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## Partner communication and role of nutrients in the arbuscular mycorrhizal symbiosis

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1 **Partner communication and function in the arbuscular mycorrhizal symbiosis**

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27 **Summary**

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

45

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

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## 61 **I. Introduction**

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

70 AMF show peculiar features: beside their obligate biotrophism, they are characterized by  
71 coenocytic hyphae and multinucleated spores (Kamel *et al.*, 2016; Lanfranco *et al.*, 2016);  
72 no sexual reproduction has been described so far, although evidence for the potential of  
73 mating-related processes has been obtained (Corradi & Brachmann, 2017). They have a  
74 rather long history of taxonomic revisions, which reflects the general difficulty in resolving  
75 the earliest branches in the fungal genealogy. Ribosomal DNA-based phylogenies placed  
76 them in the Glomeromycota phylum considered a sister group to Dikarya (Schüssler *et al.*,  
77 2001). An extensive phylogenomic study, based on kingdom-wide sampling of fungal  
78 species and genome-scale sampling of loci, placed AMF in the subphylum named  
79 Glomeromycotina with a close relationship with Mortierellomycotina (Spatafora *et al.*,  
80 2016).

81 AM is one of the most ancient and widespread symbioses in nature (Lanfranco *et al.*, 2016).  
82 The main advantage of the AM symbiosis is the exchange of nutrients: the plant provides  
83 up to 20% of the photosynthetically fixed organic carbon to the AMF (Roth & Paszkowski,  
84 2017), while the AMF transfers mineral nutrients to the plant thanks to its efficiency in  
85 exploring and acquiring these resources from the soil (Smith *et al.*, 2011). In addition,  
86 plants colonized by AMF often show higher tolerance to biotic and abiotic stresses  
87 compared to non-mycorrhizal plants and this is not a mere consequence of a better  
88 nutritional status (Jung *et al.*, 2012; Augé *et al.*, 2015). At the ecosystem level, AM  
89 improves soil quality (Rillig *et al.*, 2015) and increases plant biodiversity (van der Heijden  
90 *et al.*, 1998).

91 Root colonization by AMF occurs in successive steps. Prior to physical contact between  
92 plant and fungus, diffusible molecules mediate reciprocal recognition. When fungal hyphae  
93 touch the root epidermis, they form adhesion structures called hyphopodia. Subsequently,  
94 AMF enter the root and grow into the root cortex taking an intracellular as well as

95 intracellular route. In the cortex, hyphae penetrate single cells, where they develop  
96 arbuscules, highly branched structures (Gutjahr & Parniske, 2013; Lanfranco *et al.*, 2016).  
97 Arbuscules are surrounded by a plant derived peri-arbuscular membrane (PAM), which,  
98 together with the arbuscule-membrane, forms an extensive interface for nutrient exchange.  
99 Excellent recent reviews describe the latest advances in plant regulatory and cell biological  
100 mechanisms required for accommodation of AMF inside roots (Luginbuehl & Oldroyd,  
101 2017; MacLean *et al.*, 2017; Pimprikar & Gutjahr, in revision). Here we discuss, with  
102 special attention on the fungal partner, new findings in the understanding of molecules and  
103 mechanisms that control partner recognition, the importance of nutrients in the  
104 establishment and maintenance of AM and the role of plant-fungal genotype combinations  
105 for the outcome of the symbiosis.

106

## 107 **II. Interkingdom communication enabling symbiosis**

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

111

### 112 *Plant exudates activate the fungus*

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

129 a lower colonization level, while arbuscule morphology is normal (summarized in Waters  
130 *et al.*, 2017 and Lanfranco *et al.*, 2017).

