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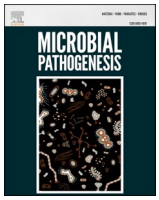

Surviving the stress: Understanding the molecular basis of plant adaptations and uncovering the role of mycorrhizal association in plant abiotic stresses

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ABSTRACT

Environmental stresses severely impair plant growth, resulting in significant crop yield and quality loss. Among various abiotic factors, salt and drought stresses are one of the major factors that affect the nutrients and water uptake by the plants, hence ultimately various physiological aspects of the plants that compromises crop yield. Continuous efforts have been made to investigate, dissect and improve plant adaptations at the molecular level in response to drought and salinity stresses. In this context, the plant beneficial microbiome presents in the rhizosphere, endosphere, and phyllosphere, also referred as second genomes of the plant is well known for its roles in plant adaptations. Exploration of beneficial interaction of fungi with host plants known as mycorrhizal association is one such special interaction that can facilitates the host plants adaptations. Mycorrhiza assist in alleviating the salinity and drought stresses of plants via redistributing the ion imbalance through translocation to different parts of the plants, as well as triggering oxidative machinery. Mycorrhiza association also regulates the level of various plant growth regulators, osmolytes and assists in acquiring minerals that are helpful in plant's adaptation against extreme environmental stresses. The current review examines the role of various plant growth regulators and plants' antioxidative systems, followed by mycorrhizal association during drought and salt stresses.

1. Introduction

The edaphic conditions rarely provide optimal conditions for plant growth. Various episodic stressors can predispose plants to the levels they would otherwise resist [1,2]. Among different stressors, soil salinity and drought alone contribute to 50 per cent of agricultural productivity loss [3]. In the 21st century, water availability and quality both imposes significant challenges in the agriculture sector that impede in enhancing the agricultural productivity [4,5]. Drought and salt stresses associated to water availibity disturb the cellular homeostasis that negatively affect the various plant processes, including growth, physiology, and metabolism [5–10]. These environmental stressors result in significant loss of economically important crops [11–13]. The disease severity or incidence caused by obligate or biotrophic pathogens are generally reduced under abiotic stresses. Additionally, these abiotic stressors can predispose the plants to various biotic stresses, such as pathogen attacks. For example, drought stress has been reported to induce Rhizoctonia bataticola mediated dry root rot, and Fusarium solani caused black root rot in chickpeas [14]. The impact of adverse effects on crops can vary depending on geographical conditions [3,5,15,16]. The abiotic stressors can predispose the plants to hemi-biotrophic pathogens, resulting in severe disease with a very low inoculum load. For example, the water status is paramount during the root and crown rots progression caused by Phytophthora. The abiotic stressors can facilitate disease progression even by weakly aggressive facultative pathogens, which otherwise behave as saprophytes or endophytes [1,14].

Identifying the mechanisms responsible for alleviating the environmental stresses is of the major challenge. Drought triggers the stomatal closure and also compromises the membrane integrity. In contrast, salinity affects the regulation of sodium (Na^+) and chloride (Cl^-) ions to counter their toxic and negative impact [3]. Drought and salinity stresses reduce the water potential and hence, the turgor pressure of the

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cell, which can negatively affect photosynthesis, plant transpiration, and root functioning [3]. Plant responses to abiotic stressors are highly complex and coordinated, that are accompanied by various morphological, physiological, biochemical, and molecular responses. These responses are manifested through the combined action of phytohormones and water potential that help in reducing the cell turgor, accumulation of reactive oxygen species (ROS), and modulation of several genes' behavior [1,17–19]. Plant growth regulators, including ethylene (ET), gibberellic acid (GA), and jasmonic acid (JA), play critical importance in drought stress by having crosstalk between the host and colonizing microbes whereas the mycorrhizal colonization is facilitated by auxins and gibberellins (GA). The ROS level during drought and salinity stress exceeds the antioxidant scavenging potential of the plant and ultimately resulting in an oxidative burst. This oxidative burst may disrupt the cellular redox homeostasis [18,20–22] which can negatively affect plant transpiration, photosynthesis, and functioning of roots [3]. Contrary to this, the regulated production of ROS assists the redox signalling, plant-microbe interactions [23], and plant growth during abiotic stresses [3,22,24–26]. Once stressed, plants often accumulate various metabolites that facilitate their adaptations [27]. These secondary metabolites are also important in food, flavours, pharmaceuticals, and other industrial sectors [28].

The role of plant-beneficial microorganisms in alleviating these environmental stresses, such as drought and salinity, is critical to increasing agricultural productivity. The beneficial microbes facilitate the host plant tolerance or adaptations against various environmental stresses [1,29–36]. The interaction between plants and 'beneficial' or 'pathogenic' microbes activates a series of dynamic and coordinated cellular responses in the plants in the rhizosphere [12,19,37] through induced systemic resistance (ISR). Depending upon their location, the plant-beneficial microbiome, categorized as endophytic, epiphytic, or rhizospheric, facilitates plant adaptations against biotic and abiotic stresses [38]. Here, our focus is limited to investing the role of mycorrhizal association drought and salinity stress mitigation of the plants [39,40]. The mycorrhiza facilitates nutrient acquisition, assists in ionic homeostasis, enhances water uptake and osmotic equilibrium, triggers the antioxidant machinery, regulates the phytohormone level which improves the photosynthetic efficiency and assist in combating the salinity and drought stress in plants [39–44].

The present study highlights the devastating effects of drought and salt stress, also explores the adaptive mechanisms of plant growth regulators and antioxidative machinery in response to drought and salinity stresses. Efforts have been made to investigate the potential role of mycorrhiza in facilitating plant physiology and reshaping the rhizosphere to alleviate these abiotic stresses.

2. Overview of plant adaptations against drought and salinity stress

Due to sessile nature of the plant, they rely on various adaptations at morphological, physiological, cellular, biochemical, and metabolic levels to counter the environmental stresses [8]. Drought, a combined and complex stress, is one of the most significant factors that can occur due to multiple factors, including loss of soil moisture, lack of precipitation, heat, soil aggregation, solar exposure, and other factors [45,46,47]. Drought causes the metabolic and physiological alterations that affects the plant root architecture, stomatal behavior, rate of photosynthesis, reproduction cycle, seed germination, composition, and even root exudates [48,47]. The plant responses to such stresses vary from species to species and can be long-term or short-term [28]. The tolerance mechanisms for the long-term responses affect the crop cycle, grain maturation, root morphogenesis, nutrient allocation, cell dehydration, and also delay senescence. In contrast, the short-term ones affect the water potential in tissues, stomatal and hydraulic conductance, osmolytes accumulation, turgor pressure, and organ growth [48]. Besides affecting plant health, drought stress also alters the microbial community organization, physiology, and habitat of microbes in the rhizophere.

In addition to water, the minerals are essential for the plant growth. However, the accumulation of mineral-soluble salts in soil can lead to ionic and osmotic stress, known as soil salinity [49]. After evaporation of water, it can cause the formation of salt scald [50]. Soil salinity is a significant concern in the arid and coastal areas [51]. Salinity and drought affect ~5 % of the global land area, which can negatively affect plant growth and development [52]. In arid and semiarid zones, soil salinity can occur due to the accumulation and deposition of dissolved salts such as sodium salts, chloride (Cl^-), carbonates (CO_3^{2-}) bicarbonates (HCO_3^-) nitrate (NO^{3-}), sulfate (SO_4^{2-}), potassium sulfate (K_2SO_4), and calcium sulfate (SO_4^{2-}), magnesium chloride ($MgCl_2$), and sulfate (SO_4^{2-}) [3,49,53]. Natural or human activities over extended periods can lead to salt accumulation in soil and groundwater. The continuous irrigation of farmland can cause the mobilization of dissolved salts from underground rocks to the rhizospheric zone, severely hampering soil fertility. Moreover, the deposition of salts can result in the degradation of farmlands where agriculture is difficult to sustain [50].

Plant responses to counter these stresses involve "avoidance and tolerance". The first involves morphological and physiological changes in root growth, leaf structure, stomatal behavior, photosynthesis, and others to minimize water loss. The morphological adaptations against drought tolerance to avoid dehydration include increased cuticle thickness, a higher number of trichomes, reduced leaf size and number, the reversible folding or curling of the leaf blades, leaf shedding, or water storage (through increased succulence), root system, increased cross-section and a number of the vessels, shorter internodes, and limited transpiration regulating stomatal behavior through abscisic acid (ABA) [31]. The underlying basis of drought resistance has been investigated in several studies [54–58]. The physiological and biochemical adaptations of the plants occur through root system architecture, an adjustment in osmotic status through water potential, growth regulators, cell membrane stability, and antioxidant defence systems [59,60] (Fig. 1).

At the cellular level, the excess salt removes the water from the cytoplasm, resulting in hypertonic conditions that can cause osmotic stress, leading to cellular dehydration and toxicity to the plant cells [28]. The disturbance in ions and water balance also impacts the hormonal level, rate of transpiration, photosynthesis, and translocation of nutrients and other biological processes [61]. The impact of environmental stresses can be assessed by investigating the responses at functional genes (transcripts) and using proteomics approaches. The re-organization of chromatin can regulate the gene's behavior in response to environmental stresses through epigenetic remodeling, such as histone modifications, DNA methylation, and formation of non-coding RNA. Moreover, the plants memorized chromatin status to combat environmental stresses can be transferred to the offspring of the next generations [62]. At the proteomics level, investigations have been used to unravel the candidate proteins and/or metabolic pathways triggered under water stress [63]. The plant responses/adaptations to drought salinity and other environmental stresses are executed through various plant growth regulators as described below.

