Chapter 2
Dynamics of Arbuscular Mycorrhizal Symbiosis and Its Role in Nutrient Acquisition: An Overview

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Abstract Arbuscular mycorrhiza constitute a heterogeneous group of diverse fungal taxa that have been reported to form mutualistic interaction with the roots of more than 90% of all plant species. Accomplishment of this symbiotic interaction requires a high degree of synchronization between the two partners and is based on a finely regulated molecular dialogue. Where plant roots exude strigolactones that stimulate fungal metabolism and branching, fungus releases signaling molecules—myc factors that trigger symbiotic responses in the host plant. Among the various benefits bestowed by this symbiotic association, transport of limiting soil nutrients including phosphorus (P), nitrogen (N), sulphur (S) in exchange for fixed carbon is considered as the key feature which occurs in arbuscule containing host cortical cells. In the last few years, novel transporters involved in this mutualistic interaction have been unravelled. This chapter briefly summarizes the signaling pathways and nutrient exchange involved in the establishment of an effective symbiosis between the host plant and fungus that could provide better insight into the role of mycorrhizal fungi in sustainable agriculture.

2.1 Introduction

In the soil rhizosphere, plant roots interact with a number of beneficial microorganisms, among which arbuscular mycorrhizal (AM) fungi are recognized as one of the most significant group of soil biota in the context of ecosystem sustainability (Jeffries and Barea 2012, Barea et al. 2013). AM fungi, belonging to the phylum Glomeromycota have been documented to form symbiosis with more than 90% of plant species belonging to Angiosperms, Gymnosperms and Pteridophytes (Read et al. 2000; Shah 2014; Prasad et al. 2017). It is an ancient type of interaction that have been believed to facilitate colonization of land even more than 460 million years ago (Redeker et al. 2000; Smith and Read 2008). Due to their widespread

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occurrence, they are considered as 'ecosystem engineers' of plant communities (Cameron 2010; Bücking and Kafle 2015) as they affect the distribution and movement of nutrients within the soil ecosystem through the activities of the interlinked and extensive soil extra-radical mycelium (ERM) (Richardson et al. 2009; Barea et al. 2014). The major flux is the transfer of carbon (C) from the host plant to fungus (and thereby to the soil) and the reciprocal movement of phosphate and ammonium (NH_4^+) from fungus to plant (Barea et al. 2014). This mutualistic interaction results in the formation of tree-shaped subcellular structures within cortical cells of plant roots called 'arbuscules' (derived from the Latin arbusculum, meaning bush or little tree), thus establishing main interface for symbiotic nutrient transfer (Parniske 2008; Gutjahr and Parniske 2013; López-Ráez and Pozo 2013). However, rather than developing on a leaf, AM interaction occurs beneath the soil surface, thus strongly hindering chances of understanding most of the early steps of their development including signal exchange that occurs between plant and the endophytic fungus (Genre 2012). Following sub sections briefly summarize the (1) events that lead to the establishment of AM symbiosis in plant rhizosphere and, (2) recent advancements in nutrient exchange and metabolite fluxes among the two symbionts.

2.1.1 AM Establishment: An Overview

AM symbiosis, which have been reviewed recently by various authors (Garg and Chandel 2010; Genre 2012; Aroca et al. 2013; Gutjahr and Parniske 2013; Barea et al. 2014; Bonfante and Desirò 2015; Mohanta and Bae 2015) is a complex and very dynamic interaction that requires a high degree of coordination between the two partners and is based on a finely regulated molecular dialogue (Hause et al. 2007; López-Ráez et al. 2010; Aroca et al. 2013; Barea et al. 2014; Pozo et al. 2015; López-Ráez 2016). The establishment of AM symbiosis can be divided into three different growth stages: (1) asymbiotic hyphal growth stage, where spores germinate and develop hyphae autonomously but for a limited period; (2) pre-symbiotic growth stage, where hyphal growth is stimulated by host signal perception; and (3) symbiotic stage, in which fungus penetrates plant root and develops both intraradical mycelium (IRM, to exchange nutrients) as well as extra-radical (ER) hyphae (to recruit nutrients in the soil and form new spores; Smith and Read 2008; López-Ráez and Pozo 2013).

Generally, it has been validated that AM fungi colonize plant roots from three main types of soil-based propagules: spores, fragments of mycorrhizal roots and ER hyphae, all of them producing more or less a well-developed mycelial network expanding in the soil (Barea et al. 2014). During the first phase, AM fungal colonization initiates with the formation of hyphae that arises from soil-borne propagules i.e. resting spores or mycorrhizal root fragments or from AM plants growing in the vicinity (Koltai and Kapulnik 2009). Following germination, fungus uses triacylglyceride (TAG) and glycogen reserves in the spore to support growth of

such a short mycelium as it is unable to uptake C from the soil organic matter (Harrison 2005; Leigh et al. 2009). However, in the absence of host (i.e. during asymbiotic phase), these germinating hyphae can grow only for a few days. Due to their obligate biotrophic nature and short life span, growth of such asymbiotic hyphae ceases before the spore reserves are depleted; as a result, in view of new germination event, mycelium retract their cytoplasm into spore (Genre 2012) and thus, return to the dormant stage.

