





Review

Arbuscular Mycorrhizal Fungi Symbiosis to Enhance Plant–Soil Interaction

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Abstract: 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. There are some obstacles impeding the beneficial formation of AMF communities, such as heavy tillage practices, high fertilizer rates, unchecked pesticide application, and monocultures. Keeping in view the stress-extenuation potential of AMF, the present review sheds light on their role in reducing erosion, nutrient leaching, and tolerance to abiotic stresses. In addition, recent advances in commercial production of AMF are discussed.

Keywords: symbiotic relationship; nutrients; abiotic stresses; stress extenuation



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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].

The symbiotic association of AMF with plants traces back to prehistoric times. In fact, there is a synchronization between the shift in plants from the aquatic to terrestrial environment and their symbiotic relationship with fungi, implying that such an association might have enabled this transition [7]. In the process of evolution, 10% of plants lost this symbiotic association [8]. AMF are present in our natural environment and beneficial in several ways. They play an essential role in enhancing plant nutrition acquisition, increasing plant tolerance to and resistance against stresses, improving soil fertility and structure, and having numerous beneficial uses in agriculture [2]. AMF make an association with several plant species [9]. AMF–halophytes associations are evident in the literature. Large quantities of *Glomus geosporum* spores were observed in saline soils, indicating that AMF can thrive in saline soils. Sea wormwood, sea plantain, salt aster, and chamomile were reported to be heavily colonized by AMF many decades ago [10]. Several *Glomus* species thrive under drought and make associations with xerophytes. Plants release strigolactone as a response to drought stress, which serves as a signalling molecule for AMF. AMF then colonize the plants and help them to fetch water from a larger surface area [11]. AMF possess an aerobic life cycle; however, these are found in association with wetland plants and aquatic species throughout the world. However, there is a poor understanding of their functionality in such ecosystems [12]. Interaction between soil microorganisms is reported to have a positive impact on plants. AMF interact with other microbes in the soil, e.g., plant growth-promoting rhizobacteria (PGPR). Studies reported the synergistic effect of AMF and PGPR in enhancing plant growth and protection against pathogens [13]. Nitrogen (N) fixation in the soil is carried by *Rhizobia*. Studies documented that AMF and *Rhizobia* share the same signalling pathway, which triggers their association with plants [14]. A positive correlation exists between AMF colonization and soil microbial diversity [15].

Many researchers defined the role of AMF spores in various contexts in relation to various crops. In a mutual context, the plant provides carbon to the fungi by transferring carbohydrates [16]. The extent to which arbuscular mycorrhiza can be beneficial to plants depends on climatic situations. A plant with AMF has an advantage over those that lack this association [17] and has more resistance to diseases [18,19]. AMF are easily adapted to various habitats and a range of hosts. Their role in protecting plants during various stresses such as drought and heat is instrumental [20]. The diverse role of the mycorrhizal association in the soil–plant environment is depicted in Figure 1. The present review focuses on the importance of AMF and their role in plant nourishment, reducing soil erosion, heavy-metal immobilization, and plant growth regulation under stress conditions. Some aspects of the commercial production of AMF are also discussed.

