Arbuscular Mycorrhizal Fungi Symbiosis to Enhance Plant–Soil Interaction

Subjects: Agronomy

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Arbuscular mycorrhizal fungi (AMF) form a symbiotic relationship with plants; a symbiotic relationship is one in which both partners benefit from each other. Fungi benefit plants by improving uptake of water and nutrients, especially phosphorous, while plants provide 10–20% of their photosynthates to fungus. AMF tend to make associations with 85% of plant families and play a significant role in the sustainability of an ecosystem. Plants' growth and productivity are negatively affected by various biotic and abiotic stresses. AMF proved to enhance plants' tolerance against various stresses, such as drought, salinity, high temperature, and heavy metals.

symbiotic relationship | nutrients | abiotic stresses

1. Introduction

Nutritional strategy can be the base of the characterization of soil-borne fungi. The majority of these fungi are saprotrophic in nature and rely on dead organic matter for their nutritional requirements. However, a small group of fungi exists that depends upon living organisms for nutrients, either by mutualism or parasitism [1]. Some others can change their feeding behaviour to seprotrophism, mutualism, or parasitism, depending upon the available circumstances. Mycorrhizal fungi need an association with plant roots to complete their life cycle; on the other hand, others can survive as free-living organisms in a natural ecosystem.

Mycorrhizal fungi form a beneficial relationship between plants and microorganisms [2]: a fungus takes nutrients (organic carbon) from the host plant to complete its growth and development. At the same time, it helps the plant absorb water and nutrients (nitrate and phosphate) and impart stress resistance. Such a mutual relationship dates back 400 million years [3]. There are two major divisions of mycorrhizal fungi based on their interactional anatomy with host plant roots. The first ones are septate fungi, which are *Basidiomycota* and *Ascomycota* and fall in the group ectomycorrhizas (hyphae of these fungi never penetrate the cell lumen; instead, these develop in epidermal cells and surround the root tips of host plants). The second group includes arbuscular mycorrhizas, ericoid, and orchid, which are regarded as endomycorrhizas (hyphae enter and develop in the cells of plant roots) [1].

Arbuscular mycorrhizal fungi (AMF) belong to *phylum Mucoromycota* and *subphylum Glomeromycotina* [4]. The colonization of AMF surrounds all woody plants, e.g., gymnosperm and angiosperm, consisting of flowering families and some non-flower-producing families. A complex hyphal network is formed by soil fungi that are efficient in mineral and water absorption from an extended surface area. Furthermore, the development of arbuscules (highly branched organs) takes place in cortical cells of roots that enable the fungi with bi-directional resource exchange with the plant [5]. This association is formed in the roots of about 80% of terrestrial plants, as fungi provide phosphorous (P) and other mineral nutrients, enhance the capacity to absorb water, improve leaf photosynthesis, and upregulate the hydraulic conductivity of plant roots. These beneficial effects impart abiotic stress tolerance in plants, enabling them to perform under adverse environmental conditions [6].

2. AMF and Nutrition Acquisition

An explicit function of AMF mutual association is the transfer and acquisition of nutrients by the plants [7]. AMF enhance the uptake of nutrients, especially P, in nearly all plants [8]. AMF improves growth and development in plants under low P and N [9]. The extent of AMF growth varies so that a lower AMP percent is realized under high soil P conditions [10]. P nutrition was enhanced by AMF symbiosis in lowland and upland rice. P uptake in rice through fungal hyphae was significantly more than direct uptake by rice roots [11]. After uptake by hyphae, polyphosphates (polyP (negatively charged liner phosphate polymers)) are assembled in the cortical cells of rice after the hydrolysis of the polyP chain upon arrival in arbuscules [11]. AMF-associated rice showed a reduction in the transcription levels of two transporter genes (*PT2* and *PT6*) involved in direct P uptake by the root. In contrast, increased transcription levels of the AMF-specific P transporter gene (*PT11*) were observed [12]. This can explain the significantly larger uptake of P by the AMF-mediated pathway rather than direct uptake by roots.

Improved N nutrition was also observed by AMF symbiosis in many studies [13][14]. Uptake of N by AMF can be accomplished in organic (amino acids) as well as inorganic forms (ammonium and nitrate ions) [15]. After being converted into positively charged arginine by the glutamine synthetase/glutamate synthase cycle, an ammonium ion is translocated to the arbuscular along with negatively charged polyP. From the arbuscules, it is transported to plant cells by ammonium transporters after being converted back into ammonium [13]. In trees and certain crops, N is the primary factor that can restrict growth. Numerous studies have shown that AMF can transfer N to adjacent plants as well [16][17].