Such exploratory hyphal development pattern changes dramatically once the hyphae reach the vicinity of a host root (pre-symbiotic growth phase) and respond to their proximity (Balestrini and Lanfranco 2006; Nasim 2013). As a result, the growth of hyphal germ tube increases substantially and hyphae ramifies intensively through the soil towards the host root (López-Ráez et al. 2012) which suggests that they have perceived something exuded from the root (Harrison 2005). Plant roots release a wide range of compounds, among which *strigolactones* (SL) have been recognized as an important 'rhizospheric plant signals' involved in stimulating the pre-symbiotic growth of AM fungi at different stages, i.e. during spore germination stage and during hyphal growth and branching stage (Fig. 2.1b; Akiyama et al. 2005; Gómez-Roldán et al. 2008; López-Ráez et al. 2012) that enhance the chances of an encounter with the host (Kumar et al. 2015), thus causing successful root colonization by AM fungi. Various studies have validated the relevance of SL in the establishment of AM symbiosis where reduction in the process of mycorrhizal colonization of mutant plants have been observed due to the impairment in SL biosynthesis (Gómez-Roldán et al. 2008; Vogel et al. 2010; Kohlen et al. 2012; López-Ráez and Pozo 2013). SL are present in extremely low concentrations in the root exudates (Akiyama and Hayashi 2006) and their concentration tends to increase under the sub-optimal growth conditions such as limited nutrition, etc., that favour mycorrhizal colonization (Yoneyama et al. 2007; Koltai and Kapulnik 2009). Yoneyama et al. (2012) revealed that biosynthesis and exudation of SL gets boosted under phosphate starvation, a condition that promotes AM colonization. Various studies have authenticated that only the molecules released from the host plant are perceived by the fungus (through a so far uncharacterized receptor) that stimulate hyphal branching in AM fungi, indicating that discrimination between host and non-host occurs at this stage (Harrison 2005; Nasim 2013). These findings clearly signify that the fungus possesses mechanism to perceive active root molecules and to switch on specific transcriptional pathways which induces morphological changes in the fungus and activate its growth (Balestrini and Lanfranco 2006; Nasim 2013). Thus, extensive hyphal branching of AM fungi, as induced under the influence of SL maximizes the chance of contact with host root and that of establishing symbiosis (Akiyama et al. 2005; Aroca et al. 2013; López-Ráez and Pozo 2013). Conversely, when AM fungus starts to proliferate in the vicinity of the root, plants perceive diffusible fungal signals, called *Myc factors* at the plant plasma membrane, due to lysine-motif (LysM) receptor kinases (Antolın-Llovera et al. 2012; Oldroyd 2013) that actively prepares the intracellular environment and induce symbiosis-specific responses in the host root, even in the absence of any physical contact (Parniske 2008; Genre and Bonfante 2010). The chemical structure

