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Responsiveness of arbuscular mycorrhizal symbiosis in plants during abiotic stress

Saumya Dubey, Tanvi Tripathi, Shikha Tripathi, Vivek Kumar, Shahrukh Hasan, Salman Khan, Avinash Pratap Singh*

Microbiology and Plant Pathology Laboratory, Department of Botany, C.M.P. Degree College, University of Allahabad, Prayagraj, India

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Correspondingauthor:

Avinash Pratap Singh

Email: avinashsinghau@gmail.com

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) can penetrate plant roots and form arbuscules for nutrient exchange. Plants have evolved a complete symbiosis system to sustain growth and development under abiotic stress. Mycorrhizal symbiosis and host plant interactions play an important role in enhancing mineral nutrient absorption, hormone production, and making the plant capable of drought tolerance, salt resistance, and mitigating heavy metal stress reduction. Research on AM symbiosis and abiotic stressors can benefit sustainable agriculture by improving plant yield and environmental safety. In this review, we discussed the role of genes responsible for the establishment of AM symbiosis and also their involvement in mineral nutrient absorption, hormonal control, resistance against heavy metals, drought and salt tolerance. This article also covered recent studies on AM symbiosis and its regulation.

Keywords: Arbuscular mycorrhizal fungi, Role of genes, AM Symbiosis, Mineral nutrients, Hormone production, Drought and salt stress, Heavy metal stress

INTRODUCTION

Mycorrhiza fungi are classified into 7 broad categories based on their physical and anatomical properties, as well as the fungus and plant species involved (Table 1). Arbuscular mycorrhizas (AMs) are the most common form of mycorrhiza found in nature, and about more than 72% of terrestrial plants play crucial roles in the rhizosphere (Genre *et al.,* 2020). According to Bonfante and Venice (2020), arbuscular mycorrhizal fungi (AMF) are placed in sub division Glomeromycota of the division Mucoromycota. AM production is the outcome of long-term co-evolution between AMF and plant roots (Genre *et al.,* 2020; Rich *et al.,* 2021). AMs consist of hyphae, arbuscules, and spores, with fewer species having vesicles and auxiliary cells.

According to Gao *et al.* (2021) and Xie *et al.* (2022), extraradical mycelia may take water and nutrients in regions not accessible to plant roots. Extrinsic mycelium enters the root of epidermal cells and cortical tissue, forming a dendritic arbuscular structure with continuous bifurcation. According to Pimprikar and Gutjahr (2018), arbuscules play a crucial role in the flow of nutrients between plant cells and fungi. Mycorrhizas are considered the most important structural component of an ecosystem. It plays a crucial role in influencing plant growth, water use, nutrition, and hormone balance in response to abiotic stimuli (Khan *et al.,* 2024). AMs play a significant role in increasing plant biomass (Chitarra *et al.,* 2016; Chen *et al.,* 2017; Huang *et al.,* 2020a; Zhang *et al.,* 2023). AMF can broaden the absorption range of host plants in soil by effectively invading root epidermal cells and forming symbionts.

Mycelia manufacture glycoproteins that provide a favorable rhizosphere environment, enhancing plant development by absorbing and transferring water and minerals from the surrounding rhizosphere (Hu *et al.,* 2017), and the rhizosphere is full of microbes, which can help the enhancement of nutrient uptake (Khan and Singh, 2024). AMF form a direct connection between the soil and the roots, which improves plant nutrition absorption, water uptake, and photosynthetic rate, reducing the negative effects of abiotic stresses like nutrient deficiency, salt, and drought (Li *et al.,* 2013; Liu *et al.,* 2018; Bahadur *et al.,* 2019; Begum *et al.,* 2022; Khan *et al.,* 2025). Application of *Rhizophagus clarus*, AM fungi responsible for facilitating nutrition exchange between the host plant and fungal symbionts through transporting aquaporin 3 to polyphosphate from hyphae to the host (Kikuchi *et al.,* 2016). In *Medicago truncatula*, the membrane protein MtPT4 in mycorrhizal roots may absorb inorganic phosphate (Pi) produced by AMF, which is advantageous to plants and required for AM symbiosis (Harrison *et al.,* 2002; Javot *et al.,* 2007). AMF not only promotes plant development and nutrient absorption but also enhances heavy metal tolerance (Gómez-Gallego *et al.,* 2019; Chen *et al.,* 2023). AMF's produce organic acids, such as citric and malic acid, which can form complexes with metals. Extrinsic mycelium can chelate and filter metal ions, making them ideal for bioremediation (Huang *et al.,* 2021). The impact of AM symbiosis on plants for abiotic stress reduction is presented in Table 2.