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

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

160

161 *Fungal chitin-based molecules elicit symbiotic plant responses*

162 AMF use GlcNAc-based molecules as pre-contact signals to activate symbiotic responses

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

170 Both Myc-COs and Myc-LCOs are able to elicit repetitive nuclear calcium ( $\text{Ca}^{2+}$ )  
171 oscillations, known as  $\text{Ca}^{2+}$ -spiking, which is considered a hallmark of symbiotic signalling  
172 (Oldroyd 2013; Sun *et al.*, 2015). So far, the biological significance of producing both  
173 Myc-COs and Myc-LCOs remains obscure. It is possible that a diversity of signaling  
174 molecules contributes to the ability of AMF to interact with a wide range of AM host plants  
175 or to the robustness of the system. However, GlcNAc-containing molecules can be  
176 produced by many microorganisms, including plant pathogens, and it is puzzling how  
177 plants can distinguish AMF from the others. One possibility are fine-tuned Myc Factors  
178 ligand-receptor specificities (Zipfel & Oldroyd, 2017). Small molecules with a GlcNAc  
179 backbone are perceived by LysM-domain containing receptor like kinases (LysM RLKs)  
180 and receptor like proteins (LyM RLPs), with different ligand specificities (Gust *et al.*,  
181 2012). The repertoire of LysM-receptors differs significantly among plant species (Zhang *et*  
182 *al.*, 2009), which may have favoured the co-evolution or maintenance of several different  
183 Myc Factors. Possibly due to the functional redundancy of AMF-responsive LysM-receptor  
184 kinases in the genome of AMF-host plants, and the multitude of different Myc Factors,  
185 definitive receptors for Myc-COs or Myc-LCOs have not emerged yet (Buendia *et al.*,  
186 2016; Zipfel & Oldroyd, 2017). Good candidates are SILYK10 from tomato and NFP from  
187 *Parasponia*: virus-induced and RNAi-mediated gene silencing of both corresponding genes,  
188 respectively, partially perturbed AM establishment (Op den Camp *et al.*, 2011; Buendia *et*  
189 *al.*, 2016). However, there is currently no evidence that both LysM-RLKs bind Myc-COs or  
190 Myc-LCOs and it cannot be excluded that VIGS and RNAi affected the expression of  
191 additional redundant LysM-RLKs. The rice OsCERK1, a LysM receptor-like kinase, which  
192 has a dual role in both interactions with pathogenic fungi and AMF (Miyata *et al.*, 2014),  
193 was shown to play a central role in the perception of Myc-CO signals because an *oscerk1*  
194 mutant does not respond to these molecules with  $\text{Ca}^{2+}$ -spiking (Carotenuto *et al.*, 2017). In  
195 addition, it fails to induce lateral roots in response to AMF (Chiu *et al.*, 2018). However,  
196 *oscerk1* root colonization is only delayed and not entirely abolished (Miyata *et al.*, 2014;



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

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

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

218

#### 219 *An emerging role for fungal effectors in AM establishment*

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

224 AMF effector candidates have been predicted from fungal genomes and transcriptomes  
225 (Sędziewska Toro & Brachmann, 2016; Kamel *et al.*, 2017). The number of identified  
226 genes depends on the criteria used to define effectors. A first criterium is the presence of a  
227 signal peptide that guides proteins towards secretion. Sędziewska Toro & Brachmann  
228 (2016) further filtered on the basis of the small size and the presence of cysteines, internal  
229 repeats and nuclear localization signals leading to the identification of 220 putative  
230 effectors from *R. irregularis*. Remarkably, a large majority of these genes is conserved in

231 the related species *R. clarus*, suggesting that a majority of putative effectors may be  
232 involved in core symbiotic functions. However, a comparison of transcriptomes from two  
233 distantly related AMF, *R. irregularis* and *Gigaspora rosea*, when colonizing three different  
234 host plants (the dicotyledon *M. truncatula*, the monocotyledon *Brachypodium distachyon*  
235 and the liverwort *Lunularia cruciata*), revealed that the expression of putative secreted  
236 proteins (SPs) can differ in function of the host plant: among 87 SPs genes expressed in the  
237 intraradical mycelium of *R. irregularis* only 33 were expressed in all three plant species  
238 (Kamel *et al.*, 2017), suggesting that these 33 fulfill core-functions, while the others may  
239 act host-specifically (Fig. 2). Host-specifically expressed effector candidates have also been  
240 observed for the endophyte *Piriformospora indica*, when colonizing roots of barley or  
241 *Arabidopsis* (Lahrmann *et al.*, 2015).

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

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

265 effectors. *RiPEIP1* expression in *Oidiodendron maius*, an ericoid endomycorrhizal fungus,  
266 for which transformation protocols are available, led to enhanced mycorrhization capacity  
267 compared to the *O. maius* wild-type strain (Fiorilli *et al.*, 2016). Further studies are needed  
268 to define the mechanisms of action of SIS1 and RiPEP1 and their specific role in the  
269 establishment of the AM symbiosis.

270 In addition to proteins, small RNAs of the pathogenic fungus *Botrytis cinerea*, were shown  
271 to target, by cross-kingdom RNAi, mRNA of defense genes in the host plant, thus acting as  
272 effectors (Wang *et al.*, 2017). It is possible that such a mechanism is also exploited by  
273 AMF. The interference with RNA metabolism of the host plant can also be envisaged for  
274 the so-called RALPH (RNase-Like Proteins associated with Haustoria) the secreted  
275 avirulence effectors described in the obligate biotroph pathogenic fungus *Blumeria*  
276 *graminis* (Spanu 2017).

277

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

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

283

#### 284 *AMF receive carbohydrates as well as lipids from the host*

285 Based on stable isotope labelling experiments, it has long been established that AMF  
286 receive carbohydrates and specifically glucose from the plant (Pfeffer *et al.*, 1999;  
287 Trépanier *et al.*, 2005). How the sugars are transported from the plant to the fungus is still  
288 unclear. A number of genes encoding sugar transporters with activities towards  
289 monosaccharides (MSTs) and sucrose (SUTs) as well as members of the SWEET family  
290 are upregulated in mycorrhizal roots (Harrison, 1996; Doidy *et al.*, 2012; Manck-  
291 Götzenberger & Requena, 2016), but genetic evidence for their function is still missing. So  
292 far only the function of the sucrose transporter SUT2 from tomato has been investigated by  
293 reverse genetics (Bitterlich *et al.*, 2014). It is localized to the PAM and roots of *sut2*  
294 antisense plants are significantly more colonized than wild-type roots. Together, this  
295 suggests that SUT2 may be involved in competition with the fungus for sucrose for  
296 example by pumping the metabolite from the peri-arbuscular space (PAS) back into the  
297 plant cell (Bitterlich *et al.*, 2014). A high affinity monosaccharide transporter MST2 from  
298 the AMF *R. irregularis* has been characterized. *RiMST2* is expressed in arbuscules and

