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DOI:10.1111/nph.15230

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New Phytologist *2018*

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Total word count: 7919
Number of Figures: 4 to be published in colour

Summary

The evolutionary and ecological success of the arbuscular mycorrhizal (AM) symbiosis relies on an efficient and multifactorial communication system for partner recognition and on a fine-tuned and reciprocal metabolic regulation of each symbiont to reach an optimal functional integration. Besides strigolactones, N-acetylglucosamine-derivatives released by the plant were recently suggested to trigger fungal reprogramming at the pre-contact stage. Remarkably, N-acetylglucosamine-based diffusible molecules (LCOs and COs) are also symbiotic signals produced by AM fungi (AMF) and clues on the mechanisms of their perception by the plant are emerging. AMF genomes and transcriptomes contain a battery of putative effector genes that may have conserved and AMF- or host plant-specific functions. Nutrient exchange is the key feature of AM symbiosis. A mechanism of phosphate transport inside fungal hyphae has been suggested and first insights into the regulatory mechanisms of root colonization in accordance with nutrient transfer and status were obtained. The recent discovery of the dependency of AMF on fatty acid transfer from the host has offered a convincing explanation for their obligate biotrophism. Novel studies highlighted the importance of plant and fungal genotypes for the outcome of the symbiosis. These findings open new perspectives for fundamental research and application of AMF in agriculture.

Key words: Arbuscular mycorrhizal fungi, effectors, lipids, natural variation, nutrients, phosphate, signalling, symbiosis

I. Introduction

Soil is a complex matrix with diverse geochemical properties that is inhabited by wide range of prokaryotic and eukaryotic organisms (Nielsen *et al.,* 2015). The soil volume in direct contact with the plant root is defined as the rhizosphere and represents a particularly biologically rich environment, in which microbial communities profit from metabolites released by roots (Sasse *et al.,* 2017). Some of the soil inhabitants, such as arbuscular mycorrhizal fungi (AMF) establish a very intimate association with plant roots leading to the formation of a mutualist interaction called the arbuscular mycorrhizal (AM) symbiosis (Martin *et al.,* 2017).

AMF show peculiar features: beside their obligate biotrophism, they are characterized by coenocytic hyphae and multinucleated spores (Kamel *et al.,* 2016; Lanfranco *et al.,* 2016); no sexual reproduction has been described so far, although evidence for the potential of mating-related processes has been obtained (Corradi & Brachmann, 2017). They have a rather long history of taxonomic revisions, which reflects the general difficulty in resolving the earliest branches in the fungal genealogy. Ribosomal DNA-based phylogenies placed them in the Glomeromycota phylum considered a sister group to Dikarya (Schüssler *et al.,* 2001). An extensive phylogenomic study, based on kingdom-wide sampling of fungal species and genome-scale sampling of loci, placed AMF in the subphylum named Glomeromycotina with a close relationship with Mortierellomycotina (Spatafora *et al.,* 2016).

AM is one of the most ancient and widespread symbioses in nature (Lanfranco *et al.,* 2016). The main advantage of the AM symbiosis is the exchange of nutrients: the plant provides up to 20% of the photosynthetically fixed organic carbon to the AMF (Roth & Paszkowski, 2017), while the AMF transfers mineral nutrients to the plant thanks to its efficiency in exploring and acquiring these resources from the soil (Smith *et al.,* 2011). In addition, plants colonized by AMF often show higher tolerance to biotic and abiotic stresses compared to non-mycorrhizal plants and this is not a mere consequence of a better nutritional status (Jung *et al.,* 2012; Augé *et al.,* 2015). At the ecosystem level, AM improves soil quality (Rillig *et al.,* 2015) and increases plant biodiversity (van der Heijden *et al.,* 1998).

Root colonization by AMF occurs in successive steps. Prior to physical contact between plant and fungus, diffusible molecules mediate reciprocal recognition. When fungal hyphae touch the root epidermis, they form adhesion structures called hyphopodia. Subsequently, AMF enter the root and grow into the root cortex taking an intracellular as well as intracellular route. In the cortex, hyphae penetrate single cells, where they develop arbuscules, highly branched structures (Gutjahr & Parniske, 2013; Lanfranco *et al.,* 2016). Arbuscules are surrounded by a plant derived peri-arbuscular membrane (PAM), which, together with the arbuscule-membrane, forms an extensive interface for nutrient exchange. Excellent recent reviews describe the latest advances in plant regulatory and cell biological mechanisms required for accommodation of AMF inside roots (Luginbuehl & Oldroyd, 2017; MacLean *et al.,* 2017; Pimprikar & Gutjahr, in revision). Here we discuss, with special attention on the fungal partner, new findings in the understanding of molecules and mechanisms that control partner recognition, the importance of nutrients in the establishment and maintenance of AM and the role of plant-fungal genotype combinations for the outcome of the symbiosis.

II. Interkingdom communication enabling symbiosis

The rhizosphere is a preferential niche for large microbial communities. Unequivocal and efficient communication systems are therefore required to enable specific interactions such as the AM symbiosis.

Plant exudates activate the fungus

AMF and plants rely on reciprocal recognition before physical contact (Nadal & Paszkowski, 2013). Plant roots, particularly under Pi limiting conditions, release strigolactones (SL), carotenoid-derived molecules with hormone functions in plants (Waters *et al.,* 2017). These stimulate AMF hyphal branching and elongation (Akiyama *et al.,* 2005; Besserer *et al.,* 2006; Fig. 1), thus promoting the chances to contact the host. Furthermore, a general activation of the fungal mitochondrial metabolism (visible as organelle division, ATP production and gene expression) has been associated to SL exposure (Besserer *et al.,* 2008; Lanfranco *et al.,* 2017). Notably, SL treatment also led to an increase in the release of chitin oligomers by AMF (Genre *et al.,* 2013), which act as signaling molecules on the plant (Sun *et al.,* 2015). SLs also contribute to the induction of fungal genes (Tsuzuki *et al.,* 2016; Kamel *et al.,* 2017). One of them, encoding a putative secreted protein 1 (SIS1), is essential for symbiosis establishment as host-induced gene silencing (HIGS) lead to stunted arbuscules and reduced root length colonization (Tsuzuki *et al.,* 2016). The fungal receptor for SL is currently unknown and its identification is a matter of active investigation. Nevertheless, the importance of SL for efficient symbiosis establishment is clear, as plants defective in the biosynthesis or the exudation of SL display a lower colonization level, while arbuscule morphology is normal (summarized in Waters *et al.,* 2017 and Lanfranco *et al.,* 2017).

