The Role of Plant Transporters in Mycorrhizal Symbioses

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Abstract

Membrane transport systems are crucial elements for plant nutrition and development as they play a key role in the absorption of mineral nutrients and water at the root level but also in the translocation within the plant. Moreover, membrane transport is involved in signalling and communication e.g. to adapt and interact with the environment. Most

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plants live in tight contact with beneficial soil microbes, such as bacteria and mycorrhizal fungi, which contribute to plant nutrition in part through modulation of the expression and functioning of plant transporter systems, as ion channels and transporters. In addition, mycorrhizal fungi largely increase the absorption surface of roots thereby promoting plant's access to soil resources as minerals and water. In turn, plants "reward" mycorrhizal fungi with sugars and/or lipids. This "fair trade" requires specific communication and a series of exchanges between the two symbiotic partners enabled by the adaptability and plasticity of their transporters. Here, we summarize recent advances allowing molecular insight in the impact of mycorrhizal symbiosis on the plant "transportome". We highlight results obtained in ecto- and endomycorrhizal associations for plant transporters involved in the absorption of mineral nutrients and water released by the fungus at the symbiotic interface, and molecular players responsible for carbon and lipid nutrition of the fungal partner. We focus also on plant membrane transport systems implicated in early communication between plant and fungal partners.

1. INTRODUCTION

Plants form mutualistic associations with specialized fungi that modulate their ability to acquire water and nutrients from the soil. Mycorrhiza is a new root structure that is formed by both symbiotic partners, and which provides a continuum between soil, fungi and plant roots. Among the different mycorrhizal associations, arbuscular mycorrhizal (AM) fungi interact with most land plants, while ectomycorrhizal (ECM) fungi colonize more specifically woody plant species, mostly from temperate and boreal forests (Smith & Read, 2008). There are also some types of mycorrhizal symbioses more specific to plant families, such as Ericaceae and Orchidaceae. These beneficial fungi can be seen as a kind of prolongation of the plant root system, enabling access to water and nutrients located outside of depletion zones around the roots (Fig. 1). Other benefits provided by mycorrhizal symbioses include protection against biotic and abiotic stresses (Miransari, 2014). In exchange, mycorrhizal fungi are fed by the plants with carbon substrates originating from photosynthesis, thus implicating regulation of plant sugar transport (Fig. 1). Nowadays, lipid transfer has also been shown in AM symbiosis (Keymer et al., 2017).

Regarding AM symbiosis, research on the mechanisms governing nutritional exchanges between the symbiotic partners has mainly focused on the plant host due to the complexity of the fungal genomes and the difficulty for handling AM fungi (Garcia, Doidy, Zimmermann, Wipf, & Courty, 2016). In contrast, studies on ECM symbiosis are more advanced on the fungal partners than on the plants due to limited tools for woody plants, with

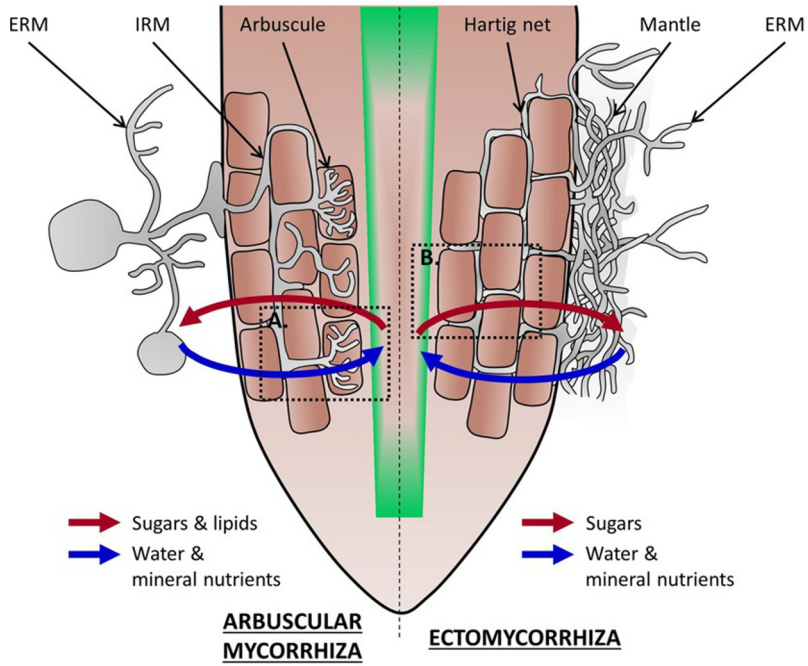

Fig. 1 Nutritional exchanges modulate the functioning of arbuscular mycorrhizal and ectomycorrhizal associations. In arbuscular mycorrhizae, the fungus absorbs water and mineral nutrients from the soil solution with its extraradical mycelium (ERM). These nutriments are transferred within the root through the intraradical mycelium (IRM) and finally transmitted to the host plant through structures within root cells, called arbuscules, that are formed by fungal and plant membranes. The plant controls the system of "reciprocal rewards" established with the fungus via the allocation of carbon compounds obtained by photosynthesis. In ectomycorrhizae, the wide ERM extends the root absorbing surface and allows a better mineral and water nutrition of the plant, which is also rewarded by the transfer of sugars to the fungus. These exchanges take place at the level of the Hartig net. Boxes (A) and (B) are further detailed in Fig. 2.

the exception of poplar, and easier handling of ECM fungi. Genomic projects such as The JGI Mycorrhizal Genomics Initiative (https://jgi.doe.gov/the-mycorrhizal-genomics-initiative-or-exploring-tree-fungal-symbioses/) recently extended our knowledge on the fungal side, which has been particularly useful in the case of ECM associations (Kohler et al., 2015). Nevertheless, ongoing researches are releasing key essential information on both the fungal and plant sides regarding the functioning of nutritional exchanges in different types of mycorrhizal symbiosis (Garcia et al., 2016).

Traditionally, there has been a great research interest on plant membrane transport systems, ion channels and transporters (cf. this book), due to their

impact on whole plant physiology, signalling, nutrient uptake and translocation, and agricultural outputs (Schroeder et al., 2013). At first, they have been extensively studied in the model plant *Arabidopsis thaliana*. Translational research is expanding this field to crop species, such as *Medicago* sp., tomato, potato, rice or maize, all of them being known to interact with arbuscular mycorrhizal fungi. In the case of mycorrhiza involving tree species, there has been much less research efforts on characterizing membrane transport systems on the plant side, besides poplar (Courty, Doidy, Garcia, Wipf, & Zimmermann, 2017), partly because of the large size of tree genomes (Loth-Pereda et al., 2011; Neale et al., 2014). This is one of the reasons why the fungal side is more explored in this symbiotic interaction.

First molecular evidence for a tight regulation of plant transporters during mycorrhizal interactions has been found for a phosphate (Pi) transporter from tomato (Rausch et al., 2001). In the meantime, recent transcriptomic studies and further detailed analyses have underlined such a tight control of plant membrane transport systems by symbiotic fungal partners, revealing the plasticity of the plant "transportome". The importance and implication of membrane transport for communication and nutritional exchange (Fig. 1) between fungi and plant roots become more and more recognized. Within this chapter, recent knowledge on this topic is summarized and discussed.

2. ECTOMYCORRHIZAL SYMBIOSIS REQUIRES TIGHTLY REGULATED PLANT MEMBRANE TRANSPORT

ECM symbioses are mutualistic interactions between roots of ligneous plants and soil fungi mainly belonging to the Basidiomycota and Ascomycota phyla (Tedersoo & Smith, 2013). They characteristically develop around short thick lateral roots forming three structures: (i) an extraradical mycelium (ERM) in contact with the substrate, (ii) a dense fungal mantle covering the root, and (iii) the so-called Hartig net formed by the hyphae that enter the root and develop in layers around the cortex and epidermal cells (Smith & Read, 2008). The ERM explores the soil and is specialized in nutrient and water absorption, functionally substituting the root hairs, whose development is inhibited. Remarkably, ECM fungi in symbiosis with trees form an extensive hyphal network, contributing to carbon storage in the soil (Clemmensen et al., 2013, 2015). This extraradical mycelium can mobilize soil nutrients and water even under extremely unfavourable soil conditions (for example, Berruti, Lumini, Balestrini, &

Bianciotto, 2015; Landeweert, Hoffland, Finlay, Kuyper, & Van Breemen, 2001), thus improving plant tolerance to challenging environments. The fungal mantle can store nutrients and serves as a buffering compartment against environmental changes or stresses (for example, Bücking & Heyser, 2000; Bücking, Kuhn, Schröder, & Heyser, 2002; Muhsin & Zwiazek, 2002). Finally, the Hartig net hyphae have been reported to be responsible for nutritional exchanges between the fungus and the plant (Kottke & Oberwinkler, 1987). Due to the small and rather simple genomes of ECM fungi compared to those of the interacting plants, genetic and molecular research in this field is far more developed on the fungal side, whereas the plant transportome involved in symbiotic exchange largely remains to be explored.