Establishment of AM symbiosis

Arbuscular mycorrhizal symbiosis involves the production of arbuscules that facilitate nutrient exchange between plants and AM fungi. Symbiosis between plants and AMFs follows a regular pattern (Oldroyd, 2013). *Rhizophagus irregularis* is an auxotroph of fatty acids, which are required for AM colonization with plant roots. RAM2 and the ATP-binding cassette transporter have a role in transferring fatty acids between host plants and fungi (Jiang *et al.,* 2017). According to Luginbuehl *et al.* (2017), lipids are the predominant source of organic carbon transported from host plants to AMF. RAM1, a transcription factor, plays a critical role in AM symbiosis by controlling the activity of glycerol-3-phosphate acyltransferase RAM2, which transfers lipids between host plants and AMF. Plants that participate in AM symbiosis require the lipid biosynthesis enzyme FatM and the ABC transporter

(STR) during the early stages of symbiosis (Bravo *et al.,* 2017). These enzymes are conserved. ERM1 and WRI5a transcriptional activators activate FatM, STR, and STR2 genes, which are crucial for fatty acid production and transport, by binding directly to their promoters. In arbuscule-containing cells, the transcriptional regulatory complex ERM1/WRI5a-ERF12-TOPLESS is crucial for maintaining a stable and beneficial symbiosis (Zhang *et al.,* 2023). AMF may acquire both fatty acids and carbohydrates from host plants throughout their mature stage. MtSWEET1b, a member of the Sugar Will Eventually Exported Transporter (SWEET) family, is highly expressed in arbuscule-containing cells. This gene plays a crucial role in transporting glucose and stabilizing AM symbiosis in *Medicago truncatula* AM symbiosis (An *et al.,* 2019). AM symbiosis involves several genes, including those linked to fatty acid and sugar metabolism. Under low phosphorus (P) circumstances, the expression of carotenoid cleavage dioxygenases CCD7 and CCD8 increases, leading to the production of strigolactones (SLs) and their release outside the root system via the transporter PDR (Kretzschmar *et al.,* 2012). When AMF detect SLs released by plant roots, their metabolism is increased in vivo, causing mycelia to develop near the plant's root and potentially become a host (Besserer *et al.,* 2008).

Table 1. Type of mycorrhiza and its physical and anatomical properties, including the fungus and plant species (Wang *et al*., 2024)

Types	Function	Structural diversity
Arbuscular mycorrhiza (AM)	Symbiosis with 72% of terrestrial plants enhances host resistance, promotes development, and supports the survival of mycorrhizal fungi.	Hyphae invade cells, forming arbuscules, intracellular circles, and dichotomous branches.
Ectomycorrhiza (ECM)	Produce proteases, which break down proteins and deliver nitrogen to host plants.	Form a hypha diaphragm, Mycoclena, and Hartig net
Ect-endomycorrhizas (EEM)	Responsible for both AM and ECM tasks.	Hyphae invade cells, forming a diaphragm, mycelia, hartig net, and an intracellular mycelium circle.
Arbutoid mycorrhizas (ARM)	Symbiosis with Arbutus menziesii, Arctostaphylos uvaursi, and Pyrola to improve host nutrition and stress resistance	Hyphae penetrate cells, forming the hypha diaphragm, mycoclena, Hartig net, and intracellular hypha circle.
Monotropoid mycorrhiza (MM)	Symbiosis with Monotropa plants provides a carbon source for host plants.	Hypha enters cells, forming the hypha diaphragm, mycoclena, and Hartig net.
Ericoid mycorrhizas (ERM)	Symbiosis with Ericaceae and Epacridaceae enhances nutrient uptake and tolerance to heavy metal contamination in host plants.	Hypha enters cells, forming a diaphragm and an intracellular hypha circle.
Orchid mycorrhiza (OM)	Symbiosis with Orchidaceae to enhance seed germination, nutrient transport, signal transduction, and stress resistance of orchids.	Hypha enters cells, forming a diaphragm and an intracellular hypha circle.

