

## **Drought Stress Genetic Mediation Mechanism of Arbuscular Mycorrhiza Fungi (AMF)**

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### **Abstract**

Plant development and productivity are adversely impacted by drought, a severe and complicated abiotic stress. Many research endeavors seek to identify the primary modulators of molecular and biochemical mechanisms linked to drought stress tolerance response. The development of drought stress tolerance involves the induction of several genes with diverse roles. AMF-induced production of drought-responsive genes in plants, such as aquaporins, dehydrins, and transcription factors involved in water transport, osmotic adjustment, and stress regulation. Therefore, in this review, we emphasized these three droughts-related genes. We also discussed the roles played by phytohormones, especially the strigolactone and abscisic acid as signaling molecules that help in the colonization process.

**Keywords:** *AMF, Drought Stress, Aquaporin, Dehydrin, ABA, Strigolactones*

## Introduction

The rhizosphere-level interactions between plants and microorganisms significantly influence plant development, tolerance, and resistance to both biotic and abiotic stressors (Vidal, *et al.*, 2022). Approximately 80% of terrestrial plant species can form arbuscular mycorrhizal (AM) symbiosis, making the supportive and mutualistic interaction between plant roots and these fungi, which belong to the phylum Glomeromycota, very significant for forestry and agricultural systems (Parihar, *et al.*, 2020).

The biological and environmental factors greatly influence the interaction, which is strictly controlled by both partners at the cellular, molecular, and genetic levels (Mitra, *et al.*, 2021). According to recent research, AM symbiosis is regulated by fungal signals and the matching host plant receptor-mediated signaling (He *et al.*, 2019).

A very common relationship between most terrestrial plants' roots—including those of significant crops and members of the Glomeromycota fungus is known as arbuscular mycorrhizal (AM) symbiosis (Lanfranco, *et al.*, 2016). Since the plants receive nutrients from the fungus in

exchange for up to 20% of the carbon ingested by the plants, AM symbioses are thought to be mutualistic due to the substantial nutritional benefit that both partners receive from one another (Ebbisa, 2022). A notable example of this is the delivery of inorganic phosphate (Pi), where certain fungi supply 70–100 % of the total Pi that the plant acquires (Bhalla, *et al.*, 2022). Due to their potential significance in sustainable agro-ecosystems, AM symbioses have been shown to have a significant impact on plant performance and overall ecosystem functioning (Chourasiya, *et al.*, 2021).

AMF may have been instrumental for the transition of plants from water to land (Ortas, *et al.*, 2021). Although concurrent interaction with other ancient beneficial fungi belonging to the basal Mucoromycotina subphylum is frequently reported, extant basal liverwort species do engage in AM symbiosis (Bonfante, & Venice, 2020).

Actually, among the liverworts, the oldest diverging clade only has an association with Mucoromycotina (Rimington, *et al.*, 2019). This indicates a change in fungal dominance throughout vascular plant diversification from Mucoromycotina to AM fungi (AMF),

although it is yet unclear what reasons caused this change (Albornoz, *et al.*, 2022). As plant body complexity and size increased during evolution, it is possible that the two forms of fungi differed in their ability to supply the mineral demands of their hosts, which may have been selected for the more efficiently nourishing fungal partner.

The persistence of AM symbiosis accounts for the widespread dispersion that exists today throughout the kingdom of plants, regardless of the reason for the preference (Bahram, & Netherway, 2022). A minority of non-mycorrhizal plant species emerged later in evolutionary history as a result of losses in the capacity to develop AM associates (Brundrett, & Tedersoo, 2020). It seems that this loss is inherited.

Recent phylogenomic studies on host and non-host genomes have shown that this loss appears to be genetically determined. These studies have revealed a suite of genes that are present in mycorrhizal plant species and absent from non-mycorrhizal plant species (Genre, *et al.*, 2020). The bulk of AM-associated genes, according to reverse genetics investigations, are thought to be important for the formation of symbioses (Ji *et al.*, 2023). This means that there is a gene

pool from which the molecular mechanisms underpinning AM symbioses can be deduced (Moreno. *et al.*, 2023).

The process of developing an AM symbiosis is extremely dynamic and can be broken down into distinct phases, which include (a) presymbiotic communication, (b) outer cortex invasion, (c) contact and penetration, (d) arbuscule production, and (e) vesicle and spore creation (Kuyper, *et al.*, 2021). Even while these phases happen consecutively at specific infection sites on a whole-root level, all of the aforementioned phases of AM symbiosis exist simultaneously, making it a non-synchronous process (Choi, *et al.*, 2018). Thus, to coordinate the intricate development of this interaction, delicate and well-coordinated signaling pathways are required. Molecular geneticists have been interested in understanding the molecular foundations of AM symbioses for over ten years (Genre, *et al.*, 2020).

