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REVIEW

Role of Arbuscular Mycorrhizal Fungi in Biological Nitrogen Fixation and Nitrogen Transfer from Legume to Companion Species

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The production of food crops in sustainable agriculture demands the use of renewable resources, which include the potential role of arbuscular mycorrhiza fungi (AMF) and Biological Nitrogen Fixation (BNF) for supplying nitrogen (N) for crops. Associative action of AMF in legumes has a great impact on root, shoot development and phosphorous uptake which results in the enhancement of nodulation and nitrogen fixation. Biological nitrogen fixing crops can contribute N to the neighbouring crops by N transfer. N compounds (NH_4^+, NO_3^-, amino acids, ureides, peptides and proteins) released from nodulated roots, decomposed legume debris, or root exudates to soil solution are absorbed by AM hyphae as the first direct pathway of N transfer. Absorbed N by AMF is translocated as NH_4^+, amino acids, and peptides from fungal cell to neighbouring plant cells. This transfer could involve NH_4^+ and NO_3^- transporters, amino acid permeases and peptide transporters. Plants could be interconnected by mycorrhizal mycelia to form common AM networks that provide the another direct pathways for N transfer from one plant to another. Although the relatively small role of common AM networks in N transfer, the overall AMF contributions to N transfer are considered to be of great importance for legume and non-legume intercropping systems in sustainable agriculture.

Key words: arbuscular mycorrhizal fungi, BNF, nitrogen transfer

N_2, the most abundant, comprising 78% of the atmosphere, is not readily available to plants. Plants have developed multiple solutions to associate with diazotrophs in order to acquire atmospheric nitrogen. Diazotrophs are found in a wide variety of habitats: free-living in soil and water, associative symbioses with grasses, actinorhizal association with woody plants, cyanobacterial symbioses with various plants, and root-nodule symbioses with legumes (Dixon and Kahn, 2004). Symbiotic nitrogen fixers are divided in two main groups: root-nodule bacteria and plant growth-promoting rhizobacteria (Mus *et al.*, 2016). All organisms use the ammonia (NH_3) to manufacture amino acids, proteins, nucleic acids and other nitrogen-containing components necessary for life. N_2, which occurs in the atmosphere and released through decomposition of organic material, is converted to NH_3 by the Biological Nitrogen Fixation (BNF) which is considered as a fundamental process for maintaining soil fertility and the continued productivity of low-input cropping systems. However, the plant must supply the necessary nutrients and a significant amount of energy in the form of photosynthate that enables the bacteria to fix atmospheric N. When the plant nutrition (especially phosphorus, potassium, zinc, iron, molybdenum and cobalt) is improved, the legume responds indirectly to the increased nitrogen nutrition resulting from enhanced nitrogen fixation. In sustainable agriculture, poor plant nutrition can be corrected by the inoculation with arbuscular mycorrhizal fungi (AMF).

AMF colonize the roots of many agriculturally important food and bioenergy crops and could serve as ‘biofertilizers’ in environmentally sustainable agriculture (Bücking *et al.*, 2012). AMF is considered to be of great importance in promoting nutrient uptake through mycelium extension outside the rhizosphere, and enlarging the area that roots have to absorb water and nutrients (Tobar *et al.*, 1994; He *et al.*, 2003; Jia *et al.*, 2004; Shockley *et al.*, 2004).

Most herbaceous legumes of family *Papillionaceae* are symbiotic with nitrogen-fixing rhizobia and AMF (Javaid, 2010). Legume nodulation and BNF were enhanced when legume roots were infected by AMF (Brown and Bethlenfalvay, 1988), and AM colonization rate was enhanced in rhizobia-inoculated legume (Sanginga *et al.*, 1999). Besides satisfying their own N needs, legumes can facilitate N acquisition of neighbouring plant species (Pirhofer-Walzl *et al.*, 2012). The N transfer in intercropping systems is assumed to be enhanced if N fixation by legumes can be improved by inoculation with AMF and rhizobium (Meng *et al.*, 2015).

The direct transfer of N from one plant to another by AMF mycelium could reduce the loss of N in the soil (leaching and immobilization), and also could improve the N cycling and the growth of neighboring plant. Therefore, the present review addresses current knowledge on the role of AMF in symbiotic N fixation and N fixed transport to the associated plant.

