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REVIEW

Biotrophic transportome in mutualistic plant–fungal interactions

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Abstract Understanding the mechanisms that underlie nutrient use efficiency and carbon allocation along with mycorrhizal interactions is critical for managing croplands and forests soundly. Indeed, nutrient availability, uptake and exchange in biotrophic interactions drive plant growth and modulate biomass allocation. These parameters are crucial for plant yield, a major issue in the context of high biomass production. Transport processes across the polarized membrane interfaces are of major importance in the functioning of the established mycorrhizal association as the symbiotic relationship is based on a 'fair trade' between the fungus and the host plant. Nutrient and/or metabolite uptake and exchanges, at biotrophic interfaces, are controlled by membrane transporters whose regulation patterns are essential for determining the outcome of plant–fungus interactions and adapting to changes in soil nutrient quantity and/or quality. In the present review, we summarize the current state of the art regarding transport systems in the two major forms of mycorrhiza, namely ecto- and arbuscular mycorrhiza.

Keywords Mycorrhiza · Nutrient transport · Transporters

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Abbreviations

AAP	Amino acid permeases
AAT	Amino acid transporters
ABA	Abscisic acid
AM	Arbuscular mycorrhiza
AMT	Ammonium transporter
APC	Amino acid/polyamine/organocation
AQPs	Aquaporins
AQR1	Acids quinidine resistance 1
ATPase	Adenosine triphosphate hydrolase
DP	Direct pathway
ECM	Ectomycorrhizal
ERM	Extraradicular mycelium
EST	Expressed sequence tag
GUS	β-Glucuronidase gene
HAK	H^+ uptake permease
HIGS	Host-induced gene silencing

IRM	Intraradical mycelium
KUP	K^+ uptake permease
LPC	Lyso-phosphatidylcholine
MIP	Major intrinsic protein
MP	Mycorrhizal pathway
MSTs	Monosaccharide transporters
NCBI	National Center for Biotechnology Information
NIP	Nod 26-like intrinsic protein
NiR	Nitrite reductase
NNP	Nitrate/nitrite porter
NO_3^-	Nitrate
NR	Nitrate reductase
NT	Nitrate transporter
OPT	Oligopeptide transporter
P_i	Inorganic phosphate
PIPs	Plasma membrane intrinsic proteins
POT	Proton-coupled oligopeptide transporter
PTR	Peptide transporter
RNAi	RNA interference
SULTRs	Sulphate transporters
SUTs/ SUCs	Sucrose transporters
TCA	Trichloroacetic acid
TIPs	Tonoplast intrinsic proteins
WT	Wild type
YAT	Yeast amino acid transporter

The main resources acquired by plants in natural ecosystems are light and CO_2—through photosynthesis in the leaves—and mineral nutrients and water—through active and passive uptake into the roots. Mycorrhizal symbiosis plays a critical role for plant nutrient use efficiency in natural and cultivated ecosystems that are usually characterized by nutrient limitation, especially with regard to nitrogen and phosphate (Smith and Read 2008). Efficient mycorrhizal interactions depend on the ability of the mycobiont to take nutrients available under an inorganic and/or organic form in the soil and translocate them (as such or their corresponding metabolites) to the host plant. In turn, organic C derived from photosynthesis is transferred from the plant to the fungus, which acts as a sink site (Bago et al. 2003), and translocated to the growing margins of the extraradical mycelium and to developing spores. These exchanges mainly result in improved host plant growth through increased nutrient availability (Smith and Read 2008). There is substantial evidence that rational use of microsymbiont properties could significantly contribute to decreasing fertilizer and pesticide use in agriculture (Gianinazzi et al. 2010). The symbiotic relationship is based on a 'fair trade' between fungus and host plant. As a consequence, transport processes across the polarized membrane interfaces are of major importance in the functioning of the established mycorrhizal association. Mineral nutrients are barely accessible to the host roots, but they are efficiently taken up by the extraradical hyphae that develop through the soil and transported to the exchange interfaces where they leave fungal cells for the host transport systems. This suggests a unique reorientation of the fungal 'nutritional metabolism' at the interface between the symbiotic partners: both plant and fungal cells are locally 'reprogrammed', including with regard to the differentiation and polarization of membrane transport functions, to fulfill the tasks of a massive nutrient transfer between the two partners. In arbuscular mycorrhiza (AM) and ectomycorrhiza (ECM), nutrients have to go through several membrane barriers at the apoplastic interface before being assimilated by the partner's cells (Hahn and Mendgen 2001); proton ATPase activity on the two membranes of the symbiotic interface is a sign of active membrane transport (Gianinazzi-Pearson et al. 1991, 2000; Harrison 2005). Nutrient and/or metabolite uptake and exchanges at biotrophic interfaces are controlled by membrane transporters whose regulation patterns are essential for determining the outcome of plant–fungal interactions and adapting to changes in soil nutrient quantity and/or quality. Despite its importance, the release of nutrients taken up by the extraradical hyphae into the root apoplast occurs through widely unknown mechanisms. The aim of this review was to summarize current knowledge about macro- and micronutrient transport systems in plants in arbuscular and ectomycorrhizal interactions.

Sugar transporters

Mycorrhizal interactions involve a stable cooperation between plant and fungal partners. Besides stimulating host plant metabolism and photosynthetic activity, mycorrhizal fungi provide greater access to nutrients, which are not directly available for host roots (Bago et al. 2000; Selosse et al. 2006). As a reward, the plant redirects between 4 and 25 % of its photosynthates towards mycorrhized roots and exchanges them with the fungal partner (Graham 2000; Högberg and Högberg 2002; Hobbie 2006). For four decades, investigations into plant-to-fungus carbon flows have strongly suggested that sugars were transferred by means of either active or passive efflux mechanisms (Ho and Trappe 1973; Blee and Anderson 1998; Doidy et al. 2012a, b). Isotopic labelling and nuclear magnetic resonance spectroscopy using AM-colonized roots showed hexoses, i.e. glucose and, to a lesser extent, fructose, being taken up by the intraradical mycelium (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Pfeffer et al. 1999). Boldt et al. (2011) monitored sucrose and fructose accumulation in tomato roots colonized by *Funneliformis mosseae* and confirmed previous evidence about invertase activity in the apoplast.

The two partners in mycorrhizal interactions seem able to detect whether the resource supply follows the '*do ut des*' rule characteristic of mutualistic duties. The capability to adjust their own resource allocation according to variations in resource exchanges is thought to increase the stability of plant–fungal mutualistic interactions (Kiers et al. 2011), although the terms of trade between the partners are still under debate. Kiers et al. (2011), choosing fungal partners that interact differently with plants, showed that host plants could discriminate among fungi on the basis of the amounts of nutrients (e.g. inorganic phosphate, P_i) supplied by AM fungi, and they selectively reallocated higher amounts of photosynthates as a reward. Similarly, N uptake by AM fungi, and its transfer to the host plant, is triggered by C availability at the mycorrhizal interface (Fellbaum et al. 2012). Additionally, Walder et al. (2012) reported an unbalanced trade of C and nutrients when plants interact with different fungal partners. Their experiment showed that different plant species sharing a common mycorrhizal network benefited from increased nutrition. But the fungal partners *F. mosseae* and *Rhizophagus irregularis* showed different P and N supply patterns when interacting with plants that provided different amounts of photosynthates (Walder et al. 2012). Nowadays, the site for photosynthates exchange between mycorrhizal symbionts is commonly accepted to be at the arbuscular interface, as demonstrated for phosphate transport (Pumplin and Harrison 2009). Some authors also suggest that intercellular hyphae could also be an important C exchange site (Helber et al. 2011; Smith et al. 2001). Evidence of glucose and xylose uptake by the intra- or extraradical mycelium was reported more than a decade ago (Pfeffer et al. 1999; Bago et al. 2000; Helber et al. 2011). Although a few transport proteins have been identified at the plant–fungus interface (Fig. 1), the mechanisms that underlie sugar transport and partitioning towards the specialized interface membranes still remain largely unknown.

Sucrose partitioning in arbuscular mycorrhiza

In different plant species, the AM interaction generally augments photosynthetic activity to support the increased sink strength. In accordance with these observations, increased transcript amounts of *Medicago truncatula* sucrose synthase (*MtSucS2*) were observed during the interaction with the AM fungus *R. irregularis* (Corbière 2002); moreover, *MtSucS1* was shown to play an important role in arbuscule maturation and maintenance in *M. truncatula* roots mycorrhized by *F. mosseae* (Baier et al. 2010).

When sucrose reaches colonized roots, the phloem is unloaded by means of sucrose transporters via the apoplasmic pathway (Fig. 1), where SUT1-loading proteins (ZmSUT1; Carpaneto et al. 2005) are thought to unload the phloem towards arbusculated cortical cells; besides, sucrose is unloaded via the symplasmic pathway through cell plasmodesmata (Doidy et al. 2012a). In addition, mechanisms of sucrose retrieval towards plant cells via SUT importers can also be assumed. Strikingly, in parallel to the previously described exchanges within host roots, extraradical hyphae have been shown to take up sugars (glucose (Glu) and xylose (Xyl)) in vitro through a proton-coupled mechanism; this opens a new path for the axenic culture of such fungi (Helber et al. 2011).

Higher transcript levels of sucrose transporters (SUTs), as well as accumulation of sucrose and monosaccharides in sink organs, were observed in mycorrhized roots of tomato (*Solanum lycopersicum*) and white clover (*Trifolium repens*) plants, indicating an increased movement of sucrose from photosynthesizing leaves (Wright et al. 1998; Boldt et al. 2011). Interestingly, overexpression of the phloem-loading *SoSUT1* in potato (*Solanum tuberosum*) increased *R. irregularis* colonization compared to WT plants when high-phosphate conditions were applied (Gabriel-Neumann et al. 2011). The absence of an effect on the mycorrhization rates in low-P_i conditions—even when antisense inhibition lines of *SoSUT1* were assessed—and previous evidence showing altered leaf and tuber C partitioning when the gene was overexpressed (Leggewie et al. 2003) suggest a non-direct effect of *SoSUT1* on the AM interaction. Additional evidence of the transcriptional regulation of genes involved in sucrose transport were reported in the AM interaction between tomato plants and *Rectipilus fasciculatus* (Tejeda-Sartorius et al. 2008), and more recently between *M. truncatula* and *R. irregularis* (Doidy et al. 2012b). Contrasting evidence on SUT regulation has also been reported for *LeSUT1* of tomato, which is downregulated in AM roots (Ge et al. 2008). Therefore, much work still has to be done to understand which plant SUTs or regulatory mechanisms play key roles in sucrose partitioning during mycorrhization.

Concerning the fungal partner in AM symbiosis, experiments on C fluxes support the hypothesis that sucrose is not taken up by the mycobiont in AM symbiosis (Solaiman and Saito 1997; Pfeffer et al. 1999; Bago et al. 2000). Nevertheless, a glomeromycotan sucrose transporter (*RiSUC1*) was identified from *R. irregularis* expressed sequence tag (EST) contigs by Helber et al. (2011). A full characterization and localization of this transporter will shed light onto sugar exchanges between arbuscular mycorrhizal partners.

Sucrose partitioning in ectomycorrhiza

Enhancement of host photosynthetic activity, sucrose synthesis and sugar transfer towards roots is also reported in ECM interactions (Nylund and Wallander 1989; Loewe et al. 2000; Corrêa et al. 2011). In particular, the estimated loss of carbon reaches 20–25 % of the total sugars fixed during photosynthesis when plants interact with ECM fungi (Hobbie 2006; Nehls et al. 2010), much higher than the 3–5 % loss measured for non-mycorrhized plants.

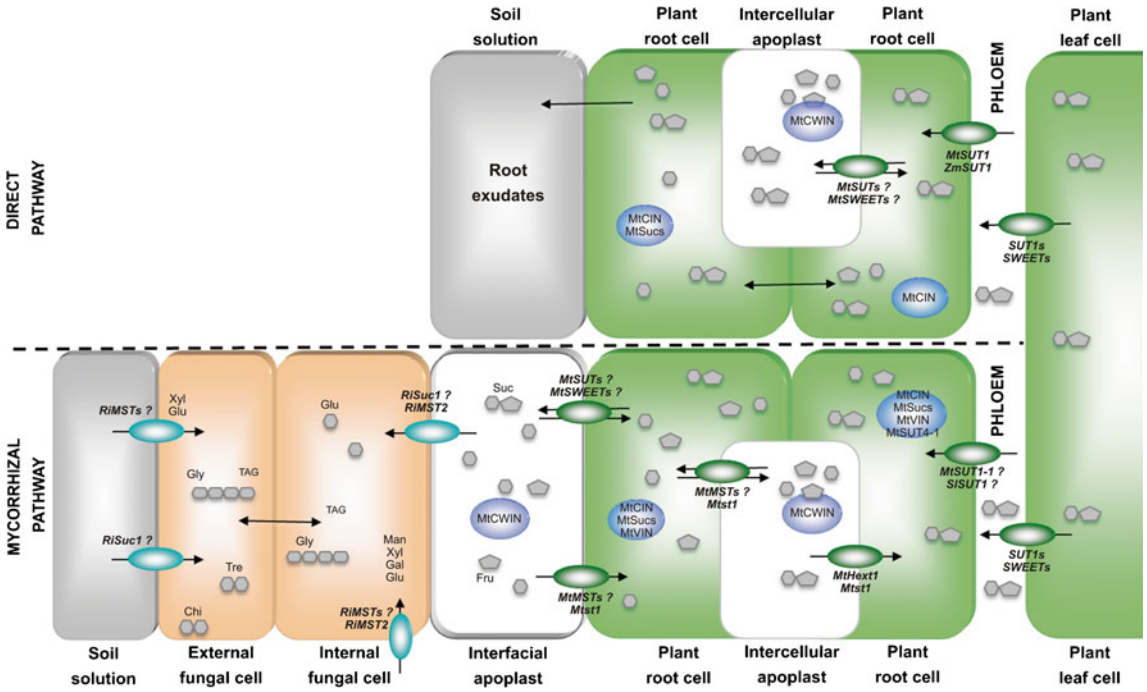

Fig. 1 Current knowledge about sugar fluxes in arbuscular mycorrhizal symbiosis: Different compartments such as the soil solution, external and internal fungal cells, interfacial apoplast, plant root and leaf cells can receive differential C allocation. To simplify the schematic representation, interactions between *M. truncatula* and *R. irregularis* are mainly reported. *Ri Rhizophagus irregularis*, *Mt Medicago truncatula*, *Zm Zea mays*, *MST* monosaccharide transporter, *SUC/SUT* sucrose transporter, *Hext* hexose transporter, *Chi* chitin, *Gal* galactose, *Glu* glucose, *Gly* glycogen, *Man* mannose, *TAG* triacylglycerol, *Tre* trehalose, *Xyl* xylose

Recently, a transcriptomic approach to determine the metabolome of the ECM interaction between quaking aspen (*Populus tremuloides*) and *Laccaria bicolor* (Larsen et al. 2011) showed a general stimulation of the carbohydrate metabolism. In particular, increased expression of the plant genes associated with starch and sucrose metabolism was observed, as well as increased expression of different sugar transporter genes. In the same work, *L. bicolor* carbohydrate metabolism was also enhanced, although no evidence of sucrose transporter genes from ECM fungi is yet available in the currently sequenced genomes (Martin et al. 2008, 2010; Larsen et al. 2011). Earlier works showed that sucrose utilization by the ECM fungi *Amanita muscaria* and *Hebeloma crustuliniforme* depended on their host's cell wall-bound invertases (Salzer and Hager 1991). Similarly, Chen and Hampp (1993) showed that sucrose and mannitol were not taken up by protoplasts of the ECM fungus *A. muscaria.* These results suggest that monosaccharides are the prevalent C form taken up by ECM fungi.

