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MYCORRHIZAL BIOFERTILIZERS AND HEAT STRESS TOLERANCE IN CEREAL CROPS

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ABSTRACT

Rising global temperatures, primarily driven by anthropogenic activities, pose a serious threat to agricultural productivity, soil health, and ecosystem stability. Cereal crops such as wheat and rice, particularly in tropical and temperate regions, are increasingly vulnerable to heat stress. This stress impairs physiological functions, leading to reduced growth and yield. As an eco-friendly and cost-effective solution, arbuscular mycorrhizal fungi (AMF) have gained attention for enhancing plant resilience under abiotic stress conditions. AMF improve host plant performance through various molecular and physiological mechanisms, including enhanced nutrient uptake, increased antioxidant production, chaperone activity and upregulation of stress-responsive genes. This review highlights the role of AMF as biofertilizers in mitigating heat stress in cereal crops, emphasizing their potential in sustainable agriculture.

Keywords: Arbuscular mycorrhizal fungi, Biofertilizers, Chaperones, Heat stress, Oxidative stress, Nutrient uptake, Sustainable agriculture

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Crop productivity is susceptible to climatic variations in the environment. Rising temperatures, increasing CO_2 levels and changed precipitation levels have reduced the crop yield (Yadav *et al.,* 2021). Main agricultural concern today is the gradual rise in average earth temperature due to anthropogenic activities. The amount of carbon dioxide, methane and other greenhouse gases in the atmosphere have risen by 30% and 150%, respectively, during the past 250 years (Hassan *et al*., 2021). Agriculture emerges as the most susceptible sector to the impacts of climate change due to its extensive scale and sensitivity to various weather conditions, consequently leading to substantial economic repercussions. (Gomez-Zavaglia *et al*., 2020). Increased levels of these gases have triggered more frequent and severe heatwaves. This directly affects plant physiology and soil health, leading to yield losses and long-term ecological imbalances. Parameters such as wind speed and rainfall, also play crucial roles in crop yield determination and estimations of climate change costs (Durodola and Mourad, 2020).

This decline in the crop yield can trigger food prices, profoundly impacting the global agricultural welfare, with estimations suggesting an annual global GDP loss of 0.3% by 2100 (Paudel *et al.,* 2023). In India, projections indicate a rise in temperatures by 2.33 °C to 4.78 °C, coupled with increased CO_2 concentrations and prolonged heatwaves, pose significant risks to the agriculture sector (Kumari and Sangha, 2021). By the end of the 21st century, global temperatures are expected to rise by 1.3 to 8.0°C annually, further exacerbating these challenges (Scafetta, 2024).

Crops like wheat, maize, rice, barley, oats, millet, rye and sorghum are major dietary staples, providing nutrients like vitamins, minerals, carbohydrates, fats, protein and fiber which are crucial for energy and overall health. As key sources of food energy, they help sustain the global population's health and well-being (Poole *et al*., 2021). These crops belong to the Gramineae (Poaceae) family and contribute significantly to the world's food supply with 760.92 million metric tons produced globally in 2020-21 (Bamania *et al*., 2024). But the increase in the world's population has necessitated the need to generate more produce (Srivastav, 2020). FAO projections indicate that by 2050, the global population could reach 9.8 billion, a sharp rise from the current 2.3 billion. Additionally, modern agriculture relies heavily on chemical inputs to maintain high yields, raising sustainability concerns (Edwards, 2020). This prompts the need for eco-friendly alternatives and cost-effective farming strategies.

Soil microorganisms play a vital role in maintaining soil health and supporting plant

