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Review

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Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks

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Summary

Arbuscular mycorrhiza (AM) symbiosis occurs between obligate biotrophic fungi of the phylum Glomeromycota and most land plants. The exchange of nutrients between host plants and AM fungi (AMF) is presumed to be the main benefit for the two symbiotic partners. In this review article, we outline the current concepts of nutrient exchanges within this symbiosis (mechanisms and regulation). First, we focus on phosphorus and nitrogen transfer from the fungal partner to the host plant, and on the reciprocal transfer of carbon compounds, with a highlight on a possible interplay between nitrogen and phosphorus nutrition during AM symbiosis. We further discuss potential mechanisms of regulation of these nutrient exchanges linked to membrane dynamics. The review finally addresses the common mycorrhizal networks formed AMF, which interconnect plants from similar and/or different species. Finally the best way to integrate this knowledge and the ensuing potential benefits of AM into sustainable agriculture is discussed.

I. Introduction

The evolutionary history of land plants and the evolution of arbuscular mycorrhizal fungi (AMF) are inextricably linked. Arbuscular mycorrhiza (AM) is an ancestral mutualistic symbiosis that appeared around 400 Ma with the emergence of the first terrestrial plants (Redecker *et al.*, 2000), and it established between soilborne fungi of the subphylum *Glomeromycotina* (Spatafora *et al.*, 2016) and host plant roots. AM symbiosis affects ≤ 80% of terrestrial plants, most of which are cultivated plants. AMF hyphae penetrate the root epidermis to colonize cortical cells and form arbuscules, composed of fungal hyphae ensheathed in a modified form of the cortical cell plasma membrane termed the periarbusclar membrane. This interaction allows plants to improve the use of the soil natural resources and to better respond to the abiotic constraints (Gianinazzi *et al.*, 2010; Lenoir *et al.*, 2016) they encounter in their environment, notably climatic changes (Torres *et al.*, 2018), drought stress (Symanczik *et al.*, 2018), water deficit (Balestrini *et al.*, 2018), salinity (Ruiz-Lozano *et al.*, 2012) or heavy metal contamination (Shi *et al.*, 2018; Torres *et al.*, 2018). Moreover, mycorrhizal plants also respond better to biotic constraints and often show increased tolerance to

pathogens – mycorrhiza-induced resistance – which occurs in a wide variety of plant species including important crop species (Pozo & Azcon-Aguilar, 2007; Cameron *et al.*, 2013).

The management and valuation of the ecosystem services provided by AMF is going to become one of the major challenges for optimizing plant production qualitatively and quantitatively in the context of an agriculture with limited synthetic chemical inputs. The optimal management of AMF in an ecological engineering of plant production systems and in the selection of plants that maximize their benefits requires an understanding of the complex mechanisms underlying the establishment and functioning of AM symbiosis (Gianinazzi *et al.*, 2010).

II. Nutrient transfer mechanisms in AM symbiosis

1. Nutrient transfer mechanisms between AMF and host plants in AM symbiosis

Improved mineral nutrition is considered as the main benefit of AM symbiosis, especially as regards phosphorus (P) and nitrogen (N) nutrition of mycorrhizal plants: these two essential macro-elements are needed in large amounts by plants, and most plants constantly cope with low N and P concentrations in natural environments (Elser *et al.*, 2007). AM-symbiosis-compatible plants are assumed to have a specific 'mycorrhizal phosphate uptake' (MPU) pathway besides the direct phosphate uptake by the root epidermal cells (Fig. 1) that provides most of their phosphate.

Although labelling experiments clearly demonstrated that AMF hyphae take up and transfer organic and inorganic N from the soil to the host plant, the mycorrhizal N uptake pathway(s) are less understood than the MPU pathway.

Phosphorus Improved P nutrition is the most recognized benefit of AM symbiosis for host plants. Most of the soil P (Rausch & Bucher, 2002) is bound inside organic molecules or to mineral surfaces, or precipitated in the form of poorly soluble phosphate salts (Fig. 1), hence inaccessible to plants. Plants can only take up orthophosphate (Pi) from the soil solution via specific phosphate transporter proteins expressed in the roots, belonging to the 'direct phosphate uptake (DPU) pathway' (Fig. 1). The uptake of soluble Pi from the zone around the plant roots results in a Pi-depletion zone nearby the root surface as a consequence of the low mobility of Pi in soils. The intensive growth of roots beyond this depletion zone is a way to access new Pi sources.

Apart from the DPU pathway described above, most plants can take up P via the MPU pathway (Bucher, 2007). AMF hyphae grow beyond the Pi depletion zone and thus have access to Pi resources inaccessible to plant roots. AMF hyphae or microorganisms associated to AMF hyphae also can hydrolyze organic P, and thereby increase the soil organic P turnover (Fig. 1). Inorganic P is taken up by AMF hyphae, transferred to intraradicular fungal structures, and released into the periarbuscular space in arbuscule-containing cells. H^+/Pi and putative Na^+/Pi symporters have been described in the analysis of AMF transcripts of *Rhizophagus irregularis*, *Funneliformis mosseae* and *Rhizophagus clarus*. However, even if one Na^+/Pi transporter (*R. irregularis* RiPT5) was suggested to be involved in Pi export from the AMF into the apoplastic interface, the mechanisms remain unknown (Garcia *et al.*, 2016).

Phosphorus is then taken up by plant cells through specific P transporter proteins (Fig. 2). Pi transport from the rhizosphere to other plant organs or sink tissues is mediated by P transporters from the Phosphate transporter (PHT) protein family, which consists of four subfamilies (PHT1–4) (Rausch & Bucher, 2002; Nagy *et al.*, 2005). The PHT1 subfamily contains PHT proteins that mediate Pi uptake from the soil via DPU. However, PHT1 members cluster into three subgroups, and most of the PHT1s clustered in subgroup 2 are induced in AM roots (Wang *et al.*, 2017a,b). Such phosphate transporter genes transcriptionally induced in AM roots have been described In several plant species such as *Solanum tuberosum* (Rausch *et al.*, 2001), *Medicago truncatula* (Harrison *et al.*, 2002), *Oryza sativa* (Paszkowski *et al.*, 2002), *Lycopersicon esculentum* (Xu *et al.*, 2007), *Petunia axillaris* (Breuillin *et al.*, 2010), *Astragalus sinicus* (Xie *et al.*, 2013), *Sorghum bicolor* (Walder *et al.*, 2015), *Lotus japonicus* (Volpe *et al.*, 2016) and *Zea mays* (Liu *et al.*, 2018). A well-studied member of subgroup 2 is *M. truncatula* MtPT4, which is localized at the periarbuscular membrane and mediates Pi uptake from the periarbuscular space (Javot *et al.*, 2007). In addition to the role of AM-induced PHT plant genes in Pi acquisition, roles have been suggested in regulating arbuscule morphogenesis, maintaining symbiosis, mediating arbuscule lifespan (Breuillin-Sessoms *et al.*, 2015) and in the Pi-sensing machinery in root tips (Volpe *et al.*, 2016). The intensity of the P flow at the arbuscule interface may depend on the P supplied at the level of the extraradical mycelium (Fiorilli *et al.*, 2013), but also depends on the capability of the AMF to reabsorb Pi or to leave it in the periarbuscular space, thus exerting a control over the amount of P delivered to the host (Balestrini *et al.*, 2007; Walder *et al.*, 2016). Finally, Pi dependency is selectively different among plants, but depends also on the responsiveness and effectiveness of the interaction between the plant and the AMF species (Janos, 2007).

