iScience

CellPress
OPEN ACCESS

Review

Plant-fungus synergy against soil salinity: The cellular and molecular role of arbuscular mycorrhizal fungi

Gökhan Boyno,[1] Younes Rezaee Danesh,[1,*] Rojbin Çevik,[1] Necmettin Teniz,[2] Semra Demir,[1] Oktay Calayır,[1]
Beatrice Farda,[3] Amedeo Mignini,[3] Debasis Mitra,[4] Marika Pellegrini,[3] Rosa Porcel,[5] and José M. Mulet[5,*]
[1]Department of Plant Protection, Faculty of Agriculture, Van Yuzuncu Yil University, Van 65090, Türkiye
[2]Department of Agricultural Biotechnology, Faculty of Agriculture, Van Yuzuncu Yil University, Van 65090, Türkiye
[3]Department of Life, Health and Environmental Sciences, University of L'Aquila, 67100 L'Aquila, Italy
[4]Department of Microbiology, Graphic Era (Deemed to be University), Dehradun, Uttarakhand, India
[5]Instituto de Biología Molecular y Celular de Plantas, Universitat Politècnica de València-Consejo Superior de Investigaciones Científicas, 46022 Valencia, Spain
*Correspondence: y.rdanesh@yahoo.com (Y.R.D.), jmmulet@ibmcp.upv.es (J.M.M.)
https://doi.org/10.1016/j.isci.2025.113384

SUMMARY

Arbuscular mycorrhizal fungi (AMF) play a crucial role in disease control by establishing symbiotic relationships with plant roots. AMF improve salinity tolerance in plants by regulating the Na^+/K^+ ratio through selective ion transport and mediate osmotic regulation by inducing the accumulation of osmotic-compatible solutes such as glycine betaine and proline to enable plant cells to maintain water content and the metabolic balance. AMF can also activate antioxidant defense responses by stimulating enzymes that protect plant cells from harmful oxidation and pathological infections. Plant salinity tolerance induced by AMF depends on abscisic acid (ABA)-dependent signaling mechanisms, calcium-calmodulin-dependent pathways, and reactive oxygen species (ROS)-modulated mitogen-activated protein kinase (MAPK) cascades. Therefore, future research should focus on optimizing the production and field efficacy of AMF-based inoculants, including their combined use with microbial biostimulants, to support the implementation of sustainable agricultural practices.

INTRODUCTION

AMF (arbuscular mycorrhizal fungi) are a kind of soil-dwelling fungi that form symbiotic relationships with most terrestrial plants.[1] Fungi-plant interaction is one of the most critical components affecting the standard plant developmental program and ecological and farming practices. The cooperation between arbuscular mycorrhiza and fungi leads to the most prevalent plant-fungus mutualistic relationship, which has been known since the Cambrian period.[2] Plants establish symbiotic mutualistic associations with AMF in natural and artificial ecosystems: mycorrhizal root invasion involves the formation of arbuscules, the fungal structures that interact with intracellular plant roots. The symbiosis allows the plant to get essential nutrients like phosphorus and nitrogen in the form of organic compounds that are usually scarce in normal soil conditions or appear in insoluble forms. The nutrient exchange manifests this symbiosis: the plant transfers carbohydrates generated during photosynthesis to the fungus. This partnership is a significant essential component maintaining the fluxes of nutrients and energy in the ecosystem; nevertheless, it also enriches the ability of the plants and the fungi to survive in the ecosystem. AMF play an unprecedented role in natural systems for recycling nutrients and signaling exchange between plants.[3] This shared mycelial network formed by AMF allows the redistribution of soil resources, enhancing the overall productivity and resilience of the ecosystem.[4] In addition, this system is essential for carbon sequestration, as soil is a sink for atmospheric carbon, and the presence of AMF enhances carbon sequestration.[5] In agriculture, the use of AMF for crop management has been considered an essential element that promotes plants' health and crop productivity,[6] which can be used in conventional, organic, or integrative farming. The plant symbiosis with AMF leads to changes throughout the plant, impacting its developmental cycle and output performance.[7] As awareness grows, there is a boom in the commercial production of AMF inoculates, with more and more farmers taking advantage of the added value these fungi provide to crop management.[8] The phylogenetic records of the plant AMF symbiosis go back 400 million years ago. Scientific evidence indicates that, during the transition of plants from aquatic to terrestrial life, arbuscular mycorrhizal fungi played a vital role in the process.[9] By inducing plant resistance against abiotic factors, AMF can help the plants respond to different environmental cues.[10] Saline-alkali soils currently affect over 800 million hectares worldwide, representing a serious threat to both ecological balance and agricultural productivity due to soil structure degradation, nutrient limitations, and yield decline. These problematic soils

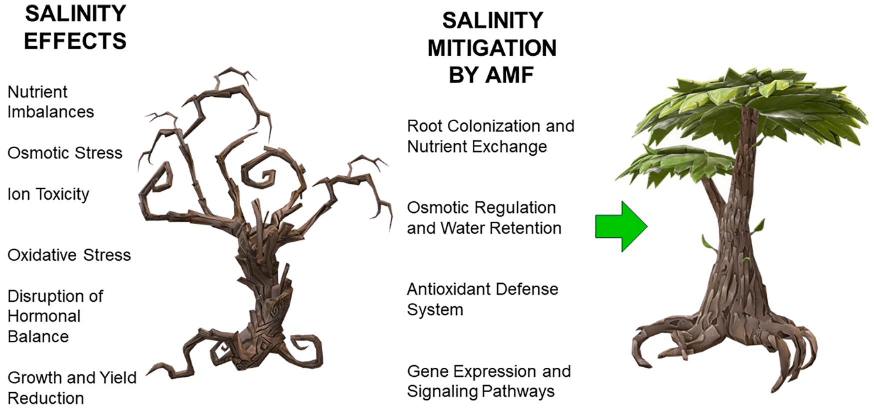

Figure 1. Diagram summarizing the functional mechanisms of AMF in improving plant salinity tolerance

are most widespread in arid and semi-arid regions of Asia, Africa, and Australia.[11] AMF establish a symbiotic relationship with plants in such a harsh environment to promote their thriving growth (Figure 1). Gaining deeper insights into the distribution and functional roles of AMF in saline environments is therefore essential for designing sustainable agricultural strategies to cope with salinity stress. Of the many abiotic stresses that agricultural systems must cope with, the most prevalent is field salinization, which significantly threatens cultivable lands worldwide. The world is feared to lose around 50% of the arable land to salinization in the next 40 years.[11] Salt in soil compromises crop yield and water uptake and alters minerals' normal plant metabolism distribution. This review primarily focuses on neutral salt stress, with particular attention to sodium chloride, the most prevalent salt in agricultural soils. Nonetheless, it is important for future research to also explore the effects of alkaline salts such as sodium carbonate and sodium bicarbonate, as these compounds pose distinct physiological challenges to plants. Another prominent event is the imbalance between salt stress and the production of some photoassimilates and plant circulation. The cell molecular machinery that defends the plant by accumulating these toxic ions and/or releasing them includes ABC transporters, ion channels, and antiporters. This review aims to investigate how AMF boost plant salt resistance by triggering complex physiological processes and biochemical reactions.

EFFECTS OF SOIL SALINITY ON PLANTS AND THE ROLE OF AMF

Soil salinity is a major agronomical problem, depriving plants' capacity to develop and affecting many agricultural ecosystems.[12] The presence of salt in the soil causes osmotic stress due to the ability of ions to sequester water. Moreover, excessive salt concentrations can alter the ionic composition of the soil solution by causing precipitation or deposition of nutrients, thereby reducing the bioavailability of essential ions such as K^+, calcium ion (Ca^{2+}), and Mg^{2+}. This phenomenon hampers root absorption capacity and impairs nutrient signaling. The Na^+, when it enters the plant, induces ion toxicity and nutrient imbalances, ultimately leading to diminished plant growth or plant death.[13] Alongside sodium ions (Na^+), chloride ions (Cl^-) also play a significant role in ion toxicity under neutral salt stress. When present in excess, Cl^- tends to accumulate in plant tissues, where it can damage cellular membranes, impair photosynthetic processes, and disrupt nutrient balance—particularly by interfering with nitrate uptake and metabolism. Plant tolerance to abiotic stress, including salinity, is reinforced by AMF, which utilize multiple mechanisms to accomplish this effect (Figure 2). For example, they can degrade 1-aminocyclopropane-1-carboxylate (ACC), a precursor to the stress hormone ethylene, by the enzyme ACC deaminase present in many microbial genomes. This helps to mitigate the detrimental effects of ethylene accumulation and improves plant growth and resilience under saline conditions.[14] Additionally, AMF can promote the absorption and translocation of limited nutrients in many instances, such as nitrogen, which may be very significant in most saline soils. Reversing the nutrient state ensures that the plant can withstand salt and protect the metabolic pathways and the expected physiological program. AMF support ion homeostasis by sequestering toxic ions such as Na^+ and Cl^- into vacuoles, thereby mitigating cytoplasmic toxicity. At the same time, they enhance the uptake of essential ions like K^+, Ca^{2+}, and Mg^{2+} by modulating specific ion transporters and membrane channels. Notably, AMF influence the expression of high-affinity potassium transporters, sodium/proton antiporters (NHX), and salt overly sensitive (SOS) genes, thus promoting selective ion transport mechanisms that preserve osmotic balance and membrane integrity under saline conditions. When the mycorrhizal fungi colonize the root, the fungi use the plant as a source of sugar and proline.[15] Furthermore, mycorrhizal fungi help by improving the soil structure and adhering to soil particles that increase water-holding capacity and nutrient availability, thereby indirectly fostering plant growth in saline environments.[12,16] Therefore, plant growth conditions improve upon microbial colonization. Having observed the potential of AMF, scientists have established a sustainable, eco-friendly tactic to combat the unwanted consequences of soil salinity during the last few decades. Ongoing work contributes immensely to comprehending the intricacies of how plants, fungi, and the soil environment interact at the co-microbiome level, which eventually aims to develop microbiome-based solutions for agriculture under saline conditions.[17] Literature has demonstrated that AMF play a significant role in plant tolerance to saline soils, enhancing general crop productivity in salt-stressed habitats. AMF can induce salt-tolerance mechanisms by improving nutrient procurement and maintenance. Mycorrhizal symbiosis plays a vital role in this context because, for example, the arbuscular development within the root cortical cells of the host plant is crucial. After all, this is where the plant-fungus nutrient transfer occurs. For example, the ability of AMF to improve phosphorus uptake relies on the development of arbuscules inside root cortical cells because this establishes the exchange region for plant-fungus nutrient transfers. Studies reveal