Monosaccharide partitioning in arbuscular mycorrhiza

During AM symbiosis, due to the fact that most AM fungi lack invertase machinery (Hatakeyama and Ohmasa 2004; Daza et al. 2006), it is commonly accepted that sucrose is hydrolyzed evenly into glucose and fructose by plant-derived sucrose-cleaving enzymes (i.e. cell wall invertase CWIN; Schaarschmidt et al. 2006). Although evidence suggests that sucrose cleavage can be done either in the intercellular apoplast or inside the host cell by sucrose synthases and/or invertases (SucS: Hohnjec et al. 2003; Ravnskov et al. 2003; Baier et al. 2010; cytosolic CIN and vacuolar VIN: Schaarschmidt et al. 2006, 2007), the exact site of sucrose cleavage is not yet directly identified (Fig. 1). Although the upregulation of AM-affected sucrose-cleaving enzymes has been evidenced in different plants (Blee and Anderson 2002; Hohnjec et al. 2003; Ravnskov et al. 2003; Schubert et al. 2004; Schaarschmidt et al. 2006; Garcia-Rodriguez et al. 2007; Tejeda-Sartorius et al. 2008), few works have addressed transcript accumulation or the promoter activity of these genes during AM symbiosis (Tejeda-Sartorius et al. 2008).

Wright et al. (1998) observed increased photosynthetic and invertase activity in white clover, coupled with sugar accumulation in sink organs, indicating a mycorrhizal-driven increased sink and C allocation for root and mycobiont development. Similarly, Schaarschmidt et al. (2007) observed an altogether enhanced metabolism in mycorrhized tomato, but the increased invertase activity and hexose levels in the roots did not affect *R. irregularis* colonization; therefore, C supply through sucrose breakdown may not be the limiting factor for a functional interaction.

Following hydrolysis, monosaccharides can be taken up by the host plant or the mycorrhizal fungus. Plant

monosaccharide transporters (MSTs) are a vast group of transporters whose phylogenetic classification and clade nomenclature remain ambiguous (for a comprehensive review, see Doidy et al. 2012a). Although the roles of MSTs in hexose partitioning have been extensively studied, reports on AM-specific or induced/regulated MSTs are still scarce.

Mtst1 of *M. truncatula* encodes a transport protein with high affinity for glucose and fructose. It is regulated in response to colonization by *Diversispora epigaea* (Harrison 1996). Increased transcript levels were observed in *M. truncatula* and *Medicago sativa* following mycorrhizal colonization, but not in *myc* mutants of the two plants, suggesting that *Mtst1* upregulation is potentially linked with a functioning symbiosis. Greater differences in cell type-specific expression, particularly in arbusculated and adjacent cortical cells, suggest that *Mtst1* is involved in sugar supply to the AM interaction (Fig. 1; Harrison 1996). Moreover, the recently identified family of sucrose and monosaccharide uniporters defined as 'SWEET transporters' seems to play a role in mediating sugar efflux from plant cells in plant–microbe interactions (Baker et al. 2012; Chen et al. 2012; Fig. 1), so a role in mycorrhizal associations can be speculated.

The complex expression pattern of monosaccharide transporters in tomato was recently assessed by Ge et al. (2008): the hexose transporter *LeHT2* was downregulated in tomato roots colonized by the AM fungi *Glomus caledonium* or *R. irregularis*, whilst different responses of the putative MST *LeST3* were observed when plants were mycorrhized by different fungi (Garcia-Rodríguez et al. 2005; Ge et al. 2008). Interestingly, when plants were cultivated at high P_i (0.5 mM) levels, reduced transcript accumulation of *LeHT2* and *LeST3* was observed in the roots, whilst increased transcripts of *LeHT2* were measured in the leaves (Ge et al. 2008). Other results highlight the effect of human selection on crop plants; indeed, the maize transporter *ZmMST1* was found upregulated at sub-micromolar P concentrations in an African cultivar adapted to low nutrient, but not in the European cultivar usually grown in high-input agricultural systems (Wright et al. 2005b). MSTs were also found differentially regulated in the non-arbusculated cortical cells of colonized roots. Indeed, plasma membrane glucose transporters from the STP clade (MtHext1 and Mtst1) were activated in non-colonized cells neighbouring arbusculated cells (Gaude et al. 2012). The activation of the monosaccharide import pathway, coupled with the reallocation of sugars stored in vacuoles, may result in cytosolic sugar enrichment in non-arbusculated cells and, thus, indirectly feed arbusculated cells through symplasmic pathways (Fig. 1).

Interestingly, the monosaccharide transporter CAD31121, isolated in the detergent-resistant membrane fraction of *M. truncatula* roots, was downregulated upon mycorrhization (Lefebvre et al. 2007). Raft-associated proteins, and along with them the membrane dynamics, could therefore play a role in the regulation of trophic exchanges during AM interaction. This opens new perspectives for future research.

The phylogenetic reconstruction of the invertase gene family in numerous fungal phyla highlighted a strong negative correlation between the presence of invertase genes and the degree of mutualism of the interaction (Parrent et al. 2009). AM fungi have a low cell wall-degrading activity compared to ECM and ericoid mycorrhizal fungi, and they lack invertase activity. Altogether, this makes them strongly dependent on their plant host (Smith and Read 2008). This could be a tool for the photobiont to control and tune this type of interaction. There are many demonstrations that AM fungi can take up glucose and fructose at the plant–fungus interface (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Pfeffer et al. 1999). Within glomeromycotan fungal species, the first symbiosis-related glucose transporter was identified in *Geosiphon pyriformis* in interaction with *Nostoc punctiforme* (Kluge et al. 1991; Schüßler et al. 2002, 2006). This unique symbiotic model allowed for the isolation of *GpMST1* (Schüßler et al. 2006, 2007), characterized as an H^+ glucose transporter with highest affinity for glucose and mannose, followed by galactose and fructose. The information obtained from this model, together with the available glomeromycotan genomic data, recently led to the isolation of three MSTs (*RiMST2*, *RiMST3* and *RiMST4*; Fig. 1) from the widely used model species *R. irregularis* (Helber et al. 2011), which predominantly transports glucose and, to a lower extent, fructose (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Pfeffer et al. 1999; Boldt et al. 2011). Therefore, the excess of fructose in colonized roots may be redirected towards other sink organs.

RiMST2 has been characterized as a high-affinity functional H^+ glucose transporter expressed in arbuscules and intraradical mycelium (Fig. 1). It is also present in intraradical hyphae, where it could mediate the uptake of monosaccharides (including Glu, Xyl, galactose and mannose) resulting from plant cell wall degradation (Schüßler et al. 2007; Helber et al. 2011). RNAi silencing of *RiMST2* by HIGS resulted in impaired mycorrhizal formation, malformed arbuscules and reduced *MtPT4* expression, suggesting that RiMST2 acts as the major component for hexose uptake by *R. irregularis* and seems indispensable for a functional AM symbiosis.

Monosaccharide partitioning in ectomycorrhiza

In ECM interactions, as in AM, the regulation of carbohydrate delivery via an apoplastic pathway and more specifically the regulation of cell wall-bound invertases provide an efficient, flexible and demand-oriented way to adjust C supply to the fungal partners (Roitsch et al. 2003; Roitsch and Gonzalez 2004). Controversial results were found about changes in invertase activity due to ECM interactions in birch (Wright et al. 2000) and Norway spruce (Schaeffer et al. 1995).

Interestingly, Schaeffer et al. (1995) reported changes in mycorrhized Norway spruce invertase activity mainly in the meristem and the elongation zone, whilst no difference was observed at the active symbiotic interface.

Enhanced expression of invertase genes and related enzymatic activities were also observed in ectomycorrhized *Populus trichocarpa* plants (Nehls et al. 2010). Unaffected glucose import capacity, coupled to increased invertase gene expression, was observed in ectomycorrhizal plants (Nehls et al. 2010). Repressed expression of hexose transporters, which can take up fructose, led to enrichment of the apoplast in fructose, and the apoplast in turn became a possible extra carbon source for the hyphae of the fungal sheath that surrounds the infected root tip. This hypothesis is consistent with the accumulation of glycogen in the fungal sheath of *Paxillus involutus* colonizing silver birch (Jordy et al. 1998).

In addition to the control of sucrose transporters and sucrose hydrolysis, the regulation of hexose transporter genes upon ECM formation enhances the competition for monosaccharides at the symbiotic interface. Such competition gives the plant an additional tool to control sugar supply at a local level (Nehls et al. 2010). Several observations point out how trees can restrict carbohydrate support when mineral nutrients are not sufficiently provided by the fungal partner (Nilsson and Wallander 2003; Nilsson et al. 2005; Hendricks et al. 2006). Moreover, the increase in transcript levels of hexose transporter genes in *Poplar* plants seems to corroborate this hypothesis (Grunze et al. 2004; Nehls et al. 2007). The impact of ECM formation on monosaccharide transporter genes has been investigated in different plant species. Compared to non-mycorrhized roots, the expression of hexose transporters from birch (*BpHEX1*, *BpHEX2*), poplar (*PttMST1.2*, *PttMST2.1*) and Norway spruce (*PaMST1*) was suppressed upon ECM establishment (Nehls et al. 2000; Wright et al. 2000; Grunze et al. 2004), whilst *PttMST3.1* from poplar was strongly upregulated. As a higher expression of *PttMST3.1* compared to the other hexose transporters was also observed in non-mycorrhized plants and the heterologous expression experiments failed to confirm its transporter activity, the authors argued about a direct regulation of this gene upon ECM interaction and suggested a posttranscriptional mechanism (Nehls et al. 2007). More recently, and in agreement with the general understanding of the biological basis for ECM interactions, Larsen et al. (2011) reported higher activity for the enzymes of the carbohydrate metabolic pathway in quaking aspen, including starch and sucrose degradation enzymes, during mycorrhizal interactions with *L. bicolor*.

A. muscaria protoplasts can take up glucose and fructose, with much higher affinity for glucose than for fructose. Although sucrose did not inhibit monosaccharide uptake, fructose uptake was strongly inhibited by glucose, but no effect on glucose uptake was observed when fructose was added to protoplasts (Chen and Hampp 1993). Similarly, preferential uptake of glucose over fructose was observed in other ECM fungi such as *Cenococcum geophilum* and undefined mycorrhizal species associated to *Picea abies* (Salzer and Hager 1993; Stülten et al. 1995). Two MSTs from *A. muscaria* (*AmMST1* and *AmMST2*) and one from *Tuber borchii* (*Tbhxt1*) have been characterized as having a high affinity for glucose, but different regulatory systems and localizations among plant tissues (Nehls et al. 1998; Wiese et al. 2000; Nehls 2004; Polidori et al. 2007). Whilst *AmMST1* and *AmMST2* were stimulated by the extracellular monosaccharide concentration and putatively located at the plant–fungus interface, *Tbhxt1* expression was stimulated during carbohydrate starvation of fungal hyphae and is probably involved in supplying sugar to the soil-growing mycelium.

L. bicolor genome sequencing (Martin et al. 2008) allowed for the identification of 15 putative MSTs (Fajardo Lopez et al. 2008). Transport properties assessed through competition experiments showed that glucose was the choice monosaccharide taken up. Moreover, MST gene expression patterns confirmed a strong induction under carbon-limiting/starving conditions, most likely to allow the fungus to compete with the host for monosaccharide uptake from the plant–fungus interface.

Other works have investigated the ECM basidiomycete *L. bicolor* S238N-H82 (Deveau et al. 2008). The author attempted to construct a comprehensive inventory of pathways involved in primary carbohydrate metabolism, thus shedding light onto the steps following hexose assimilation at the plant–fungus interface. Several genes and gene families were annotated and the transcriptional regulation of the glycolysis, pentose phosphate, TCA, trehalose and mannitol metabolism pathways was studied using whole-genome expression oligoarrays and qPCR techniques in the *L. bicolor*/*Pseudotsuga menziesii* interaction. Differential transcript regulation of the glycolytic, mannitol and trehalose metabolisms was observed upon mycorrhizal and sporocarp development (Deveau et al. 2008).