3. Molecular basis of plant adaptations against drought and salinity stress

Plant growth regulators, including ethylene (ET), gibberellic acid (GA), and jasmonic acid (JA), are of critical importance in drought stress [64,65] (Fig. 2A and C). Various transcription factors associated with plant adaptations against drought and salinity stresses have been characterized for their role in plant adaptations. For example, ethylene-responsive transcription factor (ERF) and auxin-binding protein (ABP) family have been identified for their role in drought tolerance in cotton (*Gossypium herbaceum*) [66–68], oak (*Quercus robur*) [69],

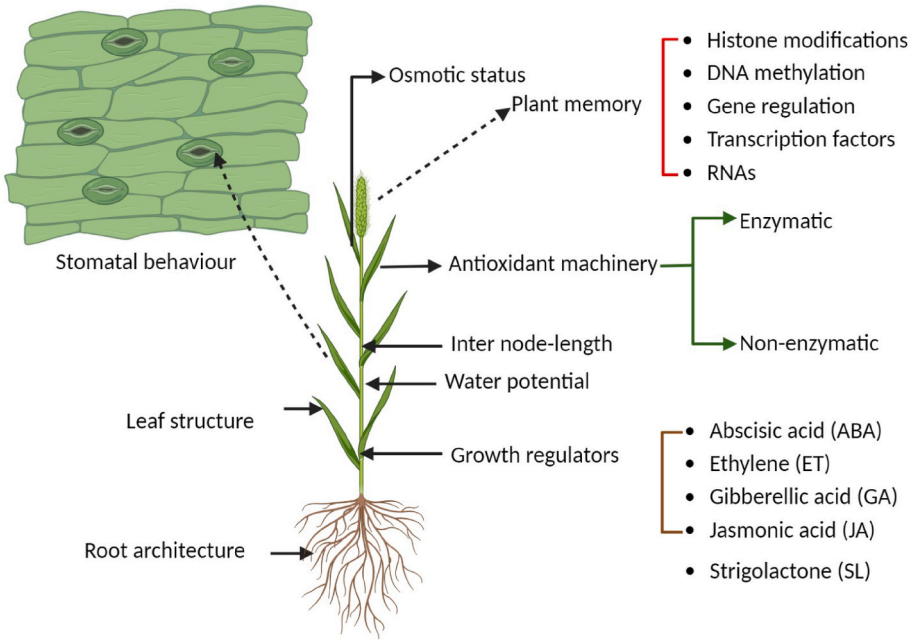

Fig. 1. Overview of morphological, physiological, biochemical, cellular, and metabolic adaptations of the plants to counter the water deficit or poor water quality stresses.

maize (*Zea mays*) [70], and other plants [71]. Transgenic plants of tobacco, rice, and Arabidopsis expressing *SodERF3* from sugarcane, *TERF1* from tomato, and *BrERF4* from *Brassica* have been explored for their role in improving the plant tolerance to salt and drought stresses, respectively [63]. These ERF receptors behave differently against drought stress; therefore, their role must be investigated. For instance, *BpERF11* negatively affects the osmotic tolerance in *Betula platyphylla* [72]. Transforming growth factor-beta (TGFβ) receptors (TGF-βreceptor) interacting protein 1 (TRIP1) receptor representing a serine/threonine kinase from *Sporobolus stapfianus* [73] has been recognized for regulating the BR signalling pathway during drought [63]. The *NtabDOG1L*, named after *Nicotiana tabacum* (Ntab) "DELAY OF GERMINATION (DOG) 1″ localized to the nucleus, cytoplasm, and cell membrane. Preferentially expressed in roots, it is induced by polyethene glycol, high salt, cold, and ABA treatments, whereas the expression of *NtabDOG1L*-T increases the drought stress tolerance in transgenic tobacco [74]. The plant adaptations to salinity include osmotic adjustments, production of growth regulators, and accumulation of secondary metabolites. For example, compared to salt-sensitive species, the resistance species accumulate higher amount of anthocyanins [75,76]. The salt tolerance alfalfa, tomato, and river mangrove plants accumulate more proline content in their roots than salt-sensitive ones [77,78]. The accumulation of endogenous JA in tomatoes [79], red peppers [80], polyphenol and polyamines accumulation in different tissues have been observed in response to biotic or abiotic stresses [28]. The role of different plant growth regulators, antioxidative systems, and other components is discussed below.

3.1. Auxins

Auxins are small organic molecules that coordinate various plant growth and developmental processes [81]. Auxin biosynthesis is achieved in two steps, where amino tryptophan is first converted into indole-3-pyruvate (IPA) by the tryptophan aminotransferase (TAA). Then, IPA is transformed into indole-3-acetic acid (IAA) by the *YUC* family of flavin monooxygenases. Enzyme assays show that *TAR* and *YUC* genes convert Trp to IPA and IPA to IAA. Therefore, the overexpression of *YUC* genes, such as *BnaYUC6a* in both *Arabidopsis* and oilseed rape has been used to enhance auxin production and increase drought resistance [82], together with the plant's endogenous IAA pool and IAA produced by plant growth promoting rhizobacterial auxin signalling results in the stimulation of cell growth and proliferation. The function of exogenous IAA is dependent on the endogenous IAA levels in plants. At optimal IAA concentration, acquiring bacterial IAA may neutralize, promote, or inhibit plant growth [83]. The role of auxin in plant growth and development in response to osmotic stressors (water deficiency, salinity, and others) and how auxin modulates its perception (*TIR/AFB*, *Aux/IAA*), biosynthesis (*YUC*, *TAA*1), transport (*PIN*), and inactivation/conjugation (*GH*3, *miR* 167, *IAR*3) and its impact on stomatal behavior, root positioning and other have been reviewed by researchers [81,84].

Further, the different components of auxin-mediated plant adaptations in response to drought [85] and salinity have been characterized by several workers [86,87]. In drought stress, the mitogen-activated protein kinases (*MPKs*) phosphorylate the auxin signalling transcriptional repressor IAA15, suppressing lateral root formation. Two *MPK*s,I.e., *MPK*3 and *MPK*6, phosphorylate the repressor IAA15 at the Ser-2 and Thr-28 residues [88] (Fig. 2B). The overexpression of stress-responsive OsMYB-R1 transcription factor in rice increases the auxin level, leading to lateral root formation and drought resistance. Moreover, it is predicted that OsMYB-R1 is a component of a complex network of transcription factors that regulates the cross behavior of auxin and salicylic acid (SA) signalling during multiple stresses [89]. The IAA-producing iaaM-OX transgenic lines and IAA pre-treatment of wild-type plants enhance drought resistance (Fig. 2B). The triple mutants for *yuc1yuc2yuc6* impair the IAA production level, decreasing the drought resistance compared to non-treated WT plants. Moreover, the endogenous and exogenous auxin positively regulates the expression of *RAB*18, *RD*22, *RD*29*A*, *RD*29*B*, *DREB*2*A*, and *DREB*2*B* genes, the antioxidant enzymatic systems and the root architecture, particularly the lateral root formation). The auxin-induced *DEEPER ROOTING* 1 (*DRO1*) promotes the formation of longer roots in rice phenotype during drought. Moreover, the insertion of *INDITTO*2 transposon at the promoter site of the *DRO*1 showed that transposon can act as an autonomous auxin-responsive promoter [90] (Fig. 2A). The role of plasma membrane-localized transporter of auxin PINFORMED1 (PIN1) in response to salt and drought stress adaptations revealed its role in regulating the flower formation and development, root hair initiation, as

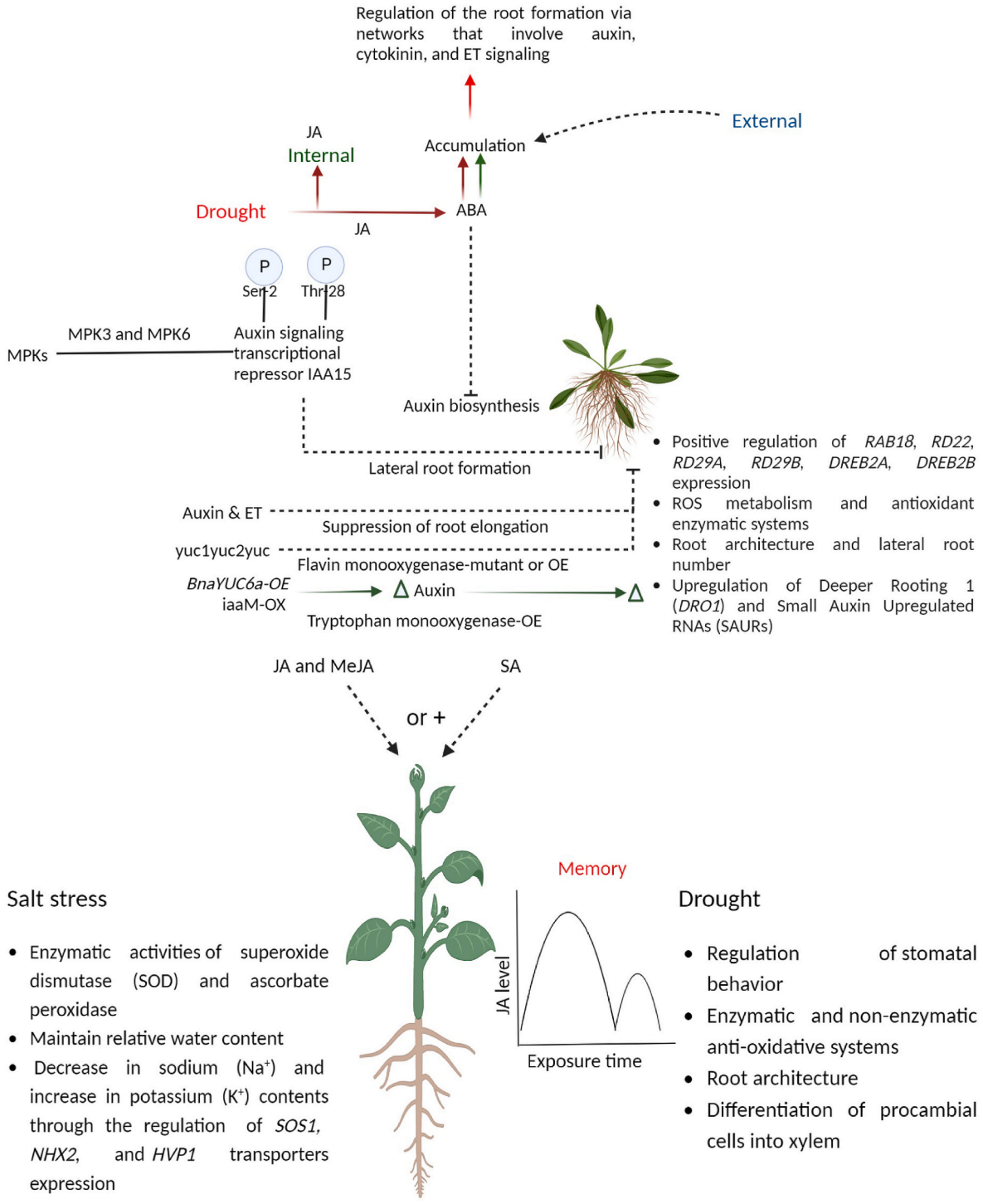

Fig. 2. Overview of plant adaptations in response to drought and salinity stress and role of plant growth regulators and their cross-talks during plant adaptations. **2A**: Auxin-mediated plant adaptations to the drought stress. The overexpression of BnaYUC6a enhances the drought resistance, whereas the triple mutants for yuc1yuc2yuc6 impair the IAA production level and subsequently decrease the drought resistance. The mitogen-activated protein kinases (MPKs) phosphorylate the auxin signalling transcriptional repressor IAA15 at the Ser-2 and Thr-28 residues responsible for suppressing the later root formation. In contrast, the stress-responsive OsMYB-R1 transcription factor overexpression enhances the later root formation. **2B**: Jasmonic acid, in combination with SA, promotes the accumulation of endogenous ABA and regulates the expression of several genes during abiotic stresses. JA is biosynthesized only for the first time against dehydration stress, and subsequent exposure of plants to dehydration lacks JA accumulations. Therefore, it is linked to memory responses in plants. The application of MeJA helps regulate the stomatal behavior, induces both the enzymatic and non-enzymatic anti-oxidative systems, modulates root architecture in response to drought, and facilitates the differentiation of procambial cells into xylem. **2C**: Salicylic acid (SA) is well known for its role in SAR and for promoting growth and abiotic stress responses, enhancing the total phenolic content and antioxidant capacity in drought-stressed plants. 2C: Cross talk of different plant growth regulators in response to drought and salinity ABA promotes the proline accumulation by regulating the activity of pyrroline-5-carboxylate reductase, promotes the enzymatic anti-oxidative system, improves the roots conductivity by inducing the gene expression of aquaporin. ABA, in combination with JA and SA signalling, also mobilizes the resources to mitigate the effects of plant stresses. Ethylene facilitates plant adaptations to stresses at the expense of growth and development.

