
Plant Hormones Improve Drought Tolerance in Plants: Outlook and Perspectives

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Abstract: In the past and in present times, human activities have triggered global warming, causing drought stresses that affect animals and plants. Plants are more defenseless against drought stress; therefore, plant development and productive output are decreased. To decrease the effect of drought stress on plants, it is very important to establish a plant feedback mechanism of resistance to drought. In plants under drought stress, the drought reflex mechanisms include the physical stature physiology and biochemical, cellular, and molecular-based processes. Improving the root system, leaf structure, osmo-balance, comparative water content and stoma adjustment are included in these procedures. In addition, the signal transduction pathway and reactive clearance of oxygen are crucial mechanisms for coping with drought stress via calcium and phytohormones (e.g., abscisic acid, salicylic acid, jasmonic acid, auxin, gibberellin, ethylene, brassinosteroids and peptide molecules). Furthermore, microorganisms, such as fungal and bacterial organisms, play a vital role in increasing resistance in plants to drought stresses. The number of characteristic loci, transgenic methods and the application of exogenous substances (nitric oxide, (C₂₈H₄₈O₆) 24-epibrassinolide, proline, glycine, and betaine) is very important for enhancing the drought resistance of plants. This review addressed the role of phytohormones and mechanisms in plants in response to drought stress.

Keywords: Phytohormones, drought stress, microorganisms, mechanisms, genes

1. Introduction

Plants are influenced by both biotic and abiotic factors, and in response to these factors, numerous internal changes occur in plants. These biotic and abiotic factors influence plant growth and development along with productivity. Biotic factors are interactions of organisms with plants that have both positive and negative effects. Positive effects may have a beneficial influence on plant growth. Negative effects may include allelopathy, herbivory influence, or pathogen infection in plants [1]. Plants defense systems with various chemical compounds help to resist those negative effects [2], as described briefly in Figure 1. Plant cell walls are proteins (antimicrobial) and secondary metabolites reservoirs with a highly weighted molecular layer of polysaccharides that resist pathogen physical penetration and growth [3].

Notably, the innate immune defense system of plants limits pathogen expansion through PTI (pattern-triggered immunity), PRRs (pattern recognition receptors), and ETI (effector-triggered immunity). ETI forms lesions on plant surfaces that restrict the further movement of pathogens from the infection site [4]. These defense systems activate a league of defense responses against pathogens in plant infection sites [5]. In response to biotic and abiotic factors, plants have growth regulatory hormones that play crucial functions [1]. Plant growth hormones, primarily known as phytohormones, are organic, natural and small lipophilic compounds. Phytohormones play a significant role in the response to different biotic and abiotic stresses along with the coordination and regulation among most developmental and growth functions in plants [6]. Also, they regulate cellular processes and respond very effectively to external stimuli and changing environmental conditions, even at very low concentrations [7]. Phytohormones with low molecular weights are more frequently adopted defense mechanisms of plants to receive external stimuli precisely against biotic stresses [8]. Based on phytohormone physiological functions and chemical structures, there were only a few regulatory hormones, namely jasmonic acid (JA), salicylic acid (SA), ethylene (ET), auxins (IAA), gibberellins (GAs), abscisic acid (ABA) and cytokinins (CKs), which have been more often

studied by plant biologists [9]. However, presently, brassinosteroids (BRs), jasmonic acid-based compounds, cytokinins based compounds (zeatin), salicylic acid-based compounds, strigolactones and peptides are also being investigated as plant hormones [10]. Based on the chemical structures of some specific groups, phytohormones are further subdivided [11] and responsible for the formation of roots and tropism and elongation. Seed and bud dormancy occurs by inhibiting phytohormones that resist abiotic stresses, and growth becomes active after the environment becomes favourable for growth [12]. Various derivatives of all phytohormones are present, such as transport, activated or inactivated storage forms, degradation metabolites and, most importantly, sugar or amino acid conjugates. The biological effects of many plant growth hormones are the result of the combined induction of more than one hormone. Free hormones show similar biological activity to these derivatives; therefore, a precise concentration is required for maximum effect estimations [13], and the estimation of the effect is shown in Figure 2.

Many techniques have been used for phytohormone separation, to study their effects more deeply. First, thin layer chromatography techniques [14] and high-performance liquid chromatography techniques are most commonly used for plant growth hormone separation [15]. GC-MS-based methods are used to profile and study phytohormone profiles in citrus species, particularly in *Citrus sinensis* L., to recognize the responses to biological and environmental stresses. Specific ionic monitoring (SIM) methods were used to evaluate the description of phytohormones. Two derivation reagents, N-Methyl-N-(trimethylsilyl) trifluoroacetamide (MSTFA) and methyl chloroformate (MCF), and one extraction solvent mixture were used. This method showed recovery with a high extraction percentage and reproducibility with a low limit of quantification and detection. With this method, they detected thirteen (13) phytohormones, such as auxins, salicylic acids, gibberellin, jasmonic acid, and abscisic acid, that belong to different groups. Jasmonic acid and auxins were only present in the vegetation of plants, abscisic acid was in the leaves and roots and salicylic acid, cytokinins and gibberellins were found in all plant. Phytohormones are present at extremely low concentrations in plants, making their analysis more difficult. Salicylic acid (SA) is the most abundant phytohormone present in various tissues, mostly ranging from 59-70% of growth hormones. BA phytohormone was the highest among SA groups, and GA7 phytohormone was the most abundant among all GA groups and was made from GA12 in the 3 β -hydroxy gibberellic acid pathway [16].