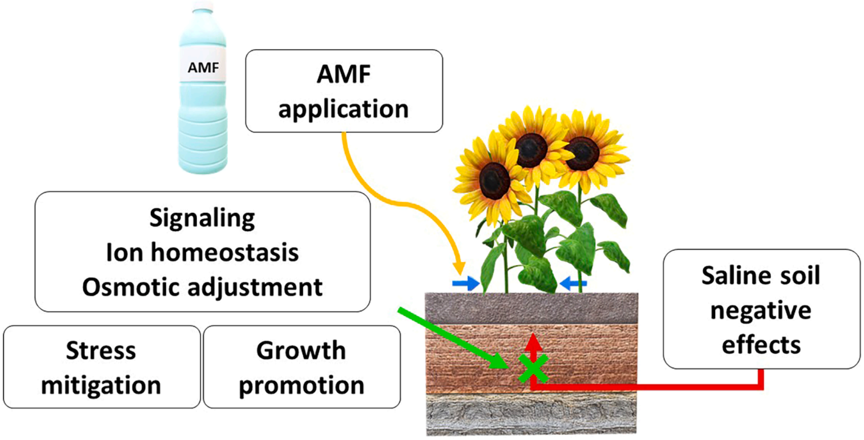

Figure 2. Salinity effects on plants and the role of AMF in its mitigation

that AMF increase the expression of membrane-bound phosphate transporter PHO1 on the host roots and enhance the phosphorus intake in salinity as well.[18] Similarly, AMF enhance nitrogen uptake by increasing the activity of nitrate transporters and promoting nitrogen assimilation pathways. One of the key functions of AMF under salinity stress is the regulation of potassium (K) and sodium (Na) homeostasis. Mycorrhizal plants exhibit increased K^+ uptake while modulating Na^+ accumulation, maintaining a higher K^+/Na^+ ratio critical for cellular function and osmotic balance.[19] This is achieved through the selective transport of K^+ via SKOR channels and the exclusion of Na^+ via SOS1 transporters in root cells. Salinity disrupts ion homeostasis by causing an excessive accumulation of Na^+ in plant tissues, leading to toxicity and nutrient imbalances.[20] Increasing potassium uptake is a known molecular strategy to counteract the toxicity of sodium.[21] Osmotic stress associated with salt stress also compromises plant water uptake and cell turgor. The osmotic imbalance can also cause a reduction in transpiration, increasing the loss of cell turgor. AMF alleviate this stress through several mechanisms: exclusion of Na^+ ions and increased K^+ uptake, which protect enzyme activity and help in osmotic regulation and overall plant health. Also, AMF cooperate with Ca^{2+} and magnesium homeostasis, which stabilizes membrane integrity and reduces oxidative damage.[15,22] AMF colonization also improves stomatal conductance and water use efficiency in plants exposed to salinity, further enhancing their drought tolerance. Another effect of salt stress is the increase in reactive oxygen species (ROS) levels, which could be responsible for oxidizing cellular structures and other essential compounds of the plant cells. AMF were shown to ameliorate plants' antioxidant defense systems by up-regulating enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase, and also carotenoid, ascorbate, and other non-enzymatic antioxidants' accumulation.[23]

CELLULAR MECHANISMS AND PLANT CELL INTERACTIONS OF AMF

The symbiosis between plants and AMF is primarily on a cellular level since the fungi build intricate networks within the cells in the cortical roots of the plant. When AMF develop arbuscules, AMF can interact directly with the plant cell and transfer nutrients and carbohydrate exchange.[24] Low amounts of strigolactones from plants activate spore germination and hyphal branching in AMF, leading to successful root colonization. The activity of AMF leads to modified expression of plant genes that control salt stress responses in addition to genes encoding transporter antioxidant enzymes and osmolyte biosynthesis pathways. Recently, it has been suggested that the high-affinity potassium transporter HAK family could have an essential role in this process.[25] AMF trigger phytohormone balance modifications that cause abscisic acid (ABA), cytokinins, and auxins to rise while helping plants adapt to saline environments.[26] Once inside the plant root, AMF establish a periarbuscular membrane, derived from the plant's plasma membrane, which encases the fungal arbuscules. This membrane is a critical interface for nutrient transfer, where plant phosphate transporters and ammonium/nitrate transporters are up-regulated to facilitate the uptake of phosphorus and nitrogen from the fungal network.[18] At the same time, the fungi receive photosynthetically derived carbon in the form of lipids and sugars, regulated by plant lipid biosynthesis genes such as RAM2, ensuring fungal survival and symbiosis maintenance.[18,27] Beyond nutrient exchange, AMF interaction also triggers plant immune responses. The plants benefit from induced systemic resistance against pathogens, which develop through jasmonic acid and ethylene signaling following mycorrhization despite some suppressed defense pathways that assist colonization. These signaling pathways are also crucial for plant adaptation to salt stress. Jasmonic acid, for instance, promotes root development and contributes to maintaining ion homeostasis under saline conditions, while ethylene signaling regulates antioxidant defenses and the transport of Na^+ and K^+. Research indicates that AMF can enhance the expression of salt-responsive genes such as *NHX* and *SOS1* through hormone-mediated pathways, thereby supporting ionic detoxification and preserving osmotic balance under salt stress. Plant resilience increases under biotic and abiotic stress situations because the expression of antioxidant defense genes and genes for osmotic adjustment and cell wall reinforcement becomes elevated through this enhancer function.[28] Molecular mechanisms described in the following paragraphs demonstrate how AMF start signal chain reactions inside plant cells, activating significant metabolites for salt resistance.[29]

THE ROLE OF AMF IN GENE EXPRESSION AND THE SIGNALING PATHWAYS GOVERNING PLANT STRESS RESPONSE

Salinity perturbs the cell mechanisms at the molecular level. Therefore, the response involves activating various successive mechanisms at plant metabolic, physiological, and molecular

Table 1. Genes activated by AMF and their functions for stress tolerance

Plant genes	Gene categories	Functions	Reference
XTH (xyloglucan endotransglucosylase-hydrolase)	glycosyl hydrolase family 16 (GH16)	increase in cell wall flexibility and strength	Zhang et al.[34]
PRP (proline-rich proteins)	cell wall structural proteins	reinforcement of cell wall durability	Puccio et al.[35]
HKT (high-affinity potassium transporter)	HKT transporter family	ion balance maintenance with sequestration of Na^+	Porcel et al.[46]
NHX (sodium/proton antiporter)	cation/proton antiporter (CPA1) family	sequestration of excess Na^+ into vacuoles	Roy et al.[47]
P5CS (Δ1-pyrroline-5-carboxylate synthase)	Δ1-pyrroline-5-carboxylate synthase family	regulation of proline biosynthesis	Guan et al.[48]
SOS1 (salt overly sensitive 1)	plasma membrane Na^+/H^+ antiporter family	regulation of sodium ion efflux	Assaha et al.[20]
LEA (late embryogenesis abundant proteins)	LEA protein family	cellular protection from dehydration	Magwanga et al.[49]
MYB (myeloblastosis transcription factor)	MYB transcription factor family	regulation of gene expression of salt tolerance	Zhang et al.[50]
SnRK2	SnRK (sucrose non-fermenting-1-related kinase) family	–	Benito et al.[51]

levels. The reactions of these cases have triggered the activation of the complex signaling pathways and morphogenic changes within the plants regarding their ability to tolerate the salt's adverse effects. In addition, the mycorrhization has a positive impact on the plant defense mechanisms.