Although SL are plant-derived, they do not appear to play an important role at the host side because rice mutants defective in the alpha-beta hydrolase SL receptor D14, are not perturbed in AM colonization (Yoshida *et al.,* 2012; Gutjahr *et al.,* 2015). During SL perception, D14 interacts with the F-box protein MAX2/D3/RMS4 in a receptor complex (Hamiaux *et al.,* 2012). MAX2/D3/RMS4 is also involved in the perception of karrikins together with the alpha-beta fold hydrolase KAI2/D14-LIKE (Nelson *et al.,* 2010; Waters *et al.,* 2012). Karrikins are butenolide molecules found in smoke extracts that promote seed germination of many plant species (Flematti *et al.,* 2004). Interestingly, rice *d3* and pea *rms4* mutants displayed aborted colonization attempts and reduced arbuscules formation, respectively (Yoshida *et al.,* 2012; Foo *et al.,* 2013; Gutjahr *et al.,* 2015) and a rice mutant defective in the karrikin receptor D14-LIKE/KAI2 is characterized by a complete absence of hyphopodia (Gutjahr *et al.,* 2015). In addition, the rice *d14l*/*kai2* mutant lacks the transcriptional response to fungal germinating spore exudates (GSEs), indicating that karrikin receptor complex may be involved in perception of the fungus. However, it is not yet clear whether a karrikin-like compound of fungal or plant origin acts as ligand of the D14L receptor in plant-AMF recognition (Gutjahr *et al.,* 2015; Waters *et al.,* 2017).

The recent discovery that an *N*-acetylglucosamine (GlcNAc) transporter of rice and maize, called NOPE1, is required for early signalling in the AM symbiosis, points to the existence of additional and GlcNAc-based diffusible plant molecules, which may trigger presymbiotic fungal reprogramming (Nadal *et al.,* 2017; Fig. 1). *nope1* mutants display very low levels of root length colonization and root exudates from the mutant differ from wild type exudates in their ability to induce transcriptome changes in the AMF *Rhizophagus irregularis* associated with the GO-term “signalling” (Nadal *et al.,* 2017). Although the exact molecular function of NOPE1 and its elusive substrate are so far unknown, the strong mycorrhizal phenotype of the *nope1* mutant indicates a crucial role in plant-fungal communication. Identification of the NOPE1 substrate will be exciting as GlcNac-based signaling molecules are currently only known from bacteria and fungi but to our knowledge not from plants.

Fungal chitin-based molecules elicit symbiotic plant responses

AMF use GlcNAc-based molecules as pre-contact signals to activate symbiotic responses in the host plant such as calcium spiking, lateral root formation, starch accumulation and gene expression (Gutjahr *et al.*, 2009; Mukherjee & Ane, 2011; Genre *et al.* 2013; Sun *et al.,* 2015; Czaja *et al.,* 2012; Camps *et al.,* 2015). These so called 'Myc Factors' include lipo-chito-oligosaccharides (Myc-LCOs, Maillet *et al.,* 2011) and short chitin tetra- and pentamers (Myc-COs; Genre *et al.,* 2013) (Fig. 1). Although the MycLCOs show strong similarity to Nod Factors released by nitrogen fixing rhizobia (Gough & Cullimore, 2011), the metabolic pathways leading to their synthesis in AMF are not yet known.

Both Myc-COs and Myc-LCOs are able to elicit repetitive nuclear calcium (Ca^{2+}) oscillations, known as Ca^{2+}-spiking, which is considered a hallmark of symbiotic signalling (Oldroyd 2013; Sun *et al.,* 2015). So far, the biological significance of producing both Myc-COs and Myc-LCOs remains obscure. It is possible that a diversity of signaling molecules contributes to the ability of AMF to interact with a wide range of AM host plants or to the robustness of the system. However, GlcNAc-containing molecules can be produced by many microorganisms, including plant pathogens, and it is puzzling how plants can distinguish AMF from the others. One possibility are fine-tuned Myc Factors ligand-receptor specificities (Zipfel & Oldroyd, 2017). Small molecules with a GlcNAc backbone are perceived by LysM-domain containing receptor like kinases (LysM RLKs) and receptor like proteins (LyM RLPs), with different ligand specificities (Gust *et al.,* 2012). The repertoire of LysM-receptors differs significantly among plant species (Zhang *et al.,* 2009), which may have favoured the co-evolution or maintenance of several different Myc Factors. Possibly due to the functional redundancy of AMF-responsive LysM-receptor kinases in the genome of AMF-host plants, and the multitude of different Myc Factors, definitive receptors for Myc-COs or Myc-LCOs have not emerged yet (Buendia *et al.,* 2016; Zipfel & Oldroyd, 2017). Good candidates are SlLYK10 from tomato and NFP from *Parasponia*: virus-induced and RNAi-mediated gene silencing of both corresponding genes, respectively, partially perturbed AM establishment (Op den Camp *et al.,* 2011; Buendia *et al.*, 2016). However, there is currently no evidence that both LysM-RLKs bind Myc-COs or Myc-LCOs and it cannot be excluded that VIGS and RNAi affected the expression of additional redundant LysM-RLKs. The rice OsCERK1, a LysM receptor-like kinase, which has a dual role in both interactions with pathogenic fungi and AMF (Miyata *et al.,* 2014), was shown to play a central role in the perception of Myc-CO signals because an *oscerk1* mutant does not respond to these molecules with Ca^{2+}-spiking (Carotenuto *et al.,* 2017). In addition, it fails to induce lateral roots in response to AMF (Chiu *et al.,* 2018). However, *oscerk1* root colonization is only delayed and not entirely abolished (Miyata *et al.,* 2014;

Zhang *et al.,* 2015; Chiu *et al.,* 2018) pointing towards redundant recognition mechanisms. By contrast, OsCEBiP, a LysM receptor-like protein (RLP), which acts as co-receptor of OsCERK1 in the perception of long-chain chitin oligomers from pathogenic fungi, is not required for the AM symbiosis and is not essential for Myc-CO-induced Ca^{2+} spiking (Carotenuto *et al.,* 2017). Therefore, an unknown LysM-containing protein likely associates with OsCERK1 to mediate specificity for the interaction with AMF.

An additional level of complexity may be added by the possibility that AMF may produce different amounts and/or a different repertoire of Myc Factors at different life-stages. Additionally, the composition of the Myc Factor cocktail may differ among AMF species. Thus, our understanding of how plants distinguish beneficial microbes and limit the invasion by detrimental ones will rely on the characterization of the blend of GlcNAc-containing molecules produced by AMF and their specific receptors and downstream signalling components.

