The Role of Arbuscular Mycorrhiza Fungi in Drought Tolerance in Legume Crops: A Review

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ABSTRACT

Legumes are low-cost but high-yielding crops, which are rich in dietary proteins, vitamins and minerals. Known as mycorrhizal plants, legumes are widely used as model organisms to explore the plant-microbe interactions, especially the symbiotic relationship between plants and rhizosphere microorganisms. Arbuscular mycorrhizal fungi (AMF), an important class of plant-associated microbes, can regulate many physiological and molecular responses of plants. To date, AMF has been commonly used as a bio-fertilizer, whose inoculation to host plants can confer tolerance to different abiotic stresses such as drought, salinity, heat and heavy metals. This review provides an overview of the responses of legumes to drought stress (DS), a summary of the mechanism of AMF-legume symbiosis and its effect on host plant drought tolerance, which taken together reveals the significance of this symbiosis in agriculture. The presented rich information will help understand how host plants benefit from AMF to increase drought tolerance while finetuning their metabolic pathways. The potential and importance of AMF as one of the most effective and environmental-friendly management approaches for enhancing legume crop productivity against DS is highlighted.

Key words: Abiotic factors, Arbuscular mycorrhizal fungi, Drought tolerance, Legume.

Abbreviations: AMF-Arbuscular mycorrhizal fungi; DS-Drought stress; ROS-Reactive oxygen species; CMN-Common mycorrhizal network; N-Nitrogen; P-Phosphorus; SOD-Superoxide dismutase; APX-Ascorbate peroxidase; GR-Glutathione reductase; IAA-Auxin; GA-Gibberellin; CTK-Cytokinin; ABA-Abscisic acid; JA-Jasmonic acid; AQPs-Aquaporins; LEA-Late embryogenesis abundant; PIPs-Plasma membrane aquaporins; TIPs-Tonoplast aquaporins.

Legumes, or pulse crops, are a valuable source of essential nutrients for the human diet because they contain essential amino acids and proteins as well as complex carbohydrates and dietary fiber (Kamboj and Nanda, 2017; Rubiales and Mikic, 2015). It has been demonstrated that pulse crops account for 12-15% of the global agricultural arable land area, contributing about 27% of the world's major food crops and 35% of the world's vegetable oil production (Mishra *et al*., 2014). Because of their agricultural importance and advantageous bioactive chemicals, legumes have been assigned economic, cultural, physiological and medical roles in addition to their nutritional quality (Graham and Vance, 2003). The consumption of legumes has also been reported to be associated with numerous beneficial health attributes (Mungai *et al*., 2016), such as hypocholesterolemic, antiatherogenic, anticarcinogenic and hypoglycemic properties (Ndidi *et al*., 2014).

Water shortage is one of the major limiting non-biological factors that restrict the growth and development of global plants, including legumes (Jafarzadeh and Abbasi, 2006). Due to the lack of water, the cell shrinks, resulting in a reduction in cellular volume. As a result, the cellular substance becomes more viscous, causing protein denaturation (Hoekstra, 2001). When leguminous plants are excessively dehydrated, they exhibit a variety of negative responses at various stages, such as (i) reduction in the efficiency of solid C (ii) osmotic stress (iii) induction of the production of reactive oxygen species (ROS) (Barzana *et al*., 2015). Plant-microbe interactions are known to be

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ubiquitous and can be beneficial or harmful to the host or microbial parasites, depending on the balance of related biotic and abiotic stress. Legumes are widely used model organisms to understand the general law of this symbiotic relationship. Microorganisms related to plant growth may be located in the rhizosphere, leaf space or even inside the host plant (endophytes). Bacteria are able to be chemo-attracted and move towards the root exudates released by the host plants, enabling them to colonize and multiply in the rhizosphere (Lugtenberg and Kamilova, 2009). It is currently well known that rhizosphere microorganisms play an important role in the growth of legumes. It is reported that mycorrhizas usually exist in roots of plants. So far, the research on arbuscular mycorrhizal fungi is far less than that of rhizobia.

The aim of this review is to summarize the interaction of arbuscular mycorrhizal fungi and legumes, the underlying

mechanisms, as well as the significant practical significance of this symbiotic relationship in mitigating the adverse effects of drought.

