TRANSPORT IN LRS

The role of phenylpropanoids in LRS is not limited to signaling to compatible rhizobia. Various compounds belonging to this class of secondary metabolites protect plants against pathogens and act to reinforce symbiosis specificity. For instance, the *M. truncatula* symbiont *Sinorhizobium meliloti* is resistant to pterocarpan medicarpin, the main phytoalexin of this plant, while *Bradyrhizobium japonicum* and *Mesorhizobium loti* are susceptible to this molecule. For further reading see Liu and Murray (2016) and Wang et al. (2018). Interestingly, it has been shown that a fullsize ABCG transporter from *M. truncatula* is involved in the translocation of medicarpin precursors (4-coumarate and liquiritigenin) (Biala et al., 2017), and its silencing affects *de novo* biosynthesis of this phytoalexin in *M. truncatula* (Banasiak et al., 2013). The role of ABCG transporters in symbioses likely extends beyond release of signaling molecules into the rhizosphere, and in the context of phenylpropanoid metabolism, is also reflected in the distribution of intermediates, joining different biosynthetic branches. Upon sensing metabolic status/external stimuli, the presence/action of such transporters, and especially those that transport the intermediates from the earlier steps in the phenylpropanoid biosynthetic pathway, offers a useful switching mechanism in different scenarios. Notably, it has been proposed that enzymes in the phenylpropanoid pathway are organized into complexes called metabolons (Bassard and Halkier, 2018), and various metabolons are spatially separated, suggesting the need for mechanisms that mediate transport between cells (for further reading see Biala and Jasinski, 2018). The channeling of intermediates by various transport mechanisms, notably membrane transporters, may provide a meaningful tool that ensures defined metabolite production. Apart from medicarpin production, the targeted distribution of phenylpropanoid intermediates during symbioses has yet to be experimentally demonstrated, and dedicated transporters remain to be identified. Such information will bridge the knowledge gaps regarding spatiotemporal details of phenylpropanoid production under various conditions, including LRS.

Colonization—contact and root penetration

Hyphopodium formation during AMS

Aliphatic compounds associated with the plant polyester cutin have been proposed to be another class of signaling molecules that are important for promoting mycorrhizal colonization. It has been reported that RAM2/GPAT protein (Required for Arbuscular Mycorrhization/Glycerol-3-Phosphate Acyl-Transferase), which is involved in cutin monomer biosynthesis, is necessary for both appropriate hyphopodium formation on the root surface and arbuscule development (Wang et al., 2012). However, it should be noted that the most recent studies point to a nutritional, rather than signaling, function of cutin-like molecules (Bravo et al., 2017; Jiang et al., 2017; Keymer et al., 2017; Luginbuehl et al., 2017; Brands et al., 2018). Several ABCG transporters were shown to be involved in the translocation of apoplastic lipid precursors associated with cutin (Panikashvili et al., 2007, 2010, 2011; McFarlane et al., 2010; Bessire et al., 2011). Therefore, it is reasonable to hypothesize that ABCG proteins are responsible for translocation of cutin monomers, regardless of their function in AMS (see the "Lipid transporters" section). It is worth noting that defects in the formation of fungal attachment structures have also been detected in *O. sativa* and *Z. mays nope1* mutants (Nadal et al., 2017) and *O. sativa* SL biosynthetic mutants (Kobae et al., 2018).

HPC distribution

Once fungal hyphae cross the epidermis, they face another barrier; the outer cortical cell layer (Sharda and Koide, 2008). In most angiosperms, this layer is suberized and is referred to as the exodermis (Peterson and Perumalla, 1990). Most of the cells within the exodermis are impenetrable to AM fungi, except for the suberin-free HPCs, which are access points for further fungal colonization of the outer cortex (Sharda and Koide, 2008; Rich et al., 2014). HPC distribution may influence root penetration by AM fungi and is controlled by hormonal signaling and environmental conditions (Sharda and Koide, 2008; Liu et al., 2019a). Recent studies have revealed that SLs cause an increased HPC density in petunia, and dysfunction of the SL transporter PaPDR1 leads to a decrease in HPC number. Conversely, abscisic acid (ABA) was observed to promote suberization of root tissues, causing a reduction in HPC number in petunia roots (Liu et al., 2019a). An important question is whether/which ABA and/or suberin monomer transporters determine the distribution of HPCs and thus affect mycorrhization efficiency. Notably, both ABA and suberin monomers in different plant

species can be translocated by half-size ABCG proteins (Kuromori et al., 2010; Landgraf et al., 2014; Yadav et al., 2014; KaNg et al., 2015; Fedi et al., 2017; Pawela et al., 2019; Shanmugarajah et al., 2019). Moreover, Reduced Culm Number 1 (RCN1)/OsABCG5 and OsABCG25 were proposed to be involved in hypodermal suberization of roots in *O. sativa* (Shiono et al., 2014; Hinrichs et al., 2017).

Rhizodermal invasion and infection thread formation during LRS

Perception of NFs initiates early symbiotic responses in host plants, such as changes in ion fluxes through the nuclear envelope (reviewed in Roy et al., 2020; Tian et al., 2020). In addition to transporters and channels involved in NF signaling, a large number of transporters are likely required to sustain the growth of enclosed bacteria inside the infection thread (IT); rhizobia within the IT are entirely cut-off from the rhizosphere and thus are completely dependent on the host for macro- and micro-nutrients. However, other than transporters involved in NF signaling, no transporters have yet been shown to be required for IT formation, although numerous candidates have been identified from root hair transcriptomic studies aimed at detecting rhizobia-induced genes. Among the candidates identified were three ABCB transporters, which are also induced in mycorrhizal roots, and the sucrose transporter (SUT) MtSWEET11 (Sugars Will Eventually be Exported Transporter 11), which could play a role in carbon supply in cells forming ITs (Breakspear et al., 2014; Kryvoruchko et al., 2016; Roy et al., 2021).

Arbuscule nutrient exchange

Mineral nutrient transporters

The major benefit of establishing AMS for the plant is improved acquisition of mineral nutrients, especially phosphate and ammonium (Wang et al., 2017). The periarbuscular membrane (PAM), which surrounds arbuscules, hosts a range of specific proteins responsible for nutrient uptake, with inorganic phosphate (Pi) transporters being the most extensively investigated.

