Review
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The Role of Arbuscular Mycorrhizal Fungi in Alleviating Heat and Drought Stress in Vegetables

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VEGETABLES have been a part of human meals due to the health benefits associated with their consumption and the presence of beneficial compounds. However, vegetable production encounters a wide range of environmental stresses, such as heat and drought, that hamper their productivity. With the frequent climate change events across agricultural farmland in the world, the problems associated with the emergence of heat and drought are expected to persist and worsen as time ticks, consequently resulting in yield loss. To abate these problems, arbuscular mycorrhizal fungi (AMF) are essential in enhancing plant nutrient intake, plant growth, increased photosynthesis rate, and reduced oxidative stress under abiotic stress. It inhibits the downregulation of important metabolic pathways and helps host plants up-regulate tolerance mechanisms. Being naturally occurring root symbionts, AMF gives host plants vital inorganic nutrients, enhancing growth and yield in both stressed and unstressed conditions. The current review gives information on the role of AMF under abiotic stress conditions.

Keywords: Abiotic stress, Arbuscular mycorrhiza fungi, Drought, Heat stress, Vegetables.

Introduction

For a long time, vegetables have been a part of human meals due to the health benefits associated with their consumption and the presence of beneficial compounds, such as vitamins and antioxidants, for the body upon consumption (Dong et al., 2020). Vegetables are consumed by both animals and humans. They can either be consumed in raw form, half cooked, or completely cooked, and are added to food to enhance the taste. In certain countries, they are consumed together with rice and bread. High consumption of vegetables has been associated with lower risks of some deadly diseases, such as cancer and heart stroke. Apart from these, vegetables play a significant role in reducing calorie intake by providing several vitamins and minerals (Shankar, 2021). Scientists have demonstrated that vegetables provide both mental and physical health benefits. This indicates a positive correlation between a high intake of vegetables and mental health, which can generally reduce the risks of certain syndromes in both children and adults. Other health advantages of

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vegetables include helping to maintain a balanced weight, good health, and good vision (Shankar, 2021). The presence of bioactive compounds such as phenolics (flavonoids) and antioxidant activity in vegetables helps to minimise the risks of chronic and degenerative diseases and maintain general health. Due to the numerous health benefits, the World Health Organization (WHO) has recommended the daily consumption of 200–250g of vegetables (Malhi et al., 2021).

In recent years, vegetable production has doubled from 0.55 billion metric tonnes in 1997 to 1.09 billion metric tonnes in 2017 (Dong et al., 2020). However, increased production capacity is required beyond the current output to meet the vegetable demand of the ever-increasing world population, which is expected to reach nine billion by 2050. Limited fertile agricultural land hinders achieving the goal of food security for vegetable production. Exacerbating the problem is the occurrence of extreme climate conditions that are unsuitable for vegetable production. Generally, vegetables are prone to a wide range of extreme climate conditions, such as heat and drought, which are the primary causes of yield loss in vulnerable regions across the globe, accounting for more than half of the yield losses (Malhi et al., 2021).

One of the significant challenges facing vegetable production is drought. Drought can be defined as a period with limited water supply or rainfall during agricultural activities, which causes a reduction in the amount of soil moisture content, thus reducing plant growth and productivity. Drought stress is expected to become severe and intense in the future due to the disappearance of fresh water, which will significantly impact the vegetable industry. By 2050, more than 50% of the world's agricultural land will be affected by drought. Drought is one of the most severe abiotic stresses, which affects the overall plant metabolism and functionality and hinders the plant from attaining the desired output. Drought-induced stress at the seedling stage disrupts the establishment and seedling survival rates. The emergence of water stress at the vegetative and reproductive stages causes a reduction in leaf formation and tillering, which consequently affects grain yield (Oyebamiji et al. 2022; Badran, 2022; Abd El-Megeed & Mohiy, 2022). Apart from morpho-physiological changes induced by drought, changes also occur at the biochemical level, causing oxidative damage in the plants (Hassan et al., 2021) .