Drought being one of the abiotic stresses is the most compelling ecological issue that significantly damages plant photosynthesis, development and growth [17]. Perennial fruit trees and crops demand well-drained soils for healthy growth and development and to obtain the maximum level of productivity. Poor drainage, even for a short time, can markedly affect the productivity of perennial fruit trees for long durations [18]. Moreover, drought stress causes an imbalance in carbon metabolism, which is the primary source of carbohydrates, leading to partial stomatal closure at carboxylation sites with less carbon dioxide availability [19]. In addition, drought stress also causes the shoot respiration level to increase, to sustain the metabolic activity. Then, a decrease in the carbohydrate reserves occurs in the storage organs of citrus plants [20].

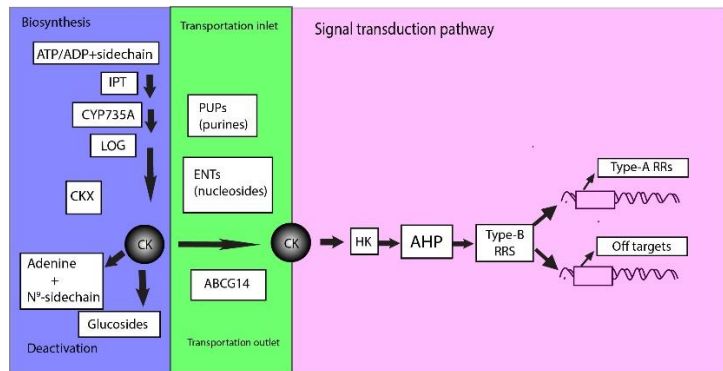
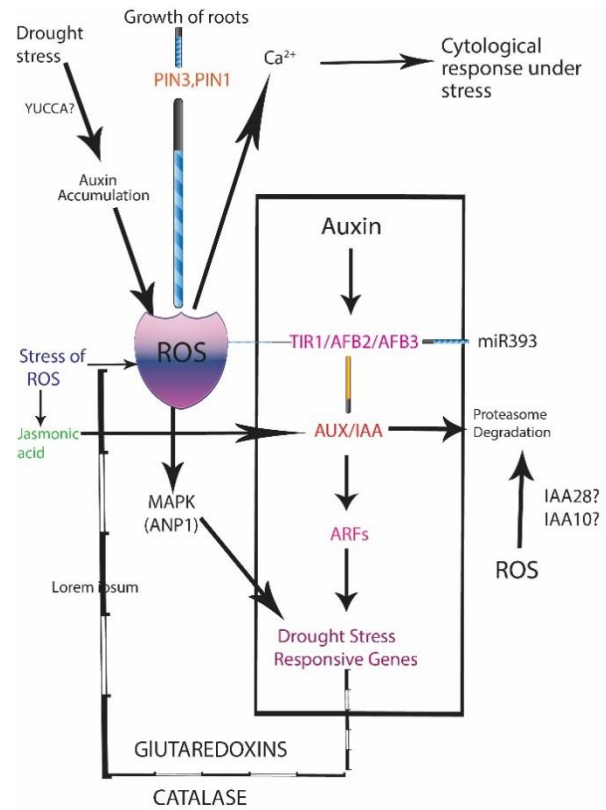


Figure 1. Crop response, from physiological and morphological perspectives to drought stress. Drought stress affects the normal functioning of plants by lowering the rate of photosynthesis. To overcome this issue, plants increase the production of hormones and photosynthesis-related components as defense mechanisms. Moderate drought stress leads to an increase in leaf soluble carbohydrate concentrations, a reduction in starch concentrations and a low photosynthesis rate in leaves. Plants may use stored carbohydrates because changes in carbon availability are observed under low photosynthesis rates. To meet the plant metabolic demand, these plants stored reservoirs that were used to overcome stressful drought conditions [21]. However, severe drought stress leads to a reduction in starch and soluble fraction levels [17]. Plants exposed to saline environments experience a reduction in plant growth because of the effect of both specific ions on metabolism and antagonistic environmental connections. Various technologies have been used to exploit citrus plant growth under drought stress. Attempts are being made through conventional breeding methods to improve plants tolerance to drought stress, and these methods are laborious and based on the prevailing genetic changeability. Recently various drought resistance genes were overexpressed in plants, and plants become tolerant to drought stress. In most of the cases, a higher yield was recorded in the transgenic plants than the wild type plants. Some of the drought-tolerant plants have been listed in Table 1.

(Table 1).