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development, especially in disturbed or stress-prone environments. Among these, arbuscular mycorrhizal fungi (AMF) are particularly significant due to their symbiotic association with the roots of many major agricultural crops, including fruit trees, cereals, legumes, and vegetables (Wahab *et al*., 2023). Host plants supply organic carbon to this fungus, directing its flow toward colonized roots under a controlled coordinated regulation. In most plants, sucrose is transported from photosynthetic tissues (shoots) to roots via companion cell complex of the phloem. Mycorrhizal colonisation in the host roots promotes greater sucrose unloading from the phloem. This is often accompanied by the upregulation of sucrose transporters (SUTs) in both leaves and colonized roots in this mutualistic relationship (Wang and Wu, 2023). Active sugar transporters are used to import carbon from host plants. For example, *GpMST1*, identified in glomeromycotan fungi, enables glucose uptake, and *RiMST2*, expressed in intraradical fungal structures, is critical for sugar transport during colonization. Once carbon is acquired, arbuscular mycorrhizal (AM) fungi must transfer it from the intraradical mycelium (IRM) to the extraradical mycelium (ERM) to support hyphal expansion and spore formation. A significant portion of this carbon is converted into fatty acids, as lipids serve as the primary carbon reserve in AM fungi (Wang *et al*., 2017). AMF enhances the plant growth by absorbing and transferring essential soil nutrients such as phosphorus, nitrogen and micronutrients like zinc, sulphur, copper, manganese and iron to plant roots in exchange for carbon. Studies using radioactive isotopes (^32P and ^33P) in dual-compartment systems demonstrated that AM fungi significantly enhance Pi transfer to plants. Several plant phosphate transporters (PTs), such as *OsPT11* in rice, *StPT3* in potato, and *MtPT4* in *Medicago truncatula*, are specifically activated during AM symbiosis to facilitate Pi transfer from the fungal interface into root cells. These PTs rely on proton gradients generated by H^+-ATPases like HA1, which energize the peri-arbuscular membrane, aiding Pi import. Pi uptake from the soil is also mediated by fungal transporters like *GvPT* and *GiPT* (Shi *et al.*, 2023). Other transporters, such as *GigmPT* from *Gigaspora margarita*, are active both in the extraradical hyphae and within root tissues. In rice, phosphorous is absorbed through transporters like *OsPT2*, *OsPT6*, and *OsPT11*, while nitrogen and zinc are taken up by fungal ammonium transporters such as *GintAMT1-3* and *GintZnT1* in *Glomus intraradices (Madrid-Delgado et al., 2021)*. Beyond nutrient exchange, AMF improve plant tolerance to abiotic stresses like drought and salinity by enhancing leaf water potential, photosynthetic efficiency, stomatal regulation and water uptake. (Boutasknit *et al.,* 2020). Furthermore, AMF induce biochemical and molecular modifications in plants, bolstering resistance against pathogens, pests, and environmental challenges (Gałązka *et al*., 2020). These fungi also promote the activity of beneficial soil microbes, contributing to carbon sequestration and improving soil structure. As bio-fertilizers, they have the potential to strengthen plants and enhance their adaptability to changing environmental conditions (Boutasknit *et al.,* 2023).

Arbuscular mycorrhizal (AM) fungi

AM fungi are symbiotic biotrophs that establish innate relationships with their host plant through the use of intracellular fungal structures called arbuscules found in the cortical cells of the roots (Wilkes, 2021). AM fungi in general are associated with > 90 % of the agricultural and horticultural crops. It grows both inside the root tissue and outside the root tissue. Their morphology improves the soil structure, its stability and functionality (Thirkell *et al*., 2020). Many crops depict mycorrhizal dependency (Kokkoris *et al*., 2020). The term 'mycorrhizal dependency' (MD) describes a host plant's inability to flourish under particular soil conditions in the absence of arbuscular mycorrhizal fungi (AMF). The most popular method of evaluating it is to compare the yields of plants grown in the same soil environment with and without mycorrhizal connections (Bhantana *et al*., 2021a). Codependency between plants and AM fungi can be understood by looking at how their abundance, species richness, and community composition relate, but each of these measures has its limitations. Abundance patterns often show that more AM fungi are found where more suitable plants grow, but this could simply be due to shared environmental preferences rather than a direct relationship. The most reliable way to detect true codependency is by studying community composition, more specifically how changing the species in one group directly affects the other (Kokkoris *et al*., 2020). AM fungi have been studied positively for agricultural productivity and soil health especially during the abiotic stress. Several crops like *Allium cepa* under drought stress, *Antirrhinum majus* under salt stress and Alfalfa (*Medicago sativa* L.) under heavy metal stress against cadmium have benefitted from this AMF colonization (Bhantana *et al*., 2021b). Specific AMF species such as *Claroideoglomus etunicatum*, *Rhizophagus intraradices*, and *Funneliformis*

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mosseae have been shown to mitigate salt stress in *Cucumis sativus* L. (Farghaly *et al*., 2022). Plant nutrition and water availability are enhanced by the AM fungal symbiosis during stress conditions, creating a favourable microenvironment in the rhizosphere (Khan *et al*., 2022a). These fungi improve root hydraulic conductivity especially at low water potential, allowing the fungal hyphae to access water and nutrients in soil pores beyond the reach of root hairs. The production of aquaporins (protein channels) regulate the movement of water and small molecules like glycerol, ammonium, CO_2, urea, and amino acids have also been observed (Chauhan *et al*., 2022).

