18 Roles and Implications of Arbuscular Mycorrhizas in Plant Nutrition

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18.1 INTRODUCTION

Symbiosis is the condition in which organisms of different species live in a closely integrated and persistent association of coexistence. At the molecular level, symbiosis is crucial to life, because the metabolic interactions within a cellular consortium are essential for closely integrated coexistence and the mutual benefit of all members of the symbiotic community.

Even if the expression of this concept may appear to be extreme, the importance of symbiosis, in evolutionary terms, is certainly more acceptable and understandable. Evolution consists mainly of changes in gene frequency between generations caused by genetic drift, gene flow, and natural selection. As early as 1909, Konstantin Merezhkowsky, who was considering the importance of extremophile organisms and extreme environments, introduced an interpretative variant to the symbiosis concept. He defined symbiogenesis as "the origin of organisms through the combination or association of two or more organisms that enter into symbiosis". According to this concept, symbiogenesis should be understood as an evolutionary mechanism, and symbiosis is how the mechanism takes place (Rosati and Vannini 2011). It is, therefore, a very different concept from that of Darwinism or modern synthetic theory. In fact, this idea emphasizes the central role of interactions among living beings, which allow the formation of new entities that incorporate one organism within another. Interactions of symbiosis are indeed widespread phenomena in the biosphere. Under natural, environmental conditions, the symbiotic associations between microorganisms (e.g., lichens) and those between microorganisms and plants (e.g., mycorrhizas, or mycorrhizae, and bacterial radical nodules) are common.

If life on our planet began in the aquatic environment, organisms would have gradually adapted to the terrestrial environment, evolving mainly in conditions of association with other organisms. Symbiosis, in fact, may have played a far greater role in terrestrial, biological evolution than was previously thought. An important symbiosis that made the colonization of land by plants possible was the

development of arbuscular mycorrhizae (Lipnicki 2015). The problems posed by this cohabitation and the competition between different organisms have represented a recurring phenomenon during millennia, but at the same time, these problems and competition of symbiosis have been, and still are, at the origin of mutual coevolution (Rodolfi et al. 2006). The meaning given to the term symbiosis is still debated: In many biology texts, reference is made exclusively to a relationship of mutual advantage between the two symbiotic organisms. Currently, however, many biologists refer to the definition of Anton de Bary who, in 1878, extended the meaning to all long-term relationships between individuals of different species, not only the advantageous ones (Oulhen et al. 2016). For this reason, the term symbiosis currently includes three major types of biological interactions between microorganisms and plants:

- Mutualism, in which both symbionts benefit from the relationship (the lichens for example), is the most restrictive meaning used in the past for symbiosis.
- Commensalism, or use of nutritional resources with advantage for the microorganism but without damage to the plant.
- Parasitism, in which the advantage of the association is in favor of one of the symbionts, at the expense of the other.

From an ecological point of view, for many heterotrophic microorganisms living plants represent a preferential habitat that are diversified in the various vegetal areas and in the seasonal phases. Living plants are potentially available and an alternative to the use of plant residues or other organic substrates of the soil, where competition with other microorganisms is high. The association of heterotrophic microorganisms with plants actually represents, for the microorganism, an adaptation that responds to primary trophic and ecological needs: an adequate source of nourishment and water, effective protection from adverse environmental factors, and a shield against actions of more aggressive competing microorganisms (Graniti 2002).

The root is the plant organ most exposed to interactions with microorganisms belonging to several phyla that are distributed in the rhizosphere. Plant roots can establish beneficial relationships with microorganisms, some of which are mycorrhizal relationships of the root with symbiotic fungi. These systems of cooperation between organisms with different genomes have achieved highly efficient and mutually beneficial integration over millions of years, resulting in well-defined structures and important, complementary physiological roles of the two partners.

Mycorrhizal symbiosis, in fact, changes the structure of the root system of the host plants: vesicular, arbuscular mycorrhizal (VAM) fungi and the root form a new structure, the mycorrhizal root, in which the fungal mycelium entirely replaces the root hairs.

Because of the different organization of the root and of the mycelial hyphae, mycorrhizal symbiosis has significant advantages. In mycorrhizal roots that result from the association of VAM fungi with plant roots, mycorrhizal fungi increase the acquisition of mineral nutrients and their translocation to the host plant. Diffuse distribution of the mycelium of the mycorrhizal fungus beyond the soil around the roots (the rhizosphere) reaches longer distances than those achieved by non-colonized roots and provides greater absorptive capacity of nutrients, particularly phosphorus (P), nitrogen (N), and potassium (K) (Classen et al. 2015). In addition, changes in root architecture with higher branching intensity increase contact surface with the soil at least 600 times that of the single root, as indicated by measurements such as 1000 m of mycelium per 1 m of the root (Plassard and Dell 2010).

As a direct consequence of increasing the root surface, mycorrhizae provide increased capacity for the plant to resist stress due to the low moisture content of the soil. Fungal hyphae allow soil–root contact to be maintained even in conditions of extreme dryness (Reid 1978) and, thanks to mycorrhizae, plants can extract water from the soil even in conditions of low soil osmotic potential, otherwise prohibitive for the single root (Brown and Carlson 1990). Coleman et al. (1990) and Guehl et al. (1992) have shown that the hydraulic conductivity of the soil-plant system is increased by mycorrhizae.

The VAM fungi, which secrete protons and enzymes with the capacity to decompose organic matter in the soil, can convert mineral elements from insoluble to soluble chemical compounds. Consequently, mycorrhizae can facilitate the dissolution of P-bearing compounds in the soil and the absorption, transport, accumulation, and utilization of P by host plants. Mycorrhizae are a key factor in making P available to plants, particularly in relatively high and low ranges of soil pH at which P is only slightly soluble.

This capability of mycorrhizae to facilitate P nutrition and the acquisition and utilization of other mineral nutrients enables mycorrhizal plants to have a competitive advantage for survival in a wide range of ecosystems (Rodolfi et al. 2006). The mycorrhizae, able to positively influence the nutritional status of the plant, contribute to the ability of the plant to utilize nitrogen, as well as carbon (C) and other essential plant nutrients, thereby indirectly contributing to the growth and productivity of the plant (Di Martino et al. 2018).

Numerous scientific investigations suggest that VAM fungi, through various metabolic strategies, reduce the virulence of fungal pathogens, altering the physiology of the host and making the roots more resistant to the pathogens themselves. Dehne (1982) estimates, in general, a decrease in fungal pathologies in 55% and 70% of all cases studied up to 1982. Although the understanding of the molecular mechanisms of the genetic matrix between mycorrhizal plant and pathogen is still under investigation, it is evident that mycorrhizal plants are less sensitive to fungal diseases.

18.2 ENDOPHYTIC FUNGI

According to the theory of Thomson (1982), the genesis of mutualism is to be found in parasitism, through a corrective adaptation over time with the host organism. In other words, natural enemies adapt to the acquired resistance characteristics of the host organism during a natural modulation and genetic mutation. Based on the hypothesis of improvement, the harmful effects caused by the parasite on its host are attenuated over time until the moment in which the host benefits from being infected (Boucher et al. 1982). This coevolutionary process is established over time and translates into symbiosis, only when both organisms take advantage of the association and increase their trophic efficiency. In this perspective, coevolution is a reciprocal process between interacting partners involved in intimate physiological and ecological interactions. The hypothesis that mutualism originates from parasitism through a series of coevolutionary changes concerning above all the reproductive systems of the two partners is confirmed by the existence of the "perfect" endophytic association (Rodolfi et al. 2006).

The endophytic fungi, unlike the other fungal groups, possess a peculiar biological behavior, because they can live as asymptomatic parasites and mutualistic symbionts completely contained in the host plant tissue where they establish effective interactions reproducing and propagating in a diversified manner (Stergiopoulos and Gordon 2014).

Endophytic fungi have been classified in the taxa Ascomycotina, Basidiomycotina, and Deuteromycotina. These endophytic associations have been identified in several vegetable terrestrial ecosystems of alpine, temperate, and tropical areas (Margulis 2010). Endophytic fungi are divided into two ecological groups in relation to their survival strategies: (1) Endophytes of herbaceous plants, called "Balansiaceae" (Schulz and Boyle 2005) or "Clavicipitaceae" (Petrini 1996; Sieber 2007) and (2) Endophytic taxa of arboreal plants "non-Balansiaceae" (Schulz and Boyle 2005) or "non-Clavicipitaceae" (Petrini 1996; Sieber 2007).

To the first group belong fungi Clavicipitaceae members of the tribe Balansiae (Ascomycotina) (Saikkonen et al. 1998), which develop in the exclusively herbaceous host plant, systemically and intercellularly inside the plant organs (except in the roots), thus resulting in vertical transmission of the endophyte through the seed. They can produce secondary metabolites and, given the ability to colonize the intercellular spaces, they depend on nutrients present in the apoplast for their growth (Schulz and Boyle 2005; Sieber 2007).

The second group brings together many fungi that generally belong to the division of the Ascomycota but can include species belonging to the Oomycetes, Deuteromycota, and Basidiomycota (Saikkonen et al. 1998; Schulz and Boyle 2005) and are generally isolated from all the plant organs of an arboreal plant. The colonization can be inter- or intracellular (Schulz and Boyle 2005) and is generally highly localized in leaves, peduncles, branches, or bark (Saikkonen et al. 1998). However, the localized infection can become more widespread in the case of conditions such as senescence of the vegetable organ (Saikkonen et al. 1998).

In the case of herbaceous plants, it is known that the plumule emerging from the seed can be affected by endophytic fungi already present in the tissues of the seed before germination or by endophytic fungi that come from infected tissues belonging to the mother plant (Carroll 1988; Ragazzi 2004). In the case of arboreal plants, there is a certainty of the existence of horizontal fungal transmission, external to the host tissues, through spores transported by air (Saikkonen et al. 1998; Jongejans and Telenius 2001), hydrochory, or zoochory (Wilkinson 1997; Ragazzi 2004), largely influenced by climatic conditions in relation to spore germination and the resulting frequency of infection of host plants (Carroll 1988). On the contrary, there is no evidence of vertical transmission of systemic endophytes through seeds of already colonized plants (Petrini 1996; Ragazzi 2004).

18.3 MOLECULAR DIALOGUE AND SYMBIOTIC INTERACTION BETWEEN PLANT AND FUNGI

Although the spores of AM fungi can sprout in the absence of host plants, they are mandatory biotrophs; therefore, their life cycle depends strictly on the molecular dialogue that is generated with the photoautotrophic host and precedes the root colonization. A symbiotic reprogramming of the plant cell involves the formation of a newly discovered pre-penetration apparatus (PPA) by the plant cell in anticipation of fungal infection (Genre et al. 2008). Seven plant genes of plant cells have been cloned that allow management of the symbiotic, fungal intracellular

passage (Parniske 2008). The stimulus of the plant to induce symbiosis also occurs due to specific deficiencies of inorganic nutrients, in particular, P (Di Martino et al. 2018), resulting in the possibility of mutual exchange of nutrients and metabolite fluxes in AM fungi. The stimulatory effect of plant root exudates on AM fungal hyphae has only recently been identified. Strigolactones, classified as plant hormones or phytohormones, were found to be responsible for the induction of branching (Akiyama et al. 2005) and alterations in fungal physiology and mitochondrial activity (Besserer et al. 2006). Strigolactones can also stimulate spore germination in some AM fungi (Parniske 2008).

Epidermal cells of plant roots in contact with the fungal hypha begin to assemble the secretion mechanism that builds the compartment of the interface where the fungus will be hosted. The cytoplasm of the plant root is aggregated at the contact site and then it develops into a thick column that provides the successive route of hypha through the cell (Genre and Bonfante 2005).

All elements of the secretory pathway – abundant endoplasmic reticulum and many Golgi bodies and secretory vesicles – are concentrated in the PPA (Genre et al. 2008), but the main factor among these cytoplasmic components is the nucleus. At an early stage, movements of the nucleus to and from the contact site precede PPA development (Genre and Bonfante 2005). When the PPA is completed, the fungus begins to grow again with a hyphal tip that goes through the cell wall of the epidermis and along the path of the PPA. At this stage, it is possible that the peripheral membrane could be assembled, since the PPA secretory vesicles are expected to merge to produce an invagination of the plant's plasma membrane. The development of the perifungal membrane marks the perimeter of the symbiotic interface, the narrow intracellular compartment that allows AM fungi to grow within the plant cell without breaking its integrity (Bonfante and Anca 2009).

Cytological studies have shown that during intracellular AM infection, hyphae that traverse epidermal cells are enclosed within an apoplastic compartment of plant origin, which is composed of a plasmalemma invagination and associated matrix (Novero et al. 2002). This initial step in root colonization is then followed by extensive intraradical hyphal development, with associated arbuscule formation in the inner cortex that is considered the site of nutrient exchange, as well as by extraradical development and subsequent spore formation.

The participation of Ca^{2+} with a signaling role at the beginning of AM symbiosis has been widely demonstrated and described in the literature (Navazio et al. 2007; Genre et al. 2013). Fluctuations in intracellular free Ca^{2+} concentration, termed *calcium spiking* (Ehrhardt et al. 1996), are the power switch of the initial steps in signaling pathways activated in plants when they meet AM fungi (Navazio and Mariani 2008), pathogens (Lecourieux et al. 2006), and nitrogen-fixing bacteria (Oldroyd et al. 2005). Molecules secreted by microorganisms, after binding to specific receptors, trigger in plant cells transient changes in cytosolic Ca^{2+} level. The concept that the secreted fungal molecules transmit, through Ca^{2+}, a favorable message which can be acknowledged only by appropriate receivers, is supported by the lack of defense response induction and the upregulation of some genes essential for the AM symbiosis initiation in host plant cells (Navazio and Mariani 2008).