Changes in gene expression upon salt stress

Salt stress causes water loss, ionic imbalance, and the generation of ROS, leading to the cell's death.[30] To counteract these adverse effects, plant cells start several biochemical and genetic mechanisms in the plant, such as increased potassium uptake and sodium extrusion or compartmentalization in the vacuole, the synthesis of osmolytes, and the activity of antioxidant defenses to respond to stress.[31] As a result of the symbiotic living that they establish with plants, AMF cause changes at the transcriptional level of many genes and promote plant defense mechanisms to protect compromised plant physiological functions (Table 1).[28,32] The plant cell wall is the first line of defending the plant against external stressors. Salt stress, however, leads to structural modifications in the cell walls. Genes like xyloglucan endotransglucosylase-hydrolase and proline-rich proteins promote growth by increasing cell wall flexibility and strength.[33] One of the findings is that the AMF up-regulate these cell wall-related genes, resulting in conveyance in the durability of the cell wall, and finally improve the resistance of plants to stress.[34,35,36] Stress salinity induces excessive accumulation of Na^+ ions, disrupting the K^+/Na^+ ratio and leading to cellular toxicity.[37] To prevent this, the cell activates genes such as high-affinity potassium transporter and NHX (sodium/proton antiporter), which serve to either block the entrance of Na^+ into the cell by increasing the entry of K^+ or accumulate Na^+ into vacuoles.[38] At this level, AMF prevent the accumulation of Na^+ ions in the cytoplasm by increasing the expression levels of these genes.[39,40] In recent years, transcriptomic studies have revealed a wide array of novel AMF-inducible genes beyond the classical NHX, SOS1, and P5CS (delta-1-pyrroline-5-carboxylate synthetase), including those involved in membrane remodeling, detoxification, and signaling (e.g., aquaporins like ZmPIP2;4, lipid transfer proteins, and transcription factors such as MYB and WRKY). Some of these genes appear to be mycorrhiza specific and show consistent up-regulation under salinity in AMF-colonized roots, indicating that AMF symbiosis triggers a distinct transcriptional program for salt adaptation. Another problem is that water loss is caused by the osmotic effect of salt in the soil, which leads to a breakdown of osmotic balance, a decrease in cellular turgor, and a slowdown in metabolic processes.[41] Water retention capacity is enhanced by activating genes related to the accumulation of osmolytes, such as P5CS (Δ1-pyrroline-5-carboxylate synthase), responsible for proline biosynthesis.[42] Proline is also vital for maintaining the stability of intracellular proteins and membranes.[43] The AMF underpin the transactivation of osmoregulatory genes for water balance maintenance. Inhibition of P5CS expression results in reduced proline content, but increased proline concentration can be achieved with higher P5CS gene activation.[44,45]

The hormonal response to salt stress

Under stress conditions, plants can rapidly activate complex signaling pathways to respond to environmental changes. These responses involve, for example, hormone-based signaling pathways, Ca^{2+}-based signaling mechanisms, and ROS-associated signaling networks.[52] The most relevant of these phytohormones is ABA, responsible for all the transcriptional activation triggered by salt stress.[53] Under salt stress, ABA levels increase, eliciting several signaling cascades.[54] The ABA increase causes the stoma to close as a compensatory mechanism to prevent water and turgor loss.[55] This, in turn, leads to increased water retention and an increase in the cellular osmotic pressure in the plant cell. AMF notoriously affect ABA production, inducing high-speed ABA transport from roots to leaves and accelerating stomata closure.[56] Additionally, AMF can facilitate ABA signaling by increasing sucrose non-fermenting-related kinase 2 protein kinase activity and, in this way, influence salt stress gene expression.[51]

One of the significant roles of Ca^{2+} is as an intracellular second messenger.[57] Under stress, there is a specific increase in the Ca^{2+} levels within cells due to Ca^{2+} channels opening on the cell membrane,[39] causing rapid and transient changes in cytosolic Ca^{2+}.[58] Such Ca^{2+} spikes activate calmodulin and Ca^{2+}-dependent protein kinases (CDPK) as the primary targets.[59] AMF actuate this by helping to exert a more balanced and better direction of Ca^{2+} fluctuations. CDPK activation results in the increased activity of stress response genes.[60] AMF, hence, efficiently regulate the precise time and level of the stress processing as they mediate the transport of Ca^{2+} and signaling.[28]

On the other hand, ROS are also signaling molecules besides their toxicity. ROS are produced by stress, mainly by the damage caused by the loss of turgor to the mitochondrial and chloroplastic membrane. ROS activate MAPK (mitogen-activated protein kinase) signaling pathways in the cell, thereby leading to the expression of stress response genes.[61] AMF operate as a significant cellular ROS balance mediator and accelerate the MAPK activation.[28] This, in turn, leads to a stress response boost and diminishes oxidative damage. Also, AMF trigger the activation of the antioxidant response (for instance, SOD, CAT, and ascorbate peroxidase [APX] activation), so AMF activate ROS scavenging and activate ROS signaling.[62,63] AMF can regulate the ROS-dependent phosphorylation of MAPK, influencing plant development and stress response. This is how ROS-mediated protection is achieved, while ROS detoxification machinery activates the mentioned pathways within the plant.[28,52] AMF induces plants' responses to salt stress. AMF limit water loss by regulating ABA production and transport, accelerate stress responses by optimizing Ca^{2+}-based signaling pathways, and prevent oxidative damage by controlling ROS levels.[28,54,64] In addition, AMF's effects on regulating the signaling cascades, like gene overexpression, signal transduction, and regulatory coordination, contribute to the function of adaptation mechanisms.[32] Hence, this demonstrates that AMF interplay with plants is crucial for stress response. So, the effect of AMF can be observed at the physiological and transcriptomic levels.

THE ROLE OF AMF IN PLANT BIOCHEMISTRY

Key outcomes such as ROS scavenging and osmotic regulation represent essential components of the plant's adaptive response to salinity stress mediated by AMF. AMF establishes a mutualistic link with plant cells that alter a variety of biochemical reactions not only in roots but throughout the plant.[65] When plants face salt stress, AMF support is crucial for the antioxidant defense system and helps maintain osmotic regulation functions by managing the stress with osmotic correction mechanisms. Together, these protect plants against the harmful effects of ROS and osmotic stress.[28,32,63]

ROS and cellular effects

Under salt stress, organelles such as mitochondria, chloroplasts, and peroxisomes show metabolic imbalances in plant cells, thereby producing ROS.[66] AMF play an essential role in mitigating the impact of stress in roots, and, in the case of oxidative stress, the decisive role played by AMF is well explained. In this context, AMF protect against lipid peroxidation, protein oxidation, and DNA damage by mitigating oxidative stress through enhanced antioxidant defense mechanisms. These mechanisms help stabilize cellular structures, maintain protein functionality, and preserve genetic integrity under stress conditions. Under oxidative stress conditions, free radicals oxidize lipids in cell membranes, leading to lipid peroxidation.[67] This modification of cell membranes alters their structure and, as a result, increases their permeability, which subsequently leads to a worsening intracellular environment. AMF can prevent this process by proactively mediating free radical scavenging enzymes in the plant cells.[68] In particular, AMF can exert anti-lipid peroxidation activity by enhancing antioxidant mechanisms and preservation of structural elements, such as membrane fluidity, leading to better plant resistance.[69] Oxidative stress causes the destruction of protein structures that ultimately lead to malfunctions of enzymes and disrupt the normal course of intracellular metabolism. The most impressive feature is that AMF have a supporting capacity to raise plant anti-oxidative defense systems and, most importantly, help stabilize biomolecules.[70] This improvement has been demonstrated by the ability of plants to bind AMF, strengthening the anti-oxidative capacity, which is an environment for pathogens' growth. Such a mechanism defends proteins from oxidation by halting protein degradation. AMF are thought to repair these damages by increasing the activity of enzymes such as glutathione peroxidase and SOD.[63] DNA is an essential macromolecule in the body, but free radicals also cause irreversible oxidative damage to its structure. Most of these alterations usually damage the DNA, leading to mutations, disruption of plant development, and the death of cells. AMF act as an antioxidant by promoting the biosynthesis of redox enzymes in the plant roots. Hence, the symbiosis with AMF prevents DNA damage.[71] Besides, AMF have been identified as a key factor in treating damaged DNA by regulating the activity of select genes, which are closely linked to oxidative DNA damage.[72]

Enzymatic antioxidants

AMF enhance the activity of antioxidant enzymes to reduce oxidative stress by boosting ROS-scavenging capacities in plants.[73] AMF aid this process by supporting the antioxidative response in different parts of the plant. They convert superoxide radicals (O_2^-) into hydrogen peroxide (H_2O_2), providing the primary method of spurring oxidation-reduction reactions.[74] AMF-enriched SOD activity, especially within the chloroplast and mitochondria,[75] ensures that ROS produced by the cells' metabolism, which is their site of energy production, are neutralized; thus, it supports the energy metabolism. In peroxisomes, the CAT decomposes hydrogen peroxide into water and oxygen, preventing harmful effects.[76] CAT maintains the integrity of cell membranes primarily by limiting lipid peroxidation.[77] Increased CAT activity under the influence of AMF provides metabolic balance in cells by rapidly and effectively reducing ROS accumulation.[70] Furthermore, APX, which detoxifies H_2O_2 with the help of ascorbate, plays a critical role in the clearance of ROS formed in chloroplasts, especially during photosynthesis.[78] By increasing APX enzyme activity, AMF maintain photosynthetic efficiency and support plant growth.[79] The glutathione reductase (GR) plays a vital role in maintaining redox balance by increasing the