AM fungi also promote photosynthesis, which is closely tied to plant development, nutrient uptake, and assimilation. They increase the levels of soluble proteins, carbohydrates, and both primary and secondary metabolites in cereal crops (Khan *et al*., 2022b). It positively regulates the carbohydrate balance and osmotic equilibrium by aiding in the release of several organic compounds through osmoregulatory regulation when exposed to salt stress. Nutrient uptake in exchange of carbon is also a well-established fact briefly mentioned before as well (Singh *et al*., 2022). Adding into the knowledge, studies using ^15N-labelled compounds have demonstrated that AM fungal colonization significantly enhances nitrogen uptake in host plants. The extraradical mycelium of AM fungi absorbs inorganic nitrogen (mainly ammonium), which is subsequently assimilated into amino acids via the glutamine synthetase/glutamate synthase (GS/GOGAT) pathway (Jana, 2020). Several ammonium transporter (AMT) genes have been identified in AM fungi, including *GintAMT1*, *GintAMT2*, and *GintAMT3* in *Glomus intraradices* (now *Rhizophagus irregularis*), which are upregulated under ammonium-limited conditions. These fungal AMTs facilitate NH_4^+ uptake from the soil and rhizosphere (Calabrese *et al*., 2016). In parallel, AM symbiosis induces specific host AMT genes, such as *GmAMT4.1* in soybean and *ATM2;3* in *Medicago truncatula*, which are localized to the branch domain of the periarbuscular membrane, indicating that active NH_4^+ transfer occurs primarily at arbuscule branches (Banasiak *et al*., 2021). This fungus supports various facets of plant life including enhanced growth, stress tolerance, disease resistance and nutrition. Additionally, the hyphal networks of AM fungi enhance soil properties such as soil particle aggregation, strengthening the soil's resilience to water and wind erosion. AM fungi help to retain nutrients in soil by reducing nutrient leaching and lowering the chance of ground water contamination (Hijri and Ba, 2018). This knowledge paves the way to use AM fungal inoculum for crops.

IMPACT OF HEAT STRESS ON PLANT FUNCTIONAL HOMEOSTATSIS

Since plants are subjected to a wide range of biotic and abiotic stimuli throughout their development, these stresses have adverse impact on plant growth. Among the abiotic factors, fluctuations in soil moisture, salinity, ambient temperature, and nutrient availability are the primary contributors to compromised plant performance. These stressors disrupt physiological and metabolic processes, ultimately affecting plant yield and vitality. Extreme temperatures are the key environmental factors impacting the maintenance of plant growth (Hassan *et al*., 2021).

1. *Effect on photosynthetic apparatus*

Cereal crops experience extensive physiological, biochemical and cellular disruptions under heat stress. Physiologically, elevated temperatures lead to reduced transpiration due to stomatal closure and CO_2 accumulation. This imbalance negatively impacts the photosynthetic gas exchange, suppressing leaf expansion and triggering premature senescence. Moreover, phloem transport of assimilates from source tissues (site of synthesis) to sink tissues (site of storage) is significantly reduced under high-temperature conditions. This reduction is primarily attributed to heat-induced loss of membrane fluidity and integrity, which impairs the efficient loading and unloading of photoassimilates such as sucrose across the phloem, ultimately affecting biomass accumulation and yield (Ullah *et al*., 2022). Biochemically, heat stress leads to the inactivation of key photosynthetic enzymes, most importantly ATP synthase and ribulose-1,5-bisphosphate carboxylase/oxygenase(Rubisco). Rubisco, which catalyzes the first step in carbon fixation, operates optimally between 20°C and 30°C, with its functionality significantly reduced at elevated temperatures. During elevated temperatures, breakdown of Rubisco activase leads to diminished carboxylation and a consequent decline in net photosynthetic rate (Dos Santos *et al*., 2022). At cellular level, heat stress modifies the thylakoid membrane by changing its fluidity, affecting the membrane system inside chloroplasts where photosynthesis occurs. This alteration in fluidity results in the separation of light-harvesting complex II from photosystem II, disrupting

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the transfer of energy during the light-dependent reactions of photosynthesis (Poudel *et al.*, 2020).

2. Effect on osmotic balance

High temperatures significantly affect plant osmotic regulation by increasing evapotranspiration, which in turn stimulates the synthesis of osmolytes such as glucose, proline critical for maintaining osmotic balance under water-deficit conditions. It also disrupts cellular metabolism by impairing water homeostasis caused by excessive transpirational water loss from leaves and reduced hydraulic conductivity in roots limiting the water uptake. This imbalance leads to a decline in leaf water potential, compromising the turgor potential and cell expansion. Additionally, increases in the fluidity of membrane lipids has also been observed thereby affecting membrane stability and functionality, ultimately resulting in reduced cell integrity and impaired growth (Hassan *et al*., 2021). Increased temperatures accelerate the loss of soil moisture, which exacerbates the consequences of heat stress and drought by reducing leaf water potential and tissue moisture. High temperatures also reduce the overall rate of water absorption and the relative water content (RWC), which have a substantial negative impact on the final crop yield (Hassan *et al*., 2021).