299 intercellular hyphae and is possibly responsible for sugars uptake from the peri-fungal  
300 apoplast, as silencing of *RiMST2* led to reduced root colonization and impaired arbuscule  
301 branching (Helber *et al.*, 2011). Interestingly, expression of *RiMST2* was triggered also in  
302 the extraradical mycelium, when it was supplied with xylose. Furthermore, the extraradical  
303 mycelium was able to take up <sup>14</sup>C-labelled glucose and xylose from the medium (Bücking  
304 *et al.*, 2008; Helber *et al.*, 2011) and this uptake was inhibited by the protonophore  
305 carbonyl cyanide m-chlorophenyl hydrazone, demonstrating that it occurred by active  
306 transport and not simple diffusion across the membrane (Helber *et al.*, 2011). The finding  
307 that AMF can actively take up pentoses and hexoses from the medium challenges the  
308 notion that obligate biotrophy of AMF is based upon strict dependence on plant-derived  
309 sugars.

310 Genome and transcriptome sequencing of the first AMF species shed more light on the  
311 biology and the evolution of AMF (Tisserant *et al.*, 2013; Lin *et al.*, 2014; Kamel *et al.*,  
312 2016; Ropars *et al.*, 2016; Tang *et al.*, 2016). Surprisingly, it was found that genes  
313 encoding the cytosolic fatty acids (FA) synthase subunits, which are responsible for the  
314 bulk FA production in fungi, are absent from AMF genomes (Wewer *et al.*, 2014; Tang *et al.*,  
315 2016). In about the same period, legume mutants, with stunted arbuscules, reduced root  
316 colonization and defects in three AM-induced lipid biosynthesis genes *DISORGANIZED*  
317 *ARBUSCULES* (*DIS*), *FatM* and *REDUCED ARBUSCULAR MYCORRHIZA 2* were  
318 identified (Wang *et al.*, 2012; Bravo *et al.*, 2016; Bravo *et al.*, 2017; Jiang *et al.*, 2017;  
319 Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017). *DIS* encodes a  $\beta$ -keto-acyl-ACP synthase I  
320 (KASI), which is specific to genomes of AM-competent gymnosperms and dicots and  
321 catalyses FA chain elongation from C4 to C16 (Keymer *et al.*, 2017). *FatM* encodes a  
322 thioesterase, which terminates FA chain elongation by hydrolysis of the acyl-ACP, and  
323 *FatM* shows a preference for C16-ACP (Bravo *et al.*, 2017; Brands *et al.*, under review).  
324 *RAM2* encodes an sn-2 glycerol-3-phosphate acyltransferase 6, which transfers a fatty acyl  
325 residue to the sn-2-position of a glycerol, thereby creating  $\beta$ -mono-acyl-glycerol ( $\beta$ -MAG,  
326 Luginbuehl *et al.*, 2017). Both *FatM* and *RAM2* have been only found in genomes of AM-  
327 competent land plants (Delaux *et al.*, 2015; Bravo *et al.*, 2016). Consistent with the  
328 phenotype, the promoters of all three genes *DIS*, *FatM* and *RAM2* are specifically active in  
329 arbuscule-containing cells (Gobbato *et al.*, 2013; Bravo *et al.*, 2017; Jiang *et al.*, 2017;  
330 Keymer *et al.*, 2017).

331 Comprehensive lipid profiling in *L. japonicus* and *M. truncatula* supported the hypothesis  
332 that *DIS*, *FatM* and *RAM2* act in an AM-specific lipid-biosynthesis pathway because *ram2*