Also volatile signals may participate in the belowground communication with the plant. Fungal volatile organic compounds (VOCs) can reprogram root growth and architecture and influence the defense system of the host plants (Werner et *al.,* 2016). Using an elegant split Petri-dish system, Sun *et al.* (2015) found that volatiles, released by germinating spores of the AMF *Gigaspora margarita*, stimulated lateral root formation in *Lotus*, as well as in *Arabidopsis*, indicating that these volatiles target a receptor, which is not AM-specific. The SL biosynthesis gene *LjCCD7*, was up-regulated following exposure to these VOCs, suggesting a possible involvement of SL signaling (Sun *et al.,* 2015).

An emerging role for fungal effectors in AM establishment

In addition to GlcNAc-containing molecules, other molecules released by AMF contribute to interkingdom signaling. In analogy to pathogenic interactions, these molecules are called effectors: they serve to dampen defense responses and/or to interfere with host cellular processes to favor colonization of the host (Lo Presti *et al.,* 2015).

AMF effector candidates have been predicted from fungal genomes and transcriptomes (Sędzielewska Toro & Brachmann, 2016; Kamel *et al.,* 2017). The number of identified genes depends on the criteria used to define effectors. A first criterium is the presence of a signal peptide that guides proteins towards secretion. Sezdzielewska Toro & Brachmann (2016) further filtered on the basis of the small size and the presence of cysteines, internal repeats and nuclear localization signals leading to the identification of 220 putative effectors from *R. irregularis*. Remarkably, a large majority of these genes is conserved in the related species *R. clarus*, suggesting that a majority of putative effectors may be involved in core symbiotic functions. However, a comparison of transcriptomes from two distantly related AMF, *R. irregularis* and *Gigaspora rosea,* when colonizing three different host plants (the dicotyledon *M. truncatula*, the monocotyledon *Brachypodium distachyon* and the liverworth *Lunularia cruciata*), revealed that the expression of putative secreted proteins (SPs) can differ in function of the host plant: among 87 SPs genes expressed in the intraradical mycelium of *R. irregularis* only 33 were expressed in all three plant species (Kamel *et al.,* 2017), suggesting that these 33 fulfill core-functions, while the others may act host-specifically (Fig. 2). Host-specifically expressed effector candidates have also been observed for the endophyte *Piriformospora indica*, when colonizing roots of barley or Arabidopsis (Lahrmann *et al.,* 2015).

The seminal work by Kloppholz *et al.* (2011) provided the first functional characterization of a putative AMF effector. The protein, named secreted protein 7 (SP7), from *R. irregularis* increased the speed of root colonization by AMF, when the corresponding gene was ectopically expressed in *M. truncatula* hairy roots (Kloppholz *et al.,* 2011). It translocated to the nucleus of the plant cell where it was suggested to counteract the plant immune response by interacting with the pathogenesis-related-transcription factor ethylene response factor ERF19 (Kloppholz *et al.,* 2011). However, the *SP7* gene is not only expressed in intraradical fungal structures, but *SP7* transcripts also strongly accumulate in extraradical fungal mycelia (Kamel *et al.,* 2017), suggesting that SP7 may play a role in addition to suppressing plant immunity inside the root. SP7 contains several sequence repeats, which are separated by computationally predicted KEX2 protease cleavage motives, which could mean that SP7 can be cleaved into small peptides, which may act on the fungus or the plant (Kamel *et al.,* 2017).

Two additional fungal genes have been recently identified with a putative role in the accommodation of fungal structures in the root (Tsuzuki *et al.* 2016; Fiorilli *et al.,* 2016). The *R. irregularis* gene, encoding the putative secreted protein SIS1, was among the five genes up-regulated in both SL-treated germinating spores and symbiotic extraradical mycelium, so that it has been proposed as a marker gene for fungal SL response (Tsuzuki *et al.,* 2016). In the absence of genetic transformation protocols for AMF, SIS1 silencing was obtained by HIGS (*Host-Induced Gene Silencing*). This led to reduced colonization and stunted arbuscules. The second gene was called *RiPEIP1 (Preferentially Expressed In Planta)* since it is strongly induced in the intraradical phase, including arbuscules. It encodes a four transmembrane domain protein, which is not a common feature for

effectors. *RiPEIP1* expression in *Oidiodendron maius*, an ericoid endomycorrhizal fungus, for which transformation protocols are available, led to enhanced mycorrhization capacity compared to the *O. maius* wild-type strain (Fiorilli *et al.,* 2016). Further studies are needed to define the mechanisms of action of SIS1 and RiPEP1 and their specific role in the establishment of the AM symbiosis.
In addition to proteins, small RNAs of the pathogenic fungus *Botrytis cinerea*, were shown to target, by cross-kingdom RNAi, mRNA of defense genes in the host plant, thus acting as effectors (Wang *et al.,* 2017). It is possible that such a mechanism is also exploited by AMF. The interference with RNA metabolism of the host plant can also be envisaged for the so-called RALPH (RNase-Like Proteins associated with Haustoria) the secreted avirulence effectors described in the obligate biotroph pathogenic fungus *Blumeris graminis* (Spanu 2017).

III. Alimentary and regulatory roles of nutrients in the AM symbiosis

After the AM symbiosis has been established, both symbionts benefit from nutrient supply by the other partner. Accumulating evidence indicates that the exchanged nutrients not only function as nourishment but also act as signals that can drastically influence AM development. Thus, AM development is strongly linked to symbiotic function.

AMF receive carbohydrates as well as lipids from the host

Based on stable isotope labelling experiments, it has long been established that AMF receive carbohydrates and specifically glucose from the plant (Pfeffer *et al.,* 1999; Trépanier *et al.,* 2005). How the sugars are transported from the plant to the fungus is still unclear. A number of genes encoding sugar transporters with activities towards monosaccharides (MSTs) and sucrose (SUTs) as well as members of the SWEET family are upregulated in mycorrhizal roots (Harrison, 1996; Doidy *et al.,* 2012; Manck-Götzenberger & Requena, 2016), but genetic evidence for their function is still missing. So far only the function of the sucrose transporter SUT2 from tomato has been investigated by reverse genetics (Bitterlich *et al.,* 2014). It is localized to the PAM and roots of *sut2* antisense plants are significantly more colonized than wild-type roots. Together, this suggests that SUT2 may be involved in competition with the fungus for sucrose for example by pumping the metabolite from the peri-arbuscular space (PAS) back into the plant cell (Bitterlich *et al.,* 2014). A high affinity monosaccharide transporter MST2 from the AMF *R. irregularis* has been characterized. *RiMST2* is expressed in arbuscules and intercellular hyphae and is possibly responsible for sugars uptake from the peri-fungal apoplast, as silencing of *RiMST2* led to reduced root colonization and impaired arbuscule branching (Helber *et al.,* 2011). Interestingly, expression of *RiMST2* was triggered also in the extraradical mycelium, when it was supplied with xylose. Furthermore, the extraradical mycelium was able to take up ^{14}C-labelled glucose and xylose from the medium (Bücking *et al.,* 2008; Helber *et al.,* 2011) and this uptake was inhibited by the protonophore carbonyl cyanide m-chlorophenyl hydrazone, demonstrating that it occurred by active transport and not simple diffusion across the membrane (Helber *et al.,* 2011). The finding that AMF can actively take up pentoses and hexoses from the medium challenges the notion that obligate biotrophy of AMF is based upon strict dependence on plant-derived sugars.

