

## ARBUSCULAR MYCORRHIZAL FUNGI (AMF): BIOLOGY AND THEIR ECONOMIC IMPORTANCE

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### Abstract

Arbuscular mycorrhizal (AM) fungi are ubiquitous symbiotic organisms that are linked to approximately 80 percent of the plants on land, which have a principal role in plant nutrition and in the functioning of the ecosystem. The review summarizes the existing information about the nature, utilization characteristics, and practical importance of AM fungi in sustainable agricultural application. The AM fungi support plant growth, and productivity by enhancing uptake of vital nutrients especially phosphorus and micronutrients, due to large networks of hyphae which spread outside the root zone. They also control the main physiological functions, such as photosynthesis, transpiration and water relations, hence enhancing the performance of the plants in varying environmental conditions. Host genotype, soil characteristics, and environmental conditions are the factors that affect the functional diversity of AM fungi as an entity that dictates the colonization efficiency and symbiotic success. Moreover, AM fungi have been found to confer plant resistance to abiotic stresses like drought, salinity, heavy metal toxicity by responding to the said factor through nutrient modulation, metal sequestration, and control of stress-responsive signaling. They also have a positive impact on soil structure and help to bioremediate the contaminated soil, which is yet another ecological value of this group. Moreover, the use of AM fungi as biofertilizers and their role in increasing crop yield and quality is also discussed in this review. Although they have some benefits, the large-scale commercialization faces problems including difficulties in mass production, strain specificity, quality control, and regulation. All in all, AM fungi is an effective solution to sustainable agriculture, just more studies are required to improve the efficiency of the widespread use of this technology and its functionality in the fields.

**Key words:** Arbuscular mycorrhizal (AM) fungi; Biofertilizers; Commercialization; Inoculants; Nutrient acquisition

### Introduction

The commercial application of mycorrhizal inoculants as biofertilizers has been on the rise in recent years because they are environmentally friendly having low-toxicity as well as because consumers increasingly seek healthy, non-toxic, or organic food (Dhiman *et al.*, 2022). However, in most regions of the world, a significant percentage of the population continue to depend on synthetic fertilizers and pesticides to fulfill nutrient needs and to protect crops as well against pests and diseases. Food safety and soil health are adversely affected because of continuous use of these chemicals (Kumar, 2022). Additionally, the use of synthetic pesticides over time interferes with the native microflora, which is rich and a vital part of productive soil and plant biodiversity (González-Escobedo *et al.*, 2022). It has also been reported in the literature that approximately 1% of applied fertilizers get to their target site, with the rest being washed into the soil and water, which pollute the environment (Timilsena *et al.*, 2015; Avila-Quezada *et al.*, 2022).

Arbuscular mycorrhizal (AM) fungi are a diverse and versatile group of mycorrhizae, being common symbionts of many plants, commonly found in symbiotic relationship with about 80% of the terrestrial flora, including bryophytes and tracheophytes (Saia & Jansa, 2022; Begum *et al.*, 2019). In symbiosis, AM fungi assist in plant energy

demands by cycling nutrients and regulating phytohormones and plants offer shelter and carbohydrates to the fungi. The multifunctionality of AM fungi, such as plant stress relievers against different abiotic and biotic elements, soil quality maintainers, and soil aggregators, is well-known (Latef & Chaoping, 2011).

Moreover, AM fungi also regulate the physiological activities of plants, such as photosynthetic rate, gaseous exchange, transpiration, and water absorption in different abiotic stresses (Begum *et al.*, 2019; Abdel-Salam *et al.*, 2018). Although AM fungi significantly contribute to the development of the arbuscules, spores, and hyphae in plant roots, this hyphae complex facilitates transfer of nutrients, carbon, and phosphorus to the host plant, hence, controlling growth and development (Bowles *et al.*, 2016; Madrid-Delgado *et al.*, 2021).

Consequently, this review gives an in-depth summary of arbuscular mycorrhizal (AM) fungi, its diversity, functional properties, biofertilizer applications, and its potential in stress management of heavy metals. It also references the commercial prospects of AMF-based products and the issues related to their industrialization on a large scale (Fig. 1).

**Functional diversity of AMF:** The AM fungi are ubiquitous which include over 200 different species belonging to the phylum Glomeromycota. They are often found within the plant rhizosphere, and published reports

indicate that AMF have been found in more than two thousand plant species, with additional ones being continually discovered (Parniske, 2008; Gough *et al.*, 2020). Despite the well-characterized AM fungal groups, a significant proportion of them are yet to be explored (Kew *et al.*, 2010).

The AM fungi are quite diverse, and minor variations in the morphology of the spores have been utilized in grouping them into distinct categories (Fitter, 2005). Differences in the production of spores can also affect colonization efficiency and hypha growth. Furthermore, symbiotic behavior, metabolic activities, and ecological services mainly depend on the diversity of AM fungal communities in host plants (Begum *et al.*, 2019). Some other studies also indicate that changes in the AMF community structure can influence plant productivity and microbial community structure. It is known that species diversity among host plants makes a significant contribution to plant productivity, plant biodiversity, and the functioning of the ecosystem (Lee *et al.*, 2013). AMF inoculation enhances plant growth by improving root morphology, biomass accumulation, and photosynthetic parameters such as stomatal conductance and transpiration (Liu *et al.*, 2026) (Fig. 2).

