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Review

Advanced Study of Drought-Responsive Protein Pathways in Plants

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Abstract: Drought, the most significant environmental stressor, severely limits plant growth and development and significantly reduces crop production. Drought stress responses vary among plants, allowing them to withstand and survive adverse conditions. Plants resist drought by maintaining signaling pathways, such as the abscisic acid pathway, and activating unusual proteins, such as dehydrins. This study aims to investigate signaling pathways and the biological structures and activities of proteins involved in these processes. We also look into the occurrence of crosstalk across multiple signaling pathways and what it means for agricultural plant enhancement. By incorporating the most common components across all abiotic stress situations, this review provides insight into the evolution of drought stress tolerance in agricultural plants. This review could be helpful for crop drought stress researchers.

Keywords: drought stress; responsive proteins; responsive pathways; development

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1. Introduction

Many abiotic stressors affect plant growth and yield worldwide, including high salinity, heavy metals, and extreme temperatures. Systemic adaptations to abiotic stressors allow plants to withstand wide-ranging environmental conditions [1–3]. Drought is the most significant ecological stressor for plant growth and development, productivity, biomass accumulation, and crop production [4]. Drought can significantly impact crop yields due to decreased cell division and expansion rates, a reduced leaf size, decreased nutritional correlations, and decreased water use efficiency during crop production [5]. The development of plant species in drought-prone areas shows that plants have naturally evolved to survive drought stress through cellular, physiological, biochemical, morphological, and other adaptations [6,7]. Drought severity is influenced by several factors, including the presence and distribution of rainfall, evaporative cooling, and the soil moisture storage capacity [8]. Stress causes plants to activate several defense-related metabolic pathways. Stress-resistant plants can withstand environmental stress for extended periods [9]. Plants eschew stress through having deep roots, early flowering, a reduced leaf area, and a better water utilization efficiency mechanism [10]. Drought resistance has been defined as the ability to reproduce and survive in water shortage conditions. In agronomy, "drought resistance" refers to a plant's ability to produce an economically viable crop during times in which there is a limited water supply [11,12]. Various drought adaptation processes, including multigenic regulation, drive drought resistance.

Functional assortment, species age, and resource distribution are all essential response mechanisms [13]. Plant responses to drought stress include changes in gene expression and

transcription as well as the regulation of several functional proteins, all of which contribute to the molecular control of drought resistance [6]. Osmotic change, cellular flexibility, and cumulative protoplasmic resistance all function as adaptive elements to maintain the turgor of cells and ensure their high level of performance [14]. Various mechanisms, such as abscisic acid (ABA), osmotic change, and the stimulation of dehydrins in plants, work together to maintain a high tissue water potential, which is how drought tolerance is achieved in plants [15], as demonstrated by molecular tree physiology [8]. Plants have evolved to have a wide range of physiological and biochemical abilities that allow them to thrive on proteins involved in the ABA signaling pathway under adverse conditions, for example, phosphatases, proteins that control the activity of protein kinases in cells, and Transcription Factors (TFs), which control how genes are expressed in response to environmental stress [16,17]. Consequently, genetic studies of how plants react to drought are essential to advance efforts to breed plants using molecular techniques. Based on the most recent omics research, this review outlined how plants respond to drought stress. In addition, the proteins involved in drought stress responses, their biological structures, and their specialized roles were considered. We investigated approaches to improving drought stress resistance in crop plants by analyzing pathway crosstalk and identifying potential difficulties.

2. Plant Defense Mechanisms against Drought Stress

To activate drought resistance mechanisms, plant cells must first be subjected to an imbalance in the water supply above and below ground and water loss. Several primary and secondary plant signaling pathways respond to drought stress by transmitting stress messages across gene networks [18]. A study on chickpea roots revealed that the gene network analysis involves Ca^{2+} signaling, chromatin organization, signal transduction, and interactions between proteins and their transcription (SuperSAGE) [19]. These networks include hormone signals, proteins, and metabolic compounds such as Reactive Oxygen Species (ROS), which are frequently required for gene expression. These compounds could be developed to stop cellular genomic damage [18]. Calcium signaling, ROS, Mitogen-Activated Protein Kinase (MAPK), phosphorylation cascades, and crosstalk between various TFs are all thought to be involved in stress perception and the stimulation of resistance and acclimation pathways [8,20]. Some drought-resistant enzymes have been found in the protein profiles of maize leaves, which are especially sensitive to drought. These enzymes are involved in the lignification, glycolysis, and Krebs cycles [21].

2.1. Calcium Signaling Pathways

Researchers have discovered that drought triggers a short-lived increase in the cytosolic Ca^{2+} concentration [19]. The role of Ca^{2+} in the response of crops to various environmental stimuli, such as drought stress, has long been recognized. Calmodulin (CaM), Calcineurin B-like (CBL), and Ca^{2+}-Dependent Protein Kinases (CDPKs or CPKs) are three major calcium sensor families found in plants. CBLs are a distinct class of Ca^{2+} sensors found in plants that decode Ca^{2+} signals by triggering a group of plant-specific protein kinases identified as CBL-Interacting Protein Kinases (CIPKs) (Figure 1). CBLs are cytoplasmic Calcium-Binding Proteins (CaBs) that, by interacting with calmodulin, activate several protein kinases and phosphatases, thereby modulating downstream signaling [22–24]. CBL1, CBL4, and CBL9 are three CBL proteins that are present in most N-myristoylation patterns. These proteins play critical roles in abiotic stress signaling pathways in plants [23,25,26]. It was found that plants overexpressing *CBL1* were better able to withstand drought [19]. Compared to CaM and CBL, CDPKs are the most frequently studied calcium sensors and have a unique structure that allows them to transmit Ca^{2+} signals via phosphorylation [23,27]. They have four conserved calcium-binding motifs, a variable domain, an auto-inhibitory connector region, a Ser/Threonine protein kinase domain (Ser/Thr), and a regulatory Calmodulin-Like Domain (CaM-LD). A CaM-LD with a Ser/Thr kinase domain is another component of CDPKs. CDPKs contain four known

components that assist plants in detecting environmental stimuli, transferring calcium signals, and mediating various cellular responses [19,25,27].