Heat stress can be described as an excessive increase in the temperature that causes permanent damage to plants (Chen et al., 2021). Heat stress during germination causes poor germination, growth, and establishment (Abd El-Sattar et al., 2024). The emergence of high temperatures at the vegetative stage negatively affects photosynthetic pigments, carbon metabolism, and the transportation of organic solutes in the plants. Heat-induced stress at the reproductive stage affects the pollen and ovule number and viability, pollen germination and growth in the stigma, and the accumulation of reactive oxygen species (ROS), leading to an oxidative burst. At the molecular level, high temperatures disrupt the gene expression that is directly involved in aiding plant resistance against stress (Oyebamiji et al., 2023). In the future, the world's temperature is predicted to increase to 4ºC at the end of the current century. This will further hamper vegetable production, making it a daunting task to meet the food demand of the expected rise in the world population by 2050 (Bhantana et al., 2021). Various agronomic practices have been adopted to mitigate the impact of abiotic stresses on vegetables. Though these practices have proven to be promising and effectively enhance vegetable production, they are not eco-friendly. Hence, there is a need to adopt a sustainable and eco-friendly approach (biological approach) to mitigate the impact of these stresses on vegetables.

Recently, the biological management of agriculture using microorganisms has been given more attention due to its impact on effectively improving plant functionality under stressful conditions and its eco-friendly nature. One of the most popular microorganisms for sustainable agricultural production is AMF (Reva et al., 2021). AMF is an obligate biotroph that may establish symbiotic relationships with plant roots that are essential for boosting agricultural yield and the nutrient cycle. It is worth noting that the application of AMF can lower the amount of inorganic fertilisers and pesticides used in the agriculture sectors due to its bio-protection properties (Jumrani et al., 2022). They play a significant role in enhancing plant development, growth, and establishment. They facilitate greater uptake and absorption of immobile nutrients. Additionally, they aid in improving soil quality and reducing environmental stress on plants (Oyebamiji et al., 2023). The current review aims to discuss the role of AMF in improving vegetable production under heat and drought stress conditions and food security.

Impact of Heat and Drought Stress on Vegetable Production

Heat and drought stress significantly disrupt vegetables morpho-physiological and biochemical processes (Figure 1). Vegetables suffer damage from drought and high temperatures during their life cycle. Abiotic stress malformation of seedlings decreases plant emergence, germination percentage, seedling vigour, and radicle emergence (Oyebamiji et al., 2023). Abiotic stresses such as heat and drought stress impair the plant's vegetative growth, including the plant's height, number, and size, and also affect the rate of photosynthesis by chlorophyll reduction and leaf area index (Nasir and Toth, 2022). Under drought stress, a decrease in the plant height and stem girth of canola was reported. A reduction in the growth of plants may be attributed to a disruption in the movement of nutrients via diffusion and mass flow (Iqbal et al., 2023). Apart from the vegetative phase, abiotic stresses significantly impact the plant's reproductive phase. The development processes that occur during the reproductive stage, such as pollen and stigma viability, pollination anthesis, pollen tube growth, and early embryonic development, are highly susceptible to abiotic stress (Lamaoui et al., 2018). This can cause a reduction in the growth cycle and an overall decrease in the quantity and quality of yield (Nasirand and Toth, 2022).

The photosynthesis pathway is greatly hampered by abiotic stresses that affect plant growth and development. Photosynthesis consists of various apparatus, such as photosystems and photosynthetic pigments, the electron transport system, and CO_2 reduction pathways. Any component in these systems can be negatively impacted by stress and may cause a decline in photosynthetic efficiency. Previous literature has demonstrated that drought and heat stress, when induced alone or simultaneously, cause a reduction in photosynthetic efficiency and transpiration rates. They are primarily caused by stress-induced stomatal closure. However, it can also happen due to other non-stomatal factors such as reduced leaf growth, leaf senescence, and unsuitable functioning of the photosynthetic mechanism (Wahid et al., 2007; Saibo et al., 2009; Rahnama et al., 2010). Abiotic stresses induce the abnormal accumulation of ROS targeting lipids, proteins, and polysaccharides. Overproduction of ROS results in oxidative injury and damage to the membrane, which leads to increased membrane peroxidation. Furthermore, ROS accumulation changes membrane permeability, increasing electrolyte leakage (Hassan et al., 2020), and consequently affecting vegetable production.

