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Drought Stress and Growth Regulation: Review in the Role of Hormonal Regulation(Review Article).

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ABSTRACT

During their life cycle, plants are always exposed to multiple abiotic stresses that negatively affect their growth and development. Based on this fact, plants developed many mechanisms to reduce or tolerate those stresses. Plants undergo a wide range of morphological, physiological, and biochemical changes in response to environmental stresses. However, drought is one of many other environmental stresses which is considered to be the most significant environmental issues that affect the lives of organisms on the planet of Earth. With the recent increase in the severity of climate change, researchers have devoted their efforts to a deeper understanding of the effects of drought on the level of plant response from a physiological and biochemical standpoint. With the recent increase in the severity of climate change, the problem of drought has gotten worse. Thus, researchers have focused their efforts on developing a deeper knowledge of how drought affects plant response at the physiological and biochemical levels. The plant undergoes several significant changes, one of which is an alteration in its hormonal balance. Specific hormones become more effective and assist the plant in sustaining a tolerable level of free radicals, while other hormones become less active under non-growth-promoting environments. Abscisic acid, sometimes referred to as the stress hormone, is one of these plant hormones. Its function under stress is to slow down the plant's growth to keep it at an acceptable level of growth. The hormones ascorbic acid, glycine betaine, alpha-tocopherol, melatonin, and Jasmonic are known to be growth-stimulating substances as well as non-enzymatic antioxidants that help suppress and eliminate free radical formation. Focusing on this, this review highlighted the function of several plant hormones and the processes that accompany them in reducing the harm caused to plants by drought stress.

***Keywords*:** *Abiotic Stresses, Antioxidants, Free radicals, Plant hormones*.

INTRODUCTION

The effects of biotic and abiotic environmental stresses on agricultural crop productivity have grown due to Earth's changing climate, and this has led to a decline in agriculture worldwide, particularly in Iraq [1]. The primary impacts of climate change on field crops, including wheat, maize, sorghum, mung bean, and others. The main climate factors are high temperatures, variability in rainfall during the growing season, and lack of it. This leads to a decline in arable land productivity, which was previously thought to be 40% of dry land [1]. Drought challenges have become more widespread globally due to their impact on most arable lands. The affected areas are growing by 1% yearly. The water deficit in plant cells significantly disrupts vital processes such as photosynthesis, respiration, absorption, transpiration, etc. Therefore, drought can be categorized as multi-dimensional stress since an increase in temperature accompanies it, and both stresses are sources of biotic stress that cause plants to experience biotic stress by promoting an environment that encourages the growth of disease and insect infestations [3]. This can have disastrous consequences that plants may not be able to withstand, or the plants may even die [2]. Due to its direct impact on physiological, morphological, and biochemical processes, drought is one of the environmental factors most closely associated with the decline in growth and plant productivity, both quantitatively and qualitatively. This decrease in productivity was estimated to be worth $69 billion in the United States between 2015 and 2019 [4]. Plants under water stress produce a large number of toxic substances called free radicals, which damage vital molecules within the cell and ultimately lead to the death or damage of the plant cells.

The electron transport chain's reactions, photosynthesis, and the efficiency of antioxidant enzymes are the most significant processes that those free radicals target. Thus, biological systems and their constituents—such as proteins, lipids, DNA, and RNA—are destroyed by oxidation [5]. Along with other adaptation mechanisms, plants also possess defense mechanisms in the form of enzymatic (catalase, peroxidase, superoxide dismutase, etc.) and non-enzymatic (flavonoids, carotenoids, proline, glycine betaine, etc.) antioxidants. They alleviate the deleterious consequences of free radicals, including O^{2-}, OH, and H_2O_2 [6].

Many studies reported that the use of plant growth regulators is beneficial to plants during stresses. The application of those growth regulators is important to investigate the effects of environmental stresses to which the plant is exposed. Salicylic acid (SA), tocopherols (TOC), and melatonin are among the most significant growth regulators that contribute to plants' resistance to water stress as well as their significant activation of enzymatic and non-enzymatic antioxidants. Many reports indicate the quantitative and qualitative effects on declining crop productivity [7]. Besides, their role in controlling numerous biological and physiological processes in plants, like stomata opening and closing, photosynthesis, scavenging the effects of free radicals, and ion absorption [8]. The current review highlighted how growth regulators function to reduce oxidative stress in plants that result from water stress and to activate both enzymatic and non-enzymatic defensive mechanisms.

The role of abscisic acid in plants during drought

The hormone known as abscisic acid (ABA) is frequently linked to the main stress-related reactions in plants. Hemberg's findings confirmed that abscisic acid (ABA) is a water- and ether-soluble inhibitor that is necessary to keep potatoes and Fraxinus bud dormant [9], [10]. In 1960, abscisic acid was discovered [11]. The production and catabolism of ABA are controlled by a complex network of genes that are subject to multi-level regulation in response to environmental changes. For the preservation of botanical germplasm and biodiversity, seeds are an essential resource [12]. Numerous variables related to ABA production, metabolism, transcription, and signalling have been discovered by researchers [13], [14].