### **AMF-induced production of signaling molecules that affect genetic expression**

Numerous beneficial, potentially harmful, and commensal microorganisms make up the incredibly complex consortium of microbes associated with a plant (Compant, *et al.*, 2019).

One of the many obstacles a symbiosis must overcome is penetrating into plant cells and overcoming their defence systems (Dey, & Ghosh, 2022). In addition, it has to trigger membrane transporters that facilitate the exchange of nutrients and metabolites between two partners, as well as certain developmental pathways for symbiotic structures (Boyno, & Demir, 2022). In this section, we discuss the response of plants to fungal signals, the function of receptor molecules, and other actors that play a crucial role in the signaling pathways.

#### **Common symbiotic pathway (CSP)**

Evidence from two important beneficial plant-microbe interactions, root nodule symbiosis (RNS) and arbuscular mycorrhiza symbiosis (AMS), identified the molecular components that allow plants to establish a compatible plant-microbe symbiosis by sending signals derived from microorganisms to them (Lu, *et al.*, 2021).

Mutations in a single plant may prevent fungus and bacteria from penetrating the root, according to research conducted utilizing genetic and mutagenic techniques on legume species that may form both RNS and AMS associations (García-Soto, *et al.*, 2021). The hypothesis resulting from these investigations is that RNS and AMS

function as the machinery of a common symbiosis pathway (CSP), relying on the same genetic toolbox (Radhakrishnan, *et al.*, 2020).

To create symbiosis, the AM fungus and the host plants must interact at the molecular level (Fernández, *et al.*, 2019). The host root first generates and releases signaling chemicals into the rhizosphere (Vives-Peris, *et al.*, 2020). The fungal spores' germination and the fungal hyphae's branching are then induced by these signaling molecules, which also cause the fungus to manufacture and release fungal factors that alter the host roots' gene expression (Mitra, *et al.*, 2021).

Without getting a signal from plants, the AMF spores may still germinate, even in the absence of direct communication from the plants, AMF spores can sense environmental cues and initiate germination (Richter, *et al.*, 2023). If the fungus is unable to locate a host root, the hyphal growth will stop in order to preserve the spore reserves (Gilbert, & Parker, 2023). As a result, the fungus can proliferate once more and locate a host plant root (Hu, & Bidochka, 2021).

Conversely, the presence of specific signaling molecules (e.g., strigolactones (SLs) in the exudate of the host roots) is

indicated by the profuse hyphae branching and the notable increase in germ tube growth upon approaching a root (Taulera, 2022). There is a marked increase in respiratory activity that lasts until the spore supplies are exhausted along with this widespread branching, which enhances the chance of contact with the root (Dhiman, *et al.*, 2022).

The fungus is dedicated to forming an association with plant roots, and as a result, the signals from host plants cause the initiation of the "presymbiotic growth phase" (Hajiboland, & Ahammed, 2024). The fungus then enters the root epidermis through the fungal hyphae, which then form an appressoria-like structure called a "hyphopodium" that adheres to the root epidermis (Hajiboland, & Ahammed, 2024). According to (Ho-Plágaro, & García-Garrido, 2022), the AM hyphae at this stage release fungal factors (Myc factors) that boost the expression of many genes involved in plant symbiosis as well as Ca<sup>2+</sup> spiking.

### **Strigolactones (SLs)**

Phytohormones, which regulate growth, development, and nutrient apportioning, have a major impact on plants' capacity to adapt to various environments (Sabagh, *et*

*al.*, 2021). Often referred to as plant growth regulators, these signal molecules are biosynthesised by the plant (Bhatla, & Lal, 2023). A distinct class of phytohormones known as strigolactones (SLs) plays an ecological role in mitigating a variety of stress conditions (Bhoi, 2021).

SLs are widely involved in physiological processes such as bud outgrowth, shoot branching, nodulation, and photomorphogenesis (Faizan, *et al.*, 2020). They are first discovered in the developing seeds of parasitic weeds *Striga lutea* employed as a potent germination stimulant in root exudates (Thiombiano, *et al.*, 2023). SLs are biosynthesized from precursor carotenoids (Hossain, *et al.*, 2021). In spores that are germinating, SLs likewise influence the hyphal branching of arbuscular mycorrhizal fungus (Mitra, *et al.*, 2021).

