Review

Approaches for the amelioration of adverse effects of drought stress on crop plants

Anamika Dubey[1], Ashwani Kumar[1,2,*], Muneer Ahmad Malla[1,3], Kanika Chowdhary[4], Garima Singh[4], Gudasalamani Ravikanth[5], Harish[6], Satyawati Sharma[4], Zaki Saati-Santamaria[7], Esther Menéndez[7], Joanna Felicity Dames[2,*]

[1]Metagenomics and Secretomics Research Laboratory, Department of Botany, Dr. Harisingh Gour University (A Central University), 470003 Sagar, Madhya Pradesh, India, [2]Mycorrhizal Research Laboratory, Department of Biochemistry and Microbiology, Rhodes University, 6140 Grahamstown (Makhanda), South Africa, [3]Department of Zoology, Dr. Harisingh Gour University (A Central University), 470003 Sagar, Madhya Pradesh, India, [4]Centre for Rural Development and Technology, Indian Institute of Technology Delhi, 110016 Hauz Khas, New Delhi, India, [5]Ashoka Trust for Research in Ecology and the Environment, 560064 Bangalore, Karnataka, India, [6]Department of Botany, Mohanlal Sukhadia University, 313001 Udaipur, Rajasthan, India, [7]Microbiology and Genetics Department/CIALE, University of Salamanca, 37007 Salamanca, Spain

TABLE OF CONTENTS

1. Abstract

Climate change, water scarcity, population growth, and food shortage are some of the threatening challenges being faced in today's world. Among different types of stresses, drought stress presents a persistent challenge for global food production, however, its harshness and intensity are supposed to expand in the imminent future. The most striking effects of drought stress on plants are stunted growth, severe damage to photosynthetic apparatus, reduction in photosynthesis, reduction in seed germination, and nutrient uptake. To deal with the destructive effect of drought stress on plants, it is necessary to consider its effects, mechanisms of action, the agronomic and genetic basis for sustainable management. Therefore, there is an urgent need for sustainable solutions to cope up with the negative impact of drought stress. This review focuses on the detrimental effects of drought stress on plants' morphological, physiological, and biochemical characteristics and recommends suitable drought management techniques to reduce the severity of drought stress. We summarize the effect of drought stress on physiological and biochemical parameters (such as germination, photosynthesis, biomass, water status, and nutrient uptake) and yield. Overall, in this article, we have reviewed the role of different phytohormones, osmolytes,

exogenous compounds, proteins, plant growth-promoting microbes (PGPM), omics approaches, and genome editing technologies like clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein 9 (CRISPR-Cas9) in alleviating drought effects in plants. We also proposed that developing drought-tolerant plant varieties requires the combined use of biotechnological and agronomic approaches and cutting-edge genome editing (GE) tools.

2. Introduction

Several driving forces are reshaping global food security, including population growth, drastic climate changes, water supplies, arable land availability, food availability, and biodiversity losses [1, 2]. The plants are continually exposed to a wide range of climatic perturbations, leading to different types of abiotic stress conditions like drought, salinity, flooding, heat, cold, heavy metals contamination, and biotic stress conditions [3, 4]. Among these factors, drought stress has become the most important and the key limiting factor that negatively affects crop productivity and eventually compromises food security [5]. Drought not only causes significant losses in agricultural productivity but it also causes desertification, soil erosion, and ecological degradation. As a result, the water shortage has been identified as a critical global and environmental issue [6]. These stress conditions contribute to significant physiological, metabolic, and molecular changes in plants, causing a reduction in agricultural production [7]. Researchers have made significant progress in elucidating the genetic, biochemical, and signalling pathways involved in plant drought responses in recent years with the help of modern technology (such as molecular genetics, genomics, transcriptomics, metabolomics, and proteomics) [3, 6]. However, the complex processes that distinguish resistance from a vulnerability within a species, particularly in crops, are still completely unknown [6]. Drought stress affects several morpho-biochemical parameters, such as leaf area reduction, reduction in total chlorophyll content, wilting of leaf, elongation of the root, and production of reactive oxygen species (ROS) [4, 8, 9]. Plants generally absorb water from the soil effectively through their root system, partially shut their stomata to decrease water loss from transpiration, and change their metabolism to match the present carbon supply in the early stages of drought stress conditions [6, 10]. Under stress conditions, some osmolytes, including prolines, glycine betaine, soluble sugars, and spermine, accumulate inside plant cells to maintain cell osmotic potential [11]. Drought-stressed plants are also reported with alterations in the activity of many oxidation-protective enzymes such as catalase (CAT), superoxide dismutase (SOD), glutathione reductase (GR), and ascorbate peroxidase (APX) [12]. However, drought stress causes changes in the expression of many genes, including those associated with stress signal transduction, as well as the transcription and regulation of hundreds of functional proteins, all of which contribute to the genetic regulation of drought tolerance [13].

Thus, sustainable agro-biotechnology needs to be designed to combat abiotic stress for maintaining or increasing crop production worldwide. Several strategies have been implemented around the globe to improve drought tolerance in crops, i.e., by using genetic engineering and traditional plant breeding methods [14, 15]. Since drought stress tolerance is a multigenic and complex trait, creating transgenic drought-resistant crop varieties is a tedious job [16]. To embark on this, applying drought-tolerant bio-inoculants or plant growth-promoting rhizobacteria (PGPR) is an alternative strategy for sustainable agriculture under water deficit conditions. Many studies conducted by different researchers support the fact that PGPRs can help plants to withstand abiotic stresses by altering the responses at the gene level [17, 18]. PGPRs have great potential for amending physiological responses to water scarcity, thereby enhancing plant endurance under drought stress conditions [8, 19]. Various reports are available that demonstrates the role of PGPRs in extenuating drought stress in many crops, such as tomato, pepper, pea, maize, wheat, mung bean, and chickpea [8, 16, 20–24].

Interdisciplinary strategies are required to harness the full potential of microbes in agriculture production systems. Through advancements in computational tools, the data-driven science of multi-omics has enhanced our understanding of microbial community structure, dynamics, and composition along with their functional attributions in many complexes and diverse environments like the rhizosphere, where the community level microbial interactions direct the plant responses toward various stresses [25–27]. However, optimizing plant-microbial partnerships for improving drought tolerance in crop plants is a daunting task given the complexity of plant-microbe and microbe-microbe interactions and the dependence on environmental conditions. This review highlights different management strategies for improving drought stress tolerance in different crop plants that can be achieved by developing drought-tolerant plant genotypes, seed treatments, genetic modifications, application of plant growth microbes, plant mineral nutrients, and the use of compatible solutes.

3. Adverse impacts of drought stress on plants growth and health

Drought is a meteorological term that signifies a period with no rain, which leads to a significant reduction in soil and atmospheric humidity and elevation in ambient air temperature [28, 29]. This situation arises due to an imbalance between the water intake and evapotranspiration flux from the soil [28]. Drought stress has a direct and indirect effect on plant health. The low availability of water
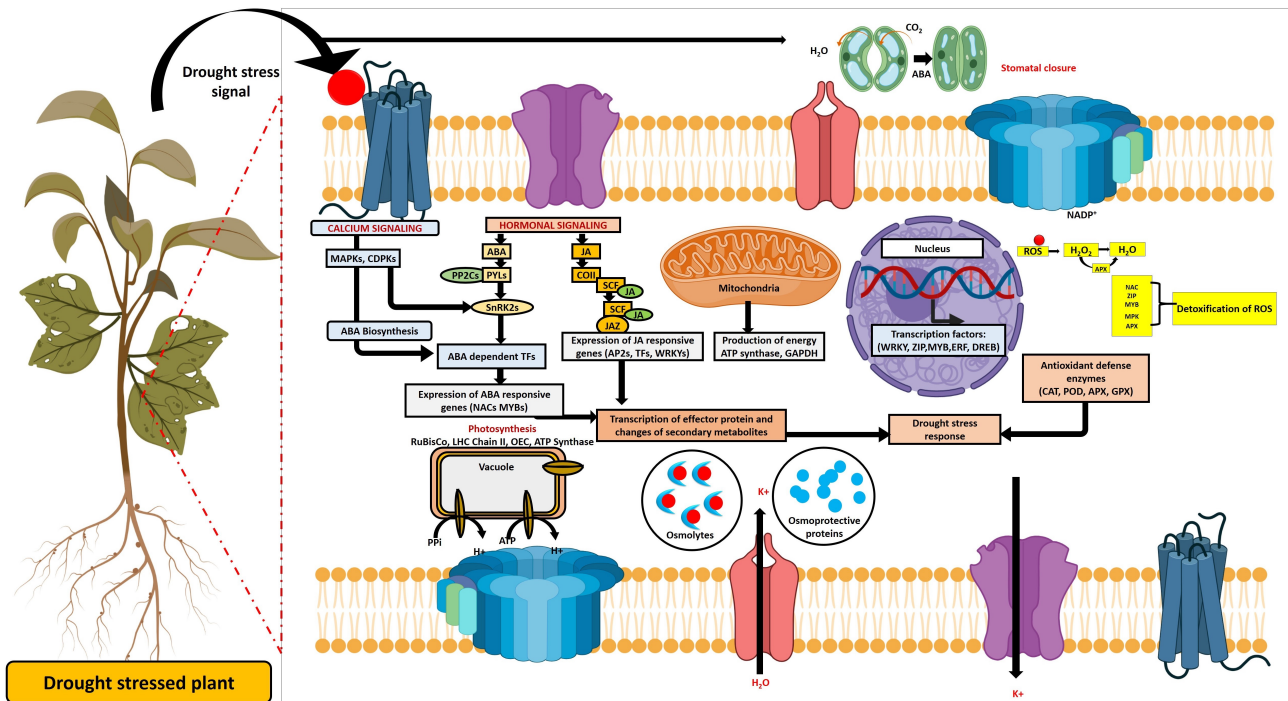
Fig. 1. Graphic representation of the mechanism of drought stress tolerance in plants. Abbreviations: ABA, Abscisic acid; APX, ascorbate peroxidase; CAT, catalase; GPX, guaiacol peroxidase; GST, glutathione-s-transferase; JA, Jasmonic Acid; MAPK, mitogen-activated protein kinase; POD, peroxidase; ROS, Reactive Oxygen Species; SOD, superoxide dismutase; TFs, Transcription Factors.

in roots and the great loss of liquid through transpiration affect the osmotic and ionic balance of plant cells, which leads to phenological changes in the plant [30]. It also affects crop development in different ways by reducing the rate of seed germination, which affects crop performance; similarly, the photosynthetic process is repressed, and the absorption capacity of nutrients is reduced, which facilitates the risk of infestation by pests [31, 32]. Drought is major abiotic stress, altering morphological, biochemical, physiological, and molecular responses by regulating protein functions and stress-induced genes [3, 7]. The study conducted by Kanwal *et al.* [33] reported drought stress adversely affects the morphology, biochemistry, and physiology of the wheat plant. Under drought conditions, cell elongation can be prevented by interrupting water passage from the xylem to the surrounding elongating cells [34]. Drought often reduces leaf area, plant height, and crop development due to impaired mitosis, cell expansion, and elongation [34, 35]. A notable impact of drought is the decrease in photosynthesis due to a decline in leaf development, and early leaf senescence decreased photosynthesis and the related loss in food production. Published research displayed that during drought stress conditions, all the vital processes such as net photosynthesis, biosynthesis of photosynthetic pigments, electron transport rates, the quantum yield of photosystem II (PSII), protein synthesis, lipid, and energy metabolism are generally ceased [36]. Drought impairs plant growth by disturbing the water balance, membrane permeability, mineral nutrition, and enzyme activity of the plant [3, 7].

Indirect effects of drought stress increase reactive oxygen species (ROS) production, resulting in oxidative damage to macromolecules [37]. The study revealed that the abscisic acid (ABA) accumulation in plants during drought stress conditions helps in the regulation of signal transduction pathway by phosphorylation/dephosphorylation and controls the transportation of K^+ and anion in the guard cells [38] (Fig. 1). In response to drought stress, plants acclimatize several physico-biochemical changes in their morphology, osmotic potential, growth rate, and enhancement in defense mechanisms [36]. Many studies have documented the negative consequences of ROS, which are produced in response to water deficiency [39–41]. ROS generation often leads to lipid peroxidation, and subsequently membrane damage, enzyme inactivation, as well as degeneration of structural and functional proteins. The study conducted by Kadioglu *et al.* [39] and Saruhan *et al.* [40] reported that H_2O_2, O_2^-, and MDA increased significantly in *Ctenanthe setose* when exposed to drought stress. Moreover, Kubiś *et al.* [42] reported that water deficiency in cucumber cells leads to membrane injury, increase in lipid peroxidation, and lipoxygenase activity. Oxidative stress may cause oxidation of protein, with a loss of enzyme activity and the generation of protease-resistant cross-linked aggregates. The study conducted by Gharibi *et al.* [43] reported the effect of drought stress on lipid peroxidation, total phenolic content, and antioxidant activity of *Achillea* species. Therefore, plants often

adopt numerous strategies to alleviate ROS-mediated injuries, like producing low molecular weight enzymatic and non-enzymatic antioxidants. The enzymatic antioxidants include catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), and glutathione-s-transferase (GST), which directly detoxify ROS [44]. Non-enzymatic antioxidants like α-tocopherol, glutathione (GSH), ascorbate (ASC), flavonoids, and carotenoids detoxify ROS. Furthermore, some other enzymes like monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR), act in the ascorbate–glutathione cycle for quenching of toxic derivatives of oxygen [44, 45] (Fig. 1).

4. Different strategies to mitigate the adverse effects of drought stress

Different studies have revealed strategies to cope with drought stress, such as (i) plant breeding and marker assistant selection [46]; (ii) improving osmotic adjustment by application of exogenously applied compounds and osmolytes like glycine, betaine, proline, or other amino acids, and polyols (sorbitol, pinitol, myo-inositol, and mannitol, among others) [47]; (iii) solicitation of plant hormones (salicylic acid, auxins, gibberellins, cytokinins, brassinosteroids, jasmonic acid, and ABA) [48, 49]; (iv) enhancing antioxidant function such as glutathione, polyamines, ascorbate, and enzymes (SOD, CAT, APX, GR, etc.) [50]; (v) generating transgenics for drought tolerance in plants and [51]; (vi) applying drought-tolerant microbes [52, 53]. Some of the strategies are discussed in the next section in detail.