Exogenous abscisic acid (ABA) has been shown to accelerate the ripening of various fruits (e.g., tomatoes, bananas, peaches, mangos, and watermelons) through modifying biological effects on several ripening-related processes. Exogenous application of ABA increases the rate of ethylene synthesis and activity. The ripening process in fruits is accelerated by the respiratory system, as supported by various studies [15], [16], [17], [18], [19]. ABA, or abscisic acid, is a plant hormone that plays a crucial role in several physiological functions of higher plants, including stomatal closure, leaf fall, and bud and seed dormancy induction [20]. It has been found that ABA decreases the pre-germination process in roots and controls the development of mature seeds in cucumbers, suggesting that it has a significant role in the development of fruit tree seeds[51]. Studies have shown that adding ABA to grape varieties during the pre-harvest stage increases their phenolic content while reducing the amount of tannin in grape skins [22]. Studies have shown that adding ABA to grape varieties during the pre-harvest stage increases their phenolic content, while reducing the amount of tannin in grape skins [23], [24]. ABA is also believed to control plant hormones and bud dormancy in plants, specifically in preserving the survival of fruit species [25]. [26]. Additionally, when ABA was applied externally to potted miniature roses, it decreased respiration and water loss while increasing the longevity of the flowers [27]. Recent research has also demonstrated that spraying seven out of nine species of bedding plants with 125 to 250 mg of ABA delayed the onset of drought-induced wilt symptoms, increasing their drought resistance [28]. As a result, plants that get exogenous abscisic acid (ABA) treatments have increased their drought resistance.In addition to controlling cell division and responses to external environmental changes, including drought, salinity, cold, UV radiation, and pathogenic organisms, the hormone ABA is crucial in controlling plant growth and development [29]. ABA is found in both higher and lower plants, and it may have the primary role in controlling plant water relations, particularly in times of drought. It's generally known that ABA can instantly close stomata. For example, ABA can activate the phospholipid pathway to signal water stress, even though it can also be a secondary signal in many other pathways. Nevertheless, his function extends beyond that. Furthermore, there might be additional ABA-related routes that are not yet discovered [30]. As in the two previously mentioned pathways, it may not be possible to accurately and completely conceptualize a sensing pathway that depends just on ABA with the information now available. This is due to the multitude of genes that are responsive to this hormone and how its mechanisms of action are entangled with various forms of biotic and abiotic stress [31]. Many genes in plants become more active in response to either osmotic stress, salt stress, or both. A significant portion of these genes is also triggered by cold or ABA treatment of the plant. Numerous genes encoding transcription factors that are instantly triggered by stress or ABA have been found. Certain genes might be dependent on other transcription factors that are constitutively expressed (constantly activated), and their proteins might be present in the cell but inactive until they are triggered by protein kinases, which then trigger the activation of transcription factors that react to stress [23]. It is well known that not all of the genes triggered by stress rely on ABA; rather, some of the genes are triggered without it. Numerous investigations on ABA-deficient mutant plants—plants that are unable to synthesize ABA—or plants that are unable to detect ABA presence at all provided evidence for this (ABA-insensitive mutants). For instance, [33] reported that these plants can still partially activate the RD29A gene in the absence of ABA. The gene's promoter, which consists of a sequence of nitrogenous bases that react to water stress, is enough to activate the gene even in the absence of ABA.

The internal Cis element is the sequence that reacts to water stress (DRE). The terminology "internal element" indicates that its focus is on triggering the same gene in which it resides. The trans elements, or external activation elements, are specific to activating other genes. Besides the ones that have the external activation elements, these could also be transcription factors or segments of DNA. The internal stress-responsive element can bind to the transcription factors DREB2A and DREB2B. (DRE). The RD29A gene's transcription is triggered independently of ABA levels [34], [35]. However, this does not imply that the DRE and ABA are separate entities. ABA activates the transcription process of the transcription factor CBF4 (Cold Responsive Element Binding Factor), determining its activity. Genes with the DRE become permanently activated when overexpression of this factor rises (normally this is not the case, but may belong to genes' rapid stress reaction and increased resistance to cold and drought in plants. This suggests that DRE and ABA have a connection, although an indirect one. It is important to determine that ABA (Figure 1) contributes to the activation of stress genes and that genes that are active independently of ABA may require ABA to control their activity. Nevertheless, there are still a lot of unanswered questions that make this image appear incomplete [36].

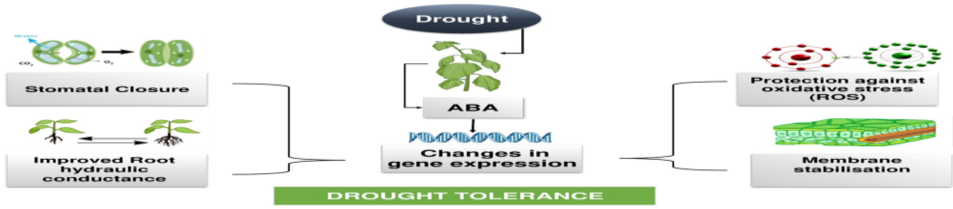

Figure 1. Mechanisms of action of abscisic acid in improving plants' ability to tolerate drought.

The role of ascorbic acid in plants during drought

Vitamin C is another name for it. After isolating a reductase from the cortex of the adrenal glands (suprarenal) and certain plants, such as oranges, the scientist A. SZENT-GYRRGYI discovered it in 1928. One of the key antioxidants is ascorbic acid, sometimes referred to as vitamin C. [37]. In 1998, it was also found in plants; it is mostly found in fruits and vegetables and promotes both the growth and development of the plant as well as its physiological functions [38]. Fruits, vegetables, and other plants contain ascorbic acid, which is regarded as one of the most vital vitamins for a human diet. Also, it helps the plant grow through several growth stages, including blooming, maturity, and others, and is engaged in physiological metabolic activities [39]. In that regard, it is superior to other antioxidants. It is soluble in water and stimulates the production of other hormones and the metabolism of carbon dioxide, among other enzymes [40]. Due to the reduction of both the fresh and dry weights of the roots, drought stress has a substantial effect on the roots. Based on the results of the studies and interactions, ascorbic acid raises the fresh and dry weight of the roots, strengthening them against drought [41]. Exogenous application of this hormone to plants stressed by drought has also been demonstrated to significantly stimulate root growth and remove active oxygen molecules from the plants [42]. Ascorbic acid controls stomata mobility in leaves and enhances carbon metabolism. Additionally, it prevents the formation of reactive oxygen compounds in the leaves, and it enhances the chlorophyll content [43], [44]. Ascorbic acid sprayed on the plant postpones the senescence of its leaves [45]. When a plant experiences drought stress, its leaves lose some of their carbohydrates, chlorophyll, and carbon dioxide content. However, these impacts were greatly mitigated when ascorbic acid was present [46]. Ascorbic acid is the most efficient antioxidant at preventing and protecting plants against stress, according to several studies on the impact of non-enzymatic antioxidants [47]. When plants are treated with ascorbic acid, stress-induced damage is decreased, growth is accelerated, and antioxidant enzymes are activated. To minimise salinity damage, plant foliar application is the most effective method of application [48]. Its application also improved the drought-stressed plants' traits by speeding up their vegetative growth, increasing grain yield, and increasing the weight of their seeds [49]. As a result, it is evident that ascorbic acid (Figure 2), one of the most significant antioxidants, improves plants that are stressed by drought and lowers stress, increasing growth rate and yield, as well as soluble sugars, amino acids, and carbohydrates. These are the detrimental impacts of stress. It is advised to apply it to all stressed plants [50].