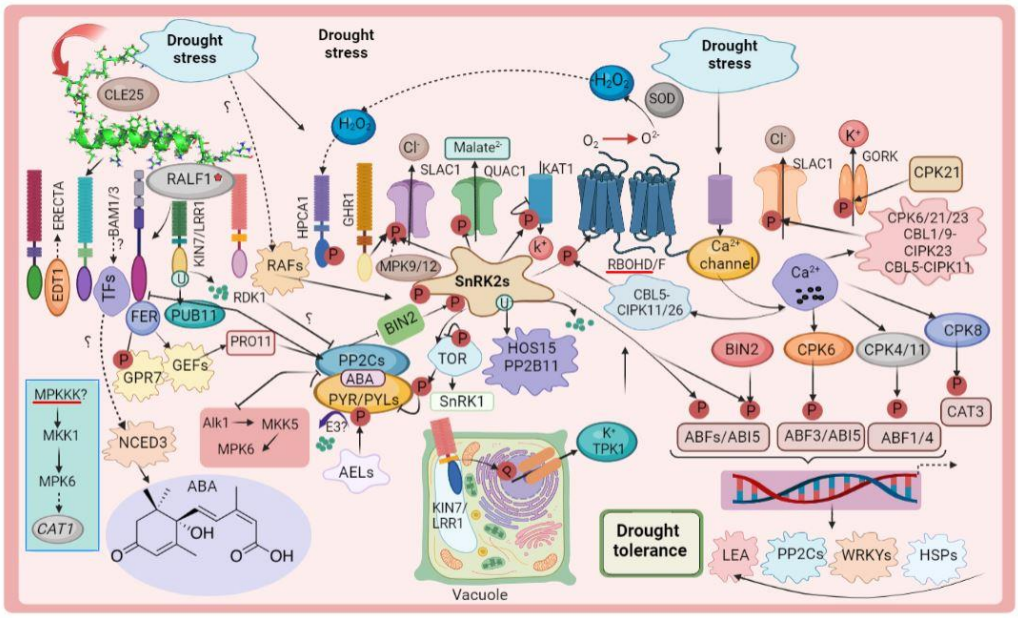

Figure 1. The PYR/Pyls/RCAR (clade A type 2C protein phosphatase receptors) are capable of recognizing ABA. The anion channels SLAC1 and QUAC1 are activated and phosphorylated by phosphorylated OST1. Calcium-dependent protein kinases can decode a particular Ca^{2+} signature under drought stress. During stress, membrane-anchored receptor-like kinases detect extracellular signals and transfer signals within cells. An interaction between RALF1, FER, and the GEF, ROP11, is required for ABI2 activation. Various protein kinases, such as CPKs and CIPKs, RLKs, SnRK2s, and MAPKs, work together to coordinate plant responses to drought stress. Positive and negative regulations are indicated by arrows and bars, respectively. Solid lines represent direct regulation, while dashed lines or unknown regulations represent indirect regulation.

2.2. Phytohormone-Mediated Pathways

The phytohormone ABA plays a key role in the complex adaptations made by plants in response to drought stress, including the closure of stomata and the activation of drought-responsive genes [28]. ABA is essential for generating hormones and osmotic signals in response to drought. This reaction conceals three primary drought-coping mechanisms: the ability to flee dry conditions, to avoid becoming dehydrated, and to tolerate dryness or desiccation [6,28,29]. It has been shown that chloroplast enzymes such Zeaxanthin Epoxidase (ZEP), Nine-Cis-Epoxycarotenoid Dioxygenase (NCED), and Abscisic Aldehyde Oxidase (AAO) contribute to the biosynthesis of ABA in plants [30]. Plants respond to drought through ABA-dependent and ABA-independent signaling pathways [31]. It is well established that NAC TFs are responsible for controlling the expression of genes that participate in the ABA pathway, Pyrabactin Resistance (*PYR*) and Pyrabactin Resistance 1-Like (*PYL*), and the induction of the production of the ABA hormone. Overexpression of the stress-responsive gene SNAC1 (STRESS-RESPONSIVE NAC 1) was shown to dramatically enhance drought resistance in transgenic rice (22–34% more) in a research area under intense drought stress at the reproductive phase without causing any phenotypic changes or yield penalty. Drought mainly causes the transcription factors NAM, ATAF, and CUC (NAC), which have transactivation activity, to be activated in guard cells [32]. OsNAP, a transcription factor that is nucleus-localized and a member of the NAC family, functions as a transcriptional activator in yeast. This gene was shown to be highly activated in rice by ABA and abiotic stressors, such as drought and low temperature, according to an analysis of *OsNAP* transcription levels. Rice plants that overexpressed *OsNAP* were not found to exhibit growth delays, but they did exhibit a considerably decreased rate of water

loss, greater tolerance to high salt, drought, and low temperature conditions during the vegetative stage and a higher yield under drought stress during the flowering stage [33].

2.3. MAPK-Dependent Pathways

The MAPKs are a family of proteins with a widespread distribution and substantial evolutionary conservation. Plant MAPK cascades control a wide range of developmental and stress-response functions. In response to various abiotic and biotic stresses, including drought, saltiness, high and low temperatures, injury, and pathogenic incursion, MAPKs are involved in several critical cellular processes [34]. Signaling cascades rely heavily on transiently phosphorylated MAPKs, including MAPK Kinases (MAPKKs) and MAPK Kinase Kinases (MAPKKKs). Multiple upstream receptors and different downstream target components are influenced by the MAPK, MAPKK, and MAPKKK network in distinct signal transduction pathways [35].

The MAPK family is activated consecutively via protein phosphorylation. An active MAPKKK stimulates an MAPKK through threonine phosphorylation during kinase activity, which stimulates an MAPK [36]. In response to different stress signals, activated MAPK phosphorylates cytoskeletal proteins and phospholipases, which leads to the expression of genes [37]. RNA-Seq research has shown that several members of the MAPK cascade change in response to drought in plants. In response to drought stress, rice produces transcripts of OsMPK4, OsMKK1, OsMKK4, OsMPK5, OsMPK7, and OsMPK8 [38]. In wheat, the levels of expression of *TaRaf44*, *TaMPK8*, *TaRaf72*, *TaRaf87*, *TaMKK1*, *TaRaf105*, *TaRaf80*, and *TaMKKK16* were shown to be altered after drought stress [39]. The transcription levels of cotton *GhMPK* gene families, such as 2, 4, 6, 7, 17, and 31, were found to be drastically reduced under drought stress conditions, whereas cotton *GhMEKK* gene families, such as 10, 12, 24, and 36 and *GhRAF4*, were shown to be increased following exposure to drought stress [39]. In addition, dry circumstances in maize triggered the expression of several drought-inducible genes, including *ZmMPK3* and *ZmMPK15*, and the *ZmMKK10-2* and *ZmMAPKKK* gene families [39]. These results show the significance of MAPKs in drought, although our understanding of their biological roles during drought stress is still unclear.