AMF symbiosis and rhizobia nodulation

Mycorrhizas are highly evolved mutualistic associations between soil fungi and plant roots (Smith and Read, 2008; Bonfante and Anca, 2009). Based on the morphological characteristics, mycorrhizae are grouped into six types: ectomycorrhiza, arbuscular mycorrhiza, arbutoid, ericoid, monotropoid and orchid (Brundrett, 2002, 2009; Smith and Read, 2008). Arbuscular mycorrhizal fungi (AMF) are obligate symbionts which form mutualistic symbioses with about 80% of land plant species (Smith and Read, 2008), including almost all species of agronomic interest and pastoral and tropical forest (Bonfante and Genre, 2008). The AM hyphae penetrate the root cortical cells and form specific ‘little tree-shaped’ fungal structures called arbuscules in the cortex (**Fig.1**). The AMF also form vesicles, which are membrane-bound organelles of varying shapes, inside or outside the cortical cells.

Symbiotic nitrogen fixers are divided in two main groups: root-nodule bacteria and plant growth-promoting rhizobacteria (Mus *et al.*, 2016). Root-nodule bacteria include rhizobia and *Frankia*. Rhizobia, classified into alpha- and beta-proteobacteria (Bomfeti *et al.*, 2011), enter into a symbiotic association with legumes. Rhizobia are known to be free-living bacteria, that are able to live in the soil. When an appropriate host crop is planted in the soil, rhizobia get entrapped within a curled root hair, penetrate the host cells and the final step involves the differentiation of rhizobium into N_2-fixing bacteroids housed in the cells of the nodule (**Figure 1**).

Many of the genes that encode for signal transduction and regulate the establishment of the N_2 fixation symbiosis in plant roots are the same genes that encode for and regulate the AMF symbiosis, which may make the AMF symbiosis inherently more common in N_2 fixers (Antunes *et al.*, 2006; Javaid, 2010). In both symbiosis, the two partners engage in a complex molecular conversation that allows AMF and rhizobia to infect the plant cells and entice the cells to undergo the developmental changes necessary for establishing the symbioses (Manchanda and Garg, 2007**)**. Although AMF and rhizobia colonize root tissues intracellularly during the symbioses, they stay separated from the plant cytoplasm by highly specialized perisymbiotic membranes (Provorov *et al.*, 2002). Across these membranes surrounding bacteroids (Day *et al.*, 2001) and arbuscules (Gianinazzi-Pearson, 1996, Harrison, 1999, Parniske, 2000), the nutrient exchange takes place between microbes and the plant .

In the AMF-Rhizobium association, the mycorrhizal mycelia may increase the absorption and translocation of nutrients (especially P) through the network to rhizobium located on plant nodules. Rhizobium fix nitrogen and provide it in the form of ammonia to the plant, which, in turn, provides carbohydrate to microsymbionts (Silveira *et al.*, 2001). These three processes are interdependent or even tightly coupled: while the rate of photosynthesis is influenced by the rates of N and P supply, the rate of N_2-fixation is influenced by the rates of photosynthate and P supply to the nodules (Jia *et al.*, 2004). However, the effectiveness of co-inoculation depends on the compatibility between interacting partners in the rhizosphere that varies greatly with physicochemical characteristics of soil, test microorganisms, plant genotypes, and substances exuded from host plant species (Javaid, 2010). Bacterial and AMF compatibility can alter symbiotic efficiency because the combination of AMF and bacterial strains can either reduce or increase efficiency in certain bacterial strains (Bonfante and Anca, 2009). Some strains of bacteria can positively influence symbiosis with AMF (Frey-Klett *et al.*, 2007). For example, Xie *et al.* (1995) demonstrated that the nodulation factors produced by *Bradyrhizobium japonicum* strain increasde by 4.5-fold the arbuscular mycorrhizal colonization in soybean roots. This phenomenon could be due to the similar signaling systems that regulated the symbiotic association of rhizobia and AMF with plant roots (Gianinazzi-Pearson and Gianinazzi, 1989; Tsai and Phillips, 1991; Xie *et al.*, 1995).