This molecular dialogue through the interaction between plant and fungi can also extend among individual plants of the same plant community. Trees of a plant community may seem separate from one another, but the soil in which they establish their roots tells us another story. The trees secretly dialogue, trade, and sometimes come into conflict with each other, thanks to an extensive hyphal network in the soil, which connects a network of host plants of the same species. In fact, through hyphal networks, trees can share many resources by creating a system that is called The Wood Wide Web or common mycorrhizal network (CMN) (Figure 18.1).

Older trees called mother plants use this network to supply sugars to younger ones, giving them a greater chance of survival. Trees that are not healthy or are dying can download the latest nutritional resources into the network; in this way the healthiest neighbors can use remobilized and shared resources (Tedersoo et al. 2020).

A CMN also plays an important role in plant-to-plant "communication" by transferring info-chemicals and warning signals between plants. Some plants that are attacked by herbivores produce volatile organic compounds that act as a repellent for aphids but attract the natural enemies of aphids to the infested leaves. These volatile compounds are only produced by the non-infested plants when they share a CMN with the infested ones (Babikova et al. 2013).

Studies indicate that orchids with little or no photosynthesis can gain the organic carbon they need for growth through specific associations with ectomycorrhizal fungi that are capable of fetching carbon mainly through the symbiotic network with other photosynthetic plants (Girlanda et al. 2011). *Juglans nigra* (eastern American black walnut), on the other hand, uses the CMNs to spread toxic chemicals such as juglone that can harm rival plants (Achatz et al. 2014). Hidden CMNs are the glue that unites an emerging community of individuals. When we enter a woodland, we remember that trees are part of a large superorganism that includes dialogue among individual trees (exchange of information) and even sharing of nutrients.

FIGURE 18.1 The Wood Wide Web, or common mycorrhizal network (CMN).

18.3.1 Carbon Flow from Host Plants to Arbuscular Mycorrhizal (AM) Fungi

Because mycorrhizal fungi do not have the capacity to fix C by photosynthesis, they are heterotrophs that must acquire C and organic compounds from photosynthetic plants. Categories of organic compounds provided by host plants to the mycorrhizal fungi include sucrose and lipids (Bravo et al. 2017). The biological role of these compounds in the fungal hosts is largely unknown, but sucrose and lipids could be involved in metabolism (i.e., in production of vitamin B_{12} or growth hormones) (Ghignone et al. 2012) and other aspects of the pre-symbiotic growth of the AMF (Salvioli et al. 2016).

18.3.1.1 Sucrose Transport and Metabolism in Mycorrhizal Roots

Most photosynthetic plants, as autotrophic organisms, synthesize C compounds in the leaves and accumulate sugars in various storage tissues and roots in the form of starch that is synthesized and stored in heterotrophic plastids (amyloplasts) (Noronha et al. 2018). In symbiosis with AM fungi, plant hosts provide highly regulated fluxes of sugars from the sites of synthesis toward roots colonized by AM fungi (Figure 18.2).

In most plants, the sugar dimer sucrose is translocated from the shoot to the roots through the phloem (Giaquinta 1983; Xu et al. 2018). However, after leaving the vascular tissue at the root, sucrose must transit the endodermis to reach the cortical cells. The forms in which C is provided in sugars from the host plant to AM fungi are still under debate, although most of the experimental evidence suggests that glucose is the main form taken up by the fungus (Shachar-Hill et al. 1995; Pfeffer et al. 1999; Ganugi et al. 2019). Because sucrose is expected to move symplastically to overcome the Casparian strip (Kaiser et al. 2014), the involvement of proteins that facilitate transmembrane transport of glucose (SWEET exporters, or SWEETs) in cortical cells containing arbuscules has been hypothesized. In order to test this hypothesis, Manck-Götzenberger and Requena (2016) decided to characterize the SWEET family of transporters in the mycorrhizal plant *Solanum tuberosum* (potato). They showed that potato contains a large SWEET family with 35 members and that mycorrhizal colonization imposes a major transcriptional regulation of SWEETs in roots. Moreover, enzymatic and promoter-reporter assays have clearly shown that mycorrhizal roots have a significant increase in cell wall-bound invertase (CWI) activity (Wright et al. 1998; Schaarschmidt et al. 2006; Manck-Götzenberger and Requena 2016). Furthermore, CWI activity is located in the apoplast surrounding arbuscule-containing cells and intercellular hyphae, suggesting that apoplastic sucrose is cleaved prior to uptake by the fungus (Schaarschmidt et al. 2006).

Sucrose (Suc) reaches arbuscule-containing cells symplastically from the endodermis by overcoming the Casparian strip via plasma cells. Sucrose can be subsequently split by sucrose synthase (SUSY) or cytoplasmic invertase (cINV) to glucose (Glc) and fructose (Fru). To

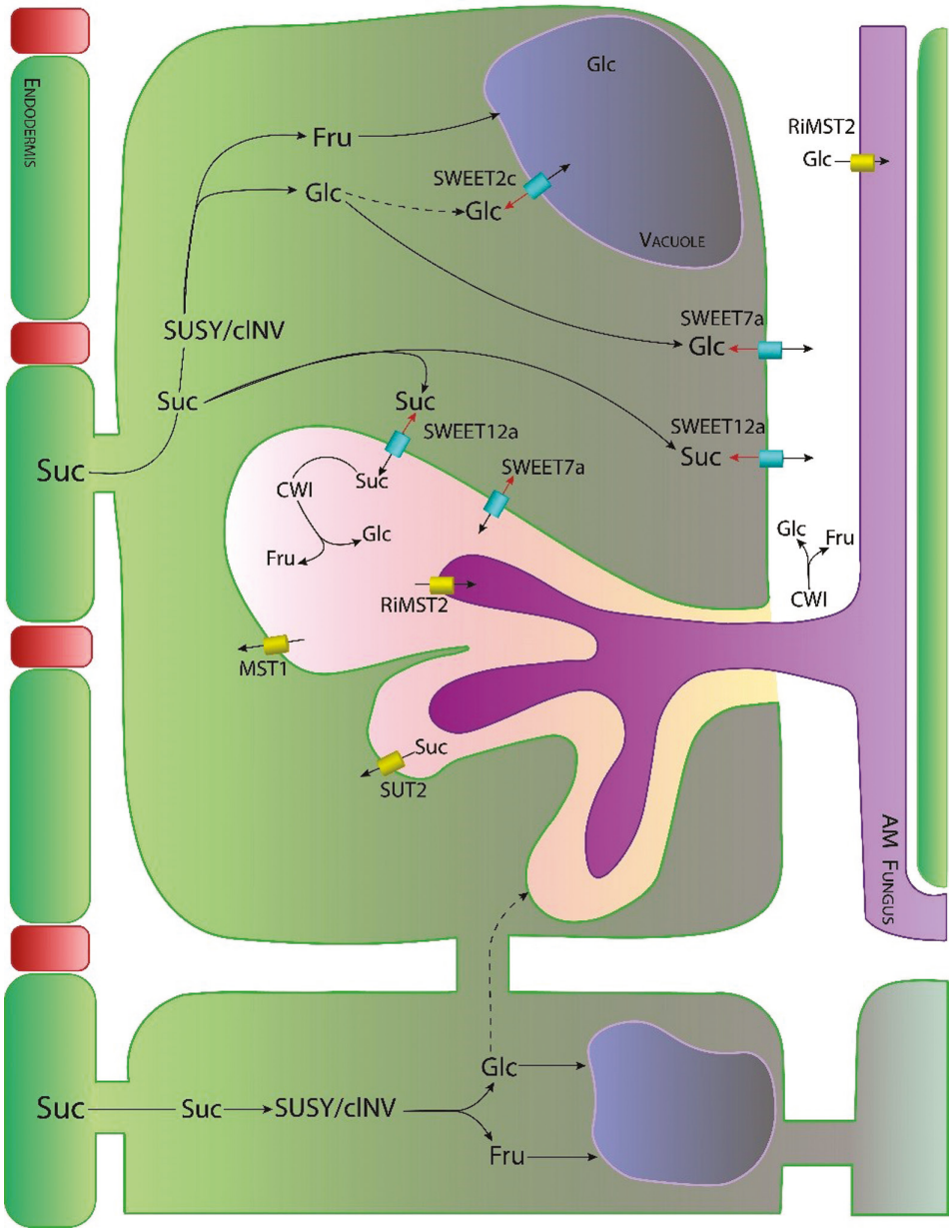

FIGURE 18.2 Model of sugar distribution during arbuscular mycorrhizal symbiosis.

maintain a favorable concentration gradient, hexoses may be translocated into the vacuole via tonoplast-located SWEETs or other transporters. This would also serve as a mechanism to control the outflow of sugar to AM fungus, which prevents parasitic behavior (Chen et al. 2015). Alternatively, it is possible that hexoses may be exported into the apoplast with the help of SWEET7a. Direct export of sucrose into the apoplast or the peri-arbuscular space could be achieved by sucrose efflux transporters as SWEET12a. In the apoplast and peri-arbuscular space, sucrose is cleaved by CWI. The sugars in the apoplast are either taken up by the fungus via monosaccharide transporters such as RiMST2 or by the plant cell via monosaccharide transporters such as MST1(shown in *M. truncatula*) (Schaarschmidt et al. 2007) and via sucrose transporters such as SUT2 (shown for *S. lycopersicum*) (Harrison, 1996; Bitterlich et al., 2014).

Carbon flow in the form of sucrose reaches the arbuscule-containing cells symplastically through the endodermis, and sucrose in such cells can be cleaved by sucrose synthase (SUSY) or cytoplasmic invertase (cINV)

to glucose (Glc) and fructose (Fru). AtSWEET2 localized at the tonoplast acts as an importer of glucose. AtSWEET2 is mainly localized in root tips, and its function has been associated with prevention of the loss of carbon into the rhizosphere. The export of sucrose into apoplast and peri-arbuscular space is reached by SWEET12a sucrose efflux transporters. Subsequently, in the apoplast as well in the peri-arbuscular space, the sucrose is cleaved by cell-wall-bound invertase (CWI). Neighboring cells might also contribute to the nutrition of the arbuscule-containing cell by providing sugars symplastically.

18.3.1.2 Lipid Transfer from Host Plants to AM Fungi

The C acquired by AM fungi from host plants, which can be more than 20% of the photoassimilated C (Bago et al. 2002), must be transported from the intraradical mycelium (IRM) to the extraradical mycelium (ERM) to allow the development of hyphae and production of spores. In addition, a large part of the sugars must be converted to fatty acids, because lipids are the main C storage compounds in AM fungi (Beilby and Kidby 1980; Becard et al. 1991).

De novo fatty acid biosynthesis in plants, predominantly from acetyl coenzyme A (acetyl-CoA), takes place in plastids. Acetyl-CoA is the basic building block of the fatty acid chains, and the malonyl-acyl carrier protein (ACP) is the C donor for all subsequent extension cycles (Ohlrogge and Browse 1995). Acetyl-CoA carboxylase (ACCase) catalyzes the formation of malonyl-CoA from acetyl-CoA, and fatty acid synthase (FAS) catalyzes the subsequent extension cycles. Two C atoms are added to the growing acyl chain in each cycle, leading to the formation of C16:0-ACP (Ohlrogge and Jaworski 1997). The acyl chains are covalently bound to the soluble ACP via a thioester during the extension cycles, and acyl-ACP thioesterases hydrolyze acyl chains and terminate the fatty acid chain elongation of fatty acids from the ACP (Jones et al. 1995; Jing et al. 2011). From the fatty acids chain, the 2-monoacylglycerols synthesized by a glycerol-3-phosphate acyltransferase (GPAT), that is, reduced arbuscular mycorrhization2 (RAM2), are likely exported by the peri-arbuscular membrane-localized heterodimeric adenosine triphosphate (ATP) binding cassette (ABC) transporters STR-STR2 into the interface space and then taken up by unknown lipid transporters into AM fungi (Jiang et al. 2017).

The core set of genes also includes the ketoacyl-ACP synthase LjDISI/MtKasII (represented by Cs5g01990), which is an essential component of the mycorrhiza-induced regulon involved in fatty acid biosynthesis, Keymer et al. 2017). This regulon has been shown to include the AM host conserved fatty acyl-acyl carrier protein (ACP) thioesterase FatM and the GPAT RAM2, involved in 16:0 β-monoacylglycerol synthesis (Wang et al. 2012; Bravo et al. 2017; Jiang et al. 2017; Luginbuehl et al. 2017). Mutants in these genes all display defects in arbuscule development. These indications support the hypothesis that plants transfer lipids to AM fungi to sustain colonization.

18.3.2 Mineral Nutrient Flow from Fungi to Host Plants

In roots associated with AM fungi, there are two pathways of nutrient uptake that involve different sites of the root, different root tissue, and different transporters. In the direct pathway, the nutrients are absorbed from the rhizosphere by root transporters in the epidermis and root hairs, close to the root surface. In the mycorrhizal pathway (Figure 18.3), the nutrients are taken up into AM fungal hyphae by fungal transporters and translocated to intracellular fungal structures (arbuscules and hyphal coils) in root cortical cells (Smith et al. 2003).