Inorganic phosphate transporters

AMS-related Pi uptake in different plant species is mediated by proton-coupled Phosphate Transporter 1 (PHT1) family members belonging to mycorrhizal-specific clade I and mycorrhizal-inducible clade III (Rausch et al., 2001; Harrison et al., 2002; Paszkowski et al., 2002; Glassop et al., 2005; Nagy et al., 2005; Maeda et al., 2006; Wegmueller et al., 2008; Breuillin et al., 2010; Xie et al., 2013; Supplemental Table S1). Transporters from the first clade (e.g. PT4 from *M. truncatula* and PT11 from *O. sativa*) are exclusively found in arbusculated cells and their expression increases as mycorrhizal colonization proceeds (Harrison et al., 2002; Paszkowski et al., 2002; Figure 2). Furthermore, analyses of transgenic plants overexpressing MtPT4 or OsPT11 fused to the green fluorescent protein (GFP) reporter, under the control of their native promoters, revealed that both proteins were located solely in the PAM domain around the arbuscule branches active in nutrient exchange (Pumplin and Harrison, 2009; Kobae and Hata, 2010; Pumplin et al., 2012). Interestingly, the polar targeting of MtPT4 to the PAM appears to be determined by its precise temporal expression, which is coordinated with arbuscule development, and involves transient changes in the secretory system (Pumplin et al., 2012). An intriguing question is whether the temporal control of MtPT4 localization to the PAM is a special case, or can it be generalized. Phenotypic characterization of *mtpt4* loss-of-function mutants and RNAi-silenced lines has provided unequivocal evidence for the pivotal role of MtPT4 in AMS maintenance (Javot et al., 2007). The *mtpt4* mutants exhibited a lower rate of mycorrhizal colonization, manifested by reduced intra- and extracellular growth of the AM fungus. Moreover, in plants with non-functional MtPT4, the infection units consisted of many septate hyphae and displayed premature arbuscule collapse. All these defects were related to the disturbance of Pi transport and led to untimely termination of the symbiosis (Javot et al., 2007). Comparable changes in arbuscule morphology and reduction of mycorrhizal colonization have also been observed in the case of the *ospt11* mutant. Tracer studies have shown that Pi is not delivered via the AM fungus to the plant in the absence of OsPT11 (Yang et al., 2012). Further studies with WT nurse plants, which act as a feeding source for the AM fungi, have revealed that premature arbuscule degeneration in *mtpt4* mutants is not associated with host carbon restriction, as previously suggested (Javot et al., 2011). Surprisingly, the low nitrogen status of the plant was sufficient to restore the WT phenotype in *mtpt4* mutants in an Ammonium Transporter 2;3 (AMT2;3)-dependent manner. It is plausible that AMT2;3 functions as a transporter involved in ammonium sensing. This observation indicates the importance of an interplay between phosphorus and nitrogen in the regulation of arbuscule lifespan (Breuillin-Sessoms et al., 2015). Additionally, recent studies suggest that PT13 from *O. sativa* can function as a non-transporting sensor related to nutrient transporter adjustment during arbuscule development to regulate Pi acquisition (Yang et al., 2012), while AsPT1 from *Astragalus sinicus* was suggested to function as a nutrient sensor with Pi transport activity (Xie et al., 2013). Moreover, mycorrhizal-inducible Pi transporters belonging to clade III (e.g. PT3 from potato [*Solanum tuberosum*] and PT3 from *Lotus japonicus*), while clearly recruited for AM functions, are not essential for symbiotic Pi acquisition (Rausch et al., 2001; Maeda et al., 2006; Supplemental Table S1).

Pi transporters located within the PAM were shown to use the H^+ electrochemical gradient generated by plasma membrane H^+-ATPases. The H^+-ATPases Os-HA1 in *O. sativa*, Mt-HA1 of *M. truncatula*, and SlHA8 from tomato (*Solanum lycopersicum*) are specifically expressed in

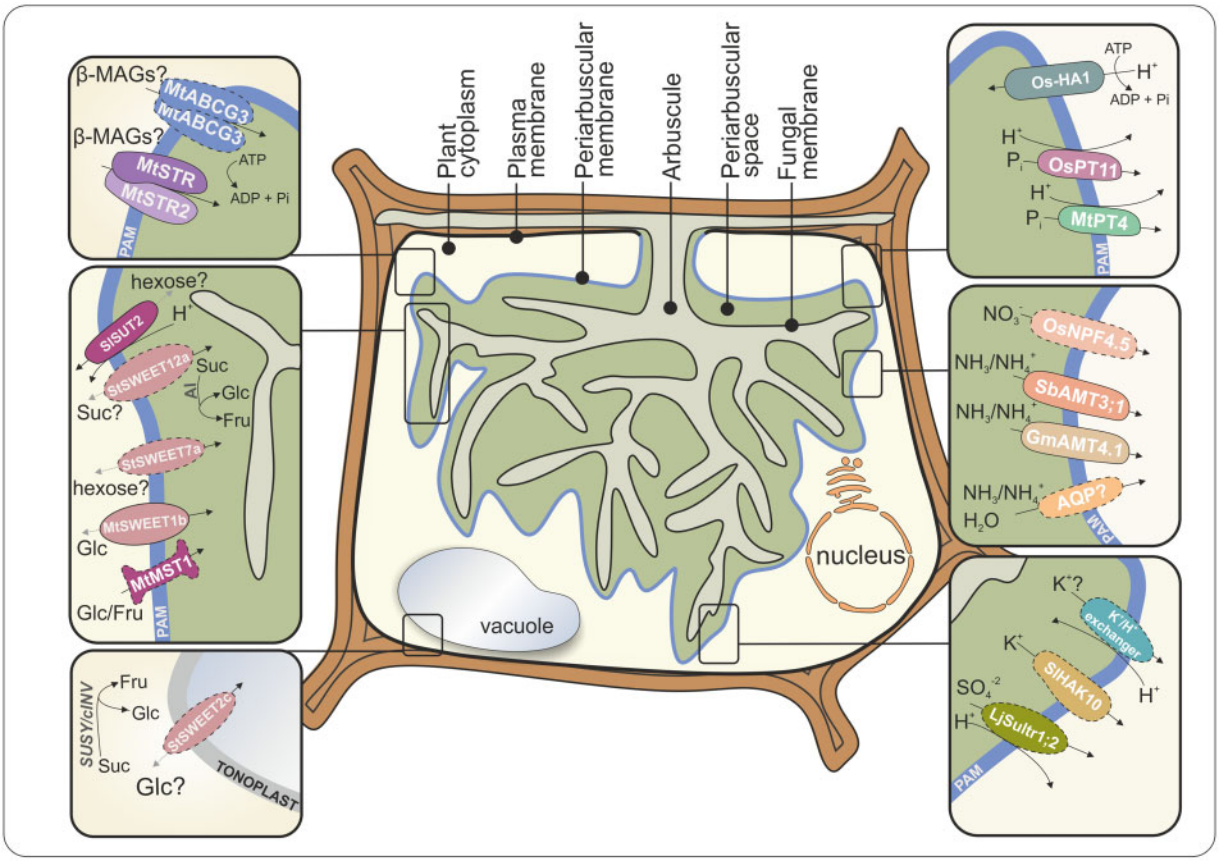

Figure 2 Schematic representation of plant membrane transporters involved in nutrient exchange across the PAM. Members of the SWEET, MST, and SUT families are responsible for carbohydrate translocation. Sucrose delivered to the periarbuscular space can be converted to hexoses by apoplastic invertase. In addition, the cytoplasmic sucrose-cleaving enzymes invertase (INV) and sucrose synthase (Suc) deliver hexoses as substrates for plant monosaccharide transporters localized to the PAM (Schaarschmidt et al., 2006; Manck-Gotzenberger and Requena, 2016). ABCG proteins have been proposed to mediate lipid delivery to the symbiotic fungus. Inorganic phosphate (Pi) symbiotic uptake is facilitated by PHT1 family members belonging to mycorrhizal-specific clade I (e.g. MtPT4 and OsPT11), which use the H^+ electrochemical gradient generated by plasma membrane H^+-ATPases. Members of the AMT and NPF protein families were proposed to take part in NH_3/NH_4^+ translocation toward the cytoplasm of arbusculated cells. Additionally, AQPs can support NH_3/NH_4^+ permeation across the PAM. A flux of sulfate and potassium out of the periarbuscular space is enabled by LjSULTR and SlHAK10 transporters. K^+/H^+ exchangers may also function in the PAM. (SWEET, Sugars Will Eventually be Exported Transporter; ABCG, G-type ABC transporters; PHT1, Phosphate Transporter 1 family; PT, Phosphate Transporter, AMT, Ammonium Transporter family; NPF, Nitrate Transporter 1/Peptide Transporter family; SULTR, Sulfate transporter; HAK, High-affinity Potassium transporter; Al, apoplastic invertase; cINV, cytoplasmic sucrose-cleaving enzymes invertase and β-MAGs, β-monoacyl glycerols). Dashed lines and questions marks indicate inferred/proposed subcellular localization or substrate, respectively.

arbuscule-containing cells and are required for appropriate nutrient uptake and a fully functional AMS (Krajinski et al., 2014; Wang et al., 2014; Liu et al., 2020a; Figure 2 and Supplemental Table S1).