3. *Effect on causing oxidative stress*

Excessive heat disrupts the redox equilibrium in plants, generating reactive oxygen species (ROS) ultimately causing oxidative stress. The accumulation of ROS under high-temperature conditions results in altered gene expression, protein denaturation, oxidative modification of biomolecules, and enzyme inactivation. ROS detoxification under stress is facilitated by ROS-scavenging enzymes such as glutathione reductase and monodehydroascorbate reductase, superoxide dismutase, catalase and ascorbate peroxidase (Raza, 2022). Among the various ROS, hydroxyl radicals (OH) exhibit high reactivity and can damage critical cellular components such as photosynthetic pigments, membrane lipids, proteins, and nucleic acids. Superoxide radicals (O^{2-}) oxidize proteins, degrade polyunsaturated fatty acids, compromise membrane integrity, and initiate lipid peroxidation, leading to decreased membrane permeability and protein dysfunction. Even moderate levels of heat stress impair photosynthetic efficiency, particularly by disrupting light reactions through enhanced electron leakage from thylakoid membranes, a process directly linked to ROS overproduction (Garcia-Caparros *et al*., 2021). Concurrently, high temperatures elevate the leaf surface temperature, diminishing enzymatic antioxidant activities and increasing malondialdehyde (MDA) levels in plant leaves which is key marker of lipid peroxidation. In wheat, significant elevations in MDA levels have been observed during both early and later stages of seedling development under heat stress conditions (Yao *et al*., 2022). ROS accumulation under sustained heat stress also promotes premature leaf senescence and induces membrane depolarization at the plasma membrane, which can culminate in cell death under severe conditions (Yadav *et al*., 2022). Beyond cellular damage, ROS also serve as signalling molecules that activate heat shock responses (HSRs). These responses include the upregulation of heat shock proteins (HSPs), which are essential for maintaining protein stability and facilitating the development of thermotolerance in crops such as rice (*Oryza sativa* L.) (He *et al*., 2021) and wheat (*Triticum aestivum* L.) (Ul Hassan *et al*., 2021).

4. Effect on synthesis of starch and protein in cereal crops

In wheat and other cereal crops, starch biosynthesis is a complex metabolic process involving key enzymes such as sucrose synthase (SuSy), soluble starch synthase (SSS**)** and granule-bound starch synthase (GBSS) **(**Irshad *et al*., 2021). However, when wheat plants are exposed to high temperatures, particularly at 40°C, the activity of soluble starch synthase decreases. This decrease in the activity negatively impacts starch synthesis and grain growth, leading to a reduction in starch concentration by approximately 30%. In maize, heat adversely affects the activity of several additional enzymes critical for carbohydrate metabolism. These include ADP-glucose pyrophosphorylase (AGPase), aldolase, acid invertase and acid phosphatase all of which exhibit decreased activity under high-temperature conditions. Furthermore, enzymes directly involved in starch metabolism such as SuSy, AGPase, glucokinase, SSS and starch branching enzyme (SBE) show reduced enzymatic activity in response to heat stress, ultimately limiting starch accumulation during grain filling. In sweet maize, heat stress also downregulates sucrose phosphate synthase (SPS) and SuSy, resulting in a significant decline in sucrose content, further restricting the substrate supply for starch biosynthesis (Yang *et al*., 2018).

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In addition to its impact on starch metabolism, heat stress significantly affects protein accumulation in cereal grains. In wheat, the endosperm comprises over 80% of the grain mass and is primarily made up of glutenins and gliadins, the two major storage proteins. Heat stress has been shown to reduce both the rate and duration of protein accumulation during grain development (Juhász *et al*., 2014). Interestingly, in maize, elevated temperatures during the grain-filling stage result in a decrease in starch content and a corresponding increase in protein concentration, indicating a shift in grain composition. This shift in grain composition occurs due to changes in enzymes involved in starch and protein synthesis (Narwal *et al*., 2022).

5. *Effect on grain filling*

Heat stress significantly influences both the rate and duration of grain filling in cereal crops, particularly in wheat. The extent of its impact is largely dependent on the timing, duration and intensity of the stress event (Hussain *et al*., 2018). The first stage of plant that can be severely impacted by heat stress (HS) is during seed germination followed by the grain filling (Ul Hassan *et al*., 2022). The early grain-filling stage is more vulnerable to high temperatures compared to later phases, with even moderate heat stress disrupting assimilate partitioning and kernel development.

In wheat, optimal grain filling occurs within a temperature range of 15-20°C, which supports an extended filling period and maximum yield potential. However, temperatures exceeding 35°C during grain filling severely reduce grain weight and lead to shrivelled, poorly filled kernels. This reduction in grain-filling duration is associated with a decline in carbohydrate accumulation, resulting in lower final grain weight. High temperatures also negatively affect seed germination and early seedling establishment by damaging embryonic tissues, especially under extreme temperatures like 45°C. Such thermal stress compromises germination efficiency, delays emergence, and contributes to a poor crop stand. Additionally, heat stress impairs the development and function of productive tillers, leading to a reduction in both tiller number (by 15.38%) and grain yield (by 53.57%) in wheat (Shaukat *et al*., 2024). In the reproductive stage of the crop's growth cycle, these effects are especially noticeable.