Strigolactones contribute to the development of nodules in the leguminous roots and the germination of the seeds of plants that are parasitic on roots, like *Orobancha*, *Phelipanche*, and *Striga* (Vurro, *et al.*, 2019). Furthermore, abiotic or biotic stress events, as well as access to nutrients, activate intrinsic and extrinsic signalling pathways of SL molecules (Boyno, & Demir, 2022).

### **AM Fungus's Response to SLs**

Root exudates containing sub-nanogram amounts of SLs stimulate AM hyphal branching and improve spore germination, most likely through lipid metabolic pathway activation (Rehman, *et al.*, 2021). When AM fungus detects SLs, it initiates its oxidative metabolism, produces ATP, and generates the energy required to stimulate growth and hyphal branching, thus putting AM fungus in a position to establish symbiosis (Chauhan, *et al.*, 2022).

SLs enhance the biochemical signals produced by fungals, like chitin oligomers (COs) (Crosino, & Genre, 2022), which cause plants to spike in Ca<sup>2+</sup> as a first indicator of a partnership. (Giovannetti *et al.* 2015) found that applying COs to plants increases the expression of several symbiotic marker genes, including the SLs biosynthesis gene (CCD7), indicating a potential synergistic effect between SLs and COs in the formation of communication between two partners (Hajiboland, & Ahammed, 2024).

The initiation of hyphal branching, fungal-symbiotic signal synthesis, and spore germination are all triggered by the fungal perception of signals originating from plants, such as strigolactones and flavonoids,

which sets up AMF colonization (Clear, & Hom, 2019).

Lastly, throughout the pre and symbiotic phases of host plant colonization, SLs control the production of many proteins released by the fungal partner (Mitra, *et al.*, 2021), that positively affect host plant colonization. AMF hyphal branches are reduced by mutations that result in defects in the production and export of SLs, which significantly lowers colonization rates compared to plants of the wild type (Alvi, *et al.*, 2022).). Reduced SL production occurs when the AM fungus has established itself in the root, most likely as a defence against the plant getting overly infested (Mitra, *et al.*, 2021).

### **AMF's Perception of the SL Signal**

It is mostly unknown how SLs perceive and transduce signals in AM fungus. According to (Taulera, 2022), the synthetic SL (GR24) causes a rapid rise in the fungus's intracellular Ca<sup>2+</sup> content.

Remarkably, the development of arbuscules is unaffected in SL-deficient or export mutants, suggesting that SLs do not appear to function as endogenous signals in plants during AM development (Hajiboland, & Ahammed, 2024). Moreover, Mashiguchi, *et*

al., 2021) report that SL-insensitive D14 rice mutants lacking the SL receptor do not show a reduction in AM colonization. These findings suggest that the early association stage, or presymbiotic stage, is the only time when SL delivered into the rhizosphere has an impact. (Hajiboland, & Ahammed, 2024)

### **AMF-induced Hormonal regulation (ABA a key drought hormone)**

Plant growth and development are governed by a range of phytohormones, which include ABA, ethylene, auxins, cytokinins, and gibberellins (Bhatt, et al., 2020). The ability to withstand drought is influenced by these plant hormones (Iqbal, et al., 2022). The increase in cytokinin levels in xylem sap during a water deficit, for instance, reduces the plant's sensitivity to ABA and promotes stomatal opening. (Salvi, et al., 2021).

When there is a shortage of water, plants tend to produce more ethylene and ABA while producing less auxin, cytokinin, and gibberellin (Bhattacharya, & Bhattacharya, 2021). According to Chandrasekaran, et al., (2021), AM symbiosis increased ABA production, which raised the amount of ABA in *Solanum lycopersicum* and further caused stomata to close, limiting

transpiration and water loss. According to (Chérel, & Gaillard, 2019), plants require higher levels of ABA to retain structural flexibility and effectively regulate transport ions. A consortium of *Rhizophagus intraradices*, *Claroideoglossum etunicatum*, and *Funneliformis mosseae* enhanced the amount of ABA in *Ephedra foliata* under drought stress conditions (Al-Arjani et al., 2020).