18.3.2.1 Nitrogen

Nitrogen, because of its electronic configuration, different oxidation states, and the ability to generate stable covalent bonds with C, is a key element in many biological organic compounds. After C, N is the most important nutritional macronutrient for plants and other living organisms, since it is fundamental for the formation of proteins, enzymes, chlorophyll, nucleic acids, and other cellular constituents. Nitrogen is a nutrient that can function in many ways, and it occupies a unique position among the essential elements in the soil, because relatively large quantities of it are assimilated by growing plants. During the absorption of N throughout the life cycle of plants, the maximum requirement of the element occurs during the period of maximum growth rate (e.g., during grain filling of cereals).

The model of mycorrhizal pathways (Figure 18.3) is based on previous models presented in the literature (Pfeffer et al. 1999; Govindarajulu et al. 2005; Tian et al. 2010; Fellbaum et al. 2012; Bücking and Kafle 2015). This model shows the P and N uptake by the fungal ERM from the soil through inorganic phosphorus (P_i), nitrate (NO_3^-) or ammonium (NH_4^+) transporters (orange). The model shows N assimilation into amino acids glutamine (Gln), glutamic acid (Glu), and arginine (Arg), the conversion of Pi into polyP, the transport of polyP from the ERM to the IRM, polyP hydrolysis and the release of Arg and P_i in the IRM, Arg breakdown to NH_4^+ via the catabolic branch of the urea cycle, and the Pi, NH_4^+, potential amino acid efflux (yellow) into the interfacial apoplast, and the plant uptake from the interface through mycorrhiza-inducible P_i or NH_4^+ transporters.

Nitrogen is one of the most important factors in agricultural production. Normally, the application of N

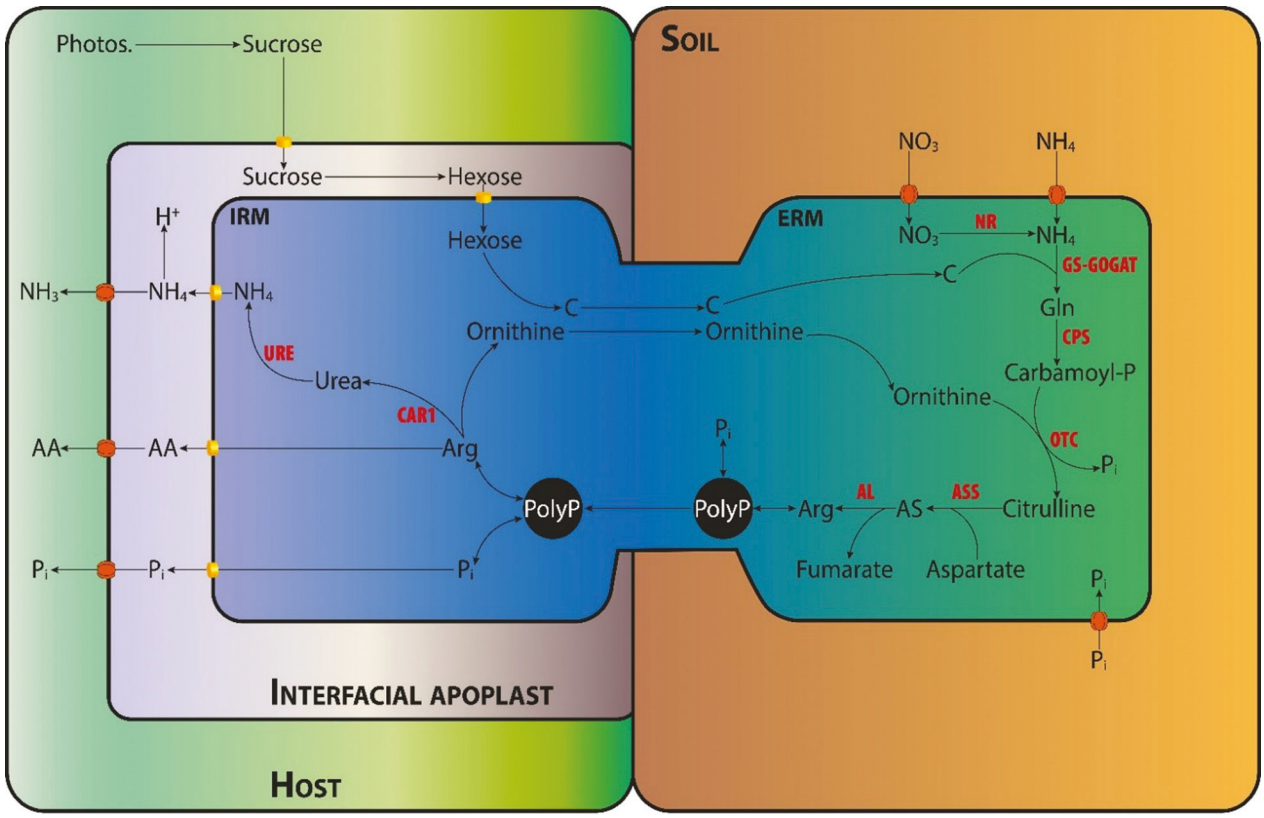

FIGURE 18.3 Summary model of transport and transfer of N and P from AM fungi to the host.

fertilizers causes a marked increase in the development of vegetative plant tissue, more intense green coloring of leaves and stems, and, ultimately, an overall increase in biomass production. However, excessive use of N fertilizers must be avoided both because it causes a substantial increase in the costs of cultivation and because it can cause serious environmental damage, such as NO_3^- pollution of groundwater and surface water (Masoni and Ercoli 2010). The use of mycorrhizal fungi in agriculture allows a more limited and eco-friendly use of N fertilizers, because mycorrhizae can compensate for a low rate of N fertilizer application by more efficiently capturing N and making it available to plants. Plants can absorb N by (1) transporters in the epidermis or root hairs or (2) the mycorrhizal-uptake pathway that absorbs nutrients by fungal transporters in the extraradical mycelium. As is the case with P, mycorrhiza-inducible N transporters are upregulated by symbiotic AM fungi (Gomez et al. 2009; Kobae et al. 2010). Furthermore, it has been recently demonstrated that the average arboreal life in *Medicago* (alfalfa or lucerne) plants is not only influenced by PT4 but also by the mycorrhiza-inducible NH_4^+ transporter AMT2,3 (Breuillin-Sessoms et al. 2015). Many studies and reports in the literature confirm that there is a positive effect of the symbiosis of AM fungi and plants on plant N nutrition, as is also evidenced for P. Moreover, recent studies suggest that the NH_4^+ uptake system of AM fungi has five times greater affinity for NH_4^+ than do N uptake systems of plants without AM fungi, enabling the fungus to take up NH_4^+ more efficiently from the soil even under low N supply conditions (Pérez-Tienda et al. 2012).

Although some investigators claim that the improvement of N nutrition of plants by AM fungi is only the result of an improvement of P nutrition, much of the literature postulates that this positive effect is independent of the contribution of these fungal isolates to P supply. There is increasing evidence that a pathway for N through the fungal hyphae to the host plant exists, even if the percentage contribution to total N nutrition of the host plant can vary considerably and is context-dependent (Smith et al. 2011; Mensah et al. 2015).

Unlike P, where access of the ERM to P sources beyond the root exhaustion zone is clearly beneficial, the ERM should not increase access to soil resources of N. In fact, concentrations of inorganic NO_3^- and NH_4^+ in the soil are relatively high, compared to P, and the rhizosphere is less likely to run out of N because of the availability of N resources in the soil outside the rhizosphere.

However, it must be said that deficiencies of N and P have similar, stimulatory effects on the development of mycorrhizae. Recent research demonstrates that both P and N are important determinants of the symbiosis of AM fungi and plants and that the colonization of the plant host is controlled by feedback mechanisms between both nutrients (Fellbaum et al. 2014). For example, both P- and N-starvation of the plant induce a nutrient stress transcriptome that is favorable for AM colonization. Under P and N stress, defensive genes of the plant are downregulated, while genes that are involved in the strigolactone biosynthesis are upregulated (Bonneau et al. 2013). Strigolactone serves as an important signal for AM fungi in the soil and stimulates hyphal branching during the pre-symbiotic growth stage (Besserer et al. 2006). High P availability often reduces AM colonization of the plant (Di Martino et al. 2018), but N starvation triggers a signal that promotes AM colonization and reverses the inhibitory effects of high P availabilities on AM colonization (Breuillin-Sessoms et al. 2015; Nouri et al. 2014). Confirming this, in several plant species, mycorrhiza-inducible NO_3^- (Hildebrandt et al. 2002) or NH_4^+ (Kobae et al. 2010; Pérez-Tienda et al. 2011; Breuillin-Sessoms et al. 2015) transporters have been identified that are able to facilitate the uptake of inorganic N from the mycorrhizal interface.

In most agricultural soils, NO_3^- is the dominant form of N that is available to plants and fungi, whereas in many undisturbed or very acidic soils, ammonium (NH_4^+) predominates and NO_3^- can be almost entirely absent in environments hostile to the action of nitrifying bacteria. For strictly bioenergetic reasons related to the oxidation state of the element, NO_3^- represents the most available source of inorganic N for most plants and for the ERM, but NH_4^+ is more easily assimilated (Johansen et al. 1996; Toussaint et al. 2004; Jin et al. 2005).

Based on pH changes induced by the ERM when hyphae were supplied with NO_3^- or NH_4^+, it has been hypothesized that the NO_3^- uptake by the hyphae is active and coupled to an H^+-symport mechanism, similar to plants and other fungi (Fuggi et al. 1984), while NH_4^+ is taken up by an antiport mechanism with a net H^+ efflux (Bago and Azcón-Aguilar 1997) in acid soil unlike in alkaline soils in which ammonium can diffuse in an unionized form as ammonia (Raven et al. 1992).

Despite the fungal preference for NH_4^+, it has been reported that when NH_4^+ was the only source N for mycorrhizal plants, the biomass of the roots and buds, the density of the length of the hyphae, and the transport of N through the hyphae to the plant were less than when N was supplied as NO_3^- (Hawkins et al. 2000). With NH_4^+ as the sole N source, the assimilation of NH_4^+ could increase the consumption of C skeletons in the root and reduce the C availability for the fungus. In fact, it was found that NH_4^+ reduced the hyphal length in the soil, but not the number of arbuscules, and it was assumed that high concentrations of NH_4^+ could also have a direct deleterious effect on the ERM (Hawkins et al. 2000). An excess of NH_4^+ as the sole source of inorganic N is often considered to be toxic for plants, and high concentrations of NH_4^+ inhibit root growth (Liu et al. 2013). The causes of NH_4^+ toxicity are related mainly to two factors:

1. A high concentration of NH_4^+ can promote and combine the glutamate dehydrogenase (GDH) activity K_M 4 mM (Kwinta et al. 2001) with the already functional glutamine synthetase-glutamate synthase (GS-GOGAT) activity, depleting the Krebs cycle of metabolic intermediates, and
2. Passive diffusion of ammonia can raise intracellular pH.

Plant GDH has a very high K_m value for ammonia, is activated by Ca^{2+}, and is localized in the mitochondria of a various different plant tissues (Turano et al. 1997).

Nitrate reduction in AM fungi converts soil NO_3^- to NH_4^+ available to the plant. After NO_3^- is transported within the root system or fungal hyphae, it is first reduced to nitrite (NO_2^-), by a nitrate reductase that is nicotinamide adenine dinucleotide (NADH)- and nicotinamide adenine dinucleotide phosphate (NADPH)- dependent. Unlike plants, in AM fungi, nitrate reductase activity is mainly driven by NADPH (Kaldorf et al. 1998), as a reductant for NO_2^- formation (Hildebrandt et al. 2002). Nitrate assimilation and nitrate reductase activity of AM plants are generally higher than in non-mycorrhizal control plants in both roots (Oliver et al. 1983; Subramanian and Charest 1998; Hawkins and George 1999) and leaves (Cliquet and Stewart 1993; Faure et al. 1998). In non-mycorrhizal plants, NO_3^- reduction primarily takes place in the leaves, while in mycorrhizal plants, NO_3^- is predominantly reduced in the roots (Vázquez et al. 2001; Di Martino et al. 2019). A gene that encodes a fungal nitrate reductase is expressed in spores, the ERM and the IRM, but the transcript levels are particularly high in the IRM. These aspects of fungal nitrate reductase lead to development of the hypothesis that NO_3^-, which is not directly assimilated in the ERM can also be reduced in the fungal tissue within the host root (Kaldorf et al. 1994; Kaldorf et al. 1998; Tisserant et al. 2012). In the next step of assimilation of N, NO_2^- is converted into NH_4^+ by nitrite reductase. A gene encoding a putative fungal nitrite reductase of the AM fungus *Rhizophagus irregularis* shows particularly high expression levels in spores and in the IRM (Tisserant et al. 2012). These high expression levels of nitrite reductase in spores and in the IRM correspond

to high transcription levels of a fungal nitrate reductase in the IRM of the AM roots (Tisserant et al. 2012).