Furthermore, when this stress occurs after anthesis it significantly accelerates plant senescence, hastens maturity, and induces programmed cell death (apoptosis) in wheat plants, thereby shortening the window for effective grain filling (Li *et al*., 2022). Significant losses in grain output can result from even a slight increase in average temperature, such as 1˚C during the reproductive stage (Lamaoui *et al*., 2018).

FUNCTIONAL ROLE OF MYCORRHIZA IN HEAT STRESS RESPONSE

Arbuscular mycorrhizal fungi (AMF) create a mutually beneficial relationship with the roots of most land plants. AMF secrete symbiotic signalling molecules known as lipo-chito-oligosaccharides, which play a crucial role in enhancing root growth and branching. These chito-oligosaccharides trigger calcium spiking within plant cells, which is detected by calcium-dependent kinases. This signalling cascade allows the plant to accommodate fungal colonization without triggering immune rejection. Once established, the arbuscules formed within root cortical cells facilitate the efficient transport of nutrients between the fungus and the host plant (Malhi *et al*., 2021). In return, the mycorrhizal hyphae of the fungi help the plants absorb nutrients from the soil, ultimately enhancing plant growth and nutrient uptake. This interaction has been found to increase various aspects of plant physiology, including water and nutrient absorption, photosynthesis, root structure, antioxidant defenses and hormonal balance, which collectively aid in coping with soil water deficits (He *et al*., 2020) as presented in the (Fig. 1). AMF also enhanced the activities of key antioxidant enzymes (superoxide dismutase, catalase, ascorbate peroxidaseand glutathione reductase) and their related compounds (glutathione and ascorbic acid), while simultaneously reducing oxidative stress markers like lipid peroxidation and hydrogen peroxide levels (Tammam *et al*., 2022).

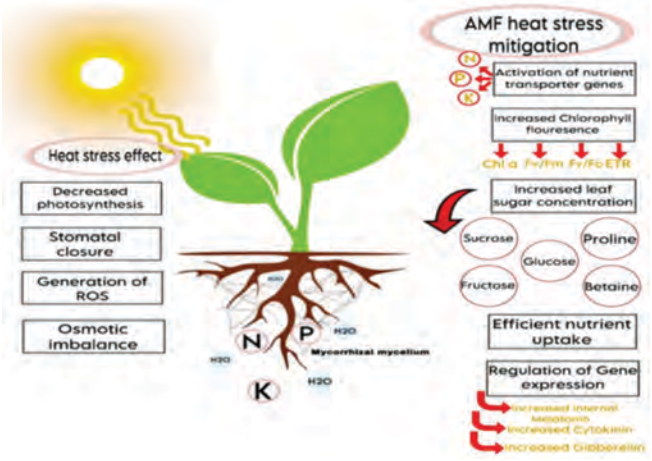

Fig 1. AMF mechanisms to alleviate heat stress in cereal crops

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1. *Activation of nutrient transporter genes*

The interaction between plants and AMF significantly influences the expression of genes involved in the uptake of key macronutrients such as nitrogen (N), phosphorus (P) and potassium (K). AMF extend their hyphae extensively in the soil, enabling them to explore a larger volume of soil than non-mycorrhizal plants, thus facilitating P uptake. The introduction of mycorrhizal fungi into the soil increases microbial biomass, leading to heightened release of CO_2, which forms H_2CO_3 in the soil solution. This weak acid aids in the dissolution of primary P-containing minerals, thereby boosting P availability. Furthermore, a synergistic relationship between P and K has been observed, wherein heightened P availability in the root zone correlates with increased K absorption in plants. Mycorrhizal fungi exhibit elevated nutrient uptake (including potassium, nitrogen, phosphorus, calcium, magnesium and iron) compared to non-mycorrhizal plants under heat stress conditions (Yeasmin *et al*., 2019).

Among the arbuscular mycorrhizal plants, there are two ways to uptake nutrients from the soil which is the direct pathway (DP) carried out by root epidermal cells and root hairs and the mycorrhizal pathway (MP) via AM fungal hyphae (Xie *et al*., 2022). For this, role of the availability of phosphorus in the soil had a significant impact on the preference of maize for different pathways of phosphorus uptake. Maize showed a preference for the mycorrhizal pathway (MP) when soil phosphorus availability was suboptimal (indicated by a preference index greater than 1). However, at both low and high levels of soil phosphorus availability, maize preferred the direct pathway (DP). Across the three tested maize genotypes, there were no significant differences observed in their preference indices under any of the soil phosphorus conditions tested. Preferential index is calculated based on P transporters, which is the ratio of gene expression levels related to the mycorrhizal pathway (ZmPT1;6) versus the direct pathway (ZmPT1;1, ZmPT1;3or ZmPT1;4) (Zhang *et al*., 2021).