The PHT family are phosphate/proton symporter proteins; phosphate uptake from the periarbuscular space by PHT proteins requires a proton gradient across the periarbuscular membrane resulting from the activity of the plasma membrane H^+-ATPase. In AM roots, a plasma membrane H^+-ATPase gene is induced (Gianinazzi-Pearson *et al.*, 2000; Krajinski *et al.*, 2002) and co-regulated with the mycorrhiza-induced PHT proteins (Gaude *et al.*, 2012). The mycorrhiza-induced H^+-ATPase was localized at the periarbuscular membrane in *M. truncatula* and rice, and its activity was proven to be essential for phosphate uptake from the periarbuscular space (Krajinski *et al.*, 2014; Wang *et al.*, 2014).

Nitrogen Nitrogen (N) is required in significant quantities as it constitutes 1–5% of the plant DW. However, plant-available N is a limiting factor in ecosystems and is heterogeneously distributed in the soil; therefore, the establishment of microbe-mediated N uptake is crucial (Courty *et al.*, 2015). Approximately one-third of the root protein N could be provided by symbiotic AMF (Govindarajulu *et al.*, 2005). This N uptake is mediated by various transport systems including transport of inorganic N in the forms of ammonium (NH_4^+) and nitrate (NO_3^-), and of organic N in the forms of amino acids and peptides (Figs 1, 2). Nitrogen ions taken

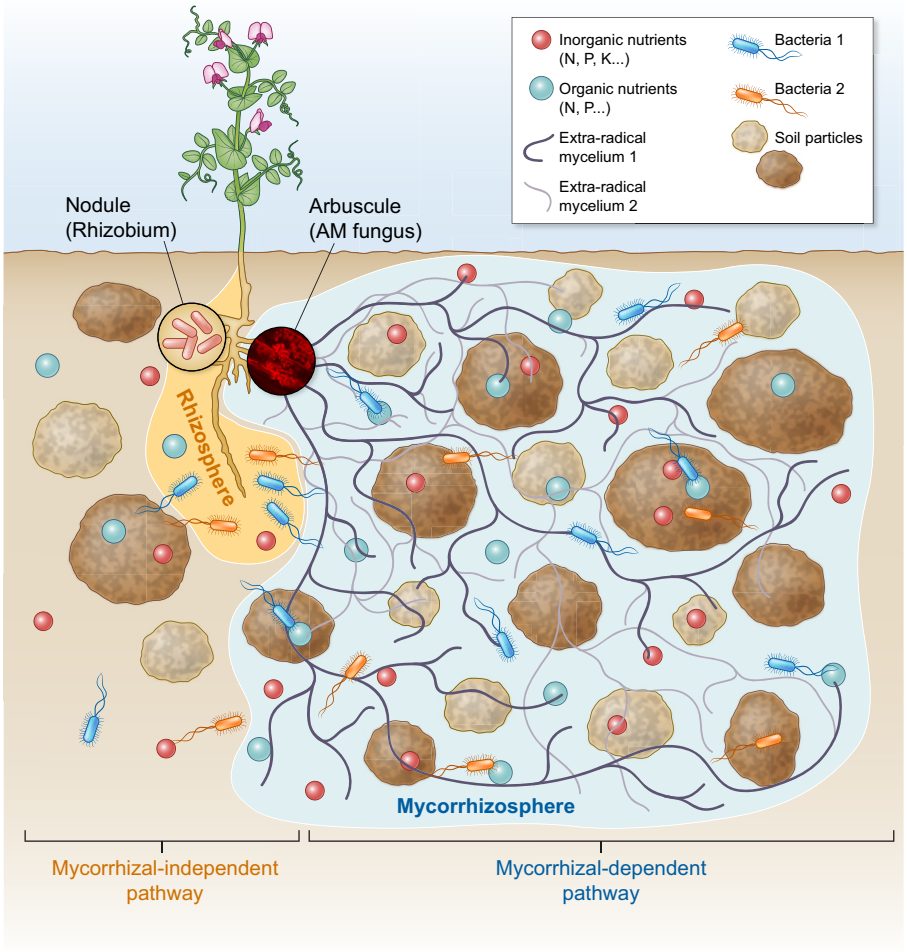

Fig. 1 Soil nutrients, bacteria and mycorrhizal vs nonmycorrhizal pathways. The extraradical mycelium 1 and 2 correspond either to two different arbuscular mycorrhizal fungal (AMF) species or two isolates from the same species. The extraradical mycelium is an extension of the root system, foraging soil that is not accessible to the root system. Some bacteria interact with the extraradical mycelium to mobilize nutrients. Leguminous plants have two different root symbioses: arbuscular mycorrhizal (AM) symbiosis and rhizobia.

up from the soil by AMF hyphae are converted into arginine and transported in this form across the hyphae towards the host roots. Then N is released into the roots without any carbon (C) links (Govindarajulu *et al.*, 2005).

Nitrate is often the main N source in fertilized soil solutions (Jämtgård *et al.*, 2010) and it is more mobile than NH_4^+. Nitrate is taken up via an energy-dependent uptake process by specific, highly regulated transporters (Fig. 2) belonging to the huge nitrate and peptide transporter families – the NPF (NRT1/PTR family; Léran *et al.*, 2014), NRT2 and NRT3 families (Orsel *et al.*, 2002; Bai *et al.*, 2013). In plants, NPF is a large protein family (85, 79 and 62 members in rice, poplar and Arabidopsis, respectively) whose members transport either NO_3^- with low affinity or di-/tripeptides (Krouk *et al.*, 2010), and also nitrite, glucosinolates or phytohormones (Bai *et al.*, 2013). In AMF, only one high-affinity transporter belonging to the NRT2 family has so far been described in *R. irregularis* (GiNT), and it was shown to be expressed in all AMF tissues (spores, extra and intraradical mycelium, arbuscules). GiNT could have a key role at the symbiotic interface by establishing a competition for NO_3^- between the plant and the AMF, through regulating bidirectional fluxes (Tian *et al.*, 2010; Koegel *et al.*, 2015). GiNT could be regulated at the plant–soil interface by the internal concentrations of NH_4^+ and/or glutamine (Fellbaum *et al.*, 2012). In roots, the regulation of NO_3^- assimilation depends on both the presence of AMF (Gomez *et al.*, 2009; Guether *et al.*, 2009), and the N and P statuses of the two partners (Hohnjec *et al.*, 2005; Drechsler *et al.*, 2017).

However, soil organisms often assimilate NH_4^+ directly because it is a more energy-efficient way than the uptake and ensuing reduction of NO_3^- to NH_4^+ (Marschner, 1995). Several plant ammonium transporters (AMTs), partly characterized as high-affinity AMTs and upregulated during AM symbiosis (reviewed by Courty *et al.*, 2015; Garcia *et al.*, 2016), are dispatched in the four AMT1/2/3/4 clades (Loqué & von Wiren, 2004) (Fig. 2). In monocots, the AM-inducible AMT3;1 seems to be conserved among plant families, suggesting that AMTs probably evolved from a common ancestor (Koegel *et al.*, 2017).