N assimilation and amino acid biosynthesis are key processes of N metabolism in AM fungi in which, as in plants, two pathways can be involved in the assimilation of NH_4^+: the NAD GDH pathway or the GS-GOGAT pathway. As in plants, NH_4^+ is predominately assimilated via the GS-GOGAT pathway in AM fungi (Johansen et al. 1996; Breuninger et al. 2004; Govindarajulu et al. 2005). Two different functional GS isoforms of *R. irregularis*, i.e., GiGS1 and GiGS2, have been characterized. GiGS1 has a lower K_M than GiGS2 and is constitutively expressed at high levels in the ERM, while GiGS2 is strongly induced by addition of NO_3^- to the ERM (Tian et al. 2010). This confirms specific adaptability of the fungi to a range of availability of N in the soil. GiGS1 is the main functional enzyme for N assimilation at low N availabilities, and that GiGS2 may play a more significant role for N assimilation under high N supply conditions (Tian et al. 2010). Furthermore, it has been found that the fungal GS genes of *Funneliformis mosseae* (GmGln1) and *R. irregularis* (GiGln1) are constitutively expressed but that the GS activities in the ERM are modulated in response to different N availabilities (Breuninger et al. 2004). This modulation in response to different N availabilities suggests that the fungal GS activity is not controlled on a transcriptional level, but that it is subjected to post-transcriptional regulation (Breuninger et al. 2004).

Indicating the GS-GOGAT pathway, intracellular ERM Gln content becomes highly labeled when $^{15}NH_4^+$ is supplied to AM fungi, representing one of the major N sinks (Rolin et al. 2001; Gachomo et al. 2009). Gln and Glu play a central role in N metabolism (1) as key N donors, (2) as precursors of many essential metabolites such as nucleic acids, amino sugars, and other amino acids, such as histidine, tyrosine, and asparagine (Asn), and (3) as key effectors for N assimilation repression and as regulators of genes involved in N metabolism (Howitt and Udvardi 2000; Forde 2000; Javelle et al. 2003; Navarro et al. 2006). Due to these important functions, the free levels of Gln in AM fungi are tightly controlled (Gachomo et al. 2009). In addition to Gln, Glu, Asn, aspartate (Asp), and alanine are abundant free amino acids in germinating spores (Gachomo et al. 2009), in the ERM (Johansen et al. 1996), or in AM roots (Rolin et al. 2001; Jin et al. 2005). Ornithine, serine, and glycine are also detectable but are in much lower concentrations (Johansen et al. 1996).

Recent studies demonstrate that Arg is the most abundant free amino acid in the ERM and can represent more than 90% of the total free amino acids in the ERM (Rolin et al. 2001). Arginine levels of up to 200 $nM \cdot mg^{-1}$ dry weight have been reported in the ERM (Jin et al. 2005). Due to its high N-to-C ratio of 4:6, Arg plays an important role for N storage and N transfer from the ERM to the IRM (Jin et al. 2005; Cruz et al. 2007). For example, Arg represents the N accumulation molecule in quiescent spores and its catabolism during spore germination provides the N and C skeletons for the biosynthesis of other amino acids or proteins necessary for the pre-symbiotic growth of the AM fungus (Gachomo et al. 2009).

Transport of N through the hyphae of the AM symbiosis can be very rapid and flux rates similar to those of P have been observed (Cruz et al. 2007). Fungal vacuoles often contain polyphosphates (polyP) and basic amino acids in equimolar concentrations (Cramer and Davis 1984; Westenberg et al. 1989), and it has been suggested that N could move in the form of Arg with fungal polyP from the ERM to the IRM (Govindarajulu et al. 2005; Cruz et al. 2007). PolyP are negatively charged polyanions, and the basic amino acid Arg could serve together with other cations such as K^+ and Mg^{2+} as counter charge and contribute to the required charge balance (Cruz et al. 2007). Studies on N transport in the AM symbiosis of *Agropyron repens*, however, also suggest that in addition to Arg, other amino acids such as Gln or Glu could be involved in the translocation of N from the ERM to the IRM (George et al. 1992).

Evidence from studies performed on gene expression supports the biosynthesis of Arg in the ERM. In fact, the ERM transcription levels of all enzymes involved in Arg biosynthesis such as fungal carbamoyl phosphate synthetase (CPS), argininosuccinate synthase (ASS), and argininosuccinate lyase (AL), are induced by NO_3^- immediately after its addition.

CPS catalyzes the formation of carbamoylphosphate from CO_2, ATP, and ammonia (NH_3), which is converted together with ornithine to citrulline and inorganic P_i by an ornithine transcarbamoylase (OTC). Citrulline and Asp are converted to argininosuccinate (AS) by ASS, and AL converts argininosuccinate to fumarate and Arg. In contrast, in the IRM, a fungal arginase (CAR1) and urease (URE) that are involved in the catabolism of Arg are upregulated (Tian et al. 2010). The biosynthesis of Arg in the ERM and the subsequent breakdown of Arg in the IRM are spatially separated, but synchronized processes, and they confirm the function of the anabolic (ERM) and catabolic part (IRM) of the urea cycle in the AM symbiosis (Bücking and Kafle 2015).

The synchronization of these processes suggests that Arg plays an important role in the N translocation from the ERM to the IRM (Cruz et al. 2007). Ultimately, it is possible to argue that ERM performs a primary function of N and P_i nutrient absorption, as well as the organization of the first forms of organic N such as Gln, Glu, and Arg. The IRM, on the other hand, through its metabolism and

through specific carriers, transfers proteins, P_i, NH_4^+, and amino acids to the interfacial apoplast.

Hence, the ERM performs a primary function of absorption of N and phosphoric inorganic nutrients, as well as the organization of the first organic N forms such as Gln, Glu, and Arg.

18.3.2.2 Phosphorus

When P represents a limiting nutrient for plant growth, it is absorbed with difficulty even if present in relatively large quantities in the soil. The poor availability of P is because of the very low solubility of phosphates of iron, aluminum, and calcium, which leads to a concentration of 10 μM or less and very low mobility. Inorganic phosphorus is acquired by plants as negatively charged ions (principally $H_2PO_4^-$ and HPO_4^{2-}), posing a further problem because the concentration in cells is about 1000-fold higher than in the soil solution and the cell membrane has an inside-negative electric potential. Uptake of P_i, therefore, requires metabolic energy and involves high-affinity transporter proteins in the Pht1 family.

As a result, plants have evolved, developing increased capacity to absorb P_i and to increase the availability of P_i in the soil (Marschner 1995). The most common of these characteristics of vascular plants is AM symbiosis. In fact, the predominant nutrient element acquired through AM is P, which is transferred to the host plant in its oxidized inorganic phosphate (P_i) forms (Karandashov and Bucher 2005; Nouri et al. 2014).

The two pathways through which AM plants absorb P have different cell types with different P_i transporters that capture P from different regions of the root and soil volumes. Direct absorption by the radical epidermis, including the root hairs when they form, accesses P_i in the soil solution near the roots. The expression of genes that code for high-affinity P_i transporters (P_iT) in these cells is highest in the root apex and in the root hairs and decreases in regions of more mature root tissue. The expression of these genes that code for P_iT is often reduced with a high P intake and by AM colonization. These reductions will lead to lower direct absorption in older regions of the root.

Therefore, mycorrhizal roots have a greater ability to absorb P_i from the soil solution than non-mycorrhizal roots because of the large capacity of extraradical hyphae to explore large volumes of soil and because of the specific biochemical and metabolic interactions at the soil–fungus and fungus–plant interfaces. (Plassard and Dell 2010). The AM pathway can reduce the impact of P_i depletion in the rhizosphere, improving plant P nutrition and growth (Smith et al. 2011). Conversely, growth differences between AM and non-mycorrhizal (NM) plants tend to disappear as available soil P is increased, because of less depletion of P in the rhizosphere (Smith and Read 2008; Smith and Smith 2011).

P fertilization has been shown to reduce mycorrhizal development of *Triticum durum* (durum wheat) (Di Martino et al. 2018). The contribution of AM fungi to P nutrition decreases with increasing soil P supply, as direct uptake increases, and this is associated with a decreasing percentage of root length colonized (Nagy et al. 2009). While AM fungi colonize roots behind the root apex, the fungi grow widely in the soil to form a well-developed hyphal network that absorbs P_i (via high fungal affinity P_iT) up to several centimeters from the root surface, often significantly extending the exhaustion zone. Phosphorus is quickly translocated via the hyphae to the roots, overcoming the slow diffusion that occurs in the soil solution (Gianinazzi et al. 1979**;** Marx et al. 1982; Dighton et al. 2005**)**. The very small diameters of fungal hyphae allow access to narrower pores of the soil, thus increasing the volume of the soil explored (Drew et al. 2003; Smith and Read 2008; Schnepf et al. 2011; Ganugi et al. 2019). The mechanisms of release of P_i from the fungus to the interfacial apoplast are not yet known, but the absorption in the plant is increasingly well understood. The P_iT genes of AM inducible plants, which are different from those of the direct path, are expressed in colonized cortical cells (Xie et al 2013).

Zhu et al. (2001) also observed a reduction in the colonization of AMF in modern wheat cultivars (*Triticum aestivum* L.) compared to older cultivars, indicating that modern agronomic techniques may have reduced the symbiotic response of younger wheat cultivars to AMF. In a study of 14 crop species, Martín-Robles et al. (2017) observed that wild strains established symbiosis with AMF in conditions of low and high P, while modern cultivars were reactive only in conditions of low availability of P. These observations support ongoing research aimed at breeding for a greater AMF colonization in organic management in which the available soil P is generally low. The different capacities of agricultural crops to sufficiently mobilize soluble P have aroused interest in the ability of certain crops to favor the assimilation of P by subsequent or antagonistic crops. The main ways in which more-P-efficient crops can promote subsequent crops is to include the accumulation of P in crop tissues followed by mineralization of P_i from organic P (P_o) available in plants, the enhancement of biomass and soil microbial activity (in particular AMF) and modification of the rhizosphere (through the exudation of carboxylates, enzymes, and/or protons that mobilize the recalcitrant P_i and P_o). Arbuscular mycorrhizal fungi have been shown to have a greater P uptake efficiency than plant roots by accessing P at lower soil solution P_i concentrations and by taking it up at increased rates (Liu et al. 2007). This ability is

attributed to a combination of factors: (i) AMF hyphae have smaller diameters than plant roots and therefore a greater surface area-to-volume ratio (Liu et al. 2007); (ii) AMF mycelia undergo constant turnover, where hyphal contents are redistributed to areas of new growth, effectively optimizing the exploitation of soil in time and space (Hamel and Plenchette 2007); (iii) AMF have a low-affinity system and a high-affinity system for P uptake, with the latter being highly efficient at P uptake (Liu et al. 2007); and (iv) once taken up by AMF hyphae, orthophosphate anions are converted into polyphosphate, which helps to maintain a concentration gradient, assisting with P uptake (Funamoto et al. 2007).

In this context, plant breeding for phosphorus use efficiency (PUE) has the potential to play a significant role in reducing the demand for P fertilizers. Cultivation programs for PUE should adopt an interdisciplinary protocol considering the complexity of genetic, environmental, and management interactions (Manschadi et al. 2014) and should include development in soils with low-soluble total P (STP) concentrations (Rowe et al. 2016). Van der Heijden et al. (1998) found that a greater number of AMF species was linked with greater ecosystem productivity and total P uptake. We know that agroecosystem management affects AMF community composition (Dai et al. 2014; Schneider et al. 2015), but the functional differences of these communities are still largely unclear. An increased understanding of AMF functional diversity and how this is affected by management is fundamental to know how we might be able to manipulate their role in agroecosystems to contribute to greater PUE (Powell et al. 2018).

One study reported that in a soil with low available P_i, the organic C/P ratio decreased over the growing season, whereas in a soil with high P_i availability it did not, suggesting that conditions of P deficiency may result in increased use of soil C by soil microorganisms and may deplete organic C (Romanyà et al. 2017). However, since the C/P ratio in soil organic matter (SOM) is not always tightly coupled (Stevenson 1986), it is possible that biochemical mineralization of P_o can occur without depleting organic C (McGill and Cole 1981; Simpson et al. 2011).

Moreover, good agricultural practice periodically brings to the soil materials with a balanced C/N ratio, such as manure and compost, which have a mixed composition, partly of animal origin and partly of vegetable origin. This condition favors decomposition and a substantial balance between mineralization and humification that are ultimately the best organic soil improvers. The presence of the barn had a decisive role in the traditional farm: this structure, aimed at the maintenance of working animals and, second, the production of milk and meat, allowed the production of large quantities of organic material that could be humified by optimizing the reuse of the straw and animal manure. The specialization of the production guidelines in market agriculture has significantly reduced this resource, increasing the production of organic materials, which individually contribute little to maintaining good levels of humus in the soil.

18.3.2.3 Potassium

Potassium (K) is one of the most abundant elements of soil and is the third most crucial component of most crop fertilizers, after nitrogen and phosphorus. However, the availability of K can be low, limiting plant growth and yield. Functions of K are important in different metabolic processes and physiological functions such as regulation in the stomatal opening, regulation of cell membrane potential, and osmotic adjustment. An important biochemical role of K is the activation of enzymes involved in important metabolic processes, such as protein synthesis and photosynthesis (Marschner 1995). Unlike N and P, which are fundamental constituents of organic macromolecules, all K is present in soluble form in the cell. K^+ is the most abundant cation in the cytosol where it is accumulated against a large transmembrane concentration gradient, maintaining an almost constant concentration of around 100–200 mM, which is its optimal cytoplasmic concentration for enzymatic activity. The high cytosolic concentration of K^+ ion explains the high percentage of K, 2–5%, of a plant´s total dry weight content (Leigh and Wyn Jones, 1984; Navarro et al. 2006). These high physiological concentrations can only be ensured by an efficient K^+ uptake by the roots from the surrounding soil. An apparent paradox of soil chemistry is that some chemical elements, although they are present in a high percentage in the earth's crust, are not very available for radical absorption in the soil. Potassium is among the soil elements that show this behavior. In fact, in the soil, K is found in four major pools with variable availability for plant absorption. This variation among the four major pools of K in the soil is due to different forms of aggregation of K in the soil that are in balance with each other, that is, K:

1. Imprisoned for the most part within the crystalline structure of primary minerals (such as K-feldspars and micas), where it represents 90–98% of the total content of K in the soil and is not available for plants.
2. Embedded in non-exchangeable positions of secondary minerals, characterized by slow release, in which the K^+ ions are absorbed in the interlayer spacing of the clay minerals, which represent 1–10% of the total K content of the soil.