Genome and transcriptome sequencing of the first AMF species shed more light on the biology and the evolution of AMF (Tisserant *et al.,* 2013; Lin *et al.,* 2014; Kamel *et al.,* 2016; Ropars *et al.,* 2016; Tang *et al.,* 2016). Surprisingly, it was found that genes encoding the cytosolic fatty acids (FA) synthase subunits, which are responsible for the bulk FA production in fungi, are absent from AMF genomes (Wewer *et al.,* 2014; Tang *et al.,* 2016). In about the same period, legume mutants, with stunted arbuscules, reduced root colonization and defects in three AM-induced lipid biosynthesis genes *DISORGANIZED ARBUSCULES* (*DIS*), *FatM* and *REDUCED ARBUSCULAR MYCORRHIZA 2* were identified (Wang *et al.,* 2012; Bravo *et al.,* 2016; Bravo *et al.,* 2017; Jiang *et al.,* 2017; Keymer *et al.,* 2017; Luginbuehl *et al.,* 2017). *DIS* encodes a ß-keto-acyl-ACP synthase I (KASI), which is specific to genomes of AM-competent gymnosperms and dicots and catalyses FA chain elongation from C4 to C16 (Keymer *et al.,* 2017). *FatM* encodes a thioesterase, which terminates FA chain elongation by hydrolysis of the acyl-ACP, and FatM shows a preference for C16-ACP (Bravo *et al.,* 2017; Brands *et al.,* under review). *RAM2* encodes an sn-2 glycerol-3-phosphate acyltransferase 6, which transfers a fatty acyl residue to the sn-2-position of a glycerol, thereby creating ß-mono-acyl-glycerol (ß-MAG, Luginbuehl *et al.,* 2017). Both *FatM* and *RAM2* have been only found in genomes of AM-competent land plants (Delaux *et al.,* 2015; Bravo *et al.,* 2016). Consistent with the phenotype, the promoters of all three genes *DIS*, *FatM* and *RAM2* are specifically active in arbuscule-containing cells (Gobbato *et al.,* 2013; Bravo *et al.,* 2017; Jiang *et al.,* 2017; Keymer *et al.,* 2017).

Comprehensive lipid profiling in *L. japonicus* and *M. truncatula* supported the hypothesis that DIS, FatM and RAM2 act in an AM-specific lipid-biosynthesis pathway because *ram2* mutants accumulate unusual phospholipids enriched in palmityl moieties, which are the products of the concerted action of DIS and FatM (Bravo *et al.,* 2017; Keymer *et al.,* 2017). AMF store lipids mainly as tri-palmityl-triacylglyerol (16:0 - TAG) and desaturate the 16:0 fatty acyl chain at a specific ω5 position, permitting distinction of fungal from plant lipids by using 16:1ω5 FAs as an AMF-specific signature (Olsson *et al.,* 2005). The lipid profile of *dis*, *fatm* and *ram2* mutants contained hardly any 16:1ω5 FAs and the fungus *R. irregularis* did not form lipid-containing vesicles in mutant roots, suggesting that the fungus was deprived of lipids (Bravo *et al.,* 2017; Keymer *et al.,* 2017). Lipid transfer from host plants to AMF was shown by two independent experimental approaches. Luginbuehl *et al.* (2017) and Jiang *et al.,* (2017) used a genetic approach and transformed *Medicago* hairy roots with the *Umbellularia californica* fatty acyl–ACP thioesterase gene (*UcFatB*) that produces the 12:0 FA lauric acid, which does neither occur in *Medicago* nor in *R. irregularis*. Transgenic *Medicago* roots carrying *UcFatB* synthesized lauric acid and it was also detected in the spores of colonizing *R. irregularis* (Luginbuehl *et al.* 2017; Jiang *et al.,* 2017), unequivocally demonstrating that lauric acid containing lipids were transferred from the host to AMF. Keymer *et al.* (2017) measured lipid transfer in non-transgenic plants by isotopolog profiling of 16:0 and 16:1 FAs as markers. To this end *Lotus* plants and carrot root organ culture were fed with ^{13}C labelled glucose. The isotopologue profile of 16:0 FAs in *Lotus* and carrot roots differed significantly. However, in each case the root profile was precisely mirrored by the 16:0 FAs in the fungal extraradical mycelium as well as by the fungus-specific 16:1 FAs (Keymer *et al.,* 2017), demonstrating that the profile was determined by the plant and therefore, the FAs were transferred from the plant to the fungus. In the *dis*, *fatm* and *ram2* mutants, lipid transfer was impaired as well as in *str* mutants, which are deficient in an ABC-half transporter gene (Bravo *et al.,* 2017; Jiang *et al.,* 2017; Keymer *et al.,* 2017). STR together with its complex partner STR2 (Zhang *et al.,* 2010) is considered a good candidate transporter for lipid transfer across the PAM (Gutjahr *et al.,* 2012; Bravo *et al.,* 2017).

Taken together, these recent findings indicate that AMF are entirely dependent on lipid supply by the plant for their growth, development and reproduction and that the dependence on lipids may be the prime reason for their obligate biotrophy. They explain why AMF store a large amount of lipids in their spores, which are probably used as resources for membrane construction during spore germination and the first phase of root colonization until the first developing arbuscules can obtain lipids from the host. These findings also change our view on the energy balance of the symbiosis, in which the burden of organic carbon compound biosynthesis is more significantly shifted towards the plant than was previously assumed.