Table 1. Transgenic crops under drought stress experienced altered yields through the phytohormone signaling pathway

Gene(s)	Expressing plant	Signaling pathway	Stress type	Environmental condition(s)	Effect on yield (Increase (%))	References
AtYUCCA6	<i>Solanum tuberosum</i>	Auxin	Drought	Greenhouse	Data not shown	[22]
LOS5ABA3	<i>Glycine max</i>	ABA	Drought	Growth chamber and field	21%	[23]
AtEDT1/HDG11	<i>Oryza sativa</i>	ABA	Drought	Greenhouse and field	16%	[24]
AtGAMT1	<i>Solanum lycopersicum</i>	GAs	Drought	Greenhouse	Data not shown	[25]
AtEDT1/HDG11	<i>Gossypium hirsutum</i>	ABA	Drought and Salinity	Laboratory, greenhouse and field	43%	[26]
GhABF2	<i>Gossypium hirsutum</i>	ABA	Drought and Salinity	Laboratory, greenhouse, and field	46%	[27]
JIOsPR10	<i>Oryza sativa</i>	JA	Drought, salt and <i>Magnaporthe oryzae</i>	Greenhouse	No change	[28]
GA2ox	<i>Oryza sativa</i>	GAs	Drought and disease	Greenhouse and field	10–30%	[29]
OsERF109	<i>Oryza sativa</i>	JA and ABA	Drought	Greenhouse	30-45%	[26]

In response to drought, plants have developed various physiology-, phenology-, morphology-, and biochemical-based mechanisms to sustain their cellular osmotic potential [30]. Studies on these mechanisms are ongoing due to the involvement of various phytohormones acting as sole mediators for avoidance, tolerance, and the adverse effect of water stress. Plant hormones vitally regulate the development and growth of plants along with drought stress reflexes throughout the lifespans of plants [31,32]. Some phytohormones are prepared in response to drought stress and transduce the pathway to manage its effects. The aforementioned plant hormones are jasmonic acid, abscisic acid, salicylic acid, ethylene and various others involved in blocking the effect of infectious and noninfectious stress [33,34]. Drought stress can also result in the release and activation of other enzymes involved in the production and destruction of reactive oxygen species [35]. These hormones act as chemo-messengers in response to various noninfectious stress conditions. As stress occurs, secreted phytohormones activate different developmental and physiological processes, such as negative phototropism in roots, osmotic balance, and closing stomata [36,37].

Exogenous applications of plant growth regulators and management are also employed to overcome these conditions. Aforementioned, phytohormones were applied to improve drought tolerance in plants (See Table 2) and to increase growth, development and productivity. Phytohormones play important roles in modifying the plant reflex

to strains at very low concentrations, and their chemical messenger properties are produced in one part of the plant and transferred to entire parts of plants. Phytohormones are natural products synthesized chemically as plant growth regulators [31].

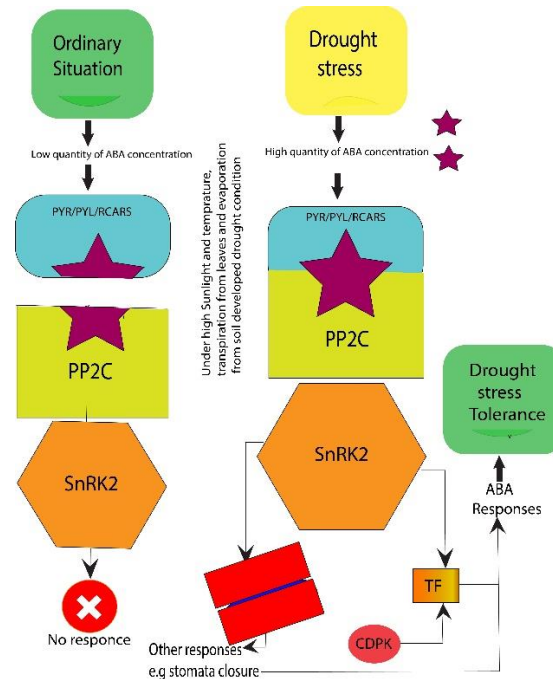


Figure 2. These hormones help plants defend against different stress conditions by increasing or decreasing their levels. Unstable levels of these hormones work within the defense mechanism of plants to ensure healthy normal growth.

Table 2. Phytohormones functions to prevent plants from drought stress.

Functions	Hormones	References
Involved in cell division, cell elongation, apical dominance, phyllotaxis and tropic responses	Auxin	[22]
Root branching	Auxin	[22]
Growth of plant parts and the flowering stage	Cytokinins	[27]
Development of female gametes and embryos	Cytokinins	[28]
Photomorphogenesis and leaf senescence	Cytokinins	[38]
Cell elongation and increasing the cell division	Gibberellins	[39]
Enhance the vegetative and reproductive stages of plants	Gibberellins	[40]
Stomatal closure, gene upregulation and compatible osmolyte synthesis	Abscisic acid (ABA)	[41]

Photosynthetic activity, stomatal regulation, root growth, and germination	Abscisic acid (ABA)	[42]
Defense responses	Salicylic acid (SA)	[43]
Progressive responses against elevated temperature stress	Salicylic acid (SA)	[44]
Stomatal closure	Salicylic acid (SA)	[45]
Drought tolerance by lessening transpiration, squeezing the aperture of the stomata, and thinning the cuticle	Ethylene	[46]
Appraisal of growth, drought tolerance, and yields	Brassinosteroids	[47]
Stomatal closing	Jasmonic Acid (JA)	[48]
Increase the antioxidant activity of plants under drought	Jasmonic Acid (JA)	[49]
Root growth, pollen tube growth, stomatal development	Peptides	[41]