2.1 Plant Root's Uptake of Mineral Nutrients and Water Transferred From Symbiotic Fungi

2.1.1 Plant Phosphate Nutrition

ECM fungi improve plant inorganic orthophosphate (Pi) nutrition through several mechanisms including the expression of membrane transport proteins at the uptake side from the soil and at the release side between the Hartig net and plant cortical cells (reviewed in Becquer, Trap, Irshad, Ali, & Plassard, 2014; Nehls & Plassard, 2018). This beneficial effect is of great importance with respect to the limiting availability of phosphorus (P) representing an increasing problem in agroecosystems. Thanks to a higher exploratory capacity provided by the fungal structure and the smaller size of fungal hyphae compared to root systems, mycorrhizal plants have the ability to access soil P in a more efficient manner than plants *per se*. In addition, fungi release Pi from the substrate through the acidification of the environment and secretion of phosphatases (Plassard & Dell, 2010). Pi absorbed by the extraradical hyphae can be transferred to the plant in the Hartig net, where as yet unknown transporters mediate its release into the apoplasm (Torres-Aquino et al., 2017). Recently, a fungal Pi transporter from *Hebeloma cylindrosporum* with a dual function likely involved in Pi absorption from the soil and in Pi secretion towards the symbiotic interface has been described (Becquer et al., 2018). However, molecular knowledge on Pi uptake by the root cells at the symbiotic interface is still missing. Loth-Pereda et al. (2011) studied several Pi transporters from ECM poplars, finding that two genes (*PtPT9* and *PtPT12*) were strongly upregulated when interacting with *Laccaria bicolor* and *Paxillus involutus*. They proposed that the corresponding transporters could perform Pi uptake in mycorrhizal

conditions, but suggested that the expression increase could be biased by the lower Pi concentrations in the symbiotic space. Similar results have been obtained by Zhang, Wen, and Ding (2017), who found four phosphate transporter genes (*PmPT1–4*) with a higher expression in *Pinus massoniana-Boletus edulis/Pisolithus tinctorius* mycorrhizae than in non-inoculated roots, especially under low Pi conditions. These authors also considered the possibility that low Pi availability was responsible for the overexpression of *PmPT1–4* genes in ectomycorrhizae. It is likely that the combination of both factors, low Pi and symbiosis, enhances the beneficial role of ECM fungi, which could be otherwise masked under high Pi conditions.

2.1.2 Ectomycorrhizal Contribution to Nitrogen Nutrition

ECM fungi contribute largely to nitrogen (N) uptake and assimilation via nitrate, ammonium, peptide and amino acid transporters (Garcia et al., 2016; Nehls & Plassard, 2018). The molecular mechanisms responsible for plant N uptake in ECM associations have been partly studied in model angiosperms and gymnosperms. In mycorrhizal poplar (*Populus trichocarpa*), the high-affinity ammonium transporter *PttAMT1.2* was upregulated when the plant was inoculated with *Amanita muscaria* in *in vitro* cultures or in field conditions when naturally associated with wild species (Selle et al., 2005) or when inoculated with *P. involutus* (Couturier et al., 2007). This transporter is believed to take up ammonium released by the fungus at the symbiotic interface. In mycorrhizal association, the related tree *Populus tremula* × *tremuloides* also undergoes an upregulation of ammonium transporters, including *PoptrAMT1.2b* which is the closest *PttAMT1.2* ortholog, as well as *PoptrAMT1.3* and *PoptrAMT1.4*. In ECM *Pinus pinaster*, ammonium uptake is believed to be mediated by *PpAMT1.3*, a high-affinity and high-capacity transporter whose transcription is induced in mycorrhizal roots (Castro-Rodríguez et al., 2016). Also, in the mycorrhizal model *Quercus robur-Piloderma croceum*, colonization induced the overexpression of one AMT (Tarkka et al., 2013).

Strikingly, a rise in the transcript abundance of the putative nitrate transporter *PttNRT2.5B* has been observed during ECM association of *P. tremula* × *tremuloides* and *A. muscaria* (Willmann, Thomfohrde, Haensch, & Nehls, 2014). Because nitrate is commonly not considered as a major form of transported N from the fungus to the host plant (Chalot, Blaudez, & Brun, 2006), it has been proposed that this transporter uses other substrates than nitrate (Willmann et al., 2014).

So far, little transcriptomic data are available on trees, whether or not they are engaged in a symbiotic interaction with an ECM fungus. The most up-to-date information led to an incomplete N model where ammonium transporters play the main role (Garcia et al., 2016). Further research is needed to confirm this function and to complete our view about the other nitrogenous compounds (nitrate, amino acids or peptides) in the N nutrition of the ECM plant.

2.1.3 Potassium

Indisputably, N and P are the main mineral nutrients acquired by mycorrhizal associations and regulating mycorrhizal establishment and functioning. However, other elements are presumably involved as well, particularly when they are scarce in the environment. For instance, some ECM plants have a better potassium (K) nutrition than non-mycorrhizal controls under shortage conditions (Garcia et al., 2014; Garcia & Zimmermann, 2014; Jentschke, Brandes, Kuhn, Schröder, & Godbold, 2001; Jourand et al., 2014), indicating a beneficial effect of this symbiotic interaction. Although the mechanisms involved in K nutrition have been well described and characterized in herbaceous plants (for a review, see Nieves-Cordones, Alemán, Martínez, & Rubio, 2014), little is known about K transport systems of ECM plants (Zhang, Yin, & Xia, 2010). These transport systems are likely to be distributed among the Shaker-like channel family (Dreyer & Uozumi, 2011) as well as the Trk/Ktr/HKT and KT/KUP/HAK transporter families (Corratgé-Faillie et al., 2010; Grabov, 2007). To date, there is only one mention of the regulation of these genes during ECM symbiosis in literature. Peter et al. (2016) found an induction of the putative Shaker-like channel *SKOR* (Stellar K^+ Outward-Rectifier) of *Pinus sylvestris* upon mycorrhization with *Cenococcum geophilum*, which could be involved in an increased xylem loading during symbiosis. Once again, most data available so far are on the fungal partner where transport proteins were identified and characterized (Corratgé et al., 2007; Garcia et al., 2014; Guerrero-Galán, Delteil, et al., 2018; Guerrero-Galán, Garcia, Houdinet, & Zimmermann, 2018). Efforts are still needed on the plant side.

2.1.4 Ectomycorrhizal Fungi Modify Root Water Transport in Plants

The association of ECM fungi with plant roots modifies deeply water uptake in the host trees. The absorption of water from the soil by plant roots is mainly controlled by radial water transport following two main paths, the apoplastic and the cell-to-cell pathways (Steudle & Peterson,

1998). The apoplastic pathway is formed by the cell wall continuum and controlled by the development of Casparian strips and suberin at the exodermis and endodermis (Barberon & Geldner, 2014). The cell-to-cell pathway occurs mainly through plasmodesmata or plasma membranes by specialized water channel proteins called aquaporins, which mediate passive water transport using the driving force due to water potential gradients. Aquaporins are membrane intrinsic proteins (MIPs) found in all plant species (Maurel et al., 2015) and in fungi (Dietz, von Bülow, Beitz, & Nehls, 2011; Nehls & Dietz, 2014; Xu et al., 2015). They are distributed among five subfamilies (PIPs, TIPs, NIPs, XIPs and SIPs) with different substrate selectivities and localizations (Chaumont & Tyerman, 2014). Among them, the most important PIP and TIP subfamilies have a prominent role in whole plant water transport (Maurel et al., 2015).