Mechanisms of phosphate transfer from AMF to plant hosts

Phosphorus (P) is predominantly present in soil as low mobile dihydrogen phosphate ion ($H_2PO_4^-$, Pi; Nussaume *et al.,* 2011) and a major macronutrient limiting plant growth. To overcome Pi starvation stress and increase access to Pi, plants have evolved several strategies. Under low Pi availability plants activate a Pi starvation response (PSR) system that regulates root and shoot architecture and physiology (Poirier & Bucher, 2002). In addition, plants can exploit the AM symbiosis to optimize Pi acquisition. The Pi contribution *via* AMF ranges from a small percentage to almost the entire acquired Pi, depending on plant/AMF combinations (Smith *et al.,* 2004). AMF are equipped with a very efficient system for Pi capture and translocation. Thanks to the extraradical hyphal network developed in the soil AMF greatly increase the absorbing surface area (up to 100-fold that of root hairs) extending well beyond the depletion zone (Javot *et al.,* 2007b). AMF were also proposed to be able to mineralize soil organic P (Feng *et al.,* 2003; Shibata & Yano, 2003); and this was supported by Sato *et al.* (2015) demonstrating that extraradical hyphae of the AMF *R. clarus* release an acid phosphatase of about 187 kDa, which may be involved in mobilizing organic P. AMF colonization also induces the expression and secretion of acid phosphatases on the plant side (Ezawa *et al.,* 2005), indicating that the symbiosis may also increase the plant ability to solubilize organic P from the soil.

Fungal Pi:H^+ symporter (PT), homologs of the yeast high-affinity transporter PHO84 (Bun-Ya *et al.,* 1991), are thought to be responsible for Pi uptake from the soil (Harrison & van Buuren, 1995; Maldonado-Mendoza *et al.,* 2001; Benedetto *et al.,* 2005; Xie *et al.,* 2016). Consistently, the fungal PT genes are expressed in the extraradical mycelium (ERM) but also in the intraradical mycelium (IRM), suggesting an additional role in Pi reabsorption from the PAS (Benedetto *et al.,* 2005; Balestrini *et al.,* 2007; Fiorilli *et al.,* 2013; Xie *et al.,* 2016).

Once absorbed by ERM, Pi is quickly converted inside vacuoles into polyphosphate (polyP) chains, linear polymers of three to hundreds Pi molecules (Solaiman *et al.,* 1999; Ezawa *et al.,* 2003). It has been hypothesized that AMF synthesize polyP through the VTC complex (Tisserant *et al.,* 2012; Tani *et al.,* 2009), as described in yeast (Hothorn *et al.,* 2009). PolyP is then translocated to the IRM *via* protoplasmatic streaming and/or along a motile a tubular vacuolar network (Olsson *et al.,* 2002; Uetake *et al.,* 2002, Hijikata *et al.,* 2010). Interesting new insights into the mechanism of long-distance polyP translocation in mycorrhizal associations were obtained from the characterization of *R. clarus* aquaporin 3 (RcAQP3), an aquaglyceroporin responsible for water transport across the plasma membrane (Kikuchi *et al.,* 2016). *RcAQP3* is strongly expressed in intraradical mycelia and down-regulation of *RcAQP3 via* VIGS through the host plant, as well as the suppression of host plant transpiration, decelerated polyP translocation. Kikuchi *et al.* (2016) proposed thus a model in which transpiration provides a primary driving force for polyP translocation by creating water flow through the fungal RcAQP3 and the mycorrhiza-inducible plant aquaporins.

PolyP breakdown in the IRM possibly involves acid and alkaline phosphatases (Ezawa *et al.,* 2001; Aono *et al.,* 2004; Kojima & Saito, 2004). The full dissociation of polyP produces large amount of negative charges. A compensatory mechanism is set up to maintain a neutral charge inside the cell: the massive accumulation of polyP in fungal mycelia is accompanied by near-synchronous and near-equivalent uptake of Na^+, K^+, Ca^{2+}, and Mg^{2+} (Kikuchi *et al.,* 2014).

Pi is delivered to the periarbuscular space, by a still unknown mechanism. It is then imported by AM-inducible, PAM-localized plant PTs, such as Medicago PT4 and rice PT11 into the cortical cells (Javot *et al.,* 2007b; Yang *et al.,* 2012). This transport is suggested to be supported by a H^+ energy gradient produced by a H^+-ATPase, that has been found to be important for arbuscule maintenance and AM-mediated phosphate uptake (Krajinski *et al.,* 2014; Wang *et al.,* 2014). AM-inducible PT genes have been identified in different host plants (Harrison *et al.,* 2002; Javot *et al.,* 2007a; Paszkowski *et al.,* 2002; Yang *et al.,* 2012; Rausch *et al.,* 2001; Nagy *et al.,* 2005; Xu *et al.,* 2007; Balestrini *et al.,* 2007; Willmann *et al.,* 2013; Sawers *et al.,* 2017; Hong *et al.,* 2012; Volpe *et al.,* 2016 ; Loth-Pereda *et al.,* 2011; Xie *et al.,* 2013; Walder *et al.,* 2015). They are homologs of the yeast PHO84 and belong to the Phosphate transporter 1 (Pht1) class (Poirier & Bucher, 2002) of the plant H^+/Pi symporters. In a phylogenetic tree of PHT1 proteins they cluster in a separate clade, which does not contain Pht1 transporters from AM-incompetent plants (Yang *et al.,* 2012; Hong *et al.,* 2012), indicating that an AM-specific PT-gene duplication was maintained in symbiotic Pi transport in the plant kingdom. Interestingly, the root endophyte *Colletotrichum tofieldiae* was shown to transfer Pi to Arabidopsis and to promote plant growth only under P-deficient conditions (Hiruma *et al.,* 2016). During colonization, several Arabidopsis PT genes of the Pht1 family were induced. It will be interesting to investigate, whether they, similarly to AM-specific PTs, localize to perifungal membranes to directly take up Pi from the fungus.

While promoters of AM-specific PT genes have been mostly reported to be specifically expressed in arbuscule-containing cells, *PT4* from *M. truncatula* and *L. japonicus* are also expressed in root tips when grown at Pi starvation conditions (Volpe *et al.,* 2016). Interestingly, *mtpt4* mutants and *Lotus* hairy roots expressing a RNAi construct which silence *PT4* do not respond to low Pi conditions with changes in lateral root formation to the same extend as the wild type (Volpe *et al.,* 2016), suggesting that PT4 is involved in root architecture responses to low Pi, in addition to symbiotic Pi uptake.