2. *Activation of chlorophyll fluorescence*

Chlorophyll fluorescence analysis is a widely adopted technique for assessing the impact of abiotic stressors, including heat stress, on the photosynthetic apparatus. Under high-temperature conditions, Chl a fluorescence induction kinetics is altered, reflecting disruptions in the efficiency of photosystem II (PSII) (Faseela *et al*., 2020). Heat stress slows electron transport through PSII, compromising photochemical efficiency. However, colonization by AMF has been shown to modulate electron flow within PSII, reducing PSII side heterogeneity and providing thermal protection in crops such as rice (Mathur and Jajoo, 2020). Two key parameters commonly used to evaluate PSII photochemistry are F_v/F_m (maximum quantum efficiency of PSII) and F_v/F_o (potential photochemical efficiency). An increase in F_v/F_{min} AMF-colonized plants is often attributed to the enhanced sink strength resulting from AM symbiosis. Improved nutrient acquisition facilitated by AMF may contribute to the observed enhancement in photochemical efficiency (Jajoo and Mathur, 2021). In general, AMF-colonized plants exhibit elevated chlorophyll fluorescence parameters Including F_v/F_m, F_v/F_o, increased electron transport rate (ETR), and improved photochemical quenching. These enhancements translate into higher photosynthetic efficiency, which supports greater seed yield and promotes superior overall plant growth. In *Triticum aestivum* L., AMF inoculation has demonstrated the capacity to mitigate the detrimental effects of heat stress, thereby improving crop resilience and productivity (Gupta *et al*., 2021).

3. *Changes in osmolyte concentration in the crop*

Heat stress induces differential accumulation of key osmolytes such as sucrose, fructose, betaine and proline, which play crucial roles in osmotic adjustment and stress resilience. Elevated temperatures alter leaf sugar concentrations, disrupting the plant's osmotic balance. AMF treatment has been shown to significantly increase the concentrations of sucrose (by 268.14%), glucose (by 334.56%), and fructose (by 36.55%) in leaves compared to non-inoculated plants (Liu *et al*., 2023). Inoculation with *Diversispora versiformis*, a species of AMF, has also been associated with significant enhancements in betaine and proline levels, both of which are central to osmotic regulation under stress.

In AMF-colonized plants, the activity of sucrose phosphate synthase (SPS) is upregulated, maintaining an adequate carbon supply for downstream metabolic processes (Liu *et al*., 2023). Proline functions as a molecular chaperone, aiding in redox homeostasis and scavenging ROS, while betaine contributes to the stabilization of proteins and plasma membrane integrity. Both molecules serve as essential osmoregulators, mitigating cellular dehydration and membrane damage during heat

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stress. The observed elevation in proline and betaine levels in AMF-colonized plants, relative to non-mycorrhizal controls, indicates a superior osmotic adjustment capacity in mycorrhizal plants under high-temperature conditions. This enhancement helps preserve membrane fluidity, protein conformation and cellular hydration (Zivcak *et al.,* 2016). Moreover, heat-tolerant wheat cultivars typically sustain higher activity of antioxidant enzymes particularly superoxide dismutase (SOD) and glutathione reductase (GR) and elevated proline content during heat stress. This response contributes to enhanced heat resistance through the modulation of chloroplastic Cu/Zn-SOD**,** Fe-SOD, and mitochondrial Mn-SOD expression (Wang *et al*., 2014). High levels of jasmonic acid enhance carbohydrate accumulation in the shoot, thereby, influencing the root osmotic potential. Moreover, AMF also amplify the plant's response to drought stress by modulating hormonal pathways, including strigolactones and auxins (Diagne *et al*., 2020).

4. *Mitigation of stomatal closure*

The decline in photosynthetic efficiency and transpiration rates under stress conditions is largely attributed to stomatal closure, which is a typical plant response triggered by abiotic stress signals. This limits the gas exchange water loss and restricts CO_2 uptake, thereby impairing photosynthesis (Oyebamiji *et al*., 2024). It is demonstrated that mycorrhizal fungi contribute to improved drought stress tolerance by modulating stomatal function. This regulation occurs through the involvement of 14-3-3 proteins within the abscisic acid (ABA) signalling pathway, which plays a central role in plant responses to water deficit (Ouledali *et al*., 2019). Inoculation with AM fungi was shown to significantly lower ABA accumulation in maize (*Zea mays* L.) leaves, thereby delaying reductions in both photosynthetic activity and stomatal conductance. This indicates that AM symbiosis enhances stomatal stability and gas exchange efficiency under stress conditions, ultimately supporting plant physiological resilience (Ren *et al*., 2019). Under drought stress, inoculation with *Funneliformis mosseae* and *Rhizophagus irregularis* in *Solanum lycopersicum* has been shown to enhance plant height, stomatal conductance, water use efficiency, total biomass, and proline accumulation. In the case of heat stress, inoculation with *Septoglomus deserticola* and *Septoglomus constrictum* in tomato plants led to increased stomatal conductance and biomass production, contributing to improved thermotolerance (Malhi *et al*., 2021).