This shows that SLs are not the only relevant signaling molecules in the pre-contact period (Nadal *et al.,* 2017). DELLA protein interacts with CCaMK and CYCLOPS, activating the downstream GRAS transcription factor RAM1 in *Medicago sativa*. This reduces the arbuscular growth of the ram1 mutant (Park *et al.,* 2015; Jin *et al.,* 2016; Pimprikar *et al.,* 2016). Rice arbuscule formation requires OsADK1, a new kinase (Guo *et al.,* 2022). Mutations in DIPI, NSP1, NSP2, MIG1, and other transcription factors can impact the formation of intracellular AMs, indicating their importance in arbuscular mycorrhizal symbiosis (Maillet *et al.,* 2011; Delaux *et al.,* 2013; Yu *et al.,* 2014; Heck *et al.,* 2016).

Regulatory functions of AMF in plants

AMF improves drought resilience of host plants

Drought is a major abiotic factor that hinders plant growth and threatens global food security (Zhang *et al.,* 2018). It can significantly impact plant biomass and growth due to inability of water. (Aroca *et al.,* 2008). Previous research has demonstrated that AM symbiosis can help plants respond to drought stress (Bahadur *et al.,* 2019).

Table 2. Impact of AM symbiosis on plant abiotic stress reduction in several plants

Plant species	Effects of influence	Mechanisms of influence	References
Lactuca sativa	Enhanced drought stress tenacity.	Better regulation of the ABA levels	Aroca *et al.*, 2008
Pistachio (*Pistacia vera*)	Increased nutrient absorption during drought stress.	Improved absorption of PO$_4^{2-}$ and Zn^{2+} to maintain osmotic balance.	Bagheri *et al.*, 2012
Tobacco (*Nicotiana tabacum* L.)	Increased drought stress resistance	Improved secondary metabolism, osmolyte buildup, and antioxidant system.	Begum *et al.*, 2022
Sorghum (*Sorghum bicolor* L.)	Enhanced ammonium transfer	High expression of GintAMT3	Calabrese *et al.*, 2016
Cucumber (*Cucumis sativus* L.)	Improved growth, nutrient uptake, and photosynthesis	Upregulated RuBisCO, FBPase, F6P, Ru5PK, and related gene expression	Chen S. *et al.*, 2017
Black locust (*Robinia pseudoacacia* L.)	Reduced salt stress	Improved photosynthesis, water status, and KC/NaC homeostasis	Chen J. *et al.*, 2017
Tomato (*Solanum lycopersicum*)	Enhanced water stress tolerance	Regulated ABA and associated gene expression levels	Chitarra *et al.*, 2016
Phoebe zhennan	Damage from salt stress was reduced.	Improved photosynthetic capability.	Cui *et al.*, 2021
Suaeda salsa	Improved halophytes' NaCl accumulation	Changed of metabolic pathways related to gene expression.	Diao *et al.*, 2021
Zea mays L.	Improved plant drought resistance	RiHog1-RiMsn2-STREs module regulated drought stress-responsive genes in the AM fungal symbiont	Fan *et al.*, 2023
Malus robusta	Increased calcium uptake	Activated hormones and Ca$_2$Cl signal transduction pathways.	Fu *et al.*, 2023
Lotus japonicus	Improved plant sulfate nutritional status under S starvation.	LjSultr1;2 encoded a key protein involved in plant sulfate uptake.	Giovannetti *et al.*, 2014
Chicory (*Cichorium intybus* L.)	Increased fitness of host plants under Cu deficient and toxic conditions	Changed expression of RiCTR1, RiCTR2 and RiCTR3A	Gómez-Gallego *et al.*, 2019
Maize (*Zea mays*)	Mitigated the changes induced by Cu toxicity.	Increased expression of the HMA genes and balance mineral nutrient uptake.	Gómez-Gallego *et al.*, 2022
Lotus japonicus	Enhanced the organic N transfer	Improved plant re-uptake and recycling of amino acids by LjLHT1.2	Guether *et al.*, 2022
Lycium barbarum	Influenced water stress tolerance	Maintained normal photochemical processes and higher expression levels of Rir-AQP2	Hu *et al.*, 2017
Apple (*Malus domestica*)	Enhanced drought resistance	Regulated genes in the MAPK pathway	Huang *et al.*, 2020a
Apple (*Malus domestica*)	Improved drought resistance	MdIAA24 regulated strigolactones biosynthesis and mycorrhization	Huang *et al.*, 2020b
Apple (*Malus domestica*)	Reduced cadmium resistance	Reduced cadmium resistance.	Huang *et al.*, 2021
Maize (*Zea mays*)	Enhanced the host plant's N uptake	ZmAMT3;1 transferred substantial quantities of N from AMF to plan.	Hui *et al.*, 2022
Maize (*Zea mays*)	Enhanced water transport via AMF to the host plants	Increased expression of aquaporin gene GintAQPF1 and GintAQPF2	Li *et al.*, 2013
Maize (*Zea mays*)	Enhanced plant drought tolerance	IPS and 14-3GF are involved in the activation of 14-3-3 protein and aquaporins	Li *et al.*, 2016