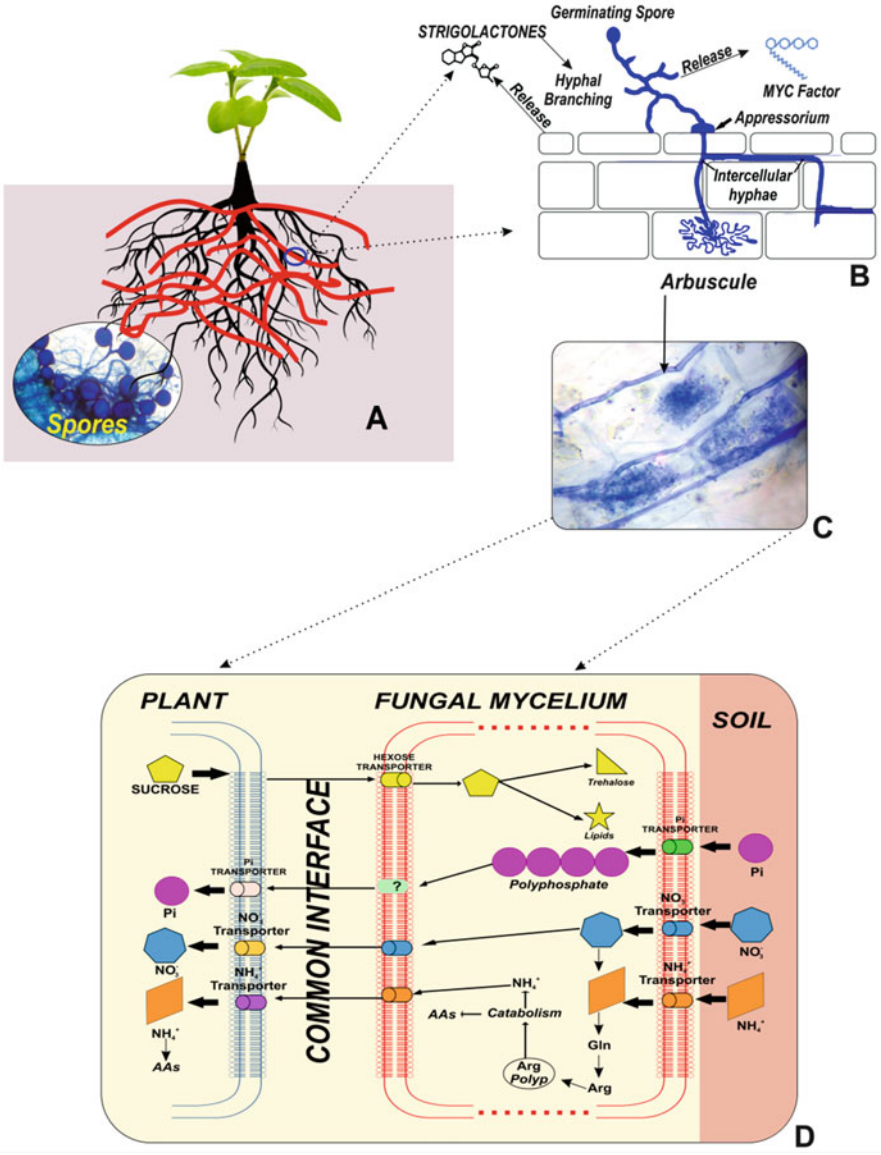

Fig. 2.1 The scheme illustrates (**a**) plant colonized with AM fungi and fungal spores (**b**) Different steps of AM establishment: Roots of host plant exude *strigolactones* which induce spore germination and hyphal branching. In response, fungus releases *Myc* factors that induce calcium oscillations in root epidermal cells and activate plant *SYM* genes, thus leads to the formation of *hyphopodium*, consequently *arbuscule*. (**c**) Arbuscule formation and (**d**) Bidirectional transfer of nutrients (C, P, N) at plant-fungus interface as well as AM fungus-soil interface: At the plant-fungus interface, carbon (C) is imported from plant *via* hexose transporters to the fungal mycelium where it is stored either in the form of trehalose, glycogen and lipids. In return, fungus helps in acquisition of mineral nutrients including phosphorus (P), nitrogen (N). Different forms of N such

of these elusive Myc factors was identified as a mixture of sulphated and non-sulphated lipochito-oligosaccharides (Myc-LCO) that shares structural similarities with rhizobial Nod factors (Maillet et al. 2011). In addition to the up-regulation of genes involved in signal transduction, Myc factors are also known to activate a number of plant responses including stimulation of lateral root development, starch accumulation and repeated calcium oscillation in epidermal cells, in analogy with *Rhizobium*-legume symbiosis (Kosuta et al. 2008; Gutjahr et al. 2009; Maillet et al. 2011; Gutjahr and Parniske 2013; Bonfante and Desirò 2015).

Pre-symbiotic phase is trailed by direct plant–fungus contact i.e. symbiotic phase, which results in the setup of novel developmental and cellular modifications in both partners. Perception of Myc factor induces nuclear Ca^{2+}-spiking that is decoded by a nuclear localized calcium-calmodulin kinase (CCaMK) and leads to phosphorylation of transcription factor—CYCLOPS which in turn cause transcriptional activation of symbiosis-related genes (Genre et al. 2013; Singh et al. 2014; Gutjahr 2014; Carbonnel and Gutjahr 2014). The hyphae of glomeromycetes adheres to atrichoblasts of the root epidermis by forming a highly branched, swollen and flattened characteristic fungal structure called *appressorium* (also called hyphopodium) (Fig. 2.1b; Smith and Read 2008; Genre 2012) which marks the initiation of symbiotic phase of the interaction. Accordingly, root epidermal cells respond to this appressorium formation by repositioning their nucleus and re-modelling their cytoplasm, thus preparing themselves for fungal penetration (Genre et al. 2005). A proline rich protein which is encoded by ENOD11 activates the epidermal cells before, during the formation of pre-penetration apparatus (PPA) and at the late stage of mycorrhizal development and even in the arbuscule-containing cells (Mohanta and Bae 2015). From the appressorium, a penetrating hypha is formed, which reaches the root cortex by following an intracellular route across epidermal cells (Barea et al. 2014). Host cell integrity is maintained by the invagination of its plasma membrane (i.e. peri-arbuscular membrane—PAM) which proliferates and engulfs the developing hypha, physically separating fungus from the plant cytoplasm (Bonfante and Desirò 2015), there by guiding intracellular fungal passage into deeper cortical layers. For this step to be successful, three ion channel genes of *M. truncatula* DMI1 (does not make infection 1), DMI2, and DMI3 are considered essential for the induction of PPA in plants (Siciliano et al. 2007; Genre and Bonfante 2010; Mohanta and Bae 2015). In the inner cortical cells, fungal hyphae ramify repeatedly in order to differentiate into *arbuscules*—the small characteristic tree like structures (Fig. 2.1c) which represents symbiotic interface

Fig. 2.1 (continued) as inorganic as well as organic forms (NH_4^+, NO_3^-) are taken up by specialized transporters located on the fungal membrane in the extraradical mycelium (ERM) where they imported from the symbiotic interface to the host plant cells *via* selective transporters. Pi is taken into fungal ERM through Pi transporters and is converted into polyP which is transported from ERM to IRM where polyp hydrolysis occur, thus releases Pi in the IRM. From IRM, plant take up Pi *via* Pi transporter present at mycorrhizal plasma membrane

where nutrient exchange between fungus and plant is thought to occur (Smith and Read 2008). The proteins encoded by common symbiosis (SYM) genes (CCaMK and CYCLOPS) are also involved in the intracellular fungal accommodation: mutants for SYM genes are not only defective in the signalling pathway (as testified by the lack of nuclear calcium spiking), but also in the assembly of the PPA, thus subsequent fungal colonization (Bonfante and Genre 2010; Genre 2012). In addition, *VAPYRIN* is another gene, which has been reported to be potentially involved in the structural reorganization of infected cells (Gutjahr and Parniske 2013). In case of vapyrin mutants of *Medicago* and *Petunia*, rhizodermal penetration is frequently aborted and in rare cases, where cortical colonization is achieved, no arbuscules or only small hyphal protrusions into cortical cells have been observed (Reddy et al. 2007; Pumplin et al. 2010; Gutjahr and Parniske 2013). Appearance of arbuscule inside the lumen of inner cortical cells hallmarks the establishment of symbiosis between the two partners (Genre 2012). On the basis of morphological attributes, two types of AM associations have been reported which include Arum type colonization and Paris type colonization (Garg and Chandel 2010). In the Arum type, which is particularly common in legumes, and in general in those plants whose root anatomy presents extensive apoplastic channels (Genre 2012), AM fungi form extensive intercellular hyphae in well-developed air spaces between cortical cells and invaginate cells as short side branches to form arbuscules (Shah 2014). Contrastingly, in the Paris type, colonization spreads directly from cell to cell in the root and is characterized by the absence of intercellular hyphae and the development of intracellular hyphal coils that frequently have intercalary arbuscules (Shah 2014). In addition to arbuscules, some fungi also form lipid containing storage structures known as vesicles in the root apoplast (Walker 1995; Rouphael et al. 2015).