As a non-enzymatic antioxidant, ascorbic acid can alter fundamental plant processes both in the presence and absence of stress and counteract the damaging effects of free radicals (ROS) [51]. Because of plant sciences may help prevent diseases, the availability of ascorbic acid and other antioxidants has stoked interest in the field [52]. It's significant in preventing environmental stresses such as radiation, heat, heavy metal oxidation, etc. and also promotes crop productivity. Plant growth is regulated in many contexts [53]. Ascorbic acid excess in plants is also something to be cautious about, as it is one of the many stresses that prevent plant growth and increase reactive oxygen species [54]. According to [55], ascorbic acid allows plants to adjust physiologically and decreases oxidative damage when they are under abiotic stresses, including drought. It can also help citrus trees that are exposed to salt. Additionally, it reduces the quantity of aldehydes that rose as a result of drought stress. This demonstrates how ascorbic acid strengthens plants' ability to withstand drought stress [51]. When plants treated with ascorbic acid under drought stress are compared to untreated plants, the growth rate, chlorophyll content, and rate of carbon metabolism increase [57]. Its function extends beyond that of an antioxidant since many of the enzymes involved in the food-plant response view it as a cofactor [37]. It alleviates the plant's absorption of vital minerals like calcium, potassium, phosphorus, and nitrogen and decreases the accumulation of sodium in different plant parts [38]. The plant's dry and fresh weight increased as a result of the application of this acid, and the crop seeds' overall fertility also increased [39].

Figure 1. Mechanism of action of ascorbic acid in improving plants' ability to tolerate drought.

The role of Glycine Betaine in plants during drought

In 1820, glycine betaine was initially extracted from gelatin. The word "sweet" (γλυκύς) in ancient Greek is the source which connects to the prefixes glyco- and gluco, as in glycoprotein. Its formula is NH_2CH_2COOH, making it an organic chemical. Glycine betaine is the smallest of the twenty amino acids that are frequently found in proteins, having a side chain that replaces hydrogen. The genetic code's GGU, GGC, GGA, and GGG are its codons. One of the substances implicated in various additional defense mechanisms against stress-related plant diseases is glycine betaine (GB) [58], [59]. Glycine betaine (GB) is a volatile, highly water-soluble metabolite that remains electrically neutral throughout a broad pH range [60]. GB concentration in cells has a role in several halophytes' osmotic stress [61]. Compared to halophytes, glycine betaine (GB) is present in much less concentrations. However, glycine betaine (GB) can balance the oxidation osmotic potential and greatly contribute to the increase in osmotic pressure since it is only partitioned into the cytosol and hyaloplasmic organelles, which make up about 20% of the cell volume or less ([62], [63]. Glycine betaine (GB) has been shown by [64] and [65] to serve as an osmotic layer for osmotic adjustment as well as to interact with the hydrophilic and hydrophobic domains of protein complexes and membranes, helping to stabilize and maintain integrity. These molecules' structural and functional analysis, protects them from the damaging effects of highly reactive oxygen species (ROS). According to [66], GB can decrease salt-induced potassium efflux by controlling ion channels, boosting enzymatic activity in the plasma membrane, boosting phosphate uptake, and controlling phosphate homeostasis [67]. Furthermore, without impairing the original functional activities of proteins, glycine betaine (GB) could restore protein misfolding and/or aggregation and preserve the thermodynamic stability of macromolecules [68]. [69], [70], and [71] demonstrated that proline and high levels of glycine betaine (GB) are very effective in protecting plants from oxidative stress, where metabolites play a part in plant defense. Enzymes that are antioxidants play a small part in protecting ROS against salinity. The investigation has also shown that glycine betaine (GB) stabilizes the structures and functions of enzymes and protein complexes and protects the integrity of membranes from the damaging effects of excessive salt. GB is not merely a non-toxic cellular osmotic substance that increases intracellular osmosis when the cell is exposed to hyperosmotic conditions brought on by stress. Furthermore, glycine betaine (GB) has been shown through biochemical and biophysical studies to protect membranes from heat, freezing, and various chemicals. It also protects membranes from lipid peroxidation under cooling. Studies conducted by Farooq [72] and [64] have reported the significance of glycine betaine (GB) in water conservation and protecting biological membranes and proteins in higher plants subjected to osmotic, water, and oxidative stresses [73]. Researchers have also discovered that GB can enhance plant response to low-phosphate stress by maintaining a higher rate of photosynthesis and increasing sucrose transport through phloem loading [64]. Additionally, GB may regulate ion channels and transporters, leading to an increase in potassium levels and a decrease in sodium levels, thereby improving transgenic plants' ability to withstand salt stress. By adjusting metabolic imbalances brought on by stress, GB can enhance plant growth and survival (Figure 3). The external application of GB has been studied extensively in low-accumulating and non-accumulating plant species, owing to its many benefits. Owing to the advantages of glycine betaine (GB), numerous studies on low-accumulating and non-accumulating plant species have been conducted on the external application of this suitable substance. Furthermore, GB protects photosynthesis by modifying the lipid content of wheat thylakoid membranes [22]. To protect plant cells from osmotic stress brought on by salt and dehydration, it also increases soluble sugars and the synthesis of free amino acids (Vigna unguiculata, Phaseolus vulgaris, Pisum sativum) [16], [18], [74]. Moreover, GB impacts the activity of antioxidant metabolites and enzymes [15].