Ammonium, and in some cases NH_3 (as shown for *L. japonicus* LjAMT2;2; Guether *et al.*, 2009; Bücking & Kafle, 2015), is actively transferred by AMF to the acidic periarbuscular space of the sole arbuscule branches. Then, the uncharged NH_3 is released by AM-induced AMT into the cytoplasm of arbuscule-containing cells (Kobae *et al.*, 2010; Koegel *et al.*, 2013, 2017). Thus, protons remain in the periarbuscular space, and could reinforce the gradient of H^+-dependent transport processes (see Section 2.1). AMTs could differ in their functions/activities; they might have a sensing

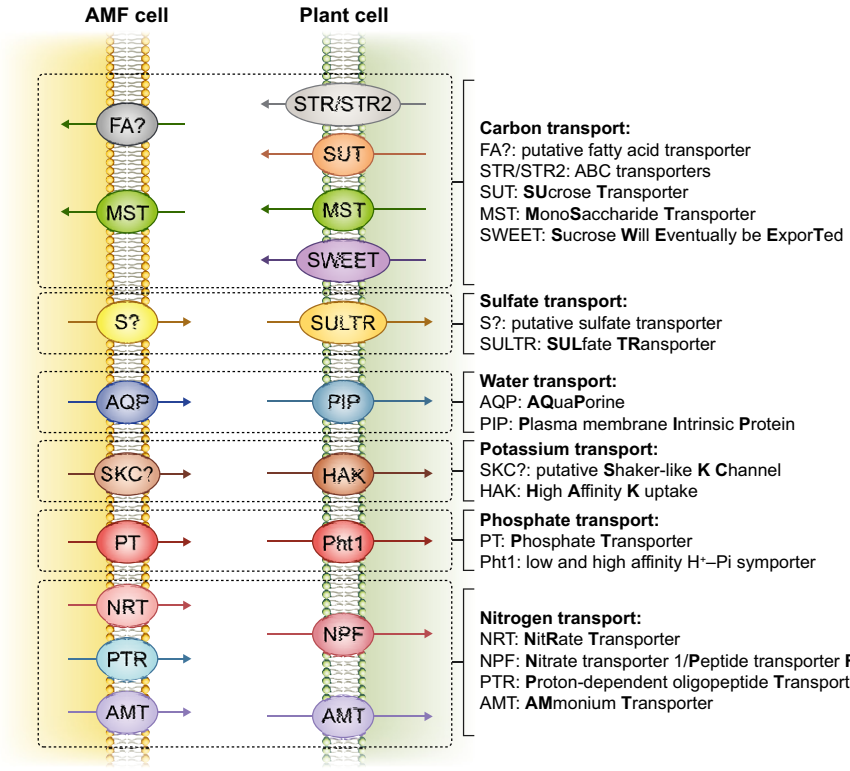

Fig. 2 Different transporters involved in carbon, nitrogen, phosphorus, sulfate, potassium and water exchanges at the biotrophic interface in the arbuscular mycorrhiza. Colours of arbuscular mycorrhizal fungal (AMF) and plant transporters involved in the transport of the same element are similar.

or signalling function, a role in the pre-penetration response, or be required for arbuscule formation and lifespan, as shown in *M. truncatula* and *L. japonicus* (Javot *et al.*, 2007, 2011; Gomez *et al.*, 2009; Breuillin-Sessoms *et al.*, 2015). Apart from arbuscules, AMF hyphae also could be involved in symbiotic N transfer; aquaporins such as Nod 26-like intrinsic protein act as low-affinity NH_4^+ transporters in hypha-colonized cortical cells in soybean and Medicago (Uehlein *et al.*, 2007; Hwang *et al.*, 2010).

The AMF species have different abilities and efficiences to take-up NH_4^+ and transfer N to host plants (Mader *et al.*, 2000), reflecting a degree of functional complementarity. Two high-affinity AMTs (*GintAMT1* (Lopez-Pedrosa *et al.*, 2006) and *GintAMT2* (Perez-Tienda *et al.*, 2011)) and one low-affinity AMT (*GintAMT3*; Calabrese *et al.*, 2016) have been identified in *R. irregularis*. *GintAMT1* could be involved in soil NH_4^+ acquisition by the extraradical mycelium when NH_4^+ is present at low concentrations, for example in acidic soils. *GintAMT2* could be involved in the recovery of NH_4^+ leakage through the fungal metabolism, as observed in yeast. The intensity of NH_4^+ transfer at the symbiotic interface through GintAMT3 could be linked to the access to a P source (Fig. 2). In addition, the regulation of the three *GintAMTs* depends on C availability, highlighting a strong interconnection between C and N transfer during AM symbiosis (Fellbaum *et al.*, 2012). Anyhow, the three NH_4^+ transporters are thought to be important for symbiotic nutrient exchanges independently of the N conditions (Calabrese *et al.*, 2017), even if the mechanisms involved in NH_4^+ transfer from the AMF into the apoplastic interface remain unknown. NH_4^+ is proposed as a candidate for fungus-to-plant-cell transfer through the apoplastic space, or inorganic N exported through voltage-dependent cation channels (Chalot *et al.*, 2006).

In the soil, AMF can draw N from organic forms in the form of amino acids such as glycine, and in the form of small peptides besides inorganic N (Cliquet *et al.*, 1997; Hodge, 2001) (Fig. 2). An amino-acid permease (GmosAAP1) involved in transporting amino acids such as proline, serine, glycine, and glutamine across fungal membranes has been identified in *F. mosseae* (Jin *et al.*, 2005; Cappellazzo *et al.*, 2008). Some di- and tripeptide transporter (PTR) genes are specifically induced in AM roots or in arbuscule-containing cells (Casieri *et al.*, 2013), and in the AMF *R. irregularis* (RiPTR2, Belmondo *et al.*, 2014). RiPT2 might play a role in the uptake of small peptides from the soil, and the reuptake of peptides from the interfacial apoplast (Belmondo *et al.*, 2014).

Is plant control of AMF colonization dependent upon inorganic phosphate and nitrogen availability? Like Pi fertilization, inorganic N fertilization in the range of ≥ 100 mg of N per kg of soil reduces root colonization by AMF (Lanowska, 1966; Blanke *et al.*, 2005). Additionally, the C allocation to the fungus can be reduced under high external N concentrations around mycorrhizal roots (Olsson *et al.*, 2005). However, the response of mycorrhiza to fertilization depends highly on the context and the availability of other nutrients. Nitrogen addition negatively affects AMF colonization of roots in soils with low N : P ratios, but positively affects AMF colonization in soils with high N : P ratios (Johnson *et al.*, 2003, 2015). A single essential resource in limiting supply could control plant production, as mentioned in the law of the minimum (von Liebig, 1843; van der Ploeg *et al.*, 1999). It has therefore been

proposed that the relative availability of soil N and P determines whether or not mycorrhizal benefits outweigh their costs (Johnson *et al.*, 2015). This trade-off model of compromise balance predicts that N fertilization only is of benefit when the plant is limited by P and there will be positive effects from providing C to the roots and the AMF. When nutrient and light availability are manipulated, inorganic N sources can indeed elicit a mutualism scenario which is predicted by the trade-off balance model, in which both the plant and the fungus will benefit from a rich N source in a P-limited system (Johnson *et al.*, 2015). Additional evidence that this response is driven by the C-to-nutrient exchange dynamics was provided by Fellbaum *et al.* (2012). In agreement with Liebig's law of the minimum, long-term P inhibition of AM symbiosis is partially suppressed under low N conditions, suggesting that plants promote AM symbiosis as long as one of the two major nutrients is available in limiting amounts (Blanke *et al.*, 2005; Nouri *et al.*, 2014). Supporting the idea that the arbuscule lifespan is partly regulated by N, premature arbuscule degeneration is relieved when plants are deprived of N (Javot *et al.*, 2011). However, the recovery of AM colonization did not lead to increased N concentrations in these plants, suggesting that N starvation triggers a signal that promotes AMF colonization (Blanke *et al.*, 2005; Nouri *et al.*, 2014; Bücking & Kafle, 2015). Consistently, a functional peri-arbuscular ammonium transporter – AMT2;3 – was required for the low-N suppression of premature arbuscule degeneration in pt4 mutants, but with unchanged symbiotic N transport (Breuillin-Sessoms *et al.*, 2015). The authors thereby proposed that Pi or NH_4^+ transport through their respective symbiotic transporters acts to deliver nutrients to the root cells, and also initiates an unknown signalling mechanism that promotes the maintenance of arbuscules. Using petunia plants inoculated with *R. irregularis*, Nouri *et al.* (2014) found that only Pi and nitrate exerted a negative influence on AM root colonization, whereas other major plant nutrients such as potassium, calcium, magnesium, sulfate and iron did not influence mycorrhizal development at elevated concentrations.