2. Plant hormones improve plant drought tolerance

2.1. Auxins (IAA)

Auxin is an important phytohormone. Auxins are involved in cell division, cell elongation and the differentiation of cellular tissues, embryogenesis, root formation, apical dominance, phyllotaxis and tropic responses. Auxin genes are important biotechnological targets for modifying plant size and shape and improving plant yield. Therefore, they play a vital role in cell and growth development events [50]. Auxins also play a dynamic role in mediating and improving plant tolerance to noninfectious stresses, such as deficiency conditions, as represented by many research reports [51]. Indole-3-acetic acid was one of the first hormones recognized in this group and is most commonly found among the auxins [52]. Indole 3-acetic acid is produced from tryptophan and is chemically similar to it. Alterations in gene expression patterns were used to control auxin-mediated growth and development. When plants are exposed to drought and other stress conditions, varied modulations in the synthesis, metabolism, transport and activity of auxins take place, as depicted in various reports [53]. A decline in the IAA level under stress conditions can increase the ABA level in plants to induce growth modulation by auxins. [54] mentioned that among auxin-coding genes recognized in rice plants, some were activated by drought stress. The researchers [55,56] mentioned the overexpression of YUC₆ in poplar and potato, which results in auxin-enhanced drought tolerance and phenotypes. Auxin also promoted root branching, which is potentially important for enhancing drought tolerance [57]. Auxins also play a role in promoting root branching and have a potential role in drought tolerance mechanisms.

The role of auxin in drought stress has been explored via TLD1/OsGH3.13 which encodes indole-3-acetic acid (IAA)-amido synthase; it then enhanced the expression of late embryogenesis abundant (LEA) genes, which then increase the resistance in plants against drought stress. In addition, genes Aux/IAA genes were identified in rice and most of these genes were expressed under drought stress. In a study, YUC6 was overexpressed in potato and poplar which showed auxin-overproduction phenotypes and enhanced drought tolerance [39]. Auxin also enhanced drought resistance by interacting with other phytohormones. For example, auxin regulates various members of the ACS (1-aminocyclopropane-1-carboxylate synthase) gene family, which is a rate-limiting enzyme in ethylene biosynthesis and this interaction enhance resistance in plants against drought stress [39].

2.2. Cytokinin (CKs)

Cytokinins were discovered in 1950, and they are the most important phytohormones that stimulate cell division and induce variations. The first natural cytokinin was *trans*-zeatin, which was isolated from maize [58]. These compounds are adenine byproducts derived from isoprene or an aromatic side chain at the N6 position of purine. Folke Skoog and his assistants isolated kinetin (the cytokinesis-promoting factor) from autoclaved herring sperm DNA [58]. These hormones are essential for the growth of plant regulation and acclimation to drought stress [59]. Cytokinins have both negative and positive impacts on drought stress [59,60].

The enhancement or reduction of the cytokinin level depends on the period and severity of the drought stress [61]. The beneficial aspects are enhanced intolerance against drought stress. CKs are also reported to stimulate transgene expression in transgenic plants, i.e., isopentenyl transferase gene expression. The transgenic plants indicated significant drought tolerance through delayed senescence by restricting drought-induced leaf senescence. Along with the positive effects, the negative effects of CK accumulation on drought tolerance have also been reported. CK oxidase/dehydrogenase (CKX) catalyzes CK and is involved in the overexpression and breakdown of CKX in *Arabidopsis*, which results in a decrease in endogenous CK contents [62]. Therefore, CKX1, CKX2, CKX3, and CKX4 were overexpressed independently in *Arabidopsis*, resulting in transgenic lines with reduced CK levels and subsequently greater drought tolerance [63].

Cytokinins are helpful in plant tissue culture techniques and support the thoughtful study of plant biological processes, such as the growth of plant parts and the flowering stage. These compounds are responsible for stimulating different processes during the growth and development of female gametes and embryos of a plant. Notably, cytokinins also take part in seed germination, vascular development, photomorphogenesis, shoot apical meristem development, floral development, and leaf senescence. It also helps plants to induce adaptive responses to drought and adverse ecological conditions [64]. The transcription of cytokinin biosynthetic genes is controlled by different hormones and macronutrients. In *Arabidopsis*, cytokinins stimulate cell division by antagonizing auxin. Auxin promotes the expression of AtIPT5 and AtIPT7, whereas cytokinins suppress the expression of AtIPT1, AtIPT3, AtIPT5, and AtIPT7 in the shoot meristem [65].

All the genes related to cytokinin in *Arabidopsis* were overexpressed individually, and transgenic lines of *Arabidopsis* with decreased levels of cytokinin gradually improved tolerance to drought conditions [63]. The current need is to elucidate the signalling and role of cytokinins under drought conditions.

2.3. Gibberellins (GAs)

Gibberellins are tetracyclic diterpenoids of carboxylic acids. The primary purpose of GAs in plants is as growth hormones and to provide resistance against drought stress and other abiotic stresses. GAs continue their functions in plants throughout the plant life cycle. The primary purpose of gibberellins is to enhance the development of plant tissues by cell elongation and increasing the cell division process enhances the immature and adult stages of plant growth. It also helps to enhance the vegetative and reproductive stages of plants [66].