In general, the presence of ECM fungi enhances the plant's root hydraulic conductivity (Lee, Calvo-Polanco, & Zwiazek, 2010; Xu et al., 2015), although other results showed no effect (Calvo-Polanco, Jones, & Zwiazek, 2009; Xu, Cooke, Kemppainen, Pardo, & Zwiazek, 2016). The increase of root water transport in the presence of ECM fungi has been mainly attributed to their effect on the symplastic water transport through upregulation of PIP aquaporins, as shown in the following associations: *A. muscaria-poplar* (Marjanović et al., 2005), *Tuber melanosporum*-poplar; (Hacquard et al., 2013), *Tuber clavery-Helianthemum almeriense* (Navarro-Rodenas et al., 2013), *L. bicolor-spruce* (Xu et al., 2015).

The effect of ECM fungi on plant water transport is fungal/host dependent. In addition, other parameters, that are not yet unravelled and well studied, might contribute to upregulation or deregulation of plant aquaporins. In particular, proper phosphorylation of aquaporins, as in AM symbiosis (Vandeleur et al., 2014), as well as their precise localization within the roots can be critical for water uptake both under control conditions and when plants are exposed to different soil stresses.

Due to the role of extraradical fungal hyphae as prolongation of the plant roots, fungal aquaporins are of importance for the uptake and transfer of water towards the plant. In line with this hypothesis, results obtained after artificial downregulation or overexpression of aquaporins from *L. bicolor* support their role in ectomycorrhizae in *Populus tremuloides* seedlings (Navarro-Ródenas, Xu, Kemppainen, Pardo, & Zwiazek, 2015) and in *Picea glauca* (Xu et al., 2015). Furthermore, fungal aquaporins have been shown to be transcriptionally regulated in ECM fungi under mycorrhizal conditions, such as in *C. geophilum* in symbiosis with *P. sylvestris* (Peter et al., 2016).

These observations support the hypothesis that fungal aquaporins are required for transport of water during symbiosis and that their expression is regulated by water needs from the host plant.

2.2 Delivering Carbon Food for the Fungal Partner

Carbon supply by the plant to the fungal partner is essential to balance the relationship between partners engaged in the mycorrhizal symbiosis. ECM fungi often derive from ancestral saprotrophic fungi (Veneault-Fourrey & Martin, 2013), which, however, have lost most genes coding for plant cell wall-degrading enzymes (Kohler et al., 2015). Therefore, their nutrition mostly relies on sugars and simple carbon compounds exuded by the plant into the root apoplasm.

Although the transport of carbohydrates in ectomycorrhizae has not been deeply explored, it has been pointed out that three families of plant transporters could be involved in this process: sucrose transporters (SUTs), monosaccharide transporters (MSTs), and sugar SWEET transporters ("sugars will eventually be exported transporter" family) (Garcia et al., 2016). Upregulation of plant SWEET members has been reported in transcriptomic studies of several ECM couples such as *Q. robur-P. croceum* (Tarkka et al., 2013), *P. trichocarpa-L. bicolor* (Plett et al., 2015) and *P. sylvestris-C. geophilum/Suillus granulatus* ectomycorrhizae (Peter et al., 2016). However, the precise process by which SWEET transporters undergo this regulation is still unknown. Initially, it has been hypothesized that sucrose would be the main substrate released by the plant to the fungus even if this latter cannot absorb sucrose. Assimilation of carbon compounds might then rely on plant invertases that hydrolyse sucrose into glucose and fructose; these two carbohydrate forms being taken up by the fungus transport systems (Nehls, Grunze, Willmann, Reich, & Küster, 2007).

To sustain a balanced sharing of resources, mechanisms controlling plant-fungal C allocation have been proposed. Grunze, Willmann, and Nehls (2004) found that *PttMST3.1*, a *P. tremula* × *tremuloides* MST gene likely involved in hexose import from the root apoplasm, is induced in *A. muscaria* ectomycorrhizae. By expressing this transporter, the plant would compete for sugars with the fungus in the symbiotic interface, thereby regulating the benefit balance of the mutualism.

To sum up, Nehls et al. (2007) suggested that the plant reaches an equilibrium in the interaction thanks to carbohydrate allocation in three ways: (i) the exudation of sucrose through a plant transporter, (ii) its hydrolysis

(in glucose and fructose) by invertases, and (iii) the competition for hexoses in the Hartig net between root and fungal cells, also mediated by plant transporters. However, this relative simple model will have to be implemented to include other substrates and mechanisms.

2.3 Communication Between Symbiotic Partners

Mutual recognition between host plants and their fungal partners constitutes the first step in the establishment of ECM symbiosis (Martin et al., 2001). Plant roots secrete a large amount of primary and secondary metabolites in the rhizosphere to attract symbiotic microbes, stimulating growth and spore germination of ECM fungi (Ali & Jackson, 1988; Fries, Serck-Hanssen, Dimberg, & Theander, 1987; Melin & Rama Das, 1954). For example, seven flavonoids exuded by *Pinus densiflora* roots stimulate germination of *Suillus bovinus* spores (Kikuchi, Matsushita, Suzuki, & Hogetsu, 2007), and rutin secreted by *Eucalyptus globulus* roots enhances the hyphal growth of two *Pisolithus* strains (Lagrange, Jay-Allemand, & Lapeyrie, 2001). Rutin and quercitin from poplar roots trigger the expression of an effector protein in the ECM fungus *L. bicolor* (Plett & Martin, 2012). Carbon-derived compounds are also exuded by the plant and can be taken up by ECM fungi growing at the root vicinity (Nehls, 2008). Although it was thought for a long time that root exudates are passively exported from roots into the rhizosphere, it becomes clear that an active transport involving plant transporters also occurs (Baetz & Martinoia, 2014; Sasse, Martinoia, & Northen, 2018). For example, ABC-type transporters allow exudation of secondary metabolites in the non-mycorrhizal plant *A. thaliana* (Baudri et al., 2008; Ziegler, Schmidt, Strehmel, Scheel, & Abel, 2017), or flavonoids in soybean (Sugiyama, Shitan, & Yazaki, 2007). Although plant transporters obviously play a key role in root exudation processes, only a few of these transporters have been reported and characterized so far. In particular, no data are currently available regarding their role in exudation of compounds that stimulate the germination and growth of ECM fungi.

It is also hypothesized that nutrients themselves play an important role for the early recognition between host plants and ECM fungi (Garcia, Delaux, Cope, & Ané, 2015). The dual trophic and signalling role of nutrients was already observed in AM symbiosis (cf. Section 3.1; Carbonnel & Gutjahr, 2014). In ECM plants, it has been demonstrated that nutrient availability

affects the establishment of the symbiotic interaction (Arnebrant, 1994; Plassard, Bonafos, & Touraine, 2000; Plassard & Dell, 2010), but the molecular players involved still remain unknown. Becquer et al. (2018) recently characterized a Pi transporter from the ECM fungus *H. cylindrosporum* that is primarily involved in Pi acquisition from the soil and its transfer towards the plant. Excitingly, it was observed that downregulation of *HcPT2* inhibits ECM formation, suggesting that a less cooperative fungus can be sanctioned by the host and that nutrients themselves are key regulators of ECM symbiosis. On the plant side, although Pi transporters are differentially regulated upon ECM colonization in poplar (Loth-Pereda et al., 2011), reverse genetic experiments are still missing to validate their role in both Pi transport and signalization in symbiosis.

3. ARBUSCULAR MYCORRHIZAL FUNGI CONTROL PLANT ION CHANNELS AND TRANSPORTERS

Arbuscular mycorrhizal symbiosis is largely widespread and occurs between a wide range of land plants and AM fungi belonging to the Glomeromycota group (Smith & Read, 2008). The principle of their relationship relies on mutual exchanges like the ones described for the ECM symbiosis, the fungi providing water and minerals, mainly phosphorus and nitrogen, while getting carbon resources from the plant (MacLean, Bravo, & Harrison, 2017). However, in contrast to the ECM association (cf. Section 2), the interface for exchange between AM fungi and the plant is not formed between the root cells. The AM fungi rather enter the plant cells and produce an expanded membrane surface within the root cell. During the symbiotic interaction, AM fungi grow in two different structures: the extraradical mycelium (ERM) and the intraradical mycelium (IRM).