Phosphate influences AM development

When a fungal *PT* or plant *PT* genes essential for symbiosis are mutated or silenced most arbuscules are stunted (Javot *et al.,* 2007a; Yang *et al.,* 2012; Xie *et al.,* 2016; Volpe *et al.,* 2016), due to accelerated arbuscule turnover (Javot *et al.,* 2007a). This indicates that the plant removes an arbuscule, which does not deliver Pi, possibly as a mechanism to avoid fungal parasitism (Gutjahr & Parniske, 2017). Interestingly, the accelerated arbuscule turnover in the *Medicago pt4* mutant can be suppressed when the plant is grown in nitrogen starvation conditions (Javot *et al.,* 2011; Breullin-Sessoms *et al.,* 2015), indicating that under these conditions symbiotic nitrogen delivery becomes an advantage even if Pi is not delivered, according to Liebig's law of the minimum (Gutjahr & Parniske, 2017). However, a double mutant of *MtPT4* and the PAM-localized ammonium transporter *MtAMT2.3* (Breullin-Sessoms *et al.,* 2015) retained a majority of stunted arbuscules, pointing towards a particular importance of ammonium as compared to nitrate, at least in Medicago. Together this indicates that fungus-delivered nutrients can act as cell-autonomous signals in the regulation of arbuscule maintenance. The molecular mechanism for this is currently unknown, but it has been suggested that PAM-localized PTs could act as transceptors similar to PHO84 in yeast (Popova *et al.,* 2010; Yang *et al.,* 2012; Breuillin-Sessoms *et al.,* 2015; Volpe *et al.,* 2016). This was based on the observation that the *OsPT13* gene, which is specifically expressed in arbuscule containing cells, is not required for AM-mediated Pi uptake, in contrast to the major player OsPT11 (Yang *et al.,* 2012). However, mutation of *OsPT13* still leads to accelerated arbuscule turnover, indicating that OsPT13 may be important for Pi sensing. The same may apply to ammonium transporters, as only *AMT2.3* was essential for arbuscule branching in the *pt4* mutant background, while the other AM-induced *AMT2.2*, *AMT2.4* and *AMT2.5* genes were not required, although AMT2.4 showed a higher affinity for ammonium than AMT2.3 in yeast complementation assays (Breuillin-Sessoms *et al.,* 2015). This could indicate that the receptor activity of AMT2.3 is more important than its transport activity. Remarkably, the recently described PT gene from the AMF *Gigaspora margarita*, which is expressed in both ERM and IRM, was shown to act as a transceptor (Xie *et al.,* 2016). Thus, coupling of Pi uptake and sensing therefore seems to be also important for the fungus.

An innovative RNAi-based suppressor screen for *pt4* focusing on transcription factors led to the identification of MYB1, the first transcriptional regulator of arbuscule degeneration (Floss *et al.,* 2017). MYB1 is involved in the regulation of a range of hydrolase genes possibly involved in clearing the arbuscule from the cortex cell. The *myb1* mutant does not show prolonged arbuscule life-time, although the MYB1 promoter is active in arbuscule-containing cells of the wild-type (Volpe *et al.,* 2013; Floss *et al.,* 2017), but ectopic expression of MYB1 suppresses AM development (Floss *et al.,* 2017). This indicates genetic redundancy at the level of MYB1 when Pi is delivered normally. MYB1 interacts with the GRAS proteins NODULATION SIGNALING PATHWAY1 (NSP1) and the suppressor of gibberellin signaling DELLA in binary interaction studies (Floss *et al.,* 2017), pointing towards a link between the regulation of arbuscule degeneration and plant hormone signaling.

In addition to its cell-autonomous influence on arbuscule maintenance, Pi regulates AM formation also in a systemic manner. It is long known that AM establishment is repressed when plants are grown under high Pi supply (Mosse 1973; Branscheid *et al.,* 2010; Balzergue *et al.,* 2011; Kobae *et al.,* 2016). For suppression to occur the shoot Pi level seems to be important because in split root experiments, in which only one side of the split root system was fertilized with high Pi concentrations, AM formation was suppressed on both sides (Branscheid *et al.,* 2010; Breuillin *et al.,* 2010; Balzergue *et al.,* 2011). Therefore, members of the miR399 family, which are systemic Pi-starvation signals, have been proposed as signaling molecules in the regulation of AM by Pi, as they are induced by AM fungal colonization (Branscheid *et al.,* 2010). However, miR399 overexpression did not restore AM fungal colonization at high Pi level (Branscheid *et al.,* 2010) suggesting that other mechanisms are involved. The reason of reduced AM colonization has also been searched in a perturbed early communication between plant and fungus. However, Ca^{2+} spiking in epidermal cells is still generated in response to AMF hyphopodia at high Pi conditions, indicating that the host plant maintains the ability to perceive and respond to the fungal partner (Balzergue *et al.,* 2013). On the plant side, SL biosynthesis is reduced under high-Pi conditions. However, the exogenous application of GR24, a synthetic SL analogue, failed to increase AM colonization levels at high Pi (Breullin *et al.,* 2010; Balzergue *et al.,* 2011), suggesting that other factors or phytohormones such as auxin or gibberellin may be involved in suppressing AM at high Pi (Floss *et al.,* 2013; Carbonnel & Gutjahr, 2014; Pozo *et al.,* 2015).

Interesting clues are emerging from metagenomics studies: the plant immune system (Lebeis *et al.,* 2015) and soil nutrient composition (Hacquard *et al.,* 2015; Castrillo *et al.,* 2017) were shown to play a key role in the coordination of root colonization by specific microbial taxa. Castrillo *et al.* (2017) demonstrated that the genetic network controlling the Pi stress response influences the composition of the microbial community of *A. thaliana* roots. An *Arabidopsis* double mutant defective in *PHR1* and *PHL1*, encoding two redundant master transcriptional regulators of Pi starvation responses (PSR), showed an upregulation of plant defense genes leading to an atypical composition of a synthetic bacterial community at low as well as high Pi conditions. These results are in line with the observation that *Arabidopsis* roots upregulate defense genes when colonized at high Pi conditions by the fungal endophyte *C. tofieldiae* (Hacquard *et al.,* 2016), which promotes plant growth under low Pi conditions by translocating Pi to the host (Hiruma *et al.,* 2016), reminiscent of what occurs in AM symbiosis. A similar activation of defense-related genes was observed in field grown maize when the plants were grown at high soil Pi levels; this was accompanied with alterations in the root-inhabiting fungal community and with reduced root length colonization by AMF (Yu *et al.,* 2017). It appears that lowering plant defenses at low Pi, functions in increasing the chances to recruit beneficial soil microbes to overcome the nutritional stress. Conversely, it is tempting to speculate that in Pi-sufficient plants, similar defense mechanisms may participate in suppressing AM formation.

An RNAseq analysis of *R. irregularis* colonizing *Lotus* roots represents the first investigation of fungal responses to high Pi (Sugimura & Saito, 2017). Fungal cell cycle regulatory genes, cyclin-dependent kinase CDK1 and several DNA replication- and mitosis-related genes were repressed under high Pi conditions in the IRM (Sugimura & Saito, 2017). The same genes were not regulated by a high Pi treatment in the ERM (Kikuchi *et al.,* 2014), suggesting that the transcriptional change in cell-cycle related genes may be mediated by the Pi-sufficient plant. High Pi treatment also led to down-regulation of twenty-nine putative secreted proteins, including SL-induced putative secreted protein (SlS1) (Sugimura & Saito, 2017), pointing to an effect of the reduced SL of a Pi-sufficient plant.

