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Review on Hormonal Regulation of Drought Stress Response in Plants

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Review Article

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ABSTRACT

Drought stress is a major environmental challenge that significantly impairs plant growth, productivity, and survival. Plants have evolved complex physiological and biochemical mechanisms to perceive and respond to drought conditions, with plant hormones playing pivotal roles in mediating these responses. This abstract provides an overview of the key hormones involved in drought stress regulation—abscisic acid (ABA), jasmonic acid (JA), ethylene, cytokinins (CKs), and gibberellins (Gas)—and their interactions in orchestrating drought tolerance mechanisms. Abscisic acid (ABA) is the central hormone in drought stress signalling. It accumulates rapidly under water deficit conditions, triggering stomatal closure to reduce water loss and activating the expression of drought-responsive genes. ABA's role is mediated through a complex signalling cascade involving receptors (PYR/PYL/RCAR), protein phosphatases (PP2Cs), and kinases (SnRK2s), ultimately leading to transcriptional changes that enhance stress tolerance. Jasmonic acid (JA) and its derivatives contribute to drought tolerance by modulating antioxidant defence mechanisms and osmotic adjustments. JA signalling interacts with ABA pathways to fine-tune stress responses, often

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enhancing ABA's effects on stomatal closure and gene expression. Ethylene, a gaseous hormone, exhibits dual roles in drought stress. While high levels of ethylene can promote leaf senescence and abscission, contributing to water conservation, it also interacts with ABA signalling to regulate stomatal closure and root growth, optimizing water uptake and minimizing loss. Cytokinins (CKs) generally promote cell division and growth, but under drought conditions, their levels decrease, which can lead to reduced shoot growth and enhanced root growth. This shift in resource allocation favours water uptake overgrowth, aiding plant survival during drought. CKs also interact with ABA, often antagonistically, to balance growth and stress responses. Gibberellins (Gas), known for promoting growth, are typically downregulated during drought stress to conserve energy and resources. The suppression of GA biosynthesis and signalling is crucial for maintaining growth arrest, a common drought avoidance strategy. In summary, the hormonal regulation of drought stress response in plants is a highly intricate and dynamic process involving multiple hormones and their interactions. Understanding these regulatory networks is essential for developing strategies to enhance drought tolerance in crops, thereby ensuring agricultural productivity in the face of increasing water scarcity.

Keywords: Drought stress; hormonal regulation; biosynthetic pathway.