The role of the ERM is to explore the soil by establishing an extensive hyphal network to mobilize and acquire soil water and nutrients, mainly phosphorus and nitrogen (Bompadre et al., 2013; Bonfante & Genre, 2010). Thus, establishment of AM symbiosis enables the host plants to resist short- and long-term environmental constraints, increasing the plant capacity to adapt and survive unfavourable conditions (Al-Karaki & Clark, 1998; Ruíz-Lozano, Porcel, Azcón, & Aroca, 2012; Smith & Read, 2008). The success of the interaction and the beneficial effects of AM fungi on plants vary according to the AM fungal strain and plant cultivars used, as well as to the biochemistry and microbial composition of the soil where the

interaction takes place (Burns, Anacker, Strauss, & Burke, 2015; Calvo-Polanco, Sánchez-Castro, et al., 2016; Öpik, Metsis, Daniell, Zobel, & Moora, 2009; Varela-Cevero et al., 2015). Furthermore, recent studies have demonstrated that AM symbiosis regulates plant transport systems thus allowing a tight control of nutrient exchange between both symbiotic partners as well as uptake from the soil.

The IRM creates arbuscules, and eventually vesicules, within the host's roots where molecule exchanges between symbiotic partners take place. These arbuscules are formed by hyphae crossing the cell wall of root cells but not their plasma membranes. Thus, nutrients have to move across both the fungal and the plant membranes to reach their final destination. As a result of root cell stimulation by the fungal colonization, the host plant develops a new membrane surrounding the arbuscules, called periarbuscular membrane (Aloui et al., 2018; Bravo, Brands, Wewer, Dörmann, & Harrison, 2017; Gaude, Bortfeld, Duensing, Lohse, & Krajinski, 2012). Some transport proteins are exclusively expressed here, like phosphate transporters *MtPT4* in *Medicago truncatula* and *OsPT11* in rice (Harrison, Dewbre, & Liu, 2002; Javot, Penmetsa, Terzaghi, Cook, & Harrison, 2007; Kobae & Hata, 2010).

3.1 Plant Phosphate Transporters Are Key Elements for Symbiotic Functioning

As mentioned above, acquiring nutrients allocated by the AM fungus requires specific expression and regulation of dozens of transporters in cortical cells containing an arbuscule (reviewed in Garcia et al., 2016). To date, most researches have focused on inorganic phosphate (Pi) and nitrogen (N; cf. Section 3.2.1) since these two elements play a key role in AM symbiosis due to their dual trophic and signalling roles. Several studies reported that root Pi transporters are upregulated upon AM colonization. For example, a specific upregulation of *MtPT4*, *OsPT11*, *StPt3*, *LePt1* and *ZmPt9*, all these genes coding for Pi transporters, was observed in *M. truncatula*, rice, potato, tomato and maize roots, respectively, after colonization by AM fungi (Harrison et al., 2002; Kobae & Hata, 2010; Liu et al., 2018; Rausch et al., 2001; Rosewarne, Barker, Smith, Smith, & Schachtman, 1999). Plant Pi transporters belong to the Pht1, Pht2 and Pht3 families and drive the transport of negatively charged orthophosphates (Pi) using an energy-driven mechanism (Rausch & Bucher, 2002; Smith, Mudge, Rae, & Glassop, 2003). Krajinski et al. (2014) revealed that the energy required for uptake of fungal Pi in *M. truncatula* is provided by an

H^+-ATPase. Although Na^+/Pi transporters are also suspected to be involved in Pi transport during ECM symbiosis (Casieri et al., 2013; Garcia et al., 2016), only low- and high-affinity H^+/Pi symporters clustered in two subgroups of the plant Pht1 family have been described so far during AM associations (Harrison et al., 2002; Liu et al., 2018; Yang et al., 2012). While AM-specific Pi transporters are upregulated, expression is reduced for many other transporters, particularly those that are involved in AM-independent Pi acquisition. However, the causal link between those two observations is not yet elucidated. Indeed, downregulations could simply be due to a general repression of genes upon colonization, regardless of Pi availability in soil and regulation of AM-specific Pi transporters. Although the involvement of plant transporters in Pi acquisition during AM symbiosis has been clearly established over the last decades, post-transcriptional and post-translational regulations of these transport proteins are still largely unknown and need further investigation.

A key role of Pi during mycorrhizal associations has emerged more recently, due to its dual trophic and signalling role (Carbonnel & Gutjahr, 2014; Garcia et al., 2015). Indeed, premature degeneration of arbuscules was observed in loss-of-function *mtpt4* mutants (Javot et al., 2007), indicating that the absence of Pi fluxes originating from the fungus affects the proper formation and functioning of AM symbiosis. In addition, the expression of *LjPT4* observed in root tips of *Lotus japonicus* without any fungal colonization revealed that transporters suspected to be AM-specific can also be a key part of the root Pi-sensing machinery (Volpe, Giovannetti, Sun, Fiorilli, & Bonfante, 2015).

3.2 Root Mineral Nutrient Transport Adapts to Mycorrhizal Interaction

3.2.1 Nitrogen Acquisition by the Plant in Arbuscular Mycorrhizae

Nitrogen is transported from the soil to colonized roots in organic and inorganic forms (Courty et al., 2017; Courty, Smith, Koegel, Redecker, & Wipf, 2015). Govindarajulu et al. (2005) developed a model for N assimilation that seems to be confirmed by recent research (Bücking & Kafle, 2015; Gomez et al., 2009). AM fungi absorb N mainly as ammonium, although they can also use nitrate and organic compounds. According to this model, N is incorporated into the arginine metabolic pathway and broken down in the urea cycle of the fungus to release ammonium into the periarbuscular space, where it is absorbed by the plant.

Plant AM-specific transporters involved in N uptake from fungal arbuscules have been described in several host plants. Ammonium

transporters of the AMT family were detected on the branch domain of periarbuscular membranes, but not on the trunk region where nutrient release is probably less active (Kobae, Tamura, Takai, Banba, & Hata, 2010; Koegel et al., 2013). In addition, transcriptomic studies have demonstrated an induction of *AMT* genes in arbuscular mycorrhizal roots of several plant species (Courty et al., 2017). However, studies characterizing these genes are rather scarce. The *L. japonicus AMT2;2* is strongly upregulated in mycorrhizal roots, particularly in arbusculated cells (Guether, Balestrini, et al., 2009). The transporter encoded by this gene is able to take up ammonium in the periarbuscular space, deprotonates it and transfers ammonia inside the cell (Guether, Neuhäuser, et al., 2009). Thus, the activity of *Lj*AMT2;2 helps to reduce the energetic cost of the transport and to maintain the proton gradient necessary for other transport processes. Similar gene expression patterns and transport activity have been identified for its soybean orthologue *Gm*AMT4;1 (Kobae et al., 2010). The induction of a rice gene (Koegel et al., 2017), that is phylogenetically close to *Lj*AMT2;2, underlines a conserved mechanism between monocots and dicots. However, the loss-of-function of this gene had no effect on mycorrhizal rice indicating a minor role in symbiosis.

Specific studies in grasses have highlighted the importance of mycorrhiza-induced *AMT* genes in sorghum (*Sorghum bicolor*; *SbAMT3;1* and *SbAMT4*), and other grasses (Koegel et al., 2013; Pérez-Tienda, Corrêa, Azcón-Aguilar, & Ferrol, 2014). The two *sorghum* transporters were specifically expressed in cells containing arbuscules or being adjacent to arbuscule-containing cells. In addition, the *Sb*AMT3;1 protein was observed in arbuscule-developing cells. In addition, a broader analysis investigated these two mycorrhiza-induced genes, AMT3;1 and AMT4, in five species of the *Poaceae* family; *sorghum*, rice, brome grass (*Brachypodium distachyon*), maize (*Zea mays*) and millet (*Setaria italica*) (Koegel et al., 2017). These transporters, whose activity was measured by yeast complementation, were found to be upregulated in all species analysed, suggesting that they have evolved from a common ancestor of current grasses. Furthermore, the overexpression of *AMT3;1* orthologues in mycorrhizal roots of dicots (*GmAMT3;1* in soybean; Kobae et al., 2010) indicated the conservation of this symbiosis-induced gene in both monocot and dicot clades. In rice, *OsAMT3;1* knock-down mutants had an impaired N and P nutrition and plant growth was not stimulated by mycorrhizal fungi (Koegel et al., 2017). In contrast, this gene does not seem to be essential for symbiosis establishment or arbuscule development.