5. *Melatonin biosynthesis*

Melatonin (MT) functions as a potent antioxidant and regulatory molecule in plants, playing a critical role in enhancing resistance to various abiotic stresses (Ayyaz *et al*., 2022). MT has been reported to positively influence numerous physiological and biochemical processes, including rhizogenesis**,** flower and fruit development, ROS scavenging, fruit ripening, circadian rhythm regulation, leaf senescence, stomatal movement, photosynthetic efficiency, osmoregulation and overall antioxidant capacity (Wei *et al*., 2023a). Inoculation of AMF enhanced the levels of gibberellin (GA), internal MT and cytokinin (CTK) while decreasing the levels of ABA in heat-stressed plants (Wei *et al*., 2023b). Moreover, in perennial ryegrass, the expression of melatonin biosynthetic genes (*LpASMT1*, *LpTDC1*, *LpCOMT1*, *LpTDC2*, *LpASMT3*), ABA catabolism genes, CTK and GA biosynthetic genes, and their respective signal transduction transcription factors (type-B ARRs) was significantly enhanced in response to melatonin and arbuscular mycorrhizal fungi (Sun and Shahrajabian, 2023). Melatonin enhanced the accumulation of proline and osmolytes, which are vital for stress tolerance, by modulating the expression of genes like *Oryza sativa* pyrroline-5-carboxylate synthase (OsP5CS), *Oryza sativa* sucrose synthase 7 (OsSUS7) and *Oryza sativa* sucrose phosphate synthase 1 (OsSPS1), leading to increased chlorophyll production (Lu *et al*., 2022). Melatonin not only regulates gene expression but also affects essential antioxidant enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) in cereal crops. This helps combat the accumulation of reactive oxygen species (ROS) caused by environmental stressors like superoxide radicals (O^{2-}) and hydrogen peroxide (H_2O_2), thus reducing oxidative damage in maize (Muhammad *et al*., 2022). Treatment of wheat seedlings by melatonin resulted in appreciable enhancement of activities of peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) over the control seedlings (Chattha *et al*., 2022). The primary defense mechanism against reactive oxygen species (ROS) in plants involves SOD, which converts ROS into water and oxygen by eliminating superoxide ions (O_2^-). In MT-pretreated wheat leaves, a significant increase in ascorbate peroxidase (APX) activity was noted following prolonged exposure to heat stress (6 hours). This

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indicates that APX plays a role in detoxifying H_2O_2 into water and generating malondialdehyde. This suggests that in MT-treated plants, the activities of APX and glutathione reductase (GR) increased to enhance the biosynthesis of glutathione (GSH), thereby maintaining a crucial balance between ROS accumulation and the mechanism for ROS scavenging in wheat seedlings (Buttar *et al*., 2020).

6. *Chaperon production*

The production of molecular chaperones is a fundamental strategy for preventing protein misfolding and aggregation under abiotic stress conditions. In *Rhizophagus irregularis*, the expression of stress-responsive genes such as 14-3-3 proteins and luminal binding protein (BiP) has been observed under drought and salinity stress in maize, suggesting their involvement in stress adaptation mechanisms (Estrada *et al*., 2013). Trehalose, a non-reducing disaccharide, functions as a crucial protective metabolite in fungi, acting both as a universal storage carbohydrate and a stabilizing agent under stress. During abiotic stress conditions, trehalose accumulates to stabilize cellular structures and preserve protein integrity. Once stress conditions abate, trehalose levels typically return to baseline, highlighting its role as a transient protective molecule (Ribeiro *et al.*, 2024). This implies that trehalose may contribute to the enhanced stress tolerance observed in host plants colonized by arbuscular mycorrhizal fungi (AMF) under adverse environmental conditions, including heat, drought, salinity, and chemical exposure (Sharma *et al*., 2020). Triacylglycerols (TAGs) represent the predominant form of carbon storage in arbuscular mycorrhizal fungi (AMF), accounting for up to 95% of carbon aggregates (Talaat *et al*., 2017). The transfer of carbon to the extraradical mycelium, located at the distal end of the fungal colony, primarily occurs through glycogen and TAGs. In response to heat shock, enzymes involved in trehalose metabolism undergo activation, leading to an accumulation of trehalose. Specifically, enzymes associated with the trehalose synthase complex and neutral trehalose are activated not only in response to heat stress but also in various other stress conditions. Trehalose serves a protective role by maintaining cellular structure and preserving the native conformation of proteins under heat stress. Studies have shown that mycorrhizal inoculation enhances the net photosynthetic rate (P_n), stomatal conductance (gs), transpiration rate and PSII photochemistry (as indicated by a higher F_v/F_m ratio) in maize plants compared to non-mycorrhizal ones (Jajoo and Mathur, 2021).