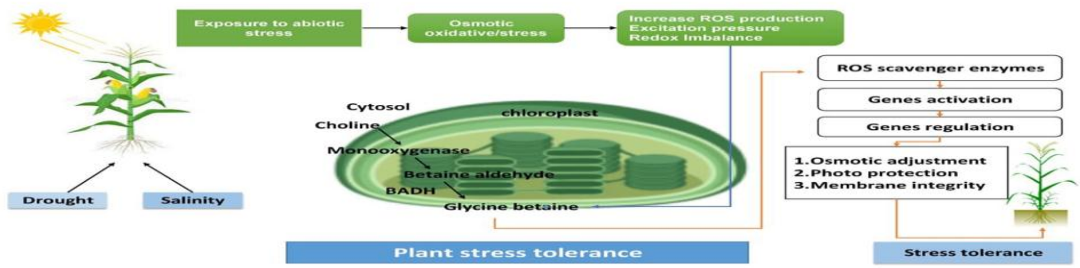

Figure 2. Mechanism of action of Glycine Betaine in improving plants' ability to tolerate drought.

The Role of α-Tocopherol in plants during drought

A substance known as "Factor Plant-derived oils are the principal sources of vitamin E, and comprise four tocopherol constituents in various quantities" was discovered in 1922 during efforts to identify the key nutritional factors for rat reproduction. Walnut oil mainly contains γ-tocopherol, whereas corn oil has larger quantities of δ-tocopherol. Almond and sunflower oils have higher levels of α-tocopherol. Notably, animals cannot synthesize tocopherol, and methylation or demethylation is not the process by which the various forms of the vitamin are converted to one another. Natural α-tocopherol is widely used in the food, pharmaceutical, and cosmetic industries since it is abundant [38]. This material is colored yellowish-brown and has a high viscosity. It is also a fat-soluble substance with no odour that is noticeable. Because tocopherols are fat-soluble, they can be obtained naturally in various food sources, although their main source is vegetable oils. Tocopherol is also present in relatively small amounts in several fruits and vegetables, although nuts are an even better source. However, because different researchers employ different analytical techniques and because variation exists because of the taxa under study, the provided values are not very exact. Moreover, the tocopherol content of vegetable oils might change during processing [75], [76]. Essential fat-soluble antioxidant vitamin E is produced from 6-chromanol. Typically, 6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid is used to produce vitamin E. The two most frequent forms of vitamin E derivatives seen in dietary supplements are succinate and acetate esters [77]. Vitamin E comprises a hydrophobic side chain with sixteen carbon atoms and a chromanol ring that comes from a phosphatidyl group (Figure 4). The Greek alphabet's first four letters, α (alpha), β (beta), γ (gamma), and δ (delta) tocopherol, are used to distinguish the four different forms of this group of tocopherols. The quantity and orientation of CH_3 groups on the chromanol head group define its distinctiveness. It can be observed that α-Tocopherol contains CH_3 groups attached to positions 5, 7, and 8 of the rings. Still, β-Tocopherol has two CH_3 groups at positions 5 and 8. γ-Tocopherol possesses two CH_3 groups at positions 7 and 8, but δ-Tocopherol only has one CH_3 group connected to position 8 from the head side [78].

The impact of tocopherol on plant roots and leaves:

Protection from oxidation: The utilization of tocopherol in plants has been found to provide several benefits. Firstly, it prevents the oxidation of cell membrane lipids, which can lead to cell death. [79] found that leaf tissues are more vulnerable to oxidative damage due to their lower levels of tocopherol compared to non-stressed tissues [79].

Regulating photosynthesis: ocopherol helps in regulating photosynthesis and chlorophyll biosynthesis, which can ultimately lead to increased plant growth and yield. It has been demonstrated that these effects [80].

Boost plant resistance to stress: tocopherol can enhance a plant's resistance to environmental stressors, such as salinity, extreme heat, and drought [81].

Delaying the senescence of leaves: tocopherol can delay the senescence of leaves by maintaining their chlorophyll content, which is crucial for photosynthesis and overall plant growth. They have highlighted the importance of chlorophyll content in water-limited environments [82].

Promoting root growth: tocopherol promotes root growth and root hair formation, leading to efficient water absorption and increased tolerance to drought conditions [81].

Protection against oxidative damage: tocopherol protects root cells from oxidative damage caused by reactive oxygen species, thus improving root functions.

Regulating gene expression: tocopherol regulates the expression of genes related to plant development and stress tolerance, as discussed by [84].