It has been hypothesized that some AMT transporters could have a signalling role, rather than a transport activity *per se*. For instance, *Mt*AMT2;3 does not complement yeasts deficient for ammonium transport but is required to prevent premature arbuscule degeneration (Breuillin-Sessoms et al., 2015). In addition to the AMT transporters, other transporter families could be involved in ammonium/ammonia transport in arbuscular mycorrhizal symbiosis. This is the case for the NIP1 (Nod 26-like intrinsic protein) aquaporin of *M. truncatula*. This channel protein is specifically expressed in arbusculated cells where it allows the entry of ammonia molecules into the cell (Hogekamp et al., 2011; Uehlein et al., 2007).

Nitrate and organic compounds are other forms of N that might be transferred but that are believed to be less significant for AM symbiosis. It is unlikely that nitrate plays a major role in plant N nutrition in this context, because of the energetic cost required for its subsequent reduction to ammonium. Although some plant NRT transporters exhibit a symbiotic regulation (Drechsler, Courty, Brulé, & Kunze, 2018; Guether, Balestrini, et al., 2009; Hildebrandt, Schmelzer, & Bothe, 2002) and a specific expression in mycorrhizal structures, it seems that they are also modulated by N and P concentrations (Chen et al., 2018; Hohnjec, Vieweg, Pühler, Becker, & Küster, 2005). This indicates a more complex regulation mechanism and suggests that plant and fungal nutritional status may affect the symbiotic assimilation of nitrate. However, plant nitrate assimilation in arbuscular mycorrhizae should not be dismissed until more thorough studies are conducted.

Among the three families of putative nitrate transporters, NPF (NRT1/PTR) members are also able to transport various N-containing compounds, including oligopeptides (Corratgé-Faillie & Lacombe, 2017; Léran et al., 2014). AM roots and arbusculated cells show specific upregulation of genes coding for di- and tripeptide transporters (PTR; Garcia et al., 2016). Transcriptomic analyses of mycorrhizal *L. japonicus* roots have identified nine putative NPF (PTR) transporters upregulated by interaction with fungi, of which the most upregulated one is exclusively expressed in arbusculated cells at the transcript level (Guether, Balestrini, et al., 2009). Likewise, several NPF (PTR) candidates of *M. truncatula* respond positively to fungal colonization, and at least one is specific of arbuscule-containing cells according to Gomez et al. (2009) and Benedito et al. (2010). Moreover, Hogekamp et al. (2011) found 11 members of this family that could also be related to plant N nutrition in arbuscular mycorrhizae, two of which were present in arbusculated cells.

In conclusion, most knowledge on N compounds in AM symbiosis is about the transcriptional regulation of genes in colonized roots and symbiotic structures. The lack of information on the functional role of these membrane transporters hampers the development of a complete model for N nutrition in this particular symbiosis. The model proposed by Govindarajulu et al. (2005) and mentioned above was recently reviewed and refined by Bücking and Kafle (2015) and Chen et al. (2018). This model provides hints regarding the path that should be followed to elucidate the complete role of AM fungi in plant N nutrition.

3.2.2 Potassium Transport in Arbuscular Mycorrhizae

K nutrition under mycorrhizal symbioses has received little attention so far, but there are increasing evidence illustrating its importance for plant performance (Garcia & Zimmermann, 2014). Recent research highlighted the need for specific nutritional conditions, such as nutrient deprivation or environmental stress, to amplify the benefit gain by the host plant from the AM fungi (Garcia, Chasman, Roy, & Ane, 2017; Zhang, Wei, Hu, Xiao, & Tang, 2017). For instance, *M. truncatula* plants colonized with *Rhizophagus irregularis* accumulated more biomass than control plants when exposed to K deprivation (Garcia et al., 2017). A transcriptomic analysis uncovered one upregulated putative K^+/H^+ exchanger (CHX) that could be responsible for this increased K absorption, as well as a protein phosphatase that is likely regulating the function of K channels. In *Lycium barbarum*, Zhang, Wei, et al. (2017) identified two Shaker-like channels, *LbKT1* and *LbSKOR*, whose expression is induced in *R. irregularis* mycorrhizal roots. *Lb*KT1 is an orthologue of the AKT1 transporter involved in K uptake in roots (Nieves-Cordones et al., 2014), whereas *Lb*SKOR is closely related to SKOR (Ahmad & Maathuis, 2014; Gaymard et al., 1998), known to be responsible for the translocation of K to the xylem sap in *A. thaliana*. An unknown K transporter was also found to be strongly upregulated in *L. japonicus*-*Gigaspora margarita* mycorrhizae (Guether, Balestrini, et al., 2009). In conclusion, proteins responsible for K uptake from the periarbuscular space have not been characterized yet, but promising candidates are to explore.

3.2.3 Transport of Metal Nutrients

The transport of other nutrients, such as metals, has been given less attention due to the importance of P and N transport in arbuscular mycorrhizae, and remains largely unexplored. Some researchers have identified putative

symbiosis-related genes possibly involved in metal transport, but so far none of these transport proteins has been studied in the context of symbiosis. A thorough summary on the knowledge accumulated on putative metal transporters has been published recently by Ferrol, Tamayo, and Vargas (2016). See also chapter "Metal transport in the developing plant seed" by Eroglu, in this volume.

3.3 Water Transport Is Regulated by Symbiotic Partners

As previously reported for ECM fungi, the symbiotic association between plants and AM fungi regulates the uptake of water both under control conditions and in the presence of different soil stresses. Overall, AM symbioses modify the root hydraulic conductivity of their host plants (Bárzana, Aroca, Bienert, Chaumont, & Ruíz-Lozano, 2014; Calvo-Polanco, Molina, Zamarreno, Garcia-Mina, & Aroca, 2014; Calvo-Polanco, Sánchez-Castro, et al., 2016; Calvo-Polanco, Sánchez-Romera, et al., 2016; Quiroga et al., 2018; Sánchez-Romera et al., 2018; Sánchez-Romera, Ruíz-Lozano, Zamarreño, García-Mina, & Aroca, 2016) and result in altered rates of water transfer in-and-out of the host plants (Augé, 2001).

In particular, AM fungi have been shown to increase plant resistance to several soil stresses such as drought (Azcón, Gomez, & Tobar, 1996; Bárzana et al., 2012; Calvo-Polanco, Sánchez-Romera, et al., 2016; Porcel, Azcón, & Ruíz-Lozano, 2004; Quiroga et al., 2018; Sheng et al., 2008), salt (Ruíz-Lozano et al., 2012; Saxena, Shukla, & Giri, 2017) or flooding (Calvo-Polanco et al., 2014). Thus, increase in tolerance to these conditions causes improvement of plant productivity (Abbaspour, Saeidi-Sar, Afshari, & Abdel-Wahhab, 2012; Navarro-Fernández, Aroca, & Barea, 2011) and plant nutrient status (Farzaneh, Vierheilig, Lössl, & Kaul, 2011; Lee, Muneer, Avice, Jin, & Kim, 2012). This effect has been largely attributed to the action of AM fungi on water transport and particularly on aquaporins. Indeed, the presence of AM fungi triggers specific changes in aquaporin gene expression and protein abundance in many host plants (Aroca, Porcel, & Ruíz-Lozano, 2007; Bárzana et al., 2014; Calvo-Polanco et al., 2014; Calvo-Polanco, Sánchez-Castro, et al., 2016; Calvo-Polanco, Sánchez-Romera, et al., 2016; Chitarra et al., 2016; Jahromi, Aroca, Porcel, & Ruíz-Lozano, 2008; Sánchez-Romera et al., 2016, 2018). Moreover, the effects of AM fungi on plant aquaporins are specific to the environmental conditions plants are exposed to (El-Mesbahi, Azcon, Ruíz-Lozano, & Aroca, 2012). Hence, aquaporins belonging to the same subgroup

may exhibit distinct expression patterns when exposed to similar circumstances (Aroca et al., 2007) or may be similarly regulated under various stress conditions (Bárzana et al., 2014; Guo et al., 2006). The high propensity of aquaporins to adapt their expression and function according to the environmental context is likely accounting for differences in described results. In fact, discrepancies are commonly observed in studies where aquaporins are differentially expressed during AM even when the same combinations of plant and AM fungal species are being used (Aroca et al., 2007; Sánchez-Romera et al., 2016).