More recently, Qian et al., (2023) showed that under drought stress, *Paris polyphylla* var. *yunnanensis*'s ABA content rose upon colonization with *Rhizophagus irregularis*. Reduced ABA catabolism under drought stress prevents ABA from entering the rhizosphere and phloem, which causes a boost in ABA concentrations. (Castro, et al., 2019). One example is the correlation between decreased stomatal conductance and elevated ABA concentration, which was caused by re-watering in guard cells (Liu, et al., 2023).

Drought stress causes the level of ABA in vegetative tissues to rise, improving drought tolerance (Ali, et al., 2020). Although (Silva, 2023) indicated as well that the inoculums of *Bacillus sp.* and AMF (*Rhizophagus clarus*) can work synergically and were able to improve proline content and reduce ABA



concentration in the corn plant subjected to drought stress during flowering and seed filling. Nevertheless, it has also been demonstrated that, in AMF-colonized plants, ABA content may decrease in response to stress, suggesting that ABA regulation in the AMF-colonized host plants may differ (Cheng, *et al.*, 2020).

After inoculating *Rhizophagus irregularis* under drought stress, ABA content in *Cichorium intybus* was found to be reduced (Langeroodi, *et al.*, 2020). Reduced ABA concentration in *Catalpa bungei* following *Rhizophagus intraradices* inoculation under drought stress was similarly found by Chen *et al.* (2020). Similarly, compared to control plants, *Olea europaea* colonized by *R. irregularis* had a lower ABA concentration (Tekaya, *et al.* 2022). The function of ABA in the development of fungal mycelium in host plants may account for the decrease in ABA content in the mycorrhizal plants (Chen, *et al.* 2020).

The results of transcriptome analysis show that drought stress causes many genes to either up- or down-regulate their expression levels (Jia, *et al.*, 2020). Functionally speaking, these genes can be divided into two groups: genes producing proteins directly related to drought tolerance are in

one group, and genes encoding proteins that control stress signaling are in the other group (Mahmood, *et al.*, 2019).

A large deal of uncertainty surrounds the underlying mechanisms generating the signaling molecules that interact with the plant-fungus interaction (Bahadur, *et al.*, 2019). Under drought, AMF symbiotic plants produce more ABA, a phytohormone known as the "abiotic stress hormone," to help them deal with the corresponding stress. ABA is known to be a key player in the modulation of drought responses in plants and involvement of both ABA-dependent and ABA-independent pathways has been observed during drought (Muhammad *et al.*, 2022).

*Rhizophagus intraradices* were found to activate 14-3-3 protein and aquaporins (GintAQPF1 and GintAQPF2) in response to an increase in the expression of plant genes producing D-myo-inositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF), which were responsible for ABA signaling transmission (Saxena *et al.*, 2022; Han *et al.*, 2022). These findings suggest that the symbiotic partners' synergistic effects on plant drought tolerance are caused by the coexpression of IPS and 14-3GF (Bahadur *et al.*, 2019). Numerous



studies have focused mechanistic insights into enhanced ABA production in the AMF host plant to confer drought stress resistance (Mathur & Roy 2021).

### **Induction of drought-responsive gene (aquaporins, dehydrins and transcription factors) under AMF Colonization**

AMF-induced production of drought-responsive genes in plants, such as aquaporins, dehydrins, and transcription factors involved in water transport, osmotic adjustment, and stress regulation (Wang, *et al.*, 2023). Plant responses to drought stress are manifested by the crosstalk between phytohormones, metabolites, transcription factors and small RNAs (Patel, *et al.*, 2019). An important plant hormone, ABA controls a number of processes in plants, from flowering to seed dormancy (Ali, *et al.*, 2022).

It is well known that ABA production confers osmotic stress tolerance and is markedly enhanced in the presence of abiotic stressors (Bharath, *et al.*, 2021). Plant responses to drought stress are frequently divided into two groups: ABA-dependent and ABA-independent mechanisms (Soma, *et al.*, 2021). The process by which ABA binds to its receptor

and initiates a signaling cascade that results in the activation of ABA-responsive genes is known as the ABA-dependent pathway (Cuming, 2019).

On the other hand, the ABA-independent pathway is triggered by some environmental conditions, including cold stress, salt, and drought, and it involves the activation of certain transcription factors that attach to cis-acting sites in the promoter regions of genes that respond to ABA (Hussain, *et al.*, 2021). ABA triggers a variety of physiological processes such as stomatal closure, root system modulation, organizing soil microbial communities, activation of transcriptional and post-transcriptional gene expression, and metabolic alterations (Muhammad, *et al.*, 2022).