Effect of drought stress on legume crops

Climate change, food shortage, water scarcity and population growth are some of the threatening challenges being faced in today's world. An increase in global temperature is accompanied by the intensification of drought stress, leading to the expansion of arid and semi-arid regions. Drought stress (DS) is a constant threat to crops and has been considered as the most important constraint to global agricultural productivity; its intensity and severity are predicted to increase in the near future. Due to this reason, the area suitable for the growth of legume crops is correspondingly reduced (Stephen Beebe, 2011). Among the various abiotic stresses, water deficit is the most important and uncontrollable factor. Grain legumes are extremely vulnerable to drought stress, which ultimately affects their grain production. Therefore, it is important to improve legumes for drought resilience. Drought affects the growth and development of legumes at various stages. The plant responses to drought stress vary between species and are affected by plant development stage and environmental conditions (Demirevska et al., 2009). Prolonged drought has adverse effects on many aspects such as seed germination, root and leaf development, photosynthetic efficiency, stoma control, flowering period and reproduction, which gives destructive effects during pod filling and hence affect the yield (Delmer, 2005; Pushpavalli et al., 2015). The germination rate in soybean (Liu et al., 2020) and chickpea (Nisha et al., 2019; Ruth Muruiki, 2018) was severely reduced due to water deficit, however, in faba bean, DS commonly occurs at the seedling stage and significantly affects yield (Li et al., 2018).

Photosynthesis is the vital pathway of energy metabolism of organisms, which has important biological significance for the growth and development of legumes. It is also reported that the water deficiency interfered with the activities of various enzymes related to carbon reactions in legumes, such as PPDK, PEPCase, EBPase and Rubisco, thereby inhibiting normal photosynthesis and ultimately reducing the net yield of grains and legumes (Farooq et al., 2014). Recent research results show that a certain degree of drought stress in soybean caused a decrease in net photosynthetic rate, the number of pods, the seed setting rate and the accumulation of dry matter, which ultimately reduced crop yields (Wang et al., 2018). Furthermore, the internal chlorophyll content and photosynthetic rate decreased significantly under drought, affecting their normal growth and development in broad beans (Siddiqui et al., 2015).

Drought also has an impact on the germination and growth of legume leaves. It was discovered in the 1980s that a lack of water promoted leaf senescence, the delay of the germination cycle of new leaves and the fall of old leaves (Karamanos, 1982). During the entire growth cycle of legumes, the flowering and reproduction periods are more susceptible to drought (Fang et al., 2010; Nezar et al., 2011). A certain intensity of drought stress shortened the flowering period and reduced the quantity and quality of nectar (Al-Ghzawi et al., 2009). At the same time, insufficient water may inhibit the germination of pollen grains and the growth of pollen tubes. In severe cases, drought led to infertility of pollen grains (Al-Ghzawi et al., 2009; Fang et al., 2010; Gusmao et al., 2012).

Studies have shown that water deficit also affects the nutrition and quality of crops, such as reducing the protein content in the grain (Singh, 2007). Furthermore, drought can also affect the content and composition of legume fatty acids (Bellaloui et al., 2013). It has been discovered that the severe drought had significantly reduced the oil and oleic acid content in soybeans (Shaheen et al., 2016). Drought hinders protein synthesis and promotes the content of free amino acids and hence ultimately affects the yield of cowpea (Mohammad Abass, 2016).

Arbuscular mycorrhizal fungi and their agricultural and ecological importance

History and classification of AMF

Arbuscular mycorrhizal fungi (AMF) are widely distributed in nature, which usually resides in the root cortex cells of the host and exist in the form of tiny branches (Bever et al., 2001). AMF-plant symbiosis has been documented to exist for at least 4 million years (Marc-André Selosse, 2015). AMF's symbiotic relationship is a classic example of a mutualistic relationship that can regulate plant growth and development. The theory of AMF's origin has been supported by a large of number fossil records, palaeobotanical data and phylogenetic analysis based on DNA sequences (James et al., 2006; Purahong et al., 2017). AMF can co-exist with nearly 80% of the roots of various types of plants on the planet and it can survive in high-stress conditions (Kivlin et al., 2011). A series of studies on various forms of Arbuscular were conducted at the beginning of the 20th century, which resulted in the classification of Arbuscular into two types: Paris and Arum (Smith, 1997). Currently, there are three forms of arbuscular structure: Arum, Paris and Intermediate. Mycorrhiza was originally proposed in 1885, followed by arbuscules in 1905. The preliminary classification system was finally completed as AMF (Smith, 1997).