Table 2. Efficiency of several AMF species on salt stress

AMF species	Combination with other treatments	Target plant	Reference
Rhizophagus irregularis	co-inoculation with plant growth-promoting rhizobacteria (PGPR)	tomato (*Solanum lycopersicum*)	Dastogeer et al.[98]
Funneliformis mosseae	combination with organic biostimulants	wheat (*Triticum aestivum*)	Rouphael et al.[95]
Funneliformis mosseae	co-inoculation with PGPR	maize (*Zea mays*)	Ain et al.[99]
Rhizoglomus irregulare	combination with compost	wheat (*Triticum durum*)	Ikan et al.[100]
Glomus mosseae	–	chickpea (*Cicer arietinum* L.)	Kundu et al.[101]
Glomus versiforme	co-inoculation with PGPR	rapeseed (*Brassica napus* L.)	Afrangan et al.[102]
Diversispora eburnea	combination with biochar	maize (*Zea mays*)	Sun et al.[94]

reduced glutathione (GSH) level in cell.[44] GSH plays a central role in ROS scavenging and regeneration of other antioxidants. AMF enhance plant resistance to oxidative stress by increasing GR activity.[80]

Non-enzymatic antioxidants and cellular functions

AMF are not only a mechanism to remove ROS but also help the plant to synthesize various non-enzymatic antioxidants.[81] An example is that in chloroplasts, the production of ascorbate (vitamin C) is enhanced by AMF, increasing the cell capacity to detoxify ROS.[82] Ascorbate, in this regard, plays a crucial role in the detoxification of H_2O_2 and protects the photosynthetic organelles.[76] GSH removes the cytoplasmic ROS and has a coordinating role in preventing the alteration of proteins under oxidative stress.[83] At the same time, GSH plays a prominent role in the biosynthesis of other antioxidants. AMF prevent the lipid peroxidation mechanism by increasing the tocopherol (vitamin E) level in the chloroplast membrane.[84] In addition, tocopherols neutralize the harmful radicals responsible for cellular stress, thus protecting the membrane from damage.[85] Finally, AMF can help to reduce ROS in the cell by increasing the amount of flavonoids and other phenolics from the biosynthesis route. These substances not only act as any other antioxidants but also provide plant resistance against attack caused by plant pathogens as a regular part of plant defense mechanisms.[86]

Osmotic regulation and ion homeostasis

AMF help to maintain intracellular water potential by promoting the accumulation of proline, glycine betaine, and soluble sugar within plant tissues.[87] Proline not only retains water in the cells but also conveys energy by checking the structure of the mitochondria and preventing protein denaturation. Glycine betaine is an amino acid derivative with a protective role, impacts membrane stability and enzyme activities, and thus makes plants more resistant to adverse conditions. Plants under salt stress suffer a loss of turgor pressure, which negatively affects the metabolic processes. To avoid this kind of scenario, AMF trigger two mechanisms by which the cellular metabolism should be maintained, and the homeostasis of the cells should remain sufficient. AMF help to stabilize osmotic pressure by regulating ion accumulation in vacuoles.[88] This increases intracellular water retention and cell resistance to water loss. In particular, the storage of Na^+ and Cl^- ions in vacuoles reduces ion toxicity in the cytoplasm and supports the sustainability of cellular metabolism.[70] AMF also increase the existing Na^+/H^+ antiporters in plant meristematic cells, which control the increase of Na^+ in the plant cells. AMF also promote the accumulation of K^+, which, in turn, helps to keep the Na^+/K^+ balance low, thus avoiding sodium toxicity.[80] Altogether, this results in an increased efficiency of the enzymatic reaction and, therefore, provides a basis for maintaining the metabolic processes. AMF increase resilience by promoting the synthesis of structural proteins and polysaccharides in the cell wall.[89] This increases the resistance of cells to external stresses and prevents cell deformations due to loss of turgor. In particular, regulating structural components such as pectin and cellulose promotes plant growth under stress conditions by increasing cell wall flexibility.[90] The role of AMF in maintaining cellular turgor is not limited to preventing plants from water loss but also has an essential effect in maintaining ion homeostasis and metabolic balance.[70,80] This increases the resilience of plants to abiotic stress conditions while ensuring the sustainability of crucial processes such as growth and productivity. In conclusion, AMF's symbiotic relationship with plants offers unique biochemical mechanisms to mitigate oxidative stress's effects and optimize osmotic balance. Effects such as strengthening antioxidant defense systems, ROS scavenging, osmolyte accumulation, and maintenance of ion balance enhance plant resilience to abiotic stress conditions and support productivity. These biochemical effects of AMF offer a promising strategy for sustainable agricultural practices. AMF also maintain high water pressure by inducing genes related to water transport. In this case, the AQP genes are responsible for water transport. Plasma membrane intrinsic proteins and tonoplast intrinsic proteins are key to regulating in-plant cell turgor.[31]

APPLICATIONS OF AMF IN SALINE SOILS

AMF applications in agricultural practices offer several contributions, such as improving soil health, supporting plant growth, and increasing environmental sustainability. Many scientific studies have endorsed several products formed by different AMF species and tested their efficacy, which has been proven in different agricultural conditions (Table 2).[91] AMF inoculation improves agricultural productivity by directly applying it to seeds, roots, or soil. In this process, selecting AMF species suitable for specific plant species and local soil characteristics is critical for optimum benefit.[92] For example, it was studied that *Rhizophagus irregularis* inoculation on drought-tolerant plant *Elaeagnus angustifolia* can enhance activities of CAT, phosphatase, urease, and saccharase in rhizosphere soil. Moreover, the inoculated root cells showed the presence of more organelles, greater integrity, and lower sodium concentrations under salt stress.[93] Several research studies have investigated using AMF inoculants to enhance plant growth and mitigate salt stress in combination with other environmental contaminants. For instance, Zarei and collaborators investigated the effects of *Claroideoglomus etunicatum* on maize plants under salt stress and boron contamination. The findings underlined that, despite abiotic stress, the colonization rate of AMF did not decrease. Moreover, the inoculation revealed significant increases in plant biomass, K^+/Na^+ ratio, and sodium and copper concentrations but reduced root boron concentrations and increased ion leakage.[94] AMF also have an essential place in integrated farming systems, constituting a valid tool for improving soil health and crop performance, especially in saline soils. When integrated with sustainable agricultural practices such as intercropping crop rotation, the productivity of both soil ecosystems and crops can be increased. Furthermore, combining AMF with organic matter, biochar, and biostimulants significantly increases the colonization rates and AMF efficacy. It has a supportive role in the performance of AMF, especially in salinity-dominated soil conditions (Table 2).[95] A case study performed by Slimani et al. reveals the advantages of using intercropping with alfalfa and co-inoculating AMF and plant growth-promoting rhizobacteria to improve the growth, yield, nutritional quality, and soil fertility of barley (*Hordeum vulgare*).[96] Emerging agricultural technologies also provide tools to support AMF applications: remote sensing, soil health diagnostics, and data-based analysis methods within precision agriculture enable AMF applications to be targeted more effectively. Especially in fields where salinity is variable, these technologies allow AMF to be applied in a way that provides optimum benefit.[97] Thus, the use of AMF in agricultural systems has the potential to be ecologically and economically sustainable.

CONCLUSIONS AND FUTURE PERSPECTIVES

Soil salinity is a complex problem that poses serious threats to agricultural production. About 20% of irrigated land worldwide faces salinity problems, complicating efforts to ensure food security.[103] High concentrations of soluble salts exert osmotic pressure on plant root systems, limiting water and nutrient uptake. Furthermore, the accumulation of toxic ions (e.g., Na^+ and Cl^-) directly affects photosynthesis and other vital metabolic processes, resulting in yield losses.[104] Traditional salinity management strategies rely on methods such as drainage and soil conditioners. However, these methods are costly, water-intensive, and environmentally unsustainable. Therefore, the search for environmentally friendly and sustainable alternative solutions has increased. AMF have emerged as critical biological agents with the potential to enhance plant resistance to salinity by establishing symbiotic relationships with plants.[105] The ability of AMF to promote plant growth, as previously described, by maintaining ion balance and improving soil structure through symbiotic relationships, has been supported by research.[65,105,106] These approaches can bridge the gap between basic research and applied agricultural strategies. Future applications of AMF have great potential for biotechnological innovations and integration into large-scale agricultural systems.[33,107]

Future advancements in this field include the identification of novel mycorrhiza-inducible genes through omics technologies, as well as the engineering of improved AMF strains or host plants to enhance symbiotic efficiency under saline conditions. Equally crucial is the large-scale production of high-quality AMF inoculants tailored to diverse soil types and environmental settings. To facilitate widespread adoption, supportive policies and dedicated farmer training programs will play a key role. Educational initiatives, government incentives, and increased awareness of the benefits of AMF-based strategies can help integrate these symbionts into both conventional and sustainable agricultural systems. In parallel, further research is needed to evaluate the long-term ecological impacts of AMF applications, particularly their interactions with native soil microbiota under salinity stress. Field-based validation and multi-season trials will be essential to translate laboratory findings into effective, real-world microbial consortia for agriculture. In conclusion, AMF offer a sustainable and environmentally friendly approach to managing saline soils and improving crop productivity. By combining integrated research, scalable technologies, and supportive policy frameworks, AMF hold great potential to reshape saline agriculture into a more resilient and productive system.