Molecular-based methods have made it possible to identify AMF diversity directly and to discover new species. Nevertheless, the genetic variation in AMF is difficult to describe because of the existence of multiple nuclei in one hypha or spore, resulting in the so-called multi-genomic structure (Kuhn *et al.*, 2001). Sanders *et al.*, (1995) were the pioneers to observe definite genetic variations even within a single spore.

The recent developments in omics technologies, such as genomics, transcriptomics, and single-cell sequencing, have provided a substantial boost to knowledge on the biology of arbuscular mycorrhizal fungi (AMF) and plant-fungus interactions. These methods can be used to identify genes, regulation pathways, and spatial-temporal interactions of nutrient exchange and symbiosis. As an example, phylogenomic studies and genome reconstructions have found complex evolution and genomic diversity in AMF (Montoliu-Nerin *et al.*, 2021) and recent co-transcriptomics studies identified clear stages of AM symbiosis in high spatial resolution (Serrano *et al.*, 2024). Additionally, new single-cell and high-resolution sequencing methods are also augmenting our knowledge about cellular interactions during AMF symbiosis (Somoza *et al.*, 2024).

Despite the well-known functionality of the various AMF strains and their mechanisms of action, the effectiveness of such strains depends on the host genotype. The AMF usually occur in the soil or in rhizosphere, and plant biochemical exudates like strigolactones (Madrid-Delgado *et al.*, 2021) and glomalin (Wu *et al.*, 2023a) have a very strong impact on the rhizosphere functioning and indigenous microflora (Begum *et al.*, 2019). Patterns of root exudation that depend on both host genotype and biotic as well as abiotic factors also influence functional interaction between plants and AMF (Kumar, 2022).

Nutrient acquisition, including carbon compounds translocation, photosynthates, and phosphorus between the host plant and AMF, are functional roles of AMF (van der Heijden *et al.*, 1998; Burleigh *et al.*, 2002). They also

determine colonization efficiency, and response of the host plants to fungal colonization (Johnson *et al.*, 1997). Though it is not clear how plants respond to AMF symbiosis, AMF inoculation has reportedly been effective in increasing plant productivity with the most common mechanisms involving phytohormone regulation and phosphate solubilization (Burleigh *et al.*, 2002; Angelard *et al.*, 2010; Lee *et al.*, 2013).

Both host plant and fungal genotypes may have a significant influence on the functional contributions of AMF. Angelard *et al.* (2010) reported that the strain *Glomus intraradices* specifically increased the rice productivity and biomass more compared to other AMF strains. Similarly, other traits, including the degree of extraradical development of mycelium and nutrient uptake also rely on AMF genotypes that result in plant growth (Wang *et al.*, 2023). The extraradical mycelium uptakes the minerals, mostly phosphorus, in the soil and relocates it to the host. However, within AMF isolates of the same source, there can be mycelial spread, viability, structure and anastomosis potential differences (Sanders *et al.*, 1977; Giovannetti *et al.*, 2001). Moreover, the existence of several families of phosphate transporters and their gene expression patterns under the regulation of phosphorus can considerably affect the nutrient uptake potential of AMF strains to their host plants (Maldonado-Mendoza *et al.*, 2001; Madrid-Delgado *et al.*, 2021).

**Functional aspect of AMF:** The efficacy of AM fungal species in the colonization process is dictated by various factors, such as the environmental conditions, such as availability of nutrients, pH, temperature, moisture content, salinity, and drought (Abd\_Allah *et al.*, 2015). Experimental evidence has shown that plant species that have mycorrhizal associations have greater acclimatization and other selective benefits than non-mycorrhizal species (Hashem *et al.*, 2016). The AM symbiosis is known since the initial stages of plant evolution, and it is found in a significant proportion of plant taxa (Chen *et al.*, 2018). Host plants have the ability to associate with various AM fungal groups or other fungi and the association may be beneficial, neutral or sometimes pathogenic. Host plant identity greatly affects the interactions, sporulation, and proliferation of AM fungi (Bever, 2002), although AM fungi tend to be relatively less selective in host colonization.

The hyphae of AMF are extremely thin and are able to extend into the soil beyond the root system of the host and into areas that would not be accessible to the root (Koide, 2000; Jakobsen *et al.*, 2003). As a result, AMF is important in promoting the growth of plants, even in nutrients deficient areas (Nouri *et al.*, 2014). Phosphorus is stored in arbuscules, which are branched structures developed in the interior cells of roots (Balestrini *et al.*, 2015). AM association has been shown to increase nutritional uptake of plants and tolerance to both abiotic and biotic stresses, including salinity and drought (Begum *et al.*, 2019), and root pathogens (Pozo *et al.*, 2009) (Fig. 3). However, high phosphorus concentration in the soil might considerably decrease the positive activity of AMF, because AMF colonization is reduced in plants in such conditions (Konvalinkova & Jansa, 2016).