3. Proteins Involved in Drought Stress Pathways

The overexpression of drought-response genes leads to the production of two main types of protein: (i) proteins that protect membranes and other proteins from damage, such as antioxidants, late embryogenesis abundant proteins, and the osmotin family; and (ii) proteins that absorb and move ions [6,40]. Water-soluble stress proteins enhance cellular hydration and resistance to stress. In addition, many TFs and stress proteins may play significant roles in drought tolerance [8,11]. Plants have developed many different types of proteins, such as aquaporin, cold shock proteins, cyclophilins, Late Embryogenesis Abundant (LEA), Heat Shock Proteins (HSPs), TFs, molecular chaperones, enzymes, functional proteins, and kinases, which form reliable stress-response pathways and signaling chain processes [11,18,41]. Drought stress encourages the buildup of ABA-Sucrose Non-Fermenting protein (SNF1)-related protein kinase 2 (SnRK2) interactions, which play vital roles in the ABA signaling pathway. The proteins PYR, PYL, and the regulatory components of ABA receptors (RCAR) are the primary regulators of the ABA signaling pathway, which involves the detection of abscisic acid. The suspension systems of ABA signals, together with the organization, function, and interplay of the PYR, PYL, and RCAR receptors with other elements of the ABA signaling pathway, all suggest that ABA is one of the fundamental factors associated with abiotic stress [42]. This leads to the formation of PYR/PYLs/RCARs-ABA-Protein Phosphatase 2C (PP2C) complexes and the release of PP2C-imposed regulation of SnRK2s (Figure 1) [43]. The existence of ABA or osmotic stress may cause the Raf-type MAPKKK to phosphorylate and activate SnRK2s [44]. The expression of genes that respond to drought, such as LEA, PP2Cs, WRKYs, and HSPs, is governed by the phosphorylation of proteins implicated in the activation of SnRK2s, including ABA-response elements (ABREs)-binding factors (ABFs), and ABA Insensitive 5 (ABI5) (Figure 1). Additionally,

phosphorylated Open Stomata 1 (OST1) can reduce the activity of the inward-rectifying K^+ channels such as the potassium channel in *Arabidopsis thaliana* 1 (KAT1), the Slow Anion Channel-Associated 1 (SLAC1), and the Quickly Activating Anion Channel 1 (QUAC1), which allows the stomata to close (Figure 1) [45,46]. Additionally, Respiratory Burst Oxidase Homologue D (RBOHD) and Respiratory Burst Oxidase Protein F (RBOHF), which are in charge of producing ROS proteins, can be phosphorylated and activated by OST1 [47]. Brassinosteroid Insensitive 2 (BIN2), the Target Of Rapamycin (TOR), and other proteins help to maintain the balance between plant growth and the stress response [48]. High Expression of Osmotically Responsive Gene 15 (HOS15) and Phloem Protein 2B11 (PP2B11), which are known for their roles in cell growth and development, are both members of the serine/threonine protein phosphatase family and can degrade SnRK2s [44]. Drought stress activates a specific Ca^{2+} pathway transcribed by CBL-interacting protein kinases or CPKs. Furthermore, CBL5-CIPK11, CBL1/9-CIPK23, and CPK6/21/23 activate and phosphorylate SLAC1 [44] (Figure 1). Furthermore, CPK21 phosphorylates the outwardly rectifying K^+ channel [49]. RBOHD/F and Catalase3 (CAT3) are both phosphorylated by CBL5-CIPK11/26 and CPK8, thereby influencing the homeostasis of H_2O_2 [50,51]. The phosphorylation activities of CPK4/11 and CPK6 increase the activity levels of ABF1/4 and ABF3/ABI5 in transcription through the nucleus (Figure 1) [52]. When a cell is under stress, Receptor-Like Kinases (RLKs) identify signals from the outside and send them inside the cell [53]. Controlling the expression of *NCED3*, Barely Any Meristem1 (*BAM1*), and *BAM3* allows them to sense the short peptide Clavata3/Embryo-Surrounding Region-Related 25 (CLE25) and, as a result, trigger ABA production (Figure 1) [54–56]. An interaction between Rapid Alkalinization Factor1 (RALF1), Feronia (FER), and the Guanine nucleotide Exchange Factor (GEF), RHO-Related Protein from Plants 11 (ROP11), is required for ABI2 activation during conditions of drought stress [57–60]. On the other hand, ABA signaling is inhibited by the Glycine-Rich Protein 7 (GRP7), which is triggered by drought stress [44]. Drought stress triggers Guard Cell Hydrogen Peroxide-Resistant1 (GHR1), a Receptor-like Pseudokinase, to activate SLAC1, regardless of the kinase activity [61].

The plasma membrane and the tonoplast harbor the kinase 7 (KIN7) enzyme which, when affected by drought stress, phosphorylates the TPK1-K^+ channel found in vacuoles, which induces stomatal closure [62]. ABA-mediated drought responses are negatively downregulated by one E3 ubiquitin ligase, Plant U-Box Protein 11 (PUB11). PUB11 binds to Leucine Rich Repeat Protein 1 (LRR1) and KIN7 to ubiquitinate them in response to drought stress (Figure 1) [63]. In conclusion, protein kinases, including SnRK2s, MAPKs, CPKs/CIPKs, and RLKs, coordinate the responses of plants to drought stress from all angles.