AM symbiosis regulates plant drought tolerance through complex processes involving several metabolites and pathways. It can improve drought resistance in plants by improving soil aggregate structures, promoting nutrient absorption, increasing water and nutrient use efficiency, improving osmotic adjustment, enhancing antioxidant capacity, and regulating hormone balances (Khan *et al.,* 2025).

After establishing a symbiotic association, AMF can increase the root capacity of host plants, improving water absorption. AMF may enhance water efficiency and root hydraulic conductivity by absorbing nutrients. Plants rely heavily on aquaporins (AQPs) to regulate water transport across cell membranes. Huang *et al.* (2020a) found that *Malus hupehensis* seedlings inoculated with *R. irregularis* had significantly higher water use efficiency during drought stress through PIPs, which are subset of AQPs. This was demonstrated by up-regulation of PIP1-3 and PIP1-4 in mycorrhizal seedling roots and Rir-AQP1 and Rir-AQP2 in the AMF compared to untreated plants. Li *et al.* (2013) discovered that drought stress greatly increased the expression of the AQP genes GintAQPF1 and GintAQPF2 in extra-root hyphae and infected mycorrhiza. This shows that AMF has a direct role in plant drought stress responses. Co-expression of D-myo-inositol-3 phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF) genes can improve maize drought tolerance by facilitating signal transmission between maize and AMF under drought stress (Li *et al.,* 2016). The transcription factor RiMsn2 from *R. irregularis* is required for arbuscule production and can improve plant drought tolerance. RiMsn2 interacts with RiHog1 to regulate STRE-controlled genes in *R. irregularis*. The RiHog1-RiMsn2-STREs module controls drought stress response genes in fungal symbionts (Fan *et al.,* 2023). Silencing three Hog1 (High Osmolarity Glycerol 1)-MAPK cascade genes from *R. irregularis*, RiSte11, RiPbs2, and RiHog1, led to reduced expression of drought-resistance genes (RiAQPs, RiTPSs, RiNTH1, and Ri14-3), inhibiting arbuscule development and host plant resistance to drought stress (Wang *et al.,* 2023). Sun *et al.* (2018) reported that the 14-3-3-like protein genes Ri14-3-3, Fm201, and RiBMH2 contribute to arbuscule production and drought stress tolerance in host plants.

AMF enhances mineral nutrient uptake by host plants

Mineral nutrients have a crucial role in plant resilience to biotic stressors, including drought stress (Shi *et al.*, 2017). Wang *et al.* (2019) found that normal nitrogen (N) supply increased antioxidant enzyme activity, prevented ROS formation, and reduced drought stress on plants.