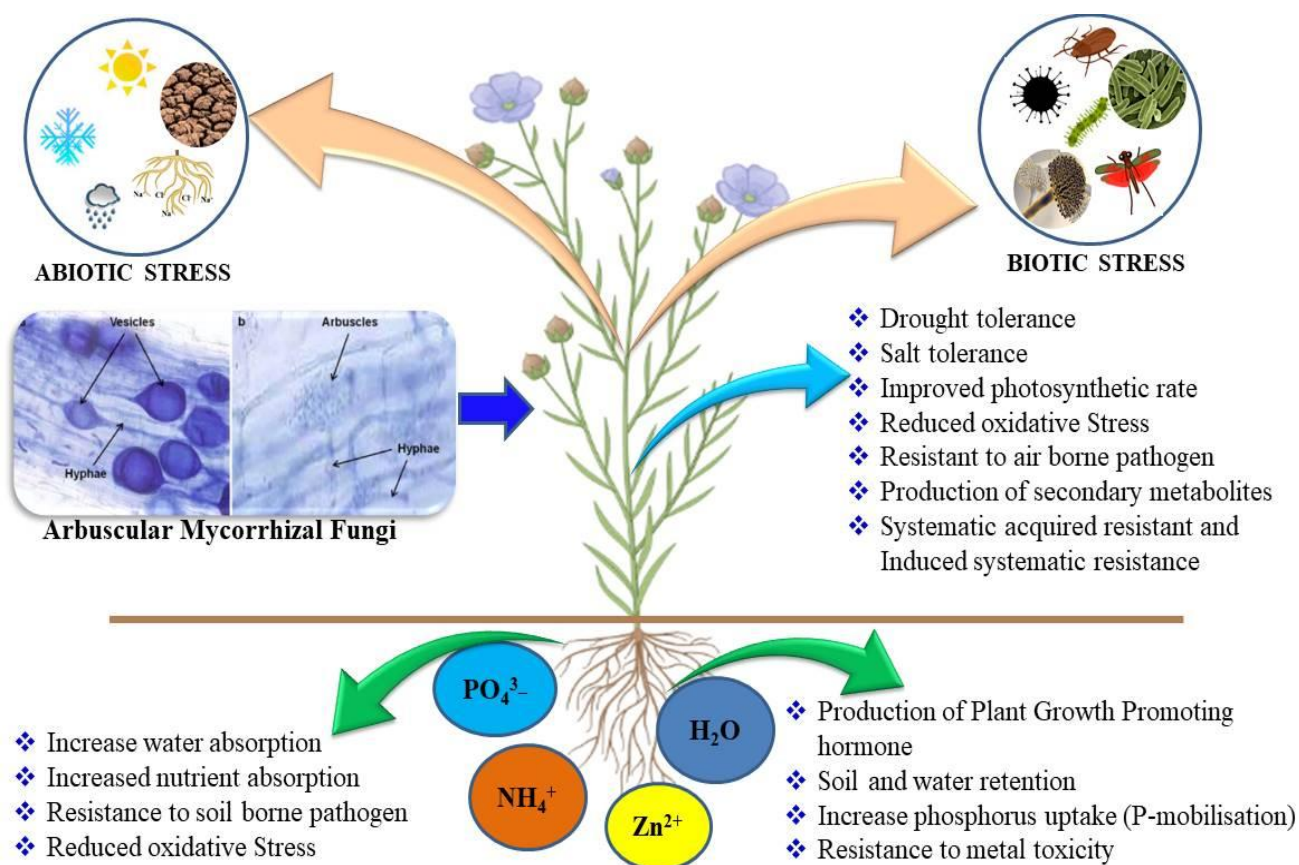


Fig. 1. An overview of arbuscular mycorrhizal fungi (AMF) and their function (created with BioRender.com).