Abiotic stresses also cause a decrease in nutrient uptake, thus causing a decline in plant development. A reduction in nutrient uptake under stress conditions may be associated with a decrease in root biomass, root hair surface, and nutrient uptake per unit root. While the decline in nutrient uptake per unit root area may be due to reduced labile carbon (non-structural carbohydrates) (Hassan et al., 2020). Furthermore, stress disrupts carbohydrate distribution to the root from the shoot, directly affecting plant roots, thus reducing the production and functions of nutrient uptake proteins (Hassan et al., 2020). The problem of heat and drought stress has become a global concern among scientists due to their impact on yield loss and the quality of yield produced. A recent study conducted by Formisano et al. (2021) reported a decrease in lettuce fresh yield by 26.9% under greenhouse irradiance. Stress-induced heat was reported to reduce the quality of tomatoes (fruit appearance, colour, and taste) (Krishna et al., 2019).

The Role of AMF in Alleviating Heat and Drought Stress

It has been demonstrated that AMF is essential to all practicing sustainable agriculture. This group of soil-borne microscopic fungi forms a beneficial association with most of the plant's roots so that colonised plants will have a new sophisticated root suitable for nutrient uptake under a wide range of environmental conditions (Reva et al., 2021). Specifically, glomeromycete fungi's beneficial relationship with the plant helps to enhance plants' water and nutrient uptake. One of the most widely distributed genera of AM fungi is the genus *Glomus.* AM fungi produce symbiotic signals (lipo-chito-oligosaccharides) to improve roots' growth and branching. The chito-ologosaccharides induce the spiking of calcium, which is sensed through kinase. As a result, the cells tolerate the fungal infection while plant cell arbuscules transport the nutrients (Malhi et al., 2021). Mycorrhizal beneficial relationship with plants has significantly enhanced plant growth and development by providing adequate nutrient supply. In return, the fungi draw food from the plant roots. AM fungi increase plant productivity