3. Interchangeable forms characterized by the rapid release, which include K^+ ions adsorbed by electrostatic forces on colloidal clay and soil surfaces, which represent 1–2% of the total K content of the soil.
4. In the soil solution, which is readily available for immediate assimilation of plants but represents only 0.1–0.2% of the total K content of the soil (Meena et al. 2014).

The last two forms of K are readily available for supply to plants and are taken up in relatively large quantities compared to the first two forms.

There are few studies that have examined the effect of AM fungi on the weathering of K-containing minerals. Arbuscular mycorrhizal fungi can increase the solubility of mineral forms of K^+ by releasing protons, H^+, or CO_2 and organic acid anions such as oxalate, malate, and citrate. This process of dissolution of K is associated with increases of N, K, Ca, and Fe in the plant leaves and fruits (Jones et al. 2009; Veresoglou et al. 2011; Yousefi et al. 2011).

Oxalic acid and acetic acid have been found in fungal hyphae, and polyols such as mannitol and arabitol are thought to be important for retaining turgor in fungal hyphae during C translocation along hydrostatic pressure gradients. High internal pressures in hyphae are thought to be an evolutionary adaptation to facilitate penetration of both plant tissues and rock surfaces (Jongmans et al. 1997). This exudation of droplets may play an important role in conditioning the immediate environment of hyphal tips, facilitating interactions with substrates and associated microorganisms, even in drier soils. Similar observations have been made by Querejeta et al. (2003) who demonstrated that water obtained by *Quercus agrifolia* plants, using a hydraulic lift, can be transferred to associated arbuscular mycorrhizal and ectomycorrhizal fungi to maintain their integrity and activity during drought, even when the fertile upper soil is dry. Carbon allocation in the form of sugars and polyols (Sun et al. 1999) may be important in generating turgor pressure in hyphae and have consequences for weathering of minerals with a lattice structure.

Transport of K^+ through plant membranes can be mediated either by K^+ channels, which use the membrane potential and electrochemical gradient to facilitate K^+ transport, or by secondary transporters with different affinities located in the plasma or organelle membranes (Gierth et al. 2005; Voelker et al. 2006; Liu et al. 2019). Genes encoding plant K^+ transporters are classified into four major families: (1) KT/HAK/KUP (K^+ transporter/high-affinity K^+ transporter/K uptake permease), (2) HKT (high-affinity K^+/Na^+ transporter), (3) KEA (K^+ exchange antiporters), and (4) CHX (cation/H^+ exchanger) (Uozumi et al. 2000; Cellier et al. 2004; Kunz et al. 2014; Aranda-Sicilia et al. 2016; Wang and Wu 2017). Several investigators have reported an improvement of the K^+ content of the plants in symbiosis with mycorrhizal fungi (Sharifi et al. 2007; Jourand et al. 2014). However, until now, transport mechanisms have not been uncovered in all cases of K^+ transport in mycorrhizal fungi. A recent study using whole-genome RNA sequencing of mycorrhizal roots of *Medicago truncatula* (barrel clover) under K^+ deficiency revealed the upregulation of several genes encoding putative transporters, including a putative K^+/H^+ exchanger, in mycorrhizal plants under K^+ deprivation (Garcia et al. 2017). However, in several transcriptome studies, no K^+ transporter was observed to be upregulated in *M. truncatula* mycorrhizal roots (Gomez et al. 2009; Gaude et al. 2012). Therefore, it would be interesting to know whether the gene regulation involved in the transfer of K^+ from the AM fungus to the plant is conserved among different plant species (Liu et al. 2019). The identification of any microbial K^+ transporter that mobilizes K^+ to the plant would have a critical role in the K^+ nutrition of plants. Besides the active role of soil microorganisms in providing the plant K^+ supply, directly (by capturing K^+ from the soil and transferring it to the plant) or indirectly (by solubilizing K^+ in the soil and making it available for plant absorption), other beneficial effects of the symbionts on plant K^+ fitness cannot be ruled out. For instance, changes in the gene expression of fungi and plants that regulates the levels of cellular signals or the production of phytohormones by the plant itself (Waqas et al. 2012) or through synthesis by the associated fungus, may occur during symbiosis (Sirrenberg et al. 2007; Xu et al. 2018). These cellular factors may induce changes in expression that may ultimately activate the K^+ transporters of the host plant itself, thereby improving its K^+ content.

18.3.2.4 Calcium

Calcium (Ca) is an important macronutrient required for plant growth and development and represents 0.1–5% of all plant dry biomass (Marschner 1995; White and Broadley 2003). Calcium's signaling role in plant cells is in response to a wide array of environmental cues and, among the inorganic nutrients, Ca may be the most involved in molecular communications and in the transmission of metabolic signals in eukaryotic cells (Thor 2019). In addition to acting as a secondary messenger, Ca has been shown to intervene as a chemical mediator in various biological processes, such as cell division, cell elongation, photomorphogenesis, and biotic and abiotic stress responses (Hepler 2005; Reddy et al. 2011). The involvement of Ca^{2+} in the triggering of the symbiotic process between plant and fungi is analogous to what is demonstrated in the *Rhizobium*-legume

symbiosis. Navazio and Mariani (2008) documented transient changes of Ca^{2+} concentration that occurred when rhizodermal cells were challenged with diffusible molecules released by AM fungi. An investigation with an experimental design based on challenging host plant cells with culture media of different AM fungi (*Gigaspora margarita*, *Glomus mosseae*, and *G. intraradices*) provided the first firm evidence that Ca^{2+} is involved as an intracellular messenger during mycorrhizal signaling, at least in a pre-contact stage. Based on these experiments, it appears that AM fungi announce their presence to the plant through the constitutive release of a chemical signal, even before experiencing proximity to the plant or its symbiotic signals to AM fungi. The notion that the secreted fungal molecules herald, through Ca^{2+}, a beneficial message which can be acknowledged only by competent receivers, is supported by (1) the lack of defense response induction and the upregulation of some genes essential for the AM symbiosis initiation in host plant cells and (2) the unresponsiveness of cultured cells from the non-host plant *Arabidopsis thaliana*. Calcium is an essential modulator in mycorrhizal colonization, and the mycorrhizal fungus increases its absorption of Ca^{2+} for host plants in Ca-deficient soils. These assumptions were confirmed a recent work on peanut (*Arachis hypogaea* L.) by Cui et al. (2019).

Yield can be limited by a deficiency of exchangeable Ca^{2+} in soil, which can also cause early embryo abortion in peanut (Yang et al. 2017; Jain et al. 2011). Cui et al. (2019) demonstrated that AM symbiosis increased the Ca^{2+} content of peanut seedlings and the development of AM symbiosis. In this study, they investigated a combination of transcriptional changes, hormone, and metabolomic analyses in roots of peanut seedlings inoculated by application of AMF and Ca^{2+}, and they compared the observed changes with those in AM plants or Ca^{2+}-treated plants. They observed that changes in secondary metabolites in roots of AM plants and Ca^{2+}-treated plants coincide with the transcriptional regulation of related biosynthesis pathways. These alternations, such as the increases in gibberellic acid (GA3) and flavonoid content, were considered to be involved in the growth enhancement of peanut seedlings by the synergy of AMF with Ca^{2+} application. Moreover, the increase in Ca^{2+} content enhanced K level in plants by enhancing the transcripts of genes encoding the K channel, and together with AM symbiosis improved plant nutrient uptake, thus increasing the shoot and root dry weight. These results indicated that the interaction between AM symbiosis and exogenous Ca^{2+} benefited the growth of peanut seedlings and could explain why Ca^{2+} application strengthens the role of AM symbiosis in plant growth by further regulating a major overlap of transcriptional changes in roots of AM plant.

18.4 CONCLUSIONS

"The plant-fungi symbiosis" is a partnership of interspecific coexistence that has developed during more than 400 million years. In nature, the strongest biological entities do not always win, and those that are best adapted to the environmental context, including climate change and nutritional resources, most often prevail. Many studies in molecular biology and biochemistry have revealed the value, functionality, and strategic advantages of mycorrhizal symbiosis. This basic research regarding a small number of AMF species and only a few completely sequenced genomes is the foundation of applied research that is beginning to produce encouraging results in the agronomic field. Future progress in utilizing plant-fungi symbiosis for agriculture, horticulture, arboriculture, and silviculture will depend on improving current knowledge through:

1. deeper understanding of how AMF function;
2. selection of AMF strains that differ in their ability to provide mineral nutrition and vegetative development with a greater number of plant species;
3. development of new AMF mixtures to covering a wider range of plant species; and
4. development of technologies that allow the massive cultivation of AMF at low production costs.

Progress in these four areas of plant-fungi symbiosis technology can lead to molecular engineering of AMF and their associated microorganisms and plant species. Applied research utilizing these improved AMF and associated microorganisms to improve plant-fungi symbiosis of modern crop production systems has the potential to increase yield and crop quality of a wide range of economically valuable plant species.

REFERENCES

Achatz, M., E. K. Morris, F. Muller, M. Hilker and M.C. Rillig. 2014. Soil hypha-mediated movement of allelochemicals: arbuscular mycorrhizae extend the bioactive zone of juglone. *Funct. Ecol.* 28: 1020–1029.

Akiyama, K., K. Matsuzaki, and H. Hayash. 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* 435:824–827. https://doi.org/10.1038/nature03608

Aranda-Sicilia, M. N., A. Aboukila , U. Armbruster , O. Cagnac, T. Schumann, H. H. Kunz, P. Jahns , M. P. Rodríguez-Rosales, H. Sze, and K. Venema. 2016. Envelope K^+/H^+ antiporters AtKEA1 and AtKEA2 function in plastid development. *Plant Physiol.* 172:441–449.

Babikova, Z., L. Gilbert, T. J. A. Bruce, M. Birkett, J. C. Caulfield, C. Woodcock, J. A. Pickett, and D. Johnson.

2013. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol. Lett.* 16:835–843. https://doi.org/10.1111/ele.12115

Bago, B. and C. Azcón-Aguilar. 1997. Changes in the rhizospheric pH induced by arbuscular mycorrhiza formation in onion (*Allium cepa* L.). *Z. Pflanzenernähr. Bodenkd*. 160:333–339.

Bago, B., W. Zipfel, R. M. Williams, J. Jun, R. Arreola, P. J. Lammers, P. E. Pfeffer, and Y. Shachar-Hill. 2002. Translocation and utilization of fungal storage lipid in the arbuscular mycorrhizal symbiosis. *Plant Physiol*. 128 :108–124.

Becard, G. L., W. Donet, D. B. Rolin, D. D. Douds and P. E. Pfeffer. 1991. Identification and quantification of trehalose in vescicular-arbuscular mycorrhizal fungi by *in vivo* ^{13}C NMR and HPLC analyses. *New Phytol*. 118:547–552.

Beilby, J. P., and D. K. Kidby. 1980. Biochemistry of ungerminated and germinated spores of the vesicular-arbuscular mycorrhizal fungus *Glomus caledonium*: Changes in neutral and polar lipids. *J. Lipid Res*. 21:739–750.

Besserer, A., V. Puech-Pagès, P. Kiefer, V. Gomez-Roldan, A. Jauneau, S. Roy, J. C. Portais, C. Roux, G. Bécard, and N. Séjalon-Delmas. 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biol*. 4:1239–1247.

Bitterlich, M., U. Krügel, K. Boldt-Burisch, P. Franken and C. Kühn. 2014. The sucrose transporter SlSUT2 from tomato interacts with brassinosteroid functioning and affects arbuscular mycorrhiza formation. *Plant J*. 78:877–889. https://doi.org/10.1111/tpj.12515

Bonfante, P., and I.A. Anca. 2009. Plants, mycorrhizal fungi, and bacteria: A network of interactions. *Annu. Rev. Microbiol*. 63:363–83. https://doi.org/10.1146/annurev.micro.091208.073504

Bonneau, L., S. Huguet, D. Wipf, N. Pauly, and H. N. Truong. 2013. Combined phosphate and nitrogen limitation generates a nutrient stress transcriptome favorable for arbuscular mycorrhizal symbiosis in *Medicago truncatula*. *New Phytol*. 199 :188–202.