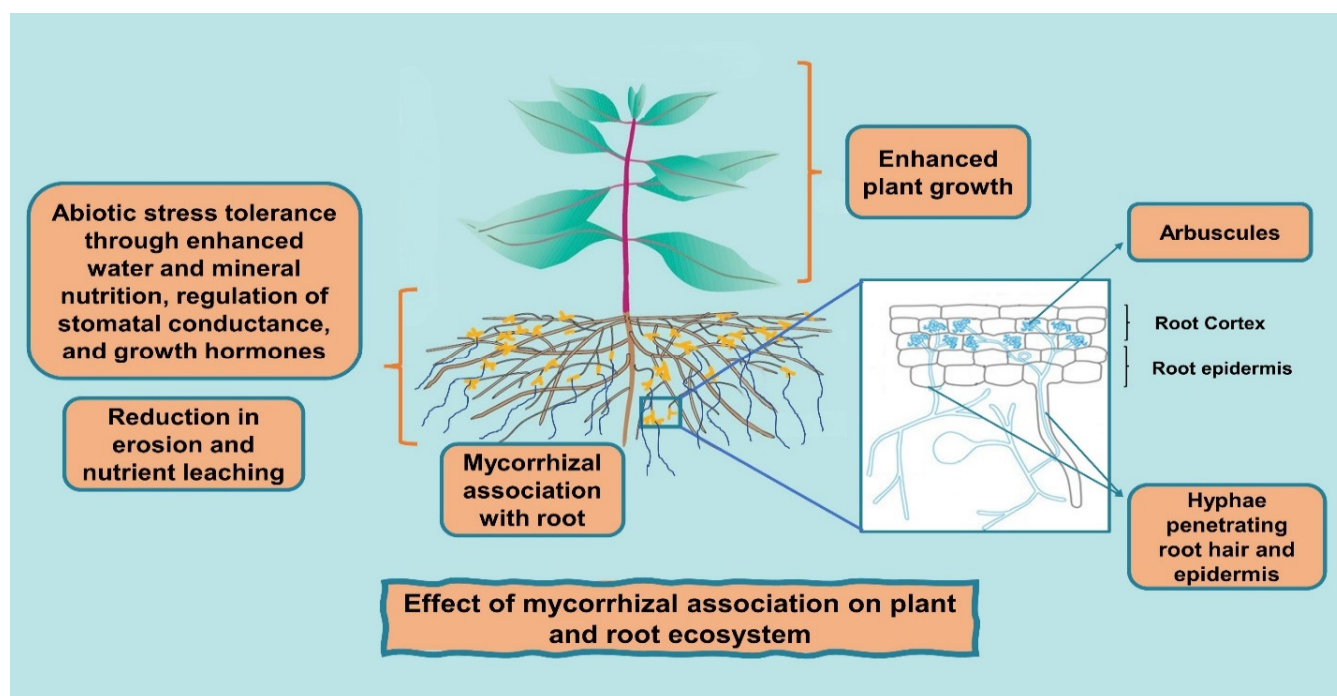


Figure 1. Graphical depiction of the effect of mycorrhizal association on plant and root ecosystem.

2. AMF and Nutrition Acquisition

An explicit function of AMF mutual association is the transfer and acquisition of nutrients by the plants [21]. AMF enhance the uptake of nutrients, especially P, in nearly all plants [22]. AMF improves growth and development in plants under low P and N [23]. The extent of AMF growth varies so that a lower AMP percent is realized under high soil P conditions [24]. 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 [25]. After uptake by hyphae, polyphosphates (polyP (negatively charged linear phosphate polymers)) are assembled in the cortical cells of rice after the hydrolysis of the polyP chain upon arrival in arbuscules [25]. 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 [26]. 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 [27,28]. Uptake of N by AMF can be accomplished in organic (amino acids) as well as inorganic forms (ammonium and nitrate ions) [29]. 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 [27]. 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 [30,31].

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 [32]. Evidence showed that inoculation of AMF in tomato plants exhibited increased K, N, P, and calcium (Ca) uptake and enhanced plant growth [33]. 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) [34,35]. AMF produce siderophores (ferricrocin, glomuferrin) [36,37], 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 [38].

Under drought environments, symbiotic association enhanced the amount of N, Fe, and P in Rose geranium [39], and pistachio plants inoculated with AMF depicted increased Zn, potassium (K), and P contents under such conditions [40]. AMF inoculated “garden mum” plants also contained a high level of N and P [41]. In addition, in Chinese ryegrass, it enhanced tissue water content and P [42]. A decreasing trend in the uptake of chlorine and sodium (Na) and an increased uptake of other nutrients were also linked to AMF [43]. Extraradical mycelium enhanced plant growth by enhancing the uptake of nutrients [44]. 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 [30].