Ammonium transporters

While Pi flux during AMS is well studied, much less is known about the transporters involved in symbiotic nitrogen acquisition. Members of two protein families: i) AMTs and ii) Nitrate Transporter 1/Peptide Transporter family (NPF) have been found to be transcriptionally induced in different plant species upon AM inoculation (Gomez et al., 2009; Kobae et al., 2010; Koegel et al., 2013; Perez-Tienda et al., 2014; Drechsler et al., 2018; Supplemental Table S1). Some of them, such as AMT2;2 from *L. japonicus*, are exclusively expressed in mycorrhizal roots. AMT2;2 has been recognized as a high-affinity NH_3/NH_4^+ transporter that acts in an acidic pH-dependent manner (Guether et al., 2009b). Its putative ortholog, AMT4.1, from *G. max* complemented an ammonium uptake-deficient yeast mutant and localized to the PAM around branched arbuscules (Kobae et al., 2010). Likewise, AMT3;1 proteins from *O. sativa* and sorghum (*Sorghum bicolor*) have been described as potential transporters involved in ammonium uptake from the periarbuscular space. Downregulation of *OsAMT3;1* and *SbAMT3;1* caused a reduction of nutrient fluxes from the AM fungus to the host and arrested the promotion of plant growth after fungal inoculation (Koegel et al., 2013, 2017). Additionally, it has been proposed that aquaporins (AQPs), besides being water channels, can also support NH_3/NH_4^+ permeation across membranes during AMS (Uehlein et al., 2007; Figure 2 and Supplemental Table S1).

It has long been thought that transfer of ammonium through the PAM is a main route of symbiotic N acquisition. However, recent studies have revealed the existence of a conserved mycorrhizal pathway for nitrate uptake, at least in gramineous species. OsNPF4.5, with demonstrated nitrate transport ability, as well as its putative orthologs from *Z. mays* and *S. bicolor*, has been shown to be transcriptionally upregulated during AM colonization. Moreover, *osnpf4.5* knockout mutants were reported to exhibit lower rates of fungal colonization and reduced growth promotion under symbiotic conditions (Wang et al., 2020b; Figure 2 and Supplemental Table S1). Further work is needed to determine whether this nitrate route operates in plants other than grasses.

Other mineral nutrient transporters

The improvement of plant nutrition through AM interactions is not limited to phosphorus and nitrogen supplementation (Sieh et al., 2013; Garcia et al., 2017). Sultr1;2 from *L. japonicus*, the transcript of which strongly accumulates upon sulfate starvation and in arbusculated cells, has been proposed to mediate both direct and symbiotic sulfur acquisition (Giovannetti et al., 2014). High-affinity Potassium Transporter 10 (SlHAK10) from *S. lycopersicum* was found to be expressed exclusively in arbuscule-containing cells, participating in mycorrhizal K^+ uptake. It has been proposed that SlHAK10 action may increase carbohydrate accumulation in roots and therefore facilitate AM fungal colonization (Liu et al., 2019b). Its putative ortholog from *L. japonicus*, LjHAK, was also shown to be AM-induced (Guether et al., 2009a). Moreover, transcriptional analysis of mycorrhizal *M. truncatula* plants grown under K^+ deprivation showed the upregulation of a gene encoding a putative K^+/H^+ exchanger (Garcia et al., 2017; Figure 2 and Supplemental Table S1). Uptake of metals such as zinc (Zn), copper (Cu), manganese (Mn), and iron (Fe), in addition to direct routes, seems to be provided by mycorrhizal pathways (Lehmann and Rillig, 2015; Coccina et al., 2019). However, our knowledge about AMS-related metal transporters is minimal. *ZIP13*, a member of the ZRT, IRT-like Protein family from barley (*Hordeum vulgare*), which encodes a potential zinc (Zn) transporter, has been shown to be up-regulated by mycorrhizal colonization (Watts-Williams and Cavagnaro, 2018), as has *ZIP5* from *M. truncatula* (Nguyen et al., 2019; Figure 2 and Supplemental Table S1). Identification of metal transporters will help elucidate the role of AMS in plant tolerance to metal stress deficiency or toxicity, and may have an impact on designing new strategies for phytoremediation.

Carbon supply during AMS

AM fungi are obligate biotrophs that require plant-sourced carbon for completion of their life cycle. For a long time, carbohydrates have been considered as the main nutrient delivered to the fungus (Pfeffer et al., 1999). However, recent findings revealed that lipids are additional, and perhaps the principle, carbon sources supplied by the host (Bravo et al., 2017; Jiang et al., 2017; Keymer et al., 2017; Luginbuehl et al., 2017; Brands et al., 2018).

Sugar transporters

Early reports demonstrated that sugars can be transported from the plant host to the AM fungus (Solaiman and Saito, 1997; Pfeffer et al., 1999). However, our knowledge of the underlying mechanism of carbohydrate delivery to the apoplastic compartment during AMS is surprisingly limited. Proteins from the SWEET family have been proposed as good candidates for symbiotic sugar transfer. Transcriptional characterization of *S. tuberosum* SWEET genes revealed that at least three of them (*SWEET2c*, *SWEET7a*, and *SWEET12a*) are symbiotically upregulated and highly expressed in arbuscule-containing cells (Manck-Gotzenberger and Requena, 2016). Similarly, the expression levels of several SWEET genes from *M. truncatula* and *G. max* were found to be elevated during AMS (Kafle et al., 2019; Zhao et al., 2019). Finally, MtSWEET1b was shown to be a glucose transporter that localizes to the PAM surrounding the trunk and fine branches of arbuscules. It is worth mentioning here that the lack of defective AMS in *mtsweet1b* might be explained by redundancy with other AM-induced *MtSWEET* genes (An et al., 2019). Another group of sugar transporters associated with AM is the SUT family, which utilizes the proton motive force present across the plasma membrane. These proteins have been proposed to contribute to carbohydrate positioning/redirection during AMS by the long-distance flow of sucrose toward the AM fungi. In *M. truncatula*, *SUT4-1* and *SUT1-1* were found to be upregulated after AM fungal colonization in leaves and roots, respectively, and both proteins were shown to import sucrose (Doidy et al., 2012). Furthermore, overexpression of *SoSUT1* from *Spinacia oleracea* in *S. tuberosum* increases AM root colonization under high Pi fertilization levels (Gabriel-Neumann et al., 2011). Interestingly, downregulation of *SlSUT2* expression in *S. lycopersicum* increases AM colonization but has a negative effect on plant growth. SlSUT2 is localized to the PAM and is probably responsible for carbohydrate retrieval by the plant, thereby limiting excessive and detrimental AM fungal expansion (Bitterlich et al., 2014). Additionally, transcripts of the Monosaccharide Transporter 1 (Mtst1/MST1) from *M. truncatula* were found to preferentially accumulate in cortical cells containing fungal structures (Harrison, 1996; Figure 2 and Supplemental Table S1).