SIDREB (drought-responsive element-binding protein) increases drought tolerance in tomatoes by decreasing the expression of gibberellin biosynthesis genes [39]. Drought tolerance is said to be enhanced if the GA level is reduced in plants. Transgenic tomatoes are produced by the overexpression of the AtGAMT1 (*Arabidopsis thaliana* GA Methyl Transferase-1) gene. AtGAMT1 encodes an enzyme that causes a breakdown in the methylation of active GA to make inactive GA methyl esters. The transgenic tomato indicated a reduction in gibberellins by enhanced drought tolerance. An increased level of water in leaves was observed in transgenic tomatoes under drought stress because of transpiration in plants [67]. The ectopic expression of GA2ox (GA 2-oxidase) increased drought tolerance. This protein also helps to enhance resistance in rice plants [68]. The DELLA proteins are the primary stimulators of GA responses in drought conditions faced by plants. The functions of this group of nuclear regulators are to suppress gibberellin stimulation in plants. Gibberellin binding to its receptor GID1 (GA insensitive dwarf 1) leads to the degradation of DELLAs by the 26S proteasome and the stimulation of gibberellin responses [69].

Drought tolerance in plants is appreciably enhanced by gibberellins, as reported in many studies. Tomatoes make the transgene by overexpressing the gene (methyltransferase 1). GAMT1 encodes an enzyme catalyzing active gibberellin methylation to form inactivated GA methyltransferase in *Arabidopsis* sp. The resulting tomato plant expressed a typical GA-deficient phenotype, which showed drought tolerance. A high-water content was prominent in transgene tomato plants because of decreased transpiration [70]. By contrast, applying hormones resulted in the reappearance of normal growth, and plants became prone to drought again [67]. In addition, the external expression of GA oxidase enzyme (GA 2-oxidase) improved drought and disease hindrance in rice plants [68]. SIDREB (drought-reflexing binding protein) also improved drought tolerance in tomatoes by suppressing the genes involved in GA biosynthesis [71]. DELLA protein factors also primarily regulate the response to GA, and this group of nuclear regulators especially act to suppress the GA response. GA binding to the insensitive dwarf 1 receptor of GA will result in DELLA degradation, similar to 26S proteasome and GA response stimulation [69].

2.4. Abscisic acid (ABA)

Abscisic acid is an important signalling phytohormone under drought stress [72]. Abscisic acid plays a significant role in regulating stomatal closure, gene upregulation and compatible osmolyte synthesis. 9-Neoxanthin cis-epoxycarotenoid dioxygenase (NCED) is used in abscisic acid synthesis and is considered a bottleneck, covering 9 neoxanthins to xanthins. This enzyme is used in the upregulation of an increased level of abscisic acid. Abscisic acid is cleaved into 8'-OH-ABA, and this process is catalyzed by an ABA 8'-hydroxylase (CYP707A) enzyme. This reaction is used to inactivate abscisic acid. ABA 8'-hydroxylase compounds are spontaneously converted into dehydrophaseic acid (DPA) and phaseic acid (PA), the primary degradation products. Another path that is used to inactivate abscisic acid pools is through conjugation to hexoses catalyzed by the ABA O-glycosyl transferase enzyme. This process yielded the ABA-glycosyl ester (ABAGE) compound [73]. After the cleavage of the ABA glycosyl ester (ABAGE) compound by an ABA glycosyl ester β -glycosidase (BG18) enzyme, active abscisic acid is released. Both species have increased levels of phasic acid (PA) and dehydrophaseic acid (DPA) under drought stress, but Cleopatra exhibited a more increased level of ABA-glycosyl ester (ABAGE).

Abscisic acid signalling pathways have vital roles in the expression of drought stress-responsive genes because various stress situations can occur in plants. Abscisic acid receptors are very important in the transduction of signals. In the subcellular state, many receptors are recognized. Under normal conditions, ABA is expressed at low concentrations in plants. SnRK2 activity in protein kinases is inhibited by the phosphatase PP₂C, leading to dephosphorylation. As plants develop ABA concentrations, they start to bind with PYRs, PYLs, and RCARs, which bind to deactivate PP₂C phosphatase activity [74]. These PYRs and PYLs are essential receptors for the abscisic acid response encoded by different genes, such as 11 genes in rice and 14 genes in *Arabidopsis* encoding these receptors [75]. The autoactivation of SnRK₂ (protein kinases that enhance the abscisic acid response) occurs when the protein is dissociated from phosphatase PP₂Cs [32,76], and the rest of the SnRKs are involved in the abscisic acid response (SnRK2.2, SnRK2.3, and SnRK2.6) [77]. In *Arabidopsis*, only the A clade participates in the signalling of abscisic acid out of seventy-six PP₂Cs. Additionally, the ABA signalling pathway is also dependent on branches of various transcription factors, such as MYC, NAC and MYBs. The responsive elements of abscisic acid also play a role in ABA signalling [78]. CDPKs (CDPKs) also proved very important in the pathway related to signalling. Calcium-dependent protein kinases also participate in ABA signalling, and 34 CDPKs have been reported in *Arabidopsis*, along with 29 in rice, 20 in wheat and 35 in maize. Two CDPKs, CPK4 and CPK11, have been reported to be involved in the regulation of ABA signalling in *Arabidopsis* [79]. SnRK₂ activation triggers the phosphorylation of down-target genes, resulting in the induction of molecular and physiological responses to ABA triggering, such as photosynthetic activity, stomatal regulation, root growth, and germination [74,80]. Abscisic acid also regulates many other genes related to drought stress to develop drought tolerance in plants. The abscisic acid-induced pathway is shown in Figure 3.