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 [45]. Furthermore, AMF enhance N and carbon acquisition under increased levels of carbon dioxide [46]. Nevertheless, the acquisition of macro and micronutrients and their distribution in olive saplings developed under a high level of manganese were associated with AMF [47]. A symbiotic association between chickpea and AMF accumulated high protein content, Zn, and Fe [48]. Studies revealed that the function of the K^+ transporter was enhanced by AMF infection in the roots of birdsfoot trefoil [49], leading to a lower accumulation of Na, magnesium, and Fe [47]. 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 [50,51]. As AMF lower the use of inorganic fertilizers, it is considered that, in the future, AMF will be a substitute for chemical fertilizers [52]. Improved nutrition by AMF symbiosis is also the key to abiotic-stress tolerance, hence maintaining normal plant growth and development.

Role of AMF in Reducing Erosion and Nutrient Leaching

Biodiversity is severely affected by uncontrolled land use that endangers ecosystem processes [33]. 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 [53]. 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 [54]. 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 [55].

Frequent use of chemical fertilizers, pesticides, and herbicides poses problems to both human and soil health [56]. AMF act as a growth regulator in most terrestrial environments, and scientists have been persuaded to use AMF as a biofertilizer [57]. 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

Enhanced water and mineral nutrition in plants and structured rhizosphere are the direct beneficial outcomes of AMF that increase plant fitness to the environment. Plant

productivity and growth are badly affected by abiotic stresses, and the intensive use of pesticides and fertilizers has a harmful effect on our ecosystem. Besides altering the gene transcription and balance of phytochromes, AMF affect the physiological functions of plants leading to modified growth, development, and metabolism. AMF symbiosis goes far beyond the standard two-way movement of carbon and P; rather, it leads to multifaceted outcomes, which increase plant resistance to abiotic stresses [1]. When AMF are inoculated in the plant, they enhance the tolerance against different stresses such as drought, heavy metal, and high-temperature stress. AMF form spores and hyphae in the rhizosphere, while inside the root tissues, they form arbuscules, hyphae, and vesicles to increase the access of plant roots to large soil surface areas by hyphal network formation with roots of plants, thereby enhancing growth in the plant. This section will discuss the abiotic-stress tolerance induced by AMF symbiosis in plants.

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 [58]. 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 [59]. At an advanced stage of tissue dehydration, normal plant growth, development, photosynthesis, nutrient absorption, and metabolism are severely impaired [60]. 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 [61]. AMF can increase water uptake in drought conditions by the stabilization of soil structure and aggregation [62]. 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 [63].

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 [64]. AMF induce the ABA responses that control plant physiological processes and stomata [65]. 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 [66].

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 [67]. A total of 1125 million hectares of area is salt-affected worldwide [68]. 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 [69].

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 [70].

Contrarily, Na accumulation in the cell is considered to be highly toxic as it disrupts the structure of several enzymes [71]. 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 [71]. Hence, major determinants of salt-stress resistance in plants are reduced Na uptake and its exclusion and compartmentation [72].

The presence of AMF has been reported in many salt-affected soils [73]. AMF-infected plants depicted increased K uptake with reduced Na absorption as compared to non-infected plants [74]. 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 sequestered in root-cell vacuoles, thus limiting the toxic effect of Na accumulation in shoot cells [75], which resulted in enhanced photosynthetic activity and improved plant biomass accumulation in AMF-infected rice plants as compared to non-infected ones [75]. 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 [76]. 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 [77]. AMF regulate the allocation of heavy metals in plant parts by hindering their transport from root to shoot [78]. 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 [79]. 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 [77]. 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 [80].

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 [81]. In the soil-plant continuum, the AMF effect chromium (Cr) translocation and transformation [82]. 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 [83]. 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. Table 1 summarises previous studies on AMF's potential to mitigate abiotic stresses such as drought, salinity, and heavy metals.

Table 1. Some case histories of plant–AMF association leading to abiotic-stress tolerance.