Plants produce tocopherol, a significant fat-soluble antioxidant that plays a crucial role in protecting them from oxidative damage. Although not naturally produced by the human body, tocopherol can be obtained through diet and has several health benefits. Tocopherols, as fat-soluble antioxidants, prevent oxidative damage to cell membranes by scavenging free radicals and reactive oxygen species (ROS) generated under stress. Overproduction of ROS-activated substances can lead to oxidation of biological components such as proteins, DNA, and lipids, resulting in cell damage and death [77], [78] By removing free radicals directly or indirectly through the glutathione ascorbate cycle, a plant antioxidant defense mechanism, tocopherols can inhibit the accumulation of reactive oxygen species. Ascorbic acid, vitamin C, and glutathione are the antioxidants and enzymes that make up the glutathione ascorbate cycle. These substances work together to eliminate reactive oxygen species (ROS) and maintain redox equilibrium in cells [85], [86], [87]. Studies on vitamin E deficiency in Arabidopsis mutants have shown that tocopherol in chloroplasts under oxidative stress has antioxidant properties [88]. However, the further roles of tocopherols in plants and animals are still unknown [89]. Tocopherol deficiencies in plants indicate a limitation in the processes of transferring synthetic chemicals from the leaves to the remaining plant, indicating that tocopherols are crucial for the transportation of sucrose[90]. Tocopherol plays a vital role in preserving the photosynthetic apparatus from oxidative damage, essential for tolerating stress during prolonged exposure to sunlight. Tocopherol prevents lipid peroxidation, which can damage the membrane and impair photosynthetic performance. In addition to defending chlorophyll from deterioration, tocopherol also helps the photosynthetic process recover from stressful situations [91]. Genetic and environmental factors both contribute to variation in plant tocopherol content. Environmental factors such as drought and high temperatures have a more significant effect on the amounts of tocopherol in seeds, while the quantities of tocopherol in leaves are known to be significantly influenced by environmental factors. For instance, soybean seeds exposed to a 5°C temperature increase during the seed-filling period showed a notable two- to three-fold rise in α-Tocopherol concentration. Similarly, heat and drought have a substantial impact on almonds' tocopherol levels [18], [92]. Furthermore, plants exposed to various abiotic stresses, such as those caused by heavy metals, salt, high light, cold, and combined light and temperature stress, have been found to have high levels of tocopherols. Under various environmental conditions, tocopherol accumulation can protect plant cells from oxidative stress damage [94], [95], [96], salt stress [97], [98], high light stress [99], cold stress [100], and combined light and temperature stress [101]. In conclusion, tocopherol has several benefits for both plants and animals. It acts as an antioxidant, preventing oxidative damage to cell membranes and protecting the photosynthetic apparatus from damage. Tocopherol deficiencies in plants can lead to limitations in the transportation of sucrose, while its accumulation under stress can protect plant cells from oxidative stress damage [102]. Numerous studies have shown that plants that have survived stress have higher amounts of tocopherol under stress, whereas plants that are sensitive to stress and are unable to resist it have lower levels of tocopherol. Furthermore, it can function as signaling molecules to trigger genes that respond to stress, enabling plants to adjust to demanding conditions. For instance, it has been demonstrated that tocopherol stimulates the expression of genes related to abscisic acid (ABA) signaling, a hormone that controls how plants react to drought stress. Additionally, applying nitrogen fertilizers to plants can raise their tocopherol concentrations [103].

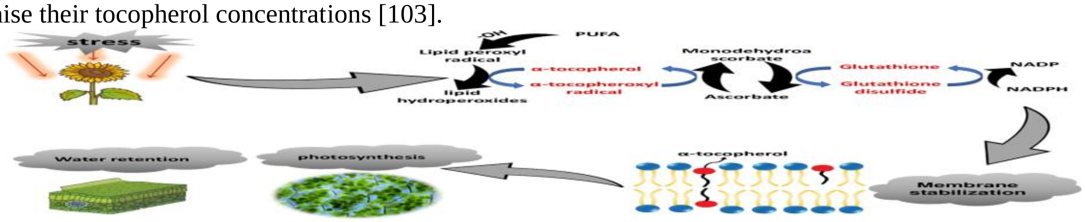

Figure 3. the process of how a-tocopherol eliminates free radicals and its interaction with glutathione, ascorbic acid, and chloroplasts to restore cell walls is illustrated.

The role of Melatonin in plants during drought

The 1958 discovery of this hormone came from the secretions of the pineal glands of cows [82]. In 1995, it was found in plants. Most of the plant's components, including the stem, leaves, roots, and seeds, also contain it. Its capacity to split fish and amphibian skin is why it was given its name. It assists plants in many ways, including physiological functions, growth and development regulation, and antioxidant defense against reactive oxygen species (ROS) [104]. The primary hormone that the pineal glands generate is thought to be MLT. It not only controls physiological processes but also acts as an immunomodulator, antioxidant, and anti-ageing substance. It also plays a significant part in blood formation [105]. It controls a significant portion of the physiological processes that impact patterns. Various impacts on the living organisms [106]. In addition to its powerful antioxidant properties, it also affects hormones [107]. Melatonin affects plants that survive under drought stress by conserving water in the leaves, reducing chlorophyll content loss and leakage, regulating stomatal movement, and enhancing the plant's ability to assimilate carbon [108]. Melatonin promotes roots, promotes root vigour and growth, and decreases ROS damage induced by water stress [114]. Melatonin also promotes root production and growth, as the results revealed that melatonin is crucial for the plant's root system [109]. Numerous studies—many of which focused on oats—have revealed that melatonin regulates growth, has a role in plant physiological processes and development, and provides plants with tolerance to drought stress [51], Pears [53], apples [56], kiwifruit [83], maize [55], tomatoes [52], cucumbers [53], wheat [54], etc. Melatonin is employed as a bio-stimulant to treat plants and has been demonstrated to boost them against biotic and abiotic challenges and the finding proved that plants can withstand drought stress [110]. Several animal functions of melatonin have been discovered, prompting research on its physiological roles in plants. Studies have shown that melatonin provides antibacterial resistance to stressors such as drought, salinity, high and low