3.1. 14-3-3-like Proteins

The 14-3-3 protein family is highly conserved and is found in all known eukaryotes [64,65]. 14-3-3 proteins play a central role in mediating a wide variety of complex signal transduction pathways in plants, including hormone crosstalk, metabolic processes, protein modification, gene transcription, and responses to stress [66]. In addition to their functions in stress responses and other signal transduction pathways, 14-3-3 proteins are essential for maintaining the electrochemical gradient across the plasma membrane [67]. The 14-3-3 genes *GF14b*, *GF14c*, *GF14e*, and *GF14f* were found to be expressed in reaction to infection with rice fungal and bacterial pathogens, confirming their roles in defense signaling responses [68]. Cotton was genetically modified to overexpress the Arabidopsis 14-3-3 protein GF14-λ, which resulted in a "stay-green" phenotype and increased the plant's resistance to water stress [69]. It is believed that the association between transporter H(+)-ATPase and the overexpression of *GF14-λ* alters stomatal conductance, leading to increased photosynthesis under conditions of dehydration [69]. Further, 14-3-3s and Hv14-3-3s have been identified as critical components of barley's quick stomatal reaction to drought [70]. According to reports, soil drought stress induces a high level of *OsGF14b* expression. The *osgf14b* mutant has been shown to have increased tolerance to drought and osmotic stress compared to the wild type (WT) through regulating the expression of

stress-relevant genes. Enhancement of the *osgf14b* mutant reinstated drought sensitivity to WT levels, whereas *OsGF14b*-overexpression lines were shown to have an increased drought and osmotic stress response. As expected, *OsGF14b*-overexpressing plants were found to be less susceptible to ABA than their *osgf14b* mutant counterparts [71].

3.2. Calcium-Mediated Proteins

It has been shown that several CaBs, such as CaMs, Calcium-Sensing Receptors (CaSRs), CDPKs, CIPKs, and Calreticulins (CRTs), are altered in response to drought [67,72]. The *CPK10* gene in Arabidopsis has been found to mediate stomatal movement in response to drought stress through the ABA and Ca^{2+} signaling pathways [22]. Furthermore, the CDPK, CIPK, and MAPK protein families have been linked to rice's resilience to stress [73–76]. For instance, the overexpression of *OsCDPK7* and *OsCIPK12* in rice increases their tolerance to drought stress during the seedling stage [73]. Furthermore, OsCIPK23, a member of the CIPK family, has been reported to play a significant role in rice pollination and drought stress responses [72]. Wei et al. [77] demonstrated that OsCPK9 enhances drought resistance by promoting stomatal closure and strengthening the plant's capacity for osmotic adaptation. These results revealed that *OsCPK9* overexpression positively affects drought tolerance and spikelet fertility because it increases rice stomatal closure, enhancing the plant's resistance to drought stress. Furthermore, OsCDPK1 controls rice's resistance to drought stress by regulating the 14-3-3 protein [77]. The CaMs/Calmodulin-Like proteins (CMLs), Ca^{2+}/CaM-based protein kinases (CCaMKs), CBL-CIPK modules, and CDPKs initiate the first step of Ca^{2+} signaling in response to drought stress [78] (Figure 2). CaMs/CMLs and CBLs serve as Ca^{2+}-sensor intermediaries, while CIPKs and CDPKs serve as sensing responses [79]. CaMs/CMLs act as versatile proteins that interact with plants' downstream targets to regulate stress conditions [80]. In plants, CBL–CIPK interactions have been shown to control various activities involving drought stress resistance [81]. The CaM-LD, Protein Kinase C (PKC, the pseudo-substrate region that binds to the inactive kinase), Ser/Thr, and the N-terminal polymorphic site are all critical features of CDPKs [82]. As a result of a conformational change triggered by Ca^{2+} interactions, the pseudo-substrate region becomes dissociated from the kinase domain, allowing the enzyme to become active [82]. The parts of the system that control the inflow and efflux processes are responsible for keeping the delicate $[Ca^{2+}]_{cyt}$ levels at the appropriate level. Ca^{2+} channels belonging to five different families have been identified in seed plants. These families include Two-Pore Channels (TPCs), Glutamate-Like Receptors (GLRs), Cyclic Nucleotide Gated Channels (CNGCs), Male Specific Lethal (MSLs), and hyperosmolality-induced $[Ca^{2+}]_{cyt}$ channels [83,84]. GLRs are nonselective Ca^{2+} channels. Their tetrameric topologies, which include an ion-pore loop and transmembranous domains, help with defensive signaling, ABA signaling, stomatal movement, carbon/nitrogen balance, root growth, nutritional homeostasis, pollen tube growth, and nutritional homeostasis [85–87]. The other proteins involved in the Ca^{2+} signaling pathway are CNGCs, which have a tetrameric architecture, six transmembranous domains, and cytosolic N- and C-termini on each monomer [88]. In plants, numerous cation transporter and channel protein families, including CNGCs, have been linked to activities that contribute to the ability of plants to withstand biotic and abiotic stress. Plant development and growth, as well as the uptake of cations such as Na(+), K(+), and Ca(2+), are all regulated by members of the CNGC family. Precise functional genomics methods have provided a new view of CNGCs. These proteins play a critical role in cellular ion homeostasis and growth pathways and as a "guard" for protection against biotic and abiotic stressors [89]. Cyclic nucleotides, such as Cyclic Adenosine Monophosphate (cAMP) and Cyclic Guanosine Monophosphate (cGMP), activate CNGCs [90] (Figure 2).