4.1 Role of phytohormones

Phytohormones are recognized to have a key role in controlling various plant responses to varied drought conditions. Additionally, salicylic acid (SA), jasmonic acid (JA), auxin (indole-3-acetic acid, IAA), ethylene (ET), cytokinins (CKs), brassinosteroids (BRs), and gibberellins (GAs) are essential plant hormones to encounter drought stress [54]. Auxins are a class of phytohormones that play an essential role in plant growth, development, and stress response [55]. Auxin production occurs mainly in leaf primordia, young leaves, developing seeds, and its biosynthesis route is mainly conserved among plants. These are delivered from the site of synthesis to the target by phloem or cell-to-cell transfer [11]. Several studies conducted by different researchers have found a positive role of auxin in developing drought tolerance. In research, Aux/IAA genes were discovered in rice, and some genes were triggered by drought stress [56].

Furthermore, one of these genes, OsIAA6, has been linked to drought stress [56]. Another study conducted by Ke *et al*. [57] and Kim *et al*. [35] in poplar

and potato, wherein *YUC6* gene was overexpressed, resulting in auxin overproduction phenotypes and improved drought tolerance. They proposed that the functioning of the *YUCCA6* gene in the auxin production pathway in potatoes might be used to manipulate plant responses to the environment [35, 57]. Auxin also increased the ramification of roots that might be critical for improving drought tolerance [58].

Cytokinins (CKs) are among the major phytohormones needed to control plant growth, development, and adaptation to environmental stressors, like drought stress [59]. Several studies reported CKs to have both beneficial and negative impacts on drought tolerance [59–62]. CK levels can also increase or decrease according to the duration and intensity of the drought. CK levels were increased endogenously in transgenic plants expressing an isopentenyl transferase gene. Drought tolerance was improved in the transgenic plants by delaying senescence and suppressing drought-induced leaf senescence. However, some studies reported that CK has a detrimental influence on drought tolerance [63]. The CK oxidase/dehydrogenase (CKX) system is well-known for the breakdown of CKs, and overexpression of CKX in *Arabidopsis* often results in the decreased endogenous CK level [63, 64]. The role of CK in drought stress and its signalling route are yet unknown.

Gibberellins (GAs) are tetracyclic diterpenoid carboxylic acids that act as growth hormones and respond to biotic and abiotic stressors. Various studies have demonstrated that the exogenous application of GA improves drought tolerance in maize [65], soybean [49], wheat [66, 67]. The study conducted by Moumita *et al*. [66] reported foliar application of Gibberellic acid stimulated glyoxalase I (Gly I) and glyoxalase II (Gly II) activity for protecting the wheat seedlings against drought stress. The combined application of GA & ABA improves stress tolerance, scavenging of ROS, and carbon-nitrogen balance in Tobacco [68].

Ethylene (ET) is a natural gaseous hormone with several activities, including fruit maturation, growth, senescence, germination of seeds, flowering, and reaction to different stimuli [69]. ET plays an active role in drought stress tolerance in plants; for example, the study conducted by Scarpecit *et al*. [70] reported that the overexpression of AtERF019 had delayed growth and senescence of plants improved *Arabidopsis'* drought tolerance. In another study conducted by the overexpression of ERF (ethylene response factor), soybean gene GmERF3 exhibited higher drought tolerance in tobacco due to higher osmolyte content than wild-type plants [71].

Different drought-responsive metabolites produced by microbes act as precursors of plant hormones, such as phenylalanine, which is a precursor for the biosynthesis of salicylic acid (SA), and another drought stress-responsive secondary metabolites [72]. For example, in the initial phases of drought, the oak tree produces secondary metabolites that play a significant role in rhizo-

sphere signalling whereas primary metabolites are produced during recovery [73]. Abscisic acid (ABA) is a strongly induced phytohormone generated in response to drought signals. ABA is generated in the roots of plants and subsequently transported to the leaves to regulate stomatal aperture, expression of ABA-responsive genes, and channel activity [73]. ABA also maintains water status in the plant by guard cell regulation and induction of genes coding for enzymes and protein associated with dehydration tolerance. By regulating stomata, guard cells respond to ABA and decrease water loss. Various membrane receptors like G-protein perceive the environmental stress signals coupled receptors (GPCRs), receptor-like kinases (RLKs), ion channels, and histidine kinases, which brings changes in the cytoplasmic Ca^{2+} levels and produces secondary messengers like reactive oxygen species (ROS), inositol phosphates (IP), abscisic acid (ABA), etc. These secondary signaling molecules initiate the phosphorylation of protein cascade by various kinases like protein kinases like CBL-interacting protein kinases (CIPKs), protein phosphatases, and calcium-dependent protein kinases (CDPKs). They activate different transcription factors like DREB/CBF, bZIP, MYC/MYB, WRKY, AREB/ABF, etc., through events of phosphorylation and de-phosphorylation. These transcription factors lead to the activation of various stress-responsive genes, which include the expression of genes that encode for late embryogenesis abundant protein (LEA), lipid transfer protein (LTPs), heat shock proteins (HSPs), ion transporters, osmolytes, and antioxidants. Finally, resistance against stresses is produced, and the damages are repaired [3, 74]. Therefore, the stress tolerance in plants is primarily induced by the generation of free radicals like ROS, production of anti-stress metabolites via. expression of stress-responsive genes [75, 76]. It was believed that ABA could induce sugar accumulation as a principal mechanism of drought stress tolerance in liverworts, which are ancestors to terrestrial plants and also specify extremely conserved drought response pathways [77]. In addition to ABA, Salicylic acid (SA) and Jasmonic acid (JA) also play an essential role in the drought stress response. JA is another plant hormone derivative of α-linolenic acid. The active derivatives of JA, known as jasmonates, play an important role in controlling plant stress responses to biotic and abiotic stressors. Jasmonates are generated in flowers and triggered in other tissues as a defensive reaction. Plants' responses to drought stress have also been reported to be improved by exogenous JA stimulation. Exogenous administration of JA enhanced antioxidant activity in wheat [78], *Cucumis melo* [79], and barley [80] under drought stress. Therefore, the study conducted by Shan *et al.* [78] reported JA significantly enhanced ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) under drought stress in wheat seedlings.

Moreover, genes responsible for jasmonic acid (JA) and salicylic acid (SA) are down-regulated during drought in sweet sorghum [81]. Salicylic acid is a potential non-enzymatic antioxidant that plays a crucial role in eliminating ROS injury. Exogenously applied SA increases SOD, APX, POD, and CAT activities in stressed plants [39]. Salicylic acid-associated exudation signals are involved in systemic resistance and the host plant-mediated selection of microbes in the rhizosphere [81]. The study conducted by Hayat *et al.* [82] and Khan *et al.* [83] reported that the drought stress tolerance is stimulated when treated with a low concentration of SA and resulted in improved photosynthetic parameters, chlorophyll content, leaf water potential, relative water content (RWC), membrane stability index (MSI), carbonic anhydrase (CA), and nitrate reductase (NR) activity. The combined application of PGPR and SA enhances the phytoremediation and drought tolerance potential of Sunflower (*Helianthus annus*) [83].

Methyl Jasmonate (MeJA) is a volatile derivative, a methyl ester of jasmonic acid (JA) and it is used as plant growth regulator. The study conducted by Anjum *et al.* [84] investigated the role of MeJA in enhancing drought stress tolerance in five different wheat cultivators and found that MeJA effectively mitigates the detrimental effects of drought stress. Glutathione plays a diverse role in physiological functions for removing harmful ROS and metal detoxification in stressed plants. Combined seed and foliar application of Methyl jasmonate (20 μM) + salicylic acid (2 mM) prevented drought-induced oxidative stress by modulating ABA and osmolytes level and antioxidant enzymes activity [85].

Brassinosteroids (BRs) modulate plant growth and development, including cell division and elongation, senescence, photomorphogenesis, vascular differentiation, and response to abiotic and biotic stresses [86]. BRs interact significantly with GA to regulate plant development. Previous studies displayed a positive role of BRs for alleviating the negative effect of drought stress in *Brassica napus*, *Arabidopsis*, and rice [87–89].

4.2 Role of exogenously applied compounds in drought stress alleviation in plants

To address global challenges in agriculture, the studies should be focused on improving the germplasm, exogenous application of hormones, and developing crop management practices to increase water use efficiency [84, 90]. ROS are valuable messengers, leading stressed plants to oxidative signaling, systemic acquired acclimation (SAA), and systemic acquired resistance (SAR). Oxidative signaling initiates a cascade of defense mechanisms and growth regulation under stress. ROS (superoxide and H_2O_2)-scavenging enzymes of plants are localized in different plant cells and function collectively. Usually, SOD acts as the first line of defense in the conversion of O_2^- to H_2O_2 [44]. Carotenoids, ascorbic acid, glu-

933

GROUPS OF OSMOPROTECTANTS

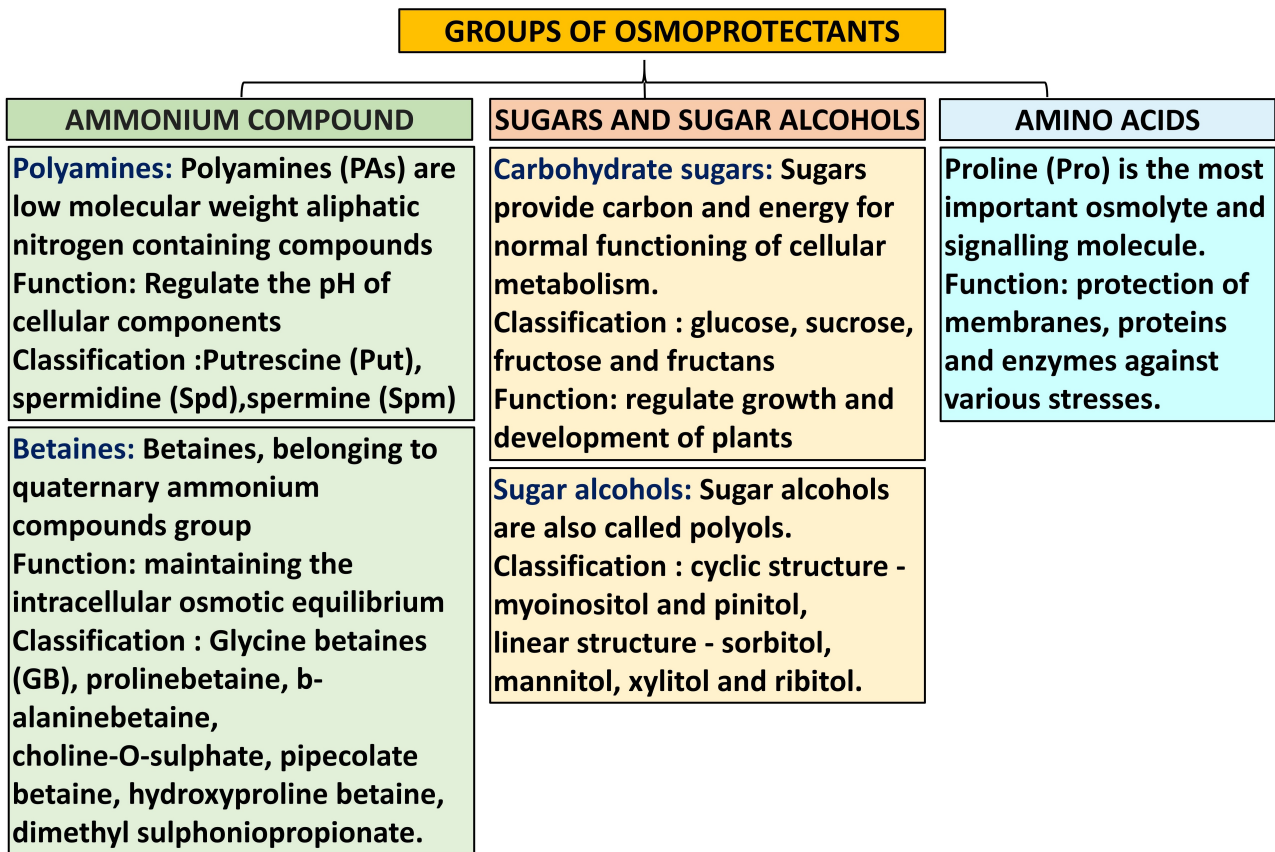| AMMONIUM COMPOUND	SUGARS AND SUGAR ALCOHOLS	AMINO ACIDS
Polyamines: Polyamines (PAs) are low molecular weight aliphatic nitrogen containing compounds **Function:** Regulate the pH of cellular components **Classification :**Putrescine (Put), spermidine (Spd),spermine (Spm)	**Carbohydrate sugars:** Sugars provide carbon and energy for normal functioning of cellular metabolism. **Classification :** glucose, sucrose, fructose and fructans **Function:** regulate growth and development of plants	**Proline (Pro)** is the most important osmolyte and signalling molecule. **Function:** protection of membranes, proteins and enzymes against various stresses.
Betaines: Betaines, belonging to quaternary ammonium compounds group **Function:** maintaining the intracellular osmotic equilibrium **Classification :** Glycine betaines (GB), prolinebetaine, b-alaninebetaine, choline-O-sulphate, pipecolate betaine, hydroxyproline betaine, dimethyl sulphoniopropionate.	**Sugar alcohols:** Sugar alcohols are also called polyols. **Classification :** cyclic structure - myoinositol and pinitol, linear structure - sorbitol, mannitol, xylitol and ribitol.	

Fig. 2. Classification of different osmolytes/osmoprotectants.

tathione, phenolics, and flavonoids are non-enzymatic antioxidants required for balancing ROS homeostasis in plants [44, 91]. The exogenous compounds alleviate stress damages by controlling and balancing ion homeostasis and oxidative machinery [92]. Glutathione plays a coordinated role in methylglyoxal detoxification, and antioxidant enzyme formation in mung bean plants under drought stress [93]. Similar study conducted by Sohag *et al.* [94] reported glutathione mediated drought stress tolerance is associated with favorable ionic homeostasis, and lower oxidative damage in in rice (*Oryza sativa* L.). Exogenous application of H_2O_2 improved drought stress tolerance in cucumber plants by activating an antioxidative defense system in plants [95]. Silicon (Si) is a beneficial element that mitigates the adverse effects of drought stress. Si-fortified fertilizers are gaining interest in recent days about their multiple roles, i.e., enhancing plant growth, photosynthetic machinery, and maintaining cellular ion homeostasis under stressed conditions [96]. Numerous putative silicon transporters have been identified in monocot and dicot plants [97]. The study conducted by Moradtalab *et al.* [98] reported combined application of Si and Arbuscular mycorrhizal fungi (AMF) enhanced strawberry plant biomass by increasing water content, water use efficiency, antioxidant enzyme activity, photosynthesis rate, and the nutritional status of mainly Zinc. Exogeneous application of Silicon

alleviates oxidative damage caused due to drought stress by increasing antioxidant enzyme activity in *Brassica napus* L. [99] and wheat plants [96]. Application of Selenium (Se) can result in the accumulation of solutes in the plants grown under water scarcity, thus decreasing the oxidative stress in plants. Furthermore, Se application can augment plant growth, increase the production of antioxidants due to senescence, and regulate the plants' water balance to tolerate drought stress [100].