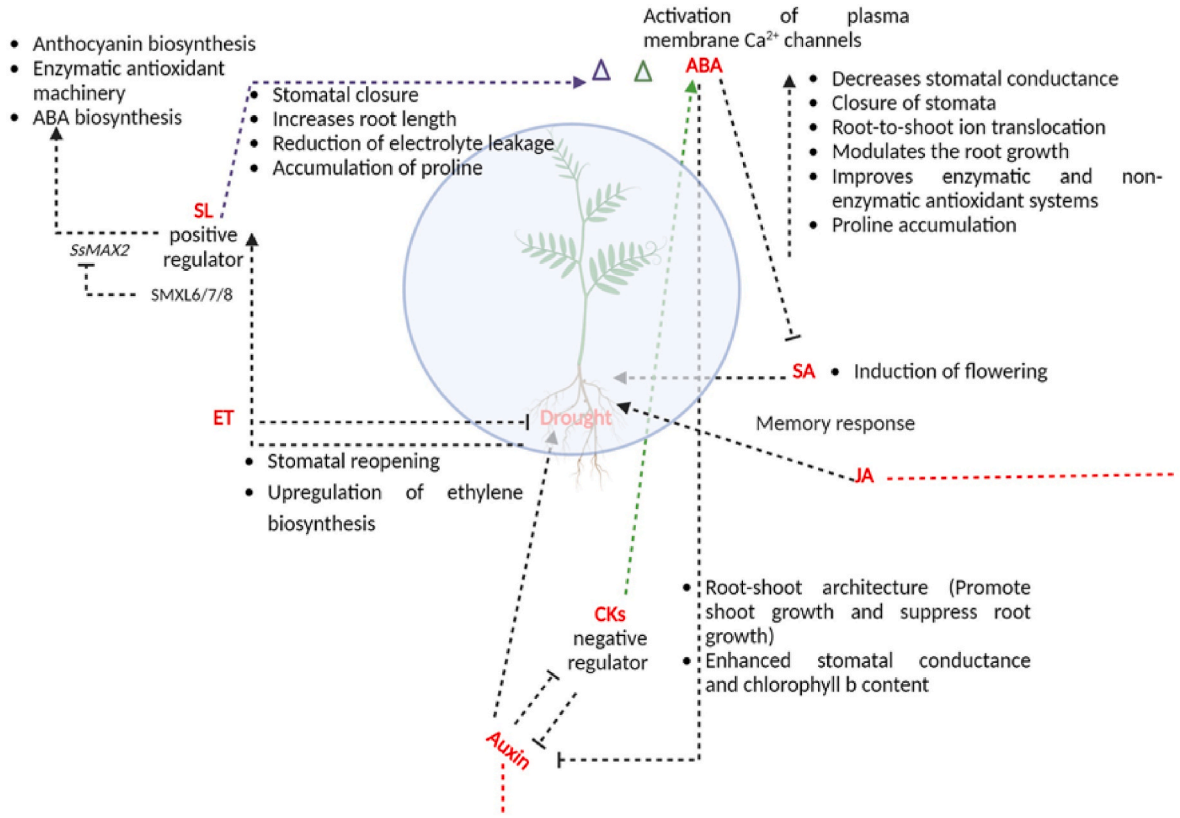

Fig. 2. (*continued*).

well as pavement cells and guard cells development and differentiation [91]. Other transcription factors, such as DNA-binding AUXIN RESPONSE FACTORS (ARFs), also regulate the soluble sugar content, root development, and chlorophyll in response to drought and salinity stress responses whereas the auxin-responsive genes; SMALL AUXIN UP-REGULATED RNAs (*SAURs*) also contribute in water stress [92].

3.2. Jasmonic acid (JA) and its derivatives

Jasmonic acid and its derivatives like jasmonoyl-amino acid, jasmonyl isoleucine (JA-Ile), JA-glucosyl ester, methyl jasmonate (MeJA), 12-hydroxyjasmonic acid sulfate (12-HSO4-JA), 12-*O*-glucosyl-JA, JA-Ile methyl ester, JA-Ile glucosyl ester, 12-carboxy-JA-IIe, 12-*O*-glucosyl-JA-IIe, and lactones of 12-hydroxy-JA-IIe), derivatives of cyclopentanones are collectively known as oxylipins [93]. The higher plants synthesize JA and MeJA. The biosynthesis, metabolism, and other aspects of JA have been discussed by the researchers [94,95]. In rice, the application of acetic acid induces root-to-shoot JA signals, similar to drought [96]. Similarly, acetic acid treatment enhances drought tolerance in apple plants by affecting the JA and ABA-induced mitogen activated protein kinase (MAPK) signalling pathway [97]. Jasmonic acid alone or in combination enhances the salt tolerance in crops such as tomato, wheat, potato and soybean, summer squash, and other crops [98–101]. JA increases relative water content and reduces sodium (Na^+) and potassium (K^+) contents by regulating the expression of *SOS*1, *NHX*2, and *HVP*1 transporters. The external application of JA counters the inhibitory effect of salt stress. Jasmonic acid also enhances the level of cytokinin (CK), and IAA and reduces the ABA. It also enhances the α-tocopherol, phenolics, and flavonoids in wheat [101,102]. In soybeans, the external application of JA alleviates the negative impact of salt stress on growth and metabolism [103]. The role of JA in plant growth and development, defence response to biotic [104], and abiotic stressors such as salt drought and other stresses have been explored in several crops including strawberries [105], oriental melon [106], earl millet [107], Chinese liquorice [108] and others plants. MeJA, in combination with SA, promotes the accumulation of endogenous ABA and osmotic adjustment substances in maize during drought responses [109–111]. Jasmonic acid regulates the expression of several genes during abiotic stresses [112]. JA is also responsible for memory response against dehydration stress. It is biosynthesized only for the first time. However, subsequent exposure of plants to dehydration lacks JA accumulations [113,114]. The treatment of *Brassica rapa* KS101 and KBS3 genotypes with JA and 24-epibrassinolide induce photosynthesis, osmolyte production, antioxidant activity, and other parameters that help in alleviating drought stress [115]. During the early phase of drought stress, the endogenous level of JA in *Arabidopsis* and citrus increases immediately, but with the prolongation of the stress, its content decreases to a basal level. The application of MeJA in broad bean and barley enhances the ability of plants against drought through the regulation of stomatal behavior whereas in cauliflower and maize, it induces both the enzymatic and non-enzymatic anti-oxidative systems [116]. Jasmonic acid is also known to modulate root architecture in response to drought. The molecular and genetic studies show that in *Arabidopsis* roots, JA interacts antagonistically and facilitates the differentiation of procambial cells into xylem [117] (Fig. 2B).

Salinity stress also induces the transcripts related to JA in sweet potatoes [118]. In MeJA-treated black locust tree theenhanced salt adaptations are linked to enzymatic activities of superoxide dismutase (SOD) and ascorbate peroxidase (APX) [112,119]. The application of nitric oxide (NO) scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO) and JA reveals that the response to drought in wheat induces the NO level and also enhances the ascorbate-glutathione (AsA-GSH) cycle through the upregulation of the ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR) and dehydroascorbate reductase (DHAR) and a decrease in malondialdehyde (MDA) content and

electrolyte leakage [120]. Various genes and transcriptional factors related to JA signalling have been characterized in plants. For example, the functional characterization using overexpression and gene silencing of *CmLOX*10 from oriental melon seedlings shows its role in drought tolerance is mediated by regulating the mediated stomatal closure and JA signalling-mediated feedback through *CmMYC*2 approach [106]. In grapevine, drought, ABA, and MeJA induce the transcription factor *VaNAC*17, which decreases the production of ROS [121].

3.3. Salicylic acid

Salicylic acid (SA) is well known for its role in systemic acquired resistance (SAR) and for promoting plant growth and abiotic stress responses. The role of SA signalling in drought and salt stress in wheat [122,123], onion [124], sweet potato [125], radish [126], Chilean wineberry [127] and other plants have been discussed earlier [128]. Besides this, SA alone has been used for inducing flowering in sweet orange or in combination with potassium [129], trehalose [130], dimethylthiourea [131], thiourea [132], spermidine [133], methyl jasmonate [110] has been used to mitigate the adverse effects of drought and other abiotic stresses (Fig. 2C). At 100 mM concentration, SA differentially enhances the nitrogen (N), phosphorus (P), and K contents of leaves in two cultivars of wheat [122]. In sweet potatoes, the SA response (at 2–4 mg/L) downregulates the ABA-related genes thus decreases the ABA level [125]. The salicylic acid application also enhances 30 % of the total phenolic content and antioxidant capacity in drought-stressed *Aristotelia chilensis* [127]. The induction of flowering in citrus plants exposed to drought stress and SA-treated plants is associated with the enrichment of differentially expressed genes related to starch sucrose metabolism and along with the upregulation of LIPOYLTRANSFERSAE 2 A homologous (*LIP*2*A*) [134]. The SA treatment of drought-stressed wheat plants induces the differential expression of various proteins related to photosynthesis, carbon assimilation, protein and amino acid metabolism, energy metabolism, redox state, signal transduction, and other biological processes that ultimately enhance drought resistance in plants [135]. Applying acetylsalicylic acid, a SA derivative, enhances drought resistance in chickpeas by activating the antioxidant system [136].