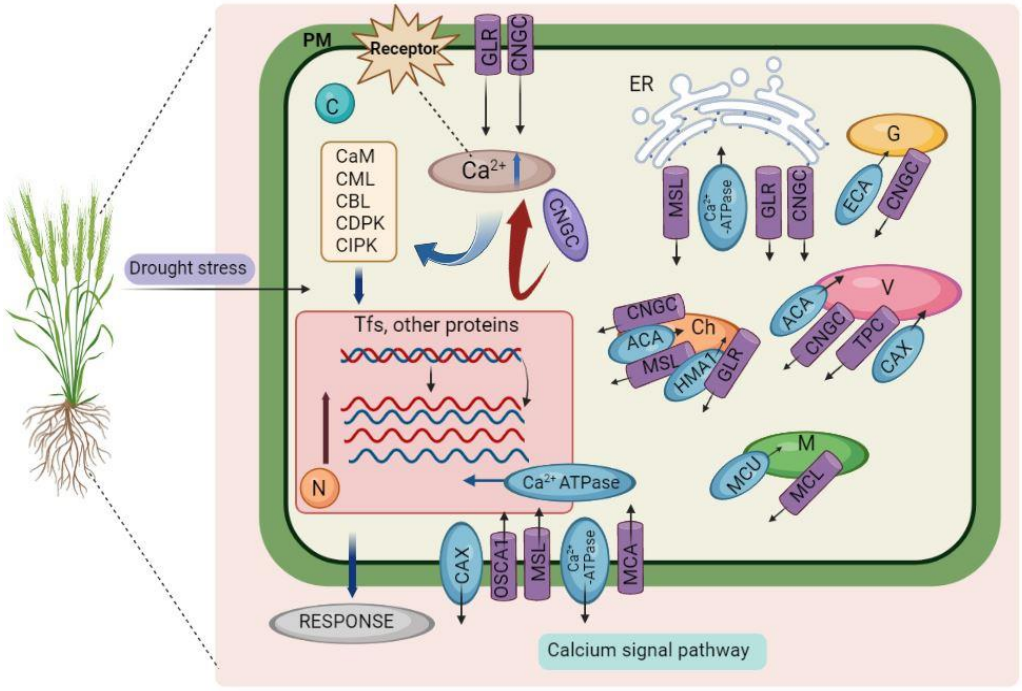

Figure 2. An illustration of the Ca^{2+} signaling system in plants. Plants use receptors on the PM to detect stress events. The receptors pick up on stimuli, which causes an increase in $[Ca^{2+}]_{cyt}$. Through EF-hands, the Ca^{2+} sensor detects the Ca^{2+} signal. The inflow systems are the CNGC, GLR, MSL, OSCA1, MCA, and TPC channels. These raise the level of $[Ca^{2+}]_{cyt}$ by delivering Ca^{2+} into the cytoplasm from extracellular spaces and subcellular compartments. The Mitochondrial Calcium Uniporter Complex (MCUC), Autoinhibited Ca^{2+}-ATPases (ACAs), ER-type Ca^{2+}-ATPases (ECAs), P1-ATPases (HMA1), and Ca^{2+} Exchangers (CAX: H^+/cation exchangers and CCX: cation/Ca^{2+} exchangers) operate as efflux mechanisms and lower the high $[Ca^{2+}]_{cyt}$ levels to sustain the Ca^{2+} concentration. The brief rises in $[Ca^{2+}]_{cyt}$ levels create Ca^{2+} signatures, which transmit stress-specific data further up the signaling pathway. PM: Plasma Membrane, C: cytosol, N: nucleus, ER: Endoplasmic Reticulum, V: vacuole, Ch: Chloroplast, G: Golgi apparatus, and M: Mitochondria.

3.3. Zinc-Finger Proteins (ZFP)

One of the most varied groups of transcription factors in plants is the ZFP family. It has been demonstrated that proteins containing finger-like structural domains are essential for plants to respond to abiotic challenges like drought [91]. In total, 176 and 189 zinc-finger proteins containing one or several zinc-finger motifs have been discovered in Arabidopsis and rice, respectively. Some zinc-finger proteins perform crucial functions in plant defense against abiotic stressors. Zat10 (STZ) and Zat12, for instance, improve plant tolerance to drought, salt, and oxidative stressors [92]. Drought-Induced Protein 19 (Di19) is a unique Cys_2/His_2 zinc-finger protein class that performs crucial functions in abiotic stress responses [92]. GhDi19-1 and GhDi19-2 have been proposed as positive regulators of crop tolerance to cold and drought stress because they are upregulated during the early stage of seedling germination and are involved in the plant response to salinity and ABA signaling in the initial phases of development [93,94]. Other studies showed that PtDi19-2 and PtDi19-7 may enhance BA-dependent signaling pathways, increasing drought resistance in transgenic plants [95]. These proteins are found throughout different tissues and regulate stress responses by, for example, reducing the stomatal density and increasing stomatal closure. Specifically, rice overexpressed with *OsZFP252* was shown to have a 74–79% greater chance of survival due to the gene's drought tolerance [6,18].

3.4. GTP-Binding Proteins (G-Proteins) and HSPs

The phytohormone signal transduction pathways rely on a group of proteins known as G-proteins. This group of proteins possesses wide structural and functional diversity [96]. Heterotrimeric G proteins link the signaling pathway between active G-Protein Coupled Receptors (GPCRs) and downstream effectors [97]. ABA signal transduction has been shown to involve a heterotrimeric G-protein through its regulation of guard cells. It has been shown that GPCRs and conventional stressors can also activate Ca^{2+} signaling pathways [98]. Multiple pathways in the Arabidopsis drought stress response, such as those involving the phytohormone ABA, the brassinosteroid ethylene, and extracellular calmodulin, have been linked to G proteins, which play a role in regulating the stomatal density during leaf development, improving the plant's ability to deal with drought [97–99]. It has also been shown that by inhibiting an AtMPK6-related pathway, the heterotrimeric G protein β subunit AGB1 negatively regulates drought tolerance and the ABA response in *Arabidopsis thaliana* [99].

On the other hand, ATP hydrolysis is an energy source required by HSP chaperone pathways. HSPs are activated by transcriptional regulators, such as Heat Shock transcription Factors (HSFs) and Calmodulin-Binding Protein Kinase 3 (CBK3). When CBK3 phosphorylates HsfA1a, it impacts HSPs and thermotolerance in Arabidopsis seedlings [100,101]. Arabidopsis FK-binding protein has been shown to bind to HSP90.1 in the cytosol under normal conditions. When cells are subjected to environmental stressors such as drought or oxygen deprivation, HSPs are activated. In addition, sugar beet HSP has been shown to be stimulated by drought stress [100,102,103]. According to some studies, the ability of rapeseed to withstand drought is associated with several different biochemical pathways. These pathways include HSP 90, V-type ATPase, plasma membrane-associated Cation Binding Protein, and EF-2 elongation factor [102,104].

3.5. Phytohormone-Mediated Proteins

Plant hormones like Auxins, Cytokinins (CK), BRs, and GAs play significant roles in determining how nutrients are used, how fast plants grow, and how well they can handle stress throughout their lives [105–107]. Arabidopsis Transcription Factor 1 or 2 (ATAF1 and ATAF2), Drought-Responsive Element Binding proteins (DREBs), Cup-shaped Cotyledon Transcending Protein (CCTP), Myelocytomatosis (MYC), Myeloblastosis (MYB), No Apical Meristem (NAM) proteins, ABREs, and ABFs are all transcription factors that are involved in ABA-mediated growth [19,108]. ABA insensitive 1 (ABI1) and OST1 are two essential components of the ABA signaling pathway that are required to act against drought stress [109].