Furthermore, posttranslational regulations of aquaporins, such as phosphorylation of specific serine residues, are necessary to adjust their activity in response to fast environmental changes (Vandeleur et al., 2014). These regulations trigger conformational changes that act on the gating of aquaporins (Johansson et al., 1998) or determine their subcellular localization and membrane targeting (Prak et al., 2008). The presence of AM fungi within roots seems to be critical for these phosphorylation events under different stresses (Calvo-Polanco, Sánchez-Romera, et al., 2016; Quiroga et al., 2018; Sánchez-Romera et al., 2018), and are believed to be a key factor during plant adaptation to stress. Conversely, de-phosphorylation of aquaporins in the presence of AM is believed to prevent water loss, giving a main role to the apoplastic pathway for water transport (Bárzana et al., 2012).

AM fungal aquaporins have been related to water transport in the extraradical mycelium, and in the periarbuscular membrane (Li et al., 2013). Thus, in AM plants, the enhanced root hydraulic conductivity could be due to the activity of the associated fungal aquaporins (Bárzana et al., 2014; Bárzana, Aroca, & Ruiz-Lozano, 2015).

It has also been suggested that water could be absorbed by the external AM mycelium and delivered to the cortical apoplast, at the symbiotic interfaces, where it would join water taken up via the root apoplastic pathway (Bárzana et al., 2012; Smith, Facelli, Pope, & Smith, 2010). Hyphal water uptake and transfer to the host plants have been demonstrated in several studies (Khalvati, Hu, Mozafar, & Schmidhalter, 2005; Marulanda, Azcón, & Ruíz-Lozano, 2003; Ruth, Khalvati, & Schmidhalter, 2011). Increased water uptake by mycorrhizal plants under drought has been related to the increased absorbing surface of growing hyphae, and mycorrhizal ability to take up water from soil pores inaccessible to roots, as AM hyphae represent a low-resistance pathway for water movement until root cells (Allen, 2009; Ruíz-Lozano, 2003).

3.4 Sugars and Lipids Are Delivered to the Fungal Partner

As discussed above, plant mineral and water nutrition by AM symbiosis is part of a kind of "fair trade" between fungi and plants including a "reciprocal reward" delivered by the host plant towards its mutualistic partner in form of carbon substrates (Fellbaum et al., 2012, 2014; Hammer, Pallon, Wallander, & Olsson, 2011; Kiers et al., 2011). In contrast to ECM fungi, AM fungi are dependent on their plant hosts and cannot be cultivated alone. It is well established that plants transfer a part of their photosynthetically produced sugars to their associated fungi. Very recently, lipids have been added to the range of substrates delivered by the plant to the fungi. In fact, the two symbiotic partners have to produce so many membranes at their root cell interface that it is not astonishing that the costs are shared between the two partners. Here, we highlight transport processes involved in fungal feeding by AM plants. Recently, Aloui et al. (2018) demonstrated that 82 plasma membrane-associated proteins are responsive to mycorrhization, and some of these are sugar transporters or proteins putatively involved in lipid biosynthesis.

3.4.1 Plant Carbohydrates Are Feeding AM Fungi

During arbuscular mycorrhization, the development of the mycelium by fungi and the development of the periarbuscular membrane by plants are costly processes requiring energy in the form of carbohydrates (Bago et al., 2003, 2002; Gaude, Schulze, Franken, & Krajinski, 2012). AM fungi are obligate biotrophs that completely rely on carbon supply by their host to grow and develop (Luginbuehl et al., 2017; Rich, Nouri, Courty, & Reinhardt, 2017; Smith & Read, 2008). Sugar transfer from plant roots to fungi has been demonstrated using ^{14}C tracer studies (Řezáčová, Konvalinková, & Jansa, 2017). In fact, during AM symbiosis, up to 20% of plant photosynthates are transferred to the fungus (Bago, Pfeffer, & Shachar-Hill, 2000), preferentially in the form of hexoses, the main substrate being glucose (Pfeffer, Douds, Bécard, & Shachar-Hill, 1999; Shachar-Hill et al., 1995). This glucose is probably released by the plant through the periarbuscular membrane where it becomes available to the fungal partner (Rich et al., 2017). Fungal transporters involved in sugar transfer from the plant towards the AM fungi have been reviewed recently (Courty et al., 2017; Garcia et al., 2016). The sugar fluxes are mediated by several transport systems described in plants, comprising sucrose transporters (SUTs), monosaccharide transporters (MSTs), and SWEETs

(Doidy, Grace, et al., 2012). The monosaccharide transporter MST2 of *Glomus* sp. is a fungal hexose transporter known to be an important actor of sugar absorption, arbuscule development and root colonization (Bago et al., 2000; Helber et al., 2011; Pfeffer et al., 1999; Rich et al., 2017). Thus, glucose is certainly released by the plant through the periarbuscular membrane to the fungus including the cleavage of plant sucrose (Rich et al., 2017). Correspondingly, several studies have focused on the analysis of plant MST expression to possibly pinpoint differentially regulated candidates in tomato and *M. truncatula* (Ge, Sun, Chen, Kapulnik, & Xu, 2008; Harrison, 1996). Differential regulation of such MSTs (MtSt1 and MtHext1) was also found in non-colonized cells and neighbouring arbuscular cells, suggesting that non-colonized adjacent cells might feed the arbuscular cells with carbon through plasmodesmata (Gaude, Bortfeld, et al., 2012).

Due to the intense transit of sugars from the plant to the fungus, mycorrhizal roots represent particularly strong carbon sinks (Gaude, Schulze, et al., 2012; Rich et al., 2017). Implication of transporters of the SUT and SWEET families in symbiotic carbon transfer has been shown for *M. truncatula* (Kafle et al., 2018). Expression of all SUT types is regulated in leaves and in colonized roots of tomato and *M. truncatula* when inoculated with AM fungi (Boldt et al., 2011; Doidy, van Tuinen, et al., 2012).

SWEET transporters, characterized as exporters of both sucrose and monosaccharides using nanosensors (Chen, 2014), were found to be specifically expressed in arbusculated cortical cells of potato roots (Manck-Götzenberger & Requena, 2016), and differently regulated in *M. truncatula* roots in tripartite interaction with the AM fungus *R. irregularis* and the N-fixing bacteria *E. meliloti* (Kafle et al., 2018). The fact that mycorrhizae represent such an important carbon sink implies that a number of plant sugar transport systems are likely to be involved in sugar translocation and transport throughout the plant body, to support the delivery function of root sugar transporters.

3.4.2 Plant Lipids Are Needed to Establish and Maintain AM Symbiosis

Other important forms for carbon transport and storage in AM fungi are lipids, in the form of triacylglycerols (Bago et al., 2003, 2002; Beilby & Kidby, 1980; Jabaji-hare, 1988; Trépanier et al., 2005). AM fungi can use hexoses to synthetize lipids by their own. This *de novo* biosynthesis of fungal fatty acids (FAs) takes place only at the IRM and not in ERM or spores (Bago et al., 1999; Pfeffer et al., 1999; Trépanier et al., 2005). Nevertheless, AM fungi are not able to complete all the lipid biosynthesis by themselves.

Indeed, recent studies showed that the type I fatty acid synthase (FAS-I), an enzyme with a key role in the initiation of *de novo* synthesis of most FAs, is absent in some AM fungi such as *R. irregularis* or *Gigaspora rosea* indicating that enzymes originating from the plant partner are required to overcome this lack (Tang et al., 2016; Wewer, Brands, & Dörmann, 2014). However, subsequent steps of the FAs synthesis *per se* (e.g. FAs elongation, desaturation) can be done by fungi alone (Trépanier et al., 2005). Interestingly, many genes involved in lipid biosynthesis in the host plant are activated and/or upregulated, especially in arbuscocytes, arbuscule-containing plant cells (Gaude, Bortfeld, et al., 2012; Gaude, Schulze, et al., 2012; Gomez et al., 2009; Hogekamp & Küster, 2013; Tang et al., 2016; Tisserant et al., 2012).