3.4. Ethylene

Ethylene (ET) induces multiple plant responses, such as leaf abscission. Synthesis of ET in response to stress may enhance plant tolerance or expedite senescence [137]. Ethylene emission rate (EER) analysis revealed that ET is a critical constraint in stomatal reopening in response to drought in *Fraxinus chinensis* [138]. Ethylene alone or in combination with other hormones acts as a critical growth regulator and activates the plant adaptations against abiotic stresses (Fig. 2A & C). The role of ET in abiotic stresses has been discussed by Chen and his colleagues, 2021a. Ethylene facilitates plant adaptations to stresses at the expense of growth and development. The editing of *PhACO* 1 and *PhACO* 3 genes responsible for ET biosynthesis genes enhanced susceptibility to salt and drought stress in petunia cv. Merage Rose [139]. The putative gene promoter analysis of gene orthologs and differential expression of ethylene-related genes (*MAT*, *ACS*, *ACO*, *ETR*, and *CTR*) from soybean revealed that *ACS* and *ACO* related to ethylene biosynthesis are upregulated. In contrast, ones related to ethylene signal transduction, such as *CTR*, are downregulated in response to water stress [140]. The overexpression and RNA interference studies have shown that the transcription factor OsERF109 negatively affects ethylene biosynthesis in rice plants during drought tolerance [141]. The *APETALA*2/ethylene responsive factor *OsEBP*89 mutant belonging to the *AP*2/*ERF* subfamily, located in the nucleus of the rice protoplast, enhances drought tolerance in rice plants [142].

Contrary to this, in maize, ZmERF21 belonging to APETALA2 (AP2)/Ethylene response factor (ERF) transcription factor, mainly expressed in the root and leaf is induced after exposure to polyethylene glycol (PEG) treatment [143]. The pre-treatment with 1-(aminocarbonyl)-1-cyclopropane carboxylic acid (ACC) (a precursor of ET) in tomato plants overexpressing mitochondrial alternative oxidase (AOX), lower H_2O_2 levels, thus establishing the role of AOX-dependent ROS signalling. The decrease in ROS signalling induces autophagy, whereas the accumulation of ROS causes programmed cell death (PCD), especially in ET-mediated drought tolerance [144]. The increased ET levels under stress inhibit the transcription of auxin response factors, which constrain plant growth. Studies show that soil bacteria producing ACC deaminase confer plants' enhanced stress tolerance and growth promotion. Plant growth-promoting rhizobacteria secrete 1-aminocyclopropane-1-carboxylase (ACC) deaminase which restricts ethylene biosynthesis in plants by catalyzing the conversion of ACC to ammonia and α-ketobutyrate [50,145].

3.5. Abscisic acid

Abscisic acid (ABA) is one of the significant and principal growth regulators that orchestrate plant responses to environmental stresses such as drought [146] by regulating the osmotic stress-responsive genes that catalyze the biosynthesis of osmoprotectants and under drought or high-salinity [62,147–149]. ABA also triggers the signalling cascade that results in large-scale transcriptional reprogramming and physiological changes, including stomata closure to reduce transpiration. Drought and ABA share an intricate dose-dependent relationship that assists the plants against drought. The role of ABA in water stress has been investigated using PEG 6000 and wheat drought-tolerant cultivar L. cvs. MV Emese and drought-sensitive cultivar GK Élet. Compared to drought-sensitive wheat cultivar GK Élet, in drought-tolerant MV Emese, the ABA level reduces significantly, indicating its role in root growth in response to osmotic stress [150]. The root's water deficiency activates the de-novo biosynthesis of ABA [151], which is then transported to the aerial plant parts such as leaves. In guard cells, ABA induces stomatal closure [152,153]. Synthesized in the root cap, ABA is actively transported to the leaves, reducing the stomatal conductance and then water loss, which helps develop drought resistance [154]. Besides stomatal closure, ABA also plays a vital role in root-to-shoot ion translocation and the modulation of root growth [48]. The external application of ABA regulates the amino acid and lipid metabolism and the accumulation of flavonoids, betaine, and other secondary metabolites. ABA also improves the enzymatic and non-enzymatic antioxidant systems and enhances the photosynthetic performance and relative water content (RWC) of plants that help the plant growth to drought resistance in crops such as maize, pearl millet, sweet potato, wheat, and other plants [107,155–157]. ABA triggers the biosynthesis of H_2O_2 in guard cells using the membrane-bound NADPH oxidase that causes stomatal closure through plasma membrane-located Ca^{2+} channels [8,158]. The different roles of ABA and ROS in guard cells have been reviewed [159].

The underlying mechanisms of water stress and its correlation with ABA levels in plants are still unclear. The decrease in turgor pressure probably results in the accumulation of ABA [160]. ABA interacts with other plant growth regulators such as auxin, GA, CK, ET, SA, and JA to combat abiotic stresses. In response to drought, a significant increase in the amount of ABA and ET has been reported [161,162]. Studies show that due to differential localization routes of ABA and auxin, their distribution in primary and lateral roots is independent. Additionally, ABA suppresses auxin biosynthesis (Fig. 2A), and its accumulation regulates auxin transportation in the root tip of *Arabidopsis* in drought [163,164]. Auxin and ET are involved in ABA-mediated response in the root [165]. The investigation of auxin/ET/ABA crosstalk showed that auxin and ET likely act linearly to affect ABA-responsive suppression of root elongation. In contrast, they probably act independently of ABA-responsive suppression of seed germination [165]. Moreover, the external application of JA enhances foliar ABA accumulation [166,167], which indicates the extensive crosstalk between JA-ABA pathways. It is also

reported that ABA level increases with decreasing water status, whereas JA level increases in the early stages of stress [8,168]. The accumulation of ABA modulates root formation via complicated signalling networks that involve auxin, CK, and ET signalling [88].

ABA upregulates the expression of aldehyde oxidase (AO) and xanthine dehydrogenase (XDH) in response to drought [169]. In addition to stomatal closure, ABA affects channel activities in guard cells, transcription of the calmodulin protein, and the expression of ABA-responsive genes during drought [170,171]. ABA promotes proline accumulation by regulating the activity of pyrroline-5-carboxylate reductase [172]. Drought and ABA also induce the expression of D1-pyrroline-5-carboxylate synthetase [173] in response to drought. ABA exposure to wheat seedlings promotes the enzymatic activity of superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, and glutathione reductase, which help reduce oxidative damage. ABA also assists in regulating the osmotic potential and improving the root's conductivity by inducing the gene expression of aquaporin. ABA, in combination with JA and SA signalling, also mobilizes the resources to mitigate the effects of plant stresses [174]. It has been observed that ABA, combined with jasmonate or benzylaminopurine, effectively promotes plant drought resistance [157,175].

The histone acetylation in response to drought plays a vital role in ABA-mediated gene regulation [8]. In Arabidopsis, ABA and drought in roots induce AtSAUR32 localized to the plasma membrane and nucleus. Yeast two-hybrid and bimolecular fluorescence complementation assays reveal that AtSAUR32 interacts with clade-A PP2C proteins (AtHAI1 and AtAIP1) to regulate ABA sensitivity [176].

3.6. Cytokinin

CK crosstalks with other hormones to meditate responses in plants (Fig. 2C) [177–179]. CK-deficient plants can better survive drought stress, suggesting that CKs act as a negative regulator [180]. Further, auxin and CK act in antagonism [179], whereas CKs crosstalk with ABA to modulate plant fitness in response to drought through complex network [181] (Fig. 2C). In poplar, the high CK activity in primary meristems, irrespective of water stress, indicates its role in meristem maintenance, whereas the decrease in CK activities in apical pith and cambium of drought-stressed contribute to primary and secondary growth [182]. CKs are of immense importance due to their crosstalk with different plant growth regulators in response to drought and salinity. CKs promote shoot growth and suppress root growth. CK levels are maintained using cytokinin glucosyl transferases [183] and cytokinin oxidase/dehydrogenase [184]. The treatment of rice plants with synthetic CK (N-2-(chloro-4-pyridyl)-*N*-phenyl urea) at 5 mg/L enhances the stomatal conductance and chlorophyll *b* content [185]. The application of phenyl-urea-based synthetic CK reduces the wilting, promotes the fresh weight and yield, and suppresses the accumulation of proteins such as SWEET5 and SWEET13 proteins, which are induced in response to drought [186]. The application of a synthetic CK, 6-benzyl amino purine (6-BA) to the perennial monocot grass tall fescue suppresses the SL-signalling genes; *FaD* 14 and *FaMax*2, which shows that 6-BA act as a drought-dependent inhibitor of SL-signalling genes [187].

3.7. Strigolactones and their role in water stress

Strigolactones (SLs) are derived from carotenoids and are known for their role in regulating plant growth and plant adaptations to drought, salinity, and other environmental cues [188,189]. Besides this, strigolactones also act as mediators during the interaction with soil microorganisms [189]. Strigolactones act as positive regulators during drought [190] (Fig. 2C). The biosynthesis of SL is linked to ABA [191]. The synthetic analogues of strigolactone GR24 induce height and root length in Jinongda 667 rice seedlings exposed to 200 mM NaCl salt [192]. Synthetic SL analogues such as GR24 at 15 μM and NO donor *S*-nitroso glutathione (GSNO) at 10 μM have been reported to promote tomato seedling growth under salt stress. The experimental investigation using TIS108, an inhibitor of strigolactone synthesis, suppresses the NO-led adaptations under salt stress, indicating that the endogenous SLs might contribute to NO-induced salt response [193]. During plant acclimation to environmental stresses, SLs intrinsically regulate the induction of stomatal closure behavior [194,195]. In apple seedlings, the SL treatment contributes to resistance against KCl stress, possibly by eliminating the ROS induced in response to KCl, accumulation of proline, and maintenance of osmotic balance. SL regulates ion homeostasis by exporting K^+ ions from the cytoplasm into the vacuole, followed by increased Na^+ and other minerals in the cytoplasm to maintain the osmotic balance under KCl stress [196]. Strigolactones-mediated drought acclimatization in shoots involves the hypersensitive response of stomata to ABA. SL is transported acropetally. However, the biosynthesis of SL is repressed in roots under drought, indicating its organ-specific metabolism. The scions of wild-type tomatoes grafted onto SL-depleted rootstocks and external application of SL establish that shoots receiving SLs from the roots cause a hypersensitive response to ABA [197]. In grapes plants, the external application of a synthetic GR24 at 1–5 μM in the presence of 7 % (w/v) PEG-6000 boosts the plant tolerance to drought via lowering the electrolyte leakage, regulating the stomatal opening, ROS level, and RWC (Fig. 2C). The application of GR24 also lowers IAA and zeatin riboside (ZR) levels, whereas it increases ABA levels in the roots and leaves of drought-stressed plants [195].