Endogone, Modicella and Glaziella are the three non-mycorrhizal genera, while Glomus, Sclerocystis, Gigaspora and Acaulospora are the four mycorrhizal genera. A new mycorrhizal genus, Entrophospora, was identified by Trappe and Schenck (Gerdemann, 1974). Later, Walker added Scutellospora to the previous mycorrhizal classification and deleted Sclerocystsis (Tadros and Laarman, 1982). Morton and Benny split the aforementioned genera into three families, Glomaceae, Acaulosporaceae and Gigasporaceae, as well as two suborders, Glomineae and Gigasporaineae (Morton,1990). Later on, they further discovered two new families and two new genera, which are Archaeospora

belonging to Archaeosporaceae and *Paraglomus* belonging to Paraglomaceae (Morton and Redecker, 2000). The AMF genus, however, is still being improved. *Racocetra*, *Kuklospora*, *Pacispora*, *Otospora*, *Geosiphon*, *Ambispora* and *Intraspora* are only a few of the novel genera found in recent years (Schüßler *et al.*, 2001).

Characteristics of AM symbiosis

Arum and Paris are the two main arbuscular mycorrhizal symbionts and their characteristics are directly opposed. Paris-type fungi coexist with plants and the hyphae grow like coils inside the cells; however, the colonization of Arum-type fungi often involves the growth of hyphae longitudinally along the air channel between cortical cells through linear expansion. In other words, the Paris type develops from cells without intercellular phases and eventually forms the fungal circle. The biggest feature of the Arum type is the arbuscular branch (Dickson *et al.*, 2007). The mycelial network of fungi spread under the roots of the plant and promotes nutrient uptake. The fungal mycelium colonises the roots of many plants, even those of different species, forming a common mycorrhizal network (CMN). This CMN is known as a major component of the terrestrial ecosystem due to its significant impact on various plant communities, particularly invasive plants (Pringle, 2009) and the fungal-mediated transport of nitrogen (N) and phosphorus (P) (Gilbert and Johnson, 2017).

Agricultural and ecological importance of AMF

It is reported that the AMF as a symbiotic fungus is found in about 90% of vascular plants and has a wide range of distribution (Gai *et al.*, 2006; Redecker *et al.*, 2013). This mutual symbiosis promotes the development of plant communities to increase yields (van der Heijden *et al.*, 2008). The symbiosis of AMF and plants can not only promote nutrient absorption, enhance soil fertility and stabilize soil structure, but also improve water absorption efficiency and drought resistance. From a microbiological perspective, AMF mycelium helps parasitic plants to extend their roots. Compared with the plants without AMF, it is more likely to enter the deep soil and absorb more water (Adriana Marulanda, 2003; Bolandnazar *et al.*, 2007; Khalvati *et al.*, 2005; Ouledali *et al.*, 2018; Pavithra and Yapa, 2018). When the environmental water is insufficient, the mycelium is destroyed and mycorrhizas, which are composed of many small and long hyphae, are connected to form a uniformly distributed absorption network, conferring more efficient water absorption than roots (de la Providencia *et al.*, 2005).

The mechanism of AMF-mediated drought resistance in legumes

General mechanisms of drought tolerance in legumes

To mitigate the negative effects of drought, plants have developed various drought resistance mechanisms. In general, drought resistance can be divided into two categories: (i) the change of morphology and organization, which help obtain more water from the external environment and reduce water loss (Siddiqui *et al.*, 2021); (ii) the synthesis of protective agents, regulators, or certain proteins and hormones, which alleviates the damage caused by drought and improves drought tolerance (Xing *et al.*, 2016).

The length, width and the number of roots, among other structural properties of drought-tolerant plants, have been proposed as early as the end of the 1960s. For the growth and development of the plant, legumes' roots absorb water from the soil and transport it from the bottom up to the leaves through their root system. Therefore, longer roots are conducive to obtaining more water from the deep soil and enhancing its drought tolerance characteristics. Taking legumes as an example, when water is in short supply, the root system of drought-tolerant legumes is relatively long and the number of fibrous roots is relatively large (Sponchiado, 1989; Garay and Wilhelm, 1983; Farooq, 2009). For example, chickpeas with longer roots tend to be more drought tolerant and have higher yields (Deepa Jaganathan, 2015). However, on the other hand, when the environmental water is limited, the expansion of root angle reduces the penetration depth of the root system to a certain extent and increases the penetration range of the soil (Meister *et al.*, 2014; Wasson *et al.*, 2012). It is also reported that the depth of the root is usually determined by its diameter. The larger the diameter, the stronger the permeability and the greater the possibility of entering the deeper layers of the soil. Improving the drought tolerance of legumes is not only an increase in water absorption but also a reduction in water loss. When legumes are under drought conditions, a series of emergency physiological reactions occur, such as rapid closure of stomata, accompanied by a decrease in leaf area and solute accumulation (Agurla *et al.*, 2018; Eremina *et al.*, 2016; Shi *et al.*, 2014).