Certain plants can adapt by triggering the drought escape (DE) response, depending on the severity and length of drought episodes (Seleiman, *et al.*, 2021). Before the drought gets too bad, DE enables plants to set seeds and hasten the floral transition (Wanga, *et al.*, 2021). Plants experiencing DE typically yield fewer fruits and seeds to avoid the potentially fatal impacts of the drought, suggesting a trade-off between plant survival and successful seed set (Srivastava, & Sahoo, 2021).

Drought stress induces many different genes in leaves, and these genes, in turn, activate subclass III SNF1-related protein kinases 2 (SnRK2s), these plant proteins are essential to the process of ABA signaling (Soma, et al., 2020). They play a part in controlling how the plant reacts to abiotic stress. Stress-responsive transcription factors, which include ABRE-BINDING FACTORS (ABFs) and ABARESPONSIVE ELEMENT BINDING PROTEINS (AREBs) are among the transcription factors that allow ABA to mediate a broad range of gene expression events (Liu, et al., 2023).

Upstream regulators of SnRK2s, RAF-like protein kinases, involved in early responses to drought stress have been elucidated by recent research (Soma, et al., 2020). In drought-responsive gene expression, ABA-responsive and ABA-independent transcriptional regulatory mechanisms are involved (Soma, et al., 2021).

The cis-acting element DEHYDRATION RESPONSIVE ELEMENT (DRE) plays a significant role in ABA-independent transcription, while the cis-acting element ABA-RESPONSIVE ELEMENT (ABRE) is involved in ABA-responsive transcription (Hussain, et al., 2021).

### **Aquaporin induction**

All physiological development depends on the roots' ability to draw water from the soil and distribute it throughout the entire plant (Scharwies, & Dinnyen, 2019). Aquaporins (AQPs) are a type of water channel that regulate and mediate the gradient-driven flow through membranes that transport water (Singh, et al., 2021). The AQPs are a family of integral membrane proteins that produce pores (Adeoye, et al., 2021). They are a part of the major intrinsic protein (MIP) family and are found in all living cells and organisms, including numerous species in plants (Bezerra-Neto, et al., 2019).

AQPs are classified into five subfamilies based on amino acid sequences: small basic intrinsic proteins (SIPs), which are only found in the endoplasmic reticulum (ER) of dicots, uncharacterized intrinsic proteins (XIPs) found in the plasma membrane, and tonoplast intrinsic proteins (TIPs), plasma membrane-intrinsic proteins (PIPs), and NOD26-like intrinsic proteins (NIPs), which were first recognized in legume symbiosomes but also exist in the endoplasmic reticulum and plasma membrane (Bezerra-Neto, et al., 2019).

Plant AQPs are important for AM symbiosis and may react differently to AMF

colonization and drought stress (Zou, *et al.*, 2019). Certain PIPs in plant roots exhibit differential expression of AQP-coding genes in response to AMF and drought stress (Bahmani-Babanari, *et al.*, 2021).

For example, extraradical mycelia of *R irregularis* and mycorrhizal roots showed significantly increased expression of two AQP genes, GintAQP1 and GintAQP2, in response to drought stress (Cheng, *et al.*, 2020). This finding supports the idea that AMF directly contributes to plant tolerance to water deprivation (Silva, *et al.*, 2023). Under drought stress, there has been consistent evidence of increased expression of AQPs genes in both root cortical cells containing arbuscules and extraradical mycelia; potential mechanisms for this phenomenon may include improved root system architecture and direct uptake of water and nutrients via extraradical hyphae (Bahadur, *et al.*, 2019).

The overexpression of the NIP AQP-encoding gene (LeNIP3;1) in tomato plants inoculated with AM fungus was found to be connected with an increase in the water transport capacity of AMF roots (Bahadur, *et al.*, 2019). On the other hand, a different study found that the mycorrhizal roots of *Lotus japonicus* had a unique up-regulation

of an NIP AQP gene (LjNIP1) in the arbuscule-containing cells (Quiroga, 2020). Comparatively, *Funneliformis mosseae* showed increased root PtTIP1;2, PtTIP1;3 and PtTIP4; of *Poncirus trifoliata* L. and lower expression levels of PtTIP2;1 and PtTIP5;1 during drought stress (Liu, *et al.*, 2019).

According to the findings, different responses to mycorrhization were found in the genes of root TIPs, indicating the various functions of AMF in water absorption during water stress (Jia-Dong, *et al.*, 2019).