In response to abiotic stresses, SLs regulate and talk with other plant hormones, including auxin, ABA, CK, and GAs [198] (Fig. 2A–C). The role of SL has been established using SL-deficient and SL-response [more axillary growth (max)] mutants of Arabidopsis, where both led to a hypersensitive response in drought and salt stress. Further, the response was linked to the plant's aerial part, i.e., shoot-rather than root [199]. The overexpression of *the SsMAX*2 homolog encoding SL signalling component from *Sapium sebiferum* in Arabidopsis improves the plant's resistance to drought, salt, and osmotic stresses. Transgenic lines such as *SsMAX*2-*OE* increase anthocyanin biosynthesis and enzymatic antioxidant machinery, leading to a significant reduction in H_2O_2 levels. Moreover, these lines also upregulate ABA biosynthesis-related genes, thus, indicating the probable role of SL and ABA during adaptation [200] (Fig. 2C). The differential expression analysis reveals that the expression of antioxidant encoding genes *APX*6, *CAT*1, *GSHPX*1 and *GSHPX*2, *POD*42, and *SODCP* is upregulated, whereas expression of *NAC* (2), *WRKY* (3), and *MYBs* (4) transcription factor is down-regulated in response to drought. Further, the essential gene of SL synthesis, D14 is induced during drought [201]. SLs treatment significantly increases photosynthesis, stomatal conductance, transpiration, and water usage in *Pennisetum purpureum*. This tropical grass helps mitigate the decrease in photosystem II efficiency and the performance index due to drought. SLs effectively increase the fresh and dry weight of the whole plant [null]. The mutation in SL-specific receptor *HvD*14 from barley revealed that its mutants are hyper-sensitive to drought stress due to alteration in ABA metabolism and/or signalling pathways, thus indicating the role of SL signalling and ABA-dependent drought stress response [202].

In Arabidopsis, SLs regulate the shoot branching by *MAX*2-dependent targeting of SUPPRESSOR OF MORE AXILLARY GROWTH2 (*MAX*2)-*LIKE*6 (*SMXL*6), *SMXL7* and *SMXL*8. However, the roles of the *SMXL*6, 7, and 8 in the SL-regulated plant response to drought still need to be determined. The experimental study on SMXL6, 7, and 8 triple mutants revealed their negative contribution to drought response. The triple mutant decreases cuticular permeability, water loss, leaf stomatal index, and the accumulation of anthocyanin biosynthesis during drought (Fig. 2C). Furthermore, the mutants were hypersensitive to ABA-induced stomatal closure [203]. *SMAX*1 and *SMAX1-LIKE*2 (*SMXL2*) promote the cuticle formation in mutants. The mutants are hypersensitive to ABA-led stomatal closure and exhibited higher ROS detoxification. Additionally, longer root hairs and a better root-to-shoot ratio were also observed in the mutants. In a nutshell, *SMAX*1 and

SMXL2 negatively impact the drought resistance [204]. Micro-RNA miR156, which acts as a mediator of ABA-dependent responses, has been identified in tomato plants in drought-stressed plants [205].

3.8. Anti-oxidative dynamics in abiotic stresses

One inevitable outcome of water scarcity is the production of ROS in cell organelles such as chloroplasts, mitochondria, and peroxisomes [206]. These are primarily toxic products produced in response to biotic and abiotic stresses [207]. At the extracellular level, ROS are primarily produced by NADPH oxidases, which are localized at the plasma membrane [208]. ROS production is also linked to photorespiration, amine oxidase, and cell wall-bound peroxidases [209]. In chloroplast, the high ratio of light absorbed to the capacity of light required for photosynthesis leads to the ROS production in photosystems I and II. ROS byproducts include singlet oxygen from PSII and superoxide radicals from PSI and PSII [11]. Other sources of ROS include xanthine dehydrogenase (XDH) (EC 1.2.1.37) and AO (EC 1.2.3.1). Using in-gel assays and mutants for XDH and AO, it has been established that XDH produces O, whereas AO produces only H_2O_2 in tomatoes and *Arabidopsis* [169]. In maize genotypes, the drought induces ROS and reactive nitrogen species (RNS) production [210] (Fig. 3).

Plant cell organelles own various ROS-producing as well as ROS-scavenging pathways. Plants evolve different mechanisms to counter the side effects of ROS [20,21,207,211]. The ROS scavenging mechanisms of halophytes, especially mangroves, and other plants, include enzymatic or non-enzymatic pathways. The enzymatic components include the production of superoxide dismutase (SOD), catalase, and peroxidase, whereas the non-enzymatic mechanisms include ascorbic acid, carotenoids, glutathione, and α-tocopherol that help in removing H_2O_2 [209,212]. The ROS and redox state dynamics of different organelles vary in response to water stress [213]. In prolonged drought stress, ROS production exceeds the scavenging of free radicals by the anti-oxidant system. The ROS response is also linked to Ca^{2+} ion fluxes and sugar sensing, which likely involve ABA-dependent signalling pathways [206]. The disturbance in the dynamics due to the accumulation of ROS peroxidates the lipids and fatty acids present on the membrane phospholipids, which enhances the membrane permeability and then causes leakage of ions followed by chlorophyll degradation, cell injury, and subsequent cell death [59]. At the gene level, a network of 152 candidate genes has been identified for ROS production in Arabidopsis [11,214]. The accumulation of apoplastic ROS and its affiliated

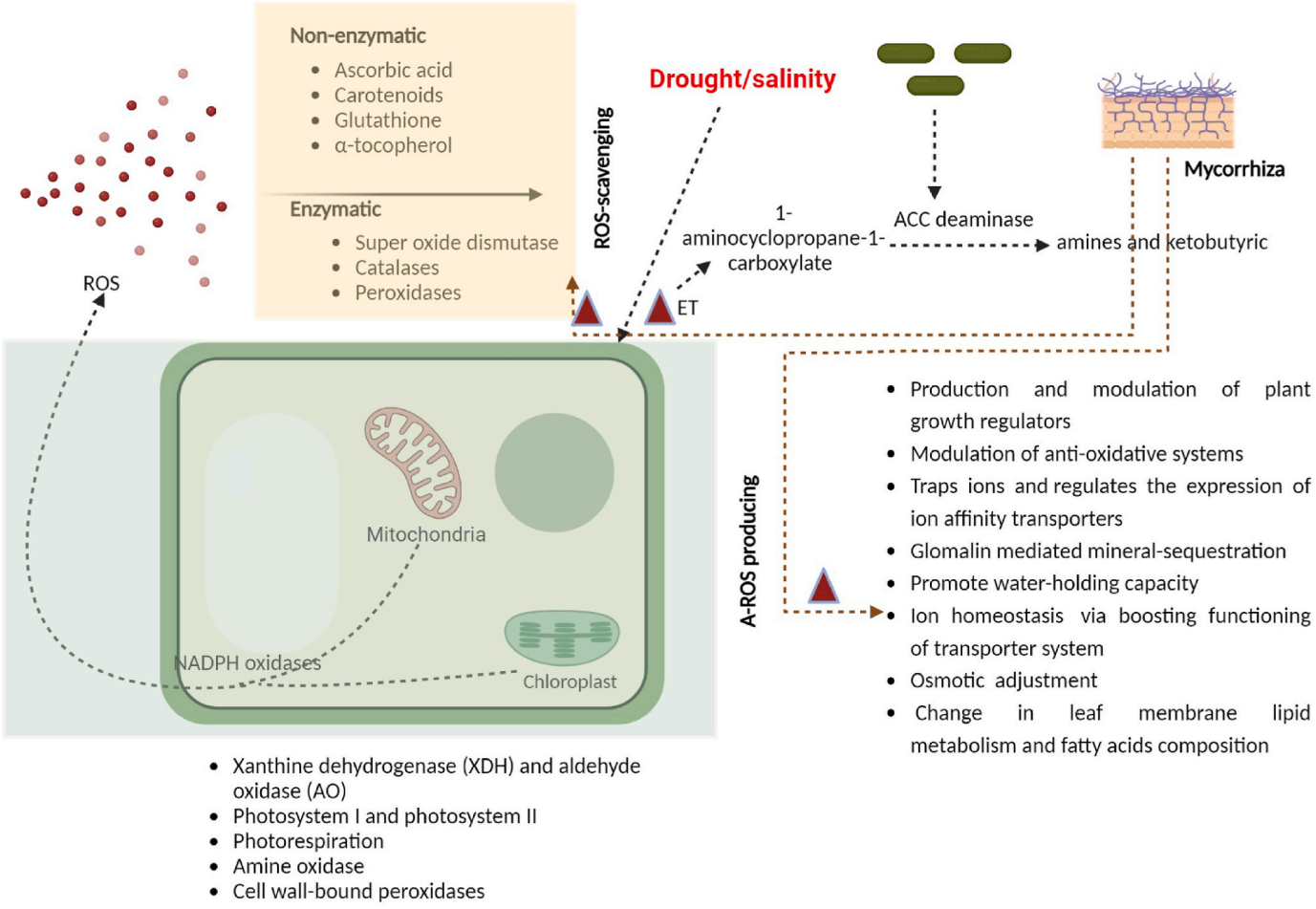

Fig. 3. Reactive oxygen species dynamics and role of mycorrhizal interactions in plant adaptations to combat drought stress. Plant cell organelles own various ROS-producing as well as ROS-scavenging pathways. The reactive oxygen species are produced in cell organelles such as chloroplasts, mitochondria, and peroxisomes, as well as by NADPH oxidases localized at the plasma membrane, photorespiration, amine oxidase, and cell wall-bound peroxidases. ROS scavenging mechanisms of plants include enzymatic or non-enzymatic pathways. The plant exudates are critical to determining the fate of mycorrhizal colonization. The strigolactones (SLs) produced by plants assist the mycorrhizal colonization. The formation of biofilm by mycorrhizal interaction facilitates the detoxification of ROS. The accumulation of unsaturated fatty acids in the chloroplast reduces cellular damage and improves plant growth in response to drought stress. In a nutshell, the mycorrhizal association improves carbon usage, osmotic status reduces the damage to the photosystems PSII and PSI structures, enhances water holding and water acquisition, photosynthesis, and stomatal conductance, and facilitates the selective exchange of ions in plants during drought and salt stress. Overall, some of the AMF responses share a similarity, whereas others are exclusive, and the magnitude of the effect varies with the fungal species.

signalling network are part of plants' early hallmarks of stomatal movement [208,215,216]. Plants evolved other mechanisms to suppress the production of ROS molecules, including adaptations at the anatomical level and leaf movement, C4 or CAM (Crassulacean Acid Metabolism) cycles, changes in the chlorophyll, downregulation of photosynthesis, photosystems, and antenna modulators [11,209] (Fig. 3).