1. INTRODUCTION

Drought stress is a critical environmental factor that significantly impacts plant growth, development, and productivity. Plants have evolved complex mechanisms to cope with water scarcity, among which hormonal regulation plays a pivotal role. This introduction will explore the various hormones involved in the drought stress response in plants, highlighting their interactions and mechanisms based on extensive literature. Abscisic acid (ABA) is widely recognized as the central hormone in drought stress response. During water deficit conditions, ABA levels increase, triggering stomatal closure to reduce water loss and inducing the expression of drought-responsive genes. The biosynthesis and signalling pathways of ABA have been extensively studied, revealing key components such as the PYR/PYL/RCAR receptors, protein phosphatase 2C (PP2C), and SNF1-related protein kinase 2 (SnRK2). Cytokinins (CKs), although generally associated with cell division and growth, also play a crucial role in modulating drought responses. CK levels typically decrease under drought stress, leading to reduced cell proliferation and growth, which is thought to conserve energy and resources. Additionally, CKs interact with ABA signalling pathways to fine-tune the balance between growth and stress responses [1]. Ethylene is another hormone that modulates plant responses to drought, often in a complex interplay with ABA. Ethylene production is generally upregulated under drought conditions, where it can influence root architecture and leaf senescence. The cross-talk between ethylene and ABA pathways is critical for optimizing drought response, as ethylene can enhance or mitigate ABA effects depending on the developmental stage and environmental context. Gibberellins (Gas) are primarily known for their role in promoting growth and development; however, their involvement in drought stress response is becoming increasingly evident [2]. Under drought conditions, GA biosynthesis is typically downregulated, leading to growth retardation and enhanced survival. This reduction in GA levels helps to prioritize stress defence mechanisms over growth. Salicylic acid (SA) is traditionally associated with pathogen defence but also contributes to drought tolerance. SA can modulate the expression of drought-responsive genes and enhance the antioxidant defence system in plants under water deficit. Moreover, the interaction between SA and other hormonal pathways, such as ABA and jasmonic acid (JA), plays a crucial role in orchestrating a coordinated response to drought stress. Jasmonic acid (JA) and its derivatives are key regulators of plant defence responses, including those against drought stress [3]. JA signalling can induce the expression of genes involved in drought tolerance and enhance the production of protective compounds such as osmolytes and antioxidants. The interplay between JA and other hormones, particularly ABA, is essential for fine-tuning drought responses. Auxins, primarily known for their role in growth and development, also influence drought stress responses [4]. Auxin signalling can modulate root architecture, promoting deeper rooting and increased water uptake under drought conditions. Additionally, the interaction between auxin and ABA pathways is crucial for regulating stomatal behaviour and growth under water-limited conditions. Brassinosteroids (BRs) are another class of hormones that have been implicated in drought tolerance. BRs can enhance stress tolerance by modulating antioxidant defences and osmoprotectant synthesis [5]. The crosstalk between BRs and other hormones, particularly ABA and ethylene, plays a significant role in optimizing plant responses to drought. Strigolactones (SLs), although primarily studied for their role in plant-microbe interactions and shoot branching, also contribute to drought stress responses. SLs can modulate root architecture and enhance water uptake under drought conditions. Additionally, SLs interact with other hormonal pathways, including ABA and auxin, to regulate plant growth and stress responses [6]. The interaction between different hormonal pathways is critical for orchestrating an effective drought response. For instance, ABA and CKs often exhibit antagonistic interactions, with ABA promoting stress responses and CKs promoting growth. Similarly, the balance between ABA and ethylene signalling can determine the extent of stomatal closure and senescence during drought. Recent studies have highlighted the importance of transcription factors in mediating hormonal responses to drought. For example, the ABA-responsive element-binding proteins (AREBs) and dehydration-responsive element-binding proteins (DREBs) are key regulators of drought-responsive gene expression [7]. These transcription factors often function downstream of hormonal signaling pathways, integrating multiple signals to coordinate a comprehensive stress response. In addition to transcriptional regulation, post-translational modifications such as phosphorylation and ubiquitination play crucial roles in modulating hormonal responses to drought [8]. Protein kinases and phosphatases, particularly those involved in ABA signalling, are key players in this regulatory network. Moreover, the ubiquitin-proteasome pathway regulates the stability of key signaling components, ensuring precise control of hormonal responses. The spatial and temporal dynamics of hormone biosynthesis, transport, and signaling are also crucial for an effective drought response [9]. For instance, root-to-shoot signaling involves the transport of hormones such as ABA and CKs, which coordinate responses between different plant organs.

2. OVERVIEW OF DROUGHT STRESS AND ITS IMPACT ON PLANT PHYSIOLOGY AND CROP PRODUCTIVITY

Drought stress is a significant environmental challenge that adversely affects plant physiology and crop productivity, leading to substantial agricultural losses worldwide. Drought stress is defined as the deficit in water availability to a level where it hampers the normal physiological processes of plants, thereby impacting their growth and yield.

2.1 Impact on Plant Physiology

Drought stress induces a variety of physiological changes in plants. One of the primary responses is stomatal closure, which reduces water loss through transpiration but also limits CO2 uptake, thereby inhibiting photosynthesis [10]. This reduction in photosynthetic activity directly impacts plant growth and biomass accumulation. In addition to stomatal regulation, drought stress affects the root system architecture. The plants often increase root depth and density to enhance water uptake from deeper soil layers. However, this adaptation can be limited by soil characteristics and the availability of resources necessary for root growth. The synthesis and accumulation of osmolytes such as proline, glycine betaine, and soluble sugars are another critical physiological response to drought stress, helping to maintain cell turgor and protect cellular structures. This osmotic adjustment is essential for sustaining metabolic activities under water deficit conditions. Oxidative stress is another consequence of drought, where the imbalance between reactive oxygen species (ROS) production and antioxidant defence mechanisms leads to cellular damage [11]. Indicate that drought stress often results in elevated ROS levels, which can damage lipids, proteins, and nucleic acids, ultimately impairing cell function and viability.

2.2 Impact on Crop Productivity

The impact of drought stress on crop productivity is profound and multifaceted. The drought can significantly reduce crop yields by affecting various growth stages, from germination to grain filling. In cereals like wheat and maize, drought stress during the flowering stage can lead to poor pollination and kernel abortion, drastically reducing yield potential [12]. Moreover, drought stress affects nutrient uptake and utilization efficiency. The reduced water availability limits the mobility of nutrients in the soil and their absorption by plant roots, leading to deficiencies that further constrain growth and productivity. Drought stress can alter the hormonal balance within plants, particularly the levels of abscisic acid (ABA), which plays a crucial role in mediating stress responses. Elevated ABA levels can induce stomatal closure and trigger the expression of stress-responsive genes, although these changes often come at the expense of growth and development [13]. Breeding and biotechnological approaches are being explored to develop drought-tolerant crop varieties. For instance, transgenic crops expressing genes for drought tolerance, such as those encoding for osmoprotectants or antioxidant enzymes, have shown promise in improving yield under water-limited conditions. Nonetheless, the adoption of such technologies is influenced by regulatory, economic, and social factors [14].