More recently, *Tuber melanosporum* sequencing and comparison with other ECM fungi showed a lower dependency on the host for monosaccharides (Martin et al. 2010). In fact, the presence of an invertase-encoding gene suggests the capability for the mycobiont to hydrolyze the sucrose delivered by the plant at the apoplastic interface. This could represent an advantage compared to the mycorrhizal symbionts that lack invertase-encoding genes, such as *L. bicolor*.

Nitrogen transporters

Nitrogen transport in arbuscular mycorrhiza

Although the role of N in AM symbiosis is less clear than that of P, it is now established that AM can play a major role in N uptake (Smith et al. 2010). Although AM fungi can

take up both NO_3^- and NH_4^+, a clear preference for NH_4^+ is at least partly explained by the extra energy the fungus has to spend to reduce NO_3^- to NH_4^+ before it can be incorporated into organic compounds (Marzluf 1997).

Molecular evidence for N uptake by AM fungi was obtained through the characterization of an ammonium transporter (AMT) in *R. irregularis* (Lopez-Pedrosa et al. 2006). *GintAMT1* encodes a functional, high-affinity NH_4^+ transporter that is expressed in the extraradicular mycelium (ERM; Lopez-Pedrosa et al. 2006). *GintAMT1* transcription increased after adding 30 μM NH_4^+, but decreased after adding 3 mM NH_4^+. The authors therefore hypothesized that this gene played a key role in NH_4^+ acquisition by the ERM when the surrounding environment was characterized by ammonium-limiting conditions, such as in acid soils. A second *R. irregularis* AMT, functionally different from *GintAMT1*, has recently been isolated and characterized (Pérez-Tienda et al. 2011). *GintAMT1* and *GintAMT2* were differentially expressed during the fungal life cycle and in response to N. In contrast to *GintAMT1*, *GintAMT2* transcript levels were higher in the intraradical fungal structures than in the ERM (Fig. 2). However, transcripts of both genes were detected in arbuscule-colonized cortical cells. *GintAMT2* showed constitutive expression in N-limiting conditions and transitory induction after N resupply (either NO_3^- or NH_4^+). It was then suggested that *GintAMT2* could be involved in retrieving NH_4^+ leaked out along with fungal metabolism. Interestingly, the expression of both genes was downregulated after adding either glucose or acetate to the root or hyphal compartment of a split Petri dish, respectively, suggesting the existence of C-dependent mechanisms of gene regulation. Fellbaum et al. (2012) investigated whether or not a reward strategy existed for nitrogen delivery in the exchange for increased sugar supply, such as the one already described for P_i (Kiers et al. 2011). By manipulating carbon availability to host and fungus in root organ cultures, the authors showed that C supplied to the host induced changes in fungal gene expression that resulted in increased nitrogen uptake and transport. Interestingly, although genes involved in N assimilation or arginine biosynthesis were induced in the ERM in response to C supply to the root compartment, a fungus NT expressed in the ERM in response to exogenous NO_3^- supply (Tian et al. 2010) was downregulated, suggesting once again that AM fungi preferentially take up NH_4^+, which is energetically less costly than NO_3^-.

Besides inorganic N uptake, AM fungi can obtain substantial amounts of N from decomposing organic materials, in particular amino acids, and that 3 % of plant N comes from that material (Hodge and Fitter 2010). Such a process could involve, among other transporters, amino acid permeases (AAP). A functional AAP from *F. mosseae* has been characterized. *GmosAAP1* expression was detected in the extraradical mycelium and its activity increased upon exposure to organic nitrogen (Cappellazzo et al. 2008; Fig. 2). GmosAAP1 can transport proline through a proton-coupled and pH- and energy-dependent process and displays a relatively specific substrate spectrum since it binds non-polar and hydrophobic amino acids. GmosAAP1 may play a role in the first steps of amino acid acquisition, allowing direct amino acid uptake from the soil and extending the range of molecular tools AM fungi use to exploit soil resources.

In plants, several transcriptomic analyses reveal that AM establishment can induce the expression of plant N transporters, mainly in arbusculated cells. However, data relying on the functional validation of putative transporters are still scarce. The first evidence of a plant functional AMT involved in N uptake during AM symbiosis was provided in *Lotus japonicus* colonized with *Gigaspora margarita* by Guether et al. (2009a). *LjAMT2;2* is exclusively expressed in mycorrhizal roots, and its transcripts are preferentially located in arbusculated cells. Interestingly, transport experiments using *Xenopus laevis* oocytes indicate that, unlike other plant AMTs, LjAMT2;2 transports NH_3 instead of NH_4^+. The authors suggest that LjAMT2;2 recruits NH_4^+ in the acidic peri-arbuscular space and releases the uncharged NH_3 into the cytoplasm of the arbuscule-containing root cortical cell. That way, protons coming from the deprotonation process remain in the peri-arbuscular space and reinforce the gradient for H^+-dependent transport processes. Moreover, NH_4^+ sensing and NH_3 transport can avoid the accumulation of NH_3/NH_4^+ at potentially toxic levels. Transcript profiling revealed another AM-induced AMT (IMGAG|1723.m00046) detected exclusively in arbusculated cells (Gomez et al. 2009). Two putative ammonium transporters were identified in *M. truncatula* (Gaude et al. 2012). Interestingly, one (medtr7g075790.2) was induced in non-colonized cortical cells, whereas the other (medtr7g140920.1) was strongly induced in arbusculated cells (Fig. 2). This latter AMT sequence is different from that of the ammonium transporter expressed in arbuscule-containing cells described recently (Gomez et al. 2009), indicating that several transporter proteins of the same family may be involved in symbiotic ammonium transfer. In contrast to *L. japonicus* and *M. truncatula*, five AM-inducible AMTs were found in *Glycine max*, and one of them was downregulated (Kobae et al. 2010). In *Lotus*, the most abundantly transcribed AMT gene, *GmAMT4.1*, an ortholog of *LjAMT2;2*, is specifically expressed in arbusculated cells. Moreover, the protein was localized only on the peri-arbuscular membranes surrounding arbuscule branches, but not on the trunk regions, indicating that active ammonium transfer occurs around the arbuscule branches (Fig. 2).

Recently, two new AMTs were identified in tomato (*LeAMT4* and *LeAMT5*) and reported to be exclusively expressed in mycorrhizal roots, but not regulated by NH_4^+, whilst the non-symbiosis-specific *LeAMT2* was induced by N treatment (Ruzicka et al. 2012). Interestingly, both *LeAMT4*

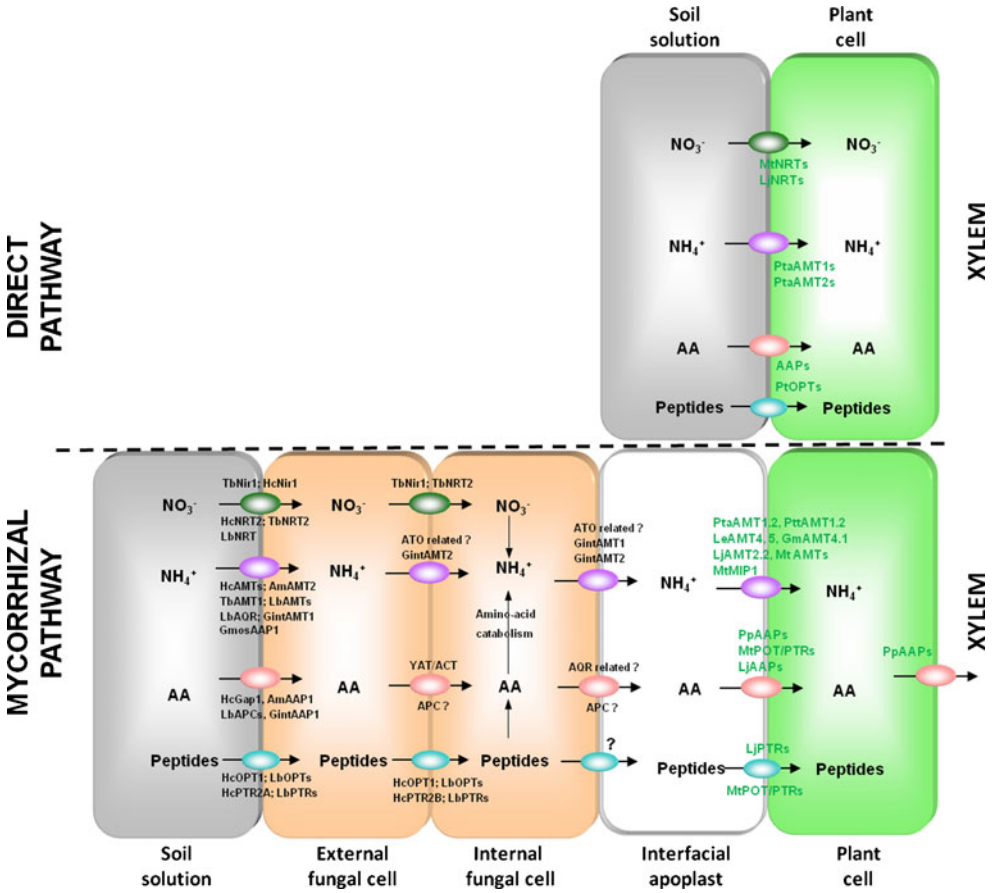

Fig. 2 Current knowledge about N transfer mechanisms in mycorrhizal interactions. Five compartments for N-compound transfer (ammonium, nitrate, amino acids and peptides) can be differentiated: the soil solution, external and internal fungal cells, the interfacial apoplast and the plant cell. The different molecules are reallocated across the different ECM compartments by several transporters that are not yet fully characterized. Hence, putative uncharacterized transporters are indicated by a *question mark*, fungal transporters in *black* and plant transporters in *green*, respectively. *NRT* nitrate transporter, *AMT* ammonium transporter, *AAP* amino acid transporter, *OPT* oligopeptide transporter, *PTR* peptide transporter, *GAP1* general amino acid permease, *ATO* ammonia (ammonium) transport outward, *AQR* aquaporin, *APC* amino acid–polyamine–organocation, *Am Amanita muscaria*, *Gint Rhizophagus irregularis*, *Gm Glycine max*, *Hc Hebeloma cylindrosporum*, *Lb Laccaria bicolor*, *Le Solanum lycopersicum*, *Lj Lotus japonicus*, *Mt Medicago truncatula*, *Tb Tuber borchii*, *Pta Populus tremula×alba*, *Ptt Populus trichocarpa*, *Pp Pinus pinaster*

and *LeAMT5* are expressed in low-N conditions, concomitantly with the transcriptional repression of direct root N uptake pathways.

The AM-induced Nod 26-like intrinsic protein (MtNIP1), an aquaporin, was reported to act as a low-affinity ammonium transporter in AM instead of facilitating water uptake (Uehlein et al. 2007). Recently, *MtNIP1* was reported to be AM-activated exclusively in arbusculated cells, whilst another NIP was activated in hyphae-containing cortical cells, suggesting that fungal hyphae could also be involved in plant N uptake (Hogekamp et al. 2011).

Although nitrate is unlikely the main form in which N is supplied to the plant by AM fungi, the AM-induced upregulation of nitrate transporter genes in various systems suggests the presence of a mechanism that supports the assimilation of nitrate by AM. In addition to the AM-induced nitrate transporter reported in tomato (Hildebrandt et al. 2002), four genes encoding nitrate transporters were also upregulated in *M. truncatula* and *L. japonicus* (Hohnjec et al. 2005; Guether et al. 2009b). However, transcriptional profiles of *M. truncatula* roots also revealed that two nitrate transporter genes were repressed (Hohnjec et al. 2005). This modulation of transporter gene expression is likely to be related to a switch in nutrient supply from direct root uptake to symbiotic uptake following changes in internal concentrations. Interestingly, in *M. truncatula*, one of the induced high-affinity nitrate transporter genes was also induced in response to high phosphate.

AM is also likely to modulate organic N transport. Among the metabolic changes observed in AM, high levels of certain amino acids (Glu, Asp, Asn) was reported in mycorrhized roots (Schliemann et al. 2008). Three genes of the AAP family were upregulated in *L. japonicus* (Guether et al. 2009a, b). In *Lotus*, ten differentially expressed genes related to di-

tripeptide transporter (PTR) genes were detected (Guether et al. 2009a, b); nine were upregulated whilst one was downregulated in mycorrhized roots. Noteworthy is that the expression of the highest induced PTR gene was exclusively located in arbuscule-containing cells.

Peptide transporters belong either to the di- and tripeptide transporter (PTR) family, also named proton-coupled oligopeptide transporter family (POT; Paulsen and Skurray 1994), or to the oligopeptide transporter (OPT) family, which transports larger peptides (Hauser et al. 2001). AM induction of four putative proton-dependent oligopeptide transporter (POT/PTR) genes was also reported in *M. truncatula* (Gomez et al. 2009; Benedito et al. 2010; Hogekamp et al. 2011). Additionally, 11 POT genes were induced in roots colonized by either *R. irregularis* or *F. mosseae* (Hogekamp et al. 2011); two of them (Mtr.7741.1.S1_at and Mtr.4863.1.S1_at) were specifically expressed in arbusculated cells.

Nitrogen transport in ectomycorrhiza

In boreal and northern temperate forests, where plants interacting with ECM fungi dominate, nitrogen is the most important growth-limiting factor and is mainly present in an organic form (Read and Perez-Moreno 2003; Smith and Read 2008). The capacity of ECM fungi to mobilize polymeric N compounds as well as take up amino acids is well documented (Wallenda and Read 1999, Plassard et al. 2002). N compounds have to pass through three membrane barriers before being assimilated into the plant cells: the soil/fungus membrane, the fungus/apoplast membrane and the apoplast/plant root membrane (Chalot et al. 2006; Fig. 2). Despite a crucial role of ECM interaction in plant N nutrition, little is known about the molecular details and, in particular, about the regulation of nitrogen transporters of the two symbionts at the three interfaces. Analysis of the *L. bicolor* genome (Martin et al. 2008) uncovered the genetic repertoire of the transportome of an ECM fungus (Lucic et al. 2008; Chalot and Plassard 2011). The following paragraphs summarize the current data about the transporters involved in N uptake and the N compounds transferred among symbionts.