Lipid transporters

The induction of plant lipid metabolism upon AMS was originally attributed to increased demand for lipids for *de novo* synthesis of PAMs (Gaude et al., 2012b). However, new findings point to the essential role of these compounds in AM fungal nutrition (Bravo et al., 2016, 2017; Jiang et al., 2017; Keymer et al., 2017;

Luginbuehl et al., 2017; Brands et al., 2018; Malar et al., 2021). For a long time, AM fungi were thought to use host-derived carbohydrates for the production of lipids, which are the main form of carbon storage and movement in the mycobiont (Bago et al., 2002). Surprisingly, analyses of the *Rhizophagus irregularis* genome and the *Gigaspora rosea* transcriptome revealed the absence of the cytoplasmic type I fatty acid synthase (FAS-I) complex required for FA synthesis (Tisserant et al., 2013; Wewer et al., 2014; Tang et al., 2016). Nonetheless, FA elongation and desaturation, as well as the production of complex lipids occurs in AM fungi (Wewer et al., 2014). It has been proposed that C16:0 sn2-monoacyl glycerol (sn2-MAG) compounds, which are structurally analogous to cutin-precursors, are transferred from plants to fungi prior to conversion to other lipids (Bravo et al., 2017). It was shown that mutation of the mycorrhizal-inducible FatM (acyl-ACP thioesterase-like protein) or RAM2/GPAT from *M. truncatula* leads to abnormal arbuscule development as a consequence of disturbance in FA and MAG biosynthesis during AMS (Wang et al., 2012; Bravo et al., 2016, 2017). Half-size ABCG transporters (also known as white–brown complex [WBC] transporters) appear to be promising candidates for lipid export to the symbiotic interface. There is a range of experimental evidence that many ABCG proteins are involved in the transport of precursors of apoplastic lipids such as cutin and suberin (Panikashvili et al., 2007, 2010, 2011; McFarlane et al., 2010). Notably, STR (Stunted Arbuscule) and STR2, which belong to the ABCG subfamily and are unique to mycorrhizal plants (Radhakrishnan et al., 2020), were found to be essential for arbuscule formation in *M. truncatula* and *O. sativa*. It has been shown that they function as heterodimers and localize specifically to the PAM. Moreover, their dysfunction contributes to a stunted arbuscule phenotype (Zhang et al., 2010; Gutjahr et al., 2012). It is tempting to speculate that sn2-MAG compounds or MAG derivatives are STR/STR2 substrates; however, direct proof has not yet been provided (Bravo et al., 2017). The nature of the molecules transported by STR/STR2 remains one of the most exciting questions in AMS research. Another transporter recruited for AMS function, and likely associated with lipid transport, is *M. truncatula* ABCG3/WBC5. The latter has been proposed to be a part of the RAM1-regulated lipid export pathway, which is indispensable for mycorrhiza formation (Luginbuehl et al., 2017). It has been shown that the expression of *MtABCG3*, together with *RAM2/GPAT*, is strongly induced after AM fungal inoculation, and their induction requires the GRAS-domain transcription factor RAM1 (Required for Arbuscular Mycorrhization 1) (Hogekamp et al., 2011; Luginbuehl et al., 2017). Moreover, MtABCG3 is expressed predominantly in arbuscule-containing cells (Hogekamp et al., 2011; Luginbuehl et al., 2017). Further, functional and mutant plant studies are needed to clarify the role of MtABCG3 in AMS (Figure 2 and Supplemental Table S1).

To sum up, it is widely speculated that RAM1, FatM, RAM2, and STR/STR2 form an AM-specific operational unit for lipid biosynthesis and transport in arbusculated cells (Bravo et al., 2017; Jiang et al., 2017; Keymer et al., 2017; Luginbuehl and Oldroyd, 2017; Rich et al., 2017). Additionally, AP2-Domain Transcription Factor WRI5 and CBX1 from *M. truncatula* and *L. japonicus*, respectively, as well as conserved WRINKLED (WRI) transcription factor from the liverwort *Marchantia paleacea*, have been shown to be regulators of lipid metabolism during AMS (Jiang et al., 2018; Xue et al., 2018; Rich et al., 2021). Moreover, it is conceivable that other ABCG proteins, besides STR/STR2, may also be involved in this scenario. Notably, phylogenetic analysis has shown that MtABCG3 clusters with AtABCG11/12/13, which are involved in the secretion of cutin-like compounds (Panikashvili et al., 2007, 2011; Banasiak and Jasinski, 2014), while STR/STR2 are more closely related to AtABCG1/2/6/20 transporters associated with deposition of suberin monomers, which are generally composed of longer carbon chains than those of cutin precursors (Banasiak and Jasinski, 2014; Yadav et al., 2014; Fedi et al., 2017; Shanmugarajah et al., 2019). Despite the fact that *str* and *str2* mutants form defective arbuscules, similar to plants lacking FatM and RAM2, the observed accumulation of 16:0 sn2-MAGs in *str* and *str2* was comparable to the WT plants (Bravo et al., 2017). This raises the intriguing question of possible alternative molecules delivered by STR/STR2 to the fungi. Additional experiments are necessary to define the substrates of STR/STR2 and MtABCG3. Direct measurement of the transport of hydrophobic molecules is technically very difficult and requires non-conventional approaches (Lefevre and Boutry, 2018). A recent report, showing ABC-mediated sn2-MAG transport, may set a path for establishing the biochemical action of STR/STR2 (Elejalde-Palmett et al., 2021). Given the central role of AM fungal lipid auxotrophy in explaining the obligate nature of the symbiosis, it is critical to fully understand how lipids are transferred in the PAM.

The nutrient exchange between the host plant and bacteroids

After release from ITs, rhizobia differentiate into large nitrogen-fixing bacteroids, which are enclosed by a host-derived membrane called the peribacteroidal membrane (symbiosome membrane, SM). SM creates a physical barrier for any fluxes of components between the symbiotic partners (Clarke et al., 2014).

Transport of fixed nitrogen

Bacteroids in nodules convert nitrogen to ammonia (NH_3) (Halbleib and Ludden, 2000), some of which is then reduced to ammonium (NH_4^+) in the acidic symbiosome space (SS) after its translocation from the bacteroid cytoplasm