2. Symbiotic C transfer to the fungus

As presented previously, AMF provide their host plants greater access to soil nutrients and water that are not directly reachable by/available to the host roots (Bago *et al.*, 2000). As a reward, the plant re-directs as much as 4% and ≤ 25% of its photosynthates towards mycorrhizal roots, to be exchanged with the fungal partner (Hobbie, 2006). AMF are obligate biotrophic organisms, which means that they cannot complete their life cycle and form new spores without intraradicular and intracellular colonization of a host plant. The basis of this biotrophy still remains to be untangled, but nutritional, physiological and genetic aspects have been considered (Bago & Bécard, 2002).

Sugar transport The sugar metabolism presumably is one of the keys to AMF biotrophy, and therefore it is essential to understand how the plant possibly controls the activity of fungal sugar transporters (Fig. 2). During the symbiotic phase, AMF receive all of the required C from their host plants, so that the specific AMF C metabolism was once considered to be the main reason for the biotrophic nature of these fungi. C-NMR spectroscopy using ^{13}C-labelled glucose or fructose initially showed that the intra- and extraradical hyphae of the AMF *R. irregularis* behaved like a metabolic bipole (Pfeffer *et al.*, 1999). Exogenously supplied hexoses such as glucose and fructose were taken up by the fungus through intraradical hyphae, but not through extraradical ones. However, the fact that no labelling was detected in extraradical hyphae by ^{13}C-NMR studies does not allow us to conclude absence of sugar transport or of some kind of metabolism as the definitive cause. Experiments using ^{14}C-labelled glucose in *R. irregularis* confirmed that the extraradical hyphae cannot take up glucose from the external medium. Enzymatic studies revealed a low activity of glycolysis enzymes (pyruvate kinase and glucose-6-P-dehydrogenase) as compared to the activity of the same enzymes in a saprophytic fungus (*Mucor mucedo*) (Shachar-Hill *et al.*, 1995; Solaiman & Saito, 1997). By contrast, neoglucogenic (glucose-6-phosphate-isomerase) activity was very high. The metabolism of extraradical hyphae thus appears very clearly directed towards glucose anabolism, indicating that hexoses are a negligible C energy source in this part of the fungus. Therefore, intraradical hyphae probably have a very different C metabolism from that of extraradical hyphae, and act like the 'energy engine' of the whole organism. However, experiments carried out on germinating spores of *R. irregularis* supplied evidence of a natural capacity to incorporate external glucose, but at very low concentrations. This transport was inhibited by high sugar concentrations, suggesting catabolic repression of the hexose transporter(s). The existence of hexose uptake in germinating spores was confirmed by the recent demonstration of the expression of a fungal mono-saccharide transporter (MST) in germinating spores (Ait Lahmidi *et al.*, 2016). Interestingly, these authors also provided for the first time experimental support for a primary role of two AMF MSTs (RiMST5 and RiMST6) in direct sugar uptake from the soil. Spore germination and initial hyphal growth during the pre-symbiotic phase do not directly depend on the presence of host roots. These findings highlight the complexity of sugar partitioning in plant–microbe interactions (PMI) in general, especially in AM as regards the obligate biotrophy of AMF.

After spore germination, hyphae can withdraw back into spores if no host root presence is sensed. AMF presumably save their limited pre-symbiotic metabolic resources through this mechanism. Subsequently, spores can re-germinate, and novel hyphae can be formed. This process of germination and hyphal withdrawal in the absence of host roots has been observed several times; it strongly suggests that AMF thus save their low C resources. Thus, an individual spore with limited resources has several timely independent chances to find a symbiotic partner.

Once a functional AM is established, arbuscules may be involved in the plant–AMF C transfer. Even if arbuscules are probably a major player in C exchanges during symbiosis, functional arbuscules do not appear to be required for fungal growth and spore production. Several plant mutants with defects in arbuscule development have been described (Ivanov *et al.*, 2012; Krajinski *et al.*, 2014; Park *et al.*, 2015), in which AMF kept growing through the root cortex. This implies that arbuscules might not be

the only site for C transfer to these C-autotroph organisms, as suggested by several publications (Smith *et al.*, 2001; Helber *et al.*, 2011; Ait Lahmidi *et al.*, 2016). Until recently (see the 'Lipid transport' section below), carbohydrates were considered as the major transport form of C to AMF (see Casieri *et al.*, 2013; Garcia *et al.*, 2016 for reviews). For > 40 yr, investigations of plant–fungus C fluxes strongly suggested that sugars were transferred through active or passive efflux mechanisms (Ho & Trappe, 1973; Doidy *et al.*, 2012a,b). Plants transport photosynthetically fixed C in the form of sucrose via the phloem into the root system, where sucrose is unloaded from the phloem and transported through the tissues (Fig. 3). Several plant SUcrose Transporter (SUT) proteins are regulated in mycorrhizal roots (Boldt *et al.*, 2011; Doidy *et al.*, 2012b; Gaude *et al.*, 2012), in line with the increased C partitioning and sink of mycorrhizal root systems. Investigations of the specific arbuscule-containing-cell transcriptome revealed no specific induction of potential sucrose transporter genes in this cell type, but increased promoter activity of putative sucrose and hexose transporter genes in cells adjacent to arbuscules or intercellular fungal hyphae (Gaude *et al.*, 2012). This shows a role of SUTs in C partitioning rather than direct C supply to the fungus in mycorrhizal roots.

Besides the key role of plant SUTs in the long-distance transport of sugars inside the host, several other families of plant and fungal sugar transporters are involved in sugar partitioning in AM (e.g. Casieri *et al.*, 2013; Garcia *et al.*, 2016). In plant sink organs, sucrose is cleaved by plant invertases, and starch is degraded into monosaccharides that are transported by MSTs, a huge family phylogenetically classified in seven clades (Lalonde *et al.*, 2004). Differently regulated MSTs potentially involved in C partitioning in AM have been identified (e.g. Harrison, 1996; Ge *et al.*, 2008). Concerning sugar uptake by the fungal partner, labelling experiments showed that AMF presumably do not take up sucrose directly from their plant host, but can take up hexoses (Bago *et al.*, 2000). Therefore, shoot-derived sucrose has to be cleaved into hexoses to be taken up by the fungal microsymbiont. Because the genomes of the so-far characterized AMF do not contain genes for known sucrose-cleaving enzymes such as sucrose synthases or invertases, sucrose has to be hydrolysed by the host cell wall invertase. Glucose is the major C form transferred to the AMF at the plant–fungal interface (Helber *et al.*, 2011; Ait Lahmidi *et al.*, 2016). The recently characterized plant SWEET (Sugars Will Eventually be Exported Transporter) family may include key players involved in the regulation of host–AMF exchanges (Chen, 2014). However, the precise transportome involved in the symbiotic efflux from host cells to the mycorrhizal apoplast remains unknown.

Fungal monosaccharide transporters were recently identified in Glomeromycota (Schüssler *et al.*, 2006; Ait Lahmidi *et al.*, 2016). Within each species, distinct MSTs seem responsible for sugar uptake at the plant–fungus and the soil–hypha interfaces, and for sugar partitioning within internal fungal structures (Garcia *et al.*, 2016). A putative Glomeromycota sucrose transporter has been identified in AMF (Helber *et al.*, 2011), but there is no demonstration of sucrose transfer into AM.