temperatures. Melatonin has also been found to play a significant role in plant growth and structure, making it a popular plant growth regulator and stimulant that enhances plant resilience to environmental challenges, especially drought stress [107]. It has gained popularity recently as a plant growth regulator and stimulant that increases plant resilience to environmental challenges, particularly drought stress [111]. Melatonin's primary function in plants is to protect them from internal and external oxidative stressors. It also regulates crop yield by boosting defense mechanisms and acts as a growth regulator for roots and shoots, promotes seed germination, aids in the production of roots, and slows down the aging process of plant leaves in the process of creating and preserving carbon in chlorophyll Arnao & Hernández-Ruiz, (2014), Melatonin also acts as an antioxidant and a plant protector against abiotic stresses,
including drought [112]. It is one of the most important hormones for reducing the harmful effects of drought stress [113]. Studies have shown that melatonin can improve plant growth traits and reduce drought stress. It can also increase the activation of peroxides and the catalase enzyme, reduce hydrogen peroxide H2O2, and help the plant adapt to drought stress and reduce oxidative damage as an antioxidant. These findings suggest that melatonin can improve field crop production by increasing yield, root growth, and protecting leaves to facilitate the process of light absorption [114], [115]. Plant productivity is decreased by abiotic stress, such as drought stress. Bio-stimulants, such as melatonin, carry out a variety of protective actions to decrease the effects of drought stress, and melatonin plays a significant part in plant activities. During seed germination and aging (Figure 5), it is a crucial antioxidant that promotes the removal of reactive oxygen species [116]. To assess the plant's response to drought stress,100 μM melatonin was also given, since this increased the plant's tolerance to the drought. In addition to preventing premature ageing of plant leaves during droughts, it also preserves chlorophyll contents from deficiency and controls the process of carbon metabolism [117].

Figure 4. Mechanism of action of Glycine Betaine in improving plants' ability to tolerate drought.

The role of Jasmonic acid in plants during drought

Plants naturally produce jasmonic acid (JA), a growth regulator that has a function in regulating certain morphological, physiological, and biochemical processes in plants [118]. In 1971, jasmonic acid was isolated from the fungus Lasiodiplodia theobromae and first found in the essential oils of Jasminum grandiflorum L. and Rosemary (Rosmarinus officinalis L.). The synthesis of jasmonic acid begins with linolenic acid to produce Jasmonic acid and the plant's plastids and peroxisomes are where it is produced (Taiz and Zeiger, 2010). Jasmonic acid is a fatty acid that comes from cyclopentanones and is a member of the oxylipins family of oxidized lipids [119]. These bioactive compounds, known as oxylipins, are generated nonenzymatically when polyunsaturated fatty acids spontaneously oxidize or enzymatically by lipoxygenases or alpha- dioxygenases [120]. Lipoxygenase (LOX) oxidizes linolenic acid to 12-oxo-phytodienoic acid, which is subsequently transformed into allene oxide synthase and allene oxide cyclase. Subsequently, three cycles of beta-oxidation and 12-oxo-phytodienoic acid reductase activity result in the synthesis of 12-oxo-PDA. Consequently, the octadecanoid pathway is the name given to the jasmonic acid production pathway [121], [122]. Plant hormone jasmonic acid is broken down into more than 30 active and inactive derivatives in the cytosol by metabolic processes. Depending on the pentanone ring, pentyl side chain, or carboxylic acid group, the compound is active [123], [124], [125], [126]. The primary forms of bioactive jasmone in plants include JA, cis-jasmone, MeJA, and JA-Ile among the series of metabolites [127], [128]. Decarboxylation of jasmone results in the production of cis-jasmone [129]. Jasmonic acid is converted to volatile MeJA by the action of carboxyl methyltransferase [130]. Plant hormones called jasmonates, which are produced from the metabolism of fatty acids in the cell membrane, attracted a lot of interest in the 1980s [131] (Figure 6). The groups of metabolites that result from the combination of
methyl jasmonate and jasmonic acid include antioxidants, quinones, terpenoids, alkaloids, phenylpropanoids, glucose glycolates, and polyamines in both free and conjugated forms [132]. Higher plants contain jasmonic in a variety of plant parts, with floral tissues containing the highest concentration of the compound. Conversely, it is present in mature leaves and roots, although less often [133]. Numerous critical biological processes in plants, including vegetative growth, cell cycle regulation, gametophyte biosynthesis, fruit ripening, senescence, inhibition of Rubisco biosynthesis, control of stomata's opening and closing, absorption of nitrogen and phosphorus, and glucose transport, are impacted by jasmonic acid [134]. It also has a role in regulating numerous genes in response to abiotic stressors as a transporter of signaling molecules.

There have been several studies that have established the relationship between jasmonic signaling pathways and the reduction of damage caused by drought stress in various plant species such as broccoli, rice, soybeans, pistachios (Arachis hypogaea),) [135] [136]. [137] Jasmonic acid (JA) has been found to make maize (Zea mays) plants more active in terms of antioxidant enzyme activity, including CAT, POD, and SOD [138]. Additionally, MeJA, a methylated derivative of JA, has been shown to improve the resistance to drought in barley (Hordeum vulgare) and beans (Vicia faba) by controlling the opening and closure of stomata [139], [140]. MeJA also enhances the activity of both enzymatic and non-enzymatic antioxidants, such as SOD, POD, CAT, APX, and glutathione reductase, thereby increasing the drought tolerance of cauliflower (B. oleracea) [129]. Moreover, a study has found that spraying JA on leaves increases the levels of anthocyanins, chlorophyll, and carotenoids in the leaves, as well as the effectiveness of the second photosynthetic system. JA also plays a significant role in regulating the opening and closing of stomata, which controls the exchange of gases and water within plants and can alter the size and form of leaves. These findings suggest that jasmonic signaling pathways could provide a promising strategy to enhance plant drought tolerance. [141].
The findings of Xing et al., (2020) investigations indicated the impact of sprayed jasmonic acid levels on the plant in most growth features and yield; the highest average in most traits of leaf area, plant height, number of leaves, dry shoot weight, and area index was obtained at a concentration of 5 mg L-1. Leaf area, stem diameter, root weight, root length, diameter, and size; total yield; chlorophyll content; and leaf concentrations of nitrogen, potassium, calcium, and magnesium. According to [143] methyl jasmonate increased the amount of H_2O_2 that accumulated in Arabidopsis guard cells, which caused the cells to close their stomatal openings in reaction to stress. They also demonstrated that jasmonic acid spraying on leaves increased watermelon seedlings' resistance to drought stress by preventing stomatal openings. Tomato plants were used in an experiment with various MeJA doses.