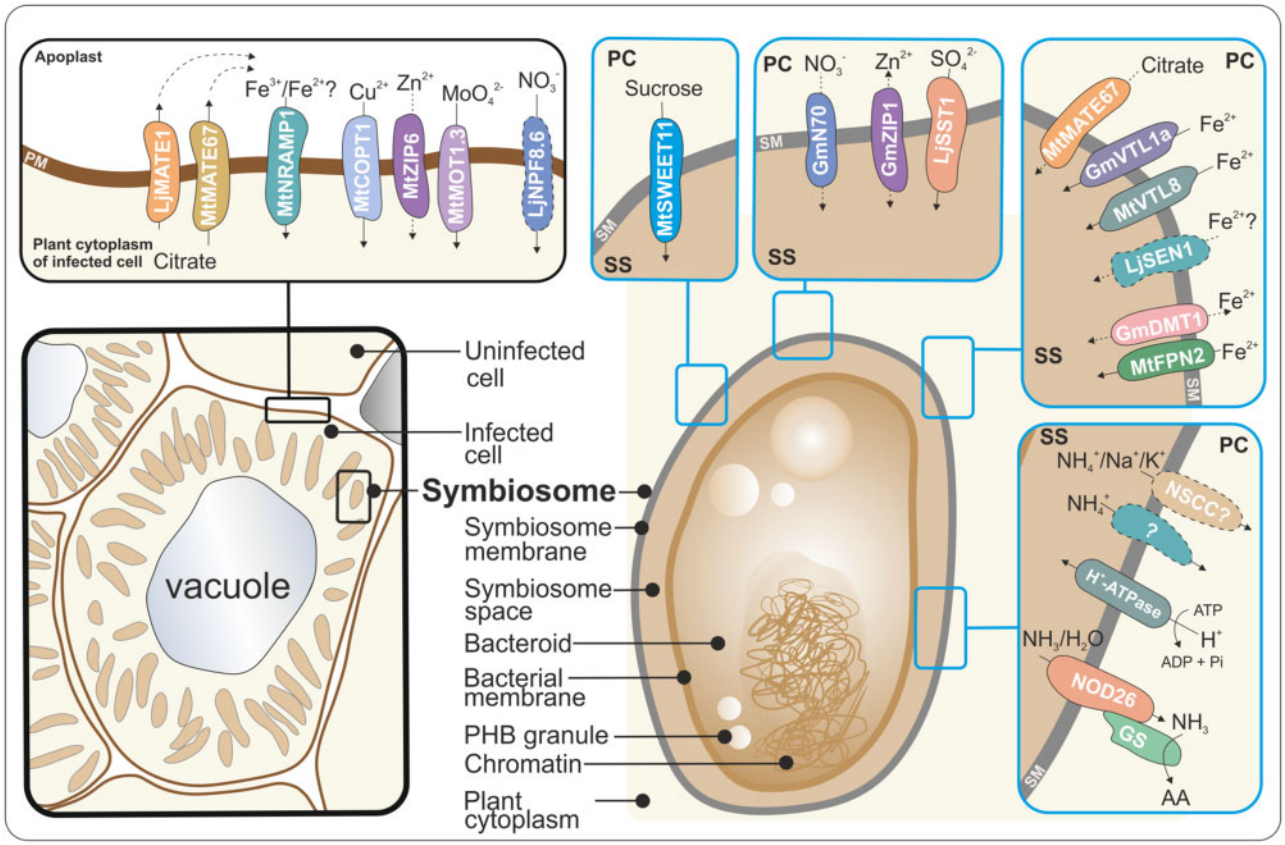

Figure 3 Schematic representation of plant membrane transporters involved in nutrient exchange across the PM of infected cells and the SM. Iron uptake into the infected cell is mediated by members of the NRAMP family and is supported by MATE proteins that release citrate into the apoplast of surrounding infected cells to support iron uptake. Other ions, such as Cu^{2+}, Zn^{2+}, and MoO_4^{2-}, are translocated across the cytoplasm of the infected cell by members of the COPT, ZIP, and MOT families, respectively. Nitrate uptake by infected cells may be facilitated by NPF family members. Rhizobia in infected cells are enclosed in a plant-derived SM, forming organelle-like structures called symbiosomes. The SM hosts a range of transporters involved in nutrient exchange. The existence of a sucrose transport in the SM has been demonstrated, but detailed characterization is limited to the MtSWEET11 transporter. Transport of nitrate into the symbiosome through the SM is mediated by N70 transporters. Zinc, sulfate, and iron ions are translocated across SM by ZIP, SST, VIT, and FPN family members, respectively. MtMATE67 may transport citrate into the SS to increase iron availability to bacteroids. Ammonia flux out of the symbiosome is facilitated by the AQP NOD26, but there is no identified transport protein for ammonium. H^+-ATPases contribute to SS acidification and NH_3 to NH_4^+ conversion. GS on the cytoplasmic side of the SM enables rapid assimilation of NH_3 to amino acids. (PM, plasma membrane; NRAMP, Natural Resistance-Associated Macrophage Protein; COPT, Copper Transporter; ZIP, ZRT and the IRT-like protein; MOT, Molybdate Transporter; NPF, Nitrate Transporter 1/Peptide Transporter family; SWEET, Sugars Will Eventually be Exported Transporter; SST, Symbiotic Sulfate Transporter; VIT, Vacuolar Iron Transporter; FPN, Ferroportin; GS, glutamine synthetase and PHB, Poly-3-Hydroxybutyrate). Dashed lines and questions marks indicate inferred/proposed subcellular localization or substrate/transporter, respectively.

(Udvardi et al., 1991). The acidification of SS, as well as proton gradient generation, which is known to drive many transport processes across SM, is possible due to H^+-ATPase activity in the membrane (Udvardi and Day, 1989; Pierre et al., 2013). Ammonia translocation across the SM is mediated by a member of the AQP family, nodulin 26 (NOD26), which is exclusively and abundantly present in the SM (Hwang et al., 2010). Nonetheless, a more important contribution of NOD26 to nitrogen homeostasis in nodules appears to be its function as a docking station for plant cytosolic glutamine synthetase. The latter enables the rapid assimilation of NH_3 into amino acids and creates a sink for further outward movement of ammonia (Masalkar et al., 2010). Up to now, AMTs in the SM have not been identified, but the presence of a voltage-activated nonselective cation channel (NSCC) that is permeable to monovalent cations (NH_4^+, K^+, Na^+) has been predicted for *G. max* and *L. japonicus* using patch clamp analyses (Roberts and Tyerman, 2002) (Figure 3 and Supplemental Table S2).

Transport of nitrate

Nitrate acts as a negative regulator of nodulation at every stage, repressing infection, nodule formation and, in mature nodules, nitrogen fixation (Streeter, 1985; Murray et al., 2017). Nitrate responses in plants, including the expression

of many nitrate transporters, are regulated by NIN-Like Protein (NLP) transcription factors, and loss of either of two NLPs in legumes results in nitrate-tolerant nodulation (Lin et al., 2018; Nishida et al., 2018). Remarkably, the nitrate transporters involved in this suppression have not been identified. Putative orthologs of Nitrate Transporter 1.1 (AtNRT1.1), considered to be the primary low-affinity nitrate transporter in Arabidopsis (*Arabidopsis thaliana*), are good candidates for this role. The role of nitrate in the suppression of nodulation is well-established, but recently an unexpected role for nitrate transport in supporting nodulation at low external concentrations through a nitrate–NO respiration pathway was discovered (Valkov et al., 2020). This provides potential insight into several previous reports that link nitrate transporters of the NPF family to nodule nitrogen fixation. The high-affinity nitrate transporter from *M. truncatula*, NPF7.6, is expressed in vascular nodule transfer cells (NTCs) upon rhizobia and nitrate treatment. Mutant nodules exhibit defects in vasculature and nitrogenase activity (Wang et al., 2020a). A low-affinity nitrate transporter, NPF8.6, was recently characterized in *L. japonicus*, and the strongest expression of *LjNPF8.6* was found to occur in mature nodules (Valkov et al., 2017). Loss of the transporter reduces nitrogen fixation efficiency, but does not affect nodule number or contribute to nitrogen-dependent inhibition of nodulation (Streeter, 1985; Valkov et al., 2017; Figure 3 and Supplemental Table S2). Interestingly, a closely related protein from *G. max*, GmNPF8.6, localizes to the SM (Clarke et al., 2015). A *L. japonicus* chlorate-tolerant mutant with decreased nitrate uptake ability was reported to have strongly decreased nodulation (Pal'ove-Balang et al., 2015). In addition to having a role in nitrogen fixation, NPF proteins may also be involved in other nodulation processes. A notable NPF identified with a role in nodulation was the *M. truncatula* high-affinity nitrate transporter MtNPF1.7, originally called Numerous Infections and Polyphenolics/Lateral root-organ Defective (NIP/LATD) (Yendrek et al., 2010; Bagchi et al., 2012). Severely affected *latd* mutants display nodule growth suppression and IT arrest in root hairs, with almost no rhizobia housed in the primordium (Veereshlingam et al., 2004; Yendrek et al., 2010; Supplemental Table S2). This suggests that either nitrate, or some yet unidentified MtNPF1.7 substrate, plays an important role in rhizobial infection.