When PYL, PYR, and RCARs are bound to ABA, these proteins can be combined with PP2Cs. As a result, these proteins can create a compound that activates downstream TFs and target genes, such as *SnRK*, which ultimately results in the phosphorylation of SnRK kinase [15,28]. The competitiveness of PYL, PYR, and RCARs coalescing with PP2Cs is strengthened after PYL, PYR, and RCARs bind to ABA. Arabidopsis, rice (*Oryza sativa* L.), and wheat (*Triticum aestivum* L.) were all shown to have dramatically enhanced drought tolerance after overexpressing the PYL, PYR, and RCAR proteins [110–112]. Furthermore, SnRK2 is required for the ABA signaling pathway, and it regulates plant development and stress responses [113,114]. In plants, the PP2Cs–SnRK2 complex controls the amount of phosphorylation caused by SnRK2, making it an important modulator of responses to abiotic stress [115]. Drought has been demonstrated to enhance PP2C and Phospholipase D (PLD) phosphorylation in *Z. mays*, suggesting that PP2C and PLD are involved in the plant response to abiotic stressors [116]. Meanwhile, PP2C is known to inhibit SnRK activity through the ABA signaling pathway, which has a negative effect on drought tolerance in plants. ABA upregulates PP2C, revealing its pivotal function in the negative regulation of drought tolerance [117]. SnRK2 phosphorylates several TFs, particularly the Basic Leucine Zipper (bZIP) TF family, to control the expression of ABA response genes [112]. Through phosphorylation, SnRK2s regulate the transcriptional activity of HAT1 (a component of

the HD-ZIP TFs), influencing the responsiveness of ABA. HAT1 is negatively regulated by ABA signaling and drought tolerance after being phosphorylated by SnRK2, activating PP2C [118]. The *HAT1*-overexpressing lines were shown to be more susceptible to ABA and less tolerant to drought stress [118].

The RLK family, which includes MRLK, LRR-RLK, and LecRLK, regulates the activity of downstream transcription factors to mediate the cellular response to various environmental factors and drought stress [106]. The genetic and molecular mechanisms underlying RLKs' role in drought responses are finally being unraveled. Furthermore, it has been demonstrated that the rice LRR-RLK gene FON1 phosphorylates and activates the ABA signaling pathway components, increasing drought tolerance in transgenic rice [106,119].

Drought stress causes an increase in CLE25 expression in the root vascular tissues of Arabidopsis. These mobile peptides can precisely convey environmental stimuli from sensor tissues to target tissues because of the peptide–receptor modules in each tissue. Dehydration stress causes changes in the root-to-shoot transmission, and a recent study found that the peptide CLE25 modulates ABA production, facilitating stomatal closure [54]. Through the induction of NCED3 expression in the leaves, root-derived CLE25 travels from the roots to the leaves and improves ABA absorption. BAM1-and BAM3-RLKs are able to detect CLE25 in the leaves. The CLE25-BAM1 and BAM3 systems control ABA absorption and responses, like stomatal closure and the activation of genes that are turned on by stress. These findings suggest that plants can integrate information about water deficits into their roots and leaves and optimize stress responses in those tissues. *NCED3* expression activated by dehydration stress is mediated by the NGATHA1 (NGA1) transcription factor [120]. The *NGA1* gene is expressed in the vasculature of leaves. This proves that NGA1 interacts directly with the CLE25-BAM1 and BAM3 signaling networks to regulate NCED3 expression [120]. ABA production rises in response to drought stress, activating stomatal closure as an initial defense mechanism to withstand water scarcity by reducing transpiration levels. The signaling cascade controlling stomatal opening is mediated by the dependent pathway protein kinase SnRK2 (OST1/SNRK2E) [121]. A loss of turgor and subsequent stomatal movement is caused by the ABA-dependent modification of ion transport in guard cells. Several proteins participate in the outflow of K^+ ions and anions from guard cells (Figure 3a). Additionally, ABA affects the expression profiles and alterations of the aquaporin genes, which control the rigidity of guard cells after stomatal closure [122,123]. Moreover, it is known that the MAPKKK18 protein, which is activated by ABA, regulates stomatal closure in Arabidopsis, in which the mutant map3k18 was associated with an increased stomata [124]. (Figure 3b).

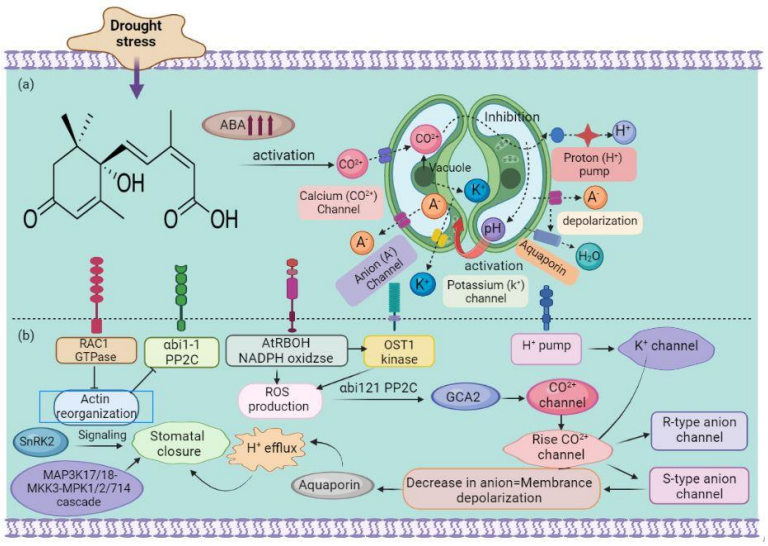

Figure 3. Many proteins and membrane transporters interact to produce stomatal closure under conditions of drought stress. (**a**) By lowering the turgor pressure in the guard cells, ABA-induced stress

triggers anions, K^+, and water to move out of the guard cells during stomatal drought. The Ca^{2+} ions brought in by abscisic-acid-mediated Ca^{2+} channel activation cause the guard cells' pH to rise by obstructing the passage of protons (H^+) via the proton pump. The alkalinity of the guard cells rises, resulting in the release of K^+ ions. (**b**) A schematic illustrating the connections between the roles of various aquaporins, ABA-mediated stomatal closure, ion transporters, and proteins and the increased abscisic acid accumulation brought on by drought stress. Under drought stress, the increase in abscisic acid accumulation regulates a set of proteins through specialized activity, and downstream signaling mediates stomatal closure.