The colonization of AMF enhances the uptake of nutrients in plants. When AMF are inoculated in the plant, they enhance macro and micro-nutrient acquisition, leading to enhanced accumulation of photosynthates. In nutrient-deficient soils, AMF play a role in the uptake of nutrients by the plants by increasing the surface absorbing capacity of the roots of host plants [18]. Evidence showed that inoculation of AMF in tomato plants exhibited increased K, N, P, and calcium (Ca) uptake and enhanced plant growth [19]. AMF form a mutual association with the roots of the plant, which, in turn, helps the uptake of many mineral nutrients such as Ca, N, P, and zinc (Zn) [20][21]. AMF produce siderophores (ferricrocin, glomuferrin) [22][23], which exhibit the ability to chelate the iron (Fe), particularly under Fe-deficient conditions. The chelated Fe is available to be up taken by plants as well as fungi [24].

Under drought environments, symbiotic association enhanced the amount of N, Fe, and P in Rose geranium [25], and pistachio plants inoculated with AMF depicted increased Zn, potassium (K), and P contents under such conditions [26]. AMF inoculated “garden mum” plants also contained a high level of N and P [27]. In addition, in Chinese ryegrass, it enhanced tissue water content and P [28]. A decreasing trend in the uptake of chlorine and sodium (Na) and an increased uptake of other nutrients were also linked to AMF [29]. Extraradical mycelium enhanced plant growth by enhancing the uptake of nutrients [30]. After developing a mutual association with the plant, AMF form extraradical mycelia extending from the plant roots to the rhizosphere, thus enhancing the nutrient uptake [16].

Interestingly, AMF can take up N from decayed and dead matter, enhancing their ability to grow and playing an essential function in the N cycle. Various researches have shown that of the total N taken up by the arbuscular mycorrhizae, about 20–75% of it is transferred to the host plant [31]. Furthermore, AMF enhance N and carbon acquisition under increased levels of carbon dioxide [32]. Nevertheless, the acquisition of macro and micronutrients and their distribution in olive saplings developed under a high level of manganese were associated with AMF [33]. A symbiotic association between chickpea and AMF accumulated high protein content, Zn, and Fe [34]. Studies revealed that the function of the K^+ transporter was enhanced by AMF infection in the roots of birdsfoot trefoil [35], leading to a lower accumulation of Na, magnesium, and Fe [33]. A symbiotic association with AMF increased the acquisition of mineral nutrients and higher carotenoid contents in the plant. AMF can be used to enhance the production of crops such as potato and maize [36][37].

Role of AMF in Reducing Erosion and Nutrient Leaching

Biodiversity is severely affected by uncontrolled land use that endangers ecosystem processes [19]. AMF can bring beneficial changes in the structure of soil that help improve its physical, chemical, and biological properties. Besides enhancing plant growth and the development of the root system, AMF protect the soil against wind and water erosion [38]. AMF form a network of hyphae with the roots of plants, which plays an important role in enhancing soil texture.

AMF play a role in conserving nutrients in the soil by reducing their loss by leaching, consequently lowering the hazards of groundwater pollution [2]. AMF have a beneficial effect on the water-holding capacity of soil and the supply of nutrients. Such benefits of AMF are more pronounced for arid regions where low soil fertility and eroded soils are major constraints on agricultural productivity. Growing such crops that develop AMF association help mitigate these problems and realize good crop yields by both improving soil condition and lowering the leaching of nutrients [39]. Leaching of nutrients is undesirable because it pollutes both surface and groundwater and lowers the fertility status of the soils. Nitrate N is often lost through leaching beyond the rhizosphere, which is retained by hyphae of AMF and is available for plant use [40].

Frequent use of chemical fertilizers, pesticides, and herbicides poses problems to both human and soil health [41]. AMF act as a growth regulator in most terrestrial environments, and scientists have been persuaded to use AMF as a biofertilizer [42]. Biofertilizers are formed from a mixture of natural substances such as microbes that enhance the growth, development, and health of plants.

3. AMF and Abiotic Stresses

3.1. Drought

The soil–plant environment continuum is the driving force for upward water fluxes. A lapse occurs in this continuum due to water deficiency in the root zone that leads to reduced leaf water potential, hence causing plants to adopt a compensation phenomenon, i.e., closure of stomata, thereby leading to reduced water loss from the plant [43]. Plant life processes are adversely influenced by drought stress: the deficiency of water lowers the transpiration rate; influences the uptake of ions, enzymatic activities, absorption of nutrients; and causes oxidative stress [44]. At an advanced stage of tissue dehydration, normal plant growth, development, photosynthesis, nutrient absorption, and metabolism are severely impaired [45]. Maintaining a continuous water supply under drought is critical to sustained plant growth. In drought-stressed soils, AMF symbiosis with *Lactuca sativa* was reported to increase water uptake as compared to plants where symbiosis was absent [46]. AMF can increase water uptake in drought conditions by the stabilization of soil structure and aggregation [47]. The porosity of soil and water retention in soil pore spaces are outcomes of aggregate stability, ultimately increasing the access of roots to water. Furthermore, extended fungal hyphae increase the root zone and directly transfer water to the plant [1]. Fungal hyphae are capable of scavenging water from narrow soil pores because the average diameter of hyphae (2–20 µm) is less than that of root hairs [48].