2.3 Recent Advances and Future Directions

Recent advances in genomics and phenomics have provided new insights into plant responses to drought stress. The role of high-throughput sequencing and phenotyping platforms in identifying drought-responsive genes and traits. These tools enable the rapid screening of large populations for drought tolerance, facilitating the development of resilient crop varieties. Moreover, climate models predict an increase in the frequency and intensity of droughts, necessitating proactive measures to safeguard crop productivity [15]. Integrating traditional breeding with modern genomic approaches and leveraging biotechnological innovations are critical for developing crops that can withstand future climatic challenges [16]. In conclusion, drought stress poses a severe threat to plant physiology and crop productivity, with significant implications for global food security. Understanding the physiological responses of plants to drought and leveraging advanced breeding and biotechnological strategies are essential for mitigating the adverse effects of drought and ensuring sustainable agricultural production. Continued research and innovation are crucial to address the complex interplay between drought stress and plant biology, ultimately enhancing the resilience of crops to water scarcity [17].

3. INTRODUCTION TO THE ROLE OF PLANT HORMONES IN MEDIATING RESPONSES TO DROUGHT STRESS

Hormonal regulation plays a critical role in mediating plant responses to drought stress, ensuring survival and adaptation. Drought stress triggers a complex network of hormonal signals, primarily involving abscisic acid (ABA), ethylene, cytokinins, auxins, gibberellins, and salicylic acid, each contributing uniquely to the plant's adaptive mechanisms. Abscisic acid (ABA) is the central hormone in the drought response. When plants experience water deficit, ABA levels increase significantly, which facilitates stomatal closure to reduce water loss through transpiration [18]. Additionally, ABA modulates the expression of drought-responsive genes, enhancing osmoprotectant synthesis and stabilizing cell structures under water-deficit conditions. The ABA-dependent signaling pathway involves the PYR/PYL/RCAR receptors, which inhibit type 2C protein phosphatases (PP2Cs), thus activating SnRK2 kinases that phosphorylate ABA-responsive element binding factors (ABFs). Ethylene, another critical hormone, exhibits a dual role under drought conditions. While ethylene production often increases in response to drought, it can either promote or inhibit stress tolerance depending on its concentration and the developmental stage of the plant [19]. Low levels of ethylene can enhance drought resistance by promoting root growth and facilitating deeper soil water extraction, whereas high ethylene levels may lead to leaf senescence and abscission, thereby reducing transpiration surface. Cytokinins generally act as negative regulators in drought stress responses. Drought conditions typically lead to reduced cytokinin levels, which helps to limit cell division and growth, thus conserving water and energy [20]. However, recent studies indicate that cytokinin signaling can also play a protective role by maintaining shoot meristem function and delaying senescence under mild drought stress. Auxins, primarily indole-3-acetic acid (IAA), are also pivotal in modulating plant architecture during drought stress. Drought conditions often lead to a redistribution of auxins, promoting root elongation and increasing root-to-shoot ratio, which enhances the plant's ability to access deeper soil moisture [21]. Furthermore, auxins interact with other hormonal pathways, such as ABA, to fine-tune the plant's stress responses and developmental processes. Gibberellins (Gas) generally promote growth and development but are downregulated during drought stress to conserve energy and resources. Reduced gibberellin levels result in growth inhibition, which is an adaptive response to limit water usage and support survival under prolonged drought conditions [22]. Salicylic acid (SA) is another hormone implicated in drought stress responses, primarily through its role in enhancing antioxidant defences and mitigating oxidative damage caused by drought-induced reactive oxygen species (ROS). SA-mediated pathways enhance the expression of antioxidant enzymes, thus protecting cellular components from oxidative stress. The intricate hormonal regulation involving ABA, ethylene, cytokinins, auxins, gibberellins, and salicylic acid forms a dynamic and interconnected network that enables plants to adapt to drought stress [23] Each hormone contributes uniquely to various aspects of the drought response, from water conservation and root architecture modification to oxidative stress mitigation and growth regulation. Understanding these hormonal pathways offers significant potential for developing crops with enhanced drought tolerance through genetic and biotechnological interventions [24]. The comprehensive insights into hormonal regulation provide a foundation for breeding and engineering crops capable of thriving under increasingly erratic climate conditions.