Osmoprotectants are generally known as osmolytes due to their cellular defensive functions against dehydration injury. Different types of osmolytes have been identified (Fig. 2). Osmolytes mainly comprise of sugars (glucose, sucrose, fructose, raffinose, trehalose, and fructans), amino acids (γ-aminobutyric acids, Pro, pipecolic acid, ectoine, etc.), polyols or sugar alcohols (glycerol, mannitol, inositol, sorbitol), betaines (glycine betaine, choline-O-sulfate, β-alanine betaine), and tertiary sulfonium compound dimethylsulfoniopropionate (DMSP) [101]. Polyamines are osmoprotectants and stabilizers of cellular biomolecules under stressful conditions. As per the literature survey, these polyamines act as biological buffers when applied exogenously in minute quantities (μm) to circumvent various stressors (Drought, salinity, heat, and metal toxicity) [42]. Glycine betaine is a compatible solute that makes osmotic adjustments in plants and protects

protein and membrane structure by functioning as an adequate oxygen radical scavenger [102] (Table 1, Ref. [66, 68, 85, 87–90, 92, 103–126]). The application of proline enhances the photosynthetic performance and antioxidant defense system of the young olive tree [127]. Exogenous application of glycine betaine [128] and proline [110] enhances seed, seed oil quality, and antioxidant enzyme activity of maize (*Zea mays* L.) under drought stress conditions. Foliar application of proline also improves plants' internal free proline content, thus increasing their drought tolerance potential [129]. Exogenous treatment of γ-aminobutyric acid (GABA) improves PEG-induced drought stress tolerance in white clover (*Trifolium repens*) [130] and sunflower [131] by increasing relative water content, reducing lipid peroxidation, leaf wilt, and electrolyte leakage. Putrescine is the precursor of the other two polyamines, namely, spermidine and spermine [90]. Polyamines like spermidine have also been proven effective for improving plant tolerance to drought stress in crops like wheat, maize, and barley [132]. The combined application of spermidine and salicylic acid (SA) mitigated the independent and combinational effects of chromium and drought stress in maize (*Zea mays* L.) [120]. The study conducted by Li *et al.* [122] and Li *et al*. [121] reported that exogenous application of spermidine enhances white clover (*Trifolium repens* L.) growth under drought stress by enhancing the antioxidant defense system and also reduced oxidative stress. Combined application of putrescine and salicylic acid improves drought stress tolerance in *Trachyspermum ammi* by increased production of total sugars, phenolics, free amino acids, chlorophyll, and carotenoids [124]. The study conducted by Kosar *et al*. [115] reported trehalose's application for enhancing photosynthetic ability, plant growth, and increasing some key osmolytes' in sunflower under drought stress conditions (Table 1).

4.3 Role of proteins in drought stress tolerance

Abiotic stress, mainly drought stress is usually linked with the dysfunctioning of different proteins and enzymes. So, under abiotic stress conditions, it is essential to avoid accretion of non-native proteins and retain the proteins' functional conformation. Therefore, the plant generally activates different genes under drought stress, producing different kinds of protein. Usually, the drought stress response is associated with the production of two kinds of proteins: (1) late embryogenesis abundant (LEA) proteins and (2) heat-shock proteins (HSPs) [77].

4.3.1 LEA or Late embryogenesis abundant proteins

LEA proteins were initially categorized in seed, but they are also present in other vegetative tissues of the plants. The Late embryogenesis abundant (LEA) gene is either induced by applying ABA or environmental stress signals such as drought, low temperature, and salinity, etc. It has been suggested that they behave as water-holding molecules in ion sequestration and can stabilize membrane and protein. LEA proteins that play an important role in the mechanism of drought stress tolerance are known as dehydrin [133, 134]. The study conducted by different scientists has characterized LEA proteins in a variety of plants like cotton [134], barley [133, 134], rice [135], and wheat [136] for investigating their functional role in drought stress tolerance.

4.3.2 Heat shock proteins (HSPs)

Plants under field conditions need to deal with many abiotic and biotic stresses simultaneously [137]. Plants respond to these stressors through continuous transcriptional and translational regulation of diverse metabolic pathways [138]. Understanding these complex plant stress response pathways is essential and involves a combined effort of a squad of molecular chaperones like Heat Shock Proteins (HSPs) [139]. HSPs are highly overexpressed in plants responding to abiotic stress, comparatively very little attention has been given to recognize their functional role in stress tolerance. The roles of these HSPs belonging have been identified in different plants like *Arabidopsis thaliana* [140], Soybean [141, 142], and Rice [143, 144]. The two Nuclear/cytosolic HSPs, GmDjp1 and DNAj in soybean, have been associated with abiotic [142] and biotic [141] stress tolerance. Proteins present in endoplasmic reticulum (ER) HSP90s is also named as glucose-regulated protein 94 (GRP94), which is responsible for drought stress tolerance in *Xerophyta viscosa*, a drought-tolerant plant [145]. Another ER-resident Hsp70s known as BiPs (luminal Binding Proteins) the overexpression of SoyBiPD (soybean BiPs) conferred drought stress tolerance in tobacco.

4.4 Role of Nanoparticles (NPs) in drought stress tolerance

Nanoparticles are highly reactive due to their high surface area, tunable pore size, and particle structure. Nanoparticles are designed to target exact cell organelles in the plant for releasing their content [146]. They are generally involved in the up-regulation of antioxidant enzymes such as CAT, SOD, POD, APX etc. Silicon-based nanoparticles (SNPs) can efficiently alleviate various abiotic stresses such as drought, heat, chilling, salt stress, and heavy metal toxicities [77]. The mechanisms involved in alleviating stresses involve (1) activation of antioxidant defense systems in plants, (2) co-precipitation of Si with toxic metal ions, (3) toxic metal ions immobilization in growth media, (4) uptake, and compartment of metal ions inside plants. The study conducted by Linh *et al.* [147] reported that metal-based (copper, iron, cobalt, zinc oxide) nanoparticles could enhance drought stress tolerance in soybean by enhancing relative water content, biomass reduction rate, and drought tolerance index. Another study conducted by Sedghi *et al*. [148] reported that the application of zinc oxide nanoparticles increases seed germination (%) and overall germinates rate, suggesting that ZnO nanopar-

Table 1. Role of osmolytes, phytohormones, and their combinations with other compounds to mitigate the effect of drought stress in different plants species.

Exogenously applied Compounds	Compounds and their combinations	Concentration of Compounds Used	Plant Species	Application	Mechanism of action	References
Osmolytes	Glycine betaine (GB)	0, 50, 100, and 200 mM	*Phoebe hunanensis*	Foliar application	Enhances permeability of cell membrane and inhibited membrane lipid peroxidase accumulation	[103]
			Maize, barley		Photosynthetic efficiency maintenance, thylakoid membrane protection, and osmotic adjustment	[104]
			Flax (*Linum usitatissimum*)	Foliar application	Increased osmolytes accumulation and enhanced antioxidative enzyme activities	[105]
	Glycine betaine (GB)	(0, 50 and 100 mM)	Wheat	Foliar application	Enhancing plant biomass, transpiration rate, nitrogen and phosphorus content in roots under drought stress	[106]
	Glycine betaine + Salicylic acid (SA)	GB 100 mM and Salicylic acid (SA) 0.724 mM	Sunflower	Foliar application	Increased the free leaf proline and oil content under drought	[107]
	Glycine betaine + Salicylic acid + Zinc	11.5 g/L GB+ 140 mg/L SA+ 4 g/L Zn	Maize	Foliar application	Increased proline and sugar accumulation as well as enhanced antioxidative enzyme activities	[108]
	Proline		Rice	Foliar application	Up-regulated antioxidants enzyme activity and glycine betaine contents and decrease in lipid peroxidation	[109]
			Maize (*Zea mays L.*)	Foliar application	Proline improved the antioxidative enzyme activities	[110]
	Proline +ABA	ABA (10 μM) and 10 mM proline	Wheat	Foliar application	Improved drought and salinity stress tolerance	[111]
	Proline + Salicylic acid	10 mM proline and 0.5 mM Salicylic acid	Barley	Foliar application	Increased plant biomass, chlorophyll concentration, relative water content, antioxidant enzyme activity, and reduces lipid peroxidation, and hydrogen peroxide (H_2O_2)	[112]
	Trehalose	(0 and 30 mM)	*Brassica,* Maize	Foliar application	Induced drought stress tolerance by up-regulation of photosynthetic and water relation characteristics as well as antioxidant enzyme activity.	[113]
		40 mM trehalose	Wheat	Foliar application	Improves the physiological status of wheat	[114]
		(0, 10, 20 and 30 mM)	Sunflower	Foliar application	Induced drought stress tolerance	[115]
	γ-Amino butyric acid (GABA) + Proline	GABA and proline (0, 0.25, 0.5, 0.75 and 1 mol/L)	Tobacco		GABA acts as an effective osmolyte to reduce the production of reactive oxygen species (ROS) under drought stress	[116]
	Mannitol + thiourea	M (15 and 30 mM) or T (3.5 and 7.0 mM)	Maize (*Zea mays L.*)	Foliar application	Scavenge the stress induce oxygen radicals and osmotic adjustment	[92]
	Mannitol	30 mM	Blackgram (*Vigna mungo L.*)	Foliar application	Scavenge the stress induce oxygen radicals and osmotic adjustment	[117]
	D-Ononitol		*Arabidopsis*		Prevent water loss in plants	[118]
	D-pinitol		*Arabidopsis*		Prevent water loss in plants	[119]
		(0.1 mM)	Maize (*Zea mays L.*)	Foliar application	Increased plant biomass, and polyamine content	[90, 120]
	Spermidine (Spd)	0.5 mmol/L	White clover (*Trifolium repens L.*)	Foliar application	Promotion of ascorbate–glutathione cycle and higher activities of antioxidant enzymes	[121]

Table 1. Continued.

Exogenously applied Compounds	Compounds and their combinations	Concentration of Compounds Used	Plant Species	Application	Mechanism of action	References
		30 μM	White clover (*Trifolium repens L.*)	Foliar application	Reduction in lipid peroxidation and enhancing the antioxidant defense system	[122]
	SA + Spd	SA + Spd (0.25 mM + 0.05 mM)	Maize (*Zea mays L.*)	Foliar application	Enhancing the antioxidant defense system and regulating endogenous polyamine metabolism	[120]
	Putrescine	20 and 40 mg/ L	*Thymus vulgaris L.*	Foliar application	Enhanced leaf water content and dry matter, reduction in cell injury indices; upregulation in antioxidant enzymatic activities. Essential oil content was found to be increased by 23%	[123]
	Putrescine + salicylic acid	Putrescine (1 ppm) +SA (100 ppm)	*Trachyspermum ammi*		Total sugars, phenolics, free amino acids, chlorophyll, and carotenoids were enhanced in shoots and roots	[124]
Phytohormones	Methyl jasmonate (MeJA) + salicylic acid (SA)	MeJA (20 μM) and SA (2 mM)	Maize (*Zea mays L.*)	Seed and foliar application	Prevented drought-induced oxidative stress by modulating ABA and osmolytes level and antioxidant enzymes activity.	[85]
	Gibberellic acid (GA)		Wheat	Foliar application	Stimulated activities of glyoxalase I (Gly I) and glyoxalase II (Gly II) for protecting the wheat seedlings against drought stress	[66]
	GA & ABA		Tobacco		Improves stress tolerance, scavenging of ROS, and carbon-nitrogen balance	[68]
	Methyl jasmonate (MeJA)	250 mg L^{-1}	Citrus		Increased chlorophyll, sugar and proline contents and significantly decreased the H_2O_2 and O_2^- levels	[125]
	Jasmonic acid + abscisic acid	JA (100 μM) and ABA (100 μM)	Soybean		Relieving the adverse effects of drought stress and regulating trypsin inhibitor	[126]
	Brassinosteroids (BRs)	0.01 μM	*Brassica napus, Arabidopsis*, and rice	Seed application	Improved leaf water economy and CO_2 assimilation	[87–89]

ticles are more effective for using seed reservoirs for seedling growth and improve drought stress tolerance. A recent study by Ali *et al*. [149] used chitosan nanoparticles to improve drought stress tolerance in *Catharanthus roseus* (L.) by biochemical and modulation of gene expression.

4.5 Microbiome mediated drought stress resistance

Plants are intimately associated with an enormous diversity of microbes present in the rhizosphere, endosphere, phyllosphere, and other components such as nectar and pollen are collectively known as the plant microbiome [9, 150]. Root exudate release by plants comprises numerous organic compounds which provide better plant absorption, increase growth, provide higher yields, and provide the home for these microbes [151, 152]. Several studies have shown that plant microbiomes play essential roles, such as the enhancement of biotic (pathogens) and abiotic (drought, salinity) stress tolerance, nutrient cycling and transformation of organic matter, and the improvement of the plant growth and yields by promoting nutrient availability, biological nitrogen fixation, and production of phytohormones and other secondary metabolites [47, 153, 154]. Plant recruitment of a drought-tolerant microbiome might be an evolved attribute, with generations of recurrent drought responses leading to the establishment of beneficial and stable plant-microbe interactions that benefit both microbe and host plant [155, 156]. The study conducted on *Brassica rapa* plants subjected to drought for generations enhanced bacterial diversity and richness around roots in dry conditions than control plants [157]. Examining previously reported plant growth-promoting microbes (PGPM) from drought-stressed plants could reveal which microbial features are likely to be beneficial to plants. Indeed, bacteria with plant growth-promoting (PGP) capacities have been detected more in soils and roots [15], particularly in persistently drought-stressed areas [155]. The use of plant growth-promoting rhizobacteria (PGPR) for alleviating the harmful effect of drought stress has been extensively studied by different scientists in different crops, such as soybean [4, 158], wheat [159, 160], chickpea [8, 161], maize [162, 163], rice [164], and mung bean [24, 165] (Table 2, Ref. [4, 8, 30, 98, 159, 161, 164–168]). A number of PGP abilities confers drought resistance, and the most studied is the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACCd). The plant hormone ethylene is maintained below inhibitory levels by ACCd activity, allowing normal root development and delaying senescence during drought [162, 169]. The study conducted by different scientists reported use of ACCd producing microbes in alleviating the negative effect of drought stress in *Vigna mungo* L. and *Pisum sativum* [21, 170], maize [162], soybean [4], and *Capsicum annuum* [171]. These PGPR microbes also synthesize other plant hormones, like auxin analog indole-3-acetic acid (IAA), which improve root and shoot growth and help in other plant developmental processes [172]. PGPB

may have a role in nutrient cycling during droughts, such as diazotrophy, siderophore production, and phosphorus solubilization [173].