From a metabolic point of view, the drought resistance mechanisms of legumes are usually divided into four categories, namely: drought escape, solute accumulation, antioxidant regulation and hormone regulation (Nadeem *et al.*, 2019). First, drought escape is a common drought resistance mechanism. In a nutshell, the main response strategy for legumes is to reduce the growth period to adjust the water potential of plant tissues. The specific manifestation is to make full use of the limited soil moisture before the arrival of severe drought, to sustain yield (Farooq *et al.*, 2014; Farooq *et al.*, 2009). Whereas solute accumulation refers to some sugars or sugar alcohols produced by legumes in response to drought stress. Mannitol is a typical sugar alcohol that is utilized to scavenge free radicals and stabilize cell structure (Stoop *et al.*, 1996). When legume crops are subjected to a particular level of drought stress, they release reactive oxygen species (ROS) and secrete several antioxidants and enzymes, including superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), to name a few, to prevent the oxidative damage caused by excessive ROS (Saglam *et al.*, 2011). In addition to producing antioxidants during growth and development, grain legumes also produce

various hormones to regulate different functional pathways. Plant hormones such as auxin (IAA), gibberellin (GA), cytokinin (CTK), abscisic acid (ABA), ethylene and jasmonic acid (JA) are involved in the resistance to drought in legumes. Various results showed that ABA has played an important role in drought resistance: (i) the concentration of ABA increases and the stomatal conductance decreases; (ii) ABA promotes root water absorption and transportation; (iii) ABA enhances antioxidant enzyme activity and relieves a series of damages caused by oxidative stress (Merilo *et al.*, 2015; Miyashita *et al.*, 2005; Park *et al.*, 2017).

At the molecular level, the drought resistance mechanism of legumes involves two well-characterized types of proteins, namely aquaporins (AQPs) and late embryogenesis abundant (LEA) proteins. AQPs were discovered as protein water channels on the cell or vacuole membrane (Park *et al.*, 2017). Different types of AQPs have different functions. For example, plasma membrane aquaporins (PIPs) are mainly responsible for water absorption and transpiration, while tonoplast aquaporins (TIPs) are responsible for regulating the osmotic pressure of plants due to drought, ensuring cell viability (Fotiadis *et al.*, 2001). When plants were challenged by drought, the activity of a significant number of AQPs decreases, resulting in increased water use efficiency and maintenance of the original water content in the tissue, which ultimately improves the plant's drought resistance. It is also proved that the expression level of AQPs is varying in different parts of plants. PIP1 and PIP2 expression levels are frequently higher in legume roots and leaves than in stems and PIP2 is more capable of transporting water (Luo *et al.*, 2019). In the later stages of plant embryo development, another type of protein called LEA is abundant. LEA accumulates in large amounts when plants are under drought stress. LEA is supposed to serve an important role in binding water molecules and chelating ions, as well as maintaining the structure of other proteins and membranes (Sofi *et al.*, 2018). Therefore, overexpression of LEA increases tolerance to osmotic stress (Sofi *et al.*, 2018).

Colonization of AMF in legumes

The symbiosis between plants and rhizosphere bacteria is better understood than that between plants and AMF. A large number of studies have shown that rhizobia are natural symbiotic bacteria of legumes, colonizing them to form functional groups by promoting the nitrogen fixation of legumes and playing an important role in plant growth and development. However, the nutrients required for the growth of legumes include also a large amount of phosphorus and other elements (Almeida *et al.*, 2000). Since the mycelium of AMF is the main place for the absorption and transportation of inorganic phosphorus, legumes often coexist with specific AMF. In fact, AMF has very low specificity for host plant selection, which exists in almost 80% of terrestrial plant roots. Most of the legumes species, such as *M. sativa* (Duan *et al.*, 2011), *M. truncatula* (Mahmoudi *et al.*, 2019), *Lotus corniculatus*

(Meghvansi *et al.*, 2008) and *P. vulgaris*, have the ability to form symbiosis system with AMF.