Stress	Host Species	Fungus	Mechanism Involved	References
Drought stress	<i>Glycine max</i>	Arbuscular mycorrhizal fungi	Increased seed fresh and dry weight and photosynthesis	[84]
	<i>Triticum aestivum</i>	<i>Gigaspora decipiens</i> , <i>Glomus mosseae</i>	Enhanced growth, chlorophyll content	[85]
	<i>Triticum durum</i>	<i>Rhizophagus intraradices</i>	In grains, increased levels of Zn, manganese, Fe, and copper (Cu)	[86,87]
	<i>Olea europaea</i>	Arbuscular mycorrhiza	Increased uptake of minerals	[88]
	<i>Zea mays</i>	<i>Rhizophagus intraradices</i>	Enhanced K, N, and P uptake	[89]
	<i>Fragaria ananassa</i>	<i>Funneliformis geosporus</i> BEG11	Enhanced water usage efficiency	[90]
	<i>Antirrhinum majus</i>	<i>Glomus deserticola</i>	Enhanced level of proline and water, number of leaves	[91]
	<i>Vigna subterranea</i>	<i>Gigaspora gregaria</i>	Enhanced level of minerals and lower level of proline	[92]
	<i>Pontius trifoliata</i>	<i>Paraglomus occultum</i>	Improved rate of water absorption and length of the hypha	[93]
	<i>Digitaria eriantha</i>	<i>Rhizophagus irregularis</i>	Improve conductivity of stomata and dry matter of shoot	[94]
	<i>Ipomoea batatas</i>	<i>Glomus</i> species	Osmotic potential adjustment	[95]
	<i>Saccharum arundinaceum</i>	<i>Glomus</i> species	Improve the uptake of water, metabolites, phenolic, and glutathione levels	[96]
	<i>Pelargonium graveolens</i>	<i>Funneliformis mosseae</i>	Increase the contents of nutrients, essential oil, and biomass of plants	[97]
	<i>Robinia pseudoacacia</i>	<i>Rhizophagus intraradices</i>	Enhanced rate of photosynthesis and water-use efficiency	[98]
	<i>Foeniculum vulgare</i>	Arbuscular mycorrhizal fungi	High production of essential oil, main the concentration of salts	[99]
Salinity stress	<i>Malus domestica</i>	Arbuscular mycorrhizal fungi	Increasing the capacity of gaseous exchange, improving the fluorescence parameters of chlorophyll	[100]
	<i>Thymus species</i>	Arbuscular mycorrhizal fungi	Increases dry weight of root and shoot, pigments of photosynthesis	[101]
	<i>Cucumis sativus</i>	<i>Glomus intraradices</i>	Improved level of antioxidant enzymes	[45]
	<i>Oryza sativa</i>	<i>Claroideoglomus etunicatum</i>	The increased conductivity of stomata and the rate of photosynthesis	[6]
	<i>Solanum lycopersicum</i>	<i>Rhizophagus irregularis</i>	Increased fresh weight of roots and shoots and number of leaves	[102]
	<i>Aleurites moluccanus</i>	<i>Claroideoglomus etunicatum</i>	Enhanced conductivity of stomata and level of soluble sugars	[103]
	<i>Acacia species</i>	<i>Glomus fasciculate</i>	Increased level of Cu, Zn, and P	[74]
	<i>Aeluropus littoralis</i>	<i>Claroideoglomus etunicatum</i>	Enhance the dry mass of roots and shoots, and conductivity of stomata	[103]
	<i>Acacia nilotica</i>	<i>Glomus fasciculate</i>	Enhance biomass of root and shoot	[74]

Table 1. Cont.

