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MINI-REVIEW

Arbuscular mycorrhizal fungi and nitrogen uptake

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Abstract Nitrogen (N) is among the most important macro-nutrients significantly affecting plant growth and yield production. Accordingly, N must be supplied adequately so that optimum amounts of yield are resulted. There are different ways of supplying N to the plant including the use of chemical and biological fertilization. The chemical properties of N make it very mobile, especially under humid conditions. Hence, N must not be overfertilized with respect to the economical and environmental points of view. N Biological fertilization includes the use of plant growth-promoting rhizobacteria (PGPR) including the N-fixing bacteria, rhizobium. There are also arbuscular mycorrhizal (AM) fungi in the soil, which are symbiotic to most terrestrial plants enhancing plant growth and yield production through increasing the uptake of water and nutrients by the host plant. Numerous experiments have indicated the important role of AM fungi in enhancing P uptake by plant. However, it is yet a matter of debate that how AM fungi may affect soil N dynamic and hence plant N uptake. Some of the most important and recent aspects regarding such effects by AM fungi are highlighted, which can be of significance to health and productivity of the ecosystem.

Keywords AM fungi · Soil N dynamic · Plant N uptake · Tripartite symbiosis · Chemical and biological fertilization

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Introduction

Plant require a range of at least 16 macro- and micro-nutrients for their growth and yield production (Marschner 1995). Among such nutrients nitrogen (N) is of particular significance because it is necessary for many different plant functioning as it is incorporated in the structure of some important macro- and micro-organic compounds in the plant such as chlorophyll and proteins and amino acids (Marschner 1995). N is a mobile element in the soil and hence under humid conditions is subjected to leaching indicating the importance of appropriate N fertilization under such conditions. On the other hand, under arid and semi arid conditions, water deficiency may limit the use of inorganic N by plant.

There are different ways of supplying N to the plant including the use of chemical and biological fertilization. In the case of chemical fertilization, proper amounts of N must be supplied with respect to the economical and environmental aspects regarding N compounds (Miransari and Mackenzie 2010a, b, c). Biological fertilization can be performed by using soil microbes such as plant growth promoting rhizobacteria (PGPR) including the N-fixing bacteria, rhizobium (Arzanesh et al. 2010; Zabihi et al. 2010; Miransari 2010a, b, c, d).

In addition, Arbuscular mycorrhizal (AM) fungi can also be used a source of biological fertilization. AM fungi are soil fungi, developing symbiotic association with most terrestrial plants. In this symbiosis, the fungi provide the host plant with water and nutrients in the exchange for carbon (Smith and Read 2008). The symbiosis between the fungi and host plant is not specific; however, some fungi-host plant associations may be more efficient under specific circumstances (Daei et al. 2009). AM fungi are able to alleviate the effects of different stresses on plant growth and yield production by significantly increasing the uptake of water and nutrients including N by the host plant (Miransari et al. 2007, 2008, 2009a, b; Daei et al. 2009).

Different research work has indicated that AM fungi can substantially enhance the uptake of different nutrients, especially phosphorous (P) by the host plant through an extensive network of hypha and some other mechanisms including the production of enzymes such as phosphatases. However, it has also been indicated that AM fungi can also influence the uptake of other nutrients necessary for plant growth and yield production including N. McFarland et al. (2010) indicated that more than 50% of plant N requirement was supplied by mycorrhizal association. As N is among the most important macro-nutrients significantly affecting plant growth and yield production, it can be pertinent to determine the contribution of AM fungi to N uptake by the host plant.

Using labeled N, it has been indicated that the hypha of AM fungi is able to utilize inorganic N efficiently (Ames et al. 1983; Frey and Schüepp 1992; Johansen et al. 1993, 1994; Subramanian and Charest 1999) and transfer it into the soil in a 10–30 cm distance. This indicates that AM fungi enable the host plant to have access to the N inorganic sources, which are not accessible by non-mycorrhizal plants (Tobar et al. 1994a, b). According to Johansen et al. (1993), the external hypha of *Glomus intraradices* was able to absorb NO_3 and NH_4 and provide them to the host plant.

The mobility of inorganic P is much lower than inorganic N including NO_3, indicating that the role of AM fungi in absorbing N may be of less significance than P. In other words, plant roots are able to absorb their necessary inorganic N by diffusion and mass flow. In addition, plants forming mycorrhizal symbiosis grow in environments with high rates of nitrification. These may all indicate that mycorrhizal symbiosis may not be considered important for the uptake of mineral N by the host plant.

