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Review article

Agricultural practices to improve nitrogen use efficiency through the use of arbuscular mycorrhizae: Basic and agronomic aspects

Julien Verzeaux[a], Bertrand Hirel[b,*], Frédéric Dubois[a], Peter J. Lea[c], Thierry Tétu[a]

[a] Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN, FRE 3498 CNRS UPJV), Laboratoire d'Agroécologie, Ecophysiologie et Biologie intégrative, Université de Picardie Jules Verne, 33 rue St Leu, 80039 Amiens Cedex, France

[b] Intitut Jean-Pierre Bourgin, Institut National de la Recherche Agronomique (INRA), Centre de Versailles-Grignon, Unité Mixte de Recherche 1318 INRA-Agro-ParisTech, Equipe de Recherche Labellisée, Centre National de la Recherche Scientifique (CNRS) 3559, RD10, F-78026 Versailles Cedex, France

[c] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, United Kingdom

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ABSTRACT

Nitrogen cycling in agroecosystems is heavily dependent upon arbuscular mycorrhizal fungi (AMF) present in the soil microbiome. These fungi develop obligate symbioses with various host plant species, thus increasing their ability to acquire nutrients. However, AMF are particularly sensitive to physical, chemical and biological disturbances caused by human actions that limit their establishment. For a more sustainable agriculture, it will be necessary to further investigate which agricultural practices could be favorable to maximize the benefits of AMF to improve crop nitrogen use efficiency (NUE), thus reducing nitrogen (N) fertilizer usage. Direct seeding, mulch-based cropping systems prevent soil mycelium disruption and increase AMF propagule abundance. Such cropping systems lead to more efficient root colonization by AMF and thus a better establishment of the plant/fungal symbiosis. In addition, the use of continuous cover cropping systems can also enhance the formation of more efficient interconnected hyphal networks between mycorrhizae colonized plants. Taking into account both fundamental and agronomic aspects of mineral nutrition by plant/AMF symbioses, we have critically described, how improving fungal colonization through the reduction of soil perturbation and maintenance of an ecological balance could be helpful for increasing crop NUE.

1. The contribution of mycorrhizal fungi to plant nitrogen nutrition

Mineral fertilizers such as nitrogen (N) are presently the main source of nutrients applied to soils, even if the contribution of animal manure remains important in areas where there are livestock nearby. Following the Green Revolution in the 1960s, N fertilizers synthesized by the Haber–Bosch process have been used extensively to increase crop yield, allowing the production of food for nearly half of the world population [1].

Despite an almost ten-fold increase in the application of mineral N fertilizers, the overall increase in yield has been less than 3-fold [2]. This indicates that N use efficiency (NUE), defined as the yield obtained per unit of available N supplied by the soil and by added N fertilizer, has declined considerably over the last 50 years. NUE is composed of the uptake efficiency, that is the ability of plants to take up N from the soil and the utilization efficiency, that is the ability of plants to use N to produce biomass, grain in particular. It has therefore become crucial that NUE should be improved worldwide, for both environmental and economic benefits [3]. One of the main reasons for the decline in NUE, has been that most modern crops were bred in the presence of non-limiting mineral fertilization conditions, in particular N. Thus, the opportunities to select productive genotypes under low levels of mineral or organic fertilization conditions have been missed. This includes the ability of genotypes to develop non-symbiotic N_2-fixing and symbiotic AMF (arbuscular mycorrhizal fungal) associations [4]. It will be necessary to enhance NUE in countries which do not have the benefit of the intensive use of N fertilizers, by the selection of productive genotypes that can grow under low N conditions, notably in tropical regions. It has also been suggested that in addition to breeding strategies for improving crop NUE, changes in government policy, including a decrease in N fertilizer usage, are needed to reduce the effect of N inputs on human health, climate and ecosystems [3].

More than 50% of the N applied to the soil is not used by the crop plant and may be taken up by the soil microbiome [5]. In the intensive agricultural production systems that are currently used worldwide, this uptake is likely to shift N accumulation towards the bacterial biomass. N is also lost by volatilization [6] or by leaching [7]. In some

* Corresponding author.
E-mail addresses: julienverzeaux@gmail.com, bertrand.hirel@versailles.inra.fr, frederic.dubois@u-picardie.fr, p.lea@lancaster.ac.uk, thierry.tetu@u-picardie.fr (B. Hirel).

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agroecosystems N volatilization can be as high as 50% [8]. The loss of N, mainly in the form of nitrate (NO_3^-), [9]), which can run off into the surface water or flow into the groundwater can have a detrimental impact on living organisms notably animals and humans [10]. In addition, NO_3^- can have a major effect on the environment by causing eutrophication of freshwater and marine ecosystems [11] and through the emission of N gases such as N_2O in heavily N fertilized agricultural soils, which has a potent greenhouse effect [9,12].