Stress	Host Species	Fungus	Mechanism Involved	References
Cd toxicity	<i>Sesbania rostrata</i>	<i>Glomus mosseae</i>	Enhances concentration of N and P	[42]
	<i>Medicago sativa</i>	<i>Glomus aggregation</i>	Enhanced concentration of N and P in shoots and reduced cadmium concentration in shoots	[104]
	<i>Oryza sativa</i>	<i>Funneliformis mosseae</i>	Decreased uptake of cadmium	[105]
	<i>Triticum aestivum</i>	<i>Indigenous</i>	Enhanced growth in plant and decreased uptake of Cd	[106]
	<i>Lycopersicon esculentum</i> L.	<i>Funneliformis mosseae</i>	Increased growth in plant and restricted translocation of Cd from root to shoot	[107]
	<i>Zea mays</i>	<i>Rhizophagus clarus</i>	Enhanced dry matter production	[108]
	<i>Trigonella foenum-graceum</i> .	<i>Glomus clarum</i> , <i>Acaulospora laevis</i>	Enhances the function of antioxidant enzymes	[109]
Pb toxicity	<i>Populus cathayana</i>	<i>Funneliformis mosseae</i>	Enhanced P uptake under stress	[110]
Cu toxicity	<i>Phragmites australis</i>	<i>Rhizophagus irregularis</i>	Improved plant growth and development and also enhanced the rate of photosynthesis	[111]
Uranium toxicity	<i>Sesbania rostrata</i>	<i>Glomus etunicatum</i>	Increased biomass of plant	[112,113]
Arsenic (As) toxicity	<i>Trifolium repens</i> L.	<i>Glomus versiforme</i>	Increased antioxidant enzymes and dry biomass of plants	[113]
Nickel (Ni) toxicity	<i>Helianthus annuus</i> L.	<i>Claroideoglomus claroideum</i>	increased growth in plant	[114]
Mercury toxicity	<i>Zea mays</i>	<i>Glomus</i> sp., fungi from <i>Glomeromycota</i>	Enhanced biomass of plant and increased content of mercury in central cylinder of AMF colonized plants	[115]
Cu toxicity	<i>Carotalaria juncea</i>	<i>Rhizophagus clarus</i>	Increased plant growth and reduced phytotoxicity	[116]
As(III), As (IV) toxicity	<i>Oryza sativa</i>	<i>Rhizophagus irregularis</i>	Increased water use efficiency and chlorophyll concentration	[117]
Ni, Cd toxicity	<i>Daucus carota</i> L., <i>Corchorus olitorius</i> L.	<i>Glomus mosseae</i> , <i>Gigaspora margarita</i>	Improved plant growth and decreased accumulation of metals	[118]
Cd, Zn toxicity	<i>Canjanus cajan</i>	<i>Rhizophagus irregularis</i>	Improved fresh weight of root and shoot and area and leaf number	[119]
Cr, Ni, Cd, Pb toxicity	<i>Zea mays</i>	<i>Rhizophagus intraradices</i> , <i>Rhizophagus fasciculatus</i>	Enhanced concentration of chlorophyll and P and improved length of root and shoot	[120]
Pb, Cd, Cu, Zn toxicity	<i>Vetiveria zizanioides</i>	<i>Glomus mosseae</i>	Increased biomass and decreased stress	[121]
Ni, Cd, Cr, Cu, Cd toxicity	<i>Helianthus annuus</i> L.	<i>Funneliformis caledonium</i>	Increased plant growth. Absorption of P and reduced concentration of heavy metal in shoots	[93]
Cold stress	<i>Solanum melongena</i>	<i>Rhizophagus irregularis</i> , <i>Funneliformis mosseae</i>	Improving photochemical reactions, reducing the damage in the membrane, and activating the antioxidants defense system	[122]

Table 1. Cont.