However, there may be situations where plant growth is limited due to reasons such as N limitation. Hence, the growth of fungal hypha in organic patches may be an effective way of supplying N for both the fungi and the host plant (Hodge et al. 2001a, b; Hodge and Fitter 2010). For example, in arid and semi arid climates, the mobility of NO_3 in soil is significantly reduced, and hence, AM fungi may behave more effectively under such conditions to absorb inorganic N (Tilman 1987; Hodge et al. 1999; Subramanian and Charest 1999; Hodge and Fitter 2010). Tobar et al. (1994a, b) indicated that under water stressed conditions AM fungi significantly increased N uptake by the host plant in comparison with well water conditions.

Interestingly, recently a plant ammonium transporter, which is activated in the presence of AM fungi, has been identified indicating that the way by which N is transferred in plant may be similar to P transfer (Guether et al. 2009). This may indicate that similar to P transporters, AM fungi may also be able to activate N transporters in plant suggesting the significance of the uptake of both nutrients by mycorrhizal plants.

The enhanced activities of nitrate reductase, glutamine synthetase, and glutamine synthase in the roots and shoots of mycorrhizal corn (*Zea mays* L.) indicate that the absorbed NO_3 by AM hypha can be directly transferred to the root cells for further utilization and incorporation into the organic structures. Such enzymatic alterations can also enhance plant resistance to drought stress (Cliquet and Stewart 1993; Subramanian and Charest 1999). This indicates that in addition to the direct effects of AM fungi on the alleviation of stresses such as drought (Auge 2001), their indirect effect such as absorbing inorganic N can also contribute to the alleviation of stress. AM fungi are able to alter plant physiological and morphological properties in a way by which plant can handle the stress (Miransari et al. 2008).

Although there are indications regarding the contributions of AM fungi to N uptake by plant, much more details must be elucidated related to such functionality by AM fungi (Atul-Nayyar et al. 2009). Different research work has indicated that AM fungi can absorb N and transfer it to the host plant roots (Tanaka and Yano 2005; Jackson et al. 2008); however, the higher rate of N uptake by mass flow may indicate that AM fungi may not be that important in the uptake of N by the host plant (Liu et al. 2007; Atul-Nayyar et al. 2009).

AM fungi can utilize the inorganic N released from organic sources (St. John et al. 1983; Hamel 2004) as well as amino acids (Hawkins et al. 2000). The presence of AM fungi on some plant tissues during the mineralization process indicated that AM fungi are able to enter the tissues through the vascular bundle and utilize the inorganic N released by soil microbes (Aristizábal et al. 2004). The ability of AM fungi to use soil organic matter as a source of inorganic N has yet to be elucidated (Jin et al. 2005; Talbot et al. 2008), however, even if AM fungi is not effective in such a process, their influence on the activity of soil mineralizing microbes may indirectly indicate their role in soil N dynamic and uptake by plant (Andrade et al. 1997; Marschner et al. 2001; Hodge 2003a, b; Aneja et al. 2006). Hodge et al. (2001a) indicated that the AM fungi, *G. hoi*, can enhance the mineralization process of soil organic matter while earning mineral N.

Atul-Nayyar et al. (2009) found that the C/N ratio of soil organic matter decreased from 17.8 to 13, resulting in higher amounts of mineralized N in the presence of AM fungi. This demonstrates that AM fungi may enhance the mineralization process (by 228%) of organic matter and hence absorbed N uptake by plant. They accordingly indicated that AM fungi may contribute to the enhanced plant growth by increasing the mineralization process of soil organic N and subsequent N uptake by plant.

The rate of N mineralization by AM fungi may be a function of plant demand for mineral N as the high rates of N in soil can decrease the growth and development of AM hypha into organic patches (Liu et al. 2000), which has been attributed to plant N uptake (Hodge et al. 2001a; Hodge 2003b). Factors affecting the process of N mineralization in the presence of AM include (1) the extension of AM hypha, (2) the production of hydrolytic enzymes such as pectinase, xyloglucanase and cellulose, which are able to decompose soil organic matter, and (3) the AM fungal effects on the activities of other soil microbes. The effects of AM fungi on soil microbes can be through different mechanisms including enhanced plant growth, induced plant resistance, and altered root exudates and hence signaling pathways (Lioussanne et al. 2008; Toljander et al. 2007). In addition, AM hypha is an important source of organic C for soil microbes (Schimel and Weintraub 2003).

N uptake by AM fungi is of significance from the following aspects: (1) the effects of AM fungi on the process of N cycling, (2) whether AM fungi can reduce the rate of NO_3 leaching, which is an important concern under humid conditions (Miransari and Mackenzie 2010a, b, c), (3) AM fungi can be considered as a source of N for plant under conditions with limitations, for example under arid and semi arid conditions where nutrient uptake by plant is limited, and (4) the proper use of chemical fertilization with respect to the use of biological fertilization.