Lipid transport In addition to sugars, C also is provided by the host plant to the AMF in the form of fatty acids (FAs) (Bravo *et al.*, 2017; Jiang *et al.*, 2017; Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017) (Fig. 3). In plants, *de novo* FA biosynthesis occurs in plastids and requires the activity of a fatty-acid synthetase complex (FAS 1). Genes encoding potential FAS 1 are absent from the genomes or transcriptomes of the so-far characterized AMF such as *R. irregularis* or *Gigaspora rosea*. Hence, AMF are assumed to depend on host plants for *de novo* FA synthesis, another potential reason for the obligate biotrophy of these organisms. The FA auxotrophy of AMF is further supported by the fact that 12 genes related to lipid biosynthesis are exclusively present in the genomes of plants forming AM symbioses (Bravo *et al.*, 2016). Recent isotope labelling experiments clearly confirmed that *R. irregularis* cannot synthesize FAs *de novo* from carbohydrates (Jiang *et al.*, 2017), which supports the obligate FA auxotrophy of AMF. A genetic approach confirmed that lipids are involved in C transfer from plants to AMF: heterologous expression of an *Umbellularia californica* fatty acyl-ACP thioesterase (UcFatB) in *M. truncatula* produced lauric acid, whose abundance is normally extremely low in wild-type mycorrhizal roots (Trepanier *et al.*, 2005). When roots with heterologous UcFatB expression were colonized by an AMF, the newly developed fungal spores contained significant amounts of lauroyl groups in the fungal lipid fraction (Luginbuehl *et al.*, 2017). Lipids represent the major C-storage compounds in AMF, and lipid bodies occur as prominent structures in AMF spores, pre-symbiotically grown germ tubes, and symbiotic hyphae (Bago *et al.*, 2002). As reviewed by Rich *et al.* (2017) and Roth & Paszkowski (2017), the AM-specific plant thioesterase FatM releases 16:0 FAs (palmitic acid) which, when attached to CoA, are used as a substrate by glycerol-3-phosphate acyl transferase (GPAT) RAM2 to produce 16:0 β-monoacylglycerol (Fig. 3). This compound can be exported across the peri-arbuscular membrane by the half-ABC transporters STR and STR2. Although the influence of Pi availability on the plant proteins that direct lipid fluxes in arbuscules have not been investigated yet, the mycorrhiza-specific GPAT was found to belong to the genes expressed in all mycorrhiza fertilized with low phosphate, but not to the mycorrhiza of the low- or high-P control roots (Breuillin *et al.*, 2010). Moreover, the expression of STR and STR2, which mediate lipid fluxes into AMF, also was repressed by high Pi concentrations (Wang *et al.*, 2017a,b). Taken together, these findings suggest that depending on the Pi supply, the symbiont may be starved for plant lipid C.

3. Mycorrhizal benefits: a mutualism-to-parasitism continuum

Not all AMF are equally beneficial for the host (Johnson *et al.*, 1997; Smith & Smith, 2013). In natural ecosystems, plants can be colonized by dozens of species, and distinguishing AMF species is difficult: spore morphological traits can be distinguished with accuracy (Mosse & Bowen, 1968; Morton & Benny, 1990;

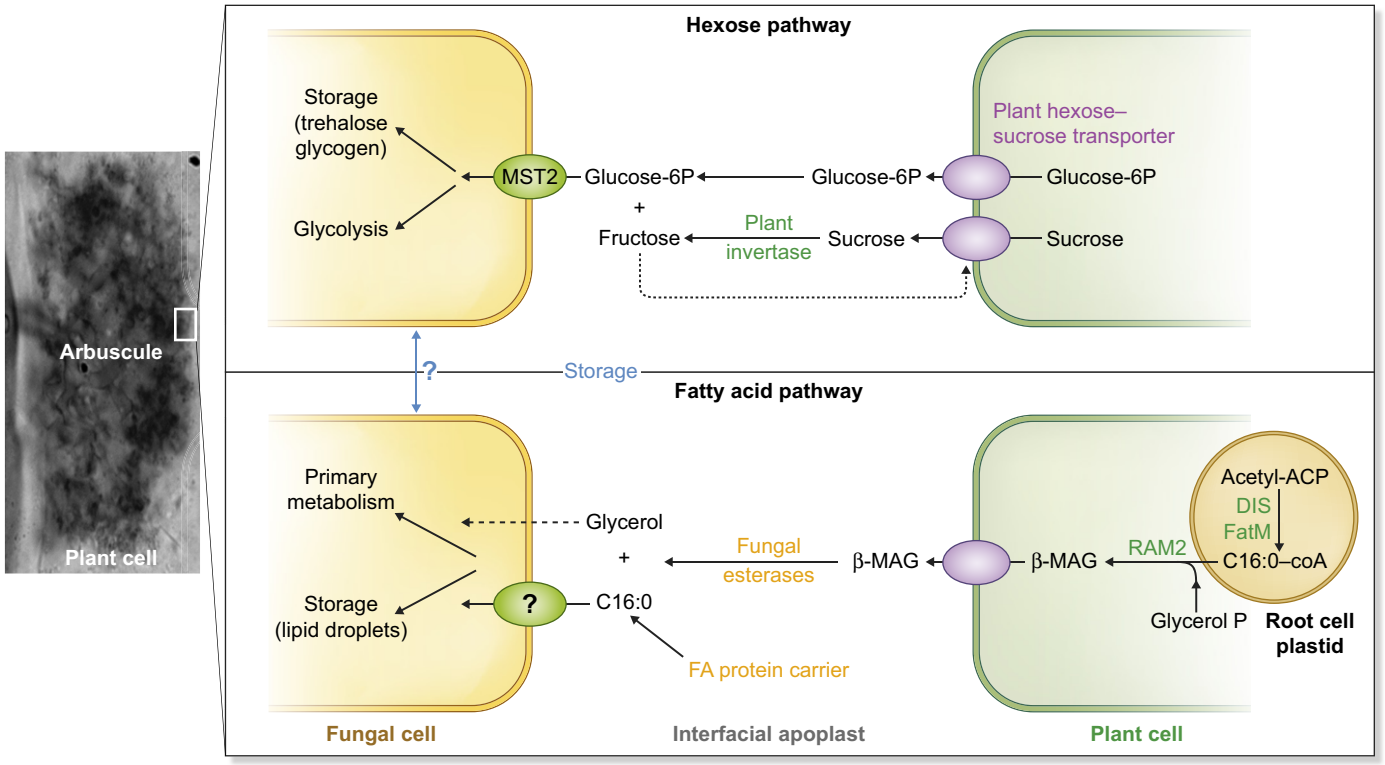

Fig. 3 Transfer of carbon as sugars and lipids at the biotrophic interface in the arbuscular mycorrhiza (AM).

Schüßler & Walker, 2010), but fungal structures (intercellular hyphae, vesicles and arbuscules) cannot. AMF species are classified mainly by sequence analysis of ribosomal RNA genes (SSU or LSU), but drawing the picture of a community's composition is problematic because of a limited number of AMF reference cultures (isolates of species) and a universal primer pair for the identification of operational taxonomic units (OTUs). A high intraspecific diversity is found in AMF. The concept of species defined by Mayr (2000) as groups of actually or potentially interbreeding natural populations that occupy a specific niche in nature is difficult to apply to Glomeromycota for three main reasons:

(1) AMF hyphae are coenocytic, so that intraindividual variation is difficult to distinguish from interindividual variation. Each fungal individual shows high genetic diversity among its own nuclei (i.e. Munkvold *et al.*, 2004; Borstler *et al.*, 2008; Mensah *et al.*, 2015). Anastomosis/hyphal fusion allow for the exchange of nuclei from genetically distinct AMF and the transmission of genetic markers in newly formed spores representing the progeny (Croll *et al.*, 2009). AMF isolates perform self-anastomosis (Giovannetti *et al.*, 2003), and > 90% of fusions are performed by wound healing within a same hypha (De La Providencia *et al.*, 2005). The capability of hyphae to perform self-anastomosis differs among AMF species (Pepe *et al.*, 2016). Moreover, anastomosis between AMF isolates depends on their vegetative compatibility or on their geographical origin (Giovannetti *et al.*, 2003).