Peptide and amino acid transporters

Peptide transporters from ECM host plants are not yet functionally characterized. Nevertheless, a comprehensive genomic analysis shows that the *Populus* genome contains 20 OPT-encoding genes; several of them cluster together, but no expression data on mycorrhized root tips are yet available (Cao et al. 2011). Gene expression regulation and the uptake capacity of two PTR transporters of the ECM fungus *Hebeloma cylindrosporum* indicate that HcPtr2A is involved in high-efficiency peptide uptake under conditions of limited N availability, whereas *HcPtr2B* is constitutively expressed (Benjdia et al. 2006; Fig. 2). The *L. bicolor* genome contains two PTR-encoding genes which are constitutively expressed in free-living tissues, one of them at a high level (Lucic et al. 2008). An oligopeptide transporter has also been isolated from an EST library of *H. cylindrosporum* mycelium (Lambilliotte et al. 2004), but has not been characterized yet (Müller et al. 2007). Nine putative OPT orthologs were identified in the *L. bicolor* genome, and expression analyses revealed different functional profiles. Four of them were constitutively expressed, two were highly and specifically upregulated in sporocarps, and two others were upregulated in sporocarps and ECM-involved mycelium. These genes could be involved in the constitutive uptake of peptides by the mycelium either in the free-living conditions or in ECM associations (Lucic et al. 2008; Fig. 2).

Amino acid uptake in mycorrhized root tips is improved, as demonstrated in *Pinus sylvestris* and *Fagus sylvatica* ECM plants (Wallenda and Read 1999). Transcriptomic data analyses from root tips of aspen colonized by *L. bicolor* revealed that organic N compounds such as glycine, glutamate and, likely, allantoin could be the forms of exchange between ectomycorrhizal symbionts (Larsen et al. 2011).

Most of the fungal amino acid transporters (AAT) have been classified into the amino acid/polyamine/organocation (APC) superfamily (Saier et al. 1999). They mediate the transfer of a broad spectrum of amino acids with overlapping specificities. The *L. bicolor* APC superfamily includes a larger number of genes (29 members; Fig. 2) compared to saprophytic or parasitic fungi (Lucic et al. 2008). These differences could be related to the dual lifestyle (symbiotic and/or saprophytic) of this ECM fungus and to its higher capacity to use organic N resources (Martin et al. 2008). AATs with high affinity for basic amino acids and lower affinity for neutral and acidic amino acids were identified in *A. muscaria* (AmAAP1; Nehls et al. 1999) and *H. cylindrosporum* (HcGap1; Wipf et al. 2002). Furthermore, *HcGAP1* was undetectable in ECM, so the authors hypothesized that this minimized the reuptake of excreted amino acids, assuming that a competition for nitrogen-based nutrients exists at mycorrhized root tips. Lucic et al. (2008) pointed out the remarkable expansion of the YAT family in *L. bicolor* and, according to their expression analysis, suggested that several of these genes could be key determinants of ECM functioning.

The mechanisms of amino acid excretion in ECM remain to be elucidated. The process could be ensured by transporters homologous to yeast AQR1 (Acids Quinidine Resistance 1), which is involved in amino acid excretion (Chalot et al. 2006; Müller et al. 2007; Fig. 2). It is worth noting that *Aqr1* homologs have been identified in both *L. bicolor* and *H. cylindrosporum* genomes and appear to be expressed in colonized root tips.

Nitrate and ammonium transporters

Nitrate is internalized by specific plasma membrane transporters via an energy-dependent uptake process. A large group of nitrate transporters, from both prokaryotes and eukaryotes, belongs to the Major Facilitator Superfamily and specifically to the NNP family. The best-characterized members of this family in ECM fungi are NRT2 from *H. cylindrosporum* (Jargeat *et al.* 2003) and NRT2 from *T. borchii* (Montanini et al. 2006; Fig. 2). They are clustered with NR- and NiR-encoding genes (Jargeat et al. 2003; Guescini et al. 2003, 2007). *TbNRT2*, *HcNRT2*, *TbNir1* and *HcNir1* were all upregulated in the presence of NO_3^- as the sole N source and under N starvation, whereas *TbNir1* was only upregulated in the presence of NO_3^- (Jargeat et al. 2000; Guescini et al. 2007). *TbNir1* and *TbNrt2* were strongly expressed in the Hartig net and the mantle, but weakly expressed in the free-living mycelium (Guescini et al. 2003; Montanini et al. 2006). Gobert and Plassard (2002, 2007) showed that the ECM fungus *Rhizopogon roseolus* displayed only high-affinity NO_3^- uptake kinetics. A single nitrate transporter is probably responsible for nitrate uptake in ECM fungal species, in contrast to plants that exhibit several nitrate transporters (Lucic et al. 2008). As recently reviewed (Chalot and Plassard 2011), direct NO_3^- uptake and transfer in ECM is under debate since measurements in field experiments demonstrated that ECM communities discriminated against NO_3^- (Clemmensen et al. 2008), whilst microcosm experiments showed ammonium to be the preferred N form transferred (Chalot and Plassard 2011). Interestingly, all the fungi that possess a single nitrate permease have multiple AMTs.

Though the soil concentration of the poorly mobile ammonium ion is generally lower than that of nitrate, ammonium is often preferred as a nitrogen source because of its lower assimilation cost (Marschner 1995). ECM fungi indeed have a preference for ammonium over nitrate in vitro (Rangel-Castro et al. 2002; Guidot et al. 2005) and in field experiments (Clemmensen et al. 2008). In addition, ammonium was proposed as a good candidate for transfer between fungal and plant cells at the apoplast interface (Chalot et al. 2006). Ammonium transport is mediated by a family of ubiquitous membrane proteins, the Mep/Amt/Rh family, found throughout all kingdoms of life (Huang and Peng 2005) and subdivided into two subfamilies in plants, AMT1 and AMT2. Analysis of the poplar genome revealed the existence of 14 AMT genes, 6 AMT1 and 8 AMT2 genes, respectively (Couturier et al. 2007). Among all these transporters, PtaAMT1;2 is ammonium-specific, with high affinity, and is highly expressed in roots (Couturier et al. 2007). More interestingly, as also observed for its homolog gene *PttAMT1.2*, it was overexpressed in ectomycorrhized roots (Selle et al. 2005; Couturier et al. 2007). Three other poplar genes coding for putative ammonium transporters were also overexpressed in ECM (Selle et al. 2005).

Three genes encoding ammonium transporters have been cloned from *H. cylindrosporum* (Javelle et al. 2001, 2003). HcAMT3 is a low-affinity AMT, whilst HcAMT1 and HcAMT2 are high-affinity ammonium transporters/sensors; the latter is induced by both N deficiency and NO_3^- supply and is repressed by glutamine. High-affinity AMTs isolated from *T. borchii* (*TbAMT1*) and *A. muscaria* (*AmAMT2*) were upregulated in N-deprived mycelium (Montanini et al. 2002) and strongly repressed when N was added (Willmann et al. 2007). The six *L. bicolor* AMT-encoding genes displayed various expression profiles (Lucic et al. 2008; Fig. 2). One was constitutively expressed in all tissues and did not respond to N starvation. It could therefore ensure a basal level of ammonium uptake independently of the external N status, as already demonstrated for the *H. cylindrosporum* ortholog *HcAMT3* (Javelle et al. 2003). Willmann et al. (2007) showed that in functional ECM, the transcript level of the high-affinity ammonium transporter *AmAMT2* of *A. muscaria* was reduced in both hyphal networks (sheath and Hartig net) and increased in the ERM. Furthermore, two genes homologous to a putative ammonium export protein of *Saccharomyces cerevisiae*, *Ato3*, are found in *A. muscaria* (Selle et al. 2005) and *L. bicolor* (Lucic et al. 2008). Such genes could be involved in the ammonium release from the fungal cells into the apoplast interface. Recently, a study highlighted the involvement of fungal aquaporins in ammonium transfer into ECM (Dietz et al. 2011). The authors described three *L. bicolor* aquaporins able to transport ammonium/ammonia—two of which are upregulated in ectomycorrhized root tips. Finally, in addition to specific AMTs, voltage-dependent cation channels such as those possibly involved in the export of fixed NH_4^+ from rhizobial bacteria to leguminous host plants (Roberts and Tyerman 2002) could be involved in the export of inorganic N to the apoplast (Chalot et al. 2006), as also supported by molecular data.

Phosphate transporters

ECM and AM fungi are known to take up P_i from the soil solution and to transfer P to the host plant. The first demonstration of P_i uptake by extramatrical hyphae and its subsequent transfer to the host plant was carried out using $^{32}P_i$ supplied to young *P. sylvestris* plants grown under sterile conditions (Melin and Nilsson 1950). Further experiments demonstrated that this P transport is unidirectional, from fungal cells to host root cells (Finlay and Read 1986). Recent results demonstrate that the so-called mycorrhizal pathway (MP), characterized by P_i transporters exclusively or predominantly induced during AM interaction (Harrison

et al. 2002), can contribute from 20 to 100 % of the plant P uptake, depending on the plant and fungal species involved and independently of the effect of fungal association on plant biomass (Smith et al. 2004, 2010; Facelli et al. 2010).

P_i transporters were first described in yeast (Persson et al. 2003), characterized as high-affinity P_i transporters encoded by the *PHO84* and *PHO89* genes (Bun-ya et al. 1991; Martinez and Persson 1998). Interestingly, PHO84 and PHO89 are respectively H^+- and Na^+-dependent transporters, a difference that is still used for classification purposes; indeed, the P_i:H^+ transporters are associated with the Pht1 family and P_i:Na^+ with the Pht2 family. High- and low-affinity transporters are found in the two families.

Phosphate transport in arbuscular mycorrhiza

AM-inducible plant P_i transporters have been identified in many monocot and dicot species, including perennial trees (Javot et al. 2007a; Loth-Pereda et al. 2011; Fig. 3 and Electronic supplementary material (ESM) Table S1). In dicots, the signal perception and the transduction pathway that mediate mycorrhiza-specific regulation of P_i transport have been described in several plant orders such as Solanales, Apiales, Fabales (Karandashov et al. 2004) and Malphigiales (Loth-Pereda et al. 2011). They cluster in subfamilies I and III of the plant Pht1 family (Fig. 3). In situ hybridization and promoter:GUS fusion studies showed that some of these AM-inducible Pht1 transporters were predominantly or exclusively expressed in arbusculated cortical cells (Rausch et al. 2001; Harrison et al. 2002; Glassop et al. 2005; Nagy et al. 2005; Maeda et al. 2006). Subfamily I *Pht1* genes are only expressed in mycorrhizal cells in perennial and annual plants, whilst subfamily III *Pht1* genes, such as *MtPT3* in *M. truncatula* and *LjPT3* in *L. japonicus*, have a basal expression in non-mycorrhized roots, but are specifically induced in cortical cells during AM symbiosis (Maeda et al. 2006; Rausch et al. 2001; Fig. 5). Transporters from the two subfamilies were immunolocalized in the peri-arbuscular membrane at the branches of arbuscules in *M. truncatula* (*MtPT4*; Harrison et al. 2002; Pumplin and Harrison 2009) or *Oryza sativa* (*OsPT11*; Kobae and Hata 2010). Interestingly, in tobacco plants colonized by AM fungi, H^+-ATPases and AM-induced P_i transporters (H^+-P_i transporters) displayed arbuscule-specific expression and distinct localizations in the plant membrane around the arbuscules (Gianinazzi-Pearson et al. 2000; Krajinski et al. 2002). Moreover, polar targeting of AM-inducible Pht1 transporters, such as MtPT4, is mediated by precise temporal expression coupled with a transient reorientation of secretion (Pumplin et al. 2012).

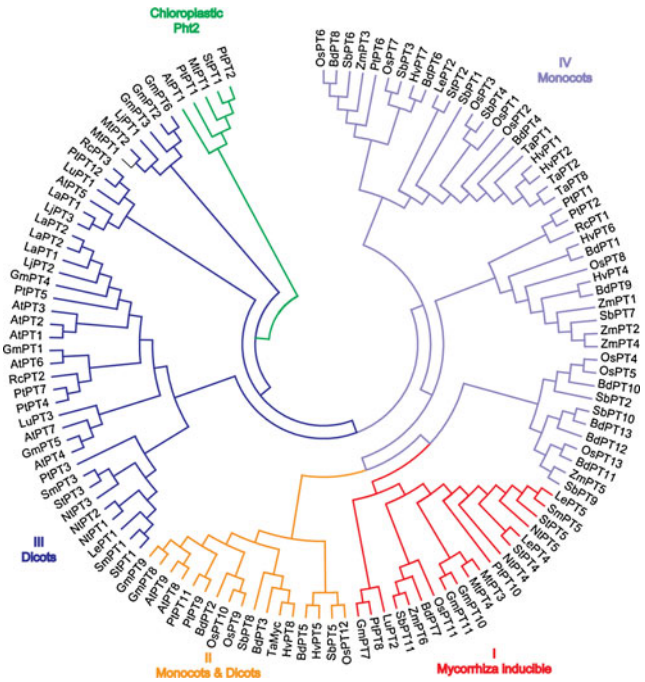

Fig. 3 Neighbour-joining tree of P_i:H^+ symporters. Members of the Pht2 family were used as an outgroup. They share high similarity with mammalian P_i:Na^+ co-transporters, but function as P_i:H^+ co-transporters in plant plastids. Subfamily I clustered the AM-inducible P_i transporters from both monocot and dicot species, suggesting they evolved before dicots and monocots separated. Some proteins from both monocots and dicots fall into the highly divergent subfamily II. Genes from plant groups were found in subfamilies III and IV, indicating their evolutionary divergence after the separation of flowering plants from their common ancestor

Analysis of the promoter region revealed the presence of the highly conserved CTTC motif in AM-inducible Pht1 genes in dicots (Karandashov et al. 2004; Chen et al. 2011; Loth-Pereda et al. 2011). However, the attempt to characterize AM-inducible Pht1 transporters by heterologous expression in yeast or by overexpression in suspension-cultured tobacco cells did not yield a clear-cut picture: the *P. trichocarpa* PtPT10 mutant exhibits a growth defect at low-P_i conditions (Loth-Pereda et al. 2011), *M. truncatula* MtPT4 is a low-affinity Pht1 transporter (668 μM; Harrison et al. 2002), and *S. tuberosum* StPT3 has a higher affinity (64 μM; Rausch et al. 2001) than MtPT4.