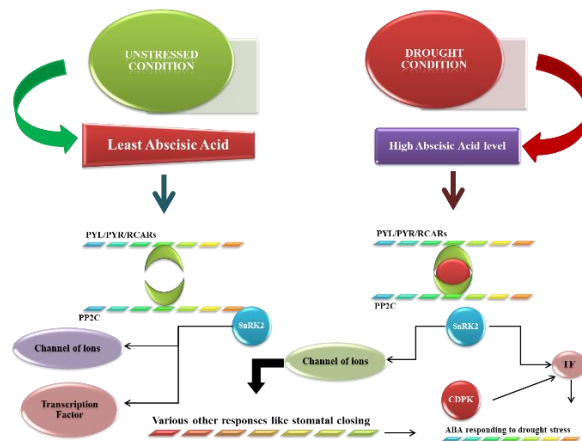


Figure 3. ABA's fundamental signalling mechanism during stressful situations. The ABA levels are lower under ideal circumstances, and the function of SnRK2 protein kinase is blocked by PP₂C phosphatases. The cellular ABA level rises during high-pressure situations, and ABA then attaches to PYR/PYL/RCARs, which connect to and deactivate PP₂Cs in response. If they are detached from PP₂C, then SnRK2s are automatically activated. Switched on SnRK2s phosphorylate the following targets and provoke molecular and physiological reactions through ABA.

2.5. Salicylic acid (SA)

The salicylic acid hormone is associated with drought stress-encouraged tolerance and signalling in plants [81]. The salicylic acid plant hormone is created in a reaction from chorismate. This reaction is catalyzed by the enzyme isochorismate synthase (ICS) and successively by the isochorismate pyruvate lyase enzyme. Salicylic acid hormone is also produced from phenylalanine. This reaction is catalyzed by the phenylalanine ammonia-lyase (PAL) enzyme [82]. Salicylic acid also plays a significant role in defense responses against biotrophic pathogens, as shown in Figure 4. PR (pathogenesis-related) genes are induced in response to high temperature and biotic stresses. Thus, salicylic acid is also induced in response to biotic stress overlay with encouraging basal thermo-tolerance through SA signalling pathways, and this study suggested *Arabidopsis* mutants [83]. Salicylic acid accumulation is caused by the exogenous application, genetic manipulation and stress. This hormone has been related to progressive responses against elevated temperature stress in different plant species, such as *Agrostis stolonifera* [84], *Avena sativa* [85], poplar [86] and grapevines [87]. Salicylic acid accumulation in plants improves the responses to various abiotic stress conditions, such as drought and salinity [81], antioxidant activity and photosynthetic machinery protection, which prevents electron leakage [33]. In another case, the Carrizo citrus plant variety showed greater tolerance to drought and heat stress in combination. Drought stress increased salicylic acid levels in the leaves of certain citrus species, such as Carrizo and Cleopatra. Chlorophyll fluorescence, gas exchange parameters and malondialdehyde (MDA) accumulation indicate that Cleopatra mandarin is susceptible to drought and heat stress [88]. Phenotypic traits of citrus plants occur in response to a combination of drought and heat stress. Whole sprouts (%) of Cleopatra and Carrizo seedlings were exposed to drought and heat stress (40°C)

in combination for ten days. For each genotype, asterisks denote statistical significance concerning the initial values at $P \leq 0.05$.

The salicylic acid levels also increased in plants when they were stressed, which may be 5 times that of the normal level recorded in evergreen shrubby plants in *Phillyrea augustifolia* [89]. The enhanced drought tolerance and disorder resistance found in mutants of *Arabidopsis* sp. such as *adr1*, *acd6*, *myb96-1*, and *cpr5* is due to the presence of salicylic acid [90,91]. In *Arabidopsis*, stomatal closing was also observed due to salicylic acid accumulation under stressed conditions because the SA-regulated induction of PR gene expression led to drought tolerance by shutting the stomatal openings [90,92], and stomatal closure occurred through the accumulation of SA under the influence of *SIZI* in *Arabidopsis*, greatly increasing the drought tolerance.

In response to drought stress, the biosynthesis of SA occurs through two pathways i.e., isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL). However, IC pathway is known to be the major pathway in the majority of plants. [72] Isochorismate synthase (ICS) converts chorismic acid to IC and enhanced ICS through the overexpression of *ICS1* and assist the plants and protect against drought stress [74]. In another study, the exogenous application of SA positively regulated *ICS1* and enhanced drought tolerance in *Arabidopsis*. Furthermore, it revealed that SA activated *WRKYs* and *TGAs* genes and enhanced the plant immune system against drought stress [75].

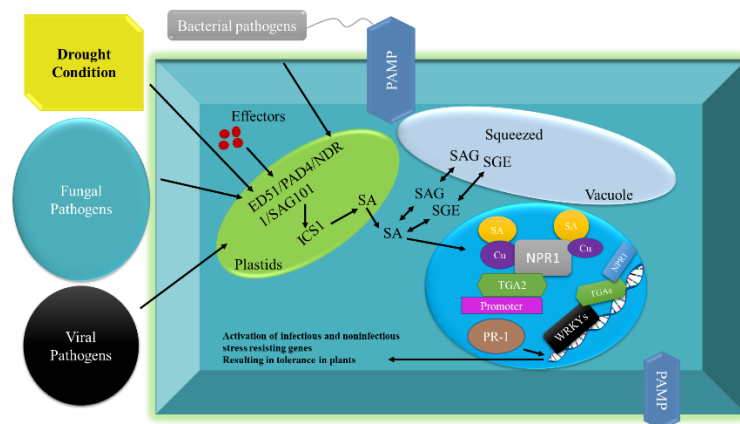


Figure 4. SA signalling pathway under different stress conditions. The accumulation of SA leads to an environment that changes multimeric NPR1 to monomerize under abiotic and biotic stresses, and this monomeric NPR1 is transported towards the nucleus. NPR1 links with SA in the nucleus, inducing a verification change that releases the C-terminal domain of activation from repression to activate transcription.