Boucher, D., S. W. James, and H. K. Keeler. 1982. The ecology of mutualism. *Annu. Rev. Ecol. Syst.* 13:315–347. https://doi.org/10.1146/annurev.es.13.110182.001531

Bravo, A., M. Brands V. Wewer, P. Dormann, and M. J. Harrison. 2017. Arbuscular mycorrhiza-specific enzymes FatM and RAM 2 fine-tune lipid biosynthesis to promote development of arbuscular mycorrhiza. *New Phytol.* 214:1631–1645. https://doi.org/10.1111/nph.14533

Breuillin-Sessoms, F., D. S. Floss, S. K. Gomez, N. Pumplin, Y. Ding, V. Levesque-Tremblay, R. D. Noar, D. A. Daniels, and A. Bravo. 2015. Suppression of arbuscule degeneration in *Medicago truncatula* phosphate transporter 4 mutants is dependent on the ammonium transporter 2 family protein AMT2,3. *Plant Cell* 27:1352–1366. https://doi.org/10.1105/tpc.114.131144

Breuninger, M., C. G. Trujillo, E. Serrano, R. Fischer, and N. Requena. 2004. Different nitrogen sources modulate activity but not expression of glutamine synthetase in arbuscular mycorrhizal fungi. *Fungal Genet. Biol*. 41: 542–552.

Brown, T. A., and G. R. Carlson. 1990. Grain yields related to stored soil water and growing season rainfall. Montana State University Agricultural Experiment Station Special Report 35, 22 p.

Bücking, H., and A. Kafle. 2015. Role of arbuscular mycorrhizal fungi in the nitrogen uptake of plants: Current knowledge and research gaps. *Agronomy* 5:587–612. https://doi.org/10.3390/agronomy5040587

Carroll, G. 1988. Fungal endophytes in stems and leaves: From latent pathogen to mutualistic symbiont. *Ecology* 69:2–9. https://doi.org/10.2307/1943154

Cellier, F., G. Conéjéro, L. Ricaud, D. T. Luu, M. Lepetit, F. Gosti and F. Casse. 2004. Characterization of AtCHX17, a member of the cation/H+ exchangers, CHX family, from *Arabidopsis thaliana* suggests a role in K^+ homeostasis. *Plant J*. 39 :834–846.

Chen, H. Y., J. H. Huh, Y. C. Yu, L. H. Ho, L. Q. Chen, D. Tholl, et al. 2015.The *Arabidopsis* vacuolar sugar transporter SWEET2 limits carbon sequestration from roots and restricts *Pythium* infection. *Plant J*. 83(6):1046–1058. https://doi.org/10.1111/tpj.12948

Classen, A. T., M. K. Sundqvist, J. A. Henning, G. S. Newman, J. A. M. Moore, and M. A. Cregger. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: what lies ahead? *Ecosphere* 6:1–21.

Cliquet, J. B., and G. R. Stewart. 1993. Ammonia assimilation in *Zea mays* L. infected with a vesicular-arbuscular mycorrhizal fungus *Glomus fasciculatum*. *Plant Physiol*. 101:865–871.

Coleman, M. D., C. S. Bledsoe, and B. A. Smit. 1990. Root hydraulic conductivity and xylem sap levels of zeatin riboside and abscisic acid in ectomycorrhizal Douglas fir seedlings. *New Phytol*. 115:275–284. https://doi.org/10.1111/j.1469–8137.1990.tb00453.x

Cramer, C. L., and H. H. Davis. 1984. Polyphosphate-cation interaction in the amino acid-containing vacuole of *Neurospora crassa*. *J. Biol. Chem*. 259:5152–5157.

Cui, L., G. Feng, J. Zhang, S. Yang, J. Meng, Y. Geng, X. Li, and S. Wan. 2019. Synergy of arbuscular mycorrhizal symbiosis and exogenous Ca^{2+} benefits peanut (*Arachis hypogaea* L.) growth through the shared hormone and flavonoid pathway. *Sci. Rep*. 9:16281. https://doi.org/10.1038/s41598-019-52630-7

Cruz, C., H. Egsgaard, C. Trujillo, P. Ambus, N. Requena, M. A. Martins-Loução, and I. Jakobsen. 2007. Enzymatic evidence for the key role of arginine in N translocation by arbuscular mycorrhizal fungi. *Plant Physiol*. 144:782–792.

Dai, M. C. Hamel, L. D. Bainard, M. St. Arnaud C. A. Grant, N. Z. Lupwayi, S. S. Malhi, and R. Lemke. 2014. Negative and positive contributions of arbuscular mycorrhizal fungal taxa to wheat production and nutrient uptake efficiency in organic and conventional systems in the Canadian prairie. *Soil Biol. Biochem*. 74 :156–166.

Dehne, H. W. 1982. Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. *Phytopathology* 72:1115–1119.

Di Martino, C., G. Palumbo, D. Vitullo, D., P. Di Santo, and A. Fuggi. 2018. Regulation of mycorrhiza development in durum wheat by P fertilization: Effect on plant N metabolism. *J. Plant Nutr. Soil Sci*. https://doi.org/10.1002/jpln.201700110

Di Martino, C, A. Fioretto, D. Palmieri, V. Torino, and G. Palumbo. 2019. Influence of tomato plant mycorrhization on nitrogen metabolism, growth and fructification on P-limited soil. *J. Plant Growth Regul*. https://doi.org/10.1007/s00344-019-09923-y

Dighton, J., J. F. White, Jr., and P. Oudemans. 2005. *The Fungal Community: Its Organization and Role in the Ecosystem*. Boca Raton, FL: CRC Press.

Drew, E. A., R. S. Murray, S. E. Smith and I. Jakobsen. 2003. Beyond the rhizosphere: growth and function of arbuscular mycorrhizal external hyphae in sands of varying pore sizes. *Plant Soil* 251 :105–114.

Ehrhardt, D.W., R. Wais, and S. R. Long. 1996. Calcium spiking in plant root hairs responding to *Rizobium* nodulation signals. *Cell* 85:673–681.

Faure, S., J. B. Cliquet, G. Thephany, and J. Boucaud. 1998. N assimilation in *Lolium perenne* colonized by the arbuscular mycorrhizal fungus *Glomus fasciculatum*. *New Phytol*. 138:411–417.

Fellbaum, C. R., E. W. Gachomo, Y. Beesetty, S. Choudhari, G. D. Strahan, P. E. Pfeffer, E. T. Kiers, and H. Bücking. 2012. Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. *Proc. Natl. Acad. Sci. USA* 109(7):2666–2671. https://doi.org/10.1073/pnas.1118650109

Fellbaum, C. R., J. A. Mensah, A. J. Cloos, G. D. Strahan, P. E. Pfeffer, E. T. Kiers, and H. Bücking, 2014. Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. *New Phytol*. 203:645–656.

Forde, B. G. 2000. Nitrate transporters in plants: Structure, function and regulation. *Biochim. Biophys. Acta* 1465:219–235.

Fuggi, A., V. Vona, V. D. Rigano, C. Di Martino, A. Martello, and C. Rigano. 1984. Evidence for two transport-systems for nitrate in the acidophilic thermophilic alga *Cyanidium caldarium*. *Arch. Microbiol.* 137:281–285.

Funamoto, R., K. Saito, H. Oyaizu, M. Saito, and T. Aono. 2007. Simultaneous *in situ* detection of alkaline phosphatase activity and polyphodphate in arbuscules within arbuscular mycorrhizal roots. *Funct. Plant Biol*. 34: 803–810.

Gachomo, E., J.W. Allen, P. E. Pfeffer, M. Govindarajulu, D. D. Douds, H. R. Jin, G. Nagahashi, P. J. Lammers, Y. Shachar-Hill, and H. Bücking. 2009. Germinating spores of *Glomus intraradices* can use internal and exogenous N sources for *de novo* biosynthesis of amino acids. *New Phytol*. 184:399–411.

Ganugi, P., A. Masoni, G. Pietramellara, and S. Benedettelli. 2019. A review of studies from the last twenty years on plant-arbuscular mycorrhizal fungi associations and their uses for wheat crops. *Agronomy* 9(12):840. https://doi.org/10.3390/agronomy9120840

Garcia, K., D. Chasman , S. Roy and J. M. Ané. 2017. Physiological responses and gene co-expression network of mycorrhizal roots under K^+ deprivation. *Plant Physiol*. 173:1811–1823.

Gaude, N., S. Bortfeld, N. Duensing, M. Lohse, and F. Krajinski. 2012. Arbuscule-containing and non-colonized cortical cells of mycorrhizal roots undergo extensive and specific reprogramming during arbuscular mycorrhizal development. *Plant J*. 69: 510–528.

Genre, A., and P. Bonfante. 2005. Building a mycorrhizal cell: How to reach compatibility between plants and arbuscular mycorrhizal fungi. *J. Plant Interact*. 1:3–13. http://doi.org/10.1080/17429140500318986

Genre, A., M. Chabaud, C. Balzergue, V. Puech-Pages, M. Novero, T. Rey, J. Fournier, S. Rochange, G. Becard, P. Bonfante, and D. G. Barker. 2013. Short-chain chitin oligomers from arbuscular mycorrhizal fungi trigger nuclear Ca^{2+} spiking in *Medicago truncatula* roots and their production is enhanced by strigolactone. *New Phytol*. 198: 179–189.

Genre, A., M. Chabaud, A. Faccio, D. G. Barker, and P. Bonfante. 2008. Prepenetration apparatus assembly precedes and predicts the colonization patterns of arbuscular mycorrhizal fungi within the root cortex of both *Medicago truncatula* and *Daucus carota*. *Plant Cell* 20:1407–1420. https://doi.org/10.1105/tpc.108.059014

George, E., K. U. Häussler, D. Vetterlein, E. Gorgus, and H. Marschner. 1992. Water and nutrient translocation by hyphae of *Glomus mosseae*. *Can. J. Bot*. 70:2130–2137.

Ghignone, S., A. Salvioli, I. Anca, E. Lumini, G. Ortu, L. Petiti, S. Cruveiller, V. Bianciotto, P. Piffanelli, L. Lanfranco, and P. Bonfante. 2012. The genome of the obligate endobacterium of an AM fungus reveals an interphylum network of nutritional interactions. *ISME Journal* 6:136–145.

Gianinazzi, S., V. Gianinazzi-Pearson, and J. Dexheimer. 1979. Enzymatic studies on the metabolism of vesicular-arbuscular mycorrhiza. III. Ultrastructural localization of acid and alkaline phosphatase in onion roots infected by *Glomus mosseae* (Nicol. and Gerd.) *New Phytol*. 82:127–132.

Giaquinta, R.T. 1983. Phloem loading of sucrose Annu. *Rev. Plant Physiol*. 34:347–387.

Gierth, M., P. Mäser, and J. I. Schroeder. 2005. The potassium transporter $AtHAK_5$ functions in K^+ deprivation-induced high-affinity K^+ uptake and AKT_1 K^+ channel contribution to K^+ uptake kinetics in *Arabidopsis* roots. *Plant Physiol.* 137:1105–1114.

Girlanda, M., R. Segreto, D. Cafasso, H. T. Liebel, M. Rodda, E. Ercole, S. Cozzolino, G. Gebauer, and S. Perotto. 2011. Photosynthetic Mediterranean meadow orchids feature partial mycoheterotrophy and specific mycorrhizal associations. *Am. J. Bot.* 98:1148–1163.

Gomez, S. K., H. Javot, P. Deewatthanawong, I. Torres-Jerez, Y. Tang, E. B. Blancaflor, M. K. Udvardi, and

M. J. Harrison. 2009. *Medicago truncatula* and *Glomus intraradices* gene expression in cortical cells harboring arbuscules in the arbuscular mycorrhizal symbiosis. *BMC Plant Biol*. 9:10.

Govindarajulu, M., P. E. Pfeffer, H. R. Jin, J. Abubaker, D. D. Douds, J. W. Allen, H. Bücking, P. J. Lammers, and Y. Shachar-Hill. 2005. N transfer in the arbuscular mycorrhizal symbiosis. *Nature* 435:819–823.

Graniti, A. 2002. L'endofitismo nei funghi: un adattamento ecologico o un modo di vita? In *Atti del Convegno "L'endofitismo di funghi e batteri patogeni in piante arboree e arbustive,"* ed. A. Franceschini and F. Marras, pp. 147–156. Sassari, Tempio Pausania, May 19–21, 2002.

Guehl, J. M., J. Garbaye, and A. Wartinger. 1992. The effects of mycorrhizal status on plant-water relations and sensitivity of leaf gas exchange to soil drought in Douglas fir (*Pseudotsuga menziesii*) seedlings. In *Mycorrhizas in Ecosystems*. ed. D. J. Read, D. H. Lewis, A. H. Fitter, and I. J. Alexander, pp. 323–332. Wallingford, Oxon, UK: CAB International.

Hamel, C., and C. Plenchette. 2007. *Mycorrhizae in Crop Production*. Binghamton, NY: HFAPP/Haworth Food & Agricultural Products Press.

Harrison, M.J. 1996. A sugar transporter from *Medicago truncatula*: altered expression pattern in roots during vesicular-arbuscular (VA) mycorrhizal associations. *Plant J*. 9:491–503. https://doi.org/10.1046/j.1365-313X.1996.09040491.x

Hawkins, H. J., and E. George. 1999. Effect of plant nitrogen status on the contribution of arbuscular mycorrhizal hyphae to plant nitrogen uptake. *Physiol. Plant*. 105:694–700.

Hawkins, H. J., A. Johansen, and E. George. 2000. Uptake and transport of organic and inorganic nitrogen by arbuscular mycorrhizal fungi. *Plant Soil* 226:275–285.