AM-induced Pht1 transporters are essential for P_i uptake via the mycorrhizal pathway. In a tomato mutant resistant to colonization by most AM fungi, *LePT3* and *LePT4* are only expressed when arbuscules are developing (Poulsen et al. 2005). The downregulation of *MtPT4* (subfamily I) caused premature arbuscule death, decreased colonization levels and ultimately led to the end of the AM relationship (Javot et al. 2007b), but also affected nitrogen metabolism (Javot et al. 2011). The mutants exhibited low total shoot P contents and an accumulation of poly-P in the arbuscules probably caused by the impairment of the symbiotic pathway. In contrast, knocking out the *LePT4* gene (subfamily III) in tomato did not inhibit arbuscule development or P_i uptake via the AM

pathway, probably due to a functional overlap with the other AM-induced Pht1 transporter *LePT3* from subfamily I (Nagy et al. 2005). The *LjPT3* knockdown mutant (subfamily III) showed reduced arbuscule development and AM-mediated P uptake (Maeda et al. 2006). Finally, mutant studies with reduced expression of the two types of AMF-inducible *Pht1* from subfamilies I and III reveal that the two subfamilies are important for AM symbiosis. However, in rice, Yang et al. (2012) showed that only OsPT11 from subfamily I was necessary and sufficient for symbiotic P_i uptake.

In addition to the effect of AM symbiosis on gene expression, *Pht1* gene expression also depends on P status. Besides AM-inducible Pht1 transporters, some other *Pht1* are downregulated, in particular those thought to be involved in direct P_i uptake. This interplay between Pht1 transporters reflects the balance between the direct and symbiotic pathways of P_i uptake. P_i absorption by root hairs and epidermis is substantially reduced in AM plants, even if the AM fungus does not provide additional P_i to the plant (Smith et al. 2003). It is currently not clear yet whether downregulation (1) is a plant-only dependent process, (2) is a direct response of the plant to symbiosis or (3) indirectly results from the AM-induced improvement of plant P acquisition (Smith and Read 2008). In *M. truncatula*, the expression of *MtPT4* was induced by *Gigaspora rosea*, *F. mosseae* and *R. irregularis*, and the other five genes coding for Pht1 transporters showed different degrees of repression that mirrored the functional differences in P nutrition by the three fungi (Grünwald et al. 2009). Furthermore, the downregulation of AM symbiosis by P is accompanied by a systemic regulation of strigolactone production, which probably affects hyphopodia differentiation and subsequent arbuscule development (Balzergue et al. 2011). Moreover, posttranscriptional regulation appears to be an important control point in response to different P conditions, meaning that transcript abundance and protein accumulation are not necessarily related, as shown by the contradictory results in *M. truncatula* (Chiou et al. 2001) and *O. sativa* (Tran and Plaxton 2008).

A series of promoter truncation and mutation analyses combined with phylogenetic footprinting of Pht1 promoters revealed that at least two *cis*-regulatory elements—the mycorrhiza transcription factor-binding sequence (Chen et al. 2011) and P1BS (Rubio et al. 2001; Schünmann et al. 2004)—mediated the transcriptional activation of AM-mediated P_i transporter genes. Deletion or partial mutation of either of the two motifs in the promoters caused a remarkable decrease, or even complete absence, of promoter activity in solanaceous species (Chen et al. 2011). The requirement of P1BS for AM inducibility of P_i transporters could explain the absence of induction under high P supply in AM plants with low colonization levels (Nagy et al. 2009; Chen et al. 2011). But other mechanisms could sustain AM symbiosis at a high P status, such as PHO2 repression mediated by miR399 accumulation in mycorrhized roots (Branscheid et al. 2010). Additionally, *Mt4*, a non-coding RNA homologous to *M. truncatula* IPS1, is rapidly downregulated in AM symbiosis (Burleigh and Harrison 1998). Therefore, components shared between P starvation signalling and AM signalling can also be differentially regulated due to AM interaction.

In AM fungi, the first P_i:H^+ transporter was described in *D. epigaea* (*DePT* on Fig. 4, subgroup III, and ESM Table S2) and had a K_m value of 18 μM P_i (Harrison and van Buuren 1995). Later, one partial cDNA (*FmPT*) and one full-length cDNA (*RiPT*) putatively coding for P_i:H^+ transporters were identified in *F. mosseae* and *R. irregularis*, respectively (Fig. 4, subgroup IV; Maldonado-Mendoza et al. 2001; Benedetto et al. 2005). The recent sequencing of the *R. irregularis* genome yielded three other genes. Two predicted polypeptides (*RiPT1* and *RiPT2*) cluster in the PHO89 subgroup (Fig 4, subgroup I), suggesting the putative presence of P_i:Na^+ transporters. However, their function is questionable as they are also very close to ScPho86, a protein involved in targeting and packaging ScPho84 in yeast (Bun-Ya et al. 1996). The third predicted polypeptide (RiPT3) clusters with the PHO87 subgroup (Fig 4, subgroup IV). It can mediate P_i uptake when expressed in quadruple-mutant yeast (*pho84*Δ, *89*Δ, *90*Δ, *91*Δ) with low affinity

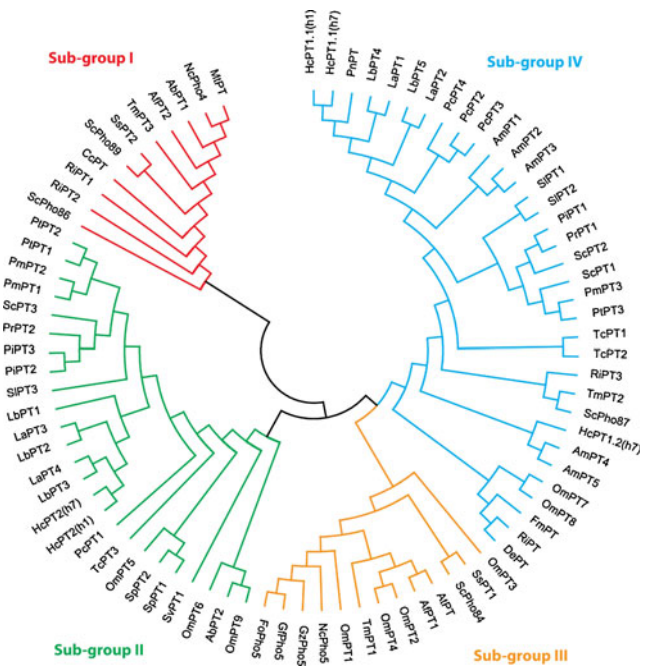

Fig. 4 Neighbour-joining tree of fungal P_i:H^+ and P_i:Na^+ transporters based on realigned amino acid sequences. Bootstrap values are from 1,000 replications. Sequence names consist of species code (first letter of the genus name and first letter of the species name, and gene name). Accession numbers of the predicted proteins are given as supporting information. The tree consists of five subgroups: subgroup I corresponds mainly to P_i:Na^+ transporters, whereas subgroups II–V correspond to P_i:H^+ transporters. Subgroup V mainly clusters P_i:H^+ transporters from ascomycetes

(216 μM; Wykoff and O'Shea 2001), suggesting that RiPT3 could encode a low-affinity P_i:H^+ transporter.

Besides Glomeromycetes, an Ascomycete species, *Oidiodendron maius*, which forms AM symbiosis with ericaceous plants (Martino et al. 2007), showed the highest number of putative P_i transporters, (http://genome.jgi.doe.gov/Oidma1/Oidma1.home.html), with nine members (*OmPT1–OmPT9*; Fig. 4 and ESM Table S2) classified as P_i:H^+ transporters.

Most fungal transcripts were predominantly detected in ERM, with their expression levels enhanced by low P availability, as in *R. irregularis* (Maldonado-Mendoza et al. 2001; Olsson et al. 2006) and *F. mosseae* (Benedetto et al. 2005). As a whole, these data suggest a role in P_i acquisition from the soil solution. Yet, Benedetto et al. (2005) and Balestrini et al. (2007) report that *FmPT* transcripts are also detected in intraradical mycelium (IRM) and in cells containing arbuscules, suggesting that the regulation of P uptake and transfer from fungal cells to host cells is far more complex than previously expected. Transcript profiling using oligoarray revealed that *R. irregularis* P_i:H^+ and P_i:Na^+ transporters were not differentially expressed in germinating spores, in the extra- and intraradical mycelium (Tisserant et al. 2012). It also appears that P delivery from the AM fungus to the plant is highly dependent of the C pool delivered by the plant, as shown for *R. irregularis* associated with root organ cultures (Hammer et al. 2011). This is confirmed by the constitutive overexpression of a potato sucrose transporter *(SoSUT1)*, which increases mycorrhizal root colonization under high P availability only (Gabriel-Neumann et al. 2011).

Phosphate transport in ectomycorrhiza

In ECM fungi, several genes putatively encoding P_i transporters have been identified (Fig. 4 and ESM Table S2; http://genome.jgi.doe.gov/Mycorrhizal_fungi/Mycorrhizal_fungi.info.html): three in *H. cylindrosporum* (*HcPT1.1*, *HcPT1.2* and *HcPT2*; Tatry et al. 2009), in *P. involutus* (*PiPT1–PiPT3*), and in *T. melanosporum* (*TmPT1–TmPT3*; Martin et al. 2010) and five in *L. bicolor* (*LbPT1–LbPT5*; Martin et al. 2008) and in *A. muscaria* (*AmPT1–AmPT5*). Most of these transporters belong to the Pht1 subfamily (P_i:H^+ transporters), suggesting that the efficiency of P_i uptake by the fungus strongly relies on external pH values. Only *T. melanosporum* stands apart, with genes encoding P_i transporters that cluster with P_i:Na^+ transporters (*TmPT3*; subgroup I in Fig. 4). This specificity could be related to the ecology of this fungal species, which can live in soils with alkaline pH values and does not strictly depend upon proton gradients thanks to these P_i transporters.

Among all P_i transporters identified so far in ECM fungi, only HcPT1 (HcPT1.1 in Figs. 4 and 5) and HcPT2 have been characterized by yeast complementation (Tatry et al. 2009). HcPT1 and HcPT2 exhibited different affinities for P_i, with K_m values of 55 and 4 μM, respectively. The apparent K_m of HcPT2 was therefore comparable to that reported for ScPho84 and even lower than that of GvPT (18 μM). It is also close to the few apparent K_m values of P_i uptake measured in ectomycorrhized pines, which ranged between 2 and 13 μM depending on the fungal species (Van Tichelen and Colpaert 2000). These two transporters differ in their kinetics, but also in their regulation according to P_i availability; *H. cylindrosporum* could use HcPT1 to mediate P_i uptake when soil P availability is low and HcPT2 when soil P availability is high (Tatry et al. 2009). The divergent phylogenetic relationships of HcPT1 and HcPT2, which cluster in subgroups II and IV (Fig. 4), respectively, and their differential transcriptional regulation suggest different functional characteristics (i.e. different affinities for P_i and/or to different regulation patterns of gene expression with P_i availability).

So far, only one study has reported the regulation of plant P_i transporters in ECM interactions. It was carried out in poplar (*P. trichocarpa*) associated with *L. bicolor* (Loth-Pereda et al. 2011). The authors showed that an alternative P_i uptake pathway distinct from AM-interacting plants allowed ectomycorrhized poplar to recruit *PtPT9* and *PtPT12* (both upregulated in poplar AM and ECM) to cope with limiting P concentrations in forest soils (Loth-Pereda et al. 2011; Fig. 5). Due to structural differences between AM and ECM roots, whether the direct and mycorrhizal uptake pathways work simultaneously in ECM has to be shown. Indeed, the presence of the fungal sheath may hinder Pi uptake by the root cells (Bücking et al. 2007), especially if the fungus is hydrophobic. However, to transfer P from the external solution to the xylem through ECM, P has to be taken up by cortical cells. That step could be mediated by specific plant Pht1 transporters such as *PtPT9* and *PtPT12* in poplar. On the other hand, the capacity of *Pinus pinaster* roots for P_i uptake strongly depends on whether ectomycorrhizae can take up P_i from the solution or not (Tatry et al. 2009). Decreased and increased net P_i uptake was measured in root portions without any ECM tips and in root portions with ECM tips, respectively, and compared to non-mycorrhized roots. The decrease in P uptake capacity in *P. pinaster* root areas grown with the symbiotic fungus but without any ectomycorrhizae could be due to the downregulation of high-affinity plant P_i transporters in the cortical cells of the whole root system, as described previously in AM plants. This suggests the occurrence of a mycorrhizal uptake pathway in ECM plants (Fig. 5).