2.6. Jasmonic Acid (JA)

Drought tolerance in plants is induced by closing stomata, shifting reactive oxygen species, and deep root growth in the case of jasmonic acid. Studies have revealed that JAs participate in stomatal closing regulation as a result of drought stress [93]. A case study revealed that treating *Arabidopsis* with 12-OPDA led to stomatal shutting. It is also involved in indirectly decreasing stomatal gaps, favouring drought tolerance. Drought also prevents the alteration of OPDAs to jasmonic acid; in this case, OPDA coupled with ABA or individually leads to the closing of stomata [94,95]. High ROS foraging was found [96] in transgenic plants overexpressing *VaNAC26*, which showed relatively more drought tolerance. JA-related genes were highly regulated in overexpressed lines under drought and ordinary conditions. The external application of JA led to a perfect reflex by plants to drought stress. External JA application was also shown to enhance the activity of antioxidants under drought stress [97]. Another case revealed that in young wheat, JA was found to be an enhancer of different enzymes, such as ascorbate peroxidases (APX), ascorbate reductases, monodehydroascorbate reductase and glutathione reductase, under stress conditions [97]. JA also plays a major role in water conductivity from soil under restricted moisture conditions. [72,85] found that the transient presence of jasmonic acid in roots is required under drought stress to increase the abscisic acid levels. However, the function of JA still must be clarified under drought stress to obtain highly tolerant plants. The exogenous application of JA increased the antioxidant activity of plants under drought conditions, as shown in Figure 5. The proteins *JAI3/JAZ* bind to various transcription factors, including *MYC2*, and limit their activity under normal conditions. However, during drought stress, the degradation of *JAZ* proteins occurs resulting in active transcription factors that up-regulate genes of JA which enhanced tolerance in plants against drought stress [78]. Moreover, JA signalling pathways interact with ABA signalling pathways, suggesting their role in response to drought stress. Recently it is revealed that JA enhanced hydraulic conductivity of plant roots under drought stress by interacting with calcium and ABA-dependent and independent signalling pathways [78].

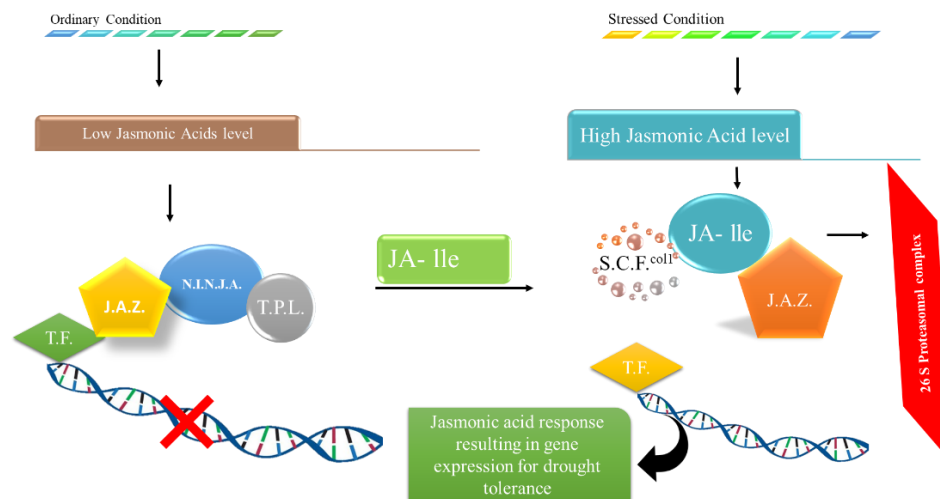


Figure 5. Changes in JA signals under stressful situations. JAI3/JAZ proteins attach to different transcription components and restrict their function along with reduced levels of JA under ideal circumstances. The JA concentrations are high and deteriorate JAZ proteins under stressful situations, leading to the activation of transcriptional components that upregulate genes associated with stress responses.

2.7. Brassinosteroids (BRs)

Brassinosteroids play a role in stress responses along with roles in plant growth and nourishment. These stresses include drought, cold, hypersalinity, metallic heaviness, raised temperature, and infectious agents [98]. It was previously mentioned that in *Arabidopsis*, wheat, and *Brassica* sp. brassinosteroids played a positive role in response to drought stress [99]. *Arabidopsis* biosynthetic gene (*DWF₄*) overexpression resulted in the appraisal of growth, drought tolerance, and yields [100]. By contrast, there was a negative response from the brassinosteroids. Additionally, mutants of Brs showed functional loss but increased drought tolerance [101,102], and knocking out BR₁ by miRNA technique led to more drought tolerance in *Brachypodium distachyon* [103]. These Phytohormones play a crucial role in drought stress tolerance, but they cannot act solely in isolation in synergism or any other combined form of assistance to synthesis and response.