4. CROSS-TALK BETWEEN HORMONES IN DROUGHT STRESS RESPONSE

The intricate network of hormonal signalling pathways plays a pivotal role in the plant response to drought stress, orchestrating a complex cross-talk that ensures survival and adaptation. Among these hormones, abscisic acid (ABA) is paramount, often referred to as the "stress hormone" due to its significant role in mediating drought responses [25]. ABA accumulates rapidly in response to drought, inducing stomatal closure to minimize water loss and activating a suite of drought-responsive genes. Cytokinins, another class of hormones, exhibit an antagonistic relationship with ABA in the context of drought stress. While ABA promotes stress adaptation, cytokinins generally encourage growth and development, leading to a finely tuned balance that affects the plant's stress tolerance [26]. Under drought conditions, the levels of cytokinins are typically reduced, which helps to prioritize the ABA-mediated stress responses overgrowth processes. Ethylene, a hormone associated with senescence and stress responses, also interacts with ABA during drought stress. Ethylene can enhance ABA biosynthesis and signaling, thereby contributing to the reinforcement of drought tolerance mechanisms. However, the relationship between ethylene and ABA is not purely synergistic; ethylene can also modulate ABA responses by influencing stomatal behaviour and gene expression [27]. Auxins, which primarily regulate growth and developmental processes, interact with ABA to modulate root architecture during drought stress. This interaction is critical for enhancing water uptake and ensuring root survival under adverse conditions. ABA can inhibit auxin transport and signalling, leading to changes in root growth patterns that favor drought resistance. Gibberellins (Gas), known for promoting growth, often exhibit an antagonistic relationship with ABA. During drought stress, the levels of Gas are usually reduced, which helps to conserve energy and resources by inhibiting growth and promoting stress-responsive pathways [28]. The interplay between ABA and Gas is crucial for balancing growth and stress responses, allowing plants to adjust their physiological processes to cope with drought . Salicylic acid (SA), primarily associated with pathogen resistance, also plays a role in drought stress responses. SA can interact with ABA to modulate stomatal behaviour and antioxidant defenses, enhancing the plant's ability to manage oxidative stress during drought [29]. Additionally, SA signalling pathways can intersect with those of other hormones, adding another layer of complexity to the hormonal cross-talk in drought stress response. Brassinosteroids (BRs), known for their role in promoting cell expansion and growth, also interact with ABA during drought stress. BRs can enhance ABA signaling, leading to improved stress tolerance through enhanced stomatal regulation and stress-responsive gene expression. This interaction exemplifies how growth-promoting hormones can be repurposed to support stress adaptation mechanisms. Jasmonates (Jas), typically associated with defence responses, are also involved in drought stress signalling. Jas can modulate ABA responses and influence stomatal behavior, contributing to the regulation of water loss and stress tolerance. The interplay between Jas and ABA highlights the dual role of these hormones in managing both biotic and abiotic stresses [30].

In drought, plants induce abscisic acid (ABA) biosynthesis genes to produce large amounts of ABA in plant roots. ABA synthesized in large quantities is directly involved in the drought-tolerant metabolism of plants through the process of ABA signaling. ABA activates the ARF transcription factor related to auxin in response to increased drought tolerance in roots, and cytokinin antagonizes ABA. In addition, the ABA-independent pathway activates the ethylene signal transduction transcription factor to help the root development.

Table 1. Cross-talk between hormones in drought stress response

Plant Hormone	Function	Transcription factors	References
ABA (Abscisic Acid)	Promotes stomatal closure to reduce water loss.	ABI5, ABI3, AREB1, ABF2	[31]
Ethylene	Modulates root growth and leaf senescence	EIN3, ERF1	[32]
Cytokinins	Delays leaf senescence and maintains cell division	ARR1, ARR2, ARR10	[33]
Auxins	Regulates root architecture and promotes lateral root formation	ARF1, ARF2, ARF7	[34]
Brassinosteroids	Enhances tolerance by modulating gene expression related to stress response	BZR1, BES1	[35]
Jasmonic Acid	Induces expression of defense-related genes	MYC2, JAZ	[36]
Gibberellins	Modulates growth responses and stress adaptation	DELLA, GAI, RGA	[37]
Salicylic Acid	Activates systemic acquired resistance (SAR)	NPR1, TGA	[38]
Strigolactones	Regulates shoot branching and root growth under stress conditions	D14, MAX2	[39]
Melatonin	Acts as an antioxidant and modulates stress-related genes	CBF1, MYB	[40]