Stress	Host Species	Fungus	Mechanism Involved	References
Heat stress	<i>Solanum lycopersicum</i>	<i>Rhizophagus irregularis</i>	Increased plant photosynthetic efficiency	[123]
Salinity-Alkali	<i>Legmus Chinensis</i>	<i>Glomus mosseae</i>	Enhanced water, P, and N concentration	[42]
Drought and salt stress	<i>Ricinus communis</i>	Arbuscular mycorrhizal fungi	Activating the growth of plant and enhancing the net stomatal conductivity, rate of transpiration, and photosynthesis, and reducing the intercellular concentration of carbon dioxide.	[93]

4. Commercial Production of AMF

Green technologies that pose a low impact on the environment and human health are gaining popularity and reducing the commercial share of agrochemicals. Plant bio-stimulants trigger plant nutrition regardless of the nutrient status of the product with an improvement in nutrient use efficiency and abiotic stress tolerance. Biostimulants can be of microbial and non-microbial origin, including AMF [124].

There is an increasing awareness and trend amongst the farming community about the beneficial effect of AMF. Many local and global ventures are preparing AMF inoculum/products that are easy to handle and can be easily transported and used for various crops. Though this practice is yet to be used on a large scale, the companies dealing with the marketing of mycorrhizal products have tremendously increased in the recent past. The main companies dealing with mycorrhizal products are present in Europe, Asia, North, and Latin America in the regional context. At present, firms dealing with the export of mycorrhizal products are mainly from U.S., Italy, Canada, and Spain. The top bio-stimulant selling market is the European market. The companies marketing AMF products have increased from 10 to about more than 75 from 1990 to 2017, as shown in Figure 2. The majority of firms are present in Italy, Spain, Belgium, France, Austria, and Switzerland, as shown in Figure 3. These products are used in agriculture, forestry, horticulture, and landscaping, as shown in Figure 4. In addition to the pure product of AMF, some products contain fungal inocula mixed with plant-promoting rhizobacteria [51].

AMF Marketing Firms in Europe

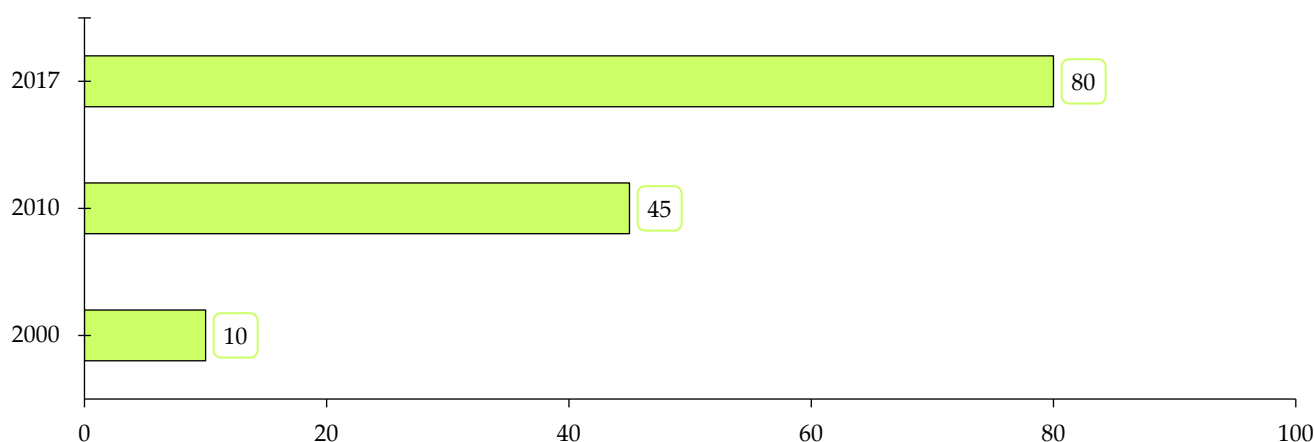


Figure 2. Arbuscular-mycorrhiza marketing firms are increasing in Europe; an internet survey was carried out on the no. of companies marketing inocula of AMF; based on foundation year, the companies were determined for three (2000, 2010, and 2017) time points (adapted from Chen et al. [125]).