The measurement of plant water flow via interconnected cell pathways is known as osmotic root hydraulic conductivity, and it is closely related to the density of the plasma membrane in the cells or the activity of the water channels (Lambers, *et al.*, 2019).

Plants typically exhibit a decrease in root hydraulic conductivity when they perceive a drought (Scharwies, & Dinneny, 2019), possibly as an adaptation strategy to stop water loss. The lack of a significant correlation between the expression of AQP genes and hydraulic conductivity implies that other processes, such as increased AQP gene expression and/or action in plants as a result of these proteins' post-translational modifications (Shivaraj, *et al.*, 2021) or

modifications to the density or size of plasmodesmata in AMF roots, may be responsible for the enhanced hydraulic conductivity in plants inoculated with AMF. A higher expression of fungal or plant AQPs may be linked to the rise in osmotic root hydraulic conductivity in AM plants (Watts-Williams, *et al.*, 2019).

The endogenous ABA sites in the host plant were necessary for the AMF's actions on the AQP genes (Sharma, *et al.*, 2021). However, despite an increase in root AMF, a water deficit in lettuce roots resulted in a decrease in GintAQP1 gene expression (Cheng *et al.*, 2020). In-depth research is needed to examine how AQP genes regulate plant water transport in response to water events (Yepes-Molina, *et al.*, 2020). This includes AQP gene roles in AMF-facilitated plant water transport as well as the distribution of water transport from AMF hyphae to the roots.

It has been observed that AMF symbiosis and instances of water stress exhibit differential regulation of AQP-encoding genes for certain PIPs in *R. irregularis* (Sharma *et al.*, 2021). Therefore, AMF symbioses cause AQP gene expression to either increase or decrease; nevertheless, little is known about how AQP functions in

mycorrhizal systems (Cheng, *et al.*, 2021). AMF symbiotic communication's improved membrane water permeability, which necessitates the upregulation of AQPs in conditions of water scarcity, may also be linked to facilitated water transport (Sharma *et al.*, 2021). Changes in the growth and water status of mycorrhizal plants indicated a general improvement in drought tolerance, which was associated with certain specific patterns of AQP regulation found in colonized roots ((Sharma. *et al.*, 2021).

### **Dehydrins Induction**

Plants have evolved complex mechanisms that enable them to quickly detect and react to abiotic stressors in response to changes in their surroundings (Sachdev, *et al.*, 2021). The broad and diversified family of late embryogenesis abundant (LEA) proteins is involved in plants' ability to withstand environmental stress Group II LEA proteins, which are stress proteins involved in the generation of defensive responses in plants against dehydration, include dehydrins (Abdul Aziz, *et al.*, 2021).

Dehydrins have been shown in certain investigations to bind lipid vesicles or metal ions. Dehydrins were found to be able to protect an enzyme's activity from harm brought on by environmental stress in *in*

*vitro* investigations (Sun, *et al.*, 2021). Despite extensive research efforts aimed at comprehending their functions in abiotic environments, the molecular role of dehydrins remains elusive (Sun, *et al.*, 2021).

Dehydrins might also be referred to as hydrophilins (Kosová, *et al.*, 2019), Tryptophan and cysteine residues are absent, and they have a low percentage of hydrophobic, non-polar residues and a high percentage of charged, polar amino acids. They are also very hydrophilic (Kosová, *et al.*, 2019). The Y-, S-, and K-segment conserved sequences allowed dehydrins to be categorized into the different sub-classes YnKn, YnSKn, KnS, SKn and Kn (Wang, 2022).

Birhanu (2020) found that transgenic tomatoes are more resilient to several abiotic stressors when the *Solanum habrochaites* dehydrins ShDHN are overexpressed. According to (Kosová, *et al.* 2019), the majority of dehydrins are found in plants together with a number of common dehydration-stress response protein types. Dehydrins, however, were also discovered to be dispersed throughout the vegetative tissues of plants cultivated in typical circumstances, indicating that the dehydrins

might be crucial for the growth of plants (Chakraborty, & Roychoudhury, 2022).

## **Functions of Dehydrin**

### **Bonding Metal Ions**

According to reports, the first member of the LEA protein family to be demonstrated to be active in the long-distance transport micronutrients is the Ricinus KS-type dehydrin ITP (Liu, *et al.*, 2019). The metal ions Fe<sup>3+</sup>, Co<sup>2+</sup>, Ni<sup>2+</sup>, Cu<sup>2+</sup>, and Zn<sup>2+</sup> can be bound by the dehydrins AtHIRD11 from *Arabidopsis thaliana* and CuCOR15 from citrus over Mg<sup>2+</sup> and Ca<sup>2+</sup> (Liu, *et al.*, 2017).