Besides NPF family members, in *L. japonicus* and *G. max*, nodulin-70 (N70) transporters from the MFS superfamily are also SM proteins. They transport nitrate and nitrite, presumably as a part of ion and membrane potential regulation in response to external nitrate availability, which is known to affect symbiosis (Streeter, 1985; Vincill et al., 2005; Figure 3 and Supplemental Table S2).

Nutrient transport in nodules

Ureides (e.g. allantoin and allantoic acid) represent one of the major reduced nitrogen transport forms in tropical nodulating legumes such as French bean (*Phaseolus vulgaris*) or *G. max*. PvUPS1 and GmUPS1 transporters, a member of Ureide Permease (UPS) family, contribute to ureide export from nodules via their translocation from the nodule cortex and vascular endodermis to the lumen of nodule xylem. RNAi silencing of *GmUPS1* expression negatively affects nodule development (Pelissier et al., 2004; Collier and Tegeder, 2012).

Nitrogen-fixing cells in nodules exhibit high levels of protein biosynthesis, which increases the demand for sulfur (Noel et al., 1982; Gaude et al., 2004). A nodule-specific SO_4^{2-} transporter has been identified in *L. japonicus*. LjSST1 (Symbiotic Sulfate Transporter 1) localizes to the SM and translocates sulfur into the SS. *Ljsst1* mutants exhibit lower nitrogen fixation rates and, as a consequence, have reduced growth in symbiotic conditions (Krusell et al., 2005; Figure 3). Nitrogen fixation rates also rely on the activity of nitrogenase, which requires molybdenum as a cofactor (Bulen and Lecomte, 1966). MtMOT1.3 (Molybdate Transporter type 1) imports molybdate into cells of the nodule interzone and nitrogen fixation zone, and MtMOT1.3 knockout mutant plants exhibit impaired growth under N-deficiency, which is associated with a reduction in nitrogenase activity (Tejada-Jimenez et al., 2017; Figure 3). Another cofactor and an element crucial for protein structure is zinc. At least three nodule-specific zinc transporters have been characterized: GmZIP1 in *G. max* localizes specifically to the SM, while *M. truncatula* MtMTP2 and MtZIP6 localize to the endomembrane compartment or plasma membrane of cells in the nodule infection and differentiation zones, respectively. Analyses of plants with disrupted zinc transporter function revealed reduced nitrogenase activity under symbiotic conditions and growth defects (Moreau et al., 2002; Abreu et al., 2017; Leon-Mediavilla et al., 2018; Figure 3). Another nodule-specific metal transporter is *M. truncatula* Copper Transporter 1 (MtCOPT1), which is expressed in the late differentiation zone, interzone, and early nitrogen fixation zone. Its mutation could have an indirect effect on nitrogen fixation and plant physiology in symbiotic conditions, likely caused by defective copper-dependent functions in bacteroids (Senovilla et al., 2018; Figure 3 and Supplemental Table S2).

Iron is a key cofactor of nitrogenase, leghemoglobin, and other proteins crucial for cell homeostasis, such as cytochromes (reviewed in Brear et al., 2013). Nodules, which can contain as much as 45% of the total plant iron (Burton et al., 1998), are capable of taking up iron as a ferrous ion (Fe^{2+}) directly from the soil (Slatni et al., 2009), or as Fe^{3+}-chelates (e.g. citrate and nicotianamine) from xylem vessels (Tiffin, 1966; Cline et al., 1982). Our knowledge about transporters facilitating iron flow within nodules was gradually increasing throughout the years (Kaiser et al., 2003; Hakoyama et al., 2012; Takanashi et al., 2013; Shen et al., 2014; Tejada-Jimenez et al., 2015), but has recently substantially expanded (Kryvoruchko et al., 2018; Escudero et al., 2020; Liu et al.,

2020b; Walton et al., 2020; Brear et al., 2020). Some key discoveries in the field are described in Box 2.

BOX 2. IRON UPTAKE DURING NODULATION

The fate of iron within nodules strictly depends on transporters located in the plasma membranes (PMs) of nodule cells, the SM, and bacterial membranes. Two citrate exporters from the MATE family were found to localize to the PMs of infected cells. LjMATE1 and MtMATE67, through citrate translocation, contribute to Fe^{3+} chelation within the apoplast to solubilize iron and mitigate its transport into infected cells (Takanashi et al., 2013; Kryvoruchko et al., 2018). As the authors postulate, MtMATE67 may also transport citrate into the SS, increasing iron availability to bacteroids (Kryvoruchko et al., 2018).

MtNRAMP1 (Natural Resistance- Associated Macrophage Protein1) is a transporter facilitating iron uptake from the apoplast to infected cells in nodule zone II, which harbors intracellular ITs. Plants with a loss-of-function *nramp1* mutation exhibit nodule growth impairment and have a decreased N-fixing potential (Tejada-Jimenez et al., 2015). An interesting iron transporter is SM-localized GmDMT1 (Divalent Metal Transporter1), which belongs to the NRAMP family and translocates ferrous iron, as demonstrated by yeast mutant complementation assays. Due to the orientation of the SM, it is postulated that the protein could also transport Fe^{2+} out of the symbiosome or work bidirectionally. *GmDMT1* expression in the nodule is highest at the onset of nitrogen fixation, later declining with nodule senescence (Kaiser et al., 2003). Its putative ortholog is also present in *Arachis hypogaea* and is important for nodule iron supply (Shen et al., 2014).

A potential iron transporter in *L. japonicus* nodules is LjSEN1 (Stationary Endosymbiont Nodule1). Its sequence similarity to known iron transporters (e.g. AtVIT1), suggests it functions in iron transport (Brear et al., 2020). The *Ljsen1* mutant develops highly vacuolated infected cells and abnormal symbiosomes with smaller bacteroids. Moreover, mutations in *LjSEN1* negatively influence nitrogen fixation (Hakoyama et al., 2012). Interestingly, the discovery that GmVTL1a (Vacuolar iron Transporter-Like 1a), a *G. max* SM iron transporter, can complement the *Ljsen1* phenotype is consistent with the proposed role of LjSEN1 as an iron transporter in the SM (Brear et al., 2020; Liu et al., 2019b); however, its SM localization awaits confirmation. Recently, the number of characterized iron transporters (e.g. GmVTL1a, MtVTL4/8, MtFPN2) that are confirmed as essential for proper nodule functioning has increased substantially (Brear et al., 2020; Escudero et al., 2020; Liu et al., 2019b; Walton et al., 2020). This is considerably important for our understanding of iron distribution in nodules and its role in nitrogen fixation (Fig. 3, Supplemental Table S2).

Symbiotic exchange of reduced carbon/carbon compounds

It is generally accepted that dicarboxylates are the primary source of reduced carbon delivered directly from the host plant to the bacteroids. Dicarboxylates (mainly malate) provide the energy for symbiotic nitrogen fixation and are used as the carbon skeletons for the synthesis of amino acids (Udvardi et al., 1988; Rosendahl et al., 1990; Mitsch et al., 2018). LjALMT4, a member of the Aluminum-Activated Malate Transporter (ALMT) family, has been shown to be expressed in parenchyma cells of nodule vascular bundles and is proposed to be involved in dicarboxylate supply to the nodule. The transporter efflux activity of malate, succinate, and fumarate, but not tricarboxylates such as citrate, was demonstrated using a *Xenopus* oocyte heterologous expression system. Additionally, LjALMT4 translocates inorganic anions, such as chloride and nitrate, in the opposite direction (Takanashi et al., 2016).