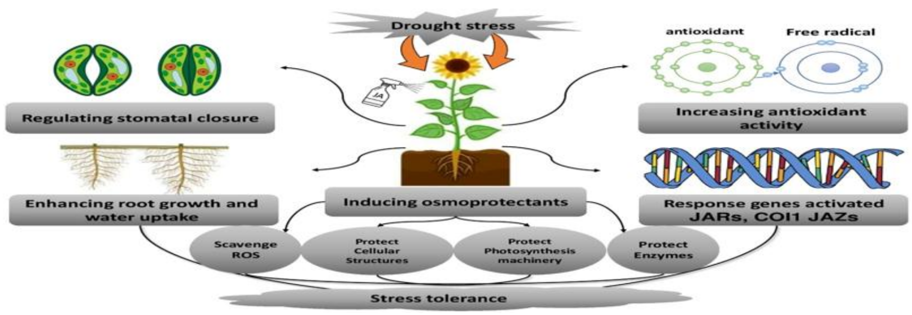

Figure 5. Mechanism of action of Glycine Betaine in improving plants' ability to tolerate drought.

The impact of MeJA on plant roots and leaves:

Jasmonic acid can develop defensive substances in plant leaves, such as phenols, alkaloids, and terpenoids. These help repel animals and pathogens from insects and other sources, thereby regulating or accelerating plant defensive responses. It has also been demonstrated to enhance plant production of proteins, carbohydrates, and starches in leaves [144].

The form of leaves can be modified by using jasmonic acid, which has been found to make them smaller and rounder. This alteration can help improve their ability to withstand wind. Furthermore, jasmonic acid can reduce the quantity of sunlight that leaves receive, which can cause them to fall in the case of heat stress [65].

. Research has shown that jasmonic acid can also reduce water usage in plants by shutting their stomata, making their water usage more efficient. Additionally, it can increase the water content of leaves, which reduces transpiration and improves the plant's resistance to drought [145].

Jasmonic acid can enhance the plant's epidermal layer by modifying the cutin layer. This can impact the plant's ability to decrease water evaporation from the leaf surface [146]. However, high levels of jasmonic acid can potentially impede the process of photosynthesis in plant leaves, which would have an adverse effect on plant growth and yield [147].
Studies have also shown that jasmonic acid application can cause plants' roots to continue growing, which is one of the hormone's effects on roots. Moreover, exposure to the hormone can improve plants' ability to absorb water and nutrients from the soil [148]. In certain plant species, high concentrations can also prevent the formation of main roots [149]. Jasmonic acid can also trigger defense mechanisms; similarly, to how it affects leaves, it can cause plant roots to create substances that aid in the defense against infections [150]. Under normal conditions, there is relatively little jasmonic acid present in the cytoplasm of a plant cell ([23]. In response to a significant reduction in its available water supply, a plant undergoes drought stress and produces and metabolizes jasmonic acid, which serves as both a mediator and a signaling molecule to activate the plant's reaction to the stress. The cytoplasm of stressed leaves contains JA-Ile, which is formed via the epimerization of jasmonic acid. In reaction to stress, JA-Ile is then translocated to the nucleus and nearby locations of leaves [151] [152]. A recent study has shown that jasmonic acid, also known as JA, plays a crucial role in enabling plants to withstand drought stress. This is achieved by regulating the expression of stress-related genes and coordinating hormonal

signals [. The transport of JA is facilitated by the jasmonic acid transport protein (JAT1), present in both the nuclear and plasma membranes of plant cells. JAT1 is responsible for transferring JA from the cytoplasm to the nucleus and apoplast, thereby controlling the dynamics of jasmonic transport during abiotic stress [154]. Moreover, plants use their vascular bundles to transport methyl and jasmonate systemically, and during this process, jasmonic is not only carried but also resynthesized [155], [156]. The phloem, for instance, produces a jasmonic precursor known as 12-oxo-PDA, as has been demonstrated in previous research [157]. Because methyl jasmonate is highly volatile and has a high potential to permeate cell membranes, it can readily travel to nearby plants and distant leaves [158]. Through the synthesis of proteins involved in stress tolerance mechanisms, such as controlling the process of opening and closing stomata, preserving water by lowering transpiration, and preserving the osmotic potential inside the cell, jasmonic acid stimulates the expression of genes responsive to drought stress (Figure 6). Maintaining the internal osmotic potential by preserving the cellular water balance and protecting against damage to the cellular membrane systems, the cell would allow the plant to stand against the detrimental consequences of drought stress [159], [160], [161]. When plants or plant organs are exposed to biotic (e.g., insects, pathogens) or abiotic (e.g., drought, light) stresses, their levels of jasmonic acid can rise significantly. Other environmental stressors include ultraviolet radiation, cold, ozone, heat, and other environmental conditions [162], [163]. Plant physiological systems are impacted by abiotic stressors in ways that include altered gene expression, cellular functions such as ion transport, DNA and protein stability, and gene expression [164]. Genes related to root growth and flower development, senescence, the creation of secondary metabolites or the production of specialized metabolites, and other metabolic pathways are expressed in response to high jasmonic acid levels [123], [124], [165]. Fruit parts, particularly the young peel, flowers, and vegetative plant parts including leaves and stems have the highest concentrations of acid [130]. In response to plant damage, jasmonic acid has been demonstrated to trigger the creation of proteinase-inhibitory proteins (Figure14) [166]. Furthermore, oxidative stress is caused by plants producing more free radicals (ROS) in response to stress. The plant's cellular components sustain chemical damage due to reactive oxygen species. It is well known that chemicals like methyl jasmonate and jasmonic acid can promote induced systemic resistance (ISR), a process that helps plants adapt to stress.