#### *4.2.1.2 Binding DNA.*

DNA binding by dehydrins was predicted by the bioinformatic study of the "Protein or Oligonucleotide Probability Profile (POPP)" (Boddington, 2019). Zinc ions are necessary for the nucleic acid binding activity of citrus dehydrin CuCOR15 (Tiwari, & Chakrabarty, 2021). The DNA-binding domains were the lysine-rich domain (GGEGAHGEEKKKKKKEKKK) and the histidine-rich domain (TTDVHHQQQYHGGEH) (Boddington, 2019). Low affinity for non-specific association with DNA was shown by Y2K-type dehydrin VrDhn1, and exogenous addition of metal ions of Zn<sup>2+</sup> or Ni<sup>2+</sup> increased the interaction (Lin, *et al.*, 2012).

### **Binding Phospholipid**

The significant stress-signaling phospholipid known as phosphatidic acid is produced in response to a number of environmental stressors, including cold, salinity, and drought (Sharma, *et al.*, 2023). In the membranes of turgescient plants, the concentration of phospholipidic acid (PA) is only around 1 %, but it rises in response to water deficiency stress (Wang, *et al.*, 2020).

Phospholipase D activity, which can be increased by ABA and dehydration, is necessary for the production of PA (Alferez, *et al.*, 2019). PA can be bound by the maize SK2-type dehydrin DHN1 (Abdul Aziz, *et al.*, 2021). The K-segment of DHN1 can adopt an  $\alpha$ -helical shape, despite the majority of the protein being disordered (Szabala, 2023). It has been suggested that the interaction is electrostatic. According to (Bartas, *et al.*, 2021), the interaction in the binding domain requires basic amino acids like arginine and lysine.

Phosphatidyl choline and other zwitterionic vesicles, as well as negatively charged phospholipids including phosphatidic acid, phosphatidyl serine, and phosphatidyl glycerol, can interact electrostatically with the Kn-type dehydrin Lti30 (Riyazuddin, *et al.*, 2022).

### **Safeguarding Proteins' Activity**

For many years, it has been hypothesized that dehydrin can attach to proteins and stop them from denaturing (Murvai, *et al.*, 2020). Numerous studies have shown that dehydrin can shield malate dehydrogenase and LDH (lactate dehydrogenase) activity from harm brought on by a variety of environmental conditions (Drira, *et al.*, 2023, Osuda *et al.*, 2023).

With the help of histidine residues, the KS-type dehydrin AtHIRD11 restores LDH activity that has been suppressed by copper (Aduse, 2021). It hasn't been discovered, nevertheless, how the dehydrins and the protected proteins interact (Bhattacharya, *et al.*, 2019).

### **Scavenging the Reactive Oxygen Species**

Dehydrins have been shown in numerous investigations to have the ability to directly scavenge free radicals. Citrus dehydrin CuCOR19 has a more robust prevention against peroxidation that is induced by free radicals (Tiwari, & Chakrabarty, 2021).

Radical-mediated oxidation targets amino acids, including glycine, histidine, and lysine (San-Segundo, 2021). The three amino acids have a high concentration of dehydrins, which can lower the ROS level.



AtHIRD11, a dehydrin of the Arabidopsis thaliana KS type, can lessen the production of ROS from copper (Sun, *et al.*, 2021). The fundamental elements that can affect this are the length of the peptides and the amount of histidine (Zhang, *et al.*, 2019).

#### **Safeguarding Photosynthetic Apparatus**

Water is vital to a cell's ability to survive since it is needed for several physiological functions, including photosynthesis, stomatal conductance, and cell expansion, thus, during drought stress, water shortage modifies all of these physiological processes as well as the general health of plants (Lambers, *et al.*, 2019). By preserving the integrity of the cell structure and the stability of the thylakoid and chloroplast membranes, dehydrin proteins play a diverse role in protecting the plant cells during drought stress.

Several overexpression studies have demonstrated that during drought stress, dehydrin proteins reduce stomatal density and increase the levels of carotenoids, soluble sugars, soluble chlorophyll a and -b, and suitable solutes like phosphorus (Shankar, *et al.*, 2024). This improves photosynthesis and maintains fresh weight.