Hepler, P. K. 2005. Calcium: A central regulator of plant growth and development. *Plant Cell*. 17(8):2142–2155. https://doi.org/10.1105/tpc.105.032508

Hildebrandt, U., E. Schmelzer, and H. Bothe. 2002. Expression of nitrate transporter genes in tomato colonized by an arbuscular mycorrhizal fungus. *Physiol. Plant*. 115:25–136.

Howitt, S. M., and M. K. Udvardi. 2000. Structure, function and regulation of ammonium transporters in plants. *Biochim. Biophys. Acta* 1465:152–170.

Javelle, A., M. Morel, B. R. Rodriguez-Pastrana, B. Botton, B. André, A. M. Marini, A. Brun, and M. Chalot. 2003. Molecular characterization, function and regulation of ammonium transporters (Amt) and ammonium-metabolizing enzymes (GS, NADP-GDH) in the ectomycorrhizal fungus *Hebeloma cylindrosporum*. *Mol. Microbiol*. 47:411–430. https://doi.org/10.1046/j.1365-2958.2003.03303.x

Jain, M., B. P. Pathak, A. C. Harmon, B. L. Tillman, and M. Gallo. 2011. Calcium dependent protein kinase (CDPK) expression during fruit development in cultivated peanut (*Arachis hypogaea*) under sufficient and deficient growth regimens. *J. Plant Physiol*. 168:2272–2277.

Jiang, Y, W. Wang, Q. Xie, N. Liu, L. Liu, D. Wang, X. Zhang, C. Yang, X. Chen, D. Tang, and E. Wang. 2017. Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi. *Science* 356(6343):1172–1175. https://doi.org/10.1126/science.aam9970

Jin, H., P. E. Pfeffer, D. D. Douds, E. Piotrowski, P. J. Lammers, and Y. Shachar-Hill. 2005. The uptake, metabolism, transport and transfer of N in an arbuscular mycorrhizal symbiosis. *New Phytol*. 168:687–696.

Jing, F., D. C. Cantu, J. Tvaruzkova, J. P.Chipman, B. J. Nikolau, M. D. Yandeau-Nelson and P. J. Reilly. 2011. Phylogenetic and experimental characterization of an acyl-ACP thioesterase family reveals significant diversity in enzymatic specificity and activity. *BMC Biochemistry* 12:44.

Johansen, A., R. D. Finlay, and P. A. Olsson. 1996. Nitrogen metabolism of external hyphae of the arbuscular mycorrhizal fungus *Glomus intraradices*. *New Phytol*. 133:705–712.

Jones, A., H. M. Davies, and T. A. Voelker. 1995. Palmitoyl-acyl carrier protein (ACP) thioesterase and the evolutionary origin of plant acyl-ACP thioesterases. *Plant Cell* 7:359–371.

Jones, D. L., C. Nguyen, and R. D. Finlay. 2009. Carbon flow in the rhizosphere: Carbon trading at the soil-root interface. *Plant Soil* 321 :5–33.

Jongejans, E., and A. Telenius. 2001. Field experiments on seed dispersal by wind in ten umbelliferous species (*Apiaceae*). *Plant Ecology* 152:67–78.

Jongmans, A. G., N. van Breemen, U. Lundstrom, P. A. W. Hees, R. D. Finlay, M. Srinivasan,T. Unestam, R. Gielser, P. A. Melkerud, and M. Olsson. 1997. Rock-eating fungi. *Nature* 389:682–683.

Jourand, P., L. Hannibal, C. Majorel, S. Mengant, M. Ducousso, and M. Lebrun. 2014. Ectomycorrhizal *Pisolithus albus* inoculation of *Acacia spirorbis* and *Eucalyptus globulus* grown in ultramafic topsoil enhances plant growth and mineral nutrition while limits metal uptake. *J. Plant. Physiol*. 171:164–172.

Kaiser, C., M. R. Kilburn, P. I. Clode, I. Fuchslueger, M. Koranda, and J. B. Cliff. 2014. Exploring the transfer of recent plant photosynthates to soil microbes mycorrhizal pathway vs direct root exudation. *New Phytol*. 205:1537–1551. https://doi.org/10.1111/nph.13138

Kaldorf, M., W. Zimmer, and H. Bothe. 1994. Genetic evidence for the occurrence of assimilatory nitrate reductase in arbuscular mycorrhizal and other fungi. *Mycorrhiza* 5:23–28.

Kaldorf, M., E. Schmelzer, and H. Bothe. 1998. Expression of maize and fungal nitrate reductase genes in arbuscular mycorrhiza. *MPMI* 11: 439–448.

Karandashov, V. and M. Bucher. 2005. Symbiotic phosphate transport in arbuscular mycorrhizas. *Trends Plant Sci*. 10:22–29.

Keymer, A., P. Pimprikar, V. Wewer, C. Huber, M. Brands, and S. I. Bucerius et al. 2017. Lipid transfer from plants to arbuscular mycorrhiza fungi. *eLife* 6:e29107 https://doi.org/10.7554/eLife.29107

Kobae, Y., Y. Tamura, S. Takai, M. Banba, and S. Hata. 2010. Localized expression of arbuscular mycorrhiza-inducible ammonium transporters in soybean. *Plant Cell Physiol*. 51:1411–1415.

Kunz, H. H., M. Gierth, A. Herdean, M. Satoh-Cruz, D. M. Kramer, C. Spetea, and J. I. Schroeder. 2014. Plastidial transporters KEA1, -2, and -3 are essential for chloroplast osmoregulation, integrity, and pH regulation in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* 111:7480–7485.

Kwinta, J., K. Bartoszewicz and W. Bielawski. 2001. Purification and characteristics of glutamate dehydrogenase (GDH) from triticale roots. *Acta Physiol. Plant.* 23: 399–405.

Lecourieux, D., R. Ranjeva, and A. Pugin. 2006. Calcium in plant defence-signalling pathways. *New Phytol.* 171:249–269.

Leigh, R. A., and R. G. Wyn Jones. 1984. A hypothesis relating critical potassium concentrations for growth to the distribution and functions on this ion in the plant cell. *New Phytol*. 97:1–13.

Lipnicki, L. I. 2015. The role of symbiosis in the transition of some eukaryotes from aquatic to terrestrial environments. *Symbiosis* 65:39–53.

Liu, J., L. Wu, S. Wei, X. Xiao, C. Su, P. Jiang, Z. Song, T. Wang, and Z. Yu. 2007. Effects of arbuscular mycorrhizal fungi on the growth, nutrient uptake and glycyrrhizin production of licorice (*Glycyrrhiza uralensis* Fisch). *Plant Growth Regul*. 52:29–39.

Liu, Y., N. Lai, K. Gao, F. Chen, L. Yuan, and G. Mi. 2013. Ammonium inhibits primary root growth by reducing the length of meristem and elongation zone and decreasing elemental expansion rate in the root apex in *Arabidopsis thaliana*. *PLoS ONE* 8: e61031.

Liu, J., J. Liu, J. Liu, M. Cui, Y. Huang, Y. Tian, A. Chen, and G. Xu. 2019. The potassium transporter S1HAK10 is involved in mycorrhizal potassium uptake. *Plant Physiol*. 180:465–479.

Luginbuehl, L. H., G. N. Menard, S. Kurup, H. Van Erp, G. V. Radhakrishnan, A. Breakspear, G. E. D. Oldroyd, and P. J. Eastmond. 2017. Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. *Science* 356:1175–1178. https://doi.org/10.1126/science.aan0081

Manck-Götzenberger, J., and N. Requena. 2016. Arbuscular mycorrhiza symbiosis induces a major transcriptional reprogramming of the potato SWEET sugar transporter family. *Front. Plant Sci*. 7:487. https://doi.org/10.3389/fpls.2016.00487

Manschadi, A. M., K. Hans-Peter, J. Vollman, J. Eitzinger, and W. Wenzel. 2014. Developing phosphorus-efficient crop varieties: An interdisciplinary research framework. *Field Crops Res*. 162:87–98. https://doi.org/10.1016/j.fcr.2013.12.016

Margulis, L. 2010. Symbiogenesis. A new principle of evolution rediscovery of Boris Mikhaylovich Kozo-Polyansky (1890–1957). In *Charles Darwin and Modern Biology*, ed. E. I. Kolchinsky, pp. 34–48. St-Petersburg: Nestor-Historia.

Marschner, H. 1995. *Mineral Nutrition of Higher Plants*, 2nd ed. San Diego, CA: Academic Press.

Martín-Robles, N., A. Lehmann, E. Seco, R. Aroca, M. C. Rillig, and R. Milla. 2017. Impacts of domestication on the arbuscular mycorrhizal symbiosis of 27 crop species. *New Phytol*. 218(1):322–334. https://doi.org/10.1111/nph.14962

Marx, C., J. Dexheimer, V. Gianinazzi-Pearson, and S. Gianninazzi. 1982. Enzymatic studies on the metabolism of vesicular-arbuscular mycorrhizas IV. Ultracytoenzymological evidence (ATPase) for active transfer process in the host-arbuscule interface. *New Phytol.* 90:37–43.

Masoni, A., and L. Ercoli. 2010. Azoto nel terreno. In *Riduzione dell'inquinamento delle acque dai nitrati provenienti dal.l'agricoltura,* ed. A. Masoni, pp. 211–241. Pisa: Felici Editore.

McGill, W. B., and C. V. Cole. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* 26:267–286.

Meena, V. S., B. R. Maurya, and J. Verma. 2014. Does a rhizospheric microorganism enhance K^+ availability in agricultural soils? *Microbiol. Res*. 169:337–347.

Mensah, J. A., A. M. Koch, P. M. Antunes, M. M. Hart, E. T. Kiers, and H. Bücking. 2015. High functional diversity within arbuscular mycorrhizal fungal species is associated with differences in phosphate and nitrogen uptake and fungal phosphate metabolism. *Mycorrhiza* 25(7):533–546. https://doi.org/10.1007/s00572-015-0631-x

Nagy, R., D. Drissner, N. Amrhein, I. Jakobsen, and M. Bucher. 2009. Mycorrhizal phosphate uptake pathway in tomato is phosphorus-repressible and transcriptionally regulated. *New Phytol*. 181: 950–959. https://doi.org/10.1111/j.1469-8137.2008.02721.x

Navarro, F. J., F. Machín, Y. Martín, and J. M. Siverio. 2006. Down-regulation of eukaryotic nitrate transporter by N-dependent ubiquitinylation. *J. Biol. Chem*. 281:13268–13274. https://doi.org/10.1074/jbc.M601253200

Navazio, L., R. Moscatiello, A. Genre, M. Novero, B. Baldan, P. Bonfante, and P. Mariani. 2007. A diffusible signal from arbuscular mycorrhizal fungi elicits a transient cytosolic calcium elevation in host plant cells. *Plant Physiol*. 144: 673–681. https://doi.org/10.1104/pp.106.086959

Navazio, L. and P. Mariani. 2008. Calcium opens the dialogue between plants and arbuscular mycorrhizal fungi. *Plant Signal Behav*. 3:229–230. https://doi.org/10.4161/psb.3.4.5093

Noronha, H., A. Silva, Z. Dai, P. Gallusci, A. D. Rombolà, S. Delrot, and H. Gerós. 2018. A molecular perspective on starch metabolism in woody tissues. *Planta* 248:559–568.

Nouri, E., F. Breuillin-Sessoms, U. Feller, and D. Reinhardt. 2014. Phosphorus and nitrogen regulate arbuscular mycorrhizal symbiosis in *Petunia hybrida*. *PLoS ONE* 9(3):e90841. https://doi.org/10.1371/journal.pone.0090841

Novero, M., A. Genre, A. Faccio, and J. Stougaard. 2002. Dual requirement of the LjSym4 gene for mycorrhizal development in epidermal and cortical cells of *Lotus japonicus* roots. *New Phytol.* 154:741–749.

Ohlrogge, J.B. and J. Browse. 1995. Lipid biosynthesis. *Plant Cell* 7: 957–970.

Ohlrogge, J.B. and J. G. Jaworski. 1997. Regulation of fatty acid synthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol*. 48:109–136.

Oldroyd, G. E. D., M. J. Harrison, and M. Udvardi. 2005. Peace talks and trade deals: Keys to long-term harmony in legume-microbe symbioses. *Plant Physiol.* 137: 1205-10.

Oliver, A. J., S. E. Smith, D. J. D. Nicholas, and W. Wallace. 1983. Activity of nitrate reductase in *Trifolium subterraneum*: Effects of mycorrhizal infection and phosphate nutrition. *New Phytol*. 94:63–79.

Oulhen, N., B. J. Schulz, and T. J. Carrier. 2016. English translation of Heinrich Anton de Bary's 1878 speech, "*Die Erscheinung der Symbiose*" ("*De la symbiose*"). *Symbiosis* 69:131–139. https://doi.org/10.1007/s13199-016-0409-8

Parniske, M. 2008. Arbuscular mycorrhiza: The mother of plant root endosymbioses. *Nat. Rev. Microbiol*. https://doi.org/10.1038/nrmicro1987

Pérez-Tienda, J., P. S. Testillano, R. Balestrini, V. Fiorilli, C. Azcón-Aguilar, and N. Ferrol. 2011. GintAMT2, a new member of the ammonium transporter family in the arbuscular mycorrhizal fungus *Glomus intraradices*. *Fungal Genet. Biol*. 48:1044–1055.

Pérez-Tienda, J., A. Valderas, G. Camañes, P. García-Agustín, and N. Ferrol. 2012. Kinetics of NH_4^+ uptake by the arbuscular mycorrhizal fungus *Rhizophagus irregularis*. *Mycorrhiza* 22:485–491.