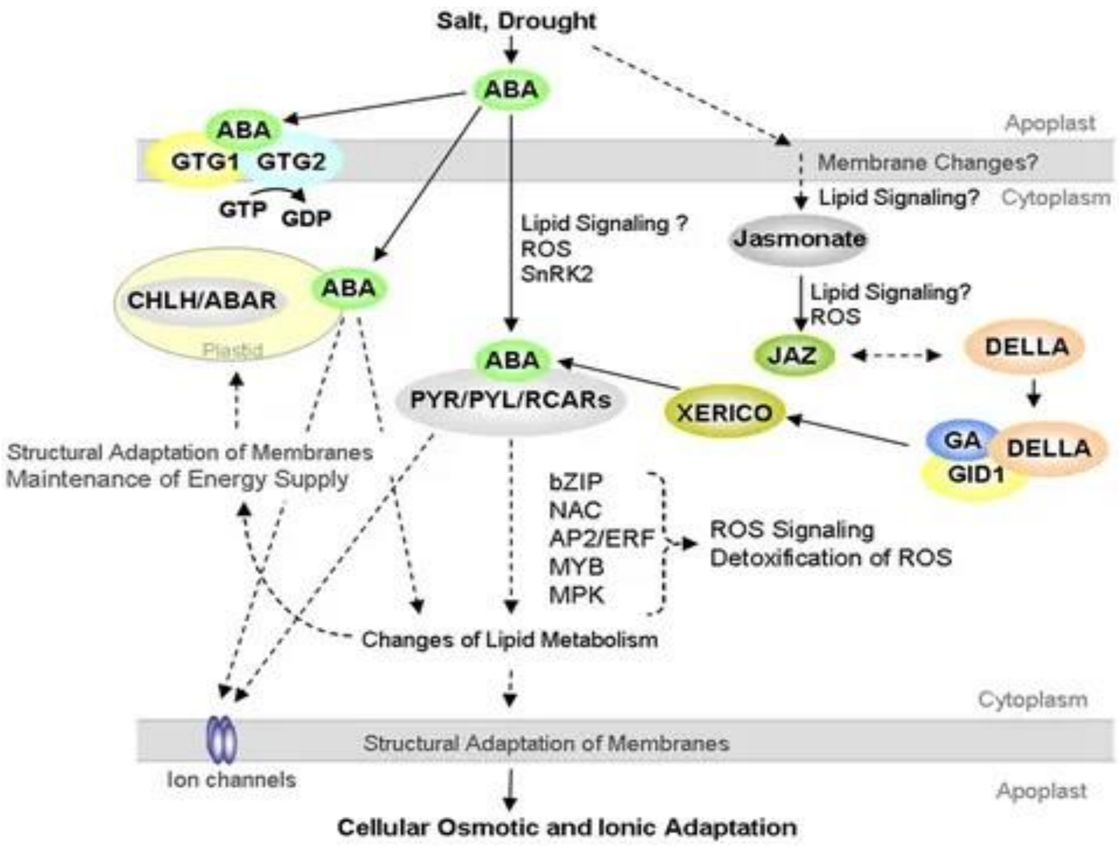

Fig. 1. Proposed model on crosstalk of abscisic acid (ABA), gibberellic acid (GA), and jasmonate signaling in plant cellular responses to the abiotic stressors drought and salt
Source. Golldack et al. [23]

5. MOLECULAR MECHANISMS UNDERLYING HORMONAL REGULATION

5.1 Signal Transduction Pathways

Signal transduction pathways play a crucial role in the hormonal regulation of drought responses in plants. One key hormone involved in this process is abscisic acid (ABA). When plants experience drought stress, ABA levels increase, which is a primary signal that initiates various adaptive responses. ABA perception begins when it binds to PYR/PYL/RCAR receptor proteins, which then inhibit protein phosphatases 2C (PP2Cs) [41]. This inhibition releases SnRK2 kinases from PP2C-mediated repression, leading to their activation. Active SnRK2s phosphorylate and activate ABA-responsive element binding factors (ABFs), which are transcription factors that regulate the expression of ABA-responsive genes. These genes encode various proteins that contribute to drought tolerance, such as late embryogenesis abundant (LEA) proteins, which protect cellular structures from dehydration [42]. Additionally, ABA signalling induces the expression of genes involved in osmoprotectant biosyntheses, such as proline and sugar alcohols, which help maintain cell turgor and protect cellular functions under drought conditions. Stomatal closure is another critical ABA-mediated response to drought. ABA triggers the efflux of anions, such as chloride and malate, from guard cells, leading to depolarization of the plasma membrane [43]. This depolarization activates outward-rectifying K+ channels, causing potassium ions to leave the guard cells. The resultant loss of solutes decreases the osmotic potential within the guard cells, leading to water efflux and stomatal closure, thereby reducing water loss through transpiration. Moreover, drought stress activates mitogen-activated protein kinase (MAPK) pathways, which further modulate ABA signalling and enhance drought response [44]. MAPKs phosphorylate various downstream targets, including transcription factors and other kinases, to fine-tune the expression of stress-responsive genes. In addition to ABA, other hormones such as ethylene, jasmonic acid, and salicylic acid also participate in the drought response, often interacting with ABA signaling pathways to coordinate complex adaptive responses. Ethylene, for instance, can modulate ABA signalling by influencing the expression of ABA biosynthetic and catabolic genes.The hormonal regulation of drought stress in plants involves intricate signal transduction pathways centered around ABA, with significant roles for PYR/PYL/RCAR receptors, PP2Cs, SnRK2 kinases, and various transcription factors [45]. These pathways integrate multiple signals and effectors to optimize plant responses and enhance survival under drought conditions.