As IRM grows, a dense net of ERM is formed simultaneously in the soil (Malbreil et al. 2014) which helps in the acquisition of mineral nutrients from the strata, particularly those nutrients whose ionic forms have poor mobility or are present in low concentration in the soil solution, such as phosphate and ammonia (Barea et al. 2005, 2014). In addition, ERM interacts with other soil micro-organisms and colonizes the root of adjacent plants belonging to the same or different species. Thus, plants and their AM fungi are interconnected through a web of roots and hyphae (Read 1998; Giovannetti et al. 2004) where exchange of water, nutrients as well as signals (Song et al. 2010) occur (Rouphael et al. 2015). Finally, ERM forms new chlamydospores and helps in the propagation of fungus, thus completing the lifecycle. Therefore, establishment of a functional AM symbiosis involves a high degree of coordination between plant and fungus, as characterized by progressive increase in the closeness of the interaction, from the exchange of long-range chemical signals in the rhizosphere to intimate intracellular association, where plant and fungus share a single cell volume (Genre 2012).

2.1.2 AM Fungi Improve Nutrient Dynamics in the Rhizosphere

Nutrient exchange is a key function that takes place at the symbiotic interface, formed in association between the roots of AM fungi and their host plants (Jakobsen and Hammer 2015) and is bidirectional in nature (Fig 2.1d). However, for many of these fungi, the specific mechanisms and gene products involved in nutrient transfer remain to be elucidated (Behie and Bidochka 2014). AM fungi are obligate biotrophs and are unable to absorb carbohydrates; as a result, they depend totally on their green host for organic C metabolism (Bonfante and Desirò 2015). In return, by acting as an extension of root system, thus increasing the plant surface area for absorption, ERM of the fungus provides host plant with access to nutrient resources such as phosphorus (P), nitrogen (N), sulphur (S) and various trace elements beyond the root depletion zone through the agency of IRM, where nutrients are exchanged at the fungus-plant interface for the fixed C (Fig. 2.1d; Marschner and Dell 1994; Smith et al. 2009; Fellbaum et al. 2014; Jakobsen and Hammer 2015). Studies have estimated that host plant transfers up to 20% of its photosynthetically fixed C to the AM fungus (Wright et al. 1998; Valentine et al. 2013; Fellbaum et al. 2014; Bücking and Kafle 2015) which is used to maintain and extend its hyphal network in the soil. However, maintenance of such cooperation has posed a paradox for evolutionary theory as it is hard to explain such kind of interaction where selfish individuals can exploit mutualisms, reaping benefits while paying no costs (Leigh 2010; Fellbaum et al. 2014). Recent studies have revealed that the flow of C to the fungus can be downregulated under sufficient nutrient regimes and that the fungus is also able to control transfer of nutrients to less than beneficial host (Kiers et al. 2011; Maillet et al. 2011; Valentine et al. 2013). Thus, it has been suggested that C to nutrient exchange in mycorrhizal symbiosis is controlled by biological market dynamics and that reciprocal reward mechanisms ensure a 'fair trade' between both the partners involved in AM symbiosis (Kiers et al. 2011; Bücking and Kafle 2015). AM fungi are able to absorb different macro-as well as -micronutrients; however, the likeliness for P uptake is higher when compared with the uptake of other nutrients which could be credited to the production of some enzymes such as phosphatase by the fungi, that enhances the solubility of insoluble P and hence it's absorption by plant (Smith and Read 2008). However, when the concentration of nutrients is higher in the rhizosphere, symbiotic efficiency usually decreases which is due to the presence of nutrient receptors in plant cellular membrane that gets adversely affected (Miransari 2013). Thus, under low and medium nutrient concentrations, the dependency of the host on glomeromycotan fungi increases (Smith and Read 1997; Valentine et al. 2013).

2.1.2.1 Phosphorus Metabolism

P is an important macronutrient that is required for energy pathways and production in plant as well as for the structure of proteins and production of cellular membranes

(Miransari 2013, Bakshi et al. 2017). It is preferentially taken up as orthophosphate (Pi) by plants, but unfortunately, this form occurs at low concentrations in soils, around 10 mM (Bieleski 1973) due to its low solubility and low mobility, leading to a rapid depletion zone around the roots (Malbreil et al. 2014). Improved uptake of P is the main benefit that plants obtain by associating with AM fungi which has been validated through the use of $^{32}P/^{33}P$-based isotope dilution approaches (Barea 2010) and has led to the conclusion that the majority of P taken up by plants comes via the fungal partner (Smith et al. 2009; Smith and Smith 2011, 2012; Barea et al. 2014). In general, plant uses two different pathways to absorb P from the soil: the direct uptake by plant roots (i.e. plant uptake pathway, PP) and the indirect uptake by glomeromycotan fungi (i.e. mycorrhizal pathway, MP). Two different phosphate transporters (PTs) are activated during the uptake of P including the ones which are located in the epidermis and root hairs (i.e. PP) and the fungal hyphal transporters, which are localized with a few centimeters in distance from the plant roots (i.e. MP) (Bücking et al. 2012; Miransari 2013). Due to much smaller diameter than roots, the individual fungal hyphae allow access to narrower soil pores and hence enhance the soil volume explored (Drew et al. 2003; Smith and Read 2008; Smith et al. 2011). The active Pi are taken up into the ERM against a large electrochemical potential gradient, high-affinity PTs and energized by H^+-ATPases (Harrison and van Buuren 1995; Ferrol et al. 2000; Bucher 2007; Javot et al. 2007ab; Smith and Read 2008; Smith and Smith 2011). P, thus absorbed by the fungal hyphae, is then translocated as polyphosphate (polyp, Fig. 2.1d) to the specialized AM fungal-plant interfaces i.e. arbuscules and hyphal coils (Smith et al. 2011) where it gets hydrolysed to free Pi that gets delivered in the apoplast, from where a specialized host plant transporter takes care of importation (Malbreil et al. 2014). Different studies have revealed that mycorrhizal pathway can deliver up to 100% of plant P uptake (Ravnskov and Jakobsen 1995; Smith et al. 2003) thus indicating that the uptake at the root epidermis is very low either due to down-regulation of direct plant PTs (Javot et al. 2007b; Yang et al. 2009; Grønlund et al. 2013) or due to the reduced Pi concentration in the rhizosphere soil solution (Jakobsen and Hammer 2015).