Plant endophytes residing in the intercellular spaces have been shown to relieve drought stress by evolving several mechanisms to sustain plant growth even under stressful conditions [174, 175]. Even when drought significantly modifies the microbial communities associated with plants, this drought-tolerant microbiota has a great positive influence on the phenological development of stressed plants [31, 153]. Thus, endophytes are considered as one of the most promising and easily available resources to improve plant tolerance under drought stress [4]. However, understanding the biochemical and physiological mechanisms of drought tolerance that act at the whole-plant level is necessary before employing these endophytes on a large scale [176]. Plants under drought stress events experience several physiological, metabolic, and molecular changes regulated or influenced by microbiota. Endophytes produce several secondary metabolites, many similar to those of the host, or regulate gene expression to overcome abiotic and biotic stresses [176, 177]. The plant microbiome positively alters the production of primary and secondary metabolites in plants during water stress conditions [47]. Endophytic microbes can synthesize different "protective" compounds like antioxidants, carbohydrates, and proline to cope with abiotic stress conditions [178]. In addition to those mechanisms detailed above, microbial endophytes also seem to confer stress tolerance by induction and regulation of stress-responsive genes, production of anti-stress metabolites as well as generation of ROS scavengers [76]. Enhanced accumulation of osmoprotectants proline, glutamine, and leucine under drought stress has been shown to impart stress tolerance [179]. Interestingly, Etesami *et al*. [180] reported that superoxide dismutase, catalase, and peroxidase enzymes showed greater activity in plants inoculated with beneficial microorganisms (i.e., *Bacillus cereus*, *B. subtilis*, and *Serratia* sp.). These enzymes are highly related to decreasing the negative effects of drought; thus, these bacterial species could be used as agents for mitigating this type of abiotic stress in plants, improving their development. Sadeghi *et al*. [181] found that the fungal endophyte (*Penicillium citrinum*, *Aureobasidium pullulans*, and *Dothideomycetes* sp.) inoculation enhances drought tolerance and reduces ROS accumulation in mandarin (*Citrus reticulata*) by increasing their scavenging via improving the redox state of glutathione and ascorbate, and promotion of antioxidant enzymes activity such as superoxide dismutase (SOD), glutathione reductase (GR), and, ascorbate peroxidase (APX). The study conducted by Martins *et al*. [166] using the three bacterial strains *Bacillus cereus*, *B. subtilis*, and *B. thuringiensis*, for mitigating the effect of drought stress in soybean and found a decrease in quantum efficiency of PSII (Fv/Fm) in control plants as compared to plants inoculated with bacterial strains. Another study

Table 2. Role of PGP microbes in the alleviation of drought stress condition.

Bacterial

S.No	Microbes	Isolated from	Target plant	Reported role	References
1.	*Bacillus cereus, Pseudomonas otitidis, and Pseudomonas sp.*	Rhizosphere	Soybean	Increased plant biomass, accumulation of proline, sugar, and decrease osmotic stress under drought stress condition	[4]
2.	*Bradyrhizobium japonicum* and *thuricin*-from *Bacillus thuringiensis*	Soybean rhizosphere	Soybean	Increase in nodule biomass, and photosynthetic rate	[167]
3.	*Bacillus cereus* UFGRB3, *B. subtilis* UFGS2, and *B. thuringiensis* UFGRB2	Soybean rhizosphere	Soybean	Differential gene expression and increased plant growth and biomass	[166]
4.	*Pseudomonas putida and Bacillus amyloliquefaciens*	Chickpea	Chickpea	Increased root biomass, which leads to higher nutrients uptake	[161]
5.	*Burkholderia phytofirmans PsJN*	Wheat rhizosphere	Wheat	Improved the antioxidant levels, ionic balance, and also increased the phosphorus, potassium, nitrogen, and protein concentration in wheat grains	[168]
6.	*Klebsiella sp., Flavobacterium sp, and Enterobacter ludwigii*	Wheat	Wheat	Increased plant biomass, accumulation of proline, sugar, and decrease osmotic stress under drought stress condition	[159]
7.	*Azotobacter chroococcum, Azospirillum brasilense*, and *Rhizobium japonicum*	Soybean rhizosphere	Soybean	Increased phytohormones production and decreases polyamine accumulated under drought stress condition	[30]
8.	*Pseudomonas aeruginosa* GGRJ21	Mung bean rhizosphere	Mung bean	Increased plant biomass, upregulation of drought stress-responsive genes, and accelerated production of proline	[165]

Fungal

S.No	Microbes	Isolated from	Target plant	Reported role	References
9.	*Piriformospora indica*	Rice	Rice	Increased chlorophyll fluorescence, accelerated production of proline and improved the antioxidant activity	[164]
10.	AMF: *Glomus etunicatum, Glomus mosseae*, and *Glomus intraradices*	Maize	Chickpea	Increased the weight and number of nodules, leghemoglobin content and nitrate reductase enzyme activity under drought stress condition	[8]
11.	AMF: *Rhizophagus clarus*	Strawberry plant	Strawberry plant	Increased plant biomass by increasing water content, water use efficiency, antioxidant enzyme activity, photosynthesis rate, and the nutritional status of mainly Zinc	[98]

conducted by Maxton *et al.* [171] used ACC deaminase-producing strains (*Bulkhorderia cepacia,* and *Citrobacter feurendii)* to mitigate the adverse effect of drought and salinity stress on *Capsicum annuum.* Melatonin accumulation, when inoculated with *Bacillus amyloliquefaciens* counter-balancing the adverse effects of drought, salinity, and cold stress [182]. This bacterial strain also reduces the transcription of tryptophan decarboxylase and serotonin. However, melatonin-producing endophytic microbes may have long-term effects on the endogenous melatonin levels in plants once they enter inside plant tissues.

Among the other mechanisms, endophytes have been shown to influence osmoregulation of tissues, regulation of stomatal conductance, and maintenance of cell-wall elasticity leading to drought tolerance [4]. In a study, arbuscular mycorrhizal fungi (AMF) colonize both C_3 (*Leymus chinensis*) and C_4 (*Hemarthria altissima*) grasses has altered the antioxidant enzyme and photosynthesis activity of plants in response to drought stress [183]. Another important root fungal endophyte, *Piriformospora indica,* isolated from plants growing in the deserts, seems to stimulate the expression of several drought stress-related genes in leaves and imparts drought tolerance to various plants, including *Arabidopsis* and Chinese cabbage [184, 185]. In

another study, Ghaffari *et al.* [184] have shown that the colonization of moisture stressed roots of barley by *P. indica* enhanced the photosystem's activity and the electron transfer chain. Further, their study using proteomic and metabolomic approaches revealed that *P. indica* also promoted the accumulation of proteins protective of photorespiration, energy modulation, primary metabolism, transporters, and autophagy during drought [184]. The beneficial effect of *P. indica* colonization on autophagy in plants exposed to drought stress may relate to alterations in the host's amino acid metabolism [184].

Similarly, Pandey *et al.* [186] showed significant alleviation of drought stress tolerance in rice by the endophyte *Trichoderma harzianum,* which significantly modulated proline levels, SOD, and upregulation of aquaporin, dehydrin, and malondialdehyde genes. A transcriptome analysis of *B. phytofirmans* PsJN colonizing potato in response to drought stress revealed the upregulation of transcripts related to transcriptional regulation, cellular homeostasis, and ROS detoxification [187]. The integration of microbiota to agricultural practices represents a promising sustainable alternative to address the food security issue under abiotic stress conditions. However, the use of these microorganisms requires several issues addressed in the field,

such as agricultural practices, microbial establishment, colonization of soil, and plant by microbial inoculants, and biosynthesis of bioactive metabolites produced by microbes involved in the regulation of plant growth, under specific conditions of soil, climate, and plant genotypes.

4.6 Deciphering the role of the unculturable microbiome

Droughts in coming time are likely to be more enduring, common, and severe than they have been in recent times, hence some novel and quickly deployable solutions for improving and convalescing drought tolerance in crops are urgently required. Terrestrial organisms, including plants, must be potent enough to adapt to the dry conditions resulting from diurnal and seasonal water fluctuations [188, 189]. Although adapted to resist, tolerate and evade the drying environments, plants tend to modify the root architecture and growth, alter their physiology, as well as shut down their stomata on their aboveground segments [190]. Recent studies have demonstrated that the interaction of plants with their above and below ground microbial partners plays an important role in augmenting plant's ability to thrive and endure under dry conditions [191, 192] and that drought significantly influences these interactions, thus altering both the structure and function of the root microbiome [193, 194]. Therefore, it can be predicted that an enhanced understanding of the complex mechanism and feedback between the plants and their microbial partners during and after drought will pave the way for harnessing the rhizosphere microbiome to augment the resilience of crop production to drought. Several studies conducted in diverse plant species have revealed that during the drought, the plant root microbiome shifts in favor of some particular microbial taxa and supplant the majority of other microbial lineages residing there in the root [194–197].

This shift in microbial communities is mainly governed by the abundance of genes involved in the degradation of complex plant polysaccharides, thus suggesting the proliferation of oligotrophic bacteria [155]. One possible reason for the proliferation of Gram-positive bacteria is that the bacteria of this group are metabolically more active and hardy enough to degrade compounds present in the drought environment [155]. Moreover, studies have also revealed that this enrichment is proportional to the duration and strength of the drought and is believed to disappear once water returns to the root system rapidly [195]. Recent advancements in omics-biology such as metagenomics, proteomics, and metabolomics allow us to binning of genomes, proteomes, and metabolomes from diverse environments to better understand the dynamics, structure, and functional including secondary metabolite biosynthesis and genes in soil microbial communities [198, 199].

Such studies will help to identify different genes, carbohydrate and secondary metabolites, transport, and metabolism pathways associated with bacterial enrichment under drought conditions. Additionally, the obtained datasets will help identify the genetic traits associated with these bacterial communities. A series of recently conducted studies revealed the role of multi-omics approaches in understanding the microbial traits in drought conditions. For example, while using metagenome-guided comparative genomics to under the dynamics of iron metabolism in drought-induced rhizosphere microbiome, concluded a linkage between drought, iron metabolism, and the plant root microbiome [200]. Similarly, Michaletti *et al.* [201], while studying the proteomics and metabolomics of spring-wheat leaf tissues, provided a detailed account of some of the key metabolites that can be used to develop ameliorated models to establish linkage between yield-associated traits and several metabolic pathways. In another study, Chmielewska *et al.* [202], while studying the proteomic and metabolomic changes in leaves and roots of two barley genotypes of different origins, indicated molecular chaperones' activity as well as osmoprotectants, elevated the resistance of these genotypes under drought stress. Gundaraniya *et al.* [203] studied the metabolomic alterations of drought-tolerant and susceptible Peanut (*Arachis hypogaea* L.) revealed that the two peanut genotypes possess different sensitivity to drought with accumulation and regulation of some metabolites, including organic acids, sugars, sugar alcohols, and fatty acids. The study conducted by Das *et al.* [204] studied metabolic alteration in different vegetative tissues of soybean under drought and heat stress conditions. This study revealed metabolites that are needed for various cellular processes, like the tricarboxylic acid (TCA) cycle, glycolysis, starch biosynthesis, and pentose phosphate pathway for regulating amino acid metabolism, peptide metabolism, carbohydrate metabolism, biosynthesis of purine and pyrimidine, were affected under heat and drought stress condition [204]. Another study conducted on soybean by Cao *et al.* [205] studied the metabolomic and transcriptomic profiling of soybean treated with melatonin under drought stress conditions during the grain-filling period through secondary metabolite biosynthesis pathways regulation.