Table 1
Examples of different genes*/transcription factors** and reactive oxygen species identified for their role in drought and salt stress tolerance in plants (from 2010 onwards till 2023 as per NCBI PubMed-database).

S. No.	Gene	Host	Role of genes, TFs and ROS in plant adaptations to the water stress	References
1.	SbNAC9*	Sorghum	Induce drought resistance in polyethylene glycol (PEG) treated plants.	[219]
2.	*ScDREB2B*-1	Sugarcane hybrid ROC22/tobacco	Upregulation of *ScDREB2B-1* in the root and leaf of ROC22 after exposure to PEG, NaCl and ABA.	[220]
3.	*SlHK2**	Tomato	Inactivation/downregulation of cytokinin receptor improved drought, heat, and combined stress tolerance	[221]
4.	*TaTIP4***	Arabidopsis and rice	Drought salinity and/or osmotic stress resistance upregulate both enzymatic and non-enzymatic anti-oxidative systems.	[222]
5.	IbBBX24-IbTOE3-IbPRX17*	Sweet potato	The transcription factor binds to its promoter, activate the expression of the class III peroxidase gene *IbPRX17*. Overexpression of both enhance tolerance to salt and drought.	[223]
6.	MeMYB108 exon*	Cassava	Facilitate the scavenging of ROS that reduce the drought-induced leaf abscission.	[224]
7.	β-amylase gene IbBAM1.1	Sweet potato/ Arabidopsis	Promote tolerance to the drought and salinity by reducing the production of H_2O_2 and O_2^- free radicals.	[225]
8.	GmNTF2B-1*	Soybean	GmNTF2B-1 interact with oxidoreductase *GmOXR17* and reduce ROS level that results in enhanced resistance.	[226]
9.	K^+/H^+ antiporters AtKEA1 and AtKEA2*	Arabidopsis	The loss of function of the chloroplast K^+ efflux via antiporters *KEA1& KEA2* in the inner envelope membrane led to inefficient photosynthesis.	[227]
10.	JrERF2-2**	Walnut	Interact with JrWRKY7 and regulate the expression of GSTs anti- oxidative system.	[228]
11.	WUSCHEL-related homeobox gene PagWOX11/12a*	Poplar	Induced in response to drought, *PagERF35* directly upregulate *PagWOX11/12a* expression and promote biomass and root elongation under drought conditions.	[229]
12.	CaCKX6*	Chickpea and Arabidopsis	Root-specific expression of cytokinin oxidase/dehydrogenase 6 (*CaCKX6*) increases the lateral roots that resulted in higher root-to-shoot biomass ratio help in drought tolerance.	[230]
13.	GmbZIP15**	Soybean	Act as a negative regulator in response to salt and drought stresses.	[58]
14.	VvNAC17*	Grapevine	The overexpression of VvNAC17-OE in Arabidopsis enhance the growth against drought.	[231]
15.	GmNAC8**	Soybean	Induce in response to drought, ABA, ET and SA treatments, its overexpression enhance drought tolerance.	[203]
16.	OsEBP89**	Rice	The mutant induce drought tolerance at all growth stages.	[142]
17.	MdERF38**	Apple	Ethylene response factors *MdERF38* induce anthocyanin biosynthesis in response to drought stress.	[232]
18.	*AtUGT76C2* *	Arabidopsis	Encoding for ck- glycosyltransferase, the overexpression of *UGT76C2* decrease the endogenous ck level that result in enhance tolerance to drought and salinity.	[181,233]
19.	AP2/ERF Transcription Factor TINY**	Arabidopsis	TF inhibit brassinosteroid-regulated growth while promote drought responses. TINY upregulate drought responses genes and also promote ABA-mediated stomatal closure.	[234]
20.	GhRaf19*	Cotton	A negative regulator of drought and salt but act as a positive regulator against cold stress modulate ROS level in cells.	[235]
21.	MsDREB6.2	Apple	Dehydration-responsive element binding factors (*MsDREB6*.2-OE) expression increases the expression of a CK catabolism related gene; *MdCKX4a* that decrease the endogenous CK levels and shoot: root ratio in response to drought adaptation.	[236]
22.	NAC-SNAC3*	Rice	Induced by drought, high temperature, salinity stress, and ABA modulates ROS level.	[237]
23.	ROS production	Maize	Drought-tolerant maize genotypes accumulate lower level of ROS and reactive nitrogen species (RNS) compared to sensitive ones.	[210]
24.	NAC - NTL4*	Arabidopsis	TF promote the ROS production after binding to the promoters of genes responsible for ROS biosynthesis in response to drought-induced leaf senescence.	[238]
25.	OsPP18*	Rice	A stress-responsive NAC1 (SNAC1)-regulate downstream gene rice protein phosphatase 18 that modulates drought and oxidative stress tolerance through ABA-independent ROS scavenging.	[239]
26.	GhWRKY17*	Cotton/Tobacco	Induce after exposure to drought, salt, H_2O_2 and ABA, its constitutive expression reduce tolerance to drought and salt stress, reduce ABA level, impair ABA-induce stomatal closure. It also reduces the level of ABA and transcript levels of ABA-inducible genes, including AREB, DREB, NCED, ERD and LEA under drought and salt stress conditions.	[240]
27.	*S*-adenosylmethionine decarboxylase (SAMDC)**	*Capsicum annuum*	CaSAMDC-OE plants accumulates polyamines, shows increase ADPH oxidase whereas suppression of RbohD and RbohF activities. Moreover, the transcription of ROS-detoxifying enzymes increases in response to drought stress in transgenic lines.	[241]
28.	CYCLIN H; 1	Arabidopsis	CYCH; 1 regulate the drought stress response in a CDKD-independent manner. I also regulate blue light-mediated stomatal opening by controlling ROS homeostasis.	[242]
29.	ThWRKY4	*Tamarix hispida*	Induced in response to ABA, salt and drought in the early phase of stress.	[218]
30.	ROS	Rice	The accumulation of proline and higher activities of monodehydroascorbate reductase, dehydroascorbate reductase, ascorbate peroxidase (APX), and glutathione transferase in the seedlings of drought-tolerant cv. Brown Gora than the sensitive cv. Malviya-36. Furthermore, drought reduces the antioxidants ascorbate and glutathione (GSH) and decreases the redox ratio (AsA/DHA and GSH/GSSG) with lesser decline in tolerant than the sensitive seedlings.	[243]
31.	NAM/ATAF1/2/CUC2 (NAC) NTL4*	Arabidopsis	Activated by drought and ABA, induces the expression of NADPH oxidase genes involved in ROS biosynthesis.	[244]
32.	OsMIOX**	Rice	Improved drought tolerance through scavenging of ROS.	[245]
33.	Raf-like MAPKKK gene DSM1**	Rice	The drought-hypersensitive mutant (drought-hypersensitive mutant 1 [dsm1]) of a putative MAPK kinase (MAPKKK) are highly sensitive compare to wild-type plants against drought.	[246]

OE-represent overexpression.

3.9. Key genes and transcription factors in response to drought and salt stress

The role of various transcription factors and crosstalk of growth regulators, such as ABA-dependent and independent signalling pathways in response to drought and salinity stress, have been reviewed by Hussain and his colleagues, 2021. For example, the dehydration-responsive element-binding protein (DREB1), a protein/C-repeat binding factors (CBFs) belonging to the APETALA2 (AP2) transcription factors family interacts with DRE/CRT *cis*-element and then regulates the stress-responsive genes. DREB1 acts as a common switch for ABA-dependent and ABA-independent pathways during plant responses to drought, salt, and other environmental stresses [214]. The treatment with ABA in salt and drought stress plants induces *PR-1*, *PR*-5, *RAB-18*, and *RD-29A* genes [146,214]. The transcription factor ZmWRKY106 belonging to the WRKY gene family from maize, which is induced exclusively in response to drought, external ABA, high temperature, and weakly induced by salt, also helps drought tolerance. The overexpression of *ZmWRKY106* regulated stress-related genes through the ABA-signalling pathway and anti-oxidative system activities [217]. The expression of a transcription factor, ThWRKY4-OE, from *Tamarix hispida* in *Arabidopsis* improves tolerance to salt and oxidative stress in ABA-treated transgenic lines. This tolerance is linked to enhancing SOD, peroxidase activity, and decreasing ROS such as O_2^- and H_2O_2 levels, protecting plant cells from death. Furthermore, microarray analysis showed that ThWRKY4 upregulates 165 and downregulates 100 genes in *Arabidopsis*. Promoter scanning analysis revealed that ThWRKY4 binds to W-box motifs in promoter regions to positively modulate abiotic stress tolerance [218]. The role of various genes and transcription factors in response to abiotic stress, such as water stress, has been described (Table 1).

In *Arabidopsis thaliana*, CYCH; 1, localized to the nucleus, positively regulates blue light-induced stomatal opening. Predominantly expressed in guard cells, its expression is substantially down-regulated by dehydration. Microarray and RT-qPCR analysis showed that CYCH; 1 did not regulate the expression of ABA-responsive genes or light-induced stomatal opening signalling determinants such as *MYB*60 and *MYB*61. The down-regulation of CYCH; 1 induces the expression of redox homeostasis genes such as lipoxygenase 3 (*LOX*3), *LOX*4, Arabidopsis glutathione peroxidase 7 (*ATGPX*7), early light-inducible protein 1 (*ELIP*1& *ELIP*2) and also increases the H_2O_2 production in guard cells. Furthermore, the functional mutations in *CDKD*;2 or *CDKD*;3 did not alter the responsiveness to drought stress, which suggests that *CYCH*;1 regulated drought stress responses are *CDKD*-independent [242]. In rice, the expression of transcription factor *SNAC*3-*OE* significantly reduces the H_2O_2, malondialdehyde (MDA), and electrolyte leakage; thus *SNAC*3 mediated stress tolerance is executed by modulating the ROS homeostasis [237]. The overexpression and virus-induced gene silencing (VIGS) of a Raf-like mitogen-activated protein kinase kinase (MAPKKK) (*GhRaf19*) in cotton showed that it negatively contributes to drought and salt stress [235]. *VvNAC17*-OE lines had lower MDA and H_2O_2 contents but higher peroxidase, superoxide dismutase, catalase activities, and higher proline content. Additionally, the upregulation of marker genes; *ABI*5, *AREB*1, *COR*15*A*, *COR*47, *P*5*CS*, *RD*22, and *RD*29*A* in the drought-stressed VvNAC17-OE lines subjected to ABA has been observed [231]. The expression of tonoplast aquaporins (intrinsic proteins, TIPs) encoding gene *TaTIP*4; 1 from wheat in *Arabidopsis* and rice enhanced the water contents and lowered the Na^+ levels, Na^+/K^+ ratio along with upregulation of enzymatic and non-enzymatic anti-oxidative systems in response to drought, salinity and/or osmotic stresses [222]. The investigation of a salt- and drought-sensitive cultivar (Aiswarya) Vyttila, a salt-tolerant (Vyttila), and a drought-tolerant rice cultivar (Vaisakh) showed that tolerant cultivars accumulate lower ROS levels, compared to sensitive plants under drought and salt stress. Furthermore, suppression of cytochrome oxidase (COX) and alternative oxidase (AOX) pathways using antimycin A and salicyl hydroxamic acid indicated that the transcription of the AOX1a in tolerant rice cultivars helped in photosynthesis, lowering of ROS, and developing stress tolerance [247]. The studies also revealed that TFs such as GmNTF2B-1 [226], WUSCHEL-related homeobox gene PagWOX11/12a SbNAC9 [219] induced by polyethylene glycol (PEG) and routinely used to mimic the dehydration responses, promoted the accumulation of chlorophyll, improved the efficiency of PSII and ROS scavenging capability [219]. The overexpression and yeast two-hybrid studies of GmNTF2B-1 belonging to the IV subgroup in the nucleus transporter family showed that it interacts with GmOXR17 to enhance the nuclear entry of GmOXR17 that ultimately contributes to the nuclear ROS scavenging [226].