A major breakthrough in mycorrhizal symbiosis was achieved when PT gene was characterized from the ER hyphae of *Glomus versiforme* (GvPT), involved in Pi uptake from soil (Harrison and van Buuren 1995; Smith and Smith 2011; Mohanta and Bae 2015). This Pi gene was induced at the transcriptional level in the presence of lower amount of Pi. Later on, another PT homolog (GmosPT) showing a similar role in Pi transport was reported from *Funneliformis mosseae* (formerly *Glomus mosseae*; Benedetto et al. 2005). Interestingly, a relatively high expression level of the transcript, independent of external Pi concentrations was observed in IR fungal structures (Benedetto et al. 2005) suggesting that the fungus may exert control over the amount of phosphate delivered to the plant inside the root cell (Balestrini and Lanfranco 2006). In addition to PTs, genes encoding alkaline phosphatases have been expressed in *R. irregularis* (formerly *Glomus intraradices*) and *G. margarita* (Tisserant et al. 1993; Aono et al. 2004). In such cases, levels of the corresponding transcripts were found to be higher in

mycorrhizal roots than in germinating spores and external hyphae, thus advocating their role in nutrient exchange with host plants (Aono et al. 2004; Mohanta and Bae 2015). Conversely, on the plant side, PTs operating at the root–soil interface have been reported to be downregulated. As a result, host plant largely depends on the phosphate delivered by the fungal symbiont (Smith et al. 2003). Various studies have highlighted the presence of PTs which are exclusively expressed during symbiosis (Harrison et al. 2002; Paszkowski et al. 2002; Karandashov and Bucher 2005; Balestrini and Lanfranco 2006). In case of *M. truncatula*, plant PT—MtPT4 was found to be located at PAM, where it likely plays an essential role in phosphate transport into the cell (Harrison et al. 2002). However, loss of MtPT4 function led to the premature death of arbuscules in *M. truncatula* plant and fungus was unable to proliferate within the host root and consequently, resulted in the termination of symbiosis (Javot et al. 2007a; Mohanta and Bae 2015). Thus, it could be established that in addition to increase in plant Pi acquisition, mycorrhizal-induced PTs play an important role in maintaining symbiosis by regulating arbuscule morphogenesis (Javot et al. 2011; Yang et al. 2012; Xie et al., 2013; Berruti et al. 2016). At present, accumulating evidence confirms that AM symbiosis specifically induces the expression of plant PTs (Harrison et al. 2002; Paszkowski et al. 2002; Nagy et al. 2005; Xie et al. 2013; Walder et al. 2015; Berruti et al. 2016). These genes include OsPT11 (*Orzya sativa* phosphate transporter11), LePT4 (*Lycopersicon esculentum* PT4), PtPT8 (*Populus trichocarpa* PT8), PtPT10 (*P. trichocarpa* PT10), StPT4 (*Solanum tuberosum* PT4), StPT5 (*S. tuberosum* PT5), LePT4 (*L. esculentum* PT4), PhPT4 (*Petunia hybrid* PT4), PhPT5 (*P. hybrid* PT5), LjPT3 (*Lotus japonicus* PT3), GmPT7 (*G. max* PT7), GmPT11 (*G. max* PT11), GmPT10 (*G. max* PT10), ZmPT6 (*Zea mays* PT6) (as reviewed by Berruti et al. 2016). Recently, Volpe et al. (2016) studied the expression of AM-induced Pi transporters in *M. truncatula* (MtPT4) and *L. japonicus* (LjPT4) and found their expression in the root tips of even non-colonized plants, thereby postulating PT4 genes as novel component of Pi-sensing machinery in the root tips. However, it has been observed that the amount and availability of P in the soil greatly affects its uptake. Under higher P availability, AM fungi may not be able to efficiently colonize host plant roots (due to decreasing arbuscule development), because under such conditions, host plant may not be willing to spend energy for the development of symbiotic association (Miransari 2013). Conversely, under P deficit conditions, fungus is able to colonize the roots of host plant efficiently, thus significantly enhances P uptake by the host plant (Smith and Read 2008).