As in mycorrhization, members of the SWEET family appear to be involved in sucrose transfer during nodulation. Notably, *L. japonicus* SWEET3 was found to be highly expressed in the vasculature of mature nodules, as well as in mycorrhizal roots. This PM-localized protein was observed to exhibit moderate sucrose influx activity; however, functional analyses using an RNAi approach did not reveal phenotypic differences between control and silenced roots (Sugiyama et al., 2017). In *M. truncatula*, a nodule-specific SUT, SWEET11, was found to be expressed, *inter alia*, in nodule vascular bundles, and constitutes a part of SM of infected cells. Loss of function of this transporter had no impact on nodule formation and nitrogen fixation (Kryvoruchko et al., 2016). The lack of a clear phenotype in knock-down and knock-out SWEET mutants in different plant species can be explained by functional redundancy among SUTs and/or the existence of alternative routes of carbon supply to nodules (Figure 3 and Supplemental Table S2). Interestingly, a member of the NPF family, Dicarboxylate Transporter (DCAT1), was located to the SM of the non-legume common alder (*Alnus glutinosa*), which establishes a symbiotic interaction with the nitrogen-fixing actinomycete *Frankia* (Jeong et al., 2004). Since the expression of NPF genes is induced in *M. truncatula* and *L. japonicus* during nodule development, it is tempting to speculate that certain members of this family are involved in supplying dicarboxylates to bacteroids (Colebatch et al., 2004; Benedito et al., 2008).

Hormone transport during symbioses

The involvement of plant hormones, such as auxin and cytokinin, in the regulation of nodulation and AM interactions

is well established, although reports of hormone translocation in nodulation are more extensive and detailed than those for AM (Foo et al., 2014; Bedini et al., 2018; Liao et al., 2018). Notably, the molecular identity of the hormone transporters involved often remains unknown, even in the case of nodulation. The role of SLs as inter-kingdom signals in the rhizosphere has been mentioned earlier (see Presymbiotic stage section).

Auxin

Auxin plays a crucial role as a mobile signal that is translocated from shoots toward the root tips, in a polar manner, and is responsible for the initiation of new lateral roots and nodules in legumes (Libbenga et al., 1973; Benkova et al., 2003; Friml, 2003).

Auxin transport is controlled by at least four classes of transport proteins: PIN (PIN-FORMED), AUX1/LAX (AUXIN1/LIKE-AUX1), PGP/MDR/ABCB (P-Glycoprotein/Multidrug resistance/ABC B), and PILS (PIN-LIKES) proteins. All of them are members of multigene families (reviewed in Mohanta et al., 2018). In the experimental model plant *A. thaliana*, eight PIN proteins have been extensively studied for their role in auxin export, most of which have well described functions in roots (Blilou et al., 2005; Paponov et al., 2005; Krecek et al., 2009). Phylogenetic analyses and sequence comparison with *A. thaliana* PIN proteins have provided clues about the putative legume PIN proteins through their assignment to orthologous groups (Schnabel and Frugoli, 2004; Kohlen et al., 2018). Interestingly, *Sinorhizobium meliloti* infection appears to modulate the expression of *M. truncatula* PIN genes both in shoots and roots (Shen et al., 2015). Disruption of *MtPIN2*, *MtPIN3*, and *MtPIN4* expression through RNAi leads to a reduction in the number of nodules, suggesting that these components of the auxin-transport machinery play a role in nodule development (Huo et al., 2006).

It is known that the action of PIN proteins mediates multiple developmental processes, including organ development (Vieten et al., 2005). Thus, the PIN-dependent transport network might enable the stabilization of auxin gradients and the development of adaptive organs, such as the nodule. There are large overlaps in the signaling components and developmental processes involved in the formation of lateral roots and nodules, making them an interesting model to study plant organ development (Schiessl et al., 2019; Soyano et al., 2019). It is worth noting that *PIN* gene expression profiles in the developing and mature nodule can vary considerably, as is the case with *MtPIN2*, which encodes the first PIN transporter described in legumes (Huo et al., 2006; Sanko-Sawczenko et al., 2016). *MtPIN2* expression in nodules starts within peripheral cells, which give birth to vascular elements. This is followed by an expression pattern covering the entire nodule at its emerging stage. Subsequently, *MtPIN2* is expressed exclusively at the base of the organ and its expression is no longer detected when the nodule is mature (Huo et al., 2006). This may be a case of nodule-associated specialization. Moreover, MtPIN2-mediated basipetal auxin transport in roots appears to be less important for successful initiation of nodulation than it is for early nodule development (Ng et al., 2020).

Studies of auxin distribution in root nodules also showed the involvement of auxin in the formation of vascular bundles (Takanashi et al., 2011). Developing vascular tissue is characterized by relatively high auxin levels and sink strength in such a system primarily depends on PIN-dependent auxin flux rates. Identification of auxin transporters, as well as other factors that influence auxin canalization during nodule vascularization, will be important to gain insights into the evolution of nodule architecture. Interestingly, it has been shown that SLs influence PIN-dependent auxin canalization in pea (*Pisum sativum*), thereby affecting vasculature formation (Zhang et al., 2020). An open question is whether, in addition to functioning as a signal in the rhizosphere, SLs and their transporters are involved in symbioses by modulating auxin distribution in roots and root-associated organs. Notably, in *A. thaliana*, it has been shown that molecular pathways coordinating root growth in response to distinct nitrogen sources involve nitrate-dependent dephosphorylation of the PIN auxin efflux carrier (Otvos et al., 2021). This provides a flexible means to regulate auxin activity in response to varying sources of N, which is an interesting area of exploration in legumes.

The export of auxin is also enabled by ABC transporters from the B subfamily. Their function overlaps partially with PIN transporters, but the flow of auxin generated by ABCB proteins is not polar (Mravec et al., 2008; Lane et al., 2016). The involvement of ABCB members in nodulation and symbiotic nitrogen fixation within *Fabaceae* still has to be determined in more detail (Molesini et al., 2014; Shen et al., 2015; Sanko-Sawczenko et al., 2016). For instance, the auxin transporter LjABCB1 from *L. japonicus* is expressed exclusively in developing nodules, and the activity of its promoter has been detected in uninfected cells neighboring the infection zone (Takanashi et al., 2012). Three ABCB transporters that are induced during both LRS and AMS were recently described, but no substrates were identified, and a triple mutant showed no overt effect on mycorrhiza, and only a slight increase in nodule formation (Roy et al., 2021).

In addition to efflux, auxin transport requires cellular influx. This occurs in part by diffusion but is also facilitated by a small multigene family of high-affinity auxin influx carriers (AUX1/LAX). In legumes, AUX/LAX transporters are ubiquitously expressed in root tissues including nodules (Shen et al., 2015; Sanko-Sawczenko et al., 2016; Roy et al., 2017). LAX2 from *M. truncatula* is one of the best characterized auxin importers. Its expression is widely detected in shoots and underground tissues of uninfected plants, but also in nodulating roots, and both developing and mature nodules (Schnabel and Frugoli, 2004; Shen et al., 2015; Sanko-Sawczenko et al., 2016). MtLAX2 plays an important role in

the formation of root nodules and lateral roots in legumes, indicating a common requirement for auxin influx activity for both forms of lateral organs (Roy et al., 2017; Supplemental Table S2).