AUTHOR CONTRIBUTIONS

All authors equally contributed to this manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

The authors used no generative AI and AI-assisted technologies while preparing this work.

REFERENCES

1. Khaliq, A., Perveen, S., Alamer, K.H., Zia Ul Haq, M., Rafique, Z., Alsudays, I.M., Althobaiti, A.T., Saleh, M.A., Hussain, S., and Attia, H. (2022). Arbuscular mycorrhizal fungi symbiosis to enhance plant–soil interaction. Sustainability *14*, 7840. https://doi.org/10.3390/su14137840.
2. Martin, F.M., and van der Heijden, M.G.A. (2024). The mycorrhizal symbiosis: research frontiers in genomics, ecology, and agricultural application. New Phytol. *242*, 1486–1506. https://doi.org/10.1111/nph.19541.
3. Begum, N., Qin, C., Ahanger, M.A., Raza, S., Khan, M.I., Ashraf, M., Ahmed, N., and Zhang, L. (2019). Role of arbuscular mycorrhizal fungi in plant growth regulation: Implications in abiotic stress tolerance. Front. Plant Sci. *10*, 1068. https://doi.org/10.3389/fpls.2019.01068.
4. Figueiredo, A.F., Boy, J., and Guggenberger, G. (2021). Common mycorrhizae network: A review of the theories and mechanisms behind underground interactions. Front. Fungal Biol. *2*, 735299. https://doi.org/10.3389/ffunb.2021.735299.
5. Agnihotri, R., Sharma, M.P., Prakash, A., Ramesh, A., Bhattacharjya, S., Patra, A.K., Manna, M.C., Kurganova, I., and Kuzyakov, Y. (2022). Glycoproteins of arbuscular mycorrhiza for soil carbon sequestration: Review of mechanisms and controls. Sci. Total Environ. *806*, 150571. https://doi.org/10.1016/j.scitotenv.2021.150571.
6. George, N.P., and Ray, J.G. (2023). The inevitability of arbuscular mycorrhiza for sustainability in organic agriculture—A critical review. Front.

Sustain. Food Syst. *7*, 1124688. https://doi.org/10.3389/fsufs.2023.1124688.

7. Fiorilli, V., Martínez-Medina, A., Pozo, M.J., and Lanfranco, L. (2024). Plant immunity modulation in arbuscular mycorrhizal symbiosis and its impact on pathogens and pests. Annu. Rev. Phytopathol. *62*, 127–156. https://doi.org/10.1146/annurev-phyto-121423-042014.
8. Ghorui, M., Chowdhury, S., Balu, P., and Burla, S. (2024). Arbuscular mycorrhizal inoculants and their regulatory landscape. Heliyon *10*, e30359. https://doi.org/10.1016/j.heliyon.2024.e30359.
9. Rosling, A., Eshghi Sahraei, S., Kalsoom Khan, F., Desirò, A., Bryson, A. E., Mondo, S.J., Grigoriev, I.V., Bonito, G., and Sánchez-García, M. (2024). Evolutionary history of arbuscular mycorrhizal fungi and genomic signatures of obligate symbiosis. BMC Genom. *25*, 529. https://doi.org/10.1186/s12864-024-10391-2.
10. Adamu, G., Gaya, E., Yakubu, M.N., and Buba, T. (2024). Drought stress genetic mediation mechanism of arbuscular mycorrhiza fungi (AMF). ATBU Journal of Environmental Technology *17*, 114.
11. Kamran, M., Parveen, A., Ahmar, S., Malik, Z., Hussain, S., Chattha, M.S., Saleem, M.H., Adil, M., Heidari, P., and Chen, J.-T. (2019). An overview of hazardous impacts of soil salinity in crops, tolerance mechanisms, and amelioration through selenium supplementation. Int. J. Mol. Sci. *21*, 148. https://doi.org/10.3390/ijms21010148.
12. Brar, B., Bala, K., Saharan, B.S., Sadh, P.K., and Duhan, J.S. (2024). Bio-boosting agriculture: Harnessing the potential of fungi-bacteria-plant synergies for crop improvement. Discov. Plants *1*, 21. https://doi.org/10.1007/s44372-024-00023-0.
13. Yuan, Z., Druzhinina, I.S., Labbé, J., Redman, R., Qin, Y., Rodriguez, R., Zhang, C., Tuskan, G.A., and Lin, F. (2016). Specialized microbiome of a halophyte and its role in helping non-host plants to withstand salinity. Sci. Rep. *6*, 32467. https://doi.org/10.1038/srep32467.
14. Chen, G., Yang, A., Wang, J., Ke, L., Chen, S., and Li, W. (2024). Effects of arbuscular mycorrhizal fungi and trehalose synergistic treatments on adaptability to salt stress in tomato seedlings. Microbiol. Spectr. *12*, e0340423. https://doi.org/10.1128/spectrum.03404-23.
15. Chun, S.C., Paramasivan, M., and Chandrasekaran, M. (2018). Proline Accumulation Influenced by Osmotic Stress in Arbuscular Mycorrhizal Symbiotic. Front. Microbiol. *9*, 2525. https://doi.org/10.3389/fmicb.2018.02525.
16. Romero-Munar, A., Aroca, R., Zamarreño, A.M., García-Mina, J.M., Perez-Hernández, N., and Ruiz-Lozano, J.M. (2023). Dual inoculation with *Rhizophagus irregularis* and *Bacillus megaterium* improves maize tolerance to combined drought and high temperature stress by enhancing root hydraulics, photosynthesis and hormonal responses. Int. J. Mol. Sci. *24*, 5193. https://doi.org/10.3390/ijms24065193.
17. Qin, Y., Druzhinina, I.S., Pan, X., and Yuan, Z. (2016). Microbially mediated plant salt tolerance and microbiome-based solutions for saline agriculture. Biotechnol. Adv. *34*, 1245–1259. https://doi.org/10.1016/j.biotechadv.2016.08.005.
18. Abbaspour, H., Pour, F.S.N., and Abdel-Wahhab, M.A. (2021). Arbuscular mycorrhizal symbiosis regulates the physiological responses, ion distribution and relevant gene expression to trigger salt stress tolerance in pistachio. Physiol. Mol. Biol. Plants *27*, 1765–1778. https://doi.org/10.1007/s12298-021-01043-w.
19. Wang, H., An, T., Huang, D., Liu, R., Xu, B., Zhang, S., Deng, X., Siddique, K.H.M., and Chen, Y. (2021). Arbuscular mycorrhizal symbioses alleviating salt stress in maize is associated with a decline in root-to-leaf gradient of Na^+/K^+ ratio. BMC Plant Biol. *21*, 457. https://doi.org/10.1186/s12870-021-03237-6.
20. Assaha, D.V.M., Ueda, A., Saneoka, H., Al-Yahyai, R., and Yaish, M.W. (2017). The role of na^+ and k^+ transporters in salt stress adaptation in glycophytes. Front. Physiol. *8*, 509. https://doi.org/10.3389/FPHYS.2017.00509.
21. Mulet, J.M., Porcel, R., and Yenush, L. (2023). Modulation of potassium transport to increase abiotic stress tolerance in plants. J. Exp. Bot. *74*, 5989–6005. https://doi.org/10.1093/jxb/erad333.
22. Razvi, S.M., Singh, N., Mushtaq, A., Dar, S., and Hussain, S. (2023). Arbuscular mycorrhizal fungi for salinity stress: Anti-stress role and mechanisms. Pedosphere *33*, 212–224. https://doi.org/10.1016/j.pedsph.2022.06.027.
23. Hasanuzzaman, M., Raihan, M.R.H., Masud, A.A.C., Rahman, K., Nowroz, F., Rahman, M., Nahar, K., and Fujita, M. (2021). Regulation of reactive oxygen species and antioxidant defense in plants under salinity. Int. J. Mol. Sci. *22*, 9326. https://doi.org/10.3390/IJMS22179326.
24. Ebbisa, A. (2023). Arbuscular mycorrhizal fungi (AMF) in optimizing nutrient bioavailability and reducing agrochemicals for maintaining sustainable agroecosystems. In Arbuscular mycorrhizal fungi in agriculture - new insights, R.N. de Sousa, ed. (IntechOpen). https://doi.org/10.5772/intechopen.106995.
25. Zhang, Y., Han, X., Ren, W., Zhang, H., and Tang, M. (2024). Arbuscular mycorrhizal fungi improve lycium barbarum potassium uptake by activating the expression of *LbHAK*. Plants *13*, 1244. https://doi.org/10.3390/plants13091244.
26. Boyno, G., Rezaee Danesh, Y., Demir, S., Teniz, N., Mulet, J.M., and Porcel, R. (2023). The complex interplay between arbuscular mycorrhizal fungi and strigolactone: mechanisms, synergies, applications and future directions. Int. J. Mol. Sci. *24*, 16774. https://doi.org/10.3390/ijms242316774.
27. Bell, C.A., Magkourilou, E., Ault, J.R., Urwin, P.E., and Field, K.J. (2024). Phytophagy impacts the quality and quantity of plant carbon resources acquired by mutualistic arbuscular mycorrhizal fungi. Nat. Commun. *15*, 801. https://doi.org/10.1038/s41467-024-45026-3.
28. Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A., Khizar, C., and Reddy, S.P.P. (2023). Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. Plants *12*, 3102. https://doi.org/10.3390/plants12173102.
29. Saharan, B.S., Brar, B., Duhan, J.S., Kumar, R., Marwaha, S., Rajput, V. D., and Minkina, T. (2022). Molecular and physiological mechanisms to mitigate abiotic stress conditions in plants. Life *12*, 1634. https://doi.org/10.3390/life12101634.
30. Ahanger, M.A., Tomar, N.S., Tittal, M., Argal, S., and Agarwal, R.M. (2017). Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. Physiol. Mol. Biol. Plants *23*, 731–744. https://doi.org/10.1007/s12298-017-0462-7.
31. Guo, X.N., Hao, Y., Wu, X.L., Chen, X., Liu, C.Y., Guo, X.N., Hao, Y., Wu, X.L., Chen, X., and Liu, C.Y. (2023). Exogenous easily extractable glomalin-related soil protein stimulates plant growth by regulating tonoplast intrinsic protein expression in lemon. Plants *12*, 2955. https://doi.org/10.3390/PLANTS12162955.
32. Mitra, D., Djebaili, R., Pellegrini, M., Mahakur, B., Sarker, A., Chaudhary, P., Khoshru, B., Gallo, M.D., Kitouni, M., Barik, D.P., et al. (2021). Arbuscular mycorrhizal symbiosis: plant growth improvement and induction of resistance under stressful conditions. J. Plant Nutr. *44*, 1993–2028. https://doi.org/10.1080/01904167.2021.1881552.
33. Bi, H., Liu, Z., Liu, S., Qiao, W., Zhang, K., Zhao, M., and Wang, D. (2024). Genome-wide analysis of wheat xyloglucan endotransglucosylase/hydrolase (XTH) gene family revealed *TaXTH17* involved in abiotic stress responses. BMC Plant Biol. *24*, 640. https://doi.org/10.1186/s12870-024-05370-4.
34. Zhang, X., Gao, H., Liang, Y., and Cao, Y. (2021). Full-length transcriptome analysis of asparagus roots reveals the molecular mechanism of salt tolerance induced by arbuscular mycorrhizal fungi. Environ. Exp. Bot. *185*, 104402. https://doi.org/10.1016/j.envexpbot.2021.104402.
35. Puccio, G., Ingraffia, R., Mercati, F., Amato, G., Giambalvo, D., Martinelli, F., Sunseri, F., and Frenda, A.S. (2023). Transcriptome changes induced