2.1.2.2 Nitrogen Metabolism

In addition to P, fungal partner also improves the performance of plant partner by providing N nutrient from both inorganic and organic N sources (Hodge et al. 2001; Leigh et al. 2009; Hodge and Fitter 2010; Matsumura et al. 2013; Kranabetter 2014; Corrêa et al. 2015; Mohanta and Bae 2015). In almost all ecosystems, availability of N limits primary productivity (Behie and Bidochka 2014). N bounded in the

organic matter is typically present in the form of peptides, proteins and free amino acids (FAA). AM fungi release peptidases and proteases into the soil that cleave organically bound N and subsequently absorb nitrogenous monomers (Nygren et al. 2007; Behie and Bidochka 2014). According to McFarland et al. (2010), mycorrhizal fungi are able to cater 50% of plant N requirement. When compared with P, N is a more mobile nutrient, hence its uptake by mycorrhizal plant may be of less importance, as N can be supplied to the host plant through mechanisms such as diffusion and mass flow (Miransari 2013). The ability of mycorrhizal fungi to utilize mineral N from organic matter and amino acids has been indicated through different studies (St. John et al. 1983; Hodge et al. 2001; Hamel 2004). However, various factors such as volume of fungal network, amount of decomposing (hydrolytic) enzymes such as xyloglucanase, pectinase, interaction with other soil microbes may affect the ability of fungus to mineralize higher amounts of organic N (Miransari 2013). In addition, by providing P, mycorrhizal fungi also improve N_2-fixation, thus representing a considerable contribution to N inputs in legume species (Azcón and Barea 2010; Barea et al. 2014).

AM fungi have been reported to directly take up and transfer N to their host plants (Bago et al. 1996; Johansen et al. 1993; He et al. 2003), thereby enhancing the utilization of different forms of N such as nitrate (NO_3^-), ammonia (NH_4^+) and urea to plants (Hodge et al. 2001). They easily translocate such different forms of N from ERM (incorporated into amino acids) to the IRM mainly as arginine via respective transporter molecule, where arginine (transported in association with polyP) would be broken down through urease cycle into NH_4^+ and thus, N is transferred to the plant without any C skeleton (Balestrini and Lanfranco 2006; Pérez-Tienda et al. 2011; Malbreil et al. 2014; Mohanta and Bae 2015). This hypothetical pathway was validated by the work of Tian et al. (2010) who demonstrated that during fungal association, arginine in roots of host plant increased threefold and was found to be the most abundant FAA owing to the presence of fungus inside the root. However, the molecular form in which N is transferred, as well as the involved mechanism is still under debate (Mohanta and Bae 2015). NO_3^- is the dominant form of N that is available to plants and fungi in most of the agricultural soils, while NH_4^+ predominates in many undisturbed or very acidic soils, where NO_3^- can be almost entirely absent (Bücking and Kafle 2015). The ERM of AM fungi can take up NH_4^+ (Frey and Schüepp, 1993) and NO_3^- (Hawkins et al. 2000), but NH_4^+ is generally preferred, because it is energetically more efficient than NO_3^-. Moreover, NH_4^+ seems to be the preferred molecule (Guether et al. 2009) as upon root colonization with *G. margarita*, the transcript of LjAMT2 (NH_4^+ transporter) was found to be up-regulated in transcriptome analysis of *L. japonicus*. Moreover, this transcript was found to be extensively expressed in mycorrhizal root, but not in the nodule (Guether et al. 2009). Recently, various transcriptome studies have revealed the expression of several fungal NH_4^+ and NO_3^- transporters in spores, ERM and IRM (Tisserant et al. 2012). Two high-affinity N transporters have been partially characterized in *R. irregularis* where the expression of GintAMT1, an NH_4^+ transporter was induced by low additions of NH_4^+ to the medium but was found to be suppressed under high NH_4^+ supply, thus suggesting

that the expression of this transporter is substrate inducible and is regulated by NH_4^+ supply as well as by fungal NH_4^+ status (López-Pedrosa et al., 2006; Bücking and Kafle 2015). However, under N limiting conditions, NH_4^+ transporter GintAMT2 was found to be constitutively expressed in the ERM (Pérez-Tienda et al. 2011). Thus, such differential localization of high transcript levels of these transporters in colonized roots suggest that both transporters may differ in their role for N uptake and transport (Bücking and Kafle 2015). High expression levels of GintAMT1 in the ERM suggest that this transporter could be primarily involved in NH_4^+acquisition of fungal hyphae from the soil, while, higher expression of GintAMT2 in the IRM signifies the role of this transporter in the re-uptake of NH_4^+ by the fungus from the symbiotic interface (Pérez-Tienda et al. 2011). The ability to transfer N has also been explored in other *Glomus* species, such as in *F. mosseae*, where AMT (GmAMT4.1) was identified during arbuscule development inside roots of *G. max* (López-Pedrosa et al. 2006; Behie and Bidochka 2014). Similarly, in case of *Medicago* mutants, it was demonstrated that in addition to PT, AMT symbiotic transporters (i.e., PT4 and AMT2; 3) did had an influence on the arbuscule lifespan (Javot et al. 2007b; Breuillin-Sessoms et al. 2015), thus speculating that the transport of Pi or NH_4^+ through these transporters not only deliver nutrients to the host root cells but also trigger signalling that enable the conditions for arbuscule maintenance (Breuillin-Sessoms et al. 2015; Berruti et al. 2016). To be further assimilated *via* glutamine synthetase/glutamate synthase (GS/GOGAT) cycle (Marzluf 1996), NO_3^- has to be converted into NH_4^+ by the sequential action of enzymes—nitrate reductase (NR) and nitrite reductase (NiR). One transcript for NR and two for NiR were identified in *R. irregularis*, all of which got expressed in ERM (Malbreil et al. 2014). Furthermore, transcripts coding for proteins that are involved in further steps to synthesize arginine were identified and were found to be highly expressed in germinating spores, ERM and IRM, thus confirming intense N cycling in this fungus (Tian et al. 2010; Tisserant et al. 2012).