333 mutants accumulate unusual phospholipids enriched in palmityl moieties, which are the  
334 products of the concerted action of DIS and FatM (Bravo *et al.*, 2017; Keymer *et al.*, 2017).  
335 AMF store lipids mainly as tri-palmityl-triacylglycerol (16:0 - TAG) and desaturate the 16:0  
336 fatty acyl chain at a specific  $\omega$ 5 position, permitting distinction of fungal from plant lipids  
337 by using 16:1 $\omega$ 5 FAs as an AMF-specific signature (Olsson *et al.*, 2005). The lipid profile  
338 of *dis*, *fatm* and *ram2* mutants contained hardly any 16:1 $\omega$ 5 FAs and the fungus *R.*  
339 *irregularis* did not form lipid-containing vesicles in mutant roots, suggesting that the  
340 fungus was deprived of lipids (Bravo *et al.*, 2017; Keymer *et al.*, 2017). Lipid transfer from  
341 host plants to AMF was shown by two independent experimental approaches. Luginbuehl  
342 *et al.* (2017) and Jiang *et al.*, (2017) used a genetic approach and transformed *Medicago*  
343 hairy roots with the *Umbellularia californica* fatty acyl-ACP thioesterase gene (*UcFatB*)  
344 that produces the 12:0 FA lauric acid, which does neither occur in *Medicago* nor in *R.*  
345 *irregularis*. Transgenic *Medicago* roots carrying *UcFatB* synthesized lauric acid and it was  
346 also detected in the spores of colonizing *R. irregularis* (Luginbuehl *et al.* 2017; Jiang *et al.*,  
347 2017), unequivocally demonstrating that lauric acid containing lipids were transferred from  
348 the host to AMF. Keymer *et al.* (2017) measured lipid transfer in non-transgenic plants by  
349 isotopolog profiling of 16:0 and 16:1 FAs as markers. To this end *Lotus* plants and carrot  
350 root organ culture were fed with <sup>13</sup>C labelled glucose. The isotopologue profile of 16:0 FAs  
351 in *Lotus* and carrot roots differed significantly. However, in each case the root profile was  
352 precisely mirrored by the 16:0 FAs in the fungal extraradical mycelium as well as by the  
353 fungus-specific 16:1 FAs (Keymer *et al.*, 2017), demonstrating that the profile was  
354 determined by the plant and therefore, the FAs were transferred from the plant to the  
355 fungus. In the *dis*, *fatm* and *ram2* mutants, lipid transfer was impaired as well as in *str*  
356 mutants, which are deficient in an ABC-half transporter gene (Bravo *et al.*, 2017; Jiang *et*  
357 *al.*, 2017; Keymer *et al.*, 2017). STR together with its complex partner STR2 (Zhang *et al.*,  
358 2010) is considered a good candidate transporter for lipid transfer across the PAM (Gutjahr  
359 *et al.*, 2012; Bravo *et al.*, 2017).

360 Taken together, these recent findings indicate that AMF are entirely dependent on lipid  
361 supply by the plant for their growth, development and reproduction and that the dependence  
362 on lipids may be the prime reason for their obligate biotrophy. They explain why AMF  
363 store a large amount of lipids in their spores, which are probably used as resources for  
364 membrane construction during spore germination and the first phase of root colonization  
365 until the first developing arbuscules can obtain lipids from the host. These findings also

366 change our view on the energy balance of the symbiosis, in which the burden of organic  
367 carbon compound biosynthesis is more significantly shifted towards the plant than was  
368 previously assumed.

369

#### 370 *Mechanisms of phosphate transfer from AMF to plant hosts*

371 Phosphorus (P) is predominantly present in soil as low mobile dihydrogen phosphate ion  
372 ( $\text{H}_2\text{PO}_4^-$ , Pi; Nussaume *et al.*, 2011) and a major macronutrient limiting plant growth. To  
373 overcome Pi starvation stress and increase access to Pi, plants have evolved several  
374 strategies. Under low Pi availability plants activate a Pi starvation response (PSR) system  
375 that regulates root and shoot architecture and physiology (Poirier & Bucher, 2002). In  
376 addition, plants can exploit the AM symbiosis to optimize Pi acquisition. The Pi  
377 contribution *via* AMF ranges from a small percentage to almost the entire acquired Pi,  
378 depending on plant/AMF combinations (Smith *et al.*, 2004). AMF are equipped with a very  
379 efficient system for Pi capture and translocation. Thanks to the extraradical hyphal network  
380 developed in the soil AMF greatly increase the absorbing surface area (up to 100-fold that  
381 of root hairs) extending well beyond the depletion zone (Javot *et al.*, 2007b). AMF were  
382 also proposed to be able to mineralize soil organic P (Feng *et al.*, 2003; Shibata & Yano,  
383 2003); and this was supported by Sato *et al.* (2015) demonstrating that extraradical hyphae  
384 of the AMF *R. clarus* release an acid phosphatase of about 187 kDa, which may be  
385 involved in mobilizing organic P. AMF colonization also induces the expression and  
386 secretion of acid phosphatases on the plant side (Ezawa *et al.*, 2005), indicating that the  
387 symbiosis may also increase the plant ability to solubilize organic P from the soil.

388 Fungal Pi:H<sup>+</sup> symporter (PT), homologs of the yeast high-affinity transporter PHO84 (Bun-  
389 Ya *et al.*, 1991), are thought to be responsible for Pi uptake from the soil (Harrison & van  
390 Buuren, 1995; Maldonado-Mendoza *et al.*, 2001; Benedetto *et al.*, 2005; Xie *et al.*, 2016).  
391 Consistently, the fungal PT genes are expressed in the extraradical mycelium (ERM) but  
392 also in the intraradical mycelium (IRM), suggesting an additional role in Pi reabsorption  
393 from the PAS (Benedetto *et al.*, 2005; Balestrini *et al.*, 2007; Fiorilli *et al.*, 2013; Xie *et al.*,  
394 2016).