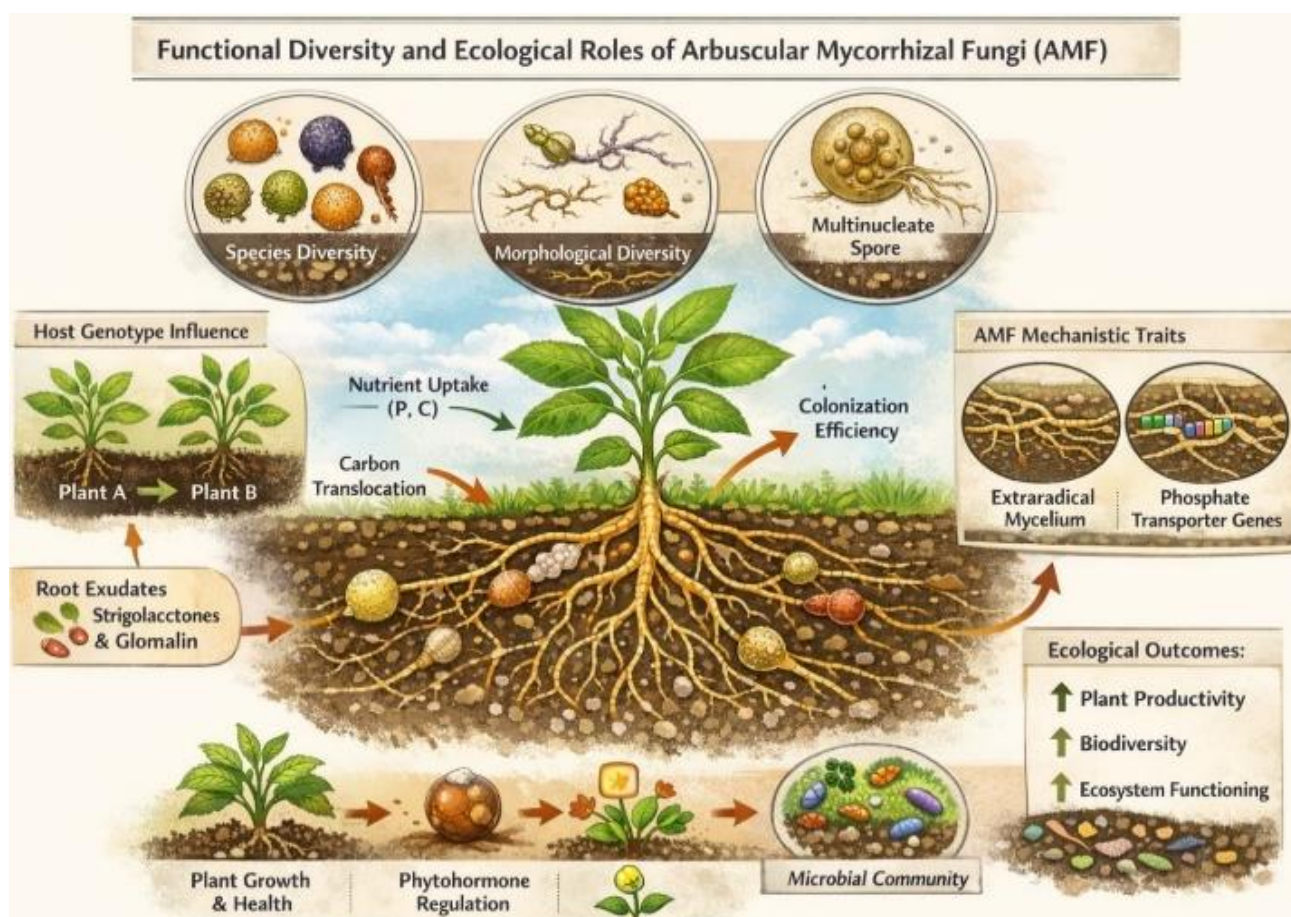


Fig. 2. Functional diversity and ecological roles of arbuscular mycorrhizal fungi (AMF) (created with BioRender.com).



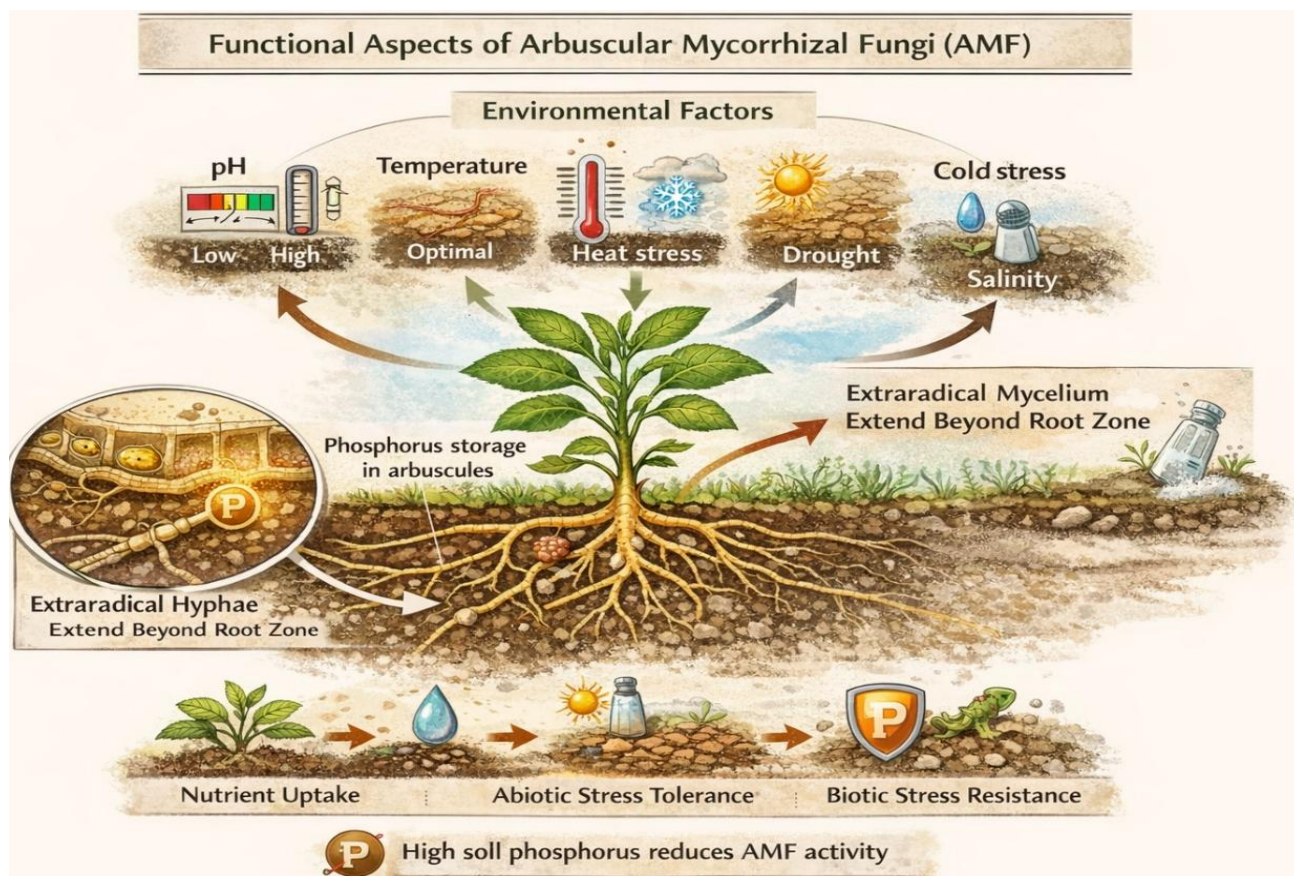


Fig. 3. Functional aspects of arbuscular mycorrhizal fungi (AMF) in plant growth and stress tolerance (created with BioRender.com).