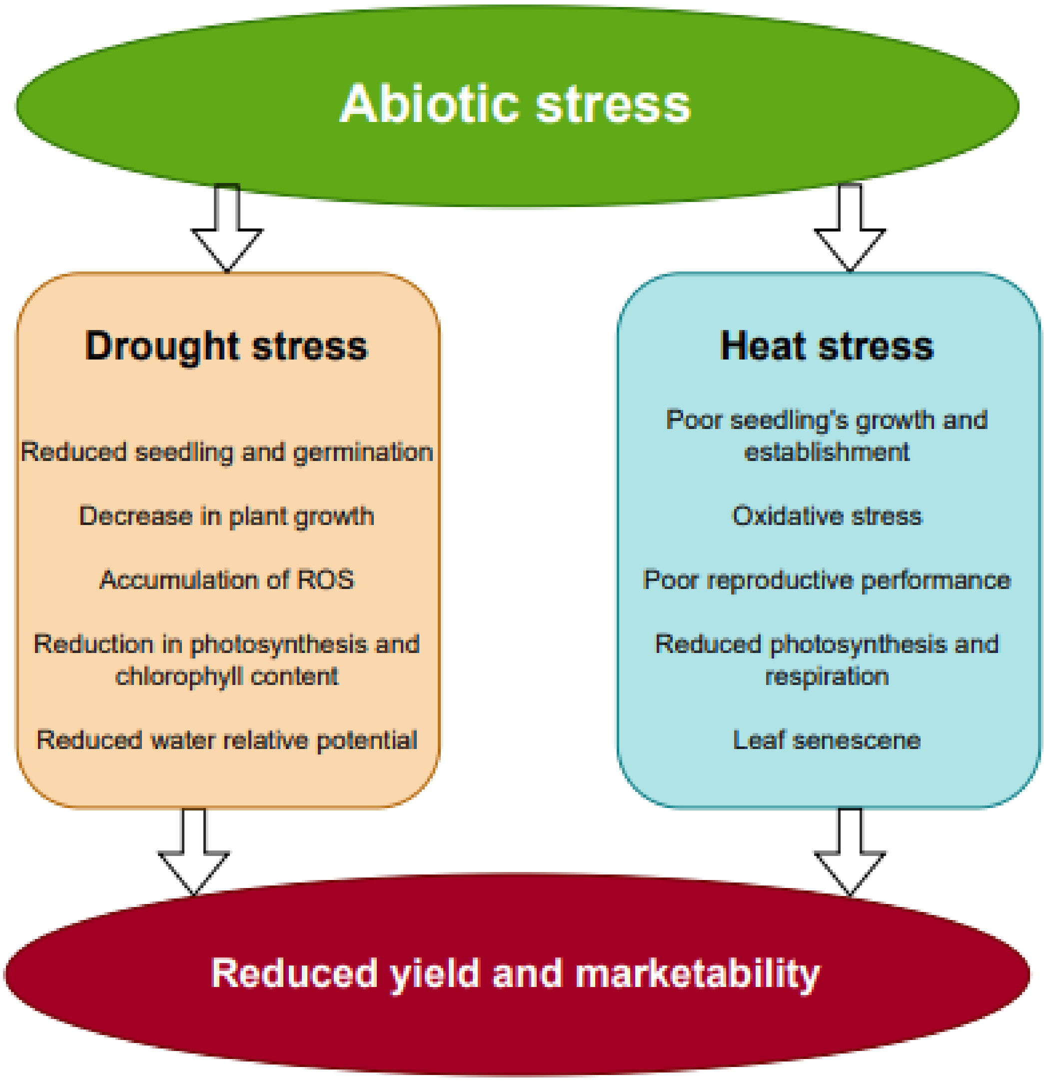

Fig.1. Impacts of Drought and Heat Stress on Vegetable Productivity.

while improving their ability to withstand stress (Malhi et al., 2021).

Under stress conditions, plants encounter a reduction in water absorption due to osmotic changes. In such cases, the inoculated AMF uses various morphological, biochemical, and physiological approaches to counteract the situation by improving the uptake of water and nutrients required for plant growth and development (Kalamulla et al., 2022). Morphologically, the improved water and nutrient absorption triggered by AMF was made possible by the induction of root volume via expanding the root length, the projected area, and the surface (Kalamulla et al., 2022) (Figure 2). The colonised plants experienced enhanced phosphorus and nitrogen assimilation. Mycorrhizal P-transporters take up phosphate and then transform it into polyphosphate before being transferred to the plant (Chauhan et al., 2022). Phosphate (Pi) uptake from soil and the PHT1 gene family mediate AMF. AMF induces Pi transporter genes during the beneficial association between plants and AMF. Overexpression of phosphate transporter (PT) genes (*LePT4* and *LePT5*) in tomatoes was induced by the inoculation of AMF, thus improving their resistance to drought stress (Israel et al., 2022). AMF also improves growth and development as well as plant establishment. They help boost immobile nutrient absorption and uptake. They also help enhance soil structure and alleviate environmental stresses in the plant (Oyebamiji et al., 2023).

A wide range of studies have demonstrated that AMF safeguards the photosynthetic processes by altering the host plant leaf stomatal behaviour, defining water vapour efflux and CO_2 gas exchange, leaf water potential and relative water content, and host plant water use efficiency, which improves host water status in drought conditions (Chauhan et al., 2022). To ensure adequate photosynthetic capacity and avoid harming the photosynthetic apparatus at high temperatures, AMF aids plants in developing their root systems for water absorption. Additionally, AMF increases plant N absorption and assimilation, thus reducing N_2O emissions (Diagne et al., 2020). AMF symbiosis reduces stress in the host plants by promoting nutrient intake, increasing the photosynthetic rate and photochemistry of PSII, osmotic adjustment, antioxidant activity, and reproductive ability (Jumrani et al., 2022). The positive correlation between AM and plant growth and development was reported to cause positive alterations to be seen when plants were injected with AM at hot temperatures. During high temperatures, plant growth traits, chlorophyll content, photosynthesis, and seed yield were improved in soybeans inoculated with AMF. To date, limited work has been conducted on the role of AM inoculation in vegetables under heat stress (Oyebamiji et al., 2023). The plant-AMF symbiosis improves gas exchange, leaf water relations, stomatal conductance, and transpiration rate. AMF also triggers ABA responses that maintain stomatal conductance and other related physiological processes (Begum et al., 2019). Under drought stress, AMF increases plant water status due to membrane and hydraulic conductivity modifications. The activation of aquaporin synthesis-related genes results in a change in membrane conductivity, which in turn increases plant water uptake. By allowing mycorrhizal hyphae to enter the soil through tiny pores where access to root hairs is possible, hydraulic conductivity is increased (Kalamulla et al., 2022).