5.2 Transcriptional Regulation, Post-Transcriptional and Post-Translational Modifications

5.2.1 Transcriptional regulation

Drought stress induces significant changes in the transcriptional regulation of hormone-responsive genes in plants. Key transcription factors (TFs) such as ABA-responsive element-binding proteins (AREB/ABF), NAC, MYB, and WRKY families are activated under drought conditions [45]. Abscisic acid (ABA), a central hormone in drought response, triggers the expression of drought-responsive genes by binding to receptors that subsequently activate TFs like ABF2/AREB1. Moreover, the dehydration-responsive element-binding (DREB) TFs, particularly DREB2A, play crucial roles by binding to DRE/CRT motifs in the promoters of drought-inducible genes [46].

5.2.2 Post-transcriptional modifications

Post-transcriptional regulation involves processes such as mRNA splicing, transport, stability, and translation, which are critical under drought stress. Alternative splicing of pre-mRNAs can generate different isoforms of proteins that might have diverse functions under stress conditions [47]. Small RNAs, including microRNAs (miRNAs) and small interfering RNAs (siRNAs), are also involved in the post-transcriptional regulation of genes during drought stress [48]. For instance, miR159 is known to target MYB TFs that are involved in ABA signaling pathways. Furthermore, RNA-binding proteins (RBPs) such as those from the glycine-rich RNA-binding protein (GRP) family play a role in stabilizing or degrading specific mRNAs in response to drought.

5.2.3 Post-translational modifications

Post-translational modifications (PTMs) such as phosphorylation, ubiquitination, sumoylation, and glycosylation are essential in modulating the activity, stability, and interactions of proteins under drought stress. Protein kinases like SnRK2 are activated by ABA and phosphorylate various TFs and other proteins to propagate the drought response signal [49]. For instance, SnRK2.6/OST1 phosphorylates the AREB/ABF TFs to enhance their transcriptional activity. Ubiquitination, mediated by E3 ubiquitin ligases such as RING-H2, targets specific proteins for degradation via the 26S proteasome pathway, thus modulating the abundance of regulatory proteins during drought. Sumoylation, involving small ubiquitin-like modifier (SUMO) proteins, affects the localization and function of various TFs, including DREB2A, thereby modulating their activity in response to drought [50]. Additionally, glycosylation can influence the stability and function of proteins like extensions, which are involved in cell wall strengthening under drought stress.

5.2.4 Integration of regulatory mechanisms

The integration of transcriptional, post-transcriptional, and post-translational modifications ensures a coordinated and efficient response to drought stress in plants. ABA signaling exemplifies this integration, where ABA not only induces the expression of TFs but also influences their stability and activity through PTMs [51]. Moreover, the interplay between different hormones such as ethylene, jasmonic acid, and salicylic acid with ABA further refines the drought response through complex regulatory networks involving multiple levels of gene regulation. By understanding these regulatory mechanisms, it becomes possible to develop strategies to enhance drought tolerance in crops, which is crucial for maintaining agricultural productivity under increasing drought conditions due to climate change [52].

6. GENETIC AND BIOTECHNOLOGICAL APPROACHES

6.1 Genetic Engineering for Hormonal Pathways such as CRISPR/Cas9 and Other Genome Editing Tools

Genetic engineering, particularly using tools such as CRISPR/Cas9, has emerged as a powerful approach for manipulating hormonal pathways to enhance drought tolerance in plants. The CRISPR/Cas9 system, which allows for precise genome editing, has been instrumental in targeting specific genes related to plant hormone pathways that are crucial for drought response [53].

One of the primary hormonal pathways involved in drought response is the abscisic acid (ABA) pathway. ABA is a key plant hormone that regulates various aspects of plant growth and stress responses, including stomatal closure, which helps to reduce water loss during drought conditions [54]. Using CRISPR/Cas9, researchers have been able to modify genes involved in ABA biosynthesis and signaling to improve drought tolerance in crops. For example, the gene NCED3, which is crucial for ABA biosynthesis, has been targeted to enhance drought resistance in rice.