N_2 fixation

Most herbaceous legumes of family *Papillionaceae* are symbiotic with nitrogen-fixing rhizobia and AMF (Javaid, 2010). Numerous studies have clearly indicated that AM symbiosis can greatly assist nodulation and N_2 fixation of numerous legumes, e.g. soybean (Hamel *et al.*, 1991a; Antunes *et al.*, 2006) black locust (Olesniewicz and Thomas, 1999), pigeon pea (Stephen *et al.*, 2013), and mung bean (Li *et al.*, 2009). Also, the N derived from N_2 fixation at harvest was greatly increased in the mycorrhizal faba bean (Qiao *et al.*, 2015). The effective AMF can enhance the performance of rhizobial infection (Tavasolee *et al.*, 2011) and affect N_2 fixation in legumes by increasing the numbers of nodules, nitrogenase activity, the leghaemoglobin content of nodules, and shoot biomass (Hodge, 2003; Garg and Chandel, 2011; Abd-Alla *et al.*, 2014).

The improved formation of arbuscular mycorrhizas increased nodulation by 54% in mung bean (Li *et al.*, 2009) and N_2 fixation by 55% in soybean (Hamel *et al.*, 1991a). The number and dry weight of nodules also significantly increased in mungbean inoculated with AMF (Xiao *et al.*, 2010). Hawkins et al. (2000); Barea *et al.* (2002) reported that the activities of N_2-fixing rhizobia with AMF increase the N_2 fixation of pigeon pea.

The effect of dual inoculation of roots with AMF and Rhizobium on N_2 fixation has been established in soybean (Bethlenfalvay *et al.*, 1990; Meng *et al.*, 2015), cowpea (Islam *et al.*, 1990; Lima *et al.*, 2011), and pea (Xavier and Germida, 2003; Stancheva *et al.*, 2006). Dual inoculation with *Rhizobium* and *Glomus fasciculatum* increased the nodule nitrogenase activity by 36-213% in *Acacia mellifera* (Lalitha *et al.*, 2011).

Under low N fertilizer inputs, soil P availability is usually the major factor limiting the rate of N_2 fixation in legume crops (Toro *et al.*, 1998). AMF can promote nutrient uptake through mycelium extension outside the rhizosphere, and enlarging the area that roots have to absorb water and nutrients (Tobar *et al.*, 1994; He *et al.*, 2003; Jia et al., 2004; Shockley *et al.*, 2004).

The role of AMF as P suppliers to legume root nodules is of great relevance for effective nodulation and N_2 fixation (Azcón *et al.*, 1991; Albrecht *et al.*, 1999; Requena *et al.*, 2001) under low soil P concentration (Barea *et al.*, 1989; Li *et al.*, 2009), at least during the early stages of the Rhizobium-legume interaction (Patterson *et al.*, 1990). The synergistic effect between AMF and rhizobia symbionts is evident from the P concentration in the nodules, which is up to three times higher than in other organs (Vadez *et al.*, 1997).

In addition to P, AMF support nitrogen fixation by providing legumes with other immobile nutrients that are essential for N fixation, such as copper and zinc (Clark and Zeto, 2000). The availability of trace metals may be critical for the nitrogen fixation. For example, iron, sulfur and molybdenum are an essential components of rhizobia nitrogenases that fixes atmospheric nitrogen in the nodules (Thorneley, 1992). Thus, enhanced plant uptake of Zn, Cu and Mo due to AMF could also promote the effectiveness of rhizobia, accelerating N_2 fixation and further promoting plant growth (Wilson and Hartnett, 1998). Mycorrhizal colonization may also alter root exudation, which could enhance the competitiveness of rhizobia and promote nodulation, thus enhancing N_2 fixation and plant growth (Javaid, 2010).

Although AMF colonize the root nodules (Baird and Caruso, 1994; Vidal-Dominguez *et al.,* 1994; Scheublin Van Der Heijden, 2006), AMF-colonized nodules did not fix N_2 (Scheublin van Der Heijden, 2006), indicating that AMF don’t deliver nutrients that are essential for N_2 fixation directly into the nodules. The extent of AMF effect on nodulation and nitrogen fixation in legumes, depends on the specific symbiont combination (Clark and Zeto, 2000), AMF species (Valdenegro *et al.*, 2001) and AM inoculants density (Azcón and El-Atrash, 1997). Wahbi *et al.* (2016) found that the total N fixed by faba bean was 27% significantly higher at the maximal mycorrhizal density compared with low inoculant and control treatments. Briefly, AMF by increasing P and other nutrients absorption, enhancing photosynthesis, beneficial interaction with rhizospheric microorganisms, and alleviation of environmental stresses improve N_2 fixation, growth and grain yield of legumes (Azcón and El-Atrash, 1997; Siviero *et al.*, 2008; Javaid, 2010).