Recent studies have revealed several genes being putatively related to lipid metabolism and transport in AM fungi-colonized plants (Bravo et al., 2017; Keymer et al., 2017; Luginbuehl et al., 2017; Rich et al., 2017). These genes, involved in both lipid metabolism and transport, are FatM (fatty acid synthase), RAM1 (Required for Arbuscular Mycorrhization 1), RAM2, STR1 (Stunted Arbuscule) and STR2.

Regarding lipid metabolism, the FAs biosynthesis takes place in the plastids of plant cells (Bravo et al., 2017; Keymer et al., 2017). Involvement of a Fat gene in AM symbiosis could be established for *FatM* in *M. truncatula*, by showing that *fatm* mutants are affected in the development of arbuscules within the root cells (Bravo, York, Pumplin, Mueller, & Harrison, 2016). The *RAM2* gene encodes a GPAT enzyme (glycerol 3-phosphate acyl transferase) and is close to *A. thaliana GPAT6* (Keymer et al., 2017). As GPAT6, RAM2 is likely to produce *sn*-2-monoacylglycerol (MAG) especially of one type, βMAG (Bravo et al., 2017; Keymer et al., 2017; Yang et al., 2010). Furthermore, the *ram2* mutation in *M. truncatula* impairs arbuscule development as the *fatm* mutation (Bravo et al., 2017; Gobbato et al., 2013; Wang et al., 2012).

Finally, initial steps have been taken in elucidating the travel of the plant lipids towards the fungal hyphae. STR1 and STR2 are ABC-type transporters specific of the periarbuscular membrane, that work together and are required for arbuscule formation (Gutjahr et al., 2012; Zhang, Blaylock, & Harrison, 2010). Their role(s) and substrate(s) remain still to be further characterized, but two research teams suggest independently that they may transport lipids, probably βMAG, from plants to fungi (Bravo et al., 2017; Keymer et al., 2017). For further information on ABC transporters, see also chapter "The ABC of ABC transporters" by Pierman, Boutry, and Lefèvre in this volume.

Moreover, RAM1 is a GRAS-domain transcription factor that can regulate many genes involved in lipid biosynthesis and transport such as FatM, RAM2 and ABC transporters (Luginbuehl et al., 2017). RAM1 was shown to be crucial for arbuscule development (Gobbato et al., 2012; Park, Floss, Levesque-Tremblay, Bravo, & Harrison, 2015).

Taken together, all of these studies indicate that plant RAM1, FatM, RAM2, STR1 and STR2 genes can form a functional unit/operational module that is regulated in AM associations and serves for lipid biosynthesis and transport particularly in arbuscocytes (Bravo et al., 2017; Keymer et al., 2017; Luginbuehl et al., 2017; Rich et al., 2017). Once more, the role of plant transporters in the functioning of the symbiotic interaction is underlined by the involvement of ABC-type transporters.

3.5 Membrane Transport Is Needed for Early Signalling to Establish Symbiosis

Besides their trophic role as described above, plant transporters can regulate the AM symbiosis by sensing nutrient availability and therefore affecting the lifespan of the symbiotic structures (Breuillin-Sessoms et al., 2015; Javot et al., 2007). Although not well described, these mechanisms are thought to play a key role in the functioning of the mutualistic association (Lanfranco, Fiorilli, & Gutjahr, 2018). Indeed, specific plant transporters appear to be crucial during the steps preceding the formation of fungal arbuscules, and even before the root colonization by hyphae. Thus, a molecular dialogue engaging the fungus and host roots must occur before any physical contact. Plant roots excrete the plant hormone strigolactone that is perceived by fungal spores, triggering their germination followed by hyphal branching (Akiyama, Matsuzaki, & Hayashi, 2005; Besserer et al., 2006). On the other side, AM fungi release a mixture of signaling molecules, including lipochitooligosaccharides and short chitooligosaccharides (Genre et al., 2013; Maillet et al., 2011), that are perceived by host plant LysM-receptor-like kinases. The signal is then transduced through various proteins, including membrane transport systems, resulting in the expression of AM-specific transcription factors (recently reviewed in Charpentier, 2018). All currently known transport proteins needed for this signalling cascade are localized on the nuclear envelope, at either or both the inner and outer nuclear membranes. Finely coordinated movements of potassium and calcium ions through the nuclear envelope are required to decode signals coming from the perception of fungal molecules. In response to unknown secondary messenger(s), calcium is released into the nucleus through calcium

channels recently described in *M. truncatula* and belonging to the CNGC family (CNGC15; Charpentier et al., 2016). In order to balance transmembrane charges due to calcium transport, the DMI1 channel (DOES NOT MAKE INFECTION 1) participates in potassium movements between the outer and inner nuclear membranes (Ané et al., 2004). A SERCA-type calcium ATPase (MCA8 in *M. truncatula*) also participates in these movements of ions (Capoen et al., 2011). It is worth noting that nucleoporins anchored in the nuclear envelope, through both membranes, were also described in *L. japonicus* to participate in calcium oscillations (Kanamori et al., 2006; Saito et al., 2007). Because all these transport proteins are localized at both inner and outer nuclear membranes, it is still unclear if calcium oscillations occur inside or outside the nucleus, or on both sides (Charpentier, 2018). The resulting calcium oscillations are finally decoded by a calcium and calmodulin-dependent kinase (CCaMK), transducing the signal to specific transcription factors and resulting in fungal colonization.

4. FIRST STEPS IN THE STUDY OF PLANT NUTRITION IN ORCHID MYCORRHIZAE

To date, little research has been done on the molecular players responsible for nutritional exchanges in orchid mycorrhizal symbiosis (Dearnaley, Perrotto, & Selosse, 2017), although C, N and P transfers have long been known in this context (e.g. Cameron, Johnson, Leake, & Read, 2007; Cameron, Leake, & Read, 2006). Recent advances in "omics" techniques have helped unravel key genes putatively involved in N transport in orchid mycorrhizae. Comparisons in gene expression in *Serapias vomeracea* protocorms colonized or not by the cosmopolitan fungus *Tulasnella calospora* have revealed interesting facts about N dynamics in the first stages of orchid development (Fochi et al., 2016).

Because it lacks nitrate transporters, it is very likely that the fungus *T. calospora* absorbs N as ammonium and/or amino acids, as suggested by the transcriptomic analysis. In the symbiotic interface, the fungus would release amino acids as a source of N for the orchid plant (*S. vomeracea*), at least in the first stages of plant development, as suggested by comparative transcriptomic analysis in which the arginine-urea pathways are not modulated. In line with such a model, two plant amino acid permeases (*Sv*AAP1 and *Sv*AAP2) and a lysine histidine transporter 1 (*Sv*LHT1) that are strongly upregulated by symbiosis are probably responsible for plant N nutrition

originated from the symbiotic fungus (Fochi, Falla, Girlanda, Perotto, & Balestrini, 2017; Fochi et al., 2016).

In general, it is believed that ammonium does not play an important role in the nutrition of *S. vomeracea*, because its ammonium transporters (*Sv*AMT1 and *Sv*AMT2) have low expression levels and only one of them, *Sv*AMT1, is slightly upregulated in symbiosis. In addition, the fungal AMT transporters (*Tc*AMT1 and *Tc*AMT2) are also expressed in the interacting organs, competing for this N resource with the plant. In a model proposed by Dearnaley and Cameron (2017), the first stages of orchid development are characterized by a loop in N transport, the fungus providing the plant with amino acids and the plant releasing NH_4^+ in return in the symbiotic interface. Apart from the already mentioned transport systems, members of the OligoPeptide Transporters (*Sv*OPT1 and *Sv*OPT2) and Peptide Transport (*Sv*PTR1 and *Sv*PTR2) families could be involved in the recovery of larger N-containing molecules by the plant (Fochi et al., 2017). In addition, it has also been proposed that intracellular fungal hyphae forming coils that increase the interface between fungus and orchid root cells, called pelotons, degrade, thus releasing nutrients in the root cell.