by Arbuscular mycorrhizal symbiosis in leaves of durum wheat (*Triticum durum Desf.*) promote higher salt tolerance. Sci. Rep. *13*, 116. https://doi.org/10.1038/s41598-022-26903-7.

36. Hsieh, C., Chen, Y.H., Chang, K.C., and Yang, S.Y. (2022). Transcriptome analysis reveals the mechanisms for mycorrhiza-enhanced salt tolerance in rice. Front. Plant Sci. *13*, 1072171. https://doi.org/10.3389/fpls.2022.1072171.
37. Hniličková, H., Hnilička, F., Orsák, M., and Hejnák, V. (2019). Effect of salt stress on growth, electrolyte leakage, Na^+ and K^+ content in selected plant species. Plant Soil Environ. *65*, 90–96. https://doi.org/10.17221/620/2018-PSE.
38. Amin, I., Rasool, S., Mir, M.A., Wani, W., Masoodi, K.Z., and Ahmad, P. (2021). Ion homeostasis for salinity tolerance in plants: a molecular approach. Physiol. Plantarum *171*, 578–594. https://doi.org/10.1111/ppl.13185.
39. Che, Y., Yao, T., Wang, H., Wang, Z., Zhang, H., Sun, G., and Zhang, H. (2022). Potassium ion regulates hormone, Ca^{2+} and H_2O_2 signal transduction and antioxidant activities to improve salt stress resistance in tobacco. Plant Physiol. Biochem. *186*, 40–51. https://doi.org/10.1016/j.plaphy.2022.06.027.
40. Liu, J., Liu, J., Liu, J., Cui, M., Huang, Y., Tian, Y., Chen, A., and Xu, G. (2019). The potassium transporter SlHAK10 is involved in mycorrhizal potassium uptake. Plant Physiol. *180*, 465–479. https://doi.org/10.1104/pp.18.01533.
41. Arif, Y., Singh, P., Siddiqui, H., Bajguz, A., and Hayat, S. (2020). Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. Plant Physiol. Biochem. *156*, 64–77. https://doi.org/10.1016/j.plaphy.2020.08.042.
42. Karimi, Z., Zarea, M.J.J., Fazeli, A., and Zarei, B. (2024). Role of sulfur in pyrroline-5-carboxylate synthase (P5CS) gene expression, proline accumulation, and antioxidant enzyme activity of wheat under water deficit conditions. Iran Agric. Res. *42*, 83–98. https://doi.org/10.22099/iar.2023.48068.1552.
43. Hnilickova, H., Kraus, K., Vachova, P., and Hnilicka, F. (2021). Salinity stress affects photosynthesis, malondialdehyde formation, and proline content in *Portulaca oleracea* L. Plants *10*, 845. https://doi.org/10.3390/PLANTS10050845.
44. Liu, Z., Bi, S., Meng, J., Liu, T., Li, P., Yu, C., and Peng, X. (2022). Arbuscular mycorrhizal fungi enhanced rice proline metabolism under low temperature with nitric oxide involvement. Front. Plant Sci. *13*, 962460. https://doi.org/10.3389/fpls.2022.962460.
45. Ni, Y., Bao, H., Zou, R., Wang, Y., Xie, K., Cheng, B., and Li, X. (2024). Aquaporin ZmPIP2;4 promotes tolerance to drought during arbuscular mycorrhizal fungi symbiosis. Plant Soil *508*, 1–20. https://doi.org/10.1007/s11104-024-06778-5.
46. Porcel, R., Aroca, R., Azcon, R., and Ruiz-Lozano, J.M. (2016). Regulation of cation transporter genes by the arbuscular mycorrhizal symbiosis in rice plants subjected to salinity suggests improved salt tolerance due to reduced Na^+ root-to-shoot distribution. Mycorrhiza *26*, 673–684. https://doi.org/10.1007/S00572-016-0704-5/FIGURES/5.
47. Roy, S., Chakraborty, A.P., and Chakraborty, R. (2021). Understanding the potential of root microbiome influencing salt-tolerance in plants and mechanisms involved at the transcriptional and translational level. Physiol. Plantarum *173*, 1657–1681. https://doi.org/10.1111/PPL.13570.
48. Guan, C., Cui, X., Liu, H.Y., Li, X., Li, M.Q., and Zhang, Y.W. (2020). Proline biosynthesis enzyme genes confer salt tolerance to switchgrass (*Panicum virgatum L.*) in cooperation with polyamines metabolism. Front. Plant Sci. *11*, 46. https://doi.org/10.3389/FPLS.2020.00046/BIBTEX.
49. Magwanga, R.O., Lu, P., Kirungu, J.N., Lu, H., Wang, X., Cai, X., Zhou, Z., Zhang, Z., Salih, H., Wang, K., and Liu, F. (2018). Characterization of the late embryogenesis abundant (LEA) proteins family and their role in drought stress tolerance in upland cotton. BMC Genet. *19*, 6–31. https://doi.org/10.1186/S12863-017-0596-1/FIGURES/9.
50. Zhang, H.C., Gong, Y.H., Tao, T., Lu, S., Zhou, W.Y., Xia, H., Zhang, X.Y., Yang, Q.Q., Zhang, M.Q., Hong, L.M., et al. (2024). Genome-wide identification of R2R3-MYB transcription factor subfamily genes involved in salt stress in rice (*Oryza sativa* L.). BMC Genom. *25*, 797. https://doi.org/10.1186/S12864-024-10693-5/FIGURES/6.
51. Benito, P., Celdrán, M., Bellón, J., Arbona, V., González-Guzmán, M., Porcel, R., Yenush, L., and Mulet, J.M. (2024). The combination of a microbial and a non-microbial biostimulant increases yield in lettuce (*Lactuca sativa*) under salt stress conditions by up-regulating cytokinin biosynthesis. J. Integr. Plant Biol. *66*, 2140–2157. https://doi.org/10.1111/jipb.13755.
52. Bhat, B.A., Mir, R.A., Mir, W.R., Hamdani, S.S., and Mir, M.A. (2024). Transcription factors-golden keys to modulate the plant metabolism to develop salinity tolerance. Plant Stress *11*, 100409. https://doi.org/10.1016/j.stress.2024.100409.
53. Muhammad Aslam, M., Waseem, M., Jakada, B.H., Okal, E.J., Lei, Z., Saqib, H.S.A., Yuan, W., Xu, W., and Zhang, Q. (2022). Mechanisms of abscisic acid-mediated drought stress responses in plants. Int. J. Mol. Sci. *23*, 1084. https://doi.org/10.3390/ijms23031084.
54. Hussain, Q., Asim, M., Zhang, R., Khan, R., Farooq, S., and Wu, J. (2021). Transcription factors interact with ABA through gene expression and signaling pathways to mitigate drought and salinity stress. Biomolecules *11*, 1159. https://doi.org/10.3390/biom11081159.
55. Raziq, A., Wang, Y., Mohi Ud Din, A., Sun, J., Shu, S., and Guo, S. (2022). A comprehensive evaluation of salt tolerance in tomato (Var. Ailsa Craig): Responses of physiological and transcriptional changes in RBOH's and ABA biosynthesis and signalling genes. Int. J. Mol. Sci. *23*, 1603. https://doi.org/10.3390/ijms23031603.
56. Saxena, B., Sharma, K., Kapoor, R., Wu, Q.-S., and Giri, B. (2022). Insights into the molecular aspects of salt stress tolerance in mycorrhizal plants. World J. Microbiol. Biotechnol. *38*, 253. https://doi.org/10.1007/s11274-022-03440-z.
57. Naz, M., Afzal, M.R., Raza, M.A., Pandey, S., Qi, S., Dai, Z., and Du, D. (2024). Calcium (Ca^{2+}) signaling in plants: A plant stress perspective. South Afr. J. Bot. *169*, 464–485. https://doi.org/10.1016/j.sajb.2024.04.047.
58. Dong, Q., Wallrad, L., Almutairi, B.O., and Kudla, J. (2022). Ca^{2+} signaling in plant responses to abiotic stresses. J. Integr. Plant Biol. *64*, 287–300. https://doi.org/10.1111/jipb.13228.
59. Luan, S., and Wang, C. (2021). Calcium signaling mechanisms across kingdoms. Annu. Rev. Cell Dev. Biol. *37*, 311–340. https://doi.org/10.1146/annurev-cellbio-120219-035210.
60. Fu, W., Yan, M., Zhao, L., Zeng, X., Cai, B., Qu, S., and Wang, S. (2023). Inoculation with arbuscular mycorrhizal fungi increase calcium uptake in *Malus robusta*. Sci. Hortic. *321*, 112295. https://doi.org/10.1016/j.scienta.2023.112295.
61. Averill-Bates, D. (2024). Reactive oxygen species and cell signaling. Review. Biochim. Biophys. Acta Mol. Cell Res. *1871*, 119573. https://doi.org/10.1016/j.bbamcr.2023.119573.
62. Porcel, R., and Ruiz-Lozano, J.M. (2004). Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. J. Exp. Bot. *55*, 1743–1750. https://doi.org/10.1093/JXB/ERH188.
63. Güneş, H., Demir, S., Durak, E.D., and Boyno, G. (2024). The effect of Arbuscular Mycorrhizal fungal species *Funneliformis mosseae* and biochar against *Verticillium dahliae* in pepper plants under salt stress. Eur. J. Plant Pathol. *170*, 669–686. https://doi.org/10.1007/s10658-024-02926-w.
64. Gong, M., Bai, N., Su, J., Wang, Y., Wei, Y., and Zhang, Q. (2024). Transcriptome analysis of Gossypium reveals the molecular mechanisms of Ca^{2+} signaling pathway on arsenic tolerance induced by arbuscular mycorrhizal fungi. Front. Microbiol. *15*, 1362296. https://doi.org/10.3389/fmicb.2024.1362296.