In addition, plants that accommodate fungal translocation of N were found to upregulate N transporters. Plant NH_4^+ transporters were found to be upregulated in arbuscule-containing cells in case of sorghum (*S. bicolor*), where expression of plant NH_4^+ transporters—SbAMT3; 1 and SbAMT4 was induced only in arbuscule-containing cells (Koegel et al. 2013). Similarly, in case of *M. truncatula*, NO_3^- transporters were expressed in arbusculated cells (Gaude et al. 2012; Behie and Bidochka 2014). Such coordinated and specific expression of both plant and fungal $NH_4^+$and NO_3^- transporters in mycorrhizal-colonized cortical cells intimate the crucial importance of fungal N transfer in plants (Behie and Bidochka 2014).

2.1.2.3 Sugar Metabolism

Carbon flux is mainly mediated from plant to the fungus as mycorrhizal fungi are incapable of breaking down complex organic compounds (Behie and Bidochka 2014) and thus, depends upon the host plant for C. Mycorrhizal fungi require C for extension of ERM, for active uptake or other energy consuming processes and for

the development of new infection units (Bücking et al. 2012). Moreover, it has been validated that supply of C by the host plant stimulates P uptake and its transfer by AM fungi (Kiers et al. 2011; Hammer et al. 2011; Bücking et al. 2012). Earlier, it was shown that C is mainly delivered by the host plant in the form of hexoses, preferentially as glucose (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Pfeffer et al. 1999; Malbreil et al. 2014) or in the form of sucrose into the apoplast, where it is converted into hexoses by acid invertase, secreted by host plant (Schaarschmidt et al. 2006) as fungus lacks the ability to secrete this enzyme (Tisserant et al. 2013). Hexoses are then transferred to the mycorrhizal fungi *via* fungal transporters that function at several symbiotic root locations (Schüβler et al. 2006; Helber et al. 2011; Mohanta and Bae 2015). In *Glomus* species, a high-affinity monosaccharide transporter (MST)—MST2 has been characterized by Bücking and Shachar-Hill (2005) whose expression pattern correlates with that of the mycorrhizal PT–PT4. Various studies have revealed that when expression of PT4 is reduced, symbiosis gets strongly impaired, resulting in malformed arbuscules, however, when incorporated, hexoses are then converted into trehalose, glycogen and lipids (Shachar-Hill et al. 1995; Pfeffer et al. 1999; Bago et al. 2000), thus signifying the fact that the amount of C received by the fungal symbiont is directly interrelated to the phosphate transfer efficiency. Moreover, many MST have been isolated and identified from different fungal species such as one MST from *G. pyriformis* (Schüβler et al. 2006), 3 MSTs as well as a sucrose transporter from *R. irregularis* (Helber et al. 2011). Triacylglycerol (TAG) is the main form of C stored by the mycobiont at all stages of its life cycle (Bago et al. 2003) which is mostly or exclusively made in IRM and gets transferred to ERM (Pfeffer et al. 1999). In vivo microscopic observations suggests that the rate of export is sufficient to account for the high levels of stored lipid in ERM (Bago et al. 2002, 2003) where glyoxylate cycle operates (Lammers et al. 2001) and converts exported TAG to carbohydrate. Trehalose and glycogen synthases were found to be present in the transcript collection of *R. irregularis* by the authors (Tisserant et al. 2012, 2013). C, thus formed in ERM, is finally used for the production of the chitinous cell wall (Lanfranco et al. 1999), for storing lipids and glycogen in the developing spores (Bonfante et al. 1994) and for long-lasting proteins like glomalin (Purin and Rillig 2007).

During the symbiotic phase, C metabolism of both the symbiotic partners get reformed at the level of gene expression (Balestrini and Lanfranco 2006). In AM-colonized roots, sucrose synthase gene was found to be up-regulated by Ravnskov et al. (2003) suggesting that the enzyme sucrose synthase plays a major role in generating sink strength (Mohanta and Bae 2015). In addition, mycorrhizal colonization has been reported to elevate the expression levels of plant sugar transporters. For instance, in the symbiotic interaction between *M. truncatula* and *R. irregularis*, increased expression of MtSucS1, a plant sucrose synthase gene, has been recorded in the surrounding internal hyphae and arbuscules (Behie et al. 2012). Besides, the expression of a family of *M. truncatula* sucrose transporters—MtSUTs increased in mycorrhizal-colonized roots. Currently, it is not possible to unravel which partner takes the first step to establish the mutualistic

C–P exchange (Smith and Smith 2012; Jakobsen and Hammer 2015). However, it has been proposed that fungus might be able to use plant cell wall sugars (Helber et al. 2011), while P reserves in spore of AM fungi could serve as signals during early colonization (Hammer et al. 2011).