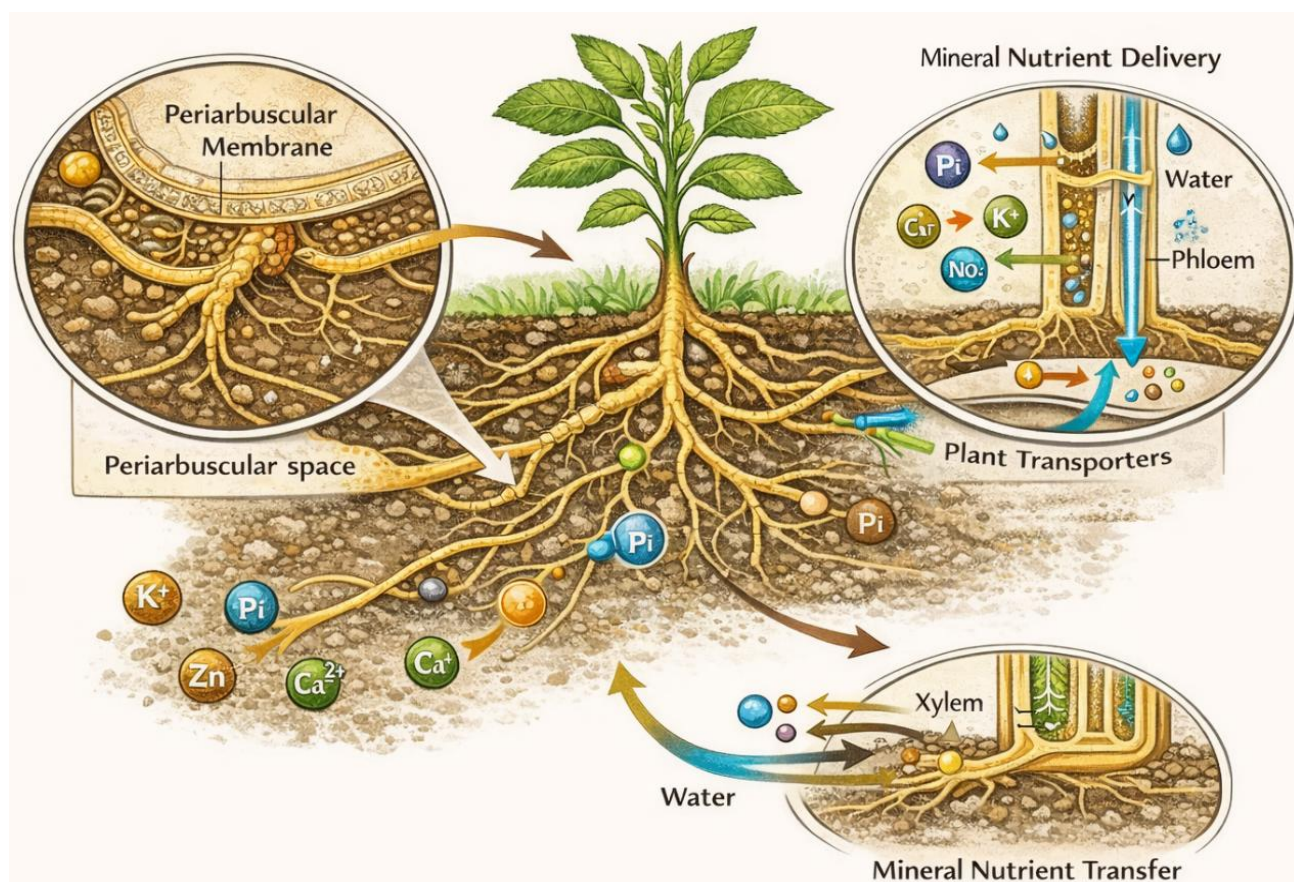


Fig. 4. Symbiotic association of arbuscular mycorrhizal fungi (AMF) with plant roots and their role in nutrient acquisition (created with BioRender.com).

### **Symbiotic association of AMF and their role in nutrient acquisition:**

Post-Endomembrane Mineral nutrient transfers in AM symbiosis are believed to happen at the periarbuscular membrane, a plant-derived membrane which encloses the arbuscule. This membrane has transporters that facilitate the absorption of mineral in the periarbuscular apoplast and the subsequent transmission of mineral to cortical cells (Bapaume & Reinhardt, 2012). The AM fungi have found extensive application in nutrient uptake of the soil and their symbiosis with crops has been reported to improve crop quality and crop productivity (Iggehon & Babalola, 2017). It has been reported that AM symbiosis enhances the transportation of important elements, including  $K^+$ , Zn, and Pi, which promote plant acclimatization and resistance to numerous abiotic stressors (Begum *et al.*, 2019; Garcia & Zimmermann, 2014). Lehmann *et al.*, (2014) reported that AM symbiosis enhanced Zn levels in different tissues of crops and this effect was dependent on soil pH, nutritional composition, and texture. Correspondingly, Lehmann & Rillig (2015) affirmed that AMF-host plant symbioses have a profound effect on the uptake of micronutrients. Successful AMF colonization forms intraradical and extraradical hyphal networks that increase the nutrient absorption area of plant roots and improve phosphorus uptake efficiency (Liu *et al.*, 2026) (Fig. 4).