#### **Transcription factor modulation**

Transcription factors (TFs) are proteins that bind to DNA and can stimulate or inhibit

transcription, which in turn regulates gene expression (Bushweller, 2019). Throughout the lifetime of a cell or organism, transcription factors are essential in controlling gene expression to guarantee that the target cells express the genes in the right amounts and at the right times (Hussain, *et al.*, 2021). Transcription factors are found in all living organisms because they are essential for regulating gene expression (Mitsis, *et al.*, 2020).

It is well-recognized that arbuscular mycorrhizal fungi (AMF) are essential to plant growth and development, particularly in situations where drought stress is prevalent (Begum, *et al.*, 2019). By controlling the expression of genes involved in stress response pathways, AMF can assist plants in coping with drought stress (Zou, *et al.* 2021). The regulation of transcription factors that control gene expression in response to drought stress is one such route, AMF can alter the way that the host plants regulate water by inducing osmolytes or hormonal signals (Wahab, *et al.*, 2023).

Stress-responsive transcription factors, such MYCs and ABA-responsive binding factors (ABFs), are essential for plant tolerance to abiotic stress (Yoon, *et al.*, 2020). They work as direct components of JA and ABA signaling. Furthermore, a multitude of investigations have discovered additional

stress-responsive transcription factors that are members of the WRKY, MYB, NAC, and AP2/ERF families that modulate a plant's abiotic stress tolerance and response (Baillo, *et al.*, 2019). Because they are necessary for controlling the expression of genes, these transcription factors are present in all living things (Oksuz, *et al.*, 2023).

### **TF Regulatory role under drought stress Tolerance**

Proteins called transcription factors are involved in the process of translating DNA into RNA. Except for RNA polymerase, they make up a diverse group of proteins that are involved in the start, regulation, and transcription of genes (Oksuz, *et al.*, 2023). DNA-binding domains, which enable TFs to bind to particular DNA regions known as enhancer or promoter sequences, are a defining characteristic of TFs (Wang, *et al.*, 2022).

Dimerization, activation, nuclear export, nuclear localization signal, and other domains are examples of additional domains (Lu, *et al.*, 2021). By attaching to regulatory enhancer sequences thousands of base pairs upstream or downstream of the gene being transcribed, or to a DNA promoter region close to the transcription start point, the TFs can start transcription (Andersson, & Sandelin 2020).

### **Conclusion**

The underlying genetic and molecular mechanisms of drought tolerance and escape are still a developing field in plant biology. Drought escape is the adaptive mechanism through which plants undergo rapid development to complete their life cycle before the onset of serious water deficits. Plants have evolved a variety of adaptive strategies at cellular and molecular levels to cope with environmental cues including drought.

Investigations into the molecular mechanisms underpinning the AMF–SL associations have uncovered complex signaling networks, regulated gene expression, and interplay amongst hormones. AMF's promotion of SL production, improved colonization and establishment of AMF in the presence of SLs, and adjustments to plant defence mechanisms and nutrient uptake were all significant factors in the reported synergistic effects. The potential for increased crop output, effective nutrient use, and soil health makes this relationship significant. It also provides chances to lessen the negative effects of agricultural operations on the environment and cut back on chemical inputs.

Due to their diverse functions in plant abiotic stress tolerance, dehydrin proteins have

attracted a lot of research lately. Dehydrins, in particular, have a well-established role in plants' ability to withstand drought stress, and recent findings have significantly improved our knowledge of this process.

Several studies have demonstrated the significance of AQPs in drought stress. In response to drought stress, the PIPs and TIPs displayed altered expression to preserve the water status of the plants. In conditions of water scarcity, the activity of AQPs is influenced by transcriptional factors, hormones, and post-translational changes like glycosylation, phosphorylation, and heterotetramerization. According to research done thus far, distinct crops react differently to drought stress by altering the expression, membrane targeting, localization, and turnover of AQPs.

Even with several developments in our understanding of AQP control in conditions of water scarcity, the mechanism underlying their regulation remains partially unclear in terms of the perception and transmission of an external signal. It will be possible to develop crops for changing climatic conditions with a better grasp of the AQP regulating mechanism.

Through simultaneous binding to the promoter regions of its various target genes, the Transcription Factor controls several

genes at once. Consequently, Transcription Factor has been viewed by the scientific community as a promising target for engineering drought stress tolerance. A better understanding of differential gene expression and its cumulative effect on a sequence of events occurring during stress progression has been made possible by several studies that have established the promising role of transcription factors in drought stress response.

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