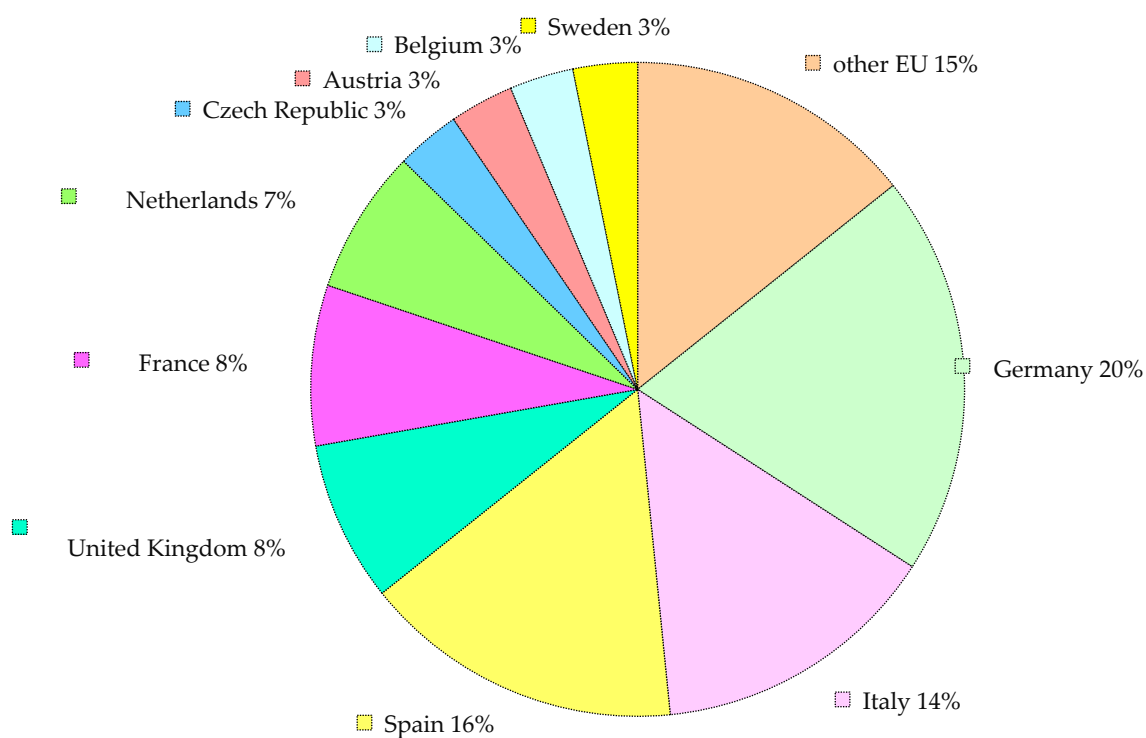


Figure 3. The pie-chart figure shows the leading countries producing AMF inocula, Germany, Italy, Spain, United Kingdom, France, and The Netherlands (adapted from Chen et al. [125]).