395 Once absorbed by ERM, Pi is quickly converted inside vacuoles into polyphosphate  
396 (polyP) chains, linear polymers of three to hundreds Pi molecules (Solaiman *et al.*, 1999;  
397 Ezawa *et al.*, 2003). It has been hypothesized that AMF synthesize polyP through the VTC  
398 complex (Tisserant *et al.*, 2012; Tani *et al.*, 2009), as described in yeast (Hothorn *et al.*,  
399 2009). PolyP is then translocated to the IRM *via* protoplasmatic streaming and/or along a

400 motile a tubular vacuolar network (Olsson *et al.*, 2002; Uetake *et al.*, 2002, Hijikata *et al.*,  
401 2010). Interesting new insights into the mechanism of long-distance polyP translocation in  
402 mycorrhizal associations were obtained from the characterization of *R. clarus* aquaporin 3  
403 (RcAQP3), an aquaglyceroporin responsible for water transport across the plasma  
404 membrane (Kikuchi *et al.*, 2016). *RcAQP3* is strongly expressed in intraradical mycelia and  
405 down-regulation of *RcAQP3* via VIGS through the host plant, as well as the suppression of  
406 host plant transpiration, decelerated polyP translocation. Kikuchi *et al.* (2016) proposed  
407 thus a model in which transpiration provides a primary driving force for polyP translocation  
408 by creating water flow through the fungal RcAQP3 and the mycorrhiza-inducible plant  
409 aquaporins.

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

416 Pi is delivered to the periarbuscular space, by a still unknown mechanism. It is then  
417 imported by AM-inducible, PAM-localized plant PTs, such as Medicago PT4 and rice  
418 PT11 into the cortical cells (Javot *et al.*, 2007b; Yang *et al.*, 2012). This transport is  
419 suggested to be supported by a H<sup>+</sup> energy gradient produced by a H<sup>+</sup>-ATPase, that has been  
420 found to be important for arbuscule maintenance and AM-mediated phosphate uptake  
421 (Krajinski *et al.*, 2014; Wang *et al.*, 2014). AM-inducible PT genes have been identified in  
422 different host plants (Harrison *et al.*, 2002; Javot *et al.*, 2007a; Paszkowski *et al.*, 2002;  
423 Yang *et al.*, 2012; Rausch *et al.*, 2001; Nagy *et al.*, 2005; Xu *et al.*, 2007; Balestrini *et al.*,  
424 2007; Willmann *et al.*, 2013; Sawers *et al.*, 2017; Hong *et al.*, 2012; Volpe *et al.*, 2016 ;  
425 Loth-Pereda *et al.*, 2011; Xie *et al.*, 2013; Walder *et al.*, 2015). They are homologs of the  
426 yeast PHO84 and belong to the Phosphate transporter 1 (Pht1) class (Poirier & Bucher,  
427 2002) of the plant H<sup>+</sup>/Pi symporters. In a phylogenetic tree of PHT1 proteins they cluster in  
428 a separate clade, which does not contain Pht1 transporters from AM-incompetent plants  
429 (Yang *et al.*, 2012; Hong *et al.*, 2012), indicating that an AM-specific PT-gene duplication  
430 was maintained in symbiotic Pi transport in the plant kingdom. Interestingly, the root  
431 endophyte *Colletotrichum tofieldiae* was shown to transfer Pi to Arabidopsis and to  
432 promote plant growth only under P-deficient conditions (Hiruma *et al.*, 2016). During  
433 colonization, several Arabidopsis PT genes of the Pht1 family were induced. It will be

434 interesting to investigate, whether they, similarly to AM-specific PTs, localize to perifungal  
435 membranes to directly take up Pi from the fungus.

436 While promoters of AM-specific PT genes have been mostly reported to be specifically  
437 expressed in arbuscule-containing cells, *PT4* from *M. truncatula* and *L. japonicus* are also  
438 expressed in root tips when grown at Pi starvation conditions (Volpe *et al.*, 2016).  
439 Interestingly, *mpt4* mutants and *Lotus* hairy roots expressing a RNAi construct which  
440 silence *PT4* do not respond to low Pi conditions with changes in lateral root formation to  
441 the same extent as the wild type (Volpe *et al.*, 2016), suggesting that PT4 is involved in  
442 root architecture responses to low Pi, in addition to symbiotic Pi uptake.