IV. The plant-fungus genotype combination determines the outcome of the symbiosis

Plant growth responses cannot be predicted by AMF phylogeny

Despite a rather modest morphological variation, AMF often show a high level of genetic variability. The characterization of ribosomal sequences revealed an unusually high sequence divergence, especially in the Internal Transcribes Spacer region (Thiéry *et al.,* 2016). Thus, the small rDNA subunit (SSU) is nowadays commonly used as a more reliable marker to define species in the Glomeromycotina (Öpik & Davidson, 2016). However, SSU rDNA may suffer from a limited resolution and many exceptions to the correlation between SSU alone and morphological species were reported. Indeed, the concept of species for AMF is currently a matter of debate and resolution of this issue will possibly require multilocus data (Bruns *et al.,* 2017).

AMF also display a high functional diversity: the efficiency of AMF genera and isolates belonging to the same species to stimulate plant growth is highly variable. Also depending on the host plant, the effect can vary in magnitude and in direction, as positive or negative effects have been recorded (Hart & Reader, 2002; Munkvold *et al.,* 2004; Feddermann *et al.,* 2008; Antunes *et al.,* 2011; Hong *et al.,* 2012; Fig. 3). However, a high functional variation, measured as the growth effect on the host plant, contrasts with the low intraspecific morphological variation shown by isolates of the same species.

In a large comparative study of AMF performance, 56 AMF isolates belonging to six different families and 17 genera were inoculated on three different host plants (Koch *et al.,* 2017) to look for relationships between fungal traits/phylogenetic position and plant growth responses. Even if most isolates originated from geographically distant areas, traits such as extraradical hyphal volume or total spore weight were relatively constant within AMF families. Surprisingly, AMF phylogeny and species identity could not predict the plant growth response. Moreover, with the exception of total spore volume, none of the considered fungal traits (total fungal volume, extra- and intraradical fungal volumes) was positively correlated with plant performance (Koch *et al.,* 2017), suggesting that molecular features such as the repertoire of signaling molecules, effectors or the abundance and efficiency of nutrient transport proteins may play a more important role for plant performance than AMF growth and morphology. Deciphering the origin of this intraspecific functional diversity is challenging and will require genomics and functional genomics investigations at intra- and interspecific levels. The effects on plant performance are likely under the control of a number of loci showing polymorphisms in coding and/or regulatory regions at the intraspecific level. As suggested by host-specific expression patterns of candidate effector genes (Kamel *et al.,* 2017) the host plant may also play a role in the regulation of such loci. In addition, plant growth promotion may not be the only trait that should be considered: other benefits such as tolerance to abiotic or biotic stresses could provide a different picture. This knowledge will be fundamental to predict the impact of AMF inoculation on plant performance.

The recent discovery of homokaryotic as well as dikaryotic strains of *R. irregularis* and the identification of putative MAT loci (Ropars *et al.,* 1016; Corradi & Brachmann, 2017) highlighted the potentials of AMF for sexual reproduction. The characterization of MAT loci will be instrumental to understand, whether they are involved in dikaryon establishment and, eventually, in karyogamy and meiosis. These new findings and expected advances in the understanding of AMF genetics and life cycle may even pave the way to genetic strain improvement for applied purposes.

Plant responsiveness to AMF is subject to genetic diversity

Not only the AMF, but also the plant genotype strongly affects the outcome of the symbiosis (Smith *et al.,* 2004; Fig. 4). The performance response of plants to AMF has been defined as responsiveness and contrasted with dependence, which describes that a genetically determined nutrient inefficiency can be compensated by AMF (Paszkowski & Boller, 2002; Janos, 2007; Sawers *et al.,* 2010). Responsiveness can differ among cultivars of the same species and, in addition, it is affected by soil nutrient content (Sawers *et al.,* 2010; Chu *et al.,* 2013), indicating a complex genotype by environment interaction. Sawers *et al.* (2017) identified a first symbiotic parameter, which may determine AM-responsiveness in maize. They investigated AM-responsiveness (R) defined as shoot dry weight of mycorrhizal plants *minus* shoot dry weight of non colonized plants ($R = SDW_M - SDW_{NC}$), in 30 American maize lines including the founder lines of a nested association mapping population (McMullen *et al.,* 2009) when colonized with the fungus *Funneliformis mosseae* in greenhouses. Interestingly, the capacity of maize lines to profit from the symbiosis in terms of shoot dry weight and shoot Pi content correlated with the amount of associated extraradical hyphae (Sawers *et al.,* 2017; Fig. 4), suggesting an influence of plant genetics on fungal growth performance and, conversely, an impact of fungal morphology on plant performance when comparisons are based on only one fungal isolate. The plant molecular mechanisms determining fungal performance are entirely unknown and may be related to the amount of carbohydrates and lipids released to the fungus. Indeed, the expression pattern of monosaccharide transporter genes from the AMF

R. irregularis in intraradical *vs.* extraradical hyphae depended on the host plant (Ait Lahmidi *et al.,* 2016), which may be symptomatic of differences in monosaccharide supply or plant signals, which influence carbohydrate uptake strategies of the fungus.

Moreover, the analysis of the same cohort of 30 maize lines for an ionomics screen for 19 mineral ions in shoots and roots allowed the identification of clusters of ions, which showed coordinated changes in response to AMF and to genotype (Ramirez-Flores *et al.,* 2017). It will be interesting to understand how the coordinated uptake of or protection from certain ions occurs and whether these correlations can also be found in a realistic field setting. Plant genetic variation also determines the root colonization level of a given fungus. However, according to our current knowledge the amount of colonization is not a major determinant of plant performance benefit (Koch *et al.,* 2017; Sawers *et al.,* 2017). In a large effort, 94 bread wheat genotypes were analysed for root length colonization by a mixed inoculum of three AMF species and six QTLs associated with colonization level were identified (Lehnert *et al.,* 2017). Interestingly, these contained genes related to defense and cell wall metabolism, which may be involved in restraining root colonization.