CHALLENGES AND FUTURE PROSPECTS

Advantages of arbuscular mycorrhizae have a very limited use due to the present chemical-based agriculture. It compromises the arbuscular mycorrhizae efficacy and symbiosis. Arbuscular mycorrhizal association, diversity and activity are hampered by high concentrations of NPK fertilizers, fungicides and pesticides. Extensive tillage practices and crop rotation with non-mycorrhizal crops reduces the arbuscular mycorrhizal flora and its colonization (Kuila and Ghosh, 2022).

Another challenge prevails in the establishment and persistence of arbuscular mycorrhizal fungi under field conditions. Commercial and laboratory AMF inoculants tested in the same field differ significantly. A commercial inoculant containing PGPR, *Trichoderma* sp. and *Beauveria* sp. applied to maize in an arable field reported by Berruti *et al*. (2017) failed to get established in the field while other research produced contradictory results, with some commercial inoculants surviving better in greenhouse environments. The type of AMF, its biotic and abiotic environment also have a considerable impact on both the survival limit and the colonization of the introduced AMF species. Since it is challenging to determine whether an introduced AMF will succeed or fail, an inoculant's chances of successfully establishing in soil with a highly diversified native AMF community must be boosted. The intrinsic characteristics of an inoculant, such as propagule type (i.e., spore, roots and hyphae), dosage and the frequency of inoculation together effect the efficacy of AMF inoculation (Basiru and Hijri, 2022).

Synergistic interaction that helps both the plant and plant growth-promoting rhizomicrobes (PGPR) is positively influenced by Mycorrhizae Helper Organisms (MHO) (Raklami *et al*., 2019). Mycorrhiza Helper Bacteria (MHB) are a group of organisms that specifically enhance the formation of mycorrhizal symbiosis. Certain bacterial isolates like *Pseudomonas fluorescens*, *Pseudomonas* sp., *Bacillus* sp, *Paenibacillus* sp., *Burkholderia* sp, *Pseudomonas monteilii* etc can positively impact the development of these symbiotic relationships, a role played by MHB. Today, MHB are recognized as plant growth-promoting rhizobacteria (PGPR) (Gupta *et al*., 2021). These organisms primarily assist mycorrhizae through cellular signaling mechanisms. Mycorrhizae attract 'mycorrhiza helper' bacterial communities that reside in the surrounding mycorrhizosphere, root and spore surface promoting their proliferation (Xu

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et al., 2019). It has been discovered that combined inoculation of various combinations of PGPR and AM species increases soil sustainability, NPK content, growth, biomass and growth-promoting hormones (El-Sawah *et al*., 2021).

A better understanding on how mycorrhiza contributes in the metabolic pathways that affect the rhizospheric interaction must be deliberated on as a step towards sustainable agriculture. Using technologies like CRISPR-Cas9 systems (clustered regularly interspaced short palindromic repeats), a large dataset can be integrated into a genome-scale model to study the molecular mechanism of an interaction and identify the key genes which can be manipulated to enhance the plant mycorrhizal interaction (Basu *et al*., 2018). Availability of more mycorrhizal genomes will thus help in comparative genomics. Construction of genetically modified AMF that is resistant to harsh environments is an avenue. It is anticipated to yield valuable insights for the discovery of significant genes associated with AMF symbiosis to produce new genetic markers for ecological studies (Martin *et al.,* 2024).

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CONCLUSION

AM symbioses are known to have favourable effects on host plant nutrition, growth and mineral cycling. They are a promising component of sustainable agricultural systems. Over a long time, AMF and their interaction with below ground microbes have been the focus for majority of the studies. But now the shift must be made to understand the AMF relationship with above-ground residents as well and whether they enhance mycorrhizal colonization and functionality or not (Kalamulla *et al*., 2022). Ecosystem greatly influences the mycorrhizal behavior. Therefore, optimal fungal inoculants with higher colonization potential must be selected for maximizing the productivity of AMF application in sustainable agriculture (Madawala, 2021). It is well known that AM fungal symbiosis plays a major role in managing agriculture and ecosystem, therefore a multitude of small- and large-scale firms are focusing on production and supply of quality AM formulations or consortia products with beneficial soil bacteria for sustainable agriculture. Interest in AM-based products is rising due to their advantageous effects on plant growth, immunity, yield and betterment in soil health (Sudheer *et al*., 2023). This promotes the requirement of appropriate information on quality mycorrhizal products, formulation, production and regulation criteria for the better supply of AM products.

Conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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