Another important hormonal pathway is the ethylene signalling pathway. Ethylene is known to play a role in regulating plant responses to various abiotic stresses, including drought [55]. By using genome editing tools to manipulate ethylene biosynthesis and signalling genes, scientists have been able to develop plants that maintain growth and productivity under drought conditions. For instance, CRISPR/Cas9-mediated editing of the ETHYLENE INSENSITIVE3 (EIN3) gene has been shown to confer drought tolerance in Arabidopsis [56].

Additionally, gibberellins (Gas), another class of plant hormones, are involved in regulating growth and development under drought stress. Manipulating GA signaling through genetic engineering can help maintain growth during drought by balancing growth and stress responses. CRISPR/Cas9 has been used to knock out GA-related genes, leading to reduced plant height and increased drought tolerance, as demonstrated in maize [57].

Besides CRISPR/Cas9, other genome editing tools such as TALENs (Transcription Activator-Like Effector Nucleases) and ZFNs (Zinc Finger Nucleases) have also been utilized to modify hormonal pathways for drought tolerance. TALENs have been employed to edit genes in the cytokinin pathway, which is another hormone involved in cell division and growth regulation under stress conditions [58]. By modifying cytokinin signaling genes, researchers have developed transgenic plants with enhanced drought resistance and improved water use efficiency. Moreover, advancements in genome editing technologies have enabled the development of multiplex editing, where multiple genes can be edited simultaneously to achieve a more robust drought tolerance phenotype. For example, using CRISPR/Cas9, scientists have simultaneously targeted multiple genes in the

ABA, ethylene, and cytokinin pathways, resulting in transgenic plants with significantly improved drought tolerance [59].

Furthermore, RNA-guided gene regulation techniques such as CRISPR interference (CRISPRi) and CRISPR activation (CRISPRa) offer additional layers of control over gene expression. CRISPRi can be used to repress the expression of negative regulators of drought tolerance, while CRISPRa can activate positive regulators, providing a dynamic approach to manage drought stress responses in plants [60]. The integration of genome editing with traditional breeding techniques and modern biotechnological approaches holds great promise for developing drought-tolerant crops. By combining precise genetic modifications with conventional breeding methods, it is possible to enhance the resilience of crops to drought while maintaining yield and quality. Genetic engineering using tools such as CRISPR/Cas9, TALENs, and ZFNs offers a powerful means to manipulate hormonal pathways and enhance drought tolerance in plants [61]. The ability to precisely edit genes involved in ABA, ethylene, gibberellin, and cytokinin pathways has already demonstrated significant potential in developing crops that can withstand drought conditions. As these technologies continue to advance, they will play a crucial role in ensuring agricultural sustainability in the face of climate change [62].

6.2 Breeding for Drought-Resilient Varieties

Breeding for drought-resilient varieties involves manipulating plant hormonal pathways to enhance their tolerance to water scarcity. Hormones like abscisic acid (ABA) play a crucial role in the plant's response to drought by regulating stomatal closure, thus reducing water loss [63]. Studies have shown that increasing ABA sensitivity in crops can significantly improve their drought tolerance. Another key hormone is cytokinin, which generally promotes cell division and growth but its levels need to be finely tuned during drought conditions to prevent excessive water loss. Research indicates that reducing cytokinin levels or modifying its signaling pathway can help plants conserve water during drought stress [64]. Additionally, ethylene is involved in the plant's drought response, often working antagonistically with ABA. Engineering plants to reduce ethylene production or sensitivity can enhance their drought resilience by maintaining growth under limited water conditions.

Gibberellins (Gas) also interact with ABA during drought stress, and modulating GA levels can help balance growth and water conservation. For example, decreasing GA levels can reduce transpiration rates and improve water use efficiency in crops [65]. The Integration of these hormonal pathways through genetic modification or selective breeding is essential for developing drought-resilient varieties. Advances in genomic technologies, such as CRISPR/Cas9, offer precise tools to edit hormone-related genes, thus accelerating the breeding process. Breeding for drought-resilient varieties by targeting hormonal regulation involves a complex interplay of various hormones, each contributing to the plant's ability to manage water use effectively [66]. By understanding and manipulating these hormonal pathways, it is possible to enhance crop resilience to drought and ensure food security under changing climate conditions.