Wu *et al.*, (2023b) found that AMF inoculation, especially members of the *Rhizophagus* genus, led to a significant increase in the leaf N, P and K concentrations, but the leaf stoichiometry was also species-specific as well as growth stage and AMF species. According to Silveira *et al.*, (2023), AMF inoculation of coffee seeds and the subsequent growth under standard substrates enhanced coffee seedling growth. Similarly, Tuheteru *et al.*, (2022) studied that AMF inoculation enhanced the availability of nutrients in *Pericopsis mooniana*. Pellegrino & Bedini (2014), also demonstrated that AMF inoculation enhanced yield and grain quality in chickpea by enhancing protein, iron (Fe) and zinc (Zn). Walder & van der Heijden (2015) noted that the degree of symbiosis and nutrient exchange was determined by the degree of mutual relationship, the level of nutrient in soil, and environmental condition.

It has been observed that AMF inoculation has been effective at increasing levels of macro- and micronutrients vital to the physiological processes of the plants. This nutrient fortification enhances further the photosynthetic production rates, which finally results in a higher plant biomass (Chen *et al.*, 2017). It has been noted in earlier research that essential elements, including Zn and Cu, are better absorbed after AMF inoculation (Smith & Read, 2008; Kayama & Yamanaka, 2014). Symanczik *et al.*, (2018) observed better nutrient uptake when AMF strains were used in *Sorghum bicolor*. Balliu *et al.*, (2015) noted better leaf area and N, K, Ca, and P concentrations in tomato seedlings inoculated with AMF. Fall *et al.*, (2023) revealed that NPK fertilization optimally coupled with AMF inoculation enhanced the growth of maize and the nutrient content of the soil.

Also, AMF are vital in promoting phosphorus availability to host roots in P-deficient condition (Bucher, 2007). In case of nutrient deficiency AMF induce transporter genes to enhance nutrient assimilation, comprising Pi transportation, hormonal communication,

and microRNA control (Mitra *et al.*, 2023). The AMF-colonized corn showed much better Pi uptake (Garcés-Ruiz *et al.*, 2017). Amiri *et al.*, (2017) observed that under drought conditions, AMF inoculation increased N, P, and Fe in *Pelargonium graveolens*, and Gomez-Bellot *et al.*, (2015) reported that AMF inoculation increased P, Ca, and K in *Euonymus japonica*. Furthermore, Wang *et al.*, (2018) reported an increase in P and N levels in *Chrysanthemum morifolium* following AMF inoculation.

The AMF genera vary in the efficiency of phosphorus uptake. For example, Tatewaki *et al.*, (2023) have found variations in nutrient uptake among *Dentiscutata cerradensis*, *Cetraspora pellucida* (Gigasporaceae), *Acaulospora morrowiae*, and *A. longuna* (Acaulosporaceae) inoculated on maize roots in Japan. Even though transfer and uptake of nutrients are a complicated process, extraradical mycelia are amongst the key players in nutrient absorption as it increased the growth and development of plants. AMF develop massive underground extraradical networks which grow beyond roots and mediate nutrient transfer (Battini *et al.*, 2017) and enhance plant performance even in stress conditions. For example, Liu *et al.*, (2023) reported that AMF inoculation enhanced salinity tolerance in tomato by controlling aquaporin and salt stress sensitive genes, and Wang *et al.*, (2023) demonstrated that AMF altered transcription factors when plants experienced drought stress. Solórzano-Acosta *et al.*, (2023) reported that *Persea americana* var. *zutano* showed increased stress tolerance after AMF inoculation. Moreover, *Diversispora spurca* showed the highest colonization rate and strongest effect on plant growth and root development (Liu *et al.*, 2026). AMF inoculation can enhance plant tolerance to stress and regulate the production of important bioactive compounds such as resveratrol, polydatin, and anthraquinones (Zhang *et al.*, 2025).

**AMF as bio-fertilizer:** Microbial-based biofertilizers are some of the most viable methods used in sustainable farming practice, as they provide a cost-effective and environmentally-friendly solution. AM fungi are widely used for nutrient acquisition, water and moisture content maintenance, mineralization as well as increased tolerance to different biotic and abiotic stresses. Traditionally, AM fungi are inoculated in the target soil directly during the agricultural production (Berruti *et al.*, 2016; Aziz *et al.*, 2023).

Last two decades have seen the use of microbial inoculants or biofertilizers or combinations of naturally occurring substances applied to agricultural fields to enhance soil fertility and plant and soil productivity. These biofertilizers have been reported to contribute enormously to the productivity of agriculture even in stressful conditions in a sustainable way (Sadhana, 2014). The positive, sustainable, and economical functions of AMF in crop yield have been emphasized by a number of studies (Ortas *et al.*, 2013; Iggehon & Babalola, 2017). Inoculation with *Glomus mosseae* and *G. intraradices* enhanced relative water content, chlorophyll and carotenoid content in *Capsicum annuum* L. significantly, even after a prolonged exposure to salt stress (Çekiç *et al.*, 2012). Inoculated tomatoes showed increase in biomass quite significantly in addition to enhancing the nutrient levels (Ortas *et al.*, 2013). Similarly, Ziane *et al.*, (2017) also reported enhanced growth and yield of tomato after AMF inoculation.