After creating a symbiotic association with host plants, AMs can increase nutrient absorption, particularly P and N (Fu *et al.,* 2023; Shi *et al.,* 2023). This is due to AMF's extra-root hyphae, which are twice as tiny as plant roots. These hyphae may penetrate deep soil to collect nutrients and broaden the absorption area, promoting root development and increasing nutrient uptake (Smith *et al.,* 2010). According to Wang *et al.* (2024), the primary function of AMF is to enhance P absorption by host plants. The *R. irregularis* Pi transporter RiPT7, which contains an SPX (SYG1/Pho81/XPR1) domain, regulates Pi input and outflow across the plasma membrane based on the Pi gradient. RiPT7 silencing reduces *R. irregularis* mycorrhizal symbiosis and Pi delivery in low-Pi settings (Xie X *et al.*, 2022). Shi *et al.* (2021) found that PSR transcription factors are necessary for mycorrhizal symbiosis and that PHR2 may control the expression of mycorrhizal symbiosis-related genes via the P1BS motif. In *R. irregularis,* the transcription factor RiPho4, which has an HLH domain and is highly increased by P-starvation, has a beneficial effect on the downstream phosphate (PHO) pathway genes RiPT1, RiPT2, and RiPT3 (Zhang *et al.,* 2023). GigmPT, a high-affinity Pi transceptor in *Gigaspora margarita,* is required for AM symbiosis. It activates both the Pi signaling pathway and the protein kinase a signaling cascade (Xie *et al.,* 2016). According to Kumar *et al.* (2008), phosphorus present in soil frequently forms a compound with calcium (Ca) and magnesium (Mg), making it difficult for plants to absorb. AMF's strong acid phosphatase activity can help liberate P from these complexes. Arbuscular mycorrhizae enhance nitrogen absorption and utilization by host plants by transferring nitrogen between the fungus and host plants via hyphal bridges (Gao *et al.,* 2021). Kobae *et al.* (2010) discovered three AMT genes (GintAMT1, GintAMT2, and GintAMT3) in *R. irregularis*, indicating that AMF have their own transport mechanism. GintAMT1 and GintAMT2 are expressed in both extraradicular and intraradicular mycelium. They play a role in absorbing ammonia (NH_3) from AMF and recovering $NH4^+$ loss at the symbiotic interface through fungal metabolism (Pérez-Tienda *et al.*, 2012). GintAMT3 is significantly stimulated in intraradicular mycelium, and expression is influenced by substrate concentration and carbon supply (Calabrese *et al.*, 2016). Plant N uptake from the peri-arbuscular space relies on peri-arbuscular membrane transporters, including the AMF-induced $NO3^-$ transporter OsNPF4.5 in *Oryza sativa*, the amino acid transporter LjLHT1.2, and the NH_4 transporter LjAMT2;2 in *Lotus japonicus* roots (Wang *et al.*, 2020, 2022b; Guether *et al.*, 2022; Zhang *et al.*, 2023).

The AMF infection upregulated the expression of NPF4.5 homologs in maize (*Zea mays*) and sorghum (*Sorghum bicolor*), demonstrating active NO_3^- absorption pathways under AM symbiosis (Wang *et al.*, 2020). Saia *et al.* (2015) found that AM symbiosis dramatically increased the expression of NRT1.1, AMT1;2, and AMT2;1 in durum wheat (*Triticum durum* Desf.). ZmAMT3;1, an AMF-inducible ammonium transporter, produced in infected cortical cells, may absorb 68-74% of the nitrogen delivered from AMF to maize plants (Hui *et al.*, 2022). Two signaling peptides in *Medicago truncatula*, C-terminally encoded peptides (CEPs) and CLAVATA3/endosperm surrounding region-related peptides (CLEs), regulate symbiotic nodule development in response to $NO3^-$ levels (Oldroyd and Leyser, 2020; Luo *et al.*, 2021). Many finding suggested that AM colonization improves plant absorption of potassium, sulfur, zinc, iron, magnesium, and calcium (Talaat and Shawky, 2011; Garcia and Zimmermann, 2014; Giovannetti *et al.*, 2014).

AMF increases the host plant's resistance to salt

Salt stress restricts the healthy expansion of agricultural sectors and the global dispersion of plants, and it impacts plant growth in many parts of the world, particularly on irrigated land (Cui *et al.*, 2021). Salinization affects around one in five of the world's irrigated land, and to make matters worse, this percentage keeps rising. The major causes of the negative impacts of salt stress on plants are the toxic effects of sodium (Na) and chlorine (Cl) on plants, which interfere with plant life processes, and the reduction in accessible water when Na builds up around the roots (Parihar *et al.*, 2015).

Plants have evolved a number of signal transduction-related adaptation mechanisms, including calcium signals, phosphatidylinositol, protein kinases, and phytohormones, to deal with salt stress. These result in adaptive reactions, including the generation of suitable solutes, ion efflux and segregation, the management of ROS (reactive oxygen species) that homeostasis, and a change in growth rate. To combat the negative impacts of salt stress, plants can also form symbiotic partnerships with beneficial rhizospheric microbes like AMF (Porcel *et al.*, 2015; Evelin *et al.*, 2019).

Transcriptome sequencing of asparagus (*Asparagus officinalis* L.) seedling roots was done by Zhang *et al.* in 2021. They discovered AMF regulated 391 differentially expressed transcripts under salt stress, which were primarily involved in the elimination of ROS, the regulation of mineral elements and water uptake, and the functional construction of cell walls. Compared to non-mycorrhizal halophytes, mycorrhizal halophyte seedlings exhibit reduced amounts of soluble sugar and sodium ions during salt stress. These variations may be connected to the control of energy and carbohydrate metabolism, such as the metabolic pathways for glyoxylate and dicarboxylic acid (Diao *et al.*, 2021). Cui *et al.* (2021) observed that AMF increased in *Phoebe zhennan's* utilization of light energy and improved the chlorophyll content of leaves, photosynthetic rate, and fluorescence correlation parameters.