DREB, representing a subgroup of the AP2/ERF family of transcription factors (TFs), is known for its role during abiotic stress responses of plants. The treatment of plants with PEG, NaCl, and ABA upregulates the expression of *ScDREB2B-1* gene in the root and leaf of the sugarcane variety ROC22. The *ScDREB2B*-1 transgenic line of *N. benthamiana* induces genes related to the ABA pathway and those regulating the intracellular ROS level through catalase, peroxidase, and superoxide dismutase, enhancing relative water, proline content and inducing the genes related to osmotic stress (NbERD and NbLEA) [248]. Another TF belonging to the APETALA2/ethylene-responsive element binding protein (AP2/EREBP) superfamily is essential due to its role in the abiotic stress response. At present, a total of 119 *AP2/EREBP* genes have been identified in *Fragaria vesca*. These were further subdivided into *AP*2 (18), *RAV* (7), *ERF* (61), *DREB* (32), and soloist subfamilies (1). Based on the phylogenetic analysis, the members of the DREB subfamily are further subcategorized into six subgroups (A-1 to A-6). The *FvDREB*6 belonging to the A-2 subgroup is down-regulated in older leaves but upregulated in young leaves during drought stress [249]. A negative regulator TF, bZIP, is linked to environmental stress tolerance. In soybean, the down-regulation of *GmbZIP*15 is suppressed under salt and drought stress, whereas the *GmbZIP*15 overexpressing line of soybean resulted in susceptibility to abiotic stress. The hypersensitive response was associated with both ABA-dependent and ABA-independent pathways, reduced antioxidant activity, and defective stomatal aperture regulation [250]. Besides various genes and TFs, potassium (K^+) is critical in modulating physiological functions through osmotic adjustments, stomatal behavior, membrane transport, photosynthesis, protein synthesis, and various other processes. The K^+ efflux antiporters *KEA*1 and *KEA*2, localized in the inner envelope, are critical in ROS homeostasis. Moreover, the glycolate oxidase, NADPH-dependent superoxide, and non-enzymatic antioxidant system also play essential roles in ROS homeostasis. Furthermore, kea1kea2 mutants exhibit high resilience to drought stress, indicating that the osmotic balance and integrity maintained by *AtKEA*1 and *AtKEA*2 are of critical importance in balancing the ROS/RNS metabolism [227].

4. Role of mycorrhizal association in response to drought and salinity stress adaptations of plants

The microbial diversity in the plant rhizosphere can facilitate plant adaptations in response to environmental stresses. The symbiotic association of fungi covers over 80 per cent of plants belonging to both angiosperms and gymnosperms. The mycorrhizal associations subcategorized as arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), ericoid mycorrhiza (ErM), and orchid mycorrhiza (OrM) subtypes assist the plant adaptations against adverse abiotic and biotic stresses [154, 251]. Different types of mycorrhizal colonization and signalling have been described in detail [252]. The study on the relationship between plant genotype and mycorrhizal richness has shown a higher richness of AMF [253]. The AM association is predominant in warm and dry climates, whereas ECM is in cold and humid climates. Hence, it is likely that AM-associated plants can exhibit better adaptations against water stress compared to ECM or non-mycorrhizal ones [254].

AMF colonization reduces the adverse effects of environmental

stresses through concerted biochemical and physiological mechanisms [255–261,262]. The colonization by the mycorrhiza is determined by the type of exudate produced. For example, the inability to produce xanthophylls in the tangerine tomato variety and reduced ABA levels negatively affect mycorrhizal colonization and root-to-shoot signalling in drought stress [263]. In return, the glomalin produced by AM fungi assists mineral sequestration during adaptations of peanuts to drought. In contrast, the root exudates could contribute to releasing glomalin-bound potassium to supply the K^+ for crops [264]. *Glomus intraradices* and *G. mosseae's* autochthonous strains promote root growth by 35–100 % [265]. The AM treatment of trifoliate orange (*Poncirus trifoliate*) seedlings with *G. versiforme* decreased the MDA concentration in leaves and roots. Also, it lowered the level of H_2O_2 and superoxide anions in roots in water-treated and water-stressed conditions. The lower H_2O_2 and superoxide anions are achieved by boosting the enzymatic and non-enzymatic oxidative machinery in response to drought tolerance [266]. AM also boosts the enzymatic and non-enzymatic oxidative systems in response to drought tolerance [266]. The response of mycorrhiza is found to be species-specific. For example, the treatment with ectomycorrhizal fungi *Descolea antarctica*, *Pisolithus tinctorius*, and *Nothofagus dombeyi* plants showed that the anti-oxidative response resulted in selective cellular damage only for *D. antartica*. The prevention and detoxification of ROS by ectomycorrhizal colonization reduces cellular damage, ultimately improving plant growth [267] (Fig. 3). The combination of mycorrhiza and carbon nanoparticles in the compost provides antioxidant, and osmo-protection to the maize plants [268]. Examples highlighting the role of AMF in regulating the plant genes' responses to symbiosis in crops of economic importance like rice, tomato, grapevine, wheat, and walnut are described in Table 2 [269]. The mycorrhizal colonized plants, in general, exhibit better stomatal conductance, better root hairs and root architecture, and IAA level with a lower root IAA efflux, better water usage and photosynthetic efficiency and capability to mitigate the oxidative burst than non-AM plants [270]; [null]; [269].

The inoculation of *Funneliformis mosseae*, AM fungi in two different maize genotypes, salt-tolerant with large roots (JD52) and salt-sensitive with small roots (FSY1), led to better growth in both genotypes at 100 mM of NaCl concentrations by maintaining the ion balance in the aerial and below-ground tissues. Further, the salt-sensitive with small roots (FSY1), AM differentially regulated the three ion transporter genes, *ZmSOS1*, *ZmHKT1*, and *ZmNHX*, which led to enhanced shoot-to-root translocation of Na^+ ions and also facilitating Na^+/K^+ distribution between shoots and roots. The enhanced shoot-to-root translocation of Na^+ ions was achieved by a comparatively higher rate of Na^+ efflux than K^+ in AM colonized shoots. Conversely, AM colonization in roots led to Na^+ influx rate [201]. Experimental data also indicated that the inoculation of AM fungi, i.e., *Funneliformis mosseae* and *Claroideoglomus etunicatum*, increased the polyphenols at 50–150 mM NaCl and 100 mM NaCl. Here, the alleviation in salinity was achieved via triggering non-enzymatic antioxidant activity by the accumulation of the flavonoid in roots and shoots and phenol in roots of Moldavian balm (*Dracocephalum moldavica*) than non-mycorrhizal plants [293]. The mechanisms of adaptations are manifested through different plant growth regulators. AMF upregulates the expression of IAA biosynthesis genes and downregulates the expression of IAA exporters in roots, leading to the accumulation of IAA, enhanced root hair growth, and subsequent drought resistance [175, 270] (Fig. 3). A species-specific behavior of mycorrhizal colonization has been observed. For example, the treatment with ectomycorrhizal fungi *Descolea antartica*, *Pisolithus tinctorius*, and *Nothofagus dombeyi* showed that the anti-oxidative response resulted in selective cellular damage only in *D. antartica*. Ectomycorrhizal-treated *N. dombeyi* plants resulted in lower oxidative stress, whereas the interaction between non-specific *P. tinctorius* and *N. dombeyi* helped metabolize the ROS. Thus, the prevention and detoxification of ROS by ectomycorrhizal colonization reduces cellular damage, ultimately improving plant growth [267].

Table 2
Applications of mycorrhiza in plant adaptation to drought and salt stresses.

S. No.	Host	Fungi	Role of mycorrhiza in plant adaptations	References
1.	False wheatgrass or Chinese rye grass	nd	Mycorrhizae improve the osmotic regulation ability and ionic balance of the seedlings that could alleviate the growth inhibition of seedlings under alkali or drought stress	[222]
2.	Lingonberry	*Oidiodendron maius* FC or *Lachnum pygmaeum* ZL6	Significantly increases biomass of lingonberry stems, roots and chlorophyll content. In addition, inoculation with *Lp*ZL6 fungi can improve drought resistance, promote root growth and increase root wet weight.	[271]
3.	Soybean	AMF $_{nd}$	The combination of biochar and AMF enhance growth, root parameters in soybean and soil enzyme activities, and water stress tolerance.	[272]
4.	*Populus simonii* × *P. nigra*	*Rhizophagus irregularis*	Mycorrhiza downregulate the expression of PsnMAPK7-2, PsnMAPK16-1, PsnMAPK19-2, and PsnMAPK20-2 which negatively regulate drought tolerance and induced specific PsnMAPKs in roots which through a cascade of events enhance drought tolerance.	[273]
5.	*Populus cathayan*	*R. intraradices*	AMF induce the expression *PcGRF10* and *PcGRF11* help in drought tolerance through antioxidant and osmotic regulation	[274]
6.	Soybean	*R. clarus*	AMF permit the plant to reduce the impairment of growth and physiological traits caused by drought.	[275]
7.	Walnut	*Diversispora spurce*	Induce low oxidative burst in drought-stressed walnut through activating antioxidant defense systems and *Hsfs* expressions.	[269]
8.	Angiosperms and gymnosperms	*Cenococcum geophilum*	Drought-sensitive strains regulate osmotic pressure by absorbing Na^+ and	[276]