(2) Obvious sexual structures are lacking in Glomeromycota, even if *c.* 85% of the core meiotic genes (i.e. HOPP2: homologous-pairing protein 2, an MND1 (meiotic nuclear division protein 1)), and the presence of homologues of putative sex-pheromone-sensing mitogen-activated protein (MAP) kinases and of mating-type gene homologues are present in the genome of *R. irregularis* DAOM197198 (Halary *et al.*, 2011; Tisserant *et al.*, 2012). As the exact function of these genes is unknown, cryptic sexuality could occur (Corradi & Bonfante, 2012).

(3) Mycoplasma-related endobacteria (MRE) belonging to a Mollicute lineage and living in the AMF cytoplasm have a widespread distribution across phylogenetic AMF lineages. However, their biological role in the physiology of their fungal hosts is largely unknown, but they could be involved in AMF functioning (i.e. vitamin B12 or growth hormone production, phosphate solubilization; Ghignone *et al.*, 2012) and in the pre-symbiotic growth phase (Salvioli *et al.*, 2016). The taxonomic composition of MRE differs among AMF individuals (Agnolucci *et al.*, 2015) and AMF species (Naito *et al.*, 2015).

This high intraspecific diversity among AMF may lead to high functional differences (extraradical hyphal extension, spore production, root colonization, water and nutrient flows) and to different mycorrhizal growth responses, without any phylogenetic support or significance (Mensah *et al.*, 2015; Koch *et al.*, 2017) (Fig. 4). We can hypothesize that the high genetic variability among different isolates could derive from a co-evolution between co-existing plant and fungal populations.

Available knowledge indicates that plants could control the degree of AMF colonization depending on their nutrient requirements. Pi and N have been identified as the major nutritional determinants of the interaction (Nouri *et al.*, 2014). The nutrients delivered to the root cortical cells are believed to trigger a signal that controls C release to the fungal partner. The rationale behind this

strategy is that a symbiont unable to deliver significant amounts of soil nutrients would only have access to low concentrations of C available in the root apoplast (Javot *et al.*, 2007). Although the nature of this signal is unknown, data from Pi-replete plants indicate that the plant host may restrict arbuscule development by reducing not only sugar, but also lipid delivery to the symbiont. Future knowledge about the regulation of this delivery upon high Pi or N fertilization regimes should shed light on the role of plant lipids in the regulation of AM symbiosis development.

4. The study of the impact of membrane lipids: a new tool to study brokers in the regulation of nutrient exchanges through symbiotic transporters?

Nutrient trades are the basis of AM symbiosis; they are regulated by transport systems present in both partners and involved in: (1) the long-distance transport of photosynthetic products from the leaves to the roots and then towards the fungal partner; and (2) the absorption/uptake of nutrients from the soil by the fungus and their transport to the plant. In this context, the incoming and outgoing nutrient flows, allowing exchanges through the soil–AMF, AMF–apoplasm and apoplasm–plant interfaces, are controlled by membrane transport proteins. These proteins are integral membrane proteins at least partially surrounded by the lipid bilayer. Membrane proteins and their functions are directly impacted by the membrane lipids through protein–lipid interactions or through the physical properties of the lipid bilayer. A rapidly emerging topic is the regulation of membrane proteins via compartmentalization in specific domains of the membrane, also called 'lipid rafts' (Simon-Plas *et al.*, 2010). According to the concept of membrane domains, biological membranes should no more be seen as homogeneous bilayers because membrane domains segregate active components inside membranes and are part of cellular processes (see Rajendran & Simons, 2005, for a review). The membrane domain concept was first established for mammalian and yeast cell membranes, but it is now also recognized in plant cell membranes. The characterization of membrane domains essentially is related to their insolubility in detergents at cold temperatures, hence their name 'Detergent-Resistant-Membranes' (DRMs). The Keystone Symposium of Lipid Rafts established a consensus definition: 'Membrane rafts are small (10–200 nm), heterogeneous, highly dynamic, sterol- and sphingolipid-enriched domains that compartmentalize cellular processes. Small rafts can sometimes be stabilized to form larger platforms through protein-protein and protein-lipid interactions' (Pike, 2004). The function of rafts is related to three different structural characteristics: (1) regulation of homomeric and heteromeric interactions by the raft proteins; (2) the bringing-together or distancing of signalling actors through the lateral compartmentalisation of the plasma membrane; or (3) a direct impact of the lipid environment (Simon-Plas *et al.*, 2010). Plant DRMs have been characterized in several plants including tobacco, Medicago and Arabidopsis (Mongrand *et al.*, 2004; Borner *et al.*, 2005; Lefebvre *et al.*, 2007): in the main, structural phospholipids are not integrated in DRMs, except polyphosphoinositides (Furt *et al.*, 2010), which also were characterized as players of signal transduction or as controllers of ion transporters and channels functioning (Liu *et al.*, 2005; Monteiro *et al.*, 2005). This highlights a possible role of DRMs in signalling and/or regulation. Sphingolipids also represent an important component of plant DRMs: plant sphingolipids can regulate ion channels and pumps (Simon-Plas *et al.*, 2010). In animal cells, there is strong evidence that lipid rafts could facilitate the assembly and functioning of signalling cascades by bringing signalling proteins, membrane receptors and ion channels close to one another. For example, the activity of the transient receptor potential (TRP) TRPM8 channel is thought to be higher outside DRMs than inside them. Concerning plant cells, less is reported about channel localization within microdomains, even if it is worth noting that several channels are present in tobacco (Morel *et al.*, 2006) or *M. truncatula* DRMs (Lefebvre *et al.*, 2007). Pumps also are present in tobacco (Mongrand *et al.*, 2004; Morel *et al.*, 2006; Stanislas *et al.*, 2009) and Arabidopsis (Shahollari *et al.*, 2004; Borner *et al.*, 2005; Minami *et al.*, 2009) DRMs. The DRM localization of pumps has to be linked to the identification of

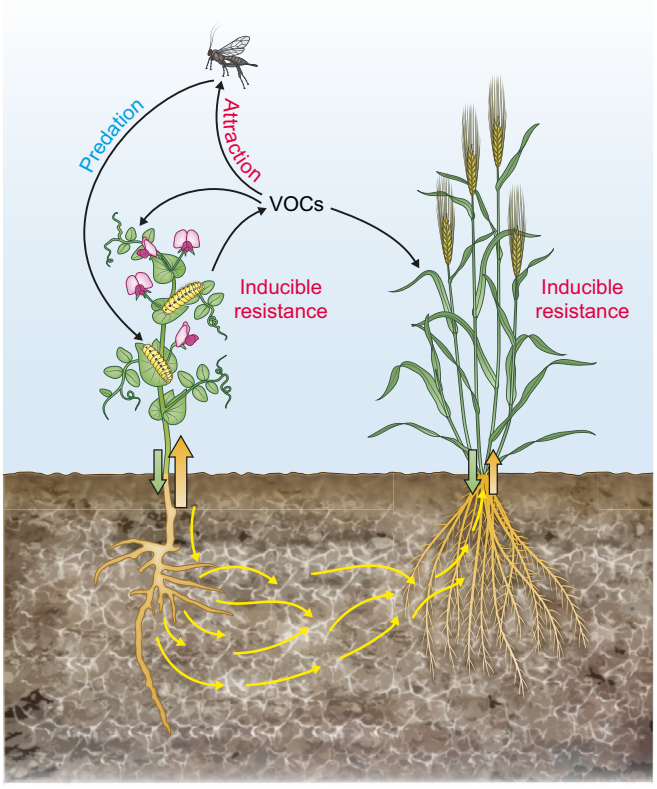

Fig. 4 Common mycorrhizal networks (CMN, whitish web in the soil) link plant roots from similar or different species and are involved in signalling and/or nutrient exchanges (VOC, volatile organic compounds). Each plant invests carbon (green arrow) into the CMN, and in return, the CMN provides nutrients (orange arrow) to the connected plants. Exchanges of nutrients are either symmetrical (green and orange arrows are similar sizes) or asymmetrical (arrows have different sizes). When a plant is attacked, here by a caterpillar, the plant produces VOCs which (black arrows) are (1) attracting insects, (2) inducing host plant resistance and (3) inducing resistance to closely related plants. Some signals also can be transmitted by the attacked plant to the other plant connected by the CMN (yellow arrows). The CMN is involved in signalling and/or nutrient exchanges (yellow arrows).