Finally, orchids have typically a mycoheterotrophic phase after germination in which they require a mycorrhizal fungus to obtain C, thanks to a symbiotic partner with a simultaneous saprotrophic or ECM lifestyle (Jacquemyn et al., 2017; Selosse, Bocayuva, Kasuya, & Courty, 2017). In this situation, the supply of amino acids from the fungus to the plant would also be a source of C towards the growing orchid.

In conclusion, although we have many clues on element fluxes in orchid mycorrhizae thanks to physiological studies, many aspects regarding nutritional exchanges and their molecular mechanisms are still ignored. The discovery of these systems will be necessary to understand this fascinating symbiosis essential for the life cycle of the largest plant family on Earth.

5. CONCLUDING REMARKS AND PERSPECTIVES

To sum up, the contribution of mycorrhizal fungi to plant nutrition and water transport becomes possible in part by the adaptation and plasticity of both fungal (reviewed recently, Garcia et al., 2016) and plant transportomes (Fig. 2). Beneficial effects of mycorrhizal fungi have been described at plant physiological level since long time. Mineral and water uptake by the fungus, delivery towards and absorption by colonized root cells, and release of plant carbohydrates and lipids to the fungus require a

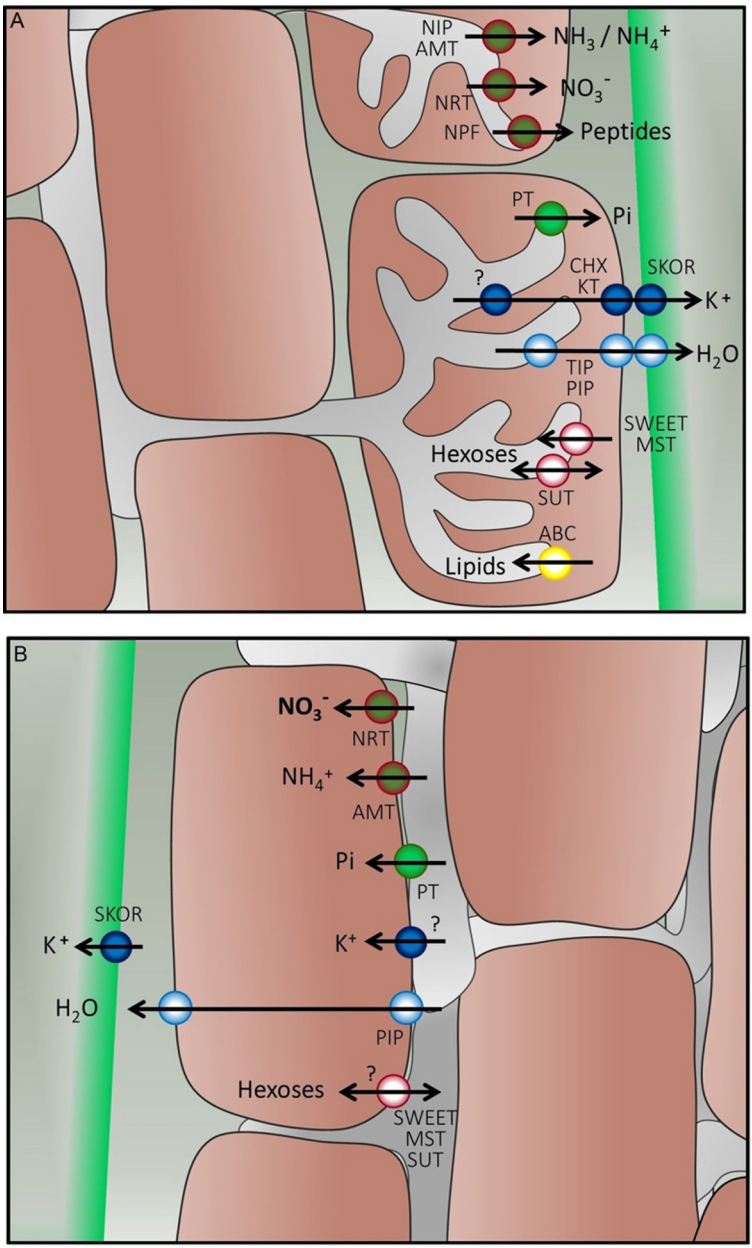

Fig. 2 Plant transporters are involved in nutritional exchanges between symbiotic fungi and root cells in arbuscular mycorrhizae (A) and ectomycorrhizae (B). A close-up from Fig. 1 shows plant transport systems that might be directly regulated and involved in nutrient exchange with mycorrhizal fungi. In addition, membrane transport is also

(Continued)

tight coordination of membrane transporters from early communication to actual resource exchanges. Molecular knowledge of all steps contributing to such an elaborate mutualistic association is increasing thanks to the number of available genomes and accumulation of transcriptomic studies. Insights into transcriptional regulation of the different transport systems involved need to be supported by functional validations to unravel the *in situ* roles of such identified candidates. Moreover, molecular mechanisms behind the polarized expression patterns and/or specific localization of symbiotic transport systems, which overall control directional transport, have still to be dissected. In particular, membrane microdomains might be responsible for a tight regulation of secretion and uptake at the interface between symbiotic fungi and host plants. Very local conditions with respect to e.g. pH or calcium could also make the difference with respect to transport directions and activities. In addition, activity of proton pumps might be closely linked to that of other transporters (Krajinski et al., 2014; Lanfranco et al., 2018). Many of these questions regarding molecular mechanisms are still awaiting answers. Progress is being made by a computational cell biology approach, which allows simulating the network of proton-coupled transporters and proton pumps in the context of AM symbiosis (Schott et al., 2016).

Fig. 2—Cont'd probably implicated in molecular communication between both symbiotic partners and in signalling. Known transport systems on the fungal side have been reported before and are not indicated here. (A) In arbuscular mycorrhizae, some plant transporters are upregulated and/or specifically expressed and could be involved in the uptake of mineral nutrients and water released by the fungus at the periarbuscular space. Some studies have indicated a role related to the absorption of N compounds in the forms of ammonium (AMT and NIP families), nitrate or peptides (NRT, NPF), phosphate (PT family) and K^+ (CHX and KT families) or its translocation to the xylem (SKOR members). It has also been proposed that arbuscular mycorrhizal fungi enhance water transport through the cell-to-cell pathway, increasing the expression and activation of plant aquaporins (TIPs and PIPs). On the release side, it has been hypothesized that hexoses (through MST, SWEET and SUT transporters) and lipids (through STR proteins) are transported to nourish the fungal partner. (B) In ectomycorrhizae, the host plant may also take up N-containing compounds, mainly ammonium (AMTs) but maybe also nitrate (NRT); phosphate (PT family) and K^+, through transport systems that are still to be elucidated. Possibly due to a higher demand for K^+ translocation to the xylem, as provoked by an enhanced K^+ nutrition, a SKOR channel has been related to the functioning of ectomycorrhizae. It has also been demonstrated that ectomycorrhizal fungi have a stimulating effect on cell-to-cell water transport (induction of PIP aquaporins). The plant is thought to secrete and take up hexoses (MST, SWEET and SUT families) from the apoplasm to feed the fungus and also to control the amount of C allocated to the fungus.

Moreover, the reality of multiple interactions under natural and field conditions is much more complex than the study of a given interaction under more or less determined artificial laboratory conditions. Such studies, taking in account e.g. tripartite interactions or different abiotic stress are coming up, and start to reveal an adapted expression of plant transporters in response to different symbionts (Kafle et al., 2018). Excitingly, it was very recently shown that the AM fungus *R. irregularis* can even feed Pi-solubilizing bacteria (*Rahnella aquatilis*) with the carbon substrate fructose to stimulate phytate mineralization (Zhang, Feng, & Declerck, 2018).

Altogether, the study of these beneficial mycorrhizal associations deserves more attention because of their ecological importance for plant health and biomass production in agriculture and agroforestry. Last, but not least, knowledge on molecular mechanisms governing beneficial associations is urgently needed with respect to plant growth under increasing environmental stress and challenging climate and soil conditions.

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