4.7 Application of genome editing tools and technologies

It is challenging to understand the mechanisms involved during damage caused due to drought stress for the development of drought stress plant varieties. Therefore, the applications of transgenic or genome editing approaches will help to introduce desired drought stress-resistant character into different crop varieties. CRISPR has emerged as an innovative tool for genome editing in plants with desired characters and improves crop production under abiotic stress conditions (Fig. 3). Recently the application of CRISPR/Cas9 has been reported in different crops: Bread wheat [206, 207], potato [208], and model plants like *Arabidopsis thaliana* [209] and rice [210]. Overexpression of
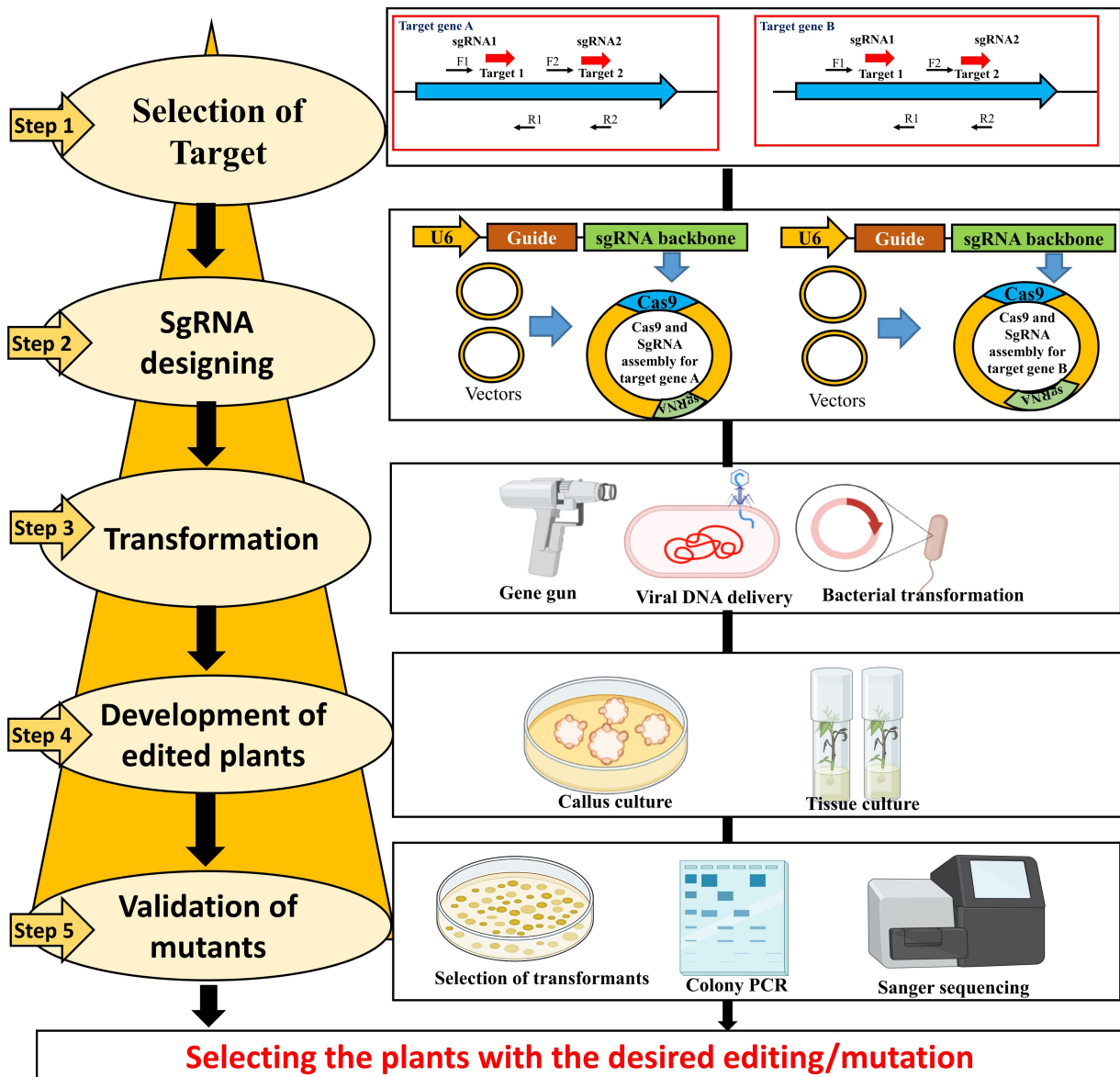
Fig. 3. Diagrammatic representation of Cas9/sgRNA genome editing (GE) approach. Sequential steps: (1) selection of target gene; (2) designing of sgRNAs using online tools; (3) Agrobacterium-mediated transformation into target plant species; (4) selection of transformants for the presence of Cas9 and sgRNA; (5) finally, selecting the plants with the desired editing/mutation by using, colony PCR and DNA sequencing.

different transcription factors (TFs) and genes associated with drought stress signalling helps to accumulate different metabolites, signalling molecules, and osmolytes, enhancing drought stress tolerance in plants.

On the other hand, sensitive (S) gene expression increases drought situations in plants by hormonal imbalance, inducing ROS production, and reducing antioxidant activity. For example, the study conducted by Fang *et al*. [210] reported *Oryza sativa* stress-related ring finger protein 1 (OsSRFP1) present in rice works as a negative regulator of drought stress, and its silencing often results in enhanced drought stress tolerance by decreasing H_2O_2 levels and by increasing antioxidant enzyme activity. Conse-

quently, natural drought tolerance could be demonstrated by negative regulation of genes that control drought stresses or by the application of genome editing approaches. The study conducted by Osakabe *et al*. [211] for the first time used the CRISPR/Cas9 genome editing approach for introducing novel alleles in the gene encodes for OPEN STOMATA 2 (OST2), an H^+ ATPase present in the plasma membrane which controls stomatal response in *Arabidopsis*.

Ethylene plays a fundamental role in regulating water scarcity conditions, therefore, the silencing 1-aminocyclopropane-1-carboxylic acid synthase 6 (ACS6), an ethylene biosynthetic gene present in maize, has resulted in high yield under drought stress conditions [212]. Another

study conducted by Shi *et al*. [213] reported that the AR-GOS family genes, i.e., AUXIN REGULATED GENE IN-VOLVED IN ORGAN SIZE 8 (ARGOS8), negatively regulates the ethylene signalling pathway and confers enhanced yield and drought stress tolerance under drought conditions. However, the endogenous expression of ARGOS8 transcript is spatially fluctuating and comparatively low in maize. Comprehensive molecular analysis has shown that ABA act as a primary factor of drought response in plants by regulating the expression of stress-related genes and controlling stomatal closure to prevent water loss [214]. Overall, these genome editing approaches will deliver new opportunities for creating nucleotide-specific alterations and might be widely explored in the future for improving drought tolerance in crops and thus will be a powerful tool for maintaining global food security.

5. Conclusions

Different approaches like PGPR and endophytes inoculation, seed priming with exogenous compounds, synthetic growth regulators, and genetic engineering are required to counter the negative impact of drought stress on crop plants. The emergence of an omics approach including genomics, metabolomics, proteomics, and transcriptomics might improve our understanding of the essential drought-tolerant genes and untangling the complex signalling cascades and gene networks involved in drought tolerance in different plants. Notably, ground-breaking methods, like CRISPR/Cas9 genome editing tools, will provide a deeper understanding and help to develop drought-resilient crops to minimize the risk of global food insecurity. Understanding of the processes through which soil microorganisms impact plant drought tolerance and recovery, as well as their relevance and application in field settings, holds a lot of promise for making crop production systems more resilient to drought. Implementing novel methods combining physiological, molecular, and genetic methods will deliver an effective solution for combating stress-related problems in the near future.

6. Author contributions

AD and AK conceived, designed, and edited the article; MM, KC, GS, GR, H, ZSS, EM, SS, and JFD contributed to different sections of the article.

7. Ethics approval and consent to participate

Not applicable.

8. Acknowledgment

9. Funding

10. Conflict of interest

The authors declare no conflict of interest.

11. References

[1] Dubey A, Malla MA, Khan F, Chowdhary K, Yadav S, Kumar A, *et al*. Soil microbiome: a key player for conservation of soil health under changing climate. Biodiversity and Conservation. 2019; 28: 2405–2429.

[2] White JC, Gardea-Torresdey J. Achieving food security through the very small. Nature Nanotechnology. 2018; 13: 627–629.

[3] Dubey A, Kumar A, Abd_Allah EF, Hashem A, Khan ML. Growing more with less: Breeding and developing drought resilient soybean to improve food security. Ecological Indicators. 2019; 105: 425–437.

[4] Dubey A, Saiyam D, Kumar A, Hashem A, Abduallah EF, Khan ML. Bacterial root endophytes: Characterization of their competence and plant growth promotion in soybean (glycine max (L.) merr.) under drought stress. International Journal of Environmental Research and Public Health. 2021; 18: 1–20.

[5] Chourasiya D, Agnihotri R, Prakash A, Pal KK, Sharma MP. Bioprotection of Soybean Plants from Drought Stress by Application of Bacterial and Fungal Endophytes. Soil Biology. 2018; 3: 281–301.

[6] Fang Y, Xiong L. General mechanisms of drought response and their application in drought resistance improvement in plants. Cellular and Molecular Life Sciences. 2015; 72: 673–689.

[7] Ahmad P, Hameed A, Abd-Allah EF, Sheikh SA, Wani MR, Rasool S, Jamsheed S, Kumar A. Biochemical and molecular approaches for drought tolerance in plants. In Physiological mechanisms and adaptation strategies in plants under changing environment (pp. 1–29). Springer: New York, NY. 2014

[8] Hashem A, Kumar A, Al-Dbass AM, Alqarawi AA, Al-Arjani AF, Singh G, *et al*. Arbuscular mycorrhizal fungi and biochar improves drought tolerance in chickpea. Saudi Journal of Biological Sciences. 2019; 26: 614–624.

[9] Dubey A, Kumar A, Khan ML. Role of Biostimulants for Enhancing Abiotic Stress Tolerance in Fabaceae Plants. The Plant Family Fabaceae. 2020; 13: 223–236.

[10] Daszkowska-Golec A, Szarejko I. Open or close the gate - stomata action under the control of phytohormones in drought stress conditions. Frontiers in Plant Science. 2013; 4: 138.

[11] Kumar A, Sharma S, Mishra S, Dames JF. Arbuscular mycorrhizal inoculation improves growth and antioxidative response of *Jatropha curcas* (L.) under Na_2SO_4 salt stress. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology. 2015; 149: 260–269.

[12] Goswami A, Banerjee R, Raha S. Drought resistance in rice seedlings conferred by seed priming: role of the anti-oxidant defense mechanisms. Protoplasma. 2013; 250: 1115–1129.

[13] Zhang X, Liu X, Zhang D, Tang H, Sun B, Li C, *et al*. Genome-wide identification of gene expression in contrasting maize inbred lines under field drought conditions reveals the significance of transcription factors in drought tolerance. PLoS ONE. 2017; 12: e0179477.

[14] Nadeem M, Li J, Yahya M, Sher A, Ma C, Wang X, *et al*. Research Progress and Perspective on Drought Stress in Legumes: a Review. International Journal of Molecular Sciences. 2019; 20: 2541.

[15] Kumar A, Dubey A. Rhizosphere microbiome: Engineering bacterial competitiveness for enhancing crop production. Journal of Advanced Research. 2020; 24: 337–352.

[16] Grover M, Nain L, Singh SB, Saxena AK. Molecular and Biochemical Approaches for Characterization of Antifungal Trait of a Potent Biocontrol Agent Bacillus subtilis RP24. Current Microbiology. 2010; 60: 99–106.

[17] Martínez-Gil M, Ramos-González MI, Espinosa-Urgel M. Roles of Cyclic Di-GMP and the Gac System in Transcriptional Control of the Genes Coding for the Pseudomonas putida Adhesins LapA and LapF. Journal of Bacteriology. 2014; 196: 1484–1495.

[18] Thao NP, Thu NBA, Hoang XLT, Van Ha C, Tran LP. Differential expression analysis of a subset of drought-responsive GmNAC genes in two soybean cultivars differing in drought tolerance. International Journal of Molecular Sciences. 2013; 14: 23828–23841.

[19] Kaushal M, Wani SP. Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. Annals of Microbiology. 2016; 66: 35–42.

[20] Mayak S, Tirosh T, Glick BR. Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. Plant Science. 2004; 166: 525–530.

[21] Zahir ZA, Munir A, Asghar HN, Shaharoona B, Arshad M. Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (Pisum sativum) under drought conditions. Journal of Microbiology and Biotechnology. 2008; 18: 958–963.

[22] Sandhya V, Ali SZ, Grover M, Reddy G, Venkateswarlu B. Effect of plant growth promoting Pseudomonas spp. on compatible solutes, antioxidant status and plant growth of maize under drought stress. Plant Growth Regulation. 2010; 62: 21–30.

[23] Kasim WA, Osman ME, Omar MN, Abd El-Daim IA, Bejai S, Meijer J. Control of Drought Stress in Wheat Using Plant-Growth-Promoting Bacteria. Journal of Plant Growth Regulation. 2013; 32: 122–130.

[24] Kumari S, Vaishnav A, Jain S, Varma A, Choudhary DK. Induced drought tolerance through wild and mutant bacterial strain Pseudomonas simiae in mung bean (Vigna radiata L.). World Journal of Microbiology & Biotechnology. 2016; 32: 4.

[25] Massawe F, Mayes S, Cheng A. Crop Diversity: an Unexploited Treasure Trove for Food Security. Trends in Plant Science. 2016; 21: 365–368.

[26] Banga SS, Kang MS. Developing Climate-Resilient Crops. Journal of Crop Improvement. 2014; 28: 57–87.

[27] Kashyap PL, Rai P, Srivastava AK, Kumar S. Trichoderma for climate resilient agriculture. World Journal of Microbiology & Biotechnology. 2017; 33: 155.

[28] Mishra AK, Singh VP. A review of drought concepts. Journal of Hydrology. 2010; 391: 202–216.

[29] Islam MS, Fahad S, Hossain A, Chowdhury MK, Iqbal MA, Dubey A, *et al*. Legumes under Drought Stress: Plant Responses, Adaptive Mechanisms, and Management Strategies in Relation to Nitrogen Fixation. Eng Toler Crop Plants Against Abiotic Stress (pp. 179–207). CRC Press: Florida. 2021.

[30] Kumar A, Gupta A, Azooz MM, Sharma S, Ahmad P, Dames J. Genetic approaches to improve salinity tolerance in plants. InSalt stress in plants (pp. 63–78). Springer: New York, NY. 2013.daptation strategies in plants under chang

[31] Etesami H, Maheshwari DK. Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. Ecotoxicology and Environmental Safety. 2018; 156: 225–246.

[32] Amna, Xia Y, Farooq MA, Javed MT, Kamran MA, Mukhtar T, *et al*. Multi-stress tolerant PGPR Bacillus xiamenensis PM14 activating sugarcane (Saccharum officinarum L.) red rot disease resistance. Plant Physiology and Biochemistry. 2020; 151: 640–649.

[33] Kanwal S, Ilyas N, Batool N, Arshad M. Amelioration of drought stress in wheat by combined application of PGPR, compost, and mineral fertilizer. Journal of Plant Nutrition. 2017; 40: 1250–1260.

[34] Nonami H. Plant water relations and control of cell elongation at low water potentials. Journal of Plant Research. 1998; 111: 373–382.

[35] Kim JI, Baek D, Park HC, Chun HJ, Oh DH, Lee MK, *et al*. Overexpression of arabidopsis YUCCA6 in potato results in high-auxin developmental phenotypes and enhanced resistance to water deficit. Molecular plant. 2013; 6: 337–349.

[36] Singh M, Kumar J, Singh S, Singh VP, Prasad SM. Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. Reviews in Environmental Science and Bio/Technology. 2015; 14: 407–426.

[37] Choudhury FK, Rivero RM, Blumwald E, Mittler R. Reactive oxygen species, abiotic stress and stress combination. the Plant Journal. 2017; 90: 856–867.