Some plant genotypes respond to AMF with growth depression. The mechanism behind the depression is not yet clear and, although it partially depends on soil conditions (Sawers *et al.,* 2010), it was in other studies on wheat and barley partially uncoupled from Pi uptake as well as from fungal growth (Li *et al.,* 2008; Grace *et al.,* 2009). It has been suggested that domestication may have decreased the ability of plants to respond positively to AMF (Lehmann *et al.,* 2012). This was investigated in a comparison of 27 crops with their wild progenitors (Martin-Robles *et al.,* 2017). Both wild and domesticated species responded to AMF at low Pi conditions, however the response was not strictly correlated to Pi in the green leaves, indicating either a variety of Pi partitioning strategies in the different species or a range of mechanisms contributing to the growth response. A subset of 14 pairs of wild and domesticated species was also tested at high Pi conditions. Interestingly, the growth response of wild progenitors to AMF was similar at low and high Pi, while it was strongly reduced at high Pi in the domesticated counterparts. In addition, suppression of root colonization at high Pi was more pronounced in the domesticated plants (Martin-Robles *et al.,* 2017). Together, this indicates that - at least in the tested species - domestication selected for AM independence at high Pi levels, which possibly increased yield in absence of a fungal carbon drain. However, as AMF provide other services to plants such as increased resistance to abiotic stress and certain pathogens, it remains to be investigated whether other stresses would enhance AM-responsiveness of domesticated plants under high Pi fertilization.

V. Perspectives

It is now commonly accepted that soil biodiversity promotes multiple ecosystem functions and that the tailored management of soil communities, including AMF, has the potential to enhance agricultural sustainability (Bender *et al.,* 2016). Understanding the biology of AMF and the AM symbiosis is instrumental for their full exploitation. We envisage in the near future a significant expansion of our knowledge in several fields of AM research.

Comparative genomics and transcriptomics from a larger number of AMF species will expand our knowledge of their genome organization, genetic and regulatory complexity. The intricacy of AMF genetics is increased by the presence of endobacteria, which live inside many AMF (Bonfante & Desirò, 2017) and may influence fungal fitness. For example, the endobacterium Candidatus *Glomeribacter gigasporarum* was shown to increase sporulation, ATP production, reactive oxygen detoxification and responsiveness to the plant signal strigolactones of the fungal host, *G. margarita* (Salvioli *et al.,* 2016). Also viruses can thrive inside AMF; however, our knowledge on the AMF virome is limited to few *Rhizophagus* species (Ikeda *et al.,* 2012; Kitahara *et al.,* 2014). In particular, Ikeda *et al.,* (2012) demonstrated that a virus-free fungal strain produced more spores and promoted plant growth more efficiently than the virus-containing strain. The full complement of the microbiota living inside AMF certainly deserves further investigation to define their influence on the metabolism of the fungal host and the potential impact on plant performance.

The characterization of AMF putative effectors and the identification of factors involved in the perception of plant signals, nutrient uptake, transport and metabolism will also be an active field of research and should involve AMF species-comparisons to foster an understanding of AMF functional diversity. Current limitations in the direct genetic manipulation of AMF can be circumvented using heterologous systems such as *Nicotiana benthamiana* leaf and legume hairy root transient assays or transgenic expression in transformable biotrophic fungi such as *O. maius* (Fiorilli *et al.,* 2016) or pathogenic oomycetes such as *Phytophtora palmivora* (Rey & Schornack, 2013). HIGS or VIGS and the emerging tool SIGS (Spray-Induced Gene Silencing; Wang & Jin, 2017) can be exploited for silencing fungal genes; however, the efficiency and reliability of these methods still need to be improved.

We expect to see progress in the description and characterization of plant receptors for

AMF signalling molecules as well as in the identification of substrates of receptors and transporters such as D14L/KAI2 and NOPE1 (Gutjahr *et al.,* 2015; Nadal *et al.,* 2017). Physiological and molecular investigation is needed to resolve mechanisms and regulation of nutrient transfer between the symbionts and, in particular, the flux of carbohydrates and lipids towards the fungus (Rich *et al.,* 2017). It becomes increasingly clear, that despite their large host range, the efficiency of AMF in promoting plant performance differs strongly among fungal species and isolates and the ability of the plant to respond to the symbiosis depends on the plant genotype. The molecular basis of AM-responsiveness is entirely unclear but it may depend on a diversity of strategies for nutrient partitioning, hormone homeostasis or (in)compatibilities of AMF effector-plant target pairs. The identification of genetic polymorphisms underlying differences in symbiotic performance of plants and AMF will be key to smart breeding for profitable application of the AM symbiosis in sustainable agricultural systems with reduced chemical fertilizer and pesticide input.

Acknowledgements

Research in LLs laboratory is supported by 60% Projects (University of Torino) and TomRes project (H2020 SFS-2016) and in CGs laboratory by the German Federal Ministry of Education and Research (BMBF, project “MAZE”), the Emmy Noether program (GU1423/1-1) and the SFB924 (project B03) of the DFG. We apologize to all those colleagues whose work was not cited because of space restrictions.

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Figure legends

Figure 1. Molecules involved in the communication between AMF and host plants. Plant roots release strigolactones (SL) which stimulate AMF metabolism and hyphal branching to promote colonization (Akiyama *et al.,* 2005; Besserer *et al.,* 2006; 2008). The recent finding that a plant *N*-acetylglucosamine (GlcNAc) transporter is required for AM early signalling suggests the existence of GlcNAc-based diffusible plant molecules, which may trigger presymbiotic fungal reprogramming (Nadal *et al.,* 2017). Also AMF use GlcNAc-based molecules, which include lipo-chito-oligosaccharides (LCO; Maillet *et al.,* 2011) and short chitin tetra- and pentamers (CO; Genre *et al.,* 2013), as pre-contact signals to activate plant symbiotic responses. AMF effector candidates, thought to interfere with host cellular processes to favor colonization at early and/or late stages of the AM symbiosis, have been predicted from fungal genomes and transcriptomes (Sędzielewska Toro & Brachmann, 2016; Kamel *et al.,* 2017). To note that SL influence the production of chitin oligomer (Genre *et al.,* 2013) and effectors (Tsuzuki *et al.,* 2016; Kamel *et al.,* 2017) by AMF. IRM: intraradical mycelium; ERM: extraradical mycelium.

Figure 2. Scheme of the variety of symbiotic effectors produced by AMF during the interaction with host plants (based on data from Kamel *et al.,* 2017). For a single AMF species some effectors are expressed in association with all plant species while others are expresssed in a host plant-specific manner. Some effectors are conserved among AMF and may play core symbiotic functions.

Figure 3. The magnitude of plant growth promotion depends on the AMF genotype.

Figure 4. Distinct plant genotypes of the same species show differences in responsiveness (R) to AMF. In maize, responsiveness is correlated with the ability of the line to promote the growth of the extraradical mycelium (ERM) of *Funnelliformis mossae* (Sawers *et al.,* 2017). Drawings of maize plants were adopted from www.clipart.co.