3.6. LEA Proteins

Plant LEA proteins are hydrophilic and glycine-rich proteins that have been discovered in various plant species [125,126]. LEA proteins can be identified by their distinct structural characteristics. One of these characteristics is a highly conserved lysine-rich domain, which is thought to be involved in hydrophobic interactions that lead to macromolecule stabilization [127]. Based on their amino acid sequence similarities and the presence of repeated sequence motifs identified in a freely available database (LEAPdb), LEA proteins are classified into at least six distinct categories [127]. LEA proteins are plants' most abundant stress proteins associated with cold and drought stress. These proteins are active in seeds with a high ABA level [128]. LEA proteins, also known as dehydrins, accumulate in response to dehydration and low temperatures. They accumulate in asexual tissues during water shortage and are biosynthesized during the seed's decaying phase. Multiple studies have identified membrane-stabilizing and LEA proteins as an additional protein category that plays a significant role in drought resistance [8,126,129,130]. For instance, LEA proteins can shield cells from the harmful effects of drought by functioning as chaperones and hydrophilic solutes [18]. OsDhn-Rab16D, a YSK2-type DHN protein, interacts in the nucleus with OsFKBP (Os02g52290), a positive transcriptional co-modulator that confers ABA-responsive drought stress resistance in *Oryza sativa* L. ssp. Japonica by influencing stress-related genes and modifying the root architecture [131].

3.7. MAPK-Mediated Proteins

The phosphorylation and activation of MAPKKs are carried out by MAPKKKs, which are MAPKs that can also be phosphorylated by MAPKKs [110,132–135]. ANP1-3, CTR1, and AtMEKK are the three main MAPKKK groups in Arabidopsis. It has been shown that abiotic stresses, such as cold, drought, and mechanical stimulation, are the central stimulators that express AtMEKK1 [136]. AtMPK1, AtMPK2, PsMPK2, ZmMPK7, and GhMPK2, as well as other groups of MAPKs, have been shown to play key roles in various signaling mechanisms associated with specific biological functions [137,138]. Lavoie et al. [139] showed that cell surface receptors or exposure to environmental stressors such as drought activate MAPKs, causing them to associate with small GTPases and/or other protein kinases and activate the MAPKKKs. *OsMPK5* and the *MAPKKK* gene *DSM1* in rice have been linked to drought resistance. A recent study showed that the overexpression of *OsMAPK5a*, a member of the MAPK family, in transgenic rice resulted in increased OsMAPK5a kinase activity and improved drought tolerance [6].

3.8. SNF1-Related Kinase Proteins

Plants' SnRK proteins are homologous to fungal SNF1. Plants have 38 members in the SnRK family, which is divided into three subfamilies (SnRK1, SnRK2, and SnRK3). *Arabidopsis thaliana* (SnRK2.1-2.10) and rice (SAPK1-10) are two plants with ten SnRK2s [121,140]. These 10 SnRK2 members may be classified into three categories based on their domain topologies. Group A consists of SnRK2.1, SnRK2.4, SnRK2.5, SnRK2.9, and SnRK2.10. Group B consists of SnRK2.7 and SnRK2.8, whereas group C consists of SnRK2.2, SnRK2.3, and SnRK2.6. The ABA-insensitive snrk2.6 mutant does not close its stomata in response to ABA [141]. By phosphorylating a conserved region identified in LEA proteins, SnRK2.10/SRK2B protein kinase was revealed to contribute to drought tolerance [142]. The

overexpression of *SRK2C* and *SnRK2.8* was shown to increase the expression of drought-responsive genes in *A. thaliana* roots and positively influence drought tolerance [143]. The overexpression of SRK2C/SnRK2.8 in *A. thaliana* was shown to boost plant growth, implying that this kinase is involved in metabolic pathways linked to plant development [144]. However, a microarray study revealed that some drought-sensitive genes involving ABRE-Binding Proteins (AREBs)/ABFs, bZIP-type transcription factors, and their targets are regulated by subclass II SnRK2s [145]. These findings reveal that SnRKs play critical roles in drought stress signaling in plants.