Petrini, O. 1996. Ecological and physiological aspect of host specificity in endophytic fungi. In: *Endophytic Fungi in Grasses and Woody Plants. Systematics, Ecology and Evolution*, ed. S. C. Redlin, and L. M. Carris. St. Paul, MN: APS Press.

Pfeffer, P. E., D. D. Douds, G. Becard, and Y. Shachar-Hill. 1999. Carbon uptake and the metabolism and transport of lipids in an arbuscular mycorrhiza. *Plant Physiol*. 120:587–598. https://doi.org/10.1104/pp.120.2.587

Plassard, C., and B. Dell. 2010. Phosphorus nutrition of mycorrhizal trees. *Tree Physiol*. 30:1129–1139.

Powell, J. R., R. P. Jeff, and C. R. Matthias. 2018. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol*. 220:1059–1075. https://doi.org/10.1111/nph.15119

Querejeta, J. I., L. M. Egerton-Warburton, and M. F. Allen. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* 134:55–64.

Ragazzi, A. 2004. Endophytism: knowns and unknowns of an age-old phenomenon. In *Endophytism in forest trees,* ed. A. Ragazzi, S. Moricca, and I. Dellavalle, pp. 15–32. Firenze: Accademia Italiana di Scienze Forestali.

Raven J. A., B. Wollenweber, and L. L. Handley. 1992. A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. *New Phytol*. 121:19–32.

Reddy A. S. N., G. S. Ali, H. Celesnik, and I. S. Day. 2011. Coping with stresses: Roles of calcium- and calcium/calmodulin-regulated gene expression. *Plant Cell* 23:2010–2032.

Reid, C. P. P. 1978. Mycorrhizae and water. In Root Physiology and Symbiosis, eds. A. Rildacher and J. Gognoire-Michaud, pp. 392–408. IUFRO Symp. Proc., Nancy, France.

Rodolfi, M., S. E. Legler, and A. M. Picco. 2006. Endofiti fungini in *Vitis vinifera* in Oltrepò Pavese. *Micologia Italiana* 35:25–31.

Rolin, D., P. E. Pfeffer, D. D. Douds, H. M. Farrell, and Y. Shachar-Hill. 2001. Arbuscular mycorrhizal symbiosis and phosphorus nutrition: Effects on amino acid production and turnover in leek. *Symbiosis* 30:1–14.

Romanyà, J., J. M. Blanco-Moreno, and F. X. Sans. 2017. Phosphorus mobilization in low-P arable soils may involve soil organic C depletion. *Soil Biol. Biochem*. 113:250–259.

Rosati, G. and C. Vannini. 2011. *Simbiosi ed evoluzione*. Pisa: Aracne Editrice.

Rowe, H., P. J. A. Withers, P. Baas, N. L. Chan, D. Doody, J. Holiman, et al. 2016. Integrating legacy soil phosphorus into sustainable nutrient management strategies for future food, bioenergy, and water security. *Nutr. Cycl. Agroecosyst*. 104:393–412. https://doi.org/10.1007/s10705-015-9726-1

Saikkonen, K., S. H. Faeth, M. Helander, and T. J. Sullivan. 1998. Fungal endophytes: A continuum of interactions with host plants. *Annu. Rev. Ecol. Syst*. 29:319–343.

Salvioli, A., S. Ghignone, M. Novero, L. Navazio, F. Venice, P. Bagnaresi, and P. Bonfante. 2016. Symbiosis with an endobacterium increases the fitness of a mycorrhizal fungus, raising its bioenergetic potential. *ISME J.* 10:130–144.

Schaarschmidt, S., T. Roitsch, and B. Hause. 2006. Arbuscular mycorrhiza induces gene expression of the apoplastic invertase LIN6 in tomato (*Lycopersicon esculentum*) roots. *J. Exp. Bot.* 57:4015–4023.

Schaarschmidt, S., J. Kopka, J. Ludwig-Müller and B. Hause. 2007. Regulation of arbuscular mycorrhization by apoplastic invertases: enhanced invertase activity in the leaf apoplast affects the symbiotic interaction. *Plant J.* 51(3):390–405. https://doi.org/10.1111/j.1365-313X.2007.03150.x

Schneider, K. D., D. H. Lynchb, K. Dunfielda, K. Khoslaa, J. Jansac, R. P. Voroney. 2015. Farm system management affects community structure of arbuscular mycorrhizal fungi. *Appl. Soil Ecol*. 96:192–200. https://doi.org/10.1016/j.apsoil.2015.07.015

Schnepf, A., S. Klepsch, and D. Leitner. 2011. Modeling phosphorus uptake by a growing and exuding root system *Vadose Zone J*. 11(3):318–327. https://doi.org/10.2136/vzj2012.0001

Schulz, B., and C. Boyle. 2005. The endophytic continuum. *Mycol. Res*. 109:661–686.

Shachar-Hill, Y., P. E. Pfeffer, D. Douds, S. F. Osman, L. W. Doner, and R. G. Ractliffe. 1995. Partitioning of intermediate carbon metabolism in VAM colonized leek. *Plant Physiol*. 108:7–15.

Sharifi, M., M. Ghorbanli, and H. Ebrahimzadeh. 2007. Improved growth of salinity-stressed soybean after

inoculation with salt pre-treated mycorrhizal fungi. *J. Plant. Physiol*. 164:1144–1151.

Sieber, T. N. 2007. Endophytic fungi in forest trees: Are they mutualists? *Fungal Biol. Rev*. 21:75–89.

Simpson, R.J., A. Oberson, R.A. Culvenor, M. H. Ryan, E. J. Veneklaas, H. Lambers et al. 2011. Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. *Plant Soil* 349:89–120. https://doi.org/10.1007/s11104-011-0880-1

Sirrenberg, A., C. Göbel, S. Grond, N. Czempinski, A. Ratzinger, P. Karlovsky, P. Santos, I. Feussner, and K. Pawlowski. 2007. *Piriformospora indica* affects plant growth by auxin production. *Physiol. Plant*. 131:581–589.

Smith, S. E., F. A. Smith, and I. Jakobsen. 2003. Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiol*. 133:16–20.

Smith, S.E., and D.J. Read. 2008. *Mycorrhizal Symbiosis,* 3rd edition. San Diego, CA: Academic Press.

Smith, S. E., and F. A. Smith. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: New paradigms from cellular to ecosystem scales. *Annu. Rev. Plant Biol*. 62:227–250.

Smith, S. E., I. Jakobsen, M. Grønlund, and F. A. Smith. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiol*. 156:1050–1057.

Stergiopoulos, I. and T. R. Gordon. 2014. Cryptic fungal infections: the hidden agenda of plant pathogens. *Front. Plant. Sci*. 5:506. https://doi.org/10.3389/fpls.2014.00506

Stevenson, F.J. 1986. *Cycles of Soils: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients*, New York: Wiley.

Subramanian, K. S., and C. Charest. 1998. Arbuscular mycorrhizae and nitrogen assimilation in maize after drought and recovery. *Physiol. Plant*. 102:285–296.

Sun, Y. P., T. Unestam, S. D. Lucas, K. J. Johanson, I. Kenne and R. D. Finlay. 1999. Exudation-reabsorption in mycorrhizal fungi, the dynamic interface for interaction with soil and other microrganism. *Mycorrhiza* 9: 137–144.

Tedersoo, L., M. Bahram, and M. Zobel. 2020. How mycorrhizal associations drive plant population and community biology. Review. *Science* 367:867–876. https://doi.org/10.1126/science.aba1223

Thomson, J. N. 1982. *Interaction and Coevolution*. New York: Wiley.

Thor, K. 2019. Calcium – Nutrient and messenger. *Front. Plant Sci*. 10:440. https://doi.org/10.3389/fpls.2019.00440

Tian, C., B. Kasiborski, R. Koul, P. J. Lammers, H. Bücking, and Y. Shachar-Hill. 2010. Regulation of the nitrogen transfer pathway in the arbuscular mycorrhizal symbiosis: Gene characterization and the coordination of expression with nitrogen flux. *Plant Physiol*. 153:1175–1187.

Tisserant, E., A. Kohler, P. Dozolme-Seddas, R. Balestrini, K. Benabdellah, A. Colard, D. Croll, C. da Silva, and S. K. Gomez. 2012. The transcriptome of the arbuscular mycorrhizal fungus *Glomus intraradices* (DAOM 197198) reveals functional tradeoffs in an obligate symbiont. *New Phytol*. 193:755–769.

Toussaint, J. P., M. St-Arnaud, and C. Charest. 2004. Nitrogen transfer and assimilation between the arbuscular mycorrhizal fungus *Glomus intraradices* Schenck & Smith and RI t-DNA roots of *Daucus carota* L. in an *in vitro* compartmented system. *Can. J. Microbiol*. 50:251–260.

Turano, F. J., S. S. Thakkar, T. Fang, and J. M. Weisemann. 1997. Characterization and expression of NAD(H)-dependent glutamate dehydrogenase genes in *Arabidopsis*. *Plant Physiol*. 113: 1329–1341. http://doi.org/10.1104/pp.113.4.1329

Uozumi, N., E. J. Kim, F. Rubio, T. Yamaguchi, S. Muto, A. Tsuboi, E. P. Bakker, T. Nakamura, and J. I. Schroeder. 2000. The *Arabidopsis* HKT1 gene homolog mediates inward Na^+ currents in *Xenopus laevis* oocytes and Na^+ uptake in *Saccharomyces cerevisiae*. *Plant Physiol.* 122:1249–1259.

Van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller et al. 1998. Mycorrhizal fungal diversity determines plant biodiversity. *Nature* 396:69–72. https://doi.org/10.1038/23932

Vázquez, M., J. Barea, and R. Azcón. 2001. Impact of soil nitrogen concentration on *Glomus* spp.-*Sinorhizobium* interactions as affecting growth, nitrate reductase activity and protein content of *Medicago sativa*. *Biol. Fertil. Soils* 34:57–63.

Veresoglou, S. D., A. P. Mamolos, B. Thornton, O. K. Voulgari, R. Sen, and S. Veresoglou. 2011. Medium-term fertilization of grassland plant communities masks plant species-linked effects on soil microbial community structure. *Plant Soil* 344:187–196.

Voelker, C., D. Schmidt , B. Mueller-Roeber, and K. Czempinski. 2006. Members of the *Arabidopsis* AtTPK/KCO family form homomeric vacuolar channels in planta. *Plant J*. 48:296–306.

Wang, E., S. Schornack, J. F. Marsh, E. Gobbato, B. Schwessinger, P. Eastmond, M. Schultze, S. Kamoun, and G. E. D. Oldroyd. 2012. A common signaling process that promotes mycorrhizal and oomycete colonization of plants. *Curr. Biol.* 22: 2242–2246.

Wang, Y., and W. H. Wu. 2017. Regulation of potassium transport and signaling in plants. *Curr. Opin. Plant Biol*. 39:123–128.

Waqas, M., A.L. Khan, M. Kamran, M. Hamayun, S. Kang, Y. Kim, and I. Lee. 2012. Endophytic fungi produce gibberellins and indolacetic acid and promotes host-plant growth during stress. *Molecules* 17:10754–10773.

Westenberg, B., T. Boller, and A. Wiemken. 1989. Lack of arginine- and polyphosphate-storage pools in a vacuole-deficient mutant (end1) of *Saccharomyces cerevisiae*. *FEBS Lett*. 254:133–136.

White P. J. and M. R. Broadley. 2003. Calcium in plants. *Ann. Bot*. 92:487–511. https://doi.org/10.1093/aob/mcg164

Wilkinson, D. M. 1997. Plant colonization: Are wind dispersed seeds really dispersed by birds at large spatial and temporal scales? *J. Biogeogr*. 24:61–65.

Wright, D. P., D.J. Read, and J.D. Scholes. 1998. Mycorrhizal sink strength influences whole plant carbon balance of *Trifolium repens* L. *Plant Cell Environ*. 21: 881–891.

Xie, X, W. Huang, F. Liu, N. Tang, Y. Liu, H. Lin, and B. Zhao. 2013. Functional analysis of the novel mycorrhiza-specific phosphate transporter AsPT1 and PHT1 family from *Astragalus sinicus* during the arbuscular mycorrhizal symbiosis. *New Phytol*. 198:836–852. https://doi.org/10.1111/nph.12188

Xu, L., C. Wu, R. Oelmüller, and W. Zhang. 2018. Role of phytohormones in *Piriformospora indica*-induced growth promotion and stress tolerance in plants: More questions than answers. *Front. Microbiol*. 9:1–13.

Yang S., L. Li, J. Zhang, Y. Geng, F. Guo, J. Wang, J. Meng, N. Sui, S. Wan, and X. Li. 2017. Transcriptome and differential expression profiling analysis of the mechanism of Ca^{2+} regulation in peanut (*Arachis hypogaea*) pod development. *Front. Plant Sci.* 8:1609. https://doi.org/10.3389/fpls.2017.01609

Yousefi, A. A., K. Khavazi, A. A. Moezi, F. Rejali and N. H. Nadian. 2011. Phosphate solubilizing bacteria and arbuscular mycorrhizal fungi impacts on inorganic phosphorus fractions and wheat growth. *World Appl. Sci. J.* 15: 1310–1318.

Zhu, Y. G., S. E. Smith, A. R. Barritt and F. A. Smith. 2001. Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. *Plant Soil* 237:249–255.