Table 1 shows the role of AMF in the management of drought and heat stress in vegetables. Numerous investigations have shown that plants under stress produce more ROS, which harms biomolecules like lipids, proteins, and DNA. Plants have developed ROS scavengers in both their non-enzymatic and enzymatic defence systems. The inoculation of AMF helps safeguard the plant under stress conditions by improving water and nutrient uptake through the hyphae (Kalamulla et al., 2022), enhancing enzymatic antioxidant production (superoxide dismutase) and the generation of phenolic compounds and secondary metabolites, which detoxify ROS, consequently reducing oxidative damage in treated plants (Chauhan et al., 2022). AMF also enhances plant defence against oxidative stress by reducing the levels of lipid peroxidation (Chauhan et al., 2022). Plant molecules required to confer drought tolerance in plants are induced by AMF. Gene expression of these molecules, including metallothioneins and polyamines, that is upregulated by AMF prevents stressed plants from cell injuries. AMF also promotes the accumulation of osmolytes, such as proline, sugar, and glycine betaine, to balance the osmotic potential (Kalamulla et al., 2022). AMF promotes the synthesis of plant hormones such as jasmonic acid and strigolactones (Begum et al., 2019). An increase in jasmonic acid increases the shoot carbohydrate level and consequently changes the root osmotic potential. Apart from jasmonic acid, AMF also enhances strigolactone and auxin responses to drought stress (Diagne et al., 2020). Under drought and heat stress, plants inoculated with AMF exhibited increased expression or upregulation of certain genes in the roots. Therefore, AM inoculation aids in reducing oxidative stress when exposed to heat stress and drought (Malhi et al., 2021).

Interaction between AMF and Other Amendments

Organic amendments, including biochar, plant residues, manures, and composts, have alleviated crop stress. For instance, combining biochar with phosphorus has been shown to enhance plant water use efficiency and photosynthesis (Oyebamiji et al., 2023). Using mineral nutrients exogenously, such as selenium (Se) has been shown to play a critical role in increasing plant performance under stress conditions by regulating the stomatal and upregulating physiological and metabolic processes (Oyebamiji et al., 2023). The interactive effects of both organic amendment and mineral nutrients when combined with AMF have been demonstrated in previous literature. For instance, combining AMF inoculation with organic amendment enhanced the plant yield and biomass (Israel et al., 2022). Moreover, the combined application of AMF with phosphorus could enhance plants' physiological traits and yield under stress conditions (Israel et al., 2022).

The inoculation of AMF has played a significant role in alleviating heat and drought stress, as explained in the current review, by enhancing plant growth and development, nutrient and water uptake, photosynthetic efficiency, increasing antioxidant enzymes and hormone production, reducing ROS generation, and improving productivity. The eco-friendly nature of AMF makes it more widely acceptable and serves as a suitable alternative. The use of AMF, combined with other agricultural practices and amendments, should be encouraged for better productivity. Further research is required on the performance of AMF (alone or with other amendments) in the natural environment, especially in arid regions where heat and drought stress are common.

Conclusion and Recommendations

The inoculation of AMF has played a significant role in alleviating heat and drought stress, as explained in the current review, by enhancing plant growth and development, nutrient and water uptake, photosynthetic efficiency, increasing antioxidant enzymes and hormone production, reducing ROS generation and improving productivity. The eco-friendly nature of AMF makes it more widely acceptable and serves as a suitable alternative. The use of AMF combined with other agricultural practices and amendments should be encouraged for better productivity. Further research is required on the performance of AMF (alone or with other amendments) in the natural environment, especially in arid regions where heat and drought stress are common.