Overview of the phosphate transportome in mycorrhized roots

Finally, gathering the data published on AM symbiosis, a simplified diagram of the possible phosphate transportome

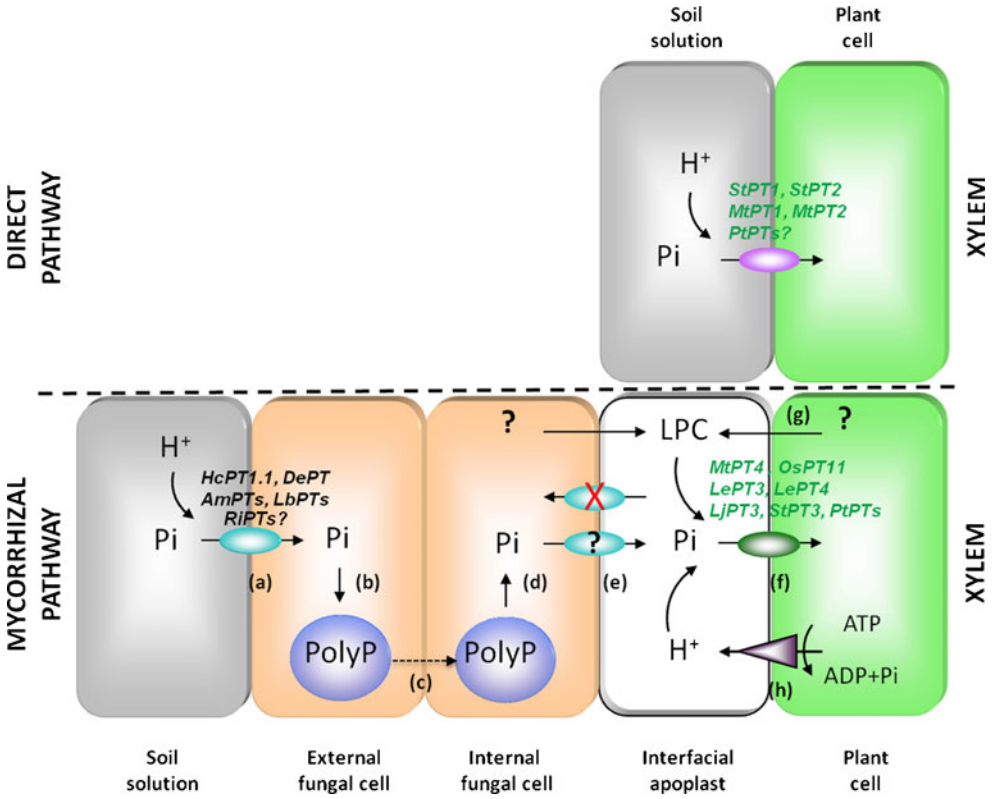

Fig. 5 Phosphate transportome during mycorrhizal interactions and P transfer mechanisms towards host cells. Expression of plant Pht1 transporters from the direct pathway could be strongly reduced in mycorrhized plants compared to non-mycorrhized plants, leading to the activation of the mycorrhizal P uptake pathway (Smith and Smith 2011). In the mycorrhizal pathway, after inorganic phosphate uptake from the soil solution through the plasma membrane, fungal Pht1 is energized by the H^+ symport (*a*), cytoplasmic P_i is accumulated in the vacuoles as polyphosphates (*b*) and transferred through hyphae via motile vacuoles (*c*) towards the intracellular fungal cells (*d*). PolyPs are probably degraded under the control of a plant signal to supply cytosol P_i which leaves the fungal cell through as yet unknown mechanisms (*e*). The mechanism could be the same fungal Pht1s whose activity is also regulated by posttranscriptional modifications, leading to the lack of apoplasmic P_i reuptake by fungal cells (*e*) and leaving P_i available for plant P uptake (*f*) through mycorrhizal-inducible Pht1 transporters. These plant mycorrhizal-inducible Pht1 transporters could be induced by lyso-phosphatidylcholines of plant or fungal origin (*g*), as shown in tomato (Drissner et al. 2007). Plant P_i uptake is energized by the proton symport resulting from plant ATPase activity (*h*) (Smith et al. 2011). *P_i* inorganic phosphate, *PolyP* polyphosphates, *LPC* lyso-phosphatidylcholine, *DP* direct pathway, *MP* mycorrhizal P uptake pathway, *Am Amanita muscaria*, *De Diversispora epigaea*, *Hc Hebeloma cylindrosporum*, *Lb Laccaria bicolor*, *Le Solanum lycopersicum*, *Lj Lotus japonicus*, *Mt Medicago truncatula*, *Os Oryza sativa*, *Pt Populus tremula*, *St Solanum tuberosum*

of mycorrhized roots is given in Fig. 5. The first impact of mycorrhizal symbiosis is the formation of a MP that can contribute to most of P uptake in mycorrhized plants (Smith et al. 2003, 2004) at the expense of the direct pathway (DP). This first effect could be mediated through the downregulation of plant Pht1 transporters located in epidermal root cells, such as reported in *M. truncatula* (MtPT1 and MtPT2; Liu et al. 1998a, b) and potato (StPT1 and StPT2; Leggewie et al. 1997; Rausch et al. 2001; Nagy et al. 2005; Fig. 5). The MP pathway first involves the uptake of P_i from the soil solution by the ERM far away from the roots. In most cases, fungal P uptake is mediated by P_i:H^+ transporters. However, the exact role of the putative P_i:Na^+ transporters identified in the *R. irregularis* genome (*RiPT1* and *RiPT2)* remains to be established. After uptake, P_i is rapidly transferred to vacuoles under the form of polyphosphate chains. Vacuoles can move from cells to cells to reach the IRM. Javot et al. (2007b) showed that polyphosphates did not accumulate in functional arbuscules, whereas they accumulated in the fungal hyphae that bear the arbuscules, suggesting that polyphosphates are degraded inside arbuscules. We can hypothesize that this recycling is under the control of plant cells, although the nature of the signals remains to be determined. This degradation of polyphosphates sustains the P_i flux delivered from the fungal cells towards the apoplastic interface between the symbionts, through as yet unknown mechanisms (Smith and Smith 2011). The detection of fungal *Pht1* in mRNA extracted from arbusculated cortical cells (Balestrini et al. 2007) strongly suggests that *Pht1* plays a role in P_i delivery at the symbiotic interface. Moreover, as shown by Koegel et al. (2013), *SbPt11* from *Sorghum bicolor* was slightly but significantly and systemically induced, indicating that a signal could be transferred to the non-colonized roots and prepare the roots for potential future colonization, as described by Gaude et al. (2012). The activity of these

transporters could be regulated by posttranslational modifications leading to an absence of apoplastic P_i reuptake by the fungus and leaving P_i available for plant P uptake via mycorrhiza-inducible *Pht1* transporters (Fig. 5). Interestingly, the expression of plant mycorrhizal-inducible Pht1 transporters was induced by lysophosphatidylcholine (LPC) from plant or fungal origin (Drissner et al. 2007). Due to the fact that LPCs are highly mobile within cells, these molecules could be the cytoplasmic messenger that activates downstream processes and gene expression in the nucleus (Bucher et al. 2009). However, roots from plants exhibiting a high P_i status are insensitive to LPC (Nagy et al. 2009), suggesting that P_i control is dominant over LPC signalling (Bucher et al. 2009). Overall, the P transportome from mycorrhizal plants appears to represent a rapid translocation system for delivering P taken up far away from roots by the external fungal cells directly into cortical cells. However, some decisive steps remain to be elucidated, especially the nature of the transport mechanisms that ensure the release of P_i from the fungal cells.

Sulphate transporters

Sulphur is a crucial macronutrient for photosynthetic organisms' growth, development and response to various abiotic and biotic stresses. It is needed to synthesize amino acids (cysteine and methionine); glutathione; thiols of proteins and peptides; membrane sulfolipids; cell walls; and secondary products like vitamins, cofactors and hormones (Foyer and Noctor 2009; Popper et al. 2011). Therefore, deficiency due to reduced S availability can have dramatic impacts on plant growth and development.

Sulphur is acquired from the soil in the form of sulphate, through an H^+-dependent co-transport process (Davidian et al. 2000), and then transported towards the sink organs under the control of different sulphate transporters classified into four groups (Fig. 6 and ESM Table S3). Due to its solubility in water, sulphate is commonly leached from soils by rainfalls (Eriksen and Askegaard 2000); as a consequence, 95 % of soil S is bound to organic compounds after being metabolized by soil microorganisms (Scherer 2001) and then no longer available for plants (Leustek 1996). S starvation or other nutrient starvation can have deleterious effects on plants, similarly to the use of increasing amounts of fertilizers on natural ecosystems (Foley et al. 2005). Therefore, different approaches to access the unavailable organic S pool present in the soil must be investigated, such

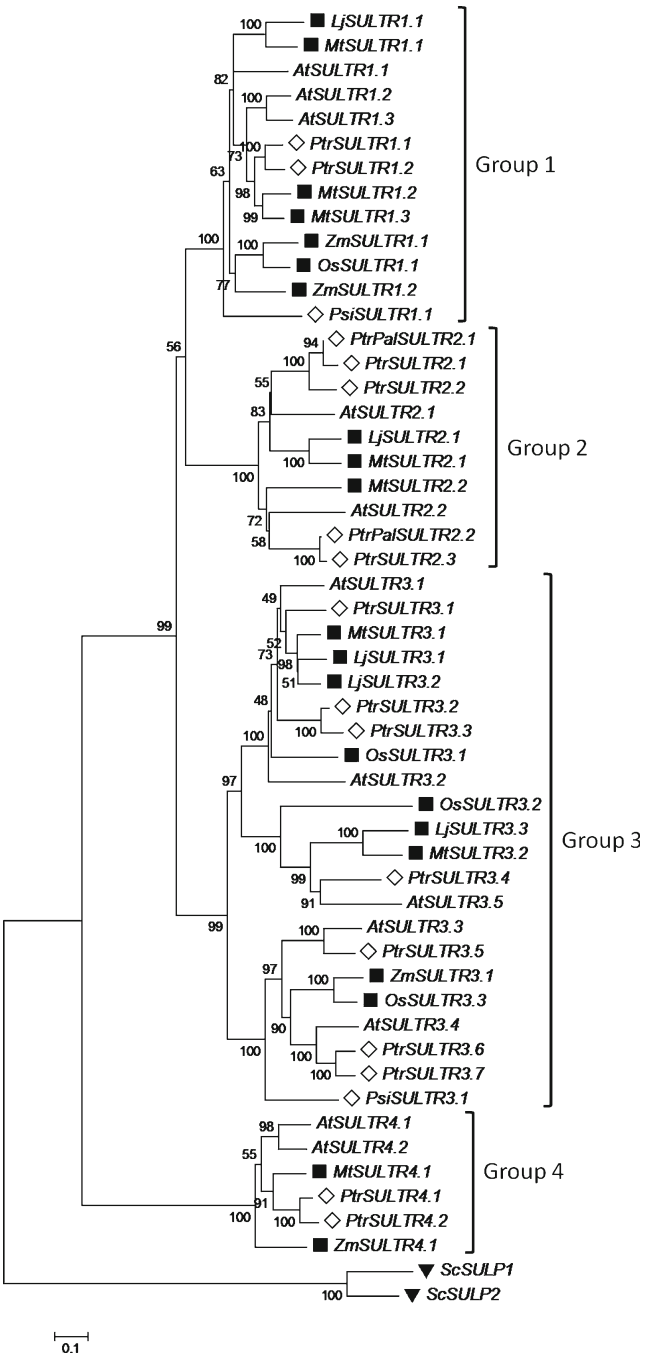

Fig. 6 Rooted phylogenetic tree of plant sulphate transporters (*SULTRs*), adapted from Casieri et al. (2012). The evolutionary history was inferred using maximum parsimony on 53 aligned amino acid sequences. *Numbers next to branches* represent the percentages of replicate trees in which the associated taxa clustered together in the bootstrap test (3,000 replicates). The evolutionary distances were computed using the Jones et al. (1992) w/freq. method and are expressed as the number of amino acid substitutions per site. Rate variation among sites was modelled with a gamma distribution (shape parameter=2). A total of 586 parsimonious informative positions were considered in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura et al. 2011). *Squares*, AM host species; *diamonds*, ECM host species; *inverted triangles*, rooting outgroup of the tree, represented by *S. cerevisiae* sulphate permeases. Species code: *At Arabidopsis thaliana*, *Lj Lotus japonicas*, *Mt Medicago truncatula*, *Os Oryza sativa*, *Zm Zea mays*, *Ptr Populus tremula*, *Ptric Populus trichocarpa*, *Ptr-Pal Populus tremula*×*Populus alba*, *Psi Picea sitchensis*

as the use of symbiotic microorganisms (i.e. AM and ECM fungi) in interaction with plant roots.

Sulphate transport in arbuscular mycorrhiza

In plants, the cross talk with AM fungi and the increased amount of available nutrients trigger a series of events such as the activation of specific mycorrhizal uptake pathways; this affects already-expressed transporters of the direct uptake pathways and increases nutrient exchanges and reallocation (Javot et al. 2007a, b; Sawers et al. 2008; Smith and Smith 2011; Smith et al. 2011).

Noteworthy is that although several papers address the importance of S uptake and of the transport of its oxidized forms or metabolic derivates inside the plant (Yoshimoto et al. 2007; Lewandowska and Sirko 2008), few studies on the effects of symbiotic interactions with AM fungi on the transcriptional regulation of plant SULTRs are reported. Growth parameters and element (C, N, S) contents of *M. truncatula* plants showed increasing S availability and starvation resistance in plants interacting with the AM fungus *R. irregularis* (Casieri et al. 2012). In the same study, transcript accumulation analysis of eight putative *M. truncatula* sulphate transporters (MtSULTRs) revealed differential regulation due to S starvation conditions (≤10 μM) and to AM interactions. It is noteworthy that the induced transcription of two transporters (*MtSULTR1.1* and *MtSULTR1.2* in Fig. 6), preferentially found in root tissues, was observed at all sulphate concentrations upon AM interaction. Similarly, other transporters (*MtSULTR2.1* and *MtSULTR2.2*) were also upregulated. Comparisons between mycorrhized and non-mycorrhized conditions, showing putative SULTRs in leguminous plants affected by AM interactions, highlighted their possible contribution to the direct or mycorrhizal-sulphate uptake pathways (Casieri et al. 2012). Although S uptake and assimilation pathways are repressed by normal or high sulphate concentrations (Vauclare et al. 2002; Buchner et al. 2004), contrasting evidence appears in mycorrhized plants where S content and uptake are enhanced whatever the sulphate concentration. Differences from the derepression mechanism observed at the transcriptional level, observed in *Arabidopsis* after supplying sulphate to S-deprived plants (Maruyama-Nakashita et al. 2003; Nikiforova et al. 2005), could suggest differences in the mechanisms that regulate plant S sensing, S assimilation and/or feedback repression due to S-containing compounds occurring in AM-interacting plants.