AMF can be artificially colonized in the root nodules of legumes. Scheublin *et al.* (2004) conducted a phylogenetic analysis of AMF on six selected plants, three non-legumes (*F. ovina, P. lanceolata* and *H. pilosella*) and three legumes (*L. corniculatus, Trifolium repens* and *Ononis repens*) (Scheublin *et al.*, 2004). Through phylogenetic analysis, the AMF sequences were classified into distinct groups. The result showed that the AMF had 28 group types, including a total of six families, of which Acaulosporaceae (14 families) and Glomeraceae (9 families) were the most numerous families. Experiments showed that the most common type of AMF sequence is from the specific group named Glo3 and the Glo8 were more common in nodules than in other parts of the roots. In addition, there may be a positive correlation between the content of Glo8 and the nitrogen concentration. For example, external application of nitrogen to plants can change the composition of the original AMF community (Eom *et al.*, 2009).

Root nodules are the site where legumes fix nitrogen (Baird and Caruso, 1994). A total of 537 root nodules from three legumes (*Trifolium repens* L., *Ononis repens* L. and *Lotus corniculatus* L.) were studied for their nitrogen fixation activity and AMF colonization, in which up to 74% of the root nodules were found to contain AMF (Scheublin and van der Heijden, 2006). De Varennes and Goss (2007) explored the influence of AMF's customized frequency on arbuscular branches, hyphae and vesicles in the root of *Medicago truncatula*, which showed that under normal growth conditions, the colonization frequency of AMF in hyphae and arbuscular branches was as high as 65% and 42%, respectively. Liu *et al.* (2009) studied the AMF of the legume species *Caragana Korshinskii* Kom in northwestern China and found that the average colonization rate of AMF in arbuscular branches and vesicles was 5.96% and 8.78%, respectively.

Mechanism of AMF-conferred water management in legumes

The growth history of AM fungi involves four processes: (i) before infection; (ii) formation of hyphae between cells; (iii) formation of symbiotic structure; (iv) formation of free radical extra mycelia. In nature, AMF spontaneously parasitizes the rhizosphere of plants and the two interact to promote plant tolerance to various stresses, such as water deficit (Zhang *et al.*, 2019). This beneficial symbiosis promotes the process of mycelium, including spore germination, hyphal differentiation, appressorium formation and other steps and finally forms mycelium, also called arbuscular structure, which promotes the exchange and absorption of nutrients and water (Goltapeh *et al.*, 2008). Mycelium is the main structure of AMF, which can penetrate the outer cortex of roots, absorb various nutrients and water from the outside and finally transport to the host plant through the free radical hyphae in the root cells (Bonfante and Genre, 2010). Sieverding (1989) discovered that plant root length is positively correlated with the detected soil volume of the

Table 1: AMF-conferred drought tolerance in legumes.

Legume species	AMF species	Effect	Reference
Common bean	*Glomus clarum* *Acaulospora scrobiculata* *Gigaspora rosea*	Increased root dry matter and root length density; Increased the expression of the aquaporin *PvPIP1;1* gene; Diminished drastically the expression of the *PvPIP1;2* and *PvPIP1;3* genes.	(Aroca *et al.*, 2007; Recchia *et al.*, 2018)
Soybean	*Rhizophagus fasciculatus* *Ambispora leptoticha*	Increased the TLA of the plant and thus the photosynthetic activity and in turn; Increased the yield production; Higher shoot dry biomass, root dry biomass and plant dry biomass; Improved nutrient supply to plants, especially in P deficient soils; Increased significantly the phosphorus concentration of the plants.	(Ashwin *et al.*, 2019; Mondal *et al.*, 2017; Rajan *et al.*, 2005)
Cowpea	*G. deserticola* *G. gigantea*	Increased mineral elements uptake and improve water relations; Increased the root hydraulic conductivity, improved stomatalregulation, osmotic adjustment in host and enabled extraction ofwater from smaller pores.	(Augé, 2001; Farahani *et al.*, 2013; Olawuyi *et al.*, 2014)

plant body. Data showed that AMF mycelium transported about 46.2% of the water into the plant (Kakouridis *et al.*, 2020). A similar study showed that when plants suffered drought, AMF hyphae was able to provide at least 1/5 of the total water (McCorkle *et al.*, 2011). In conclusion, through symbiosis, plants can develop beneficial mycelial structures in response to external stresses, enabling them to acquire more water and other nutrients.