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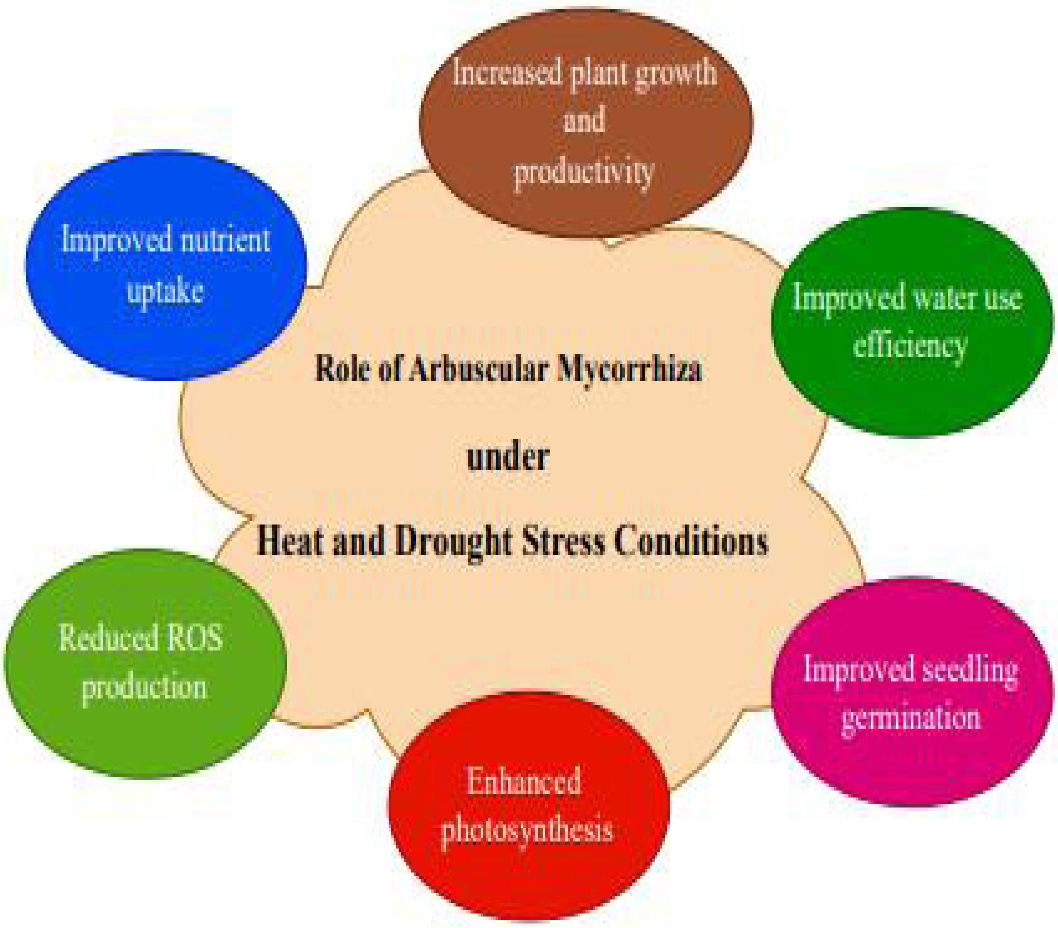

Fig. 2. Role of Arbuscular Mycorrhiza under Heat and Drought Stress Conditions.

TABLE 1. The role of AMF in the management of drought and heat stress in vegetables

Abiotic stress	AMF strains	Vegetables	Effects	References
Heat Stress	*Rhizophagusirregularis*	Tomato, pepper, and cucumber	Improved growth and productivity.	Liu et al. (2023)
Heat stress	*Diversisporaversiformis*	Cucumber	Increased growth traits, the chlorophyll index, leaf sucrose, fructose, glucose, betaine, and proline levels	Liu et al. (2023)
Drought stress	*Claroideoglomusetunicatum, Rhizophagusirregularis*, and *Funneliformismosseae*	Chickpea (*Cicerarietinum*)	Increased growth, relative water content and membrane stability, uptakes of nitrogen and phosphorus, and synthesis of chlorophyll.	Loo et al. (2022)
Drought stress	*Rhizophagusirregularis* and *Rhizophagusfasciculatus*	*Lycopersiconesculatum Capsicum annuum*	Improved root biomass, shoot length and photosynthetic pigment	Chauhan et al. (2022)
Drought stress	*Funneliformismosseae* and *Rhizophagusirregularis*	*Solanumlycopersicum*	Increase plant height, stomatal conductance, water use efficiency index, biomass, proline level, reduced ROS, and ABA level in leaf and root improvement	Chauhan et al. (2022)
Drought and Heat stress	*Rhizophagusirregularis, Funneliformismosseae*, and *Funneliformiscoronatum*	*Solanumlycopersicum*	Reduction in hydrogen peroxide and malondialdehyde content in the cells	Haddidi et al. (2020)
Drought stress	*Rhizophagusirregularis, Glomusintraradices*	Lettuce, tomato	Enhanced biomass, efficiency of photosystem II, ABA accumulation and synthesis, and strigolactone production	Begum et al. (2019)
Heat stress	*Glomusmosseae*	Cucumber	Increased root and shoot fresh weight, enhanced antioxidant activity and phenol content	Malhi et al. (2021)
Heat stress	*Penicilliumresedanum* LK6	Chilli	Increased number of leaves and biomass, nutrient uptakeproline accumulation	Malhi et al. (2021)
Heat stress	*Septoglomusdeserticola* and *Septoglomusconstrictum*	Tomato	Increased stomatal conductance and biomass production	Malhi et al. (2021)

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