Cely *et al.*, (2016) have reported the improved growth of soybean and cotton following inoculation with *Rhizophagus clarus* in the field. According to Carrara *et al.*, (2023) AMF inoculation raised potato tuber yield and antioxidant activity significantly. Javanmard *et al.*, (2023) noted that the use of AMF together with nitrogen fertilizers resulted in significant enhancement of plant height, number of nodes and leaves per plant, dry matter, and yield per plant of peppermint under varying irrigation conditions. Similarly, Alam *et al.*, (2023) reported that the root length and shoot mass of tomato plant increased after inoculation with *R. clarus* and *P. occultum* strains.

**The role of AMF in metal stress management:** Within the last two decades, rapid industrialization and anthropogenic processes resulted in the accumulation of different heavy metals in agricultural fields, thus causing toxicity that negatively impacted both soil and plant quality, and consumer health (Rai *et al.*, 2019). Though some metals are needed in optimum quantities to facilitate healthy plant physiology and metabolism, still higher levels would be toxic, which may lead to plant degradation or even plant death. Also, heavy metals are non-biodegradable and can accumulate in the tissues of edible plants, entering the human and animal food chain and causing serious health risks (Zwolak *et al.*, 2019). Cadmium in rice and the accumulation of heavy metals in vegetables are good examples of such food chain transfer that are well documented (Huang *et al.*, 2018; Tefera *et al.*, 2021).

Over the past years, different AMF species have been used to alleviate heavy metal stress (Sousa *et al.*, 2012). The predominant ones include the trapping of the toxic metals in the wall or vacuole of the cell, and others AMF species sequester metals in the cytoplasm, thus saving the host plant against heavy metal toxicity (Riaz *et al.*, 2021). The importance of AMF to reduce heavy metal stress and improve agricultural productivity has been reported in previous studies (Patel *et al.*, 2022). In addition to the decrease in the bioavailability of toxic metals, AMF inoculation positively regulates plant physiological and morphological characteristics (Miransari, 2017). Furthermore, Shen *et al.*, (2006) reported that AMF improved cadmium mobility through improving soil pH that decreases plant stress.

Moreover, AMF could be used to enhance the absorption of heavy metals by different plant species planted in polluted soils, which implies their bioremediation capability. However, there is a need to conduct more studies on the AMF community structure and metal-tolerant mycorrhizal strains that would be used with metal-accumulating plants to treat contaminated farmland (Fig. 5).

**Commercialization aspect of AM fungi and their hurdles:** In agricultural productivity, AM fungi have frequently been applied as bio-stimulants or microbial inoculants in both controlled and field systems. The industrial and commercial potential of AM fungi has taken momentum in recent years. A study revealed that the market value of mycorrhizal-based biofertilizers had reached around 2.3 billion USD in 2022, and there was an average annual growth rate of 14.08% (Basiru *et al.*, 2021).

Although technology has advanced, the world market of AMF products is still in its initial phases because of poor government policies, domination by commercial organizations, technical constraints, stringent regulations and inconsistent effectiveness of AMF products. This has been due to poor handling of the live strains following production, which may lose its viability with time or exposure to high temperatures and sunlight, leading to low efficacy. Nevertheless, the rise of consumer awareness about organic food and the activities of agricultural products with a green supply chain has sparked interest in AMF, which is one of the main biological fertilizers commonly used in sustainable farming (Fig. 6).

The absence of harmonized regulatory systems by different countries is a significant obstacle to AMF commercialization, as it limits the movement of international products. To solve this, the European Parliament is considering policies of free trade of biostimulants in the EU countries (Vosátka *et al.*, 2008). There are still growth opportunities in commercial application of AMF products since they possess multiple advantages, sustainability, economic feasibility, and low toxicity (Fig. 6).

Mycorrhizal products are still dominated by small private enterprises so the precise market statistics are hard to determine. Over the past years, a number of commercial companies have commercialized mycorrhizal products as biofertilizers or biostimulants (Vosátka *et al.*, 2008), with strong markets in North America, Europe, Asia and Latin America. The most active region is the European Union; e.g., the number of firms that promote mycorrhizal products grew to more than 75 in 2017 compared to 10 in the 1990s. In Asia, India and China serve as the primary manufacturers and retailers of mycorrhizal products (Chen *et al.*, 2018). AMF inoculation can cost between 10 and 50 cents per unit, which equates to roughly 135 USD per hectare of potato farming in the United States (Hijri, 2016) (Fig. 6).

Some AMF strains are now commercially available as biofertilizers all over the world. Their obligate and biotrophic character, however, poses a problem to large-scale commercialization. Pure AMF inoculum isolation is also technically challenging since the majority of the species are found in association with the host plants and cannot be easily cultured in axenic cultures. Commercialization is further complicated by contamination of other microbial or pathogenic species during isolation or production. Thus, the appropriate industrial production of AMF inoculants requires microscopic quality control, contamination-free transportation, and the maintenance of axenic conditions when preparing the inoculum (Vosátka *et al.*, 2012; Fernández *et al.*, 2007; Basiru *et al.*, 2021; Salomon *et al.*, 2022a) (Fig. 6).

Latest studies elucidate that the commercialization of AMF-based products is still facing numerous obstacles, such as differences in quality of inoculum, storage issues, and lack of stability in the field performance. Such concerns can be attributed to the biological complexity of AMF and challenges in sustaining viable and effective propagules at large scale. This leads to increased demand of uniform production technologies, quality control systems, and better regulatory models that would enable uniformity and effectiveness of commercial inoculants (Salomon *et al.*, 2022b).