The ability of mycorrhizal fungi to transfer N and P from organic compounds has been shown by different authors (Banerjee et al. 2003; Guo et al. 2007). Recently, the possible S uptake from organic sources by mycorrhized plants was investigated by means of ^{35}S-labelling experiments performed on transformed carrot roots (*Daucus carota*) and monoxenically grown *R. irregularis* (Allen and Shachar-Hill 2009). More generally, sulphate transfer through AM fungi was studied earlier, but different studies report contrasting results. In fact, the increase in $^{35}SO_4^{2-}$ uptake in mycorrhized red clover and maize plants was shown by Gray and Gerdemann (1973) using the AM fungus *F. mosseae*. In agreement with their report, Rhodes and Gerdemann (1978) showed mycorrhizal induction of sulphate uptake by onion using *R. fasciculatus*. However, Cooper and Tinker (1978), using white clover and onion as model plants, failed to confirm *F. mosseae*-induced $^{35}SO_4^{2-}$ transfer in two-compartment plates. The S uptake mechanisms used by the AM fungus and the specific compounds that are transferred through the fungal mycelium to allocate sulphur are still unknown. Another interesting aspect to address is how the mycobiont regulates the transfer of S-rich compounds at the plant–fungus interface. The future unraveling of the genome of the most studied AM fungus, *R. irregularis* DAOM-197198, will probably shed light on these questions and may open new perspectives regarding plant–fungus S-based nutrient exchanges.

Sulphate transport in ectomycorrhiza

Most works concerning plant nutrition and ECM interactions address the fundamental questions of how plant P and N uptake is improved thanks to the mycobiont and how much fixed C is given by the plant in return for these nutrients. Great efforts have been made to unravel the mechanisms of nutrient exchanges (see other chapters in this review), but sulphate and in general S-containing compounds have not been deeply investigated so far.

Figure 6 shows putative sulphate transporters (SULTRs) from ECM host plants and their phylogenetic relationships with AM hosts. Amino acid sequences from *Arabidopsis thaliana* SULTRs were aligned and used to construct a consensus sequence. Part of this consensus sequence, 131 amino acids with sequence identity ranging from 75 to 100 %, was blasted on the NCBI server (http://blast.ncbi.nlm.nih.gov/Blast.cgi) in order to retrieve amino acid sequences from the AM and ECM hosts most commonly used in mycorrhization experiments. The phylogenetic analysis included 61 aligned amino acid sequences, and evolutionary history was inferred using the maximum parsimony method out of a total of 785 parsimonious informative positions. In order to evaluate the number of replicate trees in which the associated taxa clustered together, bootstrap analysis (1,000 replicates) was performed. *S. cerevisiae* sulphate permeases (*ScSUL1* and *ScSUL2*; Cherest et al. 1997) were used as an outgroup to root the plants' SULTRs phylogenetic tree (Fig. 5).

ECM host SULTRs (diamonds in Fig. 6) were distributed among the four SULTR groups (as defined by Takahashi et al. 2011). *Populus tremula* interacts with different ECM fungi and, from our results, is the host species with the

highest number of putative SULTRs: two candidates in groups 1 and 4, three candidates in group 2 and eight candidates in group 3. The close phylogenetic relationship with the group 1 and 2 SULTRs from *Medicago* and *Lotus* (*MtSULTR1.1*; *MtSULTR1.2*; *LjSULTR-p chr6.CM0314.360*; *MtSULTR2.1*; and *MtSULTR2.2*), which are differentially expressed during mycorrhizal interactions (Casieri et al. 2012; Guether et al. 2009b), could indicate putative Myc-inducible SULTR candidates that play a role in sulphate uptake during ECM interactions.

Although genome-wide approaches of some ECM fungal species have been carried out (i.e. *L. bicolor*; Martin et al. 2008), there is still a knowledge gap regarding genes that control S uptake. Unraveling the contribution of ECM fungi to plant S uptake would shed light onto the complexity of nutrient exchanges during ECM interactions. For this reason, the putative SULTRs of different ECM fungi were retrieved by blasting the most conserved part of the consensus sequence from *S. cerevisiae* sulphate permeases (ScSULP) against public databases. The coding sequences were aligned and the phylogenetic relationships between SULTRs of different ECM fungi were calculated (Fig. 7 and ESM Table S4). The characterization and localization of these putative SULTRs and the sequencing and annotation of new ECM fungal species could help understand whether sulphate is the exchange form of S during plant–fungus symbiosis and how the fungus senses S and manages its allocation.

Ion transport systems—channels and transporters

In addition to the extensively described improvement of plant N and P nutrition by symbiotic fungi, physiological studies also highlight an improvement of the absorption of other ions such as potassium or various secondary macro- and microelements (Marschner and Dell 1994; Buscot et al. 2000; Cairney 2005; Smith and Read 2008). Clearly, all these nutrient exchanges between the two partners require

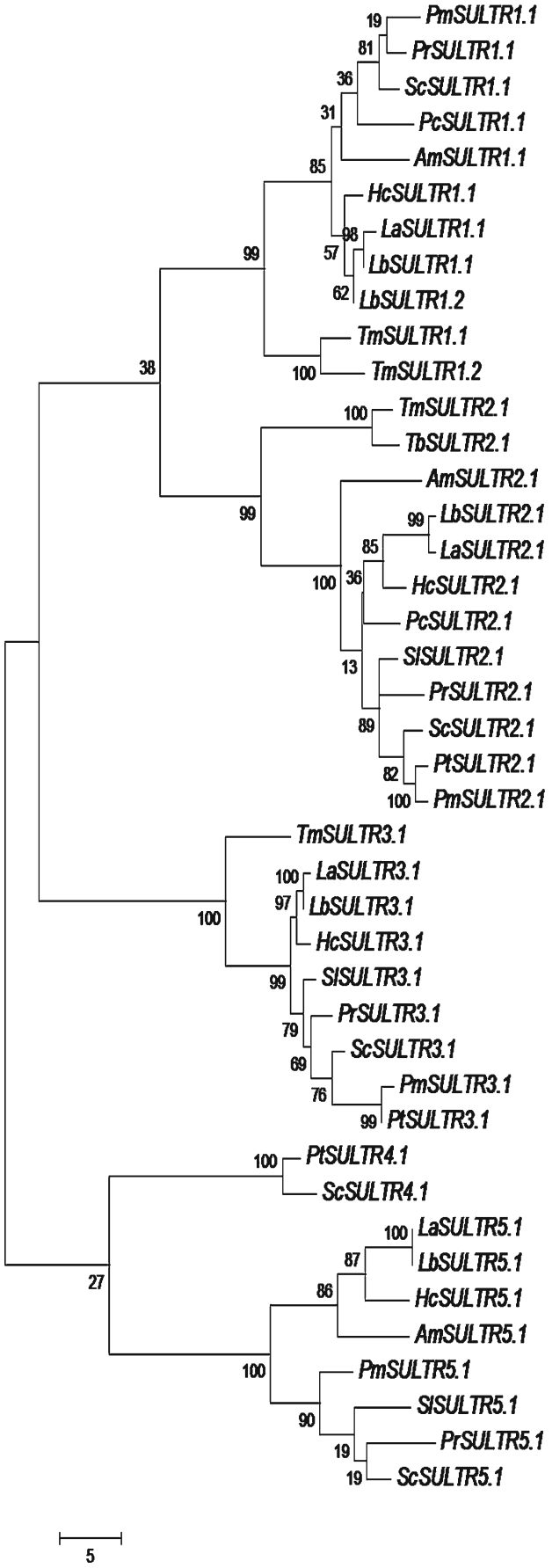

Fig. 7 Unrooted phylogenetic tree of sulphate transporters (*SULTRs*) from ECM fungi. The evolutionary history was inferred using maximum parsimony (MP) on 42 aligned amino acid sequences. The percentages of replicate trees in which the associated taxa clustered together in the bootstrap test (3,000 replicates) are shown *next to the branches* (Felsenstein 1985). The MP tree was obtained using the Subtree-Pruning-Regrafting algorithm (Nei and Kumar 2000), in which the initial trees were obtained by the random addition of sequences (100 replicates). The tree is drawn to scale, with branch lengths calculated using the average pathway method. A total of 352 parsimonious informative positions were considered in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura et al. 2011). Species code: *Am Amanita muscaria*, *Hc Hebeloma cylindrosporum*, *La Laccaria amethystina*, *Lb Laccaria bicolor*, *Pr Paxillus rubicundulus*, *Pc Piloderma croceum*, *Pm Pisolithus microcarpus*, *Pt Pisolithus tinctorius*, *Sc Scleroderma citrinum*, *Sl Suillus luteus*, *Tb Tuber borchii*, *Tm Tuber melanosporum*

a number of transport systems, both on the fungal membrane sites that take up mineral nutrients from the soil and deliver them to plant root cells and on the plant membrane interface (Smith et al. 1994; Hahn and Mendgen 2001). These membrane transport systems include ion channels and transporters that differ in their transport mechanism, selectivity, affinity and regulation. Such channels or transporters—especially for ECM fungi—have been identified (Chalot et al. 2002). In the last decade, identification has been faster thanks to the use of EST libraries from *H. cylindrosporum* (Lambilliotte et al. 2004; Wipf et al. 2003) or *P. involutus* (Morel et al. 2005; Wright et al. 2005a) and, more recently, of whole-genome sequencing data (Martin et al. 2008, 2010; Plett and Martin 2011). However, characterization of the various transport systems and assignment of their physiological roles within the symbiotic context is far from being completed. Interestingly, symbiotic ion transport has to be assessed not only in the context of nutrition but also in relation to signalling between fungi and host plants (Ramos et al. 2011a). More particularly, Ca^{2+} spiking and oscillations have been reported to be induced in host plant cells by AM fungi (Kosuta et al. 2008).

Potassium transport

Potassium, which represents the third primary mineral macronutrient and the most abundant cation in a plant cell, is pivotal for plant nutrition and growth. Its accumulation by plants is ensured by a whole set of different transport systems that contribute to maintaining cytosolic concentrations of 60–150 mM (Leigh and Jones 1984). K^+ plays a role at both cellular and whole plant levels. Potassium uptake by symbiotic fungi leading to increased plant K^+ absorption has been reported for both ECM and AM associations (Marschner and Dell 1994). However, putatively involved K channels and transporters have so far only been identified in ECM. Potassium transport has been rather well described on a molecular level in yeast and plants (Rodrìguez-Navarro 2000; Ramos et al. 2011b).

Potassium transport in arbuscular mycorrhiza

Increases in potassium uptake in AM-interacting plants have been reported (Smith and Read 2008). For example, greater K^+ uptake has been shown in mycorrhizal plants upon interaction with *R. fasciculatus* (Huang et al. 1985). Up to 10 % of the K^+ uptake in mycorrhized couch grass (*Elymus repens*) was mediated by ERM uptake (Li et al. 1991a). Significant improvements of K^+ acquisition by olive trees upon AM interaction with *R. irregularis*, *Claroideoglomus claroideum* and *F. mosseae* were 3.4-, 3.7- and 6.4-fold, respectively, and contributed to enhanced resistance against salt stress (Porras-Soriano et al. 2009). The interaction between plant K^+ status and hydraulic properties was recently studied in the AM between *Zea mays* and *R. irregularis* (El-Mesbahi et al. 2012). The authors showed that K^+ supply caused an increase in hydraulic conductivity, indicating K^+ uptake only in AM-mycorrhized plants. A specific co-localization and similar K^+/P_i ratios between in *R. irregularis* spores, hyphae (Olsson et al. 2008) and vesicles (Olsson et al. 2011) suggest an interaction between these elements and therefore a tight regulation of transport processes.

Improvement of K^+ nutrition upon AM interaction could be due to enhanced expression and activity of plant K^+ transport systems and/or the presence of efficient K^+ transporters in the ERM that extends through the soil. Indeed, a plant K^+ transporter belonging to the K^+ uptake permease (KUP) family was found 44-fold upregulated in mycorrhizal roots of *L. japonicus* (Guether et al. 2009b), whereas in *M. truncatula* a K^+ transporter from the same KUP family (Mtr. 32208.S1_at) was 28-fold induced by nodulation, but not by AM (Benedito et al. 2010).

However, direct molecular identification and characterization of K^+ transport systems for AM fungi is as yet missing. The available EST sequences from *R. irregularis* (http://mycor.nancy.inra.fr/IMGC/GlomusGenome) allow for the identification of seven short sequences related to K^+ transport systems. The BlastX on the ECM fungus *H. cylindrosporum* genome database suggests that four sequences could belong to the voltage-gated K^+ channels of the *Shaker*-like family, two sequences are probably related to β-subunits that putatively interact with K^+ channels of the *Shaker* family, and one sequence seems to be close to the KUP/HAK transporter family. Complete full-length cloning is necessary to unravel the mechanisms of K^+ transport systems in *R. irregularis*.