65. Boyno, G., Demir, S., and Danesh, Y.R. (2022). Effects of some biological agents on the growth and biochemical parameters of tomato plants infected with *Alternaria solani* (Ellis & Martin) Sorauer. Eur. J. Plant Pathol. *162*, 19–29. https://doi.org/10.1007/s10658-021-02398-2.
66. Hameed, A., Ahmed, M.Z., Hussain, T., Aziz, I., Ahmad, N., Gul, B., and Nielsen, B.L. (2021). Effects of salinity stress on chloroplast structure and function. Cells *10*, 2023. https://doi.org/10.3390/cells10082023.
67. Gebicki, J.M. (2016). Oxidative stress, free radicals and protein peroxides. Arch. Biochem. Biophys. *595*, 33–39. https://doi.org/10.1016/j.abb.2015.10.021.
68. Hashem, A., Abd_Allah, E.F., Alqarawi, A.A., Al-Huqail, A.A., and Shah, M.A. (2016). Induction of osmoregulation and modulation of salt stress in *Acacia gerrardii* Benth. by arbuscular mycorrhizal fungi and *Bacillus subtilis* (BERA 71). BioMed Res. Int. *2016*, 1–11. https://doi.org/10.1155/2016/6294098.
69. Jajoo, A., and Mathur, S. (2021). Role of arbuscular mycorrhizal fungi as an underground savior for protecting plants from abiotic stresses. Physiol. Mol. Biol. Plants *27*, 2589–2603. https://doi.org/10.1007/s12298-021-01091-2.
70. Huang, S., Gill, S., Ramzan, M., Ahmad, M.Z., Danish, S., Huang, P., Al Obaid, S., and Alharbi, S.A. (2023). Uncovering the impact of AM fungi on wheat nutrient uptake, ion homeostasis, oxidative stress, and antioxidant defense under salinity stress. Sci. Rep. *13*, 8249. https://doi.org/10.1038/s41598-023-35148-x.
71. Cadet, J., and Davies, K.J.A. (2017). Oxidative DNA damage & repair: An introduction. Free Radic. Biol. Med. *107*, 2–12. https://doi.org/10.1016/j.freeradbiomed.2017.03.030.
72. Ye, L., Zhao, X., Bao, E., Cao, K., and Zou, Z. (2019). Effects of arbuscular mycorrhizal fungi on watermelon growth, elemental uptake, antioxidant, and photosystem ii activities and stress-response gene expressions under salinity-alkalinity stresses. Front. Plant Sci. *10*, 863. https://doi.org/10.3389/fpls.2019.00863.
73. Li, Z., Zhang, Y., Liu, C., Gao, Y., Han, L., and Chu, H. (2022). Arbuscular mycorrhizal fungi contribute to reactive oxygen species homeostasis of *Bombax ceiba* L. under drought stress. Front. Microbiol. *13*, 991781. https://doi.org/10.3389/fmicb.2022.991781.
74. Sachdev, S., Ansari, S.A., Ansari, M.I., Fujita, M., and Hasanuzzaman, M. (2021). abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. Antioxidants *10*, 277. https://doi.org/10.3390/antiox10020277.
75. Luo, C., Li, Z., Shi, Y., Gao, Y., Xu, Y., Zhang, Y., and Chu, H. (2024). Arbuscular mycorrhizal fungi enhance drought resistance in *Bombax ceiba* by regulating SOD family genes. PeerJ *12*, e17849. https://doi.org/10.7717/peerj.17849.
76. Hossain, M.A., Bhattacharjee, S., Armin, S.-M., Qian, P., Xin, W., Li, H.Y., Burritt, D.J., Fujita, M., and Tran, L.S.P. (2015). Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. Front. Plant Sci. *6*, 420. https://doi.org/10.3389/fpls.2015.00420.
77. Ighodaro, O.M., and Akinloye, O.A. (2018). First line defence antioxidants-superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX): Their fundamental role in the entire antioxidant defence grid. Alexandria Journal of Medicine *54*, 287–293. https://doi.org/10.1016/j.ajme.2017.09.001.
78. Li, C., Liu, Y., Liu, X., Mai, K.K.K., Li, J., Guo, X., Zhang, C., Li, H., Kang, B.-H., Hwang, I., and Lu, H. (2021). Chloroplast thylakoid ascorbate peroxidase PtotAPX plays a key role in chloroplast development by decreasing hydrogen peroxide in *Populus tomentosa*. J. Exp. Bot. *72*, 4333–4354. https://doi.org/10.1093/jxb/erab173.
79. Yang, Y., Han, X., Liang, Y., Ghosh, A., Chen, J., and Tang, M. (2015). The combined effects of arbuscular mycorrhizal fungi (AMF) and lead (Pb) stress on Pb Accumulation, plant growth parameters, photosynthesis, and antioxidant enzymes in *Robinia pseudoacacia* L. PLoS One *10*, e0145726. https://doi.org/10.1371/journal.pone.0145726.
80. Wu, N., Li, Z., Wu, F., and Zhen, L. (2022). Sex-specific photosynthetic capacity and Na^+ homeostasis in *Populus euphratica* exposed to NaCl stress and AMF inoculation. Front. Plant Sci. *13*, 1066954. https://doi.org/10.3389/FPLS.2022.1066954/BIBTEX.
81. Chandrasekaran, M. (2022). Arbuscular mycorrhizal fungi mediated alleviation of drought stress via non-enzymatic antioxidants: A meta-analysis. Plants *11*, 2448. https://doi.org/10.3390/plants11192448.
82. Kapoor, R., and Singh, N. (2017). Arbuscular mycorrhiza and reactive oxygen species. In Arbuscular mycorrhizas and stress tolerance of plants, Q.-S. Wu, ed. (Springer Singapore), pp. 225–243. https://doi.org/10.1007/978-981-10-4115-0_10.
83. Adeoye, O., Olawumi, J., Opeyemi, A., and Christiania, O. (2018). Review on the role of glutathione on oxidative stress and infertility. JBRA Assist. Reprod. *22*, 61–66. https://doi.org/10.5935/1518-0557.20180003.
84. Begum, N., Ahanger, M.A., and Zhang, L. (2020). AMF inoculation and phosphorus supplementation alleviates drought induced growth and photosynthetic decline in Nicotiana tabacum by up-regulating antioxidant metabolism and osmolyte accumulation. Environ. Exp. Bot. *176*, 104088. https://doi.org/10.1016/j.envexpbot.2020.104088.
85. Sadiq, M., Akram, N.A., Ashraf, M., Al-Qurainy, F., and Ahmad, P. (2019). Alpha-tocopherol-induced regulation of growth and metabolism in plants under non-stress and stress conditions. J. Plant Growth Regul. *38*, 1325–1340. https://doi.org/10.1007/s00344-019-09936-7.
86. Ramaroson, M.-L., Koutouan, C., Helesbeux, J.-J., Le Clerc, V., Hamama, L., Geoffriau, E., and Briard, M. (2022). Role of phenylpropanoids and flavonoids in plant resistance to pests and diseases. Molecules *27*, 8371. https://doi.org/10.3390/molecules27238371.
87. Evelin, H., Devi, T.S., Gupta, S., and Kapoor, R. (2019). Mitigation of salinity stress in plants by arbuscular mycorrhizal symbiosis: current understanding and new challenges. Front. Plant Sci. *10*, 470. https://doi.org/10.3389/fpls.2019.00470.
88. Santander, C., Aroca, R., Ruiz-Lozano, J.M., Olave, J., Cartes, P., Borie, F., and Cornejo, P. (2017). Arbuscular mycorrhiza effects on plant performance under osmotic stress. Mycorrhiza *27*, 639–657. https://doi.org/10.1007/S00572-017-0784-X.
89. Buanafina, M.M.d.O., and Morris, P. (2022). The impact of cell wall feruloylation on plant growth, responses to environmental stress, plant pathogens and cell wall degradability. Agronomy *12*, 1847. https://doi.org/10.3390/AGRONOMY12081847.
90. Mendoza-Soto, A.B., Rodríguez-Corral, A.Z., Bojórquez-López, A., Cervantes-Rojo, M., Castro-Martínez, C., and Lopez-Meyer, M. (2022). Arbuscular mycorrhizal symbiosis leads to differential regulation of genes and miRNAs associated with the cell wall in tomato leaves. Biology *11*, 854. https://doi.org/10.3390/BIOLOGY11060854.
91. Gujre, N., Soni, A., Rangan, L., Tsang, D.C.W., and Mitra, S. (2021). Sustainable improvement of soil health utilizing biochar and arbuscular mycorrhizal fungi: A review. Environ. Pollut. *268*, 115549. https://doi.org/10.1016/J.ENVPOL.2020.115549.
92. Basiru, S., and Hijri, M. (2022). The Potential Applications of Commercial Arbuscular Mycorrhizal Fungal Inoculants and Their Ecological Consequences. Microorganisms *10*, 1897. https://www.mdpi.com/2076-2607/10/10/1897.
93. He, W., Fan, X., Zhou, Z., Zhang, H., Gao, X., Song, F., and Geng, G. (2020). The effect of *Rhizophagus irregularis* on salt stress tolerance of *Elaeagnus angustifolia* roots. J. Res. *31*, 2063–2073. https://doi.org/10.1007/S11676-019-01053-1/TABLES/2.
94. Sun, J., Jia, Q., Li, Y., Zhang, T., Chen, J., Ren, Y., Dong, K., Xu, S., Shi, N. N., and Fu, S. (2022). Effects of arbuscular mycorrhizal fungi and biochar on growth, nutrient absorption, and physiological properties of maize (*Zea mays* L.). J. Fungi *8*, 1275. https://doi.org/10.3390/JOF8121275/S1.
95. Rouphael, Y., Franken, P., Schneider, C., Schwarz, D., Giovannetti, M., Agnolucci, M., Pascale, S.D., Bonini, P., and Colla, G. (2015). Arbuscular