Nitrogen transfer

Besides satisfying their own N needs, legumes can facilitate N acquisition of neighbouring plant species (Pirhofer-Walzl *et al.*, 2012). The process of N deposition from one plant and subsequent uptake by another plant is termed N transfer (Jensen, 1996). Nitrogen transfer from one plant to another is of fundamental importance in N_2-fixing plant-based agricultural and natural ecosystems (Fujita *et al.*, 1992; Chalk, 1998; Forrester *et al.*, 2006). Non-N_2-fixing species have often been found to have better growth and yields when associated with N_2-fixing legume species (Fujita *et al.*, 1992; Ledgard and Steele, 1992). This trend is primarily caused by the transfer of a substantial amount of symbiotically fixed N in different communities including N_2-fixing and non-N_2 fixing plants (Chu *et al.*, 2004; Frankow-Lindberg and Dahlin, 2013; Jamont *et al.*, 2013).

Many researchers suggested that there were two pathways for fixed N transfer from legume to non-legume. An indirect transfer through N release from nodulated roots of the legume (Høgh-Jensen and Schjoerring, 2001; Paynel *et al.*, 2008; Mahieu *et al.*, 2014); and through the decay of aboveground litter or belowground organs (roots, nodules) (Johansen and Jensen, 1996). A direct transfer through AM hyphae followed by translocation (Smith and Read, 1997; Chu *et al.*, 2004; Bücking and Kafle, 2015); and through common AM networks that interconnect roots of legumes and non-legume plants (Smith and Read, 1997; Sierra and Nygren, 2006; He *et al.*, 2009; Mahieu *et al.*, 2014).

Several studies have shown the transfer of nitrogen from nitrogen fixers to the soil, for example Brophy and Heichel (1989) reported that alfalfa released 4.5% of symbiotically-fixed N into the root zone over its growth period. Laidlaw *et al.* (1996) found that the clover transfers 8 mg N/m^2/day to the soil. For Paynel and

Cliquet (2003), N compound exudation by legume followed by uptake by companion grass is a highly significant pathway for inter-specific N transfer between young plants.

Other studies have shown substantial transfers of fixed N from legumes to non-N_2-fixing crops through AM hyphae and common AM networks, under controlled or field conditions (He *et al.*, 2003, 2009; Chalk *et al.*, 2014; Meng *et al.*, 2015) (**Table 1**). Higher N transfer from soybean to corn was found only in mycorrhizally-inoculated plots and *G. versiforme* increased the efficiency of ^{15}N transfer from the labeled soybean plants to corn by 45% (Hamel and Smith, 1992). Mårtensson *et al.* (1998) showed that 3 to 50% of N in the chicory were transferred from pea and 20 to 34% of N in the chicory roots were transferred from red clover, with variation between used AMF isolates. Chu *et al.*, (2004) had reported that N transferred was between 6 and 13% from groundnut to rice and N could transfer along the gradient of concentration via mycorrhizal hyphae. The study of Wahbi *et al.* (2016) showed that 32-50% of fixed N were transferred from faba bean to wheat using *Rhizophagus irregularis*.

N transfers of approximately 5% through common AM networks have been reported in a white clover /ryegrass association that was inoculated with *Glomus mosseae* (Haystead *et al.*, 1988) and from berseem to maize using *Glomus intraradices* (Frey and Schuepp, 1992, 1993). 15% of N was transferred via common AM networks from pea to barley using *Glomus intraradices* (Johansen and Jensen, 1996) and 16.1% from mung bean rice using *Glomus caledonium* (Li *et al.* 2009). Martins and Cruz (1998) reported that transfer of ^{15}N mediated by AMF mycelium network, was 9.6%, from cowpea to maize plants. Moyer-Henry et al (2006) reported that transfer of N was generally very low in non-AM weed species and that N transfer occurs primarily through mycorrhizal hyphal networks. Nitrogen gradients between N-rich donors and N-limited receivers may be a driving force for unidirectional N transfers via common AM networks (Bethlenfalvay *et al.*, 1991; Frey and Schuepp, 1993).

The N transfer is assumed to be enhanced if N_2 fixation by legumes can be improved by inoculation with AMF and rhizobium (Meng *et al.*, 2015). The effect of AMF on soil microbial populations may be an important factor affecting N transfer between mycorrhizal plants (Hamel *et al.*, 1991b). Also, AMF pathway of N transfer is effected by the hyphal density or AM inoculation rates, for example, Wahbi *et al.* (2016) reported that a higher density of mycorrhizae favours N uptake by AM hyphae through vertical translocation at the expense of the lateral transfer of fixed N through common mycorrhizal networks.