[38] Osakabe Y, Yamaguchi-Shinozaki K, Shinozaki K, Tran LP. ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. The New Phytologist. 2014; 202: 35–49.

[39] Kadioglu A, Saruhan N, Sağlam A, Terzi R, Acet T. Exogenous salicylic acid alleviates effects of long term drought stress and delays leaf rolling by inducing antioxidant system. Plant Growth Regulation. 2011; 64: 27–37.

[40] Saruhan N, Saglam A, Kadioglu A. Salicylic acid pretreatment induces drought tolerance and delays leaf rolling by inducing antioxidant systems in maize genotypes. Acta Physiologiae Plantarum. 2012; 34: 97–106.

[41] Ajithkumar IP, Panneerselvam R. ROS scavenging system, osmotic maintenance, pigment and growth status of Panicum sumatrense roth. under drought stress. Cell Biochemistry and Biophysics. 2014; 68: 587–595.

[42] Kubiś J, Floryszak-Wieczorek J, Arasimowicz-Jelonek M. Polyamines induce adaptive responses in water deficit stressed cucumber roots. Journal of Plant Research. 2014; 127: 151–158.

[43] Gharibi S, Tabatabaei BES, Saeidi G, Goli SAH. Effect of Drought Stress on Total Phenolic, Lipid Peroxidation, and Antioxidant Activity of Achillea Species. Applied Biochemistry and Biotechnology. 2016; 178: 796–809.

[44] Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry. 2010; 48: 909–930.

[45] Seleiman MF, Al-Suhaibani N, Ali N, Akmal M, Alotaibi M, Refay Y, *et al*. Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants. 2021; 10: 259.

[46] Kole C, Muthamilarasan M, Henry R, Edwards D, Sharma R, Abberton M, *et al*. Application of genomics-assisted breeding for generation of climate resilient crops: Progress and prospects. Frontiers in Plant Science. 2015; 6: 563.

[47] Silvente S, Sobolev AP, Lara M. Metabolite adjustments in drought tolerant and sensitive soybean genotypes in response to water stress. PLoS ONE. 2012; 7: e38554.

[48] Arnao MB, Hernández-Ruiz J. Melatonin and its relationship to plant hormones. Annals of Botany. 2018; 121: 195–207.

[49] Hamayun M, Khan SA, Khan AL, Shin J, Ahmad B, Shin D, *et al*. Exogenous gibberellic acid reprograms soybean to higher growth and salt stress tolerance. Journal of Agricultural and Food Chemistry. 2010; 58: 7226–7232.

[50] Ahmad P, Alyemeni MN, Abass Ahanger M, Wijaya L, Alam

P, Kumar A, *et al*. Upregulation of antioxidant and glyoxalase systems mitigates NaCl stress in Brassica juncea by supplementation of zinc and calcium. Journal of Plant Interactions. 2018; 13: 151–162.

[51] Ahmad P, Ashraf M, Younis M, Hu X, Kumar A, Akram NA, *et al*. Role of transgenic plants in agriculture and biopharming. Biotechnology Advances. 2012; 30: 524–540.

[52] Ullah A, Sun H, Yang X, Zhang X. Drought coping strategies in cotton: increased crop per drop. Plant Biotechnology Journal. 2017; 15: 271–284.

[53] Rockström J. Resilience building and water demand management for drought mitigation. Physics and Chemistry of the Earth, Parts a/B/C. 2003; 28: 869–877.

[54] Chapman KM, Marchi-Werle L, Hunt TE, Heng-Moss TM, Louis J. Abscisic and Jasmonic Acids Contribute to Soybean Tolerance to the Soybean Aphid (Aphis glycines Matsumura). Scientific Reports. 2018; 8: 15148.

[55] Spaepen S, Vanderleyden J. Auxin and plant-microbe interactions. Cold Spring Harbor Perspectives in Biology. 2011; 3: 1–13.

[56] Jung H, Lee D, Choi YD, Kim J. OsIAA6, a member of the rice Aux/IAA gene family, is involved in drought tolerance and tiller outgrowth. Plant Science : an International Journal of Experimental Plant Biology. 2015; 236: 304–312.

[57] Ke Q, Wang Z, Ji CY, Jeong JC, Lee H, Li H, *et al*. Transgenic poplar expressing Arabidopsis YUCCA6 exhibits auxin-overproduction phenotypes and increased tolerance to abiotic stress. Plant Physiology and Biochemistry. 2015; 94: 19–27.

[58] Cassán F, Vanderleyden J, Spaepen S. Physiological and Agronomical Aspects of Phytohormone Production by Model Plant-Growth-Promoting Rhizobacteria (PGPR) Belonging to the Genus Azospirillum. Journal of Plant Growth Regulation. 2014; 33: 440–459.

[59] Lubovská Z, Dobrá J, Storchová H, Wilhelmová N, Vanková R. Cytokinin oxidase/dehydrogenase overexpression modifies antioxidant defense against heat, drought and their combination in Nicotiana tabacum plants. Journal of Plant Physiology. 2014; 171: 1625–1633.

[60] Ha S, Vankova R, Yamaguchi-Shinozaki K, Shinozaki K, Tran LP. Cytokinins: metabolism and function in plant adaptation to environmental stresses. Trends in Plant Science. 2012; 17: 172–179.

[61] Neil Emery RJ, Kisiala A. The roles of cytokinins in plants and their response to environmental stimuli. Plants. 2020; 9: 1158.

[62] Li W, Herrera-Estrella L, Tran LP. The Yin–Yang of Cytokinin Homeostasis and Drought Acclimation/Adaptation. Trends in Plant Science. 2016; 21: 548–550.

[63] Nishiyama R, Watanabe Y, Leyva-Gonzalez MA, Ha CV, Fujita Y, Tanaka M, *et al*. Arabidopsis AHP2, AHP3, and AHP5 histidine phosphotransfer proteins function as redundant negative regulators of drought stress response. Proceedings of the National Academy of Sciences of the United States of America. 2013; 110: 4840–4845.

[64] Nishiyama R, Watanabe Y, Fujita Y, Le DT, Kojima M, Werner T, *et al*. Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. The Plant Cell. 2011; 23: 2169–2183.

[65] Kaya C, Levent Tuna A, Alfredo ACA. Gibberellic acid improves water deficit tolerance in maize plants. Acta Physiologiae Plantarum. 2006; 28: 331–337.

[66] Moumita, Al Mahmud J, Biswas PK, Nahar K, Fujita M, Hasanuzzaman M. Exogenous application of gibberellic acid mitigates drought-induced damage in spring wheat. Acta Agrobotanica. 2019; 72: 1776.

[67] Waqas M, Khan AL, Kamran M, Hamayun M, Kang S, Kim Y, *et al*. Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. Molecules. 2012; 17: 10754–10773.

[68] Jakab G, Ton J, Flors V, Zimmerli L, Métraux J, Mauch-Mani B. Enhancing Arabidopsis Salt and Drought Stress Tolerance by Chemical Priming for its Abscisic Acid Responses. Plant Physiology. 2005; 139: 267–274.

[69] Arraes FBM, Beneventi MA, Lisei de Sa ME, Paixao JFR, Albuquerque EVS, Marin SRR, *et al*. Implications of ethylene biosynthesis and signaling in soybean drought stress tolerance. BMC Plant Biology. 2015; 15: 213.

[70] Liu C, Zhang T. Expansion and stress responses of the AP2/EREBP superfamily in cotton. BMC Genomics. 2017; 18: 118.

[71] Zhang G, Chen M, Li L, Xu Z, Chen X, Guo J, *et al*. Overexpression of the soybean GmERF3 gene, an AP2/ERF type transcription factor for increased tolerances to salt, drought, and diseases in transgenic tobacco. Journal of Experimental Botany. 2009; 60: 3781–3796.

[72] Tohge T, Watanabe M, Hoefgen R, Fernie AR. Shikimate and phenylalanine biosynthesis in the green lineage. Frontiers in Plant Science. 2013; 4: 62.

[73] Gargallo-Garriga A, Preece C, Sardans J, Oravec M, Urban O, Peñuelas J. Root exudate metabolomes change under drought and show limited capacity for recovery. Scientific Reports. 2018; 8: 12696.

[74] Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. Abiotic and biotic stress combinations. The New Phytologist. 2014; 203: 32–43.

[75] Wani SH, Kumar V, Shriram V, Sah SK. Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal. 2016; 4: 162–176.

[76] Lata R, Chowdhury S, Gond SK, White JF. Induction of abiotic stress tolerance in plants by endophytic microbes. Letters in Applied Microbiology. 2018; 66: 268–276.

[77] Ali F, Bano A, Fazal A. Recent methods of drought stress tolerance in plants. Plant Growth Regulation. 2017; 82: 363–375.

[78] Shan C, Zhou Y, Liu M. Nitric oxide participates in the regulation of the ascorbate-glutathione cycle by exogenous jasmonic acid in the leaves of wheat seedlings under drought stress. Protoplasma. 2015; 252: 1397–1405.

[79] Nafie E, Hathout T, Al Mokadem AS. Jasmonic acid elicits oxidative defense and detoxification systems in Cucumis melo L. cells. Brazilian Journal of Plant Physiology. 2011; 23: 161–174.

[80] Bandurska H, Stroiński A, Kubiś J. The effect of jasmonic acid on the accumulation of ABA, proline and spermidine and its influence on membrane injury under water deficit in two barley genotypes. Acta Physiologiae Plantarum. 2003; 25: 279–285.

[81] Varoquaux N, Cole B, Gao C, Pierroz G, Baker CR, Patel D, *et al*. Transcriptomic analysis of field-droughted sorghum from seedling to maturity reveals biotic and metabolic responses. Proceedings of the National Academy of Sciences. 2019; 116: 27124–27132.

[82] Hayat S, Ali B, Ahmad A. Salicylic acid: Biosynthesis, metabolism and physiological role in plants. Salicylic Acid: A Plant Hormone (pp. 1–14). Springer: Dordrecht. 2007.

[83] Khan N, Zandi P, Ali S, Mehmood A, Adnan Shahid M. Impact of Salicylic Acid and PGPR on the Drought Tolerance and Phytoremediation Potential of Helianthus annus. Frontiers in Microbiology. 2018; 9: 2507.

[84] Anjum SA, Tanveer M, Hussain S, Tung SA, Samad RA, Wang L, *et al*. Exogenously applied methyl jasmonate improves the drought tolerance in wheat imposed at early and late developmental stages. Acta Physiologiae Plantarum. 2016; 38: 25.

[85] Tayyab N, Naz R, Yasmin H, Nosheen A, Keyani R, Sajjad M, *et al*. Combined seed and foliar pre-treatments with exogenous methyl jasmonate and salicylic acid mitigate drought-induced stress in maize. PLos ONE2020; 15: e0232269.

[86] Chen J, Nolan TM, Ye H, Zhang M, Tong H, Xin P, *et al*. Arabidopsis WRKY46, WRKY54, and WRKY70 Transcription Factors are Involved in Brassinosteroid-Regulated Plant Growth and Drought Responses. The Plant Cell. 2017; 29: 1425–1439.

[87] Kagale S, Divi UK, Krochko JE, Keller WA, Krishna P. Brassinosteroid confers tolerance in Arabidopsis thaliana and Brassica napus to a range of abiotic stresses. Planta. 2007; 225: 353–364.

[88] Todorova D, Talaat NB, Katerova Z, Alexieva V, Shawky BT. Polyamines and brassinosteroids in drought stress responses and tolerance in plants. Water Stress and Crop Plants: A Sustainable Approach. 2016; 2: 608–627.

[89] Farooq M, Wahid A, Basra SMA, Islam-ud-Din. Improving Water Relations and Gas Exchange with Brassinosteroids in Rice under Drought Stress. Journal of Agronomy and Crop Science. 2009; 195: 262–269.

[90] Li L, Gu W, Li C, Li W, Li C, Li J, et al. Exogenous spermidine improves drought tolerance in maize by enhancing the antioxidant defence system and regulating endogenous polyamine metabolism. Crop and Pasture Science. 2018; 69: 1076.

[91] Das K, Roychoudhury A. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Frontiers in Environmental Science. 2014; 2: 53.

[92] Kaya C, sonmez O, Aydemir S, Ashraf M, Dikilitas M. Exogenous application of mannitol and thiourea regulates plant growth and oxidative stress responses in salt-stressed maize (Zea maysL.). Journal of Plant Interactions. 2013; 8: 234–241.

[93] Nahar K, Hasanuzzaman M, Alam MM, Fujita M. Glutathione-induced drought stress tolerance in mung bean: coordinated roles of the antioxidant defence and methylglyoxal detoxification systems. AoB Plants. 2015; 7: plv069.

[94] Sohag AAM, Tahjib-Ul-Arif M, Polash MAS, Belal Chowdhury M, Afrin S, Burritt DJ, et al. Exogenous Glutathione-Mediated Drought Stress Tolerance in Rice (Oryza sativa L.) is Associated with Lower Oxidative Damage and Favorable Ionic Homeostasis. Iranian Journal of Science and Technology, Transactions a: Science. 2020; 44: 955–971.

[95] Sun Y, Wang H, Liu S, Peng X. Exogenous application of hydrogen peroxide alleviates drought stress in cucumber seedlings. South African Journal of Botany. 2016; 106: 23–28.

[96] Gong H, Zhu X, Chen K, Wang S, Zhang C. Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Science. 2005; 169: 313–321.

[97] Deshmukh RK, Vivancos J, Ramakrishnan G, Guérin V, Carpentier G, Sonah H, et al. A precise spacing between the NPA domains of aquaporins is essential for silicon permeability in plants. The Plant Journal. 2015; 83: 489–500.

[98] Moradtalab N, Hajiboland R, Aliasgharzad N, Hartmann TE, Neumann G. Silicon and the Association with an Arbuscular-Mycorrhizal Fungus (Rhizophagus clarus) Mitigate the Adverse Effects of Drought Stress on Strawberry. Agronomy. 2019; 9: 41.

[99] Hasanuzzaman M, Nahar K, Anee TI, Khan MIR, Fujita M. Silicon-mediated regulation of antioxidant defense and glyoxalase systems confers drought stress tolerance in Brassica napus L. South African Journal of Botany. 2018; 115: 50–57.