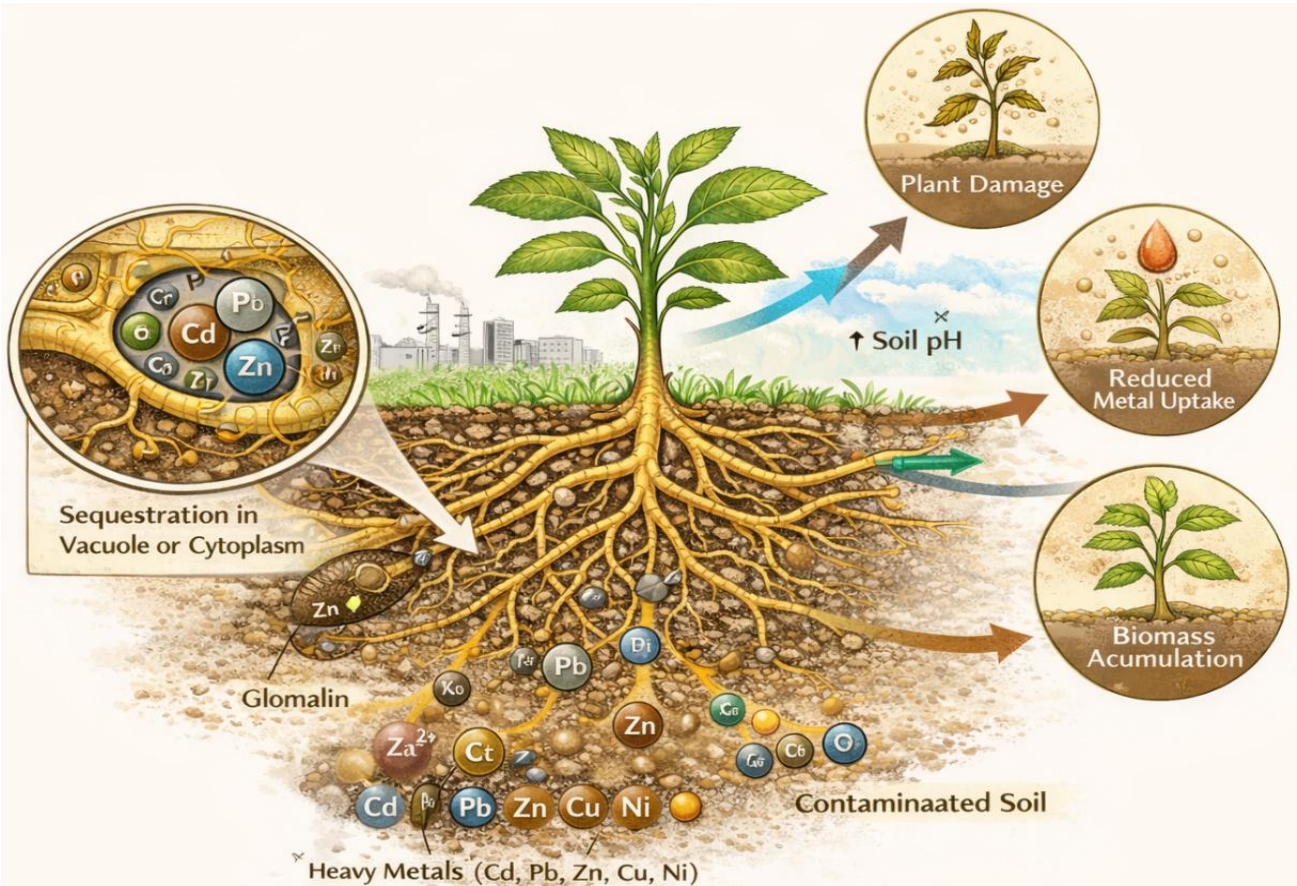


Fig. 5. Role of arbuscular mycorrhizal fungi (AMF) in alleviating heavy metal stress in plants (created with BioRender.com).



Fig. 6. Commercialization aspects and challenges of arbuscular mycorrhizal fungi (AMF) (created with BioRender.com).

## Conclusion

Arbuscular mycorrhizal (AM) fungi are an important aspect of sustainable agriculture because they have multiple purposes in plant development, nutrient uptake and soil health enhancement. Their mutualism with a large variety of plant species increases the absorption of key macro- and micronutrients, especially phosphorus, in addition to augmenting physiological functions like photosynthesis, water use efficiency, and the overall vitality of plants. The AM fungi grow large hyphae networks that greatly increase the area of the root surface, which allows plants to grow in nutrient-limited conditions. In addition to nutritional value, AM fungi are also important in alleviating abiotic stresses, such as drought, salinity, and heavy metal toxicity, via nutrient regulation, metal binding, and regulation of stress-responsive pathways. Their role in soil aggregation and maintenance of soil microbial balance further demonstrate their ecological significance and role in sustainable farming systems. Although these benefits exist, the large scale commercialization is still limited to issues like limitations in mass production, strain specificity, contamination risk, and poor field performance. Further studies should be done on the identification of highly efficient and stress resistant AMF strains, establishment of cost effective and scalable technologies in the production of inoculums as well as incorporation of AM fungi into precision agriculture and other biofertilizers. Moreover, it will be essential to standardize the regulatory framework and field validation in different agro-ecological conditions to further increase their adoption globally. By developing these areas, it will be possible to effectively convert AMF-based technologies into viable, climate-resilient agricultural solutions. Importantly, future studies incorporating state-of-the-art omics technologies with better large-scale production technologies will be needed to increase the consistency, efficiency, and international applicability of AMF-based biofertilizers.

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