Several studies showed that ammonium, amino acids, ureides, peptides and proteins have been identified in exudates of legumes (Brophy and Heichel, 1989, Murray *et al.*, 1995). AMF can modify the quality and the quantity of host root exudates (Azaizeh *et al.*, 1995) and are able to transfer substantial N to their host plant from organic N sources from the soil material (Leigh *et al.*, 2009). Kähkölä *et al.* (2012) found that AMF inoculation of cacao saplings improved N uptake from *Inga edulis* leaf litter by 0.5% and root litter by 5%.

AMF can take up free amino acids which can represent an important N source in soils, for example, aspartic acid, serine (Cliquet *et al.*, 1997), glycine, glutamic acid (Hawkins *et al.*, 2000; Whiteside *et al.*, 2012), glutamine (Breuninger *et al.*, 2004), cysteine or methionine (Allen and Shachar-Hill, 2009). Some amino acids are also taken up by germinating spores during the presymbiotic growth stage of the fungus (Gachomo *et al.*, 2009).

Ammonia formed by the Biological Nitrogen Fixation is converted by oxidation or reduction to NO_3^- and NH_4^+ respectively, which are available to plants (Zahran, 1999). Transfer of NH_4^+ or NO_3^- by AMF between N_2-fixing plants and non-N_2-fixing plants has been reported (Bethlenfalvay *et al.*, 1991; Frey and Schuepp, 1993; Johansen and Jensen, 1996; Moyer-Henry *et al.*, 2006). However, a clear preference for NH_4^+ is at least partly explained by the extra energy the fungus has to spend to reduce NO_3^- to NH_4^+ before it can be incorporated into organic compounds (Marzluf, 1997). The inorganic nitrogen taken up by the fungus outside the roots is incorporated into amino acids, translocated from the extraradical to the intraradical mycelium as arginine (Govindarajulu *et al.*, 2005). Molecular evidence for N uptake by AMF was obtained through the characterization of an ammonium transporter (AMT) (Lopez-Pedrosa *et al.*, 2006; Guether *et al.*, 2009). Two putative ammonium transporters were identified; one was induced in non-colonized cortical cells, and the other in arbusculated cells (Gaude *et al.*, 2012) (**Figure 2**). AMF can obtain substantial amounts of organic N, in particular amino acids, whereas that 3% of plant N comes from organic material (Hodge and Fitter, 2010). High levels of certain amino acids (Glutamic Acid, Aspartic Acid, Asparagine) was reported in mycorrhized roots (Schliemann *et al.*, 2008). The N uptake could involve, among other transporters, amino acid permeases (AAP) and peptide transporters that belong either to the di- and tripeptide transporter (PTR) family, also named proton-coupled oligopeptide transporter family (POT; Paulsen and Skurray, 1994), or to the oligopeptide transporter (OPT) family, which transports larger peptides (Hauser *et al.*, 2001).

Several studies showed that the transfer of symbiotically fixed N between N_2-fixing plants and non-N_2-fixing plants through AMF improved the growth of the receiver plant by the net N gains (Johansen and Jensen, 1996; Moyer-Henry *et al.*, 2006). Recently, Meng *et al.*, 2015 reported that inoculation with both AMF and rhizobium promoted N transfer from soybean to maize, resulting in the improvement of yield advantages of legume/non-legume intercropping.

Table 1: Transfer of N from legume to non-legume plant via AMF hyphae or common mycorrhizal networks.