[100] Hawrylak-Nowak B, Dresler S, Rubinowska K, Matraszek-Gawron R, Woch W, Hasanuzzaman M. Selenium biofortification enhances the growth and alters the physiological response of lamb's lettuce grown under high temperature stress. Plant Physiology and Biochemistry. 2018; 127: 446–456.

[101] Iqbal N, Nazar R. Osmolytes and plants acclimation to changing environment: Emerging omics technologies. Springer: Dordrecht. 2015.

[102] Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany. 2007; 59: 206–216.

[103] Yang Y, Huang C, Ge Z, Zhou B, Su G, Liu C, et al. Exogenous Glycine Betaine Reduces Drought Damage by Mediating Osmotic Adjustment and Enhancing Antioxidant Defense in Phoebe hunanensis. Phyton. 2022; 91: 129–148.

[104] Ashraf M, Akram NA, Al-Qurainy F, Foolad MR. Drought Tolerance. Advances in Agronomy. 2011; 131: 249–296.

[105] Gupta P, Rai R, Vasudev S, Yadava DK, Dash PK. Ex-foliar application of glycine betaine and its impact on protein, carbohydrates and induction of ROS scavenging system during drought stress in flax (Linum usitatissimum) Journal of Biotechnology. 2021; 337: 80–89.

[106] Shahbaz M, Masood Y, Perveen S, Ashraf M. Is foliar-applied glycinebetaine effective in mitigating the adverse effects of drought stress on wheat (Triticum aestivum L.)? Journal of Applied Botany and Food Quality. 2011; 84: 192.

[107] Hussain M, Malik MA, Farooq M, Ashraf MY, Cheema MA. Improving Drought Tolerance by Exogenous Application of Glycinebetaine and Salicylic Acid in Sunflower. Journal of Agronomy and Crop Science. 2008; 194: 193–199.

[108] Shemi R, Wang R, Gheith EMS, Hussain HA, Hussain S, Irfan M, et al. Effects of salicylic acid, zinc and glycine betaine on morpho-physiological growth and yield of maize under drought stress. Scientific Reports. 2021; 11: 3195.

[109] Hanif S, Saleem MF, Sarwar M, Irshad M, Shakoor A, Wahid MA, et al. Biochemically Triggered Heat and Drought Stress Tolerance in Rice by Proline Application. Journal of Plant Growth Regulation. 2021; 40: 305–312.

[110] Ali Q, Anwar F, Ashraf M, Saari N, Perveen R. Ameliorating effects of exogenously applied proline on seed composition, seed oil quality and oil antioxidant activity of maize (Zea mays L.) under drought stress. International Journal of Molecular Sciences. 2013; 14: 818–835.

[111] Kaur G, Asthir B. Impact of exogenously applied ABA on proline metabolism conferring drought and salinity stress tolerance in wheat genotypes. Cereal Research Communications. 2020; 48: 309–315.

[112] Abdelaal KAA, Attia KA, Alamery SF, El-Afry MM, Ghazy AI, Tantawy DS, et al. Exogenous application of proline and salicylic acid can mitigate the injurious impacts of drought stress on barley plants associated with physiological and histological characters. Sustainability. 2020; 12: 1736.

[113] Ali Q, Ashraf M. Induction of Drought Tolerance in Maize (Zea mays L.) due to Exogenous Application of Trehalose: Growth, Photosynthesis, Water Relations and Oxidative Defence Mechanism. Journal of Agronomy and Crop Science. 2011; 197: 258–271.

[114] Hanaa E. Ahmed, Maimona A. Kord HAY, And, Qaid EA. Exogenous Application of Trehalose Improves the Physiological Status of Wheat cv. Giza 168 grown under Stress. Egypt Journal of Botany. 2016; 56: 627–646.

[115] Kosar F, Akram NA, Ashraf M, Sadiq M, Al-Qurainy F. Trehalose-induced improvement in growth, photosynthetic characteristics and levels of some key osmoprotectants in sunflower (Helianthus annuus L.) under drought stress. Pakistan Journal of Botany. 2018; 50: 955–961.

[116] Liu C, Zhao L, Yu G. The dominant glutamic acid metabolic flux to produce γ-amino butyric acid over proline in Nicotiana tabacum leaves under water stress relates to its significant role in antioxidant activity. Journal of Integrative Plant Biology. 2011; 53: 608–618.

[117] A KP, Mini M. Water stress mitigation of blackgram (Vigna mungo L.) with exogenous application of mannitol. International Journal of Chemical Studies. 2020; 8: 1360–1364.

[118] Ahn C, Park U, Park PB. Increased salt and drought tolerance by D-ononitol production in transgenic Arabidopsis thaliana. Biochemical and Biophysical Research Communications. 2011; 415: 669–674.

[119] Ahn C, Hossain MA, Lee E, Kanth BK, Park PB. Increased salt and drought tolerance by D-pinitol production in transgenic Arabidopsis thaliana. Biochemical and Biophysical Research Communications. 2018; 504: 315–320.

[120] Naz R, Sarfraz A, Anwar Z, Yasmin H, Nosheen A, Keyani R, et al. Combined ability of salicylic acid and spermidine to mitigate the individual and interactive effects of drought and chromium stress in maize (Zea mays L.) Plant Physiology and

945

Biochemistry. 2021; 159: 285–300.

[121] Li Z, Peng Y, Zhang XQ, Pan MH, Ma X, Huang LK, *et al*. Exogenous spermidine improves water stress tolerance of white clover (Trifolium repens L.) involved in antioxidant defence, gene expression and proline metabolism. Plant Omics. 2014; 7: 517–526.

[122] Li Z, Peng Y, Zhang X, Ma X, Huang L, Yan Y. Exogenous spermidine improves seed germination of white clover under water stress via involvement in starch metabolism, antioxidant defenses and relevant gene expression. Molecules (Basel, Switzerland). 2014; 19: 18003–18024.

[123] Abd Elbar OH, Farag RE, Shehata SA. Effect of putrescine application on some growth, biochemical and anatomical characteristics of Thymus vulgaris L. under drought stress. Annals of Agricultural Sciences. 2019; 64: 129–137.

[124] Zeid FA, Omer EA, Amin AY, Hanafy Shaimaa A. Effect of Putrescine and Salicylic Acid on Ajwain Plant (Trachyspermum Ammi) at Vegetative Stage Grown under Drought Stress. International Journal of Agriculture Science Research. 2014; 4: 61–79.

[125] Xiong B, Wang Y, Zhang Y, Ma M, Gao Y, Zhou Z, *et al*. Alleviation of drought stress and the physiological mechanisms in Citrus cultivar (Huangguogan) treated with methyl jasmonate. Bioscience, Biotechnology, and Biochemistry. 2020; 84: 1958–1965.

[126] Hassanein RA, Hassanein AA, El-din AB, *et al*. Role of Jasmonic Acid and Abscisic Acid Treatments in Alleviating the Adverse Effects of Drought Stress and Regulating Trypsin Inhibitor Production in Soybean Plant. Australian Journal of Basic and Applied Sciences. 2009; 3: 904–919.

[127] Ben Ahmed C, Ben Rouina B, Sensoy S, Boukhriss M, Ben Abdullah F. Exogenous proline effects on photosynthetic performance and antioxidant defense system of young olive tree. Journal of Agricultural and Food Chemistry. 2010; 58: 4216–4222.

[128] Ali Q, Ashraf M. Exogenously applied glycinebetaine enhances seed and seed oil quality of maize (Zea mays L.) under water deficit conditions. Environmental and Experimental Botany. 2011; 71: 249–259.

[129] Semida WM, Abdelkhalik A, Rady MOA, Marey RA, Abd El-Mageed TA. Exogenously applied proline enhances growth and productivity of drought stressed onion by improving photosynthetic efficiency, water use efficiency and up-regulating osmoprotectants. Scientia Horticulturae. 2020; 272: 109580.

[130] Yong B, Xie H, Li Z, Li Y, Zhang Y, Nie G, *et al*. Exogenous Application of GABA Improves PEG-Induced Drought Tolerance Positively Associated with GABA-Shunt, Polyamines, and Proline Metabolism in White Clover. Frontiers in Physiology. 2017; 8: 1107.

[131] Abdel Razik ES, Alharbi BM, Pirzadah TB, Alnusairi GSH, Soliman MH, Hakeem KR. γ-Aminobutyric acid (GABA) mitigates drought and heat stress in sunflower (Helianthus annuus L.) by regulating its physiological, biochemical and molecular pathways. Physiologia Plantarum. 2021; 172: 505–527.

[132] Sallam A, Alqudah AM, Dawood MFA, Baenziger PS, Börner A. Drought stress tolerance in wheat and barley: Advances in physiology, breeding and genetics research. International journal of molecular sciences. 2019; 20: 3137.

[133] Kosová K, Vítámvás P, Prášil IT. Wheat and barley dehydrins under cold, drought, and salinity - what can LEA-II proteins tell us about plant stress response? Frontiers in Plant Science. 2014; 5: 343.

[134] Magwanga RO, Lu P, Kirungu JN, Lu H, Wang X, Cai X, *et al*. Characterization of the late embryogenesis abundant (LEA) proteins family and their role in drought stress tolerance in upland cotton. BMC Genetics. 2018; 19: 6.

[135] Kamarudin ZS, Yusop MR, Ismail MR, Tengku Muda Mohamed M, Harun AR, Yusuff O, *et al*. LEA Gene Expression Assessment in Advanced Mutant Rice Genotypes under Drought Stress. International Journal of Genomics. 2019; 2019: 1–8.

[136] Ali M, Gul A, Hasan H, Alipour H, Abbasi AA, Zahra Khan FT, *et al*. LEA proteins and drought stress in wheat. Climate Change and Food Security with Emphasis on Wheat. 2020; 53: 193–205.

[137] Verma AK, Tamadaddi C, Tak Y, Lal SS, Cole SJ, Hines JK, *et al*. The expanding world of plant J-domain proteins. Critical Reviews in Plant Sciences. 2019; 38: 382–400.

[138] Kissoudis C, van de Wiel C, Visser RGF, van der Linden G. Enhancing crop resilience to combined abiotic and biotic stress through the dissection of physiological and molecular crosstalk. Frontiers in Plant Science. 2014; 5: 207.

[139] Al-Whaibi MH. Plant heat-shock proteins: a mini review. Journal of King Saud University - Science. 2011; 23: 139–150.

[140] Tamura K, Takahashi H, Kunieda T, Fuji K, Shimada T, Hara-Nishimura I. Arabidopsis KAM2/GRV2 is required for proper endosome formation and functions in vacuolar sorting and determination of the embryo growth axis. The Plant Cell. 2007; 19: 320–332.

[141] Liu J, Whitham SA. Overexpression of a soybean nuclear localized type-III DnaJ domain-containing HSP40 reveals its roles in cell death and disease resistance. The Plant Journal. 2013; 74: 110–121.

[142] So H, Chung E, Lee J. Molecular characterization of soybean GmDjp1 encoding a type III J-protein induced by abiotic stress. Genes & Genomics. 2013; 35: 247–256.

[143] Ohta M, Wakasa Y, Takahashi H, Hayashi S, Kudo K, Takaiwa F. Analysis of rice ER-resident J-proteins reveals diversity and functional differentiation of the ER-resident Hsp70 system in plants. Journal of Experimental Botany. 2013; 64: 5429–5441.

[144] Ohta M, Takaiwa F. Emerging features of ER resident J-proteins in plants. Plant Signaling & Behavior. 2014; 9: e28194.

[145] Walford S-, Thomson JA, Farrant JM, Mundree SG, Musil CF. Isolation and characterisation of a novel dehydration-induced Grp94 homologue from the resurrection plant Xerophyta viscosa. South African Journal of Botany. 2004; 70: 741–750.

[146] Siddiqui MH, Al-Whaibi MH, Firoz M, Al-Khaishany MY. Role of Nanoparticles in Plants. Nanotechnology and Plant Sciences. 2015; 66: 19–35.

[147] Linh TM, Mai NC, Hoe PT, Lien LQ, Ban NK, Hien LTT, *et al*. Metal-Based Nanoparticles Enhance Drought Tolerance in Soybean. Journal of Nanomaterials. 2020; 2020: 1–13.

[148] Sedghi M, Hadi M, Toluie SG. Effect of Nano Zinc Oxide on the Germination Parameters of Soybean Seeds Under Drought Stress. Annales of West University of Timisoara. Series of Biology. 2013; 16: 73.

[149] Ali EF, El-Shehawi AM, Ibrahim OHM, Abdul-Hafeez EY, Moussa MM, Hassan FAS. A vital role of chitosan nanoparticles in improvisation the drought stress tolerance in Catharanthus roseus (L.) through biochemical and gene expression modulation. Plant Physiology and Biochemistry. 2021; 161: 166–175.

[150] Kumar A, Sharma S, Mishra S. Evaluating effect of arbuscular mycorrhizal fungal consortia and Azotobacter chroococcum in improving biomass yield of Jatropha curcas. Plant Biosystems - an International Journal Dealing with all Aspects of Plant Biology. 2016; 150: 1056–1064.

[151] van der Heijden MGA, Hartmann M. Networking in the Plant Microbiome. PLoS Biology. 2016; 14: e1002378.

[152] Moe LA. Amino acids in the rhizosphere: from plants to microbes. American Journal of Botany. 2013; 100: 1692–1705.

[153] Hare PD, Cress WA, Van Staden J. Dissecting the roles of osmolyte accumulation during stress. Plant, Cell and Environment. 1998; 21: 535–553.

[154] Kumar A, Dames JF, Gupta A, Sharma S, Gilbert JA, Ahmad P. Current developments in arbuscular mycorrhizal fungi research and its role in salinity stress alleviation: a biotechnological perspective. Critical Reviews in Biotechnology. 2015; 35: 461–474.

[155] Naylor D, Coleman-Derr D. Drought Stress and Root-Associated Bacterial Communities. Frontiers in Plant Science. 2018; 8: 2223.

[156] Naylor D, DeGraaf S, Purdom E, Coleman-Derr D. Drought and host selection influence bacterial community dynamics in the grass root microbiome. The ISME Journal. 2017; 11: 2691–2704.

[157] Terhorst CP, Lennon JT, Lau JA. The relative importance of rapid evolution for plant-microbe interactions depends on ecological context. Proceedings. Biological Sciences. 2014; 281: 20140028.