7. PRACTICAL IMPLICATIONS AND FUTURE DIRECTIONS

The study of hormonal regulation in drought resistance in plants has significant practical implications and promising future directions. Hormonal regulation plays a crucial role in plant responses to drought stress, primarily through abscisic acid (ABA), which modulates stomatal closure to reduce water loss [67]. ABA not only controls stomatal behavior but also induces the expression of drought-responsive genes, enhancing the plant's ability to cope with water scarcity. Gibberellins (Gas) are also involved, as they can regulate growth processes that are critical under drought conditions. The interplay between ABA and Gas is complex; while ABA promotes drought resistance, Gas can sometimes have antagonistic effects by promoting growth [68]. This interaction suggests that a balance between these hormones must be achieved for optimal drought resistance. Auxins and cytokinins further influence drought responses by regulating root architecture and shoot growth, thus optimizing water uptake and reducing transpiration [69]. Auxins enhance root growth and development, facilitating deeper water acquisition, which is crucial during prolonged drought periods. Conversely, cytokinins typically promote shoot growth, but under drought conditions, their levels decrease to limit leaf expansion and water loss.

Future research should focus on the genetic manipulation of these hormonal pathways to develop drought-resistant crops. Advanced genetic engineering techniques can be employed to create plants with modified hormone levels or sensitivity, improving their drought tolerance [70]. For instance, transgenic plants with enhanced ABA sensitivity have shown promising results in improving drought resistance. Another promising direction is the use of biostimulants that can modulate plant hormone levels, thus enhancing drought tolerance without genetic modification. These biostimulants can be applied as foliar sprays or soil amendments, providing a practical approach to managing drought stress in crops [71]. Understanding the hormonal crosstalk and signalling networks in plants under drought stress can also lead to the development of novel agrochemicals that specifically target these pathways. Such chemicals could mimic the action of natural plant hormones or inhibit their degradation, providing a cost-effective and environmentally friendly strategy to improve drought resistance [72].

Moreover, integrating hormonal regulation knowledge with traditional breeding programs can enhance the selection of drought-resistant varieties. By identifying and selecting traits associated with favourable hormonal responses to drought, breeders can develop crops that are better suited to withstand water-limited conditions [73]. In conclusion, hormonal regulation offers a versatile and powerful tool for improving drought resistance in plants. The practical implications of manipulating these pathways are vast, ranging from genetic engineering and biostimulants to the development of targeted agrochemicals. Future research should continue to explore these avenues, aiming to create resilient crops capable of thriving in increasingly dry environments [74].

The production and build-up of osmoprotectants, or osmotic pressures, such as soluble proteins, sugars and sugar alcohols, quaternary ammonium compounds, and amino acids, is what controls a plant's osmotic regulation at low water potential. One of the most crucial amino acids for plants in response to drought is Proline. It has powerful functions in maintaining cell homeostasis, regulating plant development and promoting stress adaptation. It is an indispensable and important indicator in drought research [75].

8. CONCLUSION

The hormonal regulation of drought stress response in plants is a complex and vital adaptive mechanism that involves multiple signalling pathways and hormonal interactions. Abscisic acid (ABA) plays a central role in mediating drought responses by regulating stomatal closure, gene expression, and osmotic adjustment [76]. Besides ABA, other hormones such as cytokinins, ethylene, auxins, gibberellins, and salicylic acid also participate in drought stress responses, often interacting synergistically or antagonistically to fine-tune plant reactions to water deficit. Cytokinins generally inhibit drought responses by promoting cell division and growth, yet under drought conditions, their levels decline, reducing their growth-promoting effects [77]. Ethylene, often associated with stress responses, can either promote or inhibit drought tolerance depending on its concentration and the plant's developmental stage. Auxins are typically involved in root growth and development, and their redistribution during drought stress can enhance root elongation and water uptake. Gibberellins, which promote growth, are generally downregulated during drought to conserve resources [78]. Salicylic acid, known for its role in pathogen defense, also modulates drought responses, often enhancing ABA signaling and promoting stress tolerance. Furthermore, cross-talk between these hormones creates a sophisticated network that allows plants to optimize their growth and survival during drought. Research has shown that genetic modifications and breeding strategies targeting hormonal pathways can enhance drought tolerance in crops. Understanding the intricate hormonal regulation mechanisms opens avenues for developing resilient plant varieties capable of withstanding adverse environmental conditions [79]. This knowledge is crucial for ensuring food security in the face of climate change-induced droughts. In conclusion, the hormonal regulation of drought stress response is an intricate and dynamic process involving a network of interactions among various hormones, primarily orchestrated by ABA, to mediate plant adaptation and survival under water-deficit conditions. Understanding these processes provides critical insights into developing drought-resistant plant varieties, a key step towards sustainable agriculture in changing climates [80].

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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