Conclusion

After going through all of the included works of literature, one can infer with great confidence that the role of various plant hormones is crucial to plant growth and development during abiotic stresses including drought. In addition to the important of the hormones that are endogenously produced within plants' cells, exogenously applied plant hormones play a similar role by boosting the capacity of plant tolerance towards the posed stress. Those hormones support plant growth and development in terms of morphological and physiological responses. More importantly, plant hormones play a crucial role in chemical responses besides, they can alter gene expression under certain abiotic stresses. Abscisic acid is confirmed to be the key hormone that regulates the responses, especially to drought and salinity. Thus, it can play a vital role in the accumulation of osmolytes (e.g., Proline, sugars, glycine betaine, etc.). besides, its role in the alteration of the activities of other antioxidants and gene expression. Ascorbic acid is a multifaced molecule that can help in plant adaptation and resistance to drought. Its role as an antioxidant, osmolyte, and regulator by which it maintains the cellular membranes and photosynthetic pigments, eventually increases the resilience against water scarcity. Therefore, the consideration of the role of ascorbic acid during drought provides an important insight into planning strategies to improve crop productivity in water-limited conditions. Glycine betaine the crucial molecule has also many functions to boost plant tolerance against water stress. Its role mainly is osmotic adjustment, plasma membrane stabilization, neutralize the ROS, gene expression alteration and regulation, and photosynthetic pigments protection. The clear benefits of these hormones should be well known to enable plant breeders to put suitable strategies for enhancing plant tolerance to cope with climate changes and water stress. What highlights the importance of the α-tocopherol, is the occurrence in the antioxidant defense system in plants. Besides, its role in protection cell plasma membranes and regulating the signaling pathways during drought stress. Thus, its role should be well investigated to set suitable strategies for increasing plant tolerance to water stress. Also, melatonin can be considered a multifunctional molecule and what made it prominent, is its role in plant adaptation to drought stress. This molecule emerged to be very important for plants as an antioxidant molecule. Besides, its role in gene expression alteration. Overall, this plant hormone boosts plant growth and enables plants to cope with drought and other abiotic stresses. Therefore, understanding its role provides a clear image of how to develop plants that can tolerate various environmental stresses. Jasmonic acid is the key hormone that regulates plant response to drought. It also has a role in stomatal control and gene expression alteration by which plants could cope with water scarcity. Understanding the complex roles of jasmonic acid definitely will give an important view for setting strategies to enhance plant tolerance in limited-water environments. In sum, plant hormones act as crucial signaling molecules that orchestrate many physiological and biochemical responses to drought. Therefore, the interplay and the cooperation between various plant hormones ending with their downstream signaling pathways is vital for evolving strategies to improve the ability of plants to tolerate the posed abiotic stresses which contribute to sustainable agriculture and support food security, especially in the coming years in which climate crises are expected to increase.

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تاثير أجهاد الجفاف وتنظيم النمو: مراجعة في دور التنظيم الهرموني(مقالة مراجعة).

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الخلاصة

تتعرض النباتات خلال فترة حياتها الى العديد من الاجهادات البيئية والتي تؤثر على نموها وتطورها بشكل سلبي، وعلى هذا الاساس طورت النباتات العديد من الاليات لتحمل او تقليل ضرر تلك الاجهادات. تحدث في النباتات العديد من التغيرات المورفولوجية والفسيولوجية والكيموحيوية كاستجابة للضغط البيئي الذي تفرضة الاجهادات البيئية المختلفة. من هذه الاجهادات البيئية المحتلفة، اجهاد الجفاف والذي يعد من اهم الاجهادات البيئية على الاطلاق واشدها تأثير على حياة الكائنات الحية على كوكب الارض. تفاقمت مشكلة الجفاف مع ازدياد شدة التغيرات المناخية مؤخرا، لذا كرس الباحثين جهودهم لفهم اعمق عن تأثيرات الجفاف على مستوى استجابة النبات من الناحية الفسلجية والكيموحيوية. من التغيرات المهمة التي تطرأ على النبات هي تغير التوازن الهرموني. أذ تزداد فعالية بعض الهرمونات والتي من شأنها المحافظة على مستوى مقبول من الجذيرات الحرة داخل النبات فيما يقل نشاط هرمونات اخرى في ظل الظروف غير المؤاتية لنموة. من هذه الهرمونات النباتية حامض الابسيسك والذي يسمى ايضا بهرمون الاجهاد ومهمته اثناء الاجهاد هي تقليل وتيرة النمو في النبات ليحافظ على مستوى معين من النمو. اما الهرمونات حامض الاسكوربيك و الكلايسين بيتاين و الالفا-توكوفيرول و الميلاتونين و حامض الجاسمونيك في بالاضافة الى كونها هرمونات منشطة للنمو الا ان لها دور في كبح الجذور الحرة المتكونة داخل النبات عن طريق دورها كمضادات اكسدة غير انزيمية. وعلى هذا الاساس في هذه المراجعة تم تسليط الضوء على دور بعض الهرمونات النباتية والاليات التي تتبعها في تخفيف ضرر اجهاد الجفاف في النباتات.

الكلمات المفتاحية: الاجهاد البيئي، مضادات الاكسدة، الهرمونات النباتية، الجذور الحرة.