[158] Kunert KJ, Vorster BJ, Fenta BA, Kibido T, Dionisio G, Foyer CH. Drought Stress Responses in Soybean Roots and Nodules. Frontiers in Plant Science. 2016; 7: 1015.

[159] Gontia-Mishra I, Sapre S, Sharma A, Tiwari S. Amelioration of drought tolerance in wheat by the interaction of plant growth-promoting rhizobacteria. Plant Biology (Stuttgart, Germany). 2016; 18: 992–1000.

[160] Barnawal D, Bharti N, Pandey SS, Pandey A, Chanotiya CS, Kalra A. Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1/TaDREB2 expression. Physiologia Plantarum. 2017; 161: 502–514.

[161] Kumar M, Mishra S, Dixit V, Kumar M, Agarwal L, Chauhan PS, et al. Synergistic effect of Pseudomonas putida and Bacillus amyloliquefaciens ameliorates drought stress in chickpea (Cicer arietinum L.). Plant Signaling & Behavior. 2016; 11: e1071004.

[162] Danish S, Zafar-Ul-Hye M, Mohsin F, Hussain M. ACC-deaminase producing plant growth promoting rhizobacteria and biochar mitigate adverse effects of drought stress on maize growth. PLos ONE. 2020; 15: e0230615.

[163] Sandhya V, Shrivastava M, Ali SZ, Sai Shiva Krishna Prasad V. Endophytes from maize with plant growth promotion and biocontrol activity under drought stress. Russian Agricultural Sciences. 2017; 43: 22–34.

[164] Saddique MAB, Ali Z, Khan AS, Rana IA, Shamsi IH. Inoculation with the endophyte Piriformospora indica significantly affects mechanisms involved in osmotic stress in rice. Rice. 2018; 11: 34.

[165] Sarma RK, Saikia R. Alleviation of drought stress in mung bean by strain Pseudomonas aeruginosa GGRJ21. Plant and Soil. 2014; 377: 111–126.

[166] Martins SJ, Rocha GA, de Melo HC, de Castro Georg R, Ulhôa CJ, de Campos Dianese É, et al. Plant-associated bacteria mitigate drought stress in soybean. Environmental Science and Pollution Research International. 2018; 25: 13676–13686.

[167] Prudent M, Salon C, Souleimanov A, Emery RJN, Smith DL. Soybean is less impacted by water stress using Bradyrhizobium japonicum and thuricin-17 from Bacillus thuringiensis. Agronomy for Sustainable Development. 2015; 35: 749–757.

[168] Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A. Drought stress amelioration in wheat through inoculation with Burkholderia phytofirmans strain PsJN. Plant Growth Regulation. 2014; 73: 121–131.

[169] Glick BR. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research. 2014; 169: 30–39.

[170] Saikia J, Sarma RK, Dhandia R, Yadav A, Bharali R, Gupta VK, et al. Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. Scientific Reports. 2018; 8: 3560.

[171] Maxton A, Singh P, Masih SA. ACC deaminase-producing bacteria mediated drought and salt tolerance in Capsicum annuum. Journal of Plant Nutrition. 2018; 41: 574–583.

[172] Xu L, Xu W, Jiang Y, Hu F, Li H. Effects of interactions of auxin-producing bacteria and bacterial-feeding nematodes on regulation of peanut growths. PLoS ONE. 2015; 10: e0124361.

[173] Kohler J, Hernández JA, Caravaca F, Roldán A. Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. Functional Plant Biology. 2008; 35: 141.

[174] Namwongsa J, Jogloy S, Vorasoot N, Boonlue S, Riddech N, Mongkolthanaruk W. Endophytic Bacteria Improve Root Traits, Biomass and Yield of Helianthus tuberosus L. under Normal and Deficit Water Conditi. Journal of Microbiology and Biotechnology. 2019; 29: 1777–1789.

[175] Dubey A, Malla MA, Kumar A, Dayanandan S, Khan ML. Plants endophytes: unveiling hidden agenda for bioprospecting toward sustainable agriculture. Critical Reviews in Biotechnology. 2020; 40: 1210–1231.

[176] Anjum SA, Xie X yu, Wang L chang, Saleem MF, Man C, Lei W. Morphological, physiological and biochemical responses of plants to drought stress. African journal of agricultural research. 2011; 6: 2026–2032.

[177] Wani ZA, Ashraf N, Mohiuddin T, Riyaz-Ul-Hassan S. Plant-endophyte symbiosis, an ecological perspective. Applied Microbiology and Biotechnology. 2015; 99: 2955–2965.

[178] Ek-Ramos MJ, Gomez-Flores R, Orozco-Flores AA, Rodríguez-Padilla C, González-Ochoa G, Tamez-Guerra P. Bioactive Products from Plant-Endophytic Gram-Positive Bacteria. Frontiers in Microbiology. 2019; 10: 463.

[179] Ahanger MA, Tyagi SR, Wani MR, Ahmad P. Drought Tolerance: Role of Organic Osmolytes, Growth Regulators, and Mineral Nutrients. Physiological Mechanisms and Adaptation Strategies in Plants under Changing Environment. 2014; 2: 25–55.

[180] Etesami H, Alikhani HA. Bacillus species as the most promising bacterial biocontrol agents in rhizosphere and endorhiza of plants grown in rotation with each other. European Journal of Plant Pathology. 2018; 150: 497–506.

[181] Sadeghi F, Samsampour D, Askari Seyahooei M, Bagheri A, Soltani J. Fungal endophytes alleviate drought-induced oxidative stress in mandarin (Citrus reticulata L.): toward regulating the ascorbate–glutathione cycle. Scientia Horticulturae. 2020; 261: 108991.

[182] Jiao J, Ma Y, Chen S, Liu C, Song Y, Qin Y, et al. Melatonin-producing endophytic bacteria from grapevine roots promote the abiotic stress-induced production of endogenous melatonin in their hosts. Frontiers in Plant Science. 2016; 7: 1387.

[183] Li J, Meng B, Chai H, Yang X, Song W, Li S, et al. Arbuscular Mycorrhizal Fungi Alleviate Drought Stress in C3 (Leymus chinensis) and C4 (Hemarthria altissima) Grasses via Altering Antioxidant Enzyme Activities and Photosynthesis. Frontiers in Plant Science. 2019; 10: 499.

[184] Ghaffari MR, Mirzaei M, Ghabooli M, Khatabi B, Wu Y, Zabet-Moghaddam M, et al. Root endophytic fungus Piriformospora indica improves drought stress adaptation in barley by metabolic and proteomic reprogramming. Environmental and Experimental Botany. 2019; 157: 197–210.

[185] Sun C, Johnson JM, Cai D, Sherameti I, Oelmüller R, Lou B. Piriformospora indica confers drought tolerance in Chinese cabbage leaves by stimulating antioxidant enzymes, the expression of drought-related genes and the plastid-localized CAS protein. Journal of Plant Physiology. 2010; 167: 1009–1017.

[186] Pandey V, Ansari MW, Tula S, Yadav S, Sahoo RK, Shukla N, et al. Dose-dependent response of Trichoderma harzianum in improving drought tolerance in rice genotypes. Planta. 2016; 243: 1251–1264.

[187] Sheibani-Tezerji R, Rattei T, Sessitsch A, Trognitz F, Mitter B. Transcriptome Profiling of the Endophyte Burkholderia phytofirmans PsJN Indicates Sensing of the Plant Environment and Drought Stress. MBio. 2015; 6: e00621–15.

[188] Schimel JP. Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. Annual Review of Ecology, Evolution, and Systematics. 2018; 49: 409–432.

[189] Becklin KM, Anderson JT, Gerhart LM, Wadgymar SM, Wessinger CA, Ward JK. Examining Plant Physiological Responses to Climate Change through an Evolutionary Lens. Plant Physiology. 2016; 172: 635–649.

[190] Gupta A, Rico-Medina A, Caño-Delgado AI. The physiology of plant responses to drought. Science. 2020; 368: 266–269.

[191] Lau JA, Lennon JT. Rapid responses of soil microorganisms improve plant fitness in novel environments. Proceedings of the National Academy of Sciences of the United States of America. 2012; 109: 14058–14062.

[192] Jez JM, Lee SG, Sherp AM. The next green movement: Plant biology for the environment and sustainability. Science. 2016; 353: 1241–1244.

[193] Edwards J, Johnson C, Santos-Medellín C, Lurie E, Podishetty NK, Bhatnagar S, et al. Structure, variation, and assembly of the root-associated microbiomes of rice. Proceedings of the National Academy of Sciences of the United States of America. 2015; 112: E911–E920.

[194] Fitzpatrick CR, Copeland J, Wang PW, Guttman DS, Kotanen PM, Johnson MTJ. Assembly and ecological function of the root microbiome across angiosperm plant species. Proceedings of the National Academy of Sciences of the United States of America. 2018; 115: E1157–E1165.

[195] Xu L, Naylor D, Dong Z, Simmons T, Pierroz G, Hixson KK, et al. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. Proceedings of the National Academy of Sciences. 2018; 115: E4284–E4293.

[196] Ault TR. On the essentials of drought in a changing climate. Science. 2020; 368: 256–260.

[197] Timm CM, Carter KR, Carrell AA, Jun S, Jawdy SS, Vélez JM, et al. Abiotic Stresses Shift Belowground Populus-Associated Bacteria toward a Core Stress Microbiome. MSystems. 2018; 3: e00070–17.

[198] Diamond S, Andeer PF, Li Z, Crits-Christoph A, Burstein D, Anantharaman K, et al. Mediterranean grassland soil C–N compound turnover is dependent on rainfall and depth, and is mediated by genomically divergent microorganisms. Nature Microbiology. 2019; 4: 1356–1367.

[199] Malla MA, Dubey A, Kumar A, Yadav S, Hashem A, Abd_Allah EF. Exploring the Human Microbiome: The Potential Future Role of Next-Generation Sequencing in Disease Diagnosis and Treatment. Frontiers in Immunology. 2019; 9: 2868.

[200] Xu L, Dong Z, Chiniquy D, Pierroz G, Deng S, Gao C, et al. Genome-resolved metagenomics reveals role of iron metabolism in drought-induced rhizosphere microbiome dynamics. Nature Communications. 2021; 12: 3209.

[201] Michaletti A, Naghavi MR, Toorchi M, Zolla L, Rinalducci S. Metabolomics and proteomics reveal drought-stress responses of leaf tissues from spring-wheat. Scientific Reports. 2018; 8: 5710.

[202] Chmielewska K, Rodziewicz P, Swarcewicz B, Sawikowska A, Krajewski P, Marczak Ł, et al. Analysis of Drought-Induced Proteomic and Metabolomic Changes in Barley (Hordeum vulgare L.) Leaves and Roots Unravels Some Aspects of Biochemical Mechanisms Involved in Drought Tolerance. Frontiers in Plant Science. 2016; 7: 1108.

[203] Gundaraniya SA, Ambalam PS, Tomar RS. Metabolomic Profiling of Drought-Tolerant and Susceptible Peanut (Arachis hypogaea L.) Genotypes in Response to Drought Stress. ACS Omega. 2020; 5: 31209–31219.

[204] Das A, Rushton PJ, Rohila JS. Metabolomic Profiling of Soybeans (Glycine max L.) Reveals the Importance of Sugar and Nitrogen Metabolism under Drought and Heat Stress. Plants. 2017; 6: 21.

[205] Cao L, Jin X, Zhang Y, Zhang M, Wang Y. Transcriptomic and metabolomic profiling of melatonin treated soybean (Glycine max L.) under drought stress during grain filling period through regulation of secondary metabolite biosynthesis pathways. PLoS ONE. 2020; 15: e0239701.

[206] Liang Z, Chen K, Li T, Zhang Y, Wang Y, Zhao Q, et al. Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. Nature Communications. 2017; 8: 14261.

[207] Zhang Z, Hua L, Gupta A, Tricoli D, Edwards KJ, Yang B, et al. Development of an Agrobacterium-delivered CRISPR/Cas9 system for wheat genome editing. Plant biotechnology journal. 2019; 17: 1623–1635.

[208] Andersson M, Turesson H, Nicolia A, Fält A, Samuelsson M, Hofvander P. Efficient targeted multiallelic mutagenesis in tetraploid potato (Solanum tuberosum) by transient CRISPR-Cas9 expression in protoplasts. Plant Cell Reports. 2017; 36: 117–128.

[209] Ryder P, McHale M, Fort A, Spillane C. Generation of stable nulliplex autopolyploid lines of Arabidopsis thaliana using CRISPR/Cas9 genome editing. Plant Cell Reports. 2017; 36: 1005–1008.

[210] Fang H, Meng Q, Xu J, Tang H, Tang S, Zhang H, et al. Knockdown of stress inducible OsSRFP1 encoding an E3 ubiquitin ligase with transcriptional activation activity confers abiotic stress tolerance through enhancing antioxidant protection in rice. Plant Molecular Biology. 2015; 87: 441–458.

[211] Osakabe Y, Watanabe T, Sugano SS, Ueta R, Ishihara R, Shinozaki K, et al. Optimization of CRISPR/Cas9 genome editing to modify abiotic stress responses in plants. Scientific Reports. 2016; 6: 26685.

[212] Habben JE, Bao X, Bate NJ, DeBruin JL, Dolan D, Hasegawa D, et al. Transgenic alteration of ethylene biosynthesis increases grain yield in maize under field drought-stress conditions. Plant Biotechnology Journal. 2014; 12: 685–693.

[213] Shi J, Gao H, Wang H, Lafitte HR, Archibald RL, Yang M, et al. ARGOS8 variants generated by CRISPR-Cas9 improve maize grain yield under field drought stress conditions. Plant Biotechnology Journal. 2017; 15: 207–216.

[214] Osakabe Y, Osakabe K, Shinozaki K, Tran LSP. Response of plants to water stress. Frontiers in Plant Science. 2014; 5: 86.

Send correspondence to:

Ashwani Kumar, Metagenomics and Secretomics Research Laboratory, Department of Botany, Dr. Harisingh Gour University (A Central University), 470003 Sagar, Madhya Pradesh, India, Mycorrhizal Research Laboratory, Department of Biochemistry and Microbiology, Rhodes University, 6140 Grahamstown (Makhanda), South Africa E-mail: ashwaniiitd@hotmail.com

Joanna Felicity Dames, Mycorrhizal Research Laboratory, Department of Biochemistry and Microbiology, Rhodes University, 6140 Grahamstown (Makhanda), South Africa, E-mail: j.dames@ru.ac.za