putative pump-regulating proteins (e.g. Plasma membrane ATPase regulating proteins, Morel *et al.*, 2006) in DRMs. Even if more pumps (e.g. members of the aquaporin family) have been reported to be localized in DRMs, there is currently no indication of a possible regulation through their association to DRMs. Concerning transporters, even if numerous reports of the regulation of animal cell membrane transporters through association to DRMs exist, few have been issued about plants (see, e.g., Morel *et al.*, 2006; Lefebvre *et al.*, 2007; Stanislas *et al.*, 2009).

Concerning a role of DRMs in PMI, some progress has been made recently concerning plant–pathogen interactions and the rhizobium–legume symbiosis. When interacting with mutualistic and/or pathogenic microbes, host plants need to keep stringent control at the cell level. This can be at least partially achieved by building 'signalling hubs' including receptors and other complex constituents (Ott, 2017). In both pathogenic and mutualistic PMIs, microbial molecule recognition is mediated by specific membrane-located receptors called pattern recognition receptors (PRRs). Several of these PRRs have been localized in nanodomains (Ott, 2017). A way to avoid cross-talk between different signalling pathways seems to be the localization of different PRRs to different nanodomains, as proposed for the Arabidopsis FLS2 and BR1 complexes (Bucherl *et al.*, 2017). In the legume–rhizobium symbiosis, nod factors (NFs) are perceived by LysM-type receptor like kinases (see Zipfel & Oldroyd, 2017, for a review) that are part of complexes present in nanodomains (Ott, 2017). Among these PRRs, it appears that immobilization of the *M. truncatula* PRR LYK3 in nanodomains requires the presence of actin and two molecular scaffold proteins, FLOT4 and SYMREM1 (Liang *et al.*, 2018), highlighting that receptors have to be recruited in nanodomains for them to function during host cell infection. There are only few indications of a possible role of DRM association in the regulation of mycorrhizal partner transport proteins. Nevertheless, a host of studies illustrate such a regulation in bacterial or animal cells, so that our vision of the membrane dynamic and its impact on transport activity has evolved. Simon-Plas *et al.* (2010) proposed that 'individual lipids and the dynamic structure and compartmentation of the bilayer as essential regulatory elements of membrane protein activity is now well established'. The recent staggering development of high-resolution imaging combined to biochemistry, physiology and genetics, should allow the scientific community to advance in the understanding of the regulation of transport activities by dynamic localization inside or outside DRMs. In the same vein, the latest knowledge acquired about DRM targeting and regulation of transport proteins in animal cells could boost this area in plant sciences. For example, five amino-acid transporter superfamilies have been identified in animals, yeasts and plants (Wipf *et al.*, 2002; Lalonde *et al.*, 2004), with both plant and animal proteins present in the ATF1/SLC38 superfamily. The similarity of animal proteins involved in neurotransmitter transport with plant members suggests that current knowledge concerning the lipid regulation of neurotransmitter transporters should help to decipher this topic in plants (e.g. Butchbach *et al.*, 2004). Concerning amino-acid transport in plants, to our knowledge only one lysine- and histidine-specific transporter (LHT) (Morel *et al.*, 2006; Stanislas *et al.*, 2009) and two oligopeptide transporters (OPTs) (Stanislas *et al.*, 2009) have been reported as being present in plant DRMs.

III. Managing common mycorrhizal networks: a tool toward a sustainable agriculture

1. Common mycorrhizal networks? What's that?

The AMF have nearly unrestricted host ranges and can associate with most plant species (Smith & Read, 2008) (Fig. 4). Annual plant species harbour higher AMF diversity than perennial plant species, and half of the currently identified AMF species are specific to one plant species (Torrecillas *et al.*, 2012). This suggests that the establishment of selected AMF communities in agricultural applications for enhanced crop productivity is no trivial issue. AMF form extraradical mycelium networks that spread from colonized roots into the surrounding soil (from 2.7 to 20.5 m g^{-1} soil), and their extension depends on the AMF species (Giovannetti & Avio, 2002; Mikkelsen *et al.*, 2008). The length of intact extraradical mycelium depends both on the AMF species and the associated plant species: the mean growth rate is 738 mm d^{-1} for *F. mosseae* in association with *Thymus vulgaris* (Giovannetti *et al.*, 2001), and 3.1–3.8 mm d^{-1} for *F. mosseae* and *Funneliformis caledonius* in association with *Trifolium subterraneum* (Mikkelsen *et al.*, 2008). The extraradical mycelium of one AMF or hyphal fusion of separate mycelia (Giovannetti *et al.*, 2004; Mikkelsen *et al.*, 2008) can colonize and further connect neighbouring plants of the same or different species within a community to form common mycorrhizal networks (CMNs) (Barto *et al.*, 2012). Earlier works suggest that CMNs could develop among plants 12–20 cm apart (Song *et al.*, 2010; Barto *et al.*, 2012; Babikova *et al.*, 2013). CMNs benefit host plants in many ways, and transfer may be bidirectional between plants, with a net flux toward one plant (Selosse *et al.*, 2006). CMNs can improve seedling establishment (van der Heijden, 2004), influence plant and microorganism community compositions (van der Heijden & Horton, 2009), induce an efficient nutrient exchange, and improve interplant nutrition (He *et al.*, 2003) and growth through plant–plant facilitation (Hartnett *et al.*, 1993). Moreover, CMNs can induce plant defence responses (defence enzyme activity and defence-related gene expression) and plant communication through a variety of phytohormones such as jasmonic acid, methyl jasmonate and zeatin riboside (Song *et al.*, 2010) (Fig. 4).

2. CMNs and plant–plant interactions

CMNs amplify intraspecific competition by altering the distribution of population size classes (Weremijewicz & Janos, 2013), a functional trait reflecting symmetrical or asymmetrical competition (Weiner & Thomas, 1986) between young and mature trees. The distribution of populations is generally symmetrical shortly after germination and evolves towards an asymmetrical distribution with plant age, reflecting the dominance of large individuals getting a disproportionate share of a limiting resource (Weiner & Thomas, 1986). CMNs play a role in plant root competition and – by extension – in mineral nutrient acquisition: plants with intact

CMNs showed asymmetrical competition whereas plants with severed CMNs showed symmetrical competition (Weremijewicz & Janos, 2013), suggesting that intact CMNs may supply nutrients such as N to large individuals that are highly photosynthetically active and provide the most C to their associated AMF (Merrild *et al.*, 2013). This reciprocal reward could depend on the rate of exchange of fungal mineral nutrients for host plant C (Kiers *et al.*, 2011). Other factors may influence the dynamics of nutrients in CMNs, such as intraspecies size hierarchy and interspecies interactions (Weremijewicz & Janos, 2013), or host sink strength (Walder & van der Heijden, 2015). However, the reciprocal reward does not seem to be a general case, as shown by Walder *et al.* (2012, 2015) in a CMN between sorghum and flax. This indicates that biological market dynamics controls resource exchanges in AM symbiosis, and there is evidence that the nutrient cost-to-benefit ratio varies among different host plant species (Walder *et al.*, 2012, 2015).