Recently, various WRKY transcription factors have been discovered in *Arabidopsis thaliana* and these transcription factors are reported to be involved in plant growth and response to drought stress. To regulate plant growth, BRs extensively interact with these transcription factors and GA in response to drought stress [83,84,85,86].

2.8. Ethylene (ET)

Ethylene was found to be actively involved in the response to creating drought tolerance in plants. In a study on cotton, ethylene-responsive genes or binding protein elements such as AP₂, EREBPs, and APETELA₂ were identified in response to heat and drought stress [104]. One analysis revealed that members of ERFs (responsive factors of ethylene), GmERF₃ isolated from *Glycine max*, whose expression was induced by drought stress, ABA, SA, JA, and ET. GmERF₃ in overexpressing tobacco plants exhibited more tolerance to drought stress because of the high contents of proline and solubilized sugar compared to those of wild plants. Transgenic plants showed increased resistance to *Ralstonia solanacearum*, *Alternaria alternata*, and tobacco mosaic virus due to the high expression of pathogenesis-related protein-coding genes [105]. The overexpression of the ERF gene (*ERF019*) in *Arabidopsis* delayed ageing and flowering time. Transgenes also exhibit drought tolerance by lessening transpiration, squeezing the aperture of the stomata, and thinning the cuticle [106]. In signal transduction, *ETR₁* codes for receptors of ET but negatively regulates the response; other receptors of this family always close down the signalling, whether ethylene is present or not [107] of the other members of the family include *ERS₁*, *ETR₂*, *EIN₄*, and *ERS₂*. *CTR₁* regulates ET signalling. In *Arabidopsis*, *CTR₁* is involved in ET signalling, while in tomato 3, *CTR₁* is involved in ET signaling. There is no evidence of a decrease in the stream substrate of *CTR₁*. When the receptor is found ethylene, it shuts off the activity of ethylene, thus leading to a reflex action for tolerance to drought conditions.

2.9. Peptides

Recently several secreted peptides were found to mediate the cellular development in plants. However, it was not clear whether these peptides mediate long-distance signalling in response to drought stress. Among the peptides, CLAVATA3 (CLV3) is a well-characterized plant peptide involved in shoot apical meristem formation. In land plants, phytohormone abscisic acid plays a significant role in the regulation of stomatal movement to prevent water loss. However, till now, no mobile signalling molecules have yet been discovered that can enhance the

abscisic acid accumulation in leaves [25]. Recently, CLE25 peptide was found to transmit water-deficiency signals through vascular tissues in Arabidopsis and affects abscisic acid biosynthesis and stomatal control of transpiration. The gene related to these peptides was expressed in the vascular tissues and enhanced root response to drought stress. These peptides move from the roots to the leaves and induce stomatal closure by modulating abscisic acid accumulation and thereby enhances resistance to drought stress. Recently another peptide gene in rice, OsDSSR1 has been discovered, which was expressed mainly in the root, stem, node, leaf, and panicle and this expression were induced by drought stress. The peptide is localized in the nucleus and cytoplasm and exhibited enhanced drought stress tolerance and decreased ABA sensitivity as compared to the wild type [26]. Other peptides such as phytosulfokine (PSK), a growth factor related to cell proliferation; rapid alkalization factor (RALF), which regulates root growth; LUREs, which guides pollen tube growth; STOMAGEN, which is related to stomatal development; and casparian strip integrity factor (CIF), which is related to the formation of the casparian strip diffusion barrier; Another peptide, AtPep3 which plays an important role in the drought and salinity stresses were also recently discovered [25,26,27].

3. Conclusion and future perspectives

Even the Green Revolution dramatically improved the yield of plants. However, the ever-growing world population and increase in drought stress due to climate changes again threatens our ability to feed the world. Therefore, climatic changes have attracted international attention due to the significant loss of crop production over the last few decades caused by drought stress. The current research aims to summarize different mechanisms of drought tolerance and further develop those processes. Plants typically react in the form of morphological, physiological, biochemical and molecular processes to drought stress. The morphological and physiological processes involve changes in the composition of the leaves, root growth and stomatal control. The biochemical process includes adjusting the levels of plant hormones, such as abscisic acid, jasmonic acid, auxin, ethylene, gibberellin, cytokinin, brassinosteroids and recently discovered small peptide molecules. Under drought stimulation, plant hormone levels normally increase and contribute to the activation of morphological, physiological and other biochemical pathways. These pathways may include MAPK signalling pathways, calcium signalling pathways, transcription factor regulation and increased levels of antioxidant enzymes and other substances to mitigate the effects of drought stress on plants. Notably, through the exogenous application of substances (nitric oxide, 24-epibrassin, proline, glycine betaine), plant breeding and transgenic processes, scientists are also attempting to develop these mechanisms further. In addition, microorganisms such as bacteria and fungi are also considered very important for improving plant growth, plant yield and resistance to drought. These approaches should be incorporated to cultivate high-yielding, drought-tolerant crops to prepare for the coming food and housing crisis. Different techniques are still being used in this regard to define high-yielding mechanisms of drought tolerance and ultimately enhance these processes. New technologies, including, next-generation sequencing and CRISPR, will enable scientists to understand and improve the drought tolerance of the major crops.

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