This reduced salt-induced damage and encouraged *P. zhennan* growth in saline–alkali soil. Furthermore, in order to maintain the osmotic equilibrium state under salt stress, AM symbiosis plants alter the Na/K ratio (Hdar *et al.,* 2023).

During salt stress, AMF colonization can improve H efflux and K influx as well as fatty acid metabolism in Jujuba root. Additionally, AM symbiosis plant's leaves and roots have higher fatty acid content, which increases salt sensitivity in wild jujube. Mycorrhizal colonization activates the plasma membrane ATPase gene ZjAHA7, which starts H efflux. ZjHAK2 expression is also up-regulated, which encourages K accumulation in AM plants to reach a high K/Na state (Ma *et al.,* 2022).

When rice plant was exposed to salt stress, mycorrhizal plants expressed more of the salt tolerance-related genes OsPRX, Os10g, OsHBP1b, and OsNCX than non-mycorrhizal plants did. This enhanced the rice capacity to scavenge reactive oxygen species and reduced the buildup of malondialdehyde (Zhang *et al*., 2023). According to Wang *et al.* (2022a), *R. irregularis* considerably increased the expression of several genes linked to ion transfer, ROS scavenging, and carbohydrate metabolism, such as HAK5, PIP1-2, MYB46, NAC43, GLP10, SKOR, CPER, and WRKY19.

Applying AMF to *Casuarina glauca* can enhance salt tolerance by increasing plant biomass, K content, and the compartmentization of Na and Cl in vacuoles through the development of certain CgNHXs and CgCLCs (Wang *et al*., 2023). By encouraging the outflow of Na from plant roots, the up-regulation of SOS1/NHX7 in *Robinia pseudoacacia* roots during AM symbiosis can improve salt stress tolerance (Chen *et al*., 2017).

When tomatoes are exposed to salt stress, AMF colonization up-regulates the salt excessively sensitive (SOS) genes SlSOS1 and SlSOS2, improving the tomato's ability to withstand salt (Liu *et al*., 2023). Ren *et al.* (2018) discovered that a variety of transcription factors, including WRKY, ERF, MYB, and TCP members, were among the hub genes in the module linked to the response to salt stress in *Sesbania cannabina* infected with AMF.

AMF regulate plant hormones to reduce abiotic stress

Plant hormones are multipurpose chemicals that are essential to the life cycle of plants, including the process of interactions between plants and AMF (Foo *et al.,* 2013; Charpentier *et al.,* 2014; Etemadi *et al.,* 2014). One essential endogenous plant hormone that is crucial to the arbuscular growth process in plants is auxin (IAA) (Etemadi *et al.,* 2014; Wang *et al.,* 2021). Meixner *et al.* (2005) observed that the IAA concentrations in soybean roots infected with AMF were noticeably greater than those in the uninoculated control. By raising levels of indole-3-acetic acid (IAA), AMF might encourage the growth of roots, particularly lateral roots (Arzanesh *et al.,* 2011). Ma *et al.* (2022) showed that AM symbiosis modifies phytohormonal levels and that salt stress lowers the amount of IAA and abscisic acid (ABA) in jujube roots, while mycorrhizal development considerably increases it.

For symbiotically associated fungi, particularly AMF, strigolactones (SL) are essential for AM association with the plant root (Mitra *et al.,* 2021). According to Ruiz Lozano *et al.* (2016), drought stress lowers the amount of SL in both AMF-colonized and non-AMF-colonized plants. By raising the number of SLs, Huang *et al.* (2020b) demonstrated that overexpression of the auxin/indole-3-acetic acid gene MdIAA24 can encourage mycorrhizal infection of apple roots, leading to a higher rate of mycorrhizal infection and increased drought resilience of transgenic lines.

According to Yoneyama *et al.* (2007), the SL contents directly control the AM symbiosis process and have a negative association with plant P status. Two GRAS transcription factors, NSP1 and NSP2, mediate the response to low P in plants by inducing the expression of genes related to SL biosynthesis. These transcription factors also participate in the AM symbiosis signaling pathway (Liu *et al.,* 2011; Luginbuehl and Oldroyd, 2017).