Legume	**Non-legume**	**inoculum**	**N**transfer **%**	**Reference**
Mung bean (*Vigna radiata*)	Rice (Oriza sativa)	*G. caledonium*	16.1	Li *et al.*, 2009
Pea *(Pisum sativum*) Red clover (*Trifolium pretense*)	Chicory (Cichorium intybus)	*8AMF isolates*	3-50 20-34	Mårtensson *et al.* (1998)
Groundnut (*Arachis villosulicarpa*)	Rice (Oriza sativa)	Glomus sp.	6-13	Chu *et al.*, 2004
Faba bean (*Vicia faba*)	wheat (Triticum turgidum)	*Rhizophagus irregularis*	32-50	Wahbi *et al.*, 2016
Soybean (*Glycine max*)	non-nodulated Soybean Sorghum (*Sorghum bicolor*) Maize (*Zea mays*) Maize (*Zea mays*) Maize (*Zea mays*)	Field soil +roots *G. mosseae* *G. versiforme* 3*Glomus* sp. *G. mosseae*	48 22.5 45 ~5.0 -	Moyer -Henry *et al.*, 2006 He, 2002 Hamel & Smith, 1992 Hamel *et al.*, 1991a,b Bethlenfalvay *et al.*, 1991
Bur clover (*Medicago polymorpha*)	Grapevine (Vitis vinifera)	Field soil +roots	5.5	Cheng & Baumgartner, 2004
Pea (*Pisum sativum*)	Barley (Hordium vulgare)	*G. intraradices*	15	Johansen & Jensen, 1996
Berseem (*Trifolium alexandrinum*)	Maize (Zea mays)	*G. intraradices*	4.7	Frey & Schuepp, 1992, 1993
White clover (*Trifolium repens*)	Ryegrass (Lolium perenne)	*G. mosseae*	~5	Haystead *et al.*, 1988
Cowpea (*Vigna unguiculata*)	Maize (Zea mays)	*G. etunicatum*	9.6	Martins & Cruz, 1998

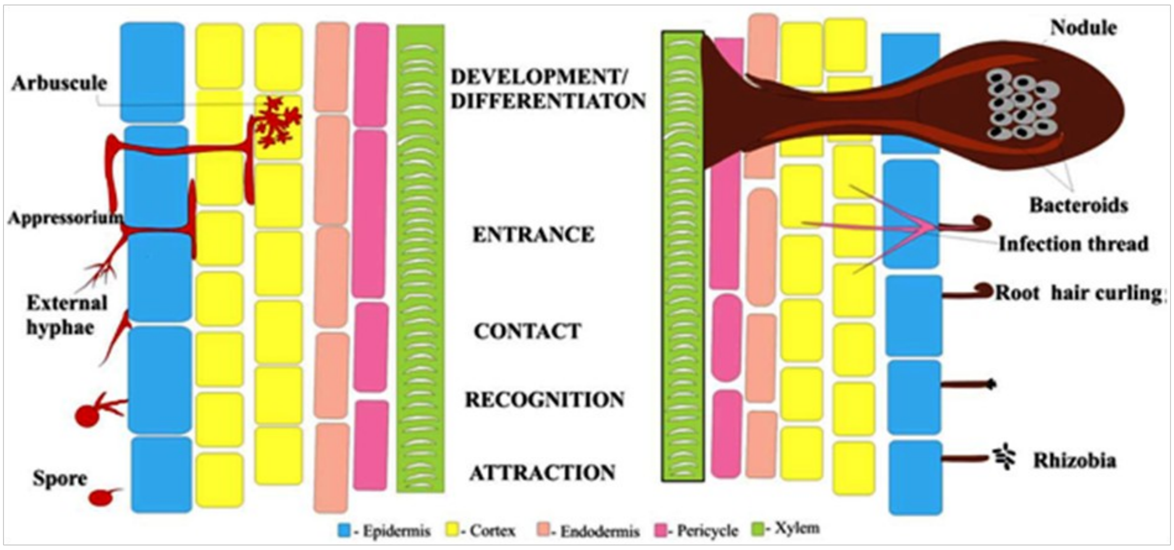

Figure 1: Schematic representation of AMF and Rhizobium-legume symbioses (Manchanda and Garg 2007).