443

#### 444 *Phosphate influences AM development*

445 When a fungal *PT* or plant *PT* genes essential for symbiosis are mutated or silenced most  
446 arbuscules are stunted (Javot *et al.*, 2007a; Yang *et al.*, 2012; Xie *et al.*, 2016; Volpe *et al.*,  
447 2016), due to accelerated arbuscule turnover (Javot *et al.*, 2007a). This indicates that the  
448 plant removes an arbuscule, which does not deliver Pi, possibly as a mechanism to avoid  
449 fungal parasitism (Gutjahr & Parniske, 2017). Interestingly, the accelerated arbuscule  
450 turnover in the *Medicago pt4* mutant can be suppressed when the plant is grown in nitrogen  
451 starvation conditions (Javot *et al.*, 2011; Breullin-Sessoms *et al.*, 2015), indicating that  
452 under these conditions symbiotic nitrogen delivery becomes an advantage even if Pi is not  
453 delivered, according to Liebig's law of the minimum (Gutjahr & Parniske, 2017). However,  
454 a double mutant of *MtPT4* and the PAM-localized ammonium transporter *MtAMT2.3*  
455 (Breullin-Sessoms *et al.*, 2015) retained a majority of stunted arbuscules, pointing towards  
456 a particular importance of ammonium as compared to nitrate, at least in *Medicago*.  
457 Together this indicates that fungus-delivered nutrients can act as cell-autonomous signals in  
458 the regulation of arbuscule maintenance. The molecular mechanism for this is currently  
459 unknown, but it has been suggested that PAM-localized PTs could act as transceptors  
460 similar to PHO84 in yeast (Popova *et al.*, 2010; Yang *et al.*, 2012; Breullin-Sessoms *et al.*,  
461 2015; Volpe *et al.*, 2016). This was based on the observation that the *OsPT13* gene, which  
462 is specifically expressed in arbuscule containing cells, is not required for AM-mediated Pi  
463 uptake, in contrast to the major player *OsPT11* (Yang *et al.*, 2012). However, mutation of  
464 *OsPT13* still leads to accelerated arbuscule turnover, indicating that *OsPT13* may be  
465 important for Pi sensing. The same may apply to ammonium transporters, as only *AMT2.3*  
466 was essential for arbuscule branching in the *pt4* mutant background, while the other AM-  
467 induced *AMT2.2*, *AMT2.4* and *AMT2.5* genes were not required, although *AMT2.4* showed



468 a higher affinity for ammonium than AMT2.3 in yeast complementation assays (Breuillin-  
469 Sessoms *et al.*, 2015). This could indicate that the receptor activity of AMT2.3 is more  
470 important than its transport activity. Remarkably, the recently described PT gene from the  
471 AMF *Gigaspora margarita*, which is expressed in both ERM and IRM, was shown to act as  
472 a transceptor (Xie *et al.*, 2016). Thus, coupling of Pi uptake and sensing therefore seems to  
473 be also important for the fungus.

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

486 In addition to its cell-autonomous influence on arbuscule maintenance, Pi regulates AM  
487 formation also in a systemic manner. It is long known that AM establishment is repressed  
488 when plants are grown under high Pi supply (Mosse 1973; Branscheid *et al.*, 2010;  
489 Balzergue *et al.*, 2011; Kobae *et al.*, 2016). For suppression to occur the shoot Pi level  
490 seems to be important because in split root experiments, in which only one side of the split  
491 root system was fertilized with high Pi concentrations, AM formation was suppressed on  
492 both sides (Branscheid *et al.*, 2010; Breuillin *et al.*, 2010; Balzergue *et al.*, 2011).  
493 Therefore, members of the miR399 family, which are systemic Pi-starvation signals, have  
494 been proposed as signaling molecules in the regulation of AM by Pi, as they are induced by  
495 AM fungal colonization (Branscheid *et al.*, 2010). However, miR399 overexpression did  
496 not restore AM fungal colonization at high Pi level (Branscheid *et al.*, 2010) suggesting  
497 that other mechanisms are involved. The reason of reduced AM colonization has also been  
498 searched in a perturbed early communication between plant and fungus. However, Ca<sup>2+</sup>  
499 spiking in epidermal cells is still generated in response to AMF hyphopodia at high Pi  
500 conditions, indicating that the host plant maintains the ability to perceive and respond to the  
501 fungal partner (Balzergue *et al.*, 2013). On the plant side, SL biosynthesis is reduced under

502 high-Pi conditions. However, the exogenous application of GR24, a synthetic SL analogue,  
503 failed to increase AM colonization levels at high Pi (Breullin *et al.*, 2010; Balzergue *et al.*,  
504 2011), suggesting that other factors or phytohormones such as auxin or gibberellin may be  
505 involved in suppressing AM at high Pi (Floss *et al.*, 2013; Carbonnel & Gutjahr, 2014;  
506 Pozo *et al.*, 2015).

507 Interesting clues are emerging from metagenomics studies: the plant immune system  
508 (Lebeis *et al.*, 2015) and soil nutrient composition (Hacquard *et al.*, 2015; Castrillo *et al.*,  
509 2017) were shown to play a key role in the coordination of root colonization by specific  
510 microbial taxa. Castrillo *et al.* (2017) demonstrated that the genetic network controlling the  
511 Pi stress response influences the composition of the microbial community of *A. thaliana*  
512 roots. An *Arabidopsis* double mutant defective in *PHR1* and *PHL1*, encoding two  
513 redundant master transcriptional regulators of Pi starvation responses (PSR), showed an  
514 upregulation of plant defense genes leading to an atypical composition of a synthetic  
515 bacterial community at low as well as high Pi conditions. These results are in line with the  
516 observation that *Arabidopsis* roots upregulate defense genes when colonized at high Pi  
517 conditions by the fungal endophyte *C. tofieldiae* (Hacquard *et al.*, 2016), which promotes  
518 plant growth under low Pi conditions by translocating Pi to the host (Hiruma *et al.*, 2016),  
519 reminiscent of what occurs in AM symbiosis. A similar activation of defense-related genes  
520 was observed in field grown maize when the plants were grown at high soil Pi levels; this  
521 was accompanied with alterations in the root-inhabiting fungal community and with  
522 reduced root length colonization by AMF (Yu *et al.*, 2017). It appears that lowering plant  
523 defenses at low Pi, functions in increasing the chances to recruit beneficial soil microbes to  
524 overcome the nutritional stress. Conversely, it is tempting to speculate that in Pi-sufficient  
525 plants, similar defense mechanisms may participate in suppressing AM formation.