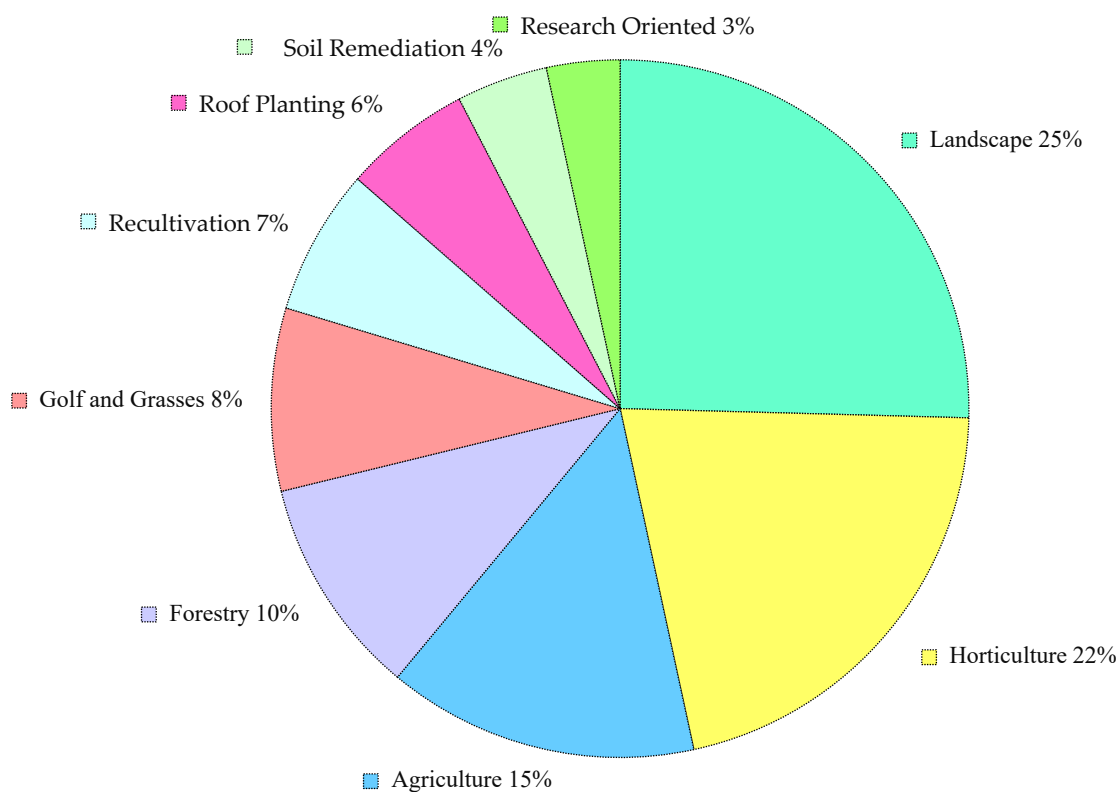


Figure 4. Area categorization on the basis of AMF product application (adapted from Chen et al. [125]).

The production of AMF is registered in the following three categories: biofertilizer, biostimulants, and bioprotectants. Any product containing microorganisms applied to

supply the major crop nutrients is termed as biofertilizers [126], and biostimulants are considered as a tool to mitigate the abiotic stresses in plants [127]. Bioprotectants are natural products that provide protection to plants against pests and pathogens [128].

Registration is carried out in accordance with the national rules of all E.U. state participants. In some instances, this monitoring procedure is costly. The International Mycorrhiza Society and The European Biostimulant Industry Council play a role in the promotion of biostimulants [125]. Basiru et al. [129] summarized seven countries to be major shareholders in AMF commercial production, including Canada, Spain, Italy, Czech Republic, United States, United Kingdom, and Germany; however, AMF commercial-production data is not available for Australia. After North America and Europe, Asia Pacific, including China, Taiwan, and India, are leading players in the AMF market. Moreover, South Africa and Kenya are leading in this market in Africa [129].

Nevertheless, more work is needed to broaden AMF-producing firms in developing countries and provide awareness about these products.

5. Conclusions and Future Prospects

Various studies proved the valuable role of AMF in improving plant growth and development under unfavourable conditions. AMF help in plant nutrient and water acquisition, reduce soil erosion, and enhance plant stress tolerance against drought, salinity, and heavy metals. AMF have been proven as a sustainable and environmentally benign source of crop supplements. It has been concluded that plants inoculated with AMF can successfully cope with different ecological extremes, including salinity, drought, low nutrient levels, and heavy metals present in the rhizosphere, and subsequently help to improve the per-hectare yield of crops. AMF can significantly help to lower dependence on synthetic fertilizers. It has a noteworthy effect in re-establishing deteriorated soils' productivity. A future insight into the underlying mechanisms controlling AMF-intervened development and signalling mechanisms will further pave the way for utilization in the agricultural system. Recognizing the systematic communications under field conditions, identifying useful strains of AMF or their blends, the impact of co-inoculation with other microbes, producing transgenic plants overexpressing the desired traits necessary to establish the symbiosis with AMF, and analysing the dynamic routes in this regard are some promising areas that need to be further explored.

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