Potassium transport in ectomycorrhiza

The beneficial effects of ECM symbiosis for plant K nutrition are widely described (Rygiewicz and Bledsoe 1984; Smith and Read 2008). Net K^+ uptake was measured for three different ECM fungi to determine their kinetic parameters and their interaction with NH_4^+ (Jongbloed et al. 1991). Potassium uptake by the fungus was also shown using ^{86}Rb as the tracer (Finlay 1992). Jentschke et al. (2001) reported that at least 5–6 % of total K^+ in Norway spruce seedlings is provided by the ECM fungus. Improvement of K^+ homeostasis by *P. involutus* in mycorrhized poplar under salt stress has also been reported recently (Li et al. 2012). Mobilization of K^+ (and other minerals) by ECM fungi represents a possible mechanism involved in the observed improvement of K^+ nutrition (Jongmans et al. 1997; Wallander and Wickman 1999; Landeweert et al. 2001). Expression regulation of plant K^+ transport systems upon ECM interaction can be assumed, but has not been reported so far. In addition, the presence of

high-capacity K^+ absorption transporters in fungi can be assumed too.

Recent sequencing data confirm the presence of a whole set of K^+ transporters in ECM fungi. Members of the K^+ transporter families Trk/Ktr/HKT (Corratgé et al. 2007; Corratgé-Faillie et al. 2010) previously identified in yeast (Gaber et al. 1988; Ko and Gaber 1991), KUP/HAK described in *Neurospora crassa*, yeast and plants (Haro et al. 1999; Grabov 2007), as well as K^+ channels from the TOK family or from the *Shaker*-like family (Lambilliotte et al. 2004) were identified partly from EST libraries and are represented in the sequenced genomes of ECM fungi. Both K^+ channel families are structurally distinct from each other. Members of the *Shaker*-like family are characterized by the presence of six transmembrane domains including a K^+-selective pore, whereas members of the TOK family harbor eight transmembrane domains and two K^+-selective pore domains. Interestingly, voltage-dependent K^+ channels from the *Shaker*-like family, originally described in animals (Papazian et al. 1987; Jan and Jan 1997) and later in plants (Sentenac et al. 1992; Gambale and Uozumi 2006), have, to our knowledge, not been found in yeast or in higher fungi.

In contrast, the TOK family was first reported in yeast (Ketchum et al. 1995), but never in animals or plants, and seems to be specific for yeast and higher fungi. Nevertheless, functional characterization has so far only been achieved for *H. cylindrosporum* K^+ transporter Trk1 (Corratgé et al. 2007). HcTrk1 complemented a K^+-deficient yeast mutant and transported K^+ and Na^+ when expressed in *Xenopus* oocytes. Functional characterization of fungal members of the *Shaker*-like family has failed so far, but functional expression of members of the TOK family is currently under investigation (Zimmermann, unpublished data). Further studies are needed to understand the localization and physiological function of these K^+ transporters in the context of symbiotic interactions. The identification of this set of K^+ transporters and channels allows us to state that Trk and KUP transporters could be involved in K^+ absorption from the soil and K^+ channels from the TOK and the *Shaker*-like family for its secretion towards the host plant.

Transport of other ions

Ca and Mg absorption and transport has been shown, e.g. for ECM mycelium (Jentschke et al. 2000, 2001). Ca accumulation as Ca-oxalate was observed in ERM from ectomycorrhized roots of *Pinus radiata* and *Eucalyptus marginata* (Malajczuk and Cromack 1982). Using a vibrating probe to measure net fluxes along non-mycorrhized and mycorrhized roots of *Eucalyptus globulus* colonized by *Pisolithus* sp, Ramos et al. (2009) found that colonized roots had a higher capacity for Ca^{2+} uptake. In addition, Ca^{2+} oscillations, which are generally involved in signalling during plant–microbe interactions, have been described as part of the signalling between symbiotic partners of the AM symbiosis between *M. truncatula* and *R. irregularis* (Kosuta et al. 2008). Copper and zinc uptake was also increased in AM-interacting plants (Manjunath and Habte 1988). Li et al. (1991b), using *T. repens*, estimated that the AM interaction accounted for up to 62 % of the total Cu uptake. Transcriptional analysis of *M. truncatula* mycorrhiza-induced transporters revealed the upregulation of a zinc–iron permease and of a Ca^{2+} channel from the TRP-CC family (Benedito et al. 2010). Besides the increased Zn uptake in deficient conditions, increased protection against toxicity was also demonstrated (Li and Christie 2001; Zhu et al. 2001). Burleigh et al. (2003) suggested that one protection mechanism could be the downregulation of the plant Zn transporter (in *M. truncatula*) when the root is colonized by AM fungi. Less is known about anion transport. Among the few pieces of evidence available, a chloride channel, belonging to the ClC family, was upregulated upon mycorrhization in *M. truncatula* (Benedito et al. 2010).

The first Zn transporters from the cation diffusion facilitator family were identified in AM fungi (*R. irregularis*; Gonzalez-Guerrero et al. 2005) and ECM fungi (*H. cylindrosporum*; Blaudez and Chalot 2011). The *H. cylindrosporum* transporter HcZnT1 is localized on ER membranes when expressed in yeast and mediates Zn storage in intracellular vesicles. These transporters could play a role in Zn homeostasis, protecting both mycobiont and host plant from Zn stress. Analysis of the *T. melanosporum* genome recently allowed for the identification of 58 metal transporters (Bolchi et al. 2011).

Water channels

Water uptake improvement is a crucial benefit for mycorrhized plants, mainly because it increases their drought resistance (Lehto and Zwiazek 2010; El-Mesbahi et al. 2012). Aquaporins (AQPs) represent a family of channel proteins that mediate the selective movement of water, but also a wide range of small neutral solutes, across the membrane of plants, animals and microbes. Presently, plant AQPs are classified into seven subfamilies, namely plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), NOD26-like intrinsic proteins (NIPs), small basic intrinsic proteins, x intrinsic proteins, hybrid intrinsic proteins and GlpF-like intrinsic proteins (Johanson and Gustavsson 2002; Wallace and Roberts 2004; Danielson and Johanson 2008; Gupta and Sankararamakrishnan 2009). Mycorrhization could stimulate the expression and/or activity of plant aquaporins (Dodd and Ruiz-Lozano 2012), but fungal aquaporins could also directly contribute to a more efficient water transfer from the soil to the host tissues.

So far, scarce data have been available about the identification and the characterization of these water channels in the mycorrhizal context and on their implication in water and solute exchanges between fungi and plants. The movement of water through ERM and between mycorrhizal symbionts is still little understood.

Water transport in arbuscular mycorrhiza

First evidence of the involvement of plant aquaporins in the altered water uptake and transport capacities of mycorrhized plants was reported by Roussel et al. (1997) and Krajinski et al. (2000), who found mycorrhiza-induced expression of TIP aquaporins in parsley and *M. truncatula*. Uehlein et al. (2007) also found that PIP and NIP aquaporin gene expression was upregulated by AM symbiosis in *M. truncatula*. In contrast to the reports of Krajinski et al. (2000) and Uehlein et al. (2007), who used well-watered conditions, several studies deal with the combined influence of AM symbiosis and abiotic stresses on aquaporin gene expression. The effect of reduced expression of the tobacco PIP gene (NtAQP1) was investigated in mycorrhized *NtAQP1*-antisense tobacco plants under drought stress and well-watered conditions (Porcel et al. 2005). Reduction of *NtAQP1* expression had no effect on the colonization by AM fungi. However, under drought stress, the shoot dry weight and the root fresh weight of the wild-type tobacco plants were higher than in the *NtAQP1*-antisense plants. Therefore, NtAQP1-mediated water transport seems to be important for the efficiency of symbiosis under drought conditions. Data from Ouziad et al. (2005) indicate a decrease in the expression of PIP and TIP aquaporins induced by AM colonization and salt stress in tomato. Porcel et al. (2006) observed decreased aquaporin expression in both non-mycorrhized and mycorrhized soybean and lettuce plants under drought stress conditions. In common bean (*Phaseolus vulgaris*), AM symbiosis interfered with aquaporin expression under drought, cold and salinity stresses and prevented stress-induced inhibition of root hydraulic conductance (Aroca et al. 2007). Under drought stress conditions, Ruiz-Lozano et al. (2009) showed that some PIP genes were upregulated by ABA in non-AM maize plants and downregulated in AM plants. However, the downregulation of another PIP gene by ABA was observed in AM plants, whilst in non-AM plants no significant changes were observed for that same gene. In contrast to the results regarding the regulation of host aquaporin expression by AM symbiosis, very few reports describe fungal aquaporins. Aroca et al. (2009) cloned the first aquaporin (GintAQP1) of the AM fungus *R. irregularis*. Its expression was increased in the ERM from the root compartment of root organ cultures when an osmotic NaCl stress was applied to the hyphal compartment. Furthermore, plant aquaporin gene expression increased when the ERM was stressed by NaCl. The authors assume that there is a communication mechanism between the extra- and intraradical mycelia and even between symbiotic partners, suggesting that a fine dialogue takes place at the plant–fungus interface to determine the water transport of the two partners (Maurel and Plassard, 2011). The recent accession of the *R. irregularis* transcriptome had allowed for the identification of two new aquaporin genes (Tisserant et al. 2012).

Water transport in ectomycorrhiza

Although plant AQPs have been extensively studied so far (Maurel et al. 2008, 2009; Wudick et al. 2009), their implication in ECM interactions is poorly understood. In a *P. tremula*×*tremuloides* cDNA library, seven aquaporin genes were identified, and functional expression in *Xenopus* oocytes confirmed their water permeability (Marjanovic et al. 2005a). The transcripts of two of them (*PttPIP1.1* and *PttPIP2.5*) were increased during symbiosis, suggesting a putative role in water uptake in symbiotic conditions. In addition, a higher transcript level of *PttPIP2.2* and *PttPIP2.4* poplar genes was described in mycorrhized plants under drought stress (Marjanovic et al. 2005b). In contrast, two *Betula pendula* major intrinsic protein (MIP) drought markers were downregulated during *P. involutus* early mantle development and Hartig net formation (Le Quéré et al. 2005). However, the expression level of these two genes became equivalent between non-mycorrhized plants and mycorrhized plants at later stages. Thus, the drought resistance mechanism that occurs during the early stage of symbiosis establishment and is characterized by the downregulation of these two MIPs was reversed. These data suggest that the protection of plants from drought stress by mycorrhization is partially mediated by a reorganization of plant aquaporin expression.

On the fungal side, a recent study deals with the role of fungal AQPs during the ECM interaction between *P. tremula*×*tremuloides* and *L. bicolor* (Dietz et al. 2011). Gene expression, protein function and the putative roles in symbiosis of several genes (one classical aquaporin, three Fps-like aquaglyceroporins and two other aquaglycoporins) were investigated. Five of these six fungal proteins were water-permeable during heterologous expression in *Xenopus* oocytes, whereas the two Fps-like aquaglyceroporins, Lacbi1:317173 and Lacbi1:391485, which were upregulated during symbiosis, were permeable to NH_3/NH_4^+ in yeast cells; these data suggest an implication of the fungal N transport towards the plant. This kind of protein was already considered as part of an alternative N transport system to the host plant (Chalot et al. 2006). However, this was the first evidence of N export out of fungal cells by AQPs, confirming the capacity of these water channels to transport not only water but also low-

molecular-weight compounds (Wudick et al. 2009). To carry on with the study of higher fungi AQPs, analyses of their membrane localization, posttranslational regulation and of their exact role in mycorrhization remain to be performed (Maurel and Plassard 2011). Recently, access to the ECM fungus *H. cylindrosporum* genome showed a panel of six AQP-like members, similar to *L. bicolor* (personal communication).

In the coming years, it will be critical to study the localization of plant and fungal AQPs in the context of mycorrhizal symbiosis to better understand their role in soil–fungus–plant water continuum fluxes.

Future challenges

Mycorrhizal fungi render a wide range of ecosystem services. Unraveling the mechanisms that underlie high nutrient use efficiency by mycorrhizal plants and carbon allocation in a context of mutualistic biotrophic interactions is therefore critical for managing croplands and forests soundly. Indeed, nutrient availability, uptake and exchange in biotrophic interactions drive plant growth and modulate biomass allocation. These parameters are central for plant yield, a major issue in the context of high biomass production. Substantial evidence on how the rational use of mycobiont properties could significantly contribute to decreasing fertilizer and pesticide use in agriculture and forestry has accumulated. Interestingly, as highlighted in the present review, in the last decade, several studies focusing on mycorrhizal interactions have identified some key transporters for nutrient uptake or metabolite transfer at the biotrophic interface. Knowledge about the transportome blueprint at the biotrophic interface has drastically increased. For example, huge progress has been made in the understanding of the P transportome of mycorrhizal plants, especially in AM symbiosis, with the evidencing of a mycorrhizal pathway (MP) different from the direct plant pathway (DP). The MP is mediated by AM-inducible plant Pht1 transporters whose deletion or impaired expression dramatically reduces arbuscule formation and plant P accumulation. In the same trend of thought, it is important to mention that although several nitrogen (ammonium, nitrate, amino acid, peptide) transporters are now identified and characterized for both plant and fungal partners, the nature of the nitrogen compounds exchanged between fungi and plant cells is still unclear. We can also note that in *Medicago*, for example, the sucrose transporter family has been identified, but no study has yet focused on the 50-odd putative monosaccharide transporters, let alone on their role in mycorrhizal association.

The transportome map with its highways and crossroads is still far from complete. Major actors of the mycorrhizal transportome of nutrient efflux at biotrophic interfaces are still missing, and the regulation of nutrient exchanges inside and between organisms is still poorly understood. However, recent advances are going to help identify and characterize the key transporters of mycorrhizal interactions. Transcriptomic and metabolomic analyses at the different interfaces (soil–fungi versus fungi/plant cells) using laser capture microdissection will be essential for determining the functional polarization of transporters at the two interfaces. New studies focusing on (1) the functional polarization of transporters at the biotrophic interfaces and (2) the understanding of how plant and fungal partners regulate reciprocal nutrient exchanges are highly required.

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