N uptake in mycorrhizal plants

Ames et al. (1983) found that the mycorrhizal fungi *Glomus mosseae* increased N uptake by mycorrhizal celery. In their experiments Tobar et al. (1994a) and Azcón et al. (2001, 2008) tested the effects of mycorrhization and P fertilization on the growth of lettuce plants as well as on N assimilation and proline content under drought stress (−0.17 MPa). They also tested the effects of AM fungi on the percentage of N uptake from N fertilization under different levels of soil N. Compared with P fertilization, AM fungi enhanced plant N concentration, the activity of nitrate reductase and proline content in plant. At the medium level of N fertilization (6 mmol N), AM fungi resulted in the higher N uptake from fertilization, relative to the lowest (3 mmol N) and highest (9 mmol N) N levels, which reduced N uptake from N fertilization. These results indicate that mycorrhizal plants can regulate plant N uptake with respect to the amounts of N in the soil. Accordingly, AM fungi can affect plant N uptake from soil and N fertilization, however, high amounts of N fertilization can significantly decrease N uptake by mycorrhizal plants affecting the fertilization strategy.

The tripartite symbiosis between the host plant, AM fungi, and N-fixing bacteria rhizobium can affect the uptake of N by the host plant. In such a symbiosis, N and P are supplied by the micro-symbionts to the host plant. Accordingly, the association between each micro- symbiont is affected by the interaction effects between the host plant and the micro-symbionts as well as by the interactions effects between the micro-symbionts. Wang et al. (2010) examined the effects of different parameters such as plant genotype and N and P levels on the tripartite symbiosis between soybean (*Glycine max* L.), AM fungi and *Bradyrhizobium japonicum*. They tested the idea that how the nutrient efficiency of soybean plans can be increased. The soybean genotypes differed in their root architecture including shallow and deep rooting genotypes. Co-inoculation of soybean plants with *Bradyrhizobium japonicum* and AM fungi may enhance the symbiotic ability of the two microbes (Xie et al. 1995). In addition to the effects of plant genotype, there may also be some interactions effects between N and P in the field affecting root morphological properties as well as the process of mycorrhization and nodulation (Kuang et al. 2005; Miransari et al. 2007, 2008, 2009a, b).

Root architecture affected mycorrhizal symbiosis and deep rooting plants had a higher rate of symbiosis with AM fungi at low P levels, compared with shallow rooting plants; however, higher nodulation was resulted at high P levels. This may indicate that N and P levels may affect the tripartite symbiosis between the host plant and the micro-symbiont. Co-inoculation with the two micro-symbionts resulted in higher plant growth and nodulation at low N and P levels and elevating fertilization levels adversely affected the contribution of the two micro-symbionts to the growth of soybean plants (Wang et al. 2010). Such results can be used for proper N and P fertilization in the field with respect to the use of biological fertilization including AM fungi and rhizobium bacteria (Miransari 2010a, b, c, d).

Hodge et al. (2001a) indicated that the AM fungi *G. hoi* enhanced the degradation of organic residues and N uptake by the host plant. In the presence of organic matter, the growth of fungal hyphal increased whether the host plant was present or not. Hawkins et al. (2000) also tested the effects of *G. mosseae* on N absorption from organic and inorganic sources. Mycorrhizal wheat absorbed organic N in the form of N-glycine by 0.2 and 6% at low and high level of N-fertilization, respectively. The higher organic N uptake at the sufficient N level fertilization was attributed to the more developed hyphal network. The fungi were also able to absorb inorganic N in the form of NO_3 and NH_4. The Ri-T-DNA transformed of mycorrhizal carrot roots was also able to absorb organic N from N-glycine and N-glutamine sources. However, the rate of N absorption in the form of organic and inorganic was not high enough to influence plant N uptake significantly.

Tian et al. (2010) also indicated that AM fungi is able to absorb both organic and inorganic N. Arginine is synthesized in the extra radical hypha and transferred to the intraradical hypha where it releases N to be absorbed by the host plant. Accordingly, 11 fungal genes related to the N absorption pathway were identified and six of them were sequenced. Such a finding indicated the role of fungal genes in N uptake and the subsequent extra- and intra-radical hypha gene expression as well as plant gene expression.

Hodge and Fitter (2010) tested and proved the hypothesis that organic matter is an important source of N for the fungi themselves. Hence, they grew the host plant both under light and shade so that less amounts of C were transferred to the fungi. Under both conditions, the fungi absorbed substantial amounts of its necessary N from the organic patch in addition to the amounts of N, which was transferred to the host plant. Both *G. hoi* and *G. mosseae* indicated such abilities. Hence, AM fungi are an important component of ecosystem in N cycling.

Conclusion

Some of the most recent advancements regarding the effects of AM fungi on the process of N uptake by the fungi themselves or by the host plant were reviewed. There are some interesting findings accordingly, which can indicate the significance of N uptake by AM fungi. N cycling, plant growth and ecosystem functioning can be affected by the influence of AM fungi on N dynamic in soil and plant N uptake. This indicates that there is a need for further research regarding the effects of AM fungi on the process of N uptake.

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