AMF manage to mitigate drought stress in many crops, such as soybean, onion, maize, wheat, and strawberry. The mutual association of AMF with a plant enhances the size and capability of roots, stomatal conductivity, and exchange of gases, and also helps the plant against adverse climatic conditions [49]. AMF induce the ABA responses that control plant physiological processes and stomata [50]. A plant having a mutual association with AMF tolerates drought stress by morphological adaptation accompanied by physiological and biochemical mechanisms. AMF maintain plant/soil water relations and enhance the structure of soil by releasing glomalin in the soil [51].

3.2 Soil Salinity

Osmotic and ionic stresses on plants are the result of soil salinity. Ionic stress results in decreased water availability to plants, ultimately leading to less photosynthesis, while specific ion toxicity and nutrient deficiency are the outcomes of ionic stress [52]. A total of 1125 million hectares of area is salt-affected worldwide [53]. A soil-salinity problem is faced under almost all climatic conditions. Salts are deposited by primary (precipitation of salt from the atmosphere, seawater, and weathering of rocks) and secondary (anthropogenic processes, i.e., mismanagement of water, irrigating the soil with brackish water, and irrigating the soil for a long time) processes. Nevertheless, cultivating shallow-rooted annual crops instead of perennial deep-root-system crops also results in increased saline groundwater [54].

Higher Na levels in saline soils result in increased Na uptake that often is at the expense of K, as both of these ions compete for the same binding sites. This Na-induced K deficiency hinders the function of many metabolic enzymes with which it acts as a cofactor [55]. Contrarily, Na accumulation in the cell is considered to be highly toxic as it disrupts the structure of several enzymes [56]. A low K:Na ratio in salt-affected soils interrupts many metabolic processes, which often results in osmotic stress, reduced photosynthesis rates, and oxidative damage [56]. Hence, major determinants of salt-stress resistance in plants are reduced Na uptake and its exclusion and compartmentation [57].

The presence of AMF has been reported in many salt-affected soils [58]. AMF-infected plants depicted increased K uptake with reduced Na absorption as compared to non-infected plants [59]. AMF are suggested to possess a buffering effect in salt-affected soil by selectively uptaking K instead of Na, hence decreasing the salt load of plant cells. In rice plants infected with AMF, Na was sequestrated in root-cell vacuoles, thus limiting the toxic effect of Na accumulation in shoot cells [60], which resulted in enhanced photosynthetic activity and improved plant biomass accumulation in AMF-infected rice plants as compared to non-infected ones [60]. Osmotic adjustments were improved in AMF-infected plants due to the accumulation of sugars, prolines, and betaines (osmoprotectants) that also develop a favourable water gradient in roots even in higher Na concentrations in soil solutions. AMF also maintain a plant’s physiological functions, e.g., its ability to absorb water efficiently under saline conditions [61]. AMF enhance salinity tolerance in plants by modifying physiological and biochemical processes, i.e., increasing photosynthetic efficiency and improving nutrient availability, water uptake, and ionic homeostasis.

3.3. Heavy Metals

The chelation of heavy metals and their sequestration by fungi is an important perspective that can be utilized to sustain plant growth and development in heavy-metal-polluted soils. Glomalin, a protein produced by the hyphae of AMF, sequesters toxic metal ions that can be used as a tool for the biostabilization of metal-polluted soils. AMF are believed to enhance tolerance against heavy metals; however, this ability is largely influenced by plant and fungal species and the type of heavy metal present in the rhizosphere [62]. AMF regulate the allocation of heavy metals in plant parts by hindering their transport from root to shoot [63]. It was reported that the retention of heavy metals (cadmium (Cd), lead (Pb), Zn) in the roots of maize plants when the plants were associated with AMF [64]. Plants associated with AMF showed minor stress symptoms even with the presence of a high level of heavy metals in their tissues, proving the toxic effect was potentially decreased due to enhanced P nutrition and growth [62]. AMF hindered heavy-metal uptake in some plants. For instance, AMF associated with *Cnadulla officinalis* attenuated the effect of heavy metals by activating the antioxidant defence system and reducing the uptake of Cd and Pb [65].

AMF-induced biogeochemical alteration in the rhizosphere resulted in the immobilization of heavy metals. Prevention of As translocation in plants and immobilization of Zn in the rhizosphere by AMF was reported in several studies [66]. In the soil–plant continuum, the AMF effect chromium (Cr) translocation and transformation [67]. The immobilization of Cr was accomplished by reduction of Cr into Cr-phosphate analogues. Transformation of heavy metals in the rhizosphere can be accomplished by AMF through root exudate alteration, precipitation, acidification, and immobilization [68]. Heavy-metal-tolerant AMF species thrive and flourish in polluted soils and play a significant role in phytoremediation, which is believed to be the sustainable and ecological sound technology for heavy-metal-polluted-soil remediation.

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