(*continued on next page*)

Table 2 (*continued*)

S. No.	Host	Fungi	Role of mycorrhiza in plant adaptations	References
			K^+ ions. Also up-regulate the genes related to the peroxisome pathway which are associated to antioxidant activity during drought. On the other side, the drought-tolerant strains up-regulate the genes related to the ubiquinone and other terpenoid-quinone biosynthesis and sphingolipid metabolism pathways	
9.	Wheat	R. irregular, Funneliformis mosseae, F. caledonium	Enhance the carbon to nitrogen ratio without affecting the P.	[277]
10.	Maize	R. irregularis	The combination of compost, mycorrhiza and carbon nanoparticles promote the mitigation of drought resistance by increasing the levels of oxalic and succinic acids, antioxidant and osmo-protectant proline and fatty acids.	[268]
11.	Velvet leaf blueberry	ERM fungi (*Pezicula ericae*, *Pezoloma ericae*, *Meliniomyces variabilis*, and *Oidiodendron maius*)	*Pezicula ericae* colonization significantly improve the drought tolerance in upland and lowland seedlings by enhancing the shoot water potential, rate of photosynthesis, and transpiration rates against drought stress.	[278]
12.	Peanut	*Gigaspora margarita*	The production of K-sequestering glomalin by AM fungal hyphae help in sequestering multiple minerals such as K- that significantly enhance the plant growth whereas the root exudates could prime the release of glomalin-bound K.	[264]
13.	Trifoliate orange	*Funneliformis mosseae*	The AM application increases H^+-ATPase activity of leaf and root, stimulates H^+-ATPase activity as well as the expression of *PtAHA2* gene expression resulted in nutrients acquisition and root growth against drought stress.	[279]
14.	Soybean	*Acaulospora laevis*, *Septoglomus deserticola*, and *R. irregularis*	AM treatment decreases ABA level and increases the gibberellin, *trans*-zeatin-riboside, and IAA alongwith strengthening of the antioxidant and osmoprotectants machinery.	[280]
15.	Wheat	G. mosseae, G. intraradices, G. etunicatum, and Scutellospora dipurpurescens	AM application promotes morphological and physiological parameters by alleviating water deficit induce oxidative stress against drought stress.	[281]
16.	Soybean	G. clarum, G. mosseae, and Gigaspora margarita and Bradyrhizobium	AM and *B. japonicum* treatment increases the yield and growth of drought stressed soybean at early pod stage (50 days from sowing) and seed development stage.	[282]
17.	Wheat	Rhizoglomus irregulare	AMF can improve the harvest index of wheat under different drought and reduced aphid pests in AM colonised plants.	[257]
18.	African cherry	Scutellospora sp. Gigaspora sp., Acaulospora sp., Sclerocystis sp. Entrophospora sp., Glomus sp.	AMF promote seedling heights, root colonization, leaf formation and higher tannin content.	[283]
19.	Oak	*Pisolithus tinctorius*	ERM mediated drought tolerance is likely contribute to leaf membrane lipid metabolism that include accumulation of chloroplast lipid and unsaturated fatty acids.	[284]
20.	Citrus	*F. mosseae*	AM treatment increases higher unsaturation index by changing the composition and unsaturation of FAs such as root methyl oleate (C18:1), methyl linoleate (C18:2) and methyl linolenate (C18:3N3) concentrations under both WW and DS conditions, and root methyl palmitoleate (C16:1) concentrations under WW, while it	[285]

(*continued on next page*)

Table 2 (*continued*)

S. No.	Host	Fungi	Role of mycorrhiza in plant adaptations	References
			decreased root methyl stearate (C18:0) levels under well-watered as well as drought which that help in reducing the oxidative damage by lower concentration of MDA and superoxide radicals.	
21.	Damask rose	–	AMF colonization can enhance growth and adaptation of rose plants in response to drought stress.	[286]
22.	Trifoliate orange	*F.s mosseae*	AMF-stimulate greater root-hair growth under drought which is independent on AMF species and is related to mycorrhiza-modulated auxin synthesis and transport that facilitates the host plant adaptations to enhance drought tolerance.	[270]
23.	Liquorice	*R. irregularis*	Stimulate the accumulation of the active ingredients, glycyrrhizin and liquiritin. Further, the effects are more pronounced under moderate drought stress.	[287]
24.	Cowpea	*G. deserticola* and *Gigaspora gigantea*	The exposure to mycorrhiza enhance the drought tolerance against charcoal rot disease.	[288]
25.	Tomato	*F. mosseae, R. intraradices*	AM symbiosis positively affects the tolerance to drought.	[289]
26.	Trifoliate orange	*F. mosseae*	Induced lower oxidative burst which is related to accumulation of antioxidant enzyme activities, root net H_2O_2 effluxes, and Ca^{2+} influxes under well-watered and drought stressed plants.	[290]
27.	Pistacia vera	*G. etunicatum*	AM colonization promotes the accumulation of osmotic adjustment compounds, nutritional and antioxidant enzyme activity that help in plant adaptations.	[291]
28.	Leymus mollis	Fungal endophytes	Abiotic stress tolerance either decreases water consumption or reactive oxygen sensitivity/ generation but do not to increase osmolytes production.	[292]

The metabolome analysis of trifoliate orange inoculated with *Rhizophagus intraradices* revealed that out of 643 metabolites, 210 and 105 are differentially regulated by association in normal water and drought stress in roots, whereas 88 and 17 metabolites were up and down-regulated in response to drought, respectively [294]. The colonization of trifoliate orange plants by *Funneliformis mosseae* has been reported for modulating the composition and unsaturation of fatty acids that helped plant adaptations to drought stress. Mycorrhizal colonized seedlings exhibited better plant growth performance, higher leaf water potential, and lower root ABA concentrations under well-watered and drought-stressed plants. Arbuscular mycorrhiza fungus inoculation significantly increases the root methyl oleate (C18:1), methyl linoleate (C18:2), and methyl linoleate (C18:3N3) concentrations under both water stressed as well as drought. At the same time, it decreased root methyl stearate (C18:0) levels under both well water and water stress conditions [285]. Similarly, the improved tolerance of ectomycorrhizal colonized oak plants against drought could be related to changes in leaf membrane lipid metabolism and fatty acids composition. The mycorrhiza colonized plants accumulate unsaturated fatty acids in the chloroplast in response to drought stress. The higher digalactosyldiacyloglycerol (DGDG)/monogalactosyldiacyloglycerol (MGDG) ratio in the non-mycorrhizal plants could enhance the plant adaptations to drought stress [284].

The molecular dissection revealed the dual role of 14-3-3 proteins encoding genes in drought tolerance and the regulation of AMF [274]. The rhythmic expression of circadian clock genes *PtPRR*7, *PtLHY*, *PtCCA*1, *PtGI*, *PtPIF*3, and *PtSRR*1 in trifoliate orange colonized by *Funneliformis mosseae* has shown that symbiosis affects the gene expression [295]. The AMF colonization of walnut plants differentially upregulates *JrHsf*03, *JrHsf*05, *JrHsf*20, *JrHsf*22*and JrHsf*24 both in the presence of water and shortage, whereas the expression of *JrHsf*03, *JrHsf*22, and *JrHsf*24 is exclusively upregulated under drought [269]. The AM symbiosis with maize changes the expression of plant aquaporins and hormone-related genes in response to drought stress. The AM induces the post-transcriptional changes in these aquaporin expressions that alter the radial water transport in host plants. In contrast, regulating IAA, SA, ABA, and JA levels may assist the plant-AM fungus interaction through feedback [296]. *Funneliformis mosseae* modulate IAA levels through the constitutive upregulation of IAA biosynthesis genes *PtYUC*3 and *PtYUC*8 of trifoliate orange in water and drought stress conditions [270]. The mycorrhiza induces the expression of *PtAHA*2 (MW239123), a plasma membrane H^+-ATPase gene, which induces drought tolerance in trifoliate orange. The AMF colonization by *Acaulospora laevis*, *Rhizophagus irregularis*, and *Septoglomus deserticola* regulates the ABA level and enhances the GA, IAA, and *trans*-zeatin-riboside in the soybean [297]. In walnuts, the AMF exposure promoted the accumulation of soluble protein and an anti-oxidative system in drought-stressed plants compared to non-inoculated ones [269]. Besides this, AMF colonization also provides osmoprotection, assists in nutrients and water acquisition, maintains ionic homeostasis, and preserves the cell's ultrastructure. The AMF-induced nutrients and water acquisition is achieved by the production of the EPS layer, whereas the ability to modulate the osmolytes and regulate the expression of the aquaporin present on the plasma membrane and tonoplast help in maintaining the high K^+/Na^+ ratio and suppressing the transport of toxic Na^+, which improves the water status of the plants [44].

In a nutshell, the mycorrhizal association improves carbon usage, osmotic status reduces the damage to the photosystem (PS) structures such as PSII and PSI, enhances water holding and water acquisition, photosynthesis, and stomatal conductance, and facilitates the selective exchange of ions in plants during drought and salt stress. Overall, some of the AMF responses share similarities, whereas others are exclusive, and the magnitude of the effect varies with the fungal species.

5. Conclusions and future perspectives

Feeding the continuously growing human population is one of the significant challenges of the present century. Water scarcity due to drought and salinity further limits and exacerbates our goal to enhance food production for the increasing world population. Consistent efforts are needed to promote plant growth against abiotic stressors to feed humans and livestock. Plants have evolved various adaptive mechanisms at different levels to counter environmental stresses. These adaptations include the upregulation of several stress-related mechanisms associated with signalling, defence enzymes, transcription factors, and others that help plants adapt and tolerate extreme conditions. Consistent efforts have been made to unravel different mechanisms of plants involved in plant adaptations to various stresses. Various biotechnological and advanced molecular breeding approaches have investigated genes/transcripts responsible for desired traits. Exploration of plant-beneficial microbes for modulating plant responses has received the attention of several researchers worldwide. Several independent studies have unraveled the role of different plant-beneficial microorganisms, such as mycorrhiza, in alleviating plant stresses. Mycorrhiza-induced plant adaptations' detailed mechanisms and components are now well established. However, transferring this knowledge from the laboratory to field production remains a significant challenge. Microbiome engineering aims to manipulate the microbiome toward a specific type of community that will optimize plant functions to meet crop production demands. A better understanding of the network dynamics of these interactions needs to be explored before crop implementation. Furthermore, the high throughput methods for phenotyping the plants to abiotic stresses and the role of beneficial microbes demand an active area of inquiry.

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