526 An RNAseq analysis of *R. irregularis* colonizing *Lotus* roots represents the first  
527 investigation of fungal responses to high Pi (Sugimura & Saito, 2017). Fungal cell cycle  
528 regulatory genes, cyclin-dependent kinase CDK1 and several DNA replication- and  
529 mitosis-related genes were repressed under high Pi conditions in the IRM (Sugimura &  
530 Saito, 2017). The same genes were not regulated by a high Pi treatment in the ERM  
531 (Kikuchi *et al.*, 2014), suggesting that the transcriptional change in cell-cycle related genes  
532 may be mediated by the Pi-sufficient plant. High Pi treatment also led to down-regulation  
533 of twenty-nine putative secreted proteins, including SL-induced putative secreted protein  
534 (SIS1) (Sugimura & Saito, 2017), pointing to an effect of the reduced SL of a Pi-sufficient  
535 plant.

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

537 *Plant growth responses cannot be predicted by AMF phylogeny*

538 Despite a rather modest morphological variation, AMF often show a high level of genetic  
539 variability. The characterization of ribosomal sequences revealed an unusually high  
540 sequence divergence, especially in the Internal Transcribes Spacer region (Thiéry *et al.*,  
541 2016). Thus, the small rDNA subunit (SSU) is nowadays commonly used as a more reliable  
542 marker to define species in the Glomeromycotina (Öpik & Davidson, 2016). However, SSU  
543 rDNA may suffer from a limited resolution and many exceptions to the correlation between  
544 SSU alone and morphological species were reported. Indeed, the concept of species for  
545 AMF is currently a matter of debate and resolution of this issue will possibly require  
546 multilocus data (Bruns *et al.*, 2017).

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

554 In a large comparative study of AMF performance, 56 AMF isolates belonging to six  
555 different families and 17 genera were inoculated on three different host plants (Koch *et al.*,  
556 2017) to look for relationships between fungal traits/phylogenetic position and plant growth  
557 responses. Even if most isolates originated from geographically distant areas, traits such as  
558 extraradical hyphal volume or total spore weight were relatively constant within AMF  
559 families. Surprisingly, AMF phylogeny and species identity could not predict the plant  
560 growth response. Moreover, with the exception of total spore volume, none of the  
561 considered fungal traits (total fungal volume, extra- and intraradical fungal volumes) was  
562 positively correlated with plant performance (Koch *et al.*, 2017), suggesting that molecular  
563 features such as the repertoire of signaling molecules, effectors or the abundance and  
564 efficiency of nutrient transport proteins may play a more important role for plant  
565 performance than AMF growth and morphology. Deciphering the origin of this  
566 intraspecific functional diversity is challenging and will require genomics and functional  
567 genomics investigations at intra- and interspecific levels. The effects on plant performance  
568 are likely under the control of a number of loci showing polymorphisms in coding and/or  
569 regulatory regions at the intraspecific level. As suggested by host-specific expression

570 patterns of candidate effector genes (Kamel *et al.*, 2017) the host plant may also play a role  
571 in the regulation of such loci. In addition, plant growth promotion may not be the only trait  
572 that should be considered: other benefits such as tolerance to abiotic or biotic stresses could  
573 provide a different picture. This knowledge will be fundamental to predict the impact of  
574 AMF inoculation on plant performance.

575 The recent discovery of homokaryotic as well as dikaryotic strains of *R. irregularis* and the  
576 identification of putative MAT loci (Ropars *et al.*, 2016; Corradi & Brachmann, 2017)  
577 highlighted the potentials of AMF for sexual reproduction. The characterization of MAT  
578 loci will be instrumental to understand, whether they are involved in dikaryon  
579 establishment and, eventually, in karyogamy and meiosis. These new findings and expected  
580 advances in the understanding of AMF genetics and life cycle may even pave the way to  
581 genetic strain improvement for applied purposes.