Another significant hormone involved in controlling alterations linked to plant P status and AM symbiosis is gibberellic acid (GA). Plant P status controls GA production; low P stress increases the transcription of DELLA genes while downregulating the expression of genes linked to GA biosynthesis (Devaiah *et al.,* 2009). Floss *et al.* (2013) observed that DELLA proteins, which function as repressors of GA signaling and increase the biomass accumulation and growth process of plants, have an impact on the process of arbuscule formation process. Gene expression levels linked to GA breakdown and signaling are significantly changed under AM symbiosis (Yu *et al.,* 2014).

Arbuscular mycorrhizal fungi are significantly important for maintaining significant plant hormone balances. By causing notable increases in IAA and cytokinin levels but decreases in ABA levels in both the roots and leaves, Zhang *et al.* (2021) found that AMF maintains hormonal balances after damaging the root under stress. This raises the ratio of fine roots and encourages root development. Furthermore, AMF can activate plant hormone signaling in response to drought stress. Improved drought tolerance and the development of AM symbiosis can result from increased ABA synthesizing capacity in stressed and AM mycorrhizal plants (Bahadur *et al.,* 2019).

When tobacco shoots are exposed to drought stress, co-inoculation with AMF and rhizobacteria can increase the ABA and IAA contents (Begum *et al.,* 2022). When watermelon was inoculated with varying numbers of AMF spores, it was found that the concentrations of ABA, IAA, GA3, and zeatin riboside (ZR) changed in distinct ways as the number of spores. For instance, when 300 spores were inoculated per plant, ABA concentrations were ABA concentration was highest and lowest after inoculation of 300 and 600 spores per plant respectively (Wu *et al.,* 2021). Liu *et al.* (2016) inoculated with AMF, the IAA and ABA contents in the leaves and roots of *Lycium barbarum* L. (Goji), maintaining the osmotic balance and enhancing salt stress tolerance. AMF-inoculated plants may control the amounts and ratios of phytohormones to reduce stress under arsenic (As) stress conditions. This includes a decrease in the GA and zeatin riboside contents and an increase in IAA and ABA contents (Zhang *et al.,* 2020).

AMF symbiosis improves the plant's resilience to heavy metals

Due the extensive use of pesticides in the agriculture industry, large-scale livestock and poultry farming, and industrial discharge, heavy metal pollution, including that of cadmium (Cd), mercury (Hg), arsenic (As), and lead (Pb), causes adverse effects in agricultural fields, and the degrading the environment (Wu *et al.,* 2018). Cadmium (Heavy metal) stress often harms plants in two different ways. Initially, heavy metals such as Cd are absorbed by plant roots, causing ionic disturbances inside the plant, interfering with regular cellular functions, and causing problems with metabolic activity. After being absorbed by plants, Cd can form complexes with proteins, enzymes, and other biological macromolecules. These complexes can replace necessary elements in the original structure of enzymes and biological macromolecules, causing them to lose their specific functions and become denatured. Plants often undertake physiological and molecular modifications to avoid protein inactivation and oxidative damage caused by ROS bursts when exposed to Cd stress (Sofo *et. al.,* 2013). AM symbiosis has been shown to improve plant tolerance to heavy metal contamination in soil, including Cd (Chen *et al.,* 2004a), Pb and uranium (Chen *et al.,* 2005), Cu (Chen *et al.,* 2007), and Zn (Chen *et al.,* 2004b).

Mycorrhizal symbiosis improves plant tolerance to heavy metals through two mechanisms: the "growth dilution effect" and "mycorrhizal immobilization." AM symbiosis can boost plant P content, promoting biomass growth and dilution of heavy metals, whereas AMF can limit heavy metals inside plant roots by precipitating polyphosphate complexes, restricting their transport to shoots (Wu *et al.,* 2015; Liu *et al.,* 2018). According to Chen *et al.* (2005), mycorrhizae under Pb stress can promote plant development by enhancing absorption and reducing toxicity by fixing more P in the roots. AMF can colonize plants in naturally polluted soils and reduce phytotoxicity (Sun *et al.,* 2016). AM symbiosis can promote methylation (Li *et al.,* 2018), potentially reducing heavy metal phytotoxicity through a novel mechanism.

According to Aloui *et al.* (2009), AMF can boost plant antioxidant enzyme activity by secreting lipids and proteins or altering the expression of heavy metal stress-related genes.