mycorrhizal fungi act as biostimulants in horticultural crops. Sci. Hortic. *196*, 91–108. https://doi.org/10.1016/J.SCIENTA.2015.09.002.

96. Slimani, A., Oufdou, K., and Meddich, A. (2023). Intercropping with alfalfa and co-inoculation of AMF and PGPR improve growth, yield, grain bioactive quality, and soil fertility of barley. Arch. Agron Soil Sci. *69*, 3469–3483. https://doi.org/10.1080/03650340.2023.2242692.
97. Phour, M., and Sindhu, S. S. (2024). Arbuscular mycorrhizal fungi: an eco-friendly technology for alleviation of salinity stress and nutrient acquisition in sustainable agriculture. In Arbuscular Mycorrhizal Fungi in Sustainable Agriculture: Nutrient and Crop Management, M. Parihar, A. Rakshit, A. Adholeya, and Y. Chen, eds. (Springer Nature Singapore), pp. 223–267.
98. Dastogeer, K.M.G., Zahan, M.I., Tahjib-Ul-Arif, M., Akter, M.A., and Okazaki, S. (2020). Plant salinity tolerance conferred by arbuscular mycorrhizal fungi and associated mechanisms: A meta-analysis. Front. Plant Sci. *11*, 588550. https://doi.org/10.3389/FPLS.2020.588550/PDF.
99. Ain, Q.U., Hussain, H.A., Zhang, Q., Maqbool, F., Ahmad, M., Mateen, A., Zheng, L., and Imran, A. (2024). Coordinated influence of *Funneliformis mosseae* and different plant growth-promoting bacteria on growth, root functional traits, and nutrient acquisition by maize. Mycorrhiza *34*, 477–488. https://doi.org/10.1007/S00572-024-01165-5.
100. Ikan, C., Ben-Laouane, R., Ouhaddou, R., Anli, M., Boutasknit, A., Lahbouki, S., Benchakour, A., Jaouad, A., Bouchdoug, M., Moatasime, A. E., et al. (2023). Interactions between arbuscular mycorrhizal fungus and indigenous compost improve salt stress tolerance in wheat (*Triticum durum*). South Afr. J. Bot. *158*, 417–428. https://doi.org/10.1016/J.SAJB.2023.05.038.
101. Kundu, V., Sarkar, M., and Kundagrami, S. (2025). Mitigation of salinity stress in chickpea (*Cicer arietinum* L.) by arbuscular mycorrhizal fungi (*Glomus mosseae*) in the Sundarbans Delta Region of India. Discov. Plants *2*, 161. https://doi.org/10.1007/s44372-025-00252-x.
102. Afrangan, F., Kazemeini, S.A., Alinia, M., and Mastinu, A. (2023). *Glomus versiforme* and *Micrococcus yunnanensis* reduce the negative effects of salinity stress by regulating the redox state and ion homeostasis in *Brassica napus* L. crops. Biologia *78*, 3049–3061. https://doi.org/10.1007/S11756-023-01479-3.
103. Shahid, S.A., Zaman, M., and Heng, L. (2018). Soil salinity: Historical perspectives and a world overview of the problem. In In guideline for salinity assessment, mitigation and adaptation using nuclear and related techniques, M. Zaman, S. A. Shahid, and L. Heng, eds. (Springer Cham), pp. 43–53. https://doi.org/10.1007/978-3-319-96190-3_2.
104. Tavakkoli, E., Rengasamy, P., and McDonald, G.K. (2010). High concentrations of Na^+ and Cl^- ions in soil solution have simultaneous detrimental effects on growth of faba bean under salinity stress. J. Exp. Bot. *61*, 4449–4459. https://doi.org/10.1093/JXB/ERQ251.
105. Porcel, R., Aroca, R., and Ruiz-Lozano, J.M. (2012). Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. Agron. Sustain. Dev. *32*, 181–200. https://doi.org/10.1007/s13593-011-0029-x.
106. Demir, S., Durak, E.D., Güneş, H., Boyno, G., Mulet, J.M., Rezaee Danesh, Y., and Porcel, R. (2023). Biological control of three fungal diseases in strawberry (Fragaria × ananassa) with arbuscular mycorrhizal fungi. Agronomy *13*, 2439. https://doi.org/10.3390/AGRONOMY13092439.
107. Boyno, G., Ansari, R.A., Durak, E.D., Güneş, H., Çevik, R., and Demir, S. (2024). Arbuscular mycorrhizal technology in sustainable agriculture: Current knowledge and challenges in agroforestry. In Mycorrhizal symbiosis and agroecosystem restoration, pp. 173–195. https://doi.org/10.1007/978-981-99-5030-0_8.