It will be necessary to increase agricultural production by 1.7-fold in 2050, if we are to feed the growing world population (FAO; http://www.fao.org/nr/nr-home/en/). The detrimental impact of the overuse of N fertilizers on the environment can be minimized if it is accompanied by sustainable agricultural practices, such as fertilizer use rationalization [13]. In addition, the use of crop rotation, the establishment of ground cover and the burial of crop residues will be of value, preferably with plants that fix dinitrogen (N_2) fixing and utilize AMF symbiotic associations [13]. Paradoxically, N_2 fixation, which is mainly carried out by the symbiotic association between seed and forage producing legumes and Rhizobiacae [14], is one of the most important sources of reduced N in agricultural systems [15]. This is also why intensive research is currently being conducted to expand symbiotic N_2 fixation to a greater diversity of crop plants [16]. An increasing number of studies have shown that conservation tillage using no-till and permanent plant cropping systems also significantly enhances the potential of plant colonization by AMF in comparison with conventional tillage [17]. The occurrence of even more efficient tripartite symbioses between legumes, Rhizobiacae and AMF has also been suggested [18]. Thus, either the use of legumes as cover crops and the development of no-till farming or both, could also be attractive to increase NUE through the beneficial action of AMF on N uptake efficiency, with regards to both soil N availability and N transfer to the host plant. The development of such sustainable agricultural practices implies that more studies are needed for a better understanding of the biological mechanisms involved in the establishment and functioning of more efficient symbioses with Rhizobiacae and AMF as they share a common initial signaling pathway when they develop a symbiotic association with a plant [19]. The knowledge gained from such studies could be used to develop future breeding and farming strategies to select and grow highly productive crops using less synthetic N fertilizer [20]. However, it will be necessary to take into account that legumes require more phosphate (P) fertilizer than cereals [21], and many are more demanding of water [22], notably in areas where water scarcity is increasing. Therefore, plant breeders and agronomists will need to determine whether increasing N_2 fixation is economically justified as, in contrast to atmospheric and synthetic N, P is not inexhaustible.

2. The complexity of nutrient uptake in a plant-fungal symbiosis

Many excellent reviews have described extensively our current knowledge of the role of mycorrhizal fungi in the uptake of nutrients by plants, notably N [23] and P [24]. In these reviews it has been emphasized that AMF play an essential role in the nutrient uptake of the majority of land plants, including many important crop species. The contribution of the AMF symbiosis to P nutrition has focused on the interplay between direct P uptake *via* the roots and uptake *via* the AMF pathway.

Whether AMF contribute similarly to the N nutrition of the host plant is discussed, taking into account that AMF can actively transfer N to their host [23], even through the contribution of AMF to plant P uptake is usually much larger than the contribution to plant N uptake [24]. Moreover, the greatest AMF benefits are realized under low P and high N fertilization, substantiating the greater role of AMF in P uptake than in N uptake [25]. The relative availability of P and N is an important driver of AMF structure and function and of the impact of AMF on host plants, whether they are present as a single species or as a community of species in various ecosystems [26].

Therefore, we will briefly cover the assimilation of mineral nutrients in mycorrhizal symbiotic associations by focusing this section on N transport and only summarizing current knowledge and future perspectives. Roots colonized by AMF have two uptake pathways for nutrients. One involves the plant, whilst the other involves the fungal symbiotic partner. The plant root takes up minerals *via* high or low affinity transport systems, allowing the uptake of nutrients present in low concentrations, or those with a low mobility such as P [27]. The AMF possess only high affinity transport systems towards P located in the extraradical mycelia for nutrient uptake, or in the hyphae colonizing the root cortex, for their translocation. The mechanisms involved in the control of P transport by the plant and the fungal uptake systems are well characterized [24,27]. In contrast, it remains to be demonstrated if, in a similar manner to P uptake, the plant NO_3^- or ammonium (NH_4^+) transport systems are down regulated when the plant is colonized by AMF [23]. Whether the fungi with their own NO_3^- or NH_4^+ transporters are able to provide enough N for optimal plant growth and development, also remains to be determined, knowing that inorganic N taken up by the fungi can be incorporated into amino acids that are further transferred to the plant [28]. Fungi are also able to obtain substantial amounts of N from decomposing organic material that can enhance their fitness to grow in such an environment (see section 3.1 for details). Moreover, the large biomass and high N demand of AM fungi means that they represent a global N pool equivalent in magnitude to fine roots and play a substantial role in the N cycle [29].

For example, several amino acids such as asparagine and arginine are transferred to the plant when *Sorghum bicolor* is colonized by AMF, suggesting the occurrence of multiple transporters in the fungus [30]. Therefore, more research will be required to characterize these putative amino acid transporters and to determine to what extent they contribute to NUE improvement in the symbiotic association. Establishing whether there is competition for N between the plant and the AMF and identifying the underlying regulatory control mechanisms seems to be a key issue for optimizing the efficiency of the symbiotic association, notably when there is low N availability in the soil [31]. Individual or combined "omics"-based techniques [32] will provide means to decipher some of the regulatory control mechanisms. However, the interpretation and integration of the generated transcriptomic, proteomic and metabolomic data under agronomic conditions will be difficult, due to the occurrence of complex mycelial networks in a single species, that are even more complex in mixtures of several species. The traits of both the roots and mycorrhizal fungi need to be jointly considered for studying regulation and optimizing nutrient foraging by the symbiotic association [33]. Initially the physiological and molecular mechanisms involved in inorganic or organic N uptake by the fungi and their transfer to the plant, should be investigated using a single plant species including N_2 fixing legumes and a single fungal partner. This research should be carried out before glasshouse or field studies using natural soils, when interaction with the microbiome and the neighboring plants are much more complex. Such investigations could be first conducted using microcosms [34] and well-controlled gnotobiotic systems similar to those recently developed for non-symbiotic N_2-fixing associations [35], (Fig. 1). These two experimental systems could then be adapted to study the interaction between a mixture of several plant species and multiple fungal partners both at the molecular and physiological levels, thus gradually increasing the complexity of the plant/AMF symbiotic association. Further on, the qualitative and quantitative impact of N nutrition and the nature of the soil used to study the plant/AMF interactions will need to be assessed in order to determine if the knowledge gained from these experimental systems can be transferred to the field under agronomic conditions.

3. The roles of arbuscular mycorrhizal fungi in agroecosystems

The association between AMF and host plants is an ancient symbiosis that arose on the earth more than 400 million years ago [36].