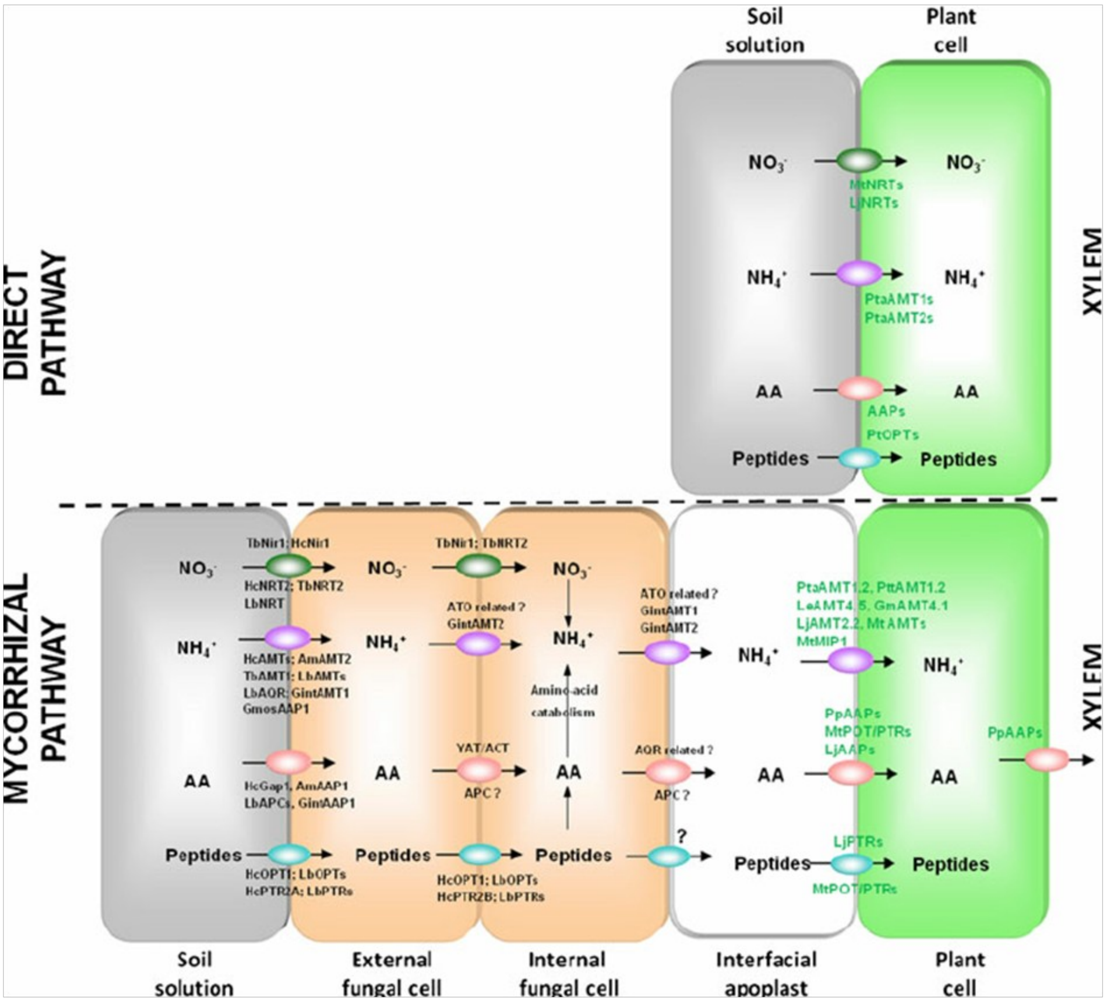

Figure 2. Current knowledge about N transfer mechanisms in mycorrhizal interactions (Casieri et al., 2013). Five compartments for N-compound transfer (ammonium, nitrate, amino acids and peptides) can be differentiated: the soil solution, external and internal fungal cells, the interfacial apoplast and the plant cell. The different molecules are reallocated across the different extraradicular mycelium compartments by several transporters that are not yet fully characterized. Hence, putative uncharacterized transporters are indicated by a question mark , fungal transporters in black and plant transporters in green, respectively. NRT nitrate transporter, AMT ammonium transporter, AAP amino acid permeases.

CONCLUSION AND PERSPECTIVES

The effective AMF can greatly assist nodulation and N_2 fixation of legumes. The overall AMF contributions to N transfer are considered to be of great importance for legume and non-legume intercropping systems in sustainable agriculture. Seeing that the rhizobia and AMF compatibility is an important factor affecting symbiotic efficiency, the combination of adapted and efficient AMF-rhizobia-legume tripartite symbiosis is of great importance for N_2 fixation and consequently for successful N transfer in sustainable agriculture especially under unfavorable environmental conditions. Thus, N transfer through AMF requires further investigations on many plant species, AMF isolates, and rhizobia strains under various field conditions.

N transfer from N_2 fixing to non N_2 fixing plant is effected by the AMF hyphal density and the presence of common AM networks. AMF hyphae are considered to be the main source of inocula when host plants are present and the soil is not disturbed. The various tillage practices used for crop production may negatively impact the survival of AMF propagules, especially AMF hyphae and common AM networks. Thus, maximizing N transfer and benefits to associated crop requires management of AMF in soil through applying agricultural practices that minimize soil distribution.

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CONFLICTS OF INTEREST

Authors declared no potential conflict of interest

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