The mycorrhizal plant response to drought can be divided into two mechanisms: mitigation and tolerance. The drought resistance of mycorrhizal plants usually causes morphological changes, such as the formation of an extensive hypha network, directly improving water absorption efficiency and indirectly maintaining the water-locking effect of plant leaves. When AMF colonizes at a certain plant, the water potential of the plant may decrease, forming a water potential difference with the external soil, which promotes water acquisition (Marulanda *et al.*, 2003). In addition, AMF symbiosis can also bring a series of indirect benefits to drought parasitic plants. For example, AMF promotes the production of polysaccharides, mannitol and other substances in plants, which can be closely combined with soil particles, promoting the formation of soil aggregates, optimizing soil structure and improving soil moisture retention (Singh *et al.*, 2013).

Taking leguminous plants as an example, first of all, AMF inoculation on mungbean's roots can mitigate the negative impact on plants due to soil water shortage by adjusting the tissue water potentials (Habibzadeh *et al.*, 2014). A study has documented that AMF can produce a glycoprotein to form soil aggregates to optimize soil structure and achieve the best effect of water retention in legumes (*Amorpha canescens* Pursh, *Lespedeza capitata* Michx, *Lupinus perennis* L., *Dalea candida* Michx and *Dalea purpurea* Vent) (Burrows, 2014). Porcel and Ruiz-lozano (2004) found that AMF inoculation can increase the level of osmoprotectants to improve the tolerance of soybean to drought stress (Porcel and Ruiz-Lozano, 2004). In Table 1,

a collection of literature reporting on the AMF-conferred drought tolerance in various legumes is presented.

Interaction between AMF and other beneficial soil microorganisms

The rhizosphere is an extremely complex environment. In simple terms, it is the interface between the plant and the root. Roots are the key organ for the symbiosis between plants and microorganisms, which includes rhizobia and AMF to help absorb water and nutrients (Gao *et al.*, 2019). The main function of AMF includes absorbing phosphorus. It is found that the content and absorption of P in the buds of mycorrhizal plants are higher than those of non-mycorrhizal plants (Yao *et al.*, 2001). Microorganisms in the roots of legumes with root nodule symbiosis and arbuscular mycorrhizal symbiosis can interact with each other (O'Brian *et al.*, 2009). This interaction can affect the rhizosphere structure and improve the activity of soil microorganisms, thus making the plants more easily obtain organic and non-polar nutrients. In addition, some researchers conducted field research and reported that the strains inoculated with rhizobia and AMF can produce more nodules and have a higher AMF infection rate than those inoculated with rhizobia or AMF alone (Marques *et al.*, 2001). Therefore, the study of the interaction between legumes and soil microorganisms, especially the interaction between nitrogen-fixing bacteria and AMF, is important (Marzban *et al.*, 2017). Studies have suggested that the colonization of rhizobia requires a high level of phosphorus, while AMF has the function of helping phosphorus absorption (Smith and Read, 2008). There is hence no wonder that the roots of legumes can simultaneously colonize AMF and nitrogen-fixing bacteria.

CONCLUSION AND FUTURE RESEARCH PERSPECTIVES

Drought stress has posed grand challenge to agriculture all around the world. The symbiosis of microorganisms, a microbiological approach, has been a useful tool to tackle

this challenge. Compared with physical, chemical and other biological measures, the microbiological method is non-destructive, effective and cost-saving. While AMF was initially considered as beneficial entities for nutrient uptake from the soil, it has recently been demonstrated to effectively combat various environmental cues, such as salinity, drought, nutrient stress, alkali stress, cold and extreme temperatures, thus helping increase the yield of a wide range of crops and vegetables (Pavithra and Yapa, 2018). At present, the beneficial rhizosphere microbial inoculants have become popularized in agricultural practices for many crops beyond the legumes. However, there may also be unfavorable relationships between different types of rhizosphere microorganisms, such as competition and antagonism. Certain types of indigenous microorganisms in the soil may have adverse reactions with externally applied microorganisms, which is counterproductive (Romdhane *et al.*, 2021). The primary focus of future research should be on the identification of genes controlling the AMF-mediated growth and development regulation under stressful conditions, both host plant and AMF specific genes that regulate symbiotic relationship, as well as the important cellular and metabolic processes under different environmental conditions. A better understanding of the AMF-induced modulations in drought tolerance and the crosstalk triggered to regulate plant performance can help improve crop productivity.

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