This reduces the harmful effects of heavy metal stress in plants. Zhang *et al.* (2019) found that AM-inoculated plants can maintain ROS homeostasis during Pb stress by down-regulating the expression of the RBOH gene MtRbohC-G. This reduces H_2O_2 buildup in *Medicago truncatula*. AMF may boost plant resilience to heavy metal stress by inducing hormone production, such as IAA, ABA, and GA. Under Cd stress, AM symbiosis regulated ABA in high Cd uptake maize cultivars and IAA in low Cd uptake maize cultivars (Chen *et al.,* 2023).

Phytohormone concentration and root traits in different cultivars of maize. The root tip concentration and the ABA concentration with high Cd uptake (Panju3) while average root diameter aur auxin concentration increases with low Cd uptake (Ludan Q). Plants use similar genes to respond to heavy metal stress through AMF-mediated pathways. Cu treated in mycorrhizal maize plants increased the expression of heavy metal ATPase (HMA) ZmHMA3a and ZmHMA4 isoforms, indicating that AM symbiosis may enhance the expression of Cu detoxification proteins to reduce Cu toxicity (Gómez-Gallego *et al.,* 2022). Gómez-Gallego *et al.* (2019) identified two Cu transporter (CTR) family member genes (RiCTR1 and RiCTR2) and a CTR-like protein (RiCTR3A) in *R. irregularis*. These genes are implicated in Cu transport and tolerance.

The Report suggested that RiCTR3A may function as a Cu receptor when exposed to Cu stress, according to further study. RiATOX1, RiSco1, and RiSSC genes in *R. irregularis* may act as chaperones, transferring Cu to ATPases, cytochrome c oxidases, and Cu or Zn superoxide dismutase (Ferrol *et al.,* 2016). Huang *et al.* (2021) found that AMF inoculation decreased Cd accumulation in apple seedlings. MdGH3-2/12 silenced seedlings had weaker Cd stress tolerance, resulting in a lower AM symbiosis ratio compared to the wild type.

CONCLUSION

Arbuscular mycorrhizal fungi (AMF) represent a fundamental component of plant life and ecosystem functioning, shaped through long-term co-evolution with their host plants. This symbiotic association contributes significantly to plant performance by enhancing nutrient uptake, particularly phosphorus, and improving tolerance to environmental stresses such as drought, salinity, and temperature extremes. In addition, AMF play a vital role in maintaining soil structure by promoting aggregate formation and water retention, thereby supporting overall soil health.

This review has highlighted the multifaceted interactions between AMF and host plants, including their influence on nutrient acquisition, hormonal regulation, and resilience to abiotic stresses such as drought, salinity, and heavy metal toxicity. These benefits collectively position AMF as a promising biological tool for improving plant productivity and sustainability in agriculture. However, despite their ecological and agronomic importance, practical application remains constrained by several biological and technological limitations, particularly their obligate biotrophic nature, which complicates large-scale production and commercialization.

FUTURE PERSPECTIVES

Future research should focus on overcoming the biological and technological constraints that limit the large-scale application of arbuscular mycorrhizal fungi (AMF). The obligate biotrophic nature of AMF remains a central challenge for mass production; therefore, continued development of efficient cultivation systems is essential. Approaches such as in vitro root organ culture, controlled symbiotic systems, and scalable bioreactor-based production offer promising directions for generating high-quality inoculum at commercial scale. Simplifying and standardizing these techniques will be critical to ensure consistency, cost-effectiveness, and wider accessibility.

Strategic selection of AMF strains tailored to specific crops and agroecological conditions should be prioritized. This includes evaluating host–fungus compatibility, colonization efficiency, and functional performance under diverse environmental stresses. Integrating molecular and omics-based tools can further improve strain identification and functional characterization, enabling more precise and efficient application in agricultural systems.

The establishment of robust quality control frameworks is equally important. Standardized protocols for assessing inoculum purity, viability, infectivity, and shelf-life will enhance the reliability and credibility of AMF-based products. In parallel, maintaining well-characterized and diverse pure culture collections will support both industrial production and ongoing research.

Future efforts should also address practical implementation challenges, including formulation development, storage stability, and field-level performance under variable conditions. In addition, economic feasibility, farmer awareness, and supportive regulatory policies will play a crucial role in facilitating large-scale adoption.

Overall, advancing AMF technology requires an integrated approach that combines microbiology, plant science, biotechnology, and agronomic practices. Strengthening collaboration between researchers, industry, and policymakers will be essential to fully realize the potential of AMF in promoting sustainable and resilient agricultural systems.

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