2.1.2.4 Sulphur Metabolism

Sulphur (S) is an essential macronutrient required for plant growth, development and response to various abiotic and biotic stresses as it plays as key role in the biosynthesis of many S-containing compounds. Sulphate represent a very small portion of soil S pull and is the only form that plant roots can uptake and mobilize through H^+-dependent co-transport processes, thereby implying the role of sulphate transporters (Casieri et al. 2012; Miransari 2013). In contrast to the other organically bound forms of S, sulphate is commonly leached from soils due to its solubility in water, thus reducing its availability to plants (Eriksen and Askegaard 2000; Casieri et al. 2012). During mycorrhizal interactions, by altering the expression of plant sulphate transporters (Casieri et al. 2012; Giovannetti et al. 2014), fungal symbiont plays an important role in the uptake of S, thereby improving S nutritional status of the host plant (Allen and Shachar-Hill 2009; Casieri et al. 2012; Sieh et al. 2013; Berruti et al. 2016). In order to understand the beneficial role of mycorrhizal interaction on *M. truncatula* plants colonized with *R. irregularis* at different sulphate concentrations, Casieri et al. (2012) analyzed the expression of genes encoding putative *Medicago* sulphate transporters (MtSULTRs) and revealed that mycorrhizal symbiosis substantially increased the rate of plant S absorption. Moreover, in silico analyses they identified and recognized eight MtSULTRs, some of which were expressed in plant leaf and root at different S concentrations, thus demonstrated the role of AM fungi on S uptake by the host plant. Recently, a sulphate transporter (A group 1 sulfate transporter, LjSultr1; 2) specifically involved in the uptake of S from arbuscules has been identified in *L. japonicus* (Giovannetti et al. 2014). However, in contrast to PTs, a single gene LjSultr1; 2, seems to mediate both direct and symbiotic pathways of S uptake in *L. japonicus*. On the contrary, the efficiency of S uptake in plant roots was directly correlated with phosphate availability, as transfer of S increased only when the phosphate content of the soil was low (Sieh et al. 2013; Behie and Bidochka 2014). In addition, the effects of mycorrhizal colonization on the S uptake by the host plant could also be explained on the basis of higher production of root exudates, increased activity of other soil microbes such as *Thiobacillus*, formation of extensive hyphal network and production of different enzymes, which may acidify the rhizosphere and hence increase the availability of S to the host plant (Miransari 2013).

2.1.2.5 Other Macro-as Well as Micro-nutrient Metabolism

Apart from P, N and S, mycorrhizal fungi are able to increase the uptake of different macro-as well as-micro nutrients including potassium (K), magnesium (Mg),

calcium (Ca), zinc (Zn), copper (Cu) and iron (Fe) under various environmental conditions. AM fungi develop an extensive network of hyphae that reaches into the even finest soil pores producing different enzymes such as phosphatases, which enhances the solubility of nutrients and hence their subsequent uptake by the host plant (Miransari 2013). In addition, enhanced uptake of water and plant growth, with a larger root medium, as observed under mycorrhization substantially increases the rate of nutrient uptake (Smith and Read 2008). In a split-plot experiment performed under field conditions, mycorrhizal fungi *R. irregularis* improved the uptake of different nutrients including K, Mg and Ca in tomato (*L. esculentum*; Cimen et al. 2010; Miransari 2013). Furthermore, several authors have reported up-regulation of a plant K^+ transporter in mycorrhizal roots of *L. japonicus* (Guether et al. 2009; Berruti et al. 2016).

In case of micronutrients, AM fungi help plant in two ways: (1) they help in the uptake of these elements which are considered to be relatively immobile, and (2) take up these elements and store them so as to prevent their concentrations to reach toxic levels (Goltapeh et al. 2008). AM fungi mobilize such micronutrients either by producing different enzymes or by interacting positively with the other soil microbes or by modifying plant rhizosphere or by affecting the morphology (i.e. root growth) and physiology of the host plant, thus affecting the production of root exudates (Miransari 2013). In one of the studies, Zaefarian et al. (2011) demonstrated the beneficial effects of different fungal species including *F. mosseae*, *G. etunicatum* and *R. irregularis* (as single treatments) and the combined treatment of *F. mosseae*, *Gigaspora hartiga* and *G. fasciculatum* on the uptake of N, P, K, Fe, Zn and Cu. In addition, two meta-analysis studies have been published recently, focusing on the contribution of mycorrhizal symbiosis to different micro-nutrient concentrations in crops (Lehmann et al. 2014; Lehmann and Rillig 2015; as reviewed by Berruti et al. 2016). According to Lehmann et al. (2014), factors such as soil texture, pH and soil nutrient concentration (i.e., Zn and Pi deficiency) influence AM-mediated Zn content in different plant tissues.

2.1.2.6 Lipid Metabolism

Glomeromycetes can be certified as 'oleogenic' fungi as approximately 25% of their dry weight consists of lipids (Bago et al. 2002; Malbreil et al. 2014). Several experiments have revealed that lipid metabolism has an unexpected and specific regulation mechanism: C is obtained from plants as hexose but mainly stored as TAG (a compact form of C storage, allowing long-distance translocation) in hyphae and more particularly in spores (Malbreil et al. 2014) and is needed when required. Various labelling experiments have disclosed that synthesis of palmitic acid (the first produced in fatty acid synthesis and precursor to longer ones) takes place in only in IRM and is used in IRM, ERM or germinating spores (Pfeffer et al. 1999; Trépanier et al. 2005). Moreover, through their study, Tisserant et al. (2012) revealed that all the genes involved in the synthesis of fatty acids are present in *R. irregularis* and the fungus did not rely on the host plant to obtain them. However,

it is not probable and might imply regulation at post-transcriptional level. Several genes related to fatty acid metabolism such as desaturase and lipase were found to be upregulated (five- and fourfold changes, respectively), out which, only 7% that belongs to lipid transport and metabolism were found to be upregulated *in planta* (Tisserant et al. 2013; Malbreil et al. 2014).

2.2 Conclusion and Future Prospects

From the above facts, it could be concluded that AM fungi are able to form effective symbiosis with host and act as an active bridge between the soil and the plant, thereby improving nutrient dynamics in the soil ecosystem. However, there is a paucity of information regarding the mechanisms that regulate the production of signal molecules under different environmental conditions. Moreover, the data regarding exchange of resources between the two symbionts, summarized in this chapter is largely based on trials with root organ cultures or with single plants that have been colonized by single AM species. Thus, in order to have a better insight about the dynamics of AM signalling as well as nutrient exchange between the symbionts, further research needs to be conducted under natural field conditions where multiple trading partners operate simultaneously. The information, thus generated could probably be used in developing new green technologies that might play an important role in sustainable agriculture.

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