582

#### 583 *Plant responsiveness to AMF is subject to genetic diversity*

584 Not only the AMF, but also the plant genotype strongly affects the outcome of the  
585 symbiosis (Smith *et al.*, 2004; Fig. 4). The performance response of plants to AMF has  
586 been defined as responsiveness and contrasted with dependence, which describes that a  
587 genetically determined nutrient inefficiency can be compensated by AMF (Paszkowski &  
588 Boller, 2002; Janos, 2007; Sawers *et al.*, 2010). Responsiveness can differ among cultivars  
589 of the same species and, in addition, it is affected by soil nutrient content (Sawers *et al.*,  
590 2010; Chu *et al.*, 2013), indicating a complex genotype by environment interaction. Sawers  
591 *et al.* (2017) identified a first symbiotic parameter, which may determine AM-  
592 responsiveness in maize. They investigated AM-responsiveness (R) defined as shoot dry  
593 weight of mycorrhizal plants *minus* shoot dry weight of non colonized plants ( $R = SDW_M -$   
594  $SDW_{NC}$ ), in 30 American maize lines including the founder lines of a nested association  
595 mapping population (McMullen *et al.*, 2009) when colonized with the fungus  
596 *Funneliformis mosseae* in greenhouses. Interestingly, the capacity of maize lines to profit  
597 from the symbiosis in terms of shoot dry weight and shoot Pi content correlated with the  
598 amount of associated extraradical hyphae (Sawers *et al.*, 2017; Fig. 4), suggesting an  
599 influence of plant genetics on fungal growth performance and, conversely, an impact of  
600 fungal morphology on plant performance when comparisons are based on only one fungal  
601 isolate. The plant molecular mechanisms determining fungal performance are entirely  
602 unknown and may be related to the amount of carbohydrates and lipids released to the  
603 fungus. Indeed, the expression pattern of monosaccharide transporter genes from the AMF

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

607 Moreover, the analysis of the same cohort of 30 maize lines for an ionomics screen for 19  
608 mineral ions in shoots and roots allowed the identification of clusters of ions, which  
609 showed coordinated changes in response to AMF and to genotype (Ramirez-Flores *et al.*,  
610 2017). It will be interesting to understand how the coordinated uptake of or protection from  
611 certain ions occurs and whether these correlations can also be found in a realistic field  
612 setting. Plant genetic variation also determines the root colonization level of a given  
613 fungus. However, according to our current knowledge the amount of colonization is not a  
614 major determinant of plant performance benefit (Koch *et al.*, 2017; Sawers *et al.*, 2017). In  
615 a large effort, 94 bread wheat genotypes were analysed for root length colonization by a  
616 mixed inoculum of three AMF species and six QTLs associated with colonization level  
617 were identified (Lehnert *et al.*, 2017). Interestingly, these contained genes related to  
618 defense and cell wall metabolism, which may be involved in restraining root colonization.

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

638 high Pi fertilization.

639

## 640 **V. Perspectives**

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

646 Comparative genomics and transcriptomics from a larger number of AMF species will  
647 expand our knowledge of their genome organization, genetic and regulatory complexity.

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

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

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

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

686

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693

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1241 **Figure legends**

1242

1243 **Figure 1.** Molecules involved in the communication between AMF and host plants. Plant  
1244 roots release strigolactones (SL) which stimulate AMF metabolism and hyphal branching to  
1245 promote colonization (Akiyama *et al.*, 2005; Besserer *et al.*, 2006; 2008). The recent  
1246 finding that a plant *N*-acetylglucosamine (GlcNAc) transporter is required for AM early  
1247 signalling suggests the existence of GlcNAc-based diffusible plant molecules, which may  
1248 trigger presymbiotic fungal reprogramming (Nadal *et al.*, 2017). Also AMF use GlcNAc-  
1249 based molecules, which include lipo-chito-oligosaccharides (LCO; Maillet *et al.*, 2011) and  
1250 short chitin tetra- and pentamers (CO; Genre *et al.*, 2013), as pre-contact signals to activate  
1251 plant symbiotic responses. AMF effector candidates, thought to interfere with host cellular  
1252 processes to favor colonization at early and/or late stages of the AM symbiosis, have been  
1253 predicted from fungal genomes and transcriptomes (Sędziewska Toro & Brachmann,  
1254 2016; Kamel *et al.*, 2017). To note that SL influence the production of chitin oligomer  
1255 (Genre *et al.*, 2013) and effectors (Tsuzuki *et al.*, 2016; Kamel *et al.*, 2017) by AMF. IRM:  
1256 intraradical mycelium; ERM: extraradical mycelium.

1257

1258 **Figure 2.** Scheme of the variety of symbiotic effectors produced by AMF during the  
1259 interaction with host plants (based on data from Kamel *et al.*, 2017). For a single AMF  
1260 species some effectors are expressed in association with all plant species while others are  
1261 expressed in a host plant-specific manner. Some effectors are conserved among AMF and  
1262 may play core symbiotic functions.

1263

1264 **Figure 3.** The magnitude of plant growth promotion depends on the AMF genotype.

1265

1266 **Figure 4.** Distinct plant genotypes of the same species show differences in responsiveness  
1267 (R) to AMF. In maize, responsiveness is correlated with the ability of the line to promote  
1268 the growth of the extraradical mycelium (ERM) of *Funnelliformis mossae* (Sawers *et al.*,  
1269 2017). Drawings of maize plants were adopted from [www.clipart.co](http://www.clipart.co).