The effects of CMNs on seedling recruitment as opposed to awaiting AMF spore germination may be beneficial. For example, AMF spore germination represents a C cost for the developing seedlings that is higher for *Gigasporaceae* than for *Glomus* species (Thomson *et al.*, 1990; Feddermann *et al.*, 2010) for the development of the intraradical and extraradical mycelia (Chagnon *et al.*, 2013). Moreover, the P resources of seedlings may be limited (Koide, 1985) and the net outcome (cost vs benefits) of the interaction between one plant and different AMF species is variable (Johnson *et al.*, 1997; Hoeksema *et al.*, 2010; Kiers *et al.*, 2011). By contrast, the effects of CMNs on plant germination (growth and chances of establishment) are positive when seedlings get trapped into the existing CMN (van der Heijden, 2004; Walder & van der Heijden, 2015). CMNs may provide faster mycorrhiza formation, limit the investment of seedlings in the construction costs of hyphal networks, give access to mineral nutrients and water, and could transfer C from one plant to another depending on the plant photosynthetic rates or the intensity of sources and sinks.

3. Plant–CMN–plant interplay and potential for crop pest control

Plant–plant signalling could be involved in food security by reducing pest-related crop losses (Fig. 4). AMF can act on competition through allelopathy (Barto *et al.*, 2012). The CMN can act rapidly (from 24 to 50 h) as a conduit for signalling compounds (Babikova *et al.*, 2013) following necrotrophic fungus attack (Song *et al.*, 2010) or caterpillar attack (Song *et al.*, 2015). The CMN helps extend the bioactive zone of allelochemicals in the soil (Barto *et al.*, 2012) or changes leaf volatile organic chemicals (Babikova *et al.*, 2013). Therefore, CMNs represent a considerable potential for crop pest control through this belowground plant–plant signalling mechanism (Babikova *et al.*, 2014). In agroecosystems, and for a direct, rapid and realistic role in pest control, CMN reliability will depend on: (1) the frequency and rapidity of pest attacks; (2) the number of attacked crop plants; (3) the signal travelling on long distances (≥ 20 cm in beans; Babikova *et al.*, 2013); (4) the putative relay of the signals among plants; and (5) the putative transfer to other CMNs. However, the most fundamental requirements for CMNs to be efficient and useful in crop pest control are (1) being warned of attacks and (2) remaining physically intact. Most cropped soils are tilled, which likely breaks up CMNs. Increasing tillage intensity decreases the mycorrhizal colonization of plants (Carpenter-Boggs *et al.*, 2003; Lumini *et al.*, 2010; Peyret-Guzzon *et al.*, 2016; Sommermann *et al.*, 2018). Tillage may change the AMF community composition by positively selecting more tolerant AMF species and by impacting on the ability of CMNs to transfer defence signals (Brito *et al.*, 2012; Brígido *et al.*, 2017). Taken together, all of these findings highlight the importance of CMNs and the imperative need for further research on their function and role, particularly in the context of agroecological management.

4. AM fungi are not alone: interactions with PGPR

Apart from AMF, plants interact with further mutualistic root microorganisms such as plant-growth-promoting rhizobacteria (PGPR), which also can impact plant development and health (Fig. 1).

The PGPR are bacteria belonging to different groups, including *Pseudomonas*, *Bacillus*, *Rhizobia* and *Azotobacter* spp. (Benizri *et al.*, 2001), that can either be free or attached to the fungal mycelium (Bianciotto *et al.*, 2001; van Overbeek & Saikkonen, 2016). They stimulate plant development through a variety of mechanisms, namely mobilization of rhizosphere-bound nutrients, fixation of atmospheric di-nitrogen, solubilization of P and synthesis of phytohormones such as IAA (Indole-3-acetic acid) (Kloepper *et al.*, 1980; Glick, 1995). PGPR also can have indirect beneficial effects by suppressing phytopathogens through siderophore synthesis or by inducing plant resistance (Benizri *et al.*, 2001). Among the fluorescent pseudomonads that exclusively colonize roots, *Pseudomonas fluorescens* is the best-known species (Duijff *et al.*, 1997). A few fluorescent pseudomonads act as mycorrhiza-helper bacteria (Mugnier & Mosse, 1987) by improving mycorrhizal root colonization (Gamalero *et al.*, 2010) and promoting the growth of extraradical hyphae, and also by enhancing spore germination (Roesti *et al.*, 2005). PGPR increase mycorrhizal colonization in cucumber (*Cucumis sativus* L.) by lowering the plant ethylene content through the synthesis of ACC deaminase (Gamalero *et al.*, 2010). Inversely, AMF impact the composition of plant root exudates, an important food source for rhizosphere microorganisms (Hegde *et al.*, 1999).

In strawberry, AMF colonization not only stimulates plant growth (Hršelová *et al.*, 1990), but also enhances photosynthesis (Borkowska, 2002), increases sugar and anthocyanin concentrations (Castellanos-Morales *et al.*, 2010), and induces early flowering and fruit production (Lu & Koide, 1994; Sohn *et al.*, 2003). Nevertheless, only few reports are available about the effects of PGPR on strawberry. Vosatka *et al.* (1992) co-inoculated strawberry plants with AMF and *Pseudomonas putida*, and reported a synergistic effect on plant growth (Vosatka *et al.*, 1992). The same authors highlighted a positive effect of *Agrobacterium radiobacter* on root colonization. Todeschini *et al.* (2018) recently reported an impact of PGPR and AMF co-inoculation on strawberry quality as well as the importance of the strains. Despite huge progress in the

understanding of PMI at the cellular and molecular levels, there is a considerable knowledge gap regarding the combined application of such beneficial microorganisms on crop productivity. AMF and PGPR are currently considered as essential actors in agronomic practices because they could help cut down chemical fertilizer and pesticide inputs, and promote the agriculture of the future, based on the implementation of practices that favour the ecosystem services rendered by beneficial microorganisms (Gianinazzi *et al.*, 2010).

IV. Conclusion and prospects

Arbuscular mycorrhizal symbiosis is the fruit of a long coevolution of AMF with their plant partners, in constant interaction with many other (abiotic and biotic) components of their environment; as such, it constitutes a major element not only of plant life, but also of agroecological production. The ecological services provided by AMF are truly broad, and suitable tools and/or markers have to be defined to phylogenetically characterize the OTUs and functionally define their contribution during the interaction. Moreover, quick and reliable tests for evaluating and monitoring their diversity and functionality in agroecosystems are still lacking.

Furthermore, the growing understanding of the mechanisms underlying AM symbiosis should not overshadow the fact that so far most results have been obtained on a small number of AM fungal species interacting with a small number of plant species. In particular, the *R. irregularis* model strain DAOM 197198, the first AMF whose genome was fully sequenced, is probably the most studied strain in research laboratories. Thus, our understanding of mycorrhizal biology is often limited to a few special cases, and any generalization of these concepts should be based on studies involving additional AMF species. Future progress will depend on the generalization of current knowledge to different Glomeromycota genera and species, through: (1) a deeper understanding of AM functioning; (2) the selection of AMF strains differing in their ability to provide ecosystem services; (3) the development of new AMF cocktails of synthetic communities covering the broadest possible range of ecosystem services; and (4) the development of technologies allowing AMF cultivation under controlled conditions. This progress will be a prelude to the development of a future 'ecological engineering of AMF and their associated microorganisms' and its integration into modern plant breeding while taking care of the ecosystem services rendered by these valuable fungi.

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