Auxin involvement in AMS has been widely discussed (Ludwig-Muller et al., 1997; Hanlon and Coenen, 2011; Ng et al., 2015; Bedini et al., 2018; Liao et al., 2018). It has been postulated that mycorrhizal fungi use auxin as a means to stimulate root growth and new lateral root development in an infection area (Bonfante and Genre, 2010). However, knowledge of the changes in auxin distribution and role of auxin transporters in arbuscule development is limited. Interestingly, expression of one *M. truncatula* full-size transporter, *ABCB1*, is induced in cells hosting arbuscules and adjacent cortical cells. The encoded transporter may be involved in transport of auxin between cells during AMS (Gaude et al., 2012a).

Cytokinins

Cytokinins are involved in many important developmental processes, including a central role in LRS (Gonzalez-Rizzo et al., 2006; Murray et al., 2007; Tirichine et al., 2007). They are considered to be signaling molecules, conveying information from symbiotic bacteria to the inner parts of the root, where they are required for cortical cell divisions (Timmers et al., 1999; Reid et al., 2017). Moreover, cytokinins act as a negative regulator of infection within the rhizodermis and as a part of systemic autoregulatory mechanisms, controlling the number of nodules (Sasaki et al., 2014; Miri et al., 2019).

In *A. thaliana*, three kinds of cytokinin transporters have been reported to date: Purine Permeases (PUP), Equilibrative Nucleoside Transporters (ENT), and ABCG transporters (Kudo et al., 2010; Girke et al., 2014; Borghi et al., 2015). Less is known about cytokinin distribution in legumes, although some transcriptome data have demonstrated that ABC and ENT family members are expressed in the rhizodermis and are upregulated by NF treatment (Damiani et al., 2016; Jardinaud et al., 2016). Recently, Jarzyniak et al. (2021) identified a full-size ABCG protein in *M. truncatula* as a cytokinin transporter. *MtABCG56* is expressed in roots and nodules, and it was proposed to be responsible for efflux of cytokinins from the epidermis upon infection. Such export may have a cell-autonomous function and may also affect distal cortical responses and nodule organogenesis. Thus, ABCG-driven cytokinin transport may be a part of scenario of early symbiotic communication between the epidermis and cortex (Supplemental Table S2). Given that genes encoding 30 full-size ABCG proteins are present in the *M. truncatula* genome and that transcriptomic analyses suggest that several of them are induced under symbiotic conditions (Jardinaud et al., 2016), other roles in LRS may be attributed to the action of ABCG transporters. Other LRS processes involving cytokinins, such as the suppression of nodulation and lateral root formation, may use ABCG proteins as hormone flow facilitators.

The role of cytokinins in AMS is not as well understood as in LRS (Bedini et al., 2018; Liao et al., 2018). This is mostly caused by the diversity of fungi and plants that take part in symbioses, and the ability of some fungi to produce cytokinins themselves, which complicates analyses of the source and function of this class of phytohormones (Barea and Azcon-Aguilar, 1982; Pons et al., 2020). The identification of cytokinin transport and/or transporters that participate in AMS would constitute an important milestone in the field.

Abscisic acid

Levels of ABA in legumes are affected by soil moisture and influence root morphology and nodulation efficiency. Upon water shortage, ABA promotes the growth of lateral roots and simultaneously modulates the nodulation process, acting as a negative regulator of the early nodulation stages by affecting epidermal NF signaling and cytokinin-activated cortical cell division (Ding et al., 2008; Gonzalez et al., 2015). ABA in roots is synthesized within vascular tissues and has to be translocated to external parts of the root (i.e. pericycle, endodermis, and inner cortex) in order to suppress nodule morphogenesis (Phillips, 1971; Endo et al., 2008; Xiao et al., 2014). The molecular basis of ABA transport has been defined, and transmembrane ABA translocation, based on diffusion and the presence of primary and secondary transporters, has been extensively studied in *A. thaliana* (Boursiac et al., 2013; Borghi et al., 2015; Kuromori et al., 2018). Several ABCG transporters, namely AtABCG25, -30, -31, and -40, have been implicated in the transport of ABA, promoting plant resistance to pathogens or modulating root architecture, seed development, and stomatal movement (Kang et al., 2010, 2015; Kuromori et al., 2010). It was recently shown that a *M. truncatula* half-size ABCG transporter, MtABCG20, is involved in ABA translocation from the root vasculature. Interestingly, nodulation tests have shown that a knock-out of *MtABCG20* results in increased nodule number compared with WT, consistent with the function of ABA as a negative regulator of infection events in the epidermis and nodule primordium formation in the root cortex tissue. The increase in nodule numbers in *mtabcg20* is likely due to reduced export of ABA from its site of biosynthesis (Ding et al., 2008; Ding and Oldroyd, 2009; Pawela et al., 2019).

Mutation of *M. truncatula* MtNPF1.7/LATD/NIP, mentioned above as a nitrate transporter, results in defects in rhizobial infection structures and non-functional nodule meristems (Yendrek et al., 2010). Interestingly, these phenotypes are rescued by the exogenous application of ABA (Zhang et al., 2014). Therefore, it has been speculated that *M. truncatula* LATD/NIP may also be involved in ABA transport (Harris and Dickstein, 2010; Supplemental Table S2).

ABA also modulates AMS. Low ABA concentrations promote AM colonization, development, and maintenance, as in the case of mild water stress. This suggests that the fungal supply of water and mineral compounds has a net benefit to the plant, despite the increased costs of the symbiosis. In contrast, high concentrations of ABA may have a negative influence on AM fungi–host plant relations, as in the case of severe drought conditions (Charpentier et al., 2014; Stec et al., 2016). The role of ABA transport, and transporters

OUTSTANDING QUESTIONS

- Which host transporters are responsible for flavonoid secretion during LRS, and do they vary between legume taxa?
- During LRS, which host transporters are required to sustain growth of bacteria enclosed within infection threads?
- Is the temporal control of MtPT4 localization to the PAM a special case, or can it be generalized?
- What is the substrate(s)/function of NOPE1?
- How does lipid transport influence AM formation?
- What is the nature of the substrate transported by STR and STR2?
- Does the mycorrhizal nitrate pathway operate in plants other than grasses?
- What is the range and potential interplay/cooperation of auxin and cytokinin transporters during nodule development?

facilitating its distribution in plants during AMS, seems to be of key importance, but is not well understood at present.

Conclusion

Despite the obvious importance of transporters in symbioses and considerable recent progress, knowledge in this area is surprisingly sporadic (see Outstanding questions). Classical genetic approaches coupled with thorough biochemical characterization have enabled the discovery of the physiological functions of many such proteins. However, deciphering the functions of members of multigene families is not an easy task due to apparent functional redundancy. The source of such redundancy can be difficult to predict since small variations in protein sequence can greatly alter transport properties. However, symbiotic studies provide particular opportunities for transport research, including: (i) organ-driven specialization (e.g. legumes and nodules); (ii) process specialization (e.g. nodulation and hormone interplay); (iii) dedicated transport of species-specific compounds (isoflavonoids and legumes), and new functionality (e.g. ABCGs and specialized metabolite intermediates distribution/channeling). Equally important are identifying the molecules that are translocated, determining which are biologically relevant, and generating direct transport data. The latter is often technically challenging (e.g. lipid provision during AMS) but is crucial for characterizing the carriers as additional transport-driven processes are uncovered.

Supplemental data

Supplemental Table S1. Comprehensive overview of transporters involved in arbuscular mycorrhiza formation.

Supplemental Table S2. Comprehensive overview of transporters involved in LRS.

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