3.9. Transcription Factor (TF) Proteins

TFs are a crucial subset of regulatory proteins involved in the transcriptional regulation of the drought stress response [2,146–148]. Transcriptome analyses have shown that many TFs are involved in plants' drought stress responses [149,150]. TFs are found in a variety of large responsive groups, such as ethylene-responsive element binding protein (EREBP), ethylene-responsive factors (ERF), APETALA type 2 (AP2), DREBs, and AREBs/ABFs. MYCs, MYBs, the NAM/ATAF/CUC TF (NAC), and WRKY binding TFs are examples of TFs [6,19,149]. In Arabidopsis, DREB2A encodes a TF with an AP2 domain that binds precisely to the DRE motif and activates genes involved in the drought response [147,151]. DRE/CRT has been shown to be one of the most vital factors in the ABA-independent signaling pathway [152]. In Arabidopsis, the overexpression of DREB1/CBF was found to induce the expression of more than 40 stress-inducible genes, which resulted in drought tolerance [153]. sDREBs in the AP2 domain, such as OsDREB and ARAG1, have been shown to enhance the response of rice to drought. ABA activates and upregulates ABF3, AREB1, and AREB2, which are members of the ABF/AREB subfamily. They are well-known for their roles in drought stress ABRE-dependent ABA signaling [147,152]. ABA-induced abiotic stress can be addressed by utilizing genes containing ACGT core sequences to activate several bZIP TFs, such as ABRE and G-box, resulting in the essential function of bZIP TFs as effectors of the ABA signaling pathway [112]. In Arabidopsis and rice, drought tolerance was discovered to be controlled by some bZIP TFs. For example, the overexpression of *ABRE1*, a gene active at the amino site R-X-X/S/T, enhances drought tolerance and leads to greater ABA sensitivity in Arabidopsis [112,154]. The overexpression of *ABF3* (the first component of bZIP) has been demonstrated to increase the expression of ABA-related genes that encode proteins such as RAB21, Hsp70, and Protein Phosphatase 2Ca (PP2CA) [155]. The binding of AtAREB3/AtDPBF3 to the Actin-Depolymerizing Factor 5 (*ADF5*) promoter increases its expression in response to drought stress and ABA treatments [11,112]. Drought resistance and the ABA response in Arabidopsis were improved by the TaFDL2-1A or TabZIP8-7A-related protein [112]. It has been reported that the *OsbZIP23* gene plays a key role in regulating the drought stress response in rice. In addition, the overexpression of the *OsbZIP42*, *OsbZIP46*, and *OsbZIP52* genes was associated with improved resistance against drought stress. Furthermore, the overexpression of *OsbZIP46-OsbZIP46CA1* has been associated with increased drought stress resistance [155,156]. NAC TF also plays a vital role in abiotic stress responses, helping plants to respond to different abiotic stressors, such as drought, salt, heat, and cold, by governing gene expression and therefore regulating physiological processes [155]. Several NAC TFs in the grapevine have been found to improve drought tolerance in Arabidopsis, including VvNAC26, VvNAC08, VvNAC17, and VaNAC17 [151]. Moreover, Movahedi et al. [2] revealed that the overexpression of *CarNAC3* in poplars exhibited significantly enhanced salinity and drought stresses. The overexpression of three well-known NAC stress-responsive genes, ANAC019, ANAC055, and RD26/ANAC07, has also been associated with increased drought tolerance in Arabidopsis [157]. In Arabidopsis, NAC016 reduces the transcription of AREB1 in response to drought stress, enhancing the response of plants to stress [158]. An inhibitor of NAC-like (NAP) triggered by AP3/PI in a trident-feed-forward modulatory loop, NAC016 suppresses AREB1 transcription [158].

3.10. Other Drought-Related Proteins in Plants

Dehydration-responsive proteins from W89 of wheat, the SAM binding protein, and methyltransferase have shown homology, which suggests that W89 plays an essential role in the early stages of drought stress by controlling the expression of stress-responsive genes [19]. Actin-depolymerizing factors, rubisco activase, S-like RNase homologs, and proteins similar to isoflavone reductase have been found to be part of four new drought-responsive pathways in rice leaves [21,130]. Several major Differentially Accumulated Proteins (DAPs) were found in NC47 wheat (*Triticum aestivum* L. "Ningchun 47" wheat), including enolase, fibrillin-like protein, 6-phosphogluconate dehydrogenase, HSP 70, OEE2, and 2-Cys peroxiredoxin BAS1, which all play essential roles in the drought-stress response [159]. Transgenic Arabidopsis plants expressing Acetylserotonin O-methyltransferase 1 (*ASMT1*) or Serotonin N-acetyltransferase 5 (*SNAT5*) have been demonstrated to have lower levels of endogenous ROS than wild-type plants, resulting in enhanced drought stress tolerance [157]. Aquaporins, or water channel proteins, contribute to drought tolerance by increasing their water intake by opening a water channel, aiding in plant survival in dry areas [11,18]. According to a research study, the basic helix-loop-helix domain gene *OsbHLH148* in rice contributes to jasmonate signaling, which makes the plant more drought-resistant. Moreover, after treatment with Methyl Jasmonate (MeJA) or abscisic acid and exposure to abiotic conditions such as dehydration, high salinity, low temperature, and wounding, high OsbHLH148 transcription levels were identified [160].

4. Crosstalk of Phytohormone and Early Osmotic-Stress Pathways

Standard parts of signal transduction pathways are perception, signaling at the level of proteins or through second messengers, and changes in the expression levels of target genes. In terms of how plants respond to drought stress, dynamic changes in cellular metabolism, phytohormones, or other signaling molecules are only part of the story. ABA is an essential phytohormone used by plants in response to drought stress. It does this by closing stomata and activating stress-responsive genes. Hence, it has been postulated that ABA signaling has an important impact on plant dehydration stress responses. The RCAR-type ABA receptor, PP2C, PYR, PYL, and SnRK2 are the three primary components of early ABA signaling [161]. A genetic search for ABA sensitivity produced Arabidopsis mutants with ABI. It was discovered that ABI1 and ABI2 encode homologous PP2C, demonstrating the impact of protein phosphorylation in ABA signaling [162]. The ABA-insensitive mutants *abi1*-1 and *abi2*-1 are the sources of ABI1 and ABI2, two members of the Group A subfamily of plant PP2Cs [162]. Nevertheless, more recent studies discovered that altering either the *ABI1* or *ABI2* genes affects ABA hypersensitivity [163]. In ABA-hypersensitive mutants, researchers found additional PP2Cs, such as AHG1 and AHG3/PP2CA [164]. Consequently, it was found that group A PP2Cs are negative modulators of ABA signaling. It has been suggested that group A PP2Cs could be operationally responsible for ABA signaling in various ways. For instance, *abi1*-1 and *abi2*-1 display an ABA-insensitive phenotype that underlies ABA reactions, such as seed dormancy, seedling growth, ABA-responsive gene expression, and stomatal closure, which indicates that both ABI1 and ABI2 play roles in these plant tissues [162]. For this reason, PP2C family members play vital roles in plants as regulators of ABA signaling [162]. The 14 PYR, PYL, and RCAR genes have been identified in Arabidopsis [165]. Furthermore, it has been proposed that these individuals perform partially overlapping functions in different plant tissues. Because of their shared hydrophobic properties, the PYR, PYL, and RCAR proteins can all recognize ABA as a ligand. PYR, PYL, and RCAR interact with group A PP2Cs and prevent their protein phosphatase activity due to these conformational changes [165]. The SnRK2 family of proteins has been discovered to play a role in ABA-activated protein kinases in plants, supplementing the function of PP2C in this pathway [166]. Arabidopsis contains ten SnRK2 family members, which are classified into three groups. Subclass III SnRK2s (SRK2I/SnRK2.3, SRK2D/SnRK2.2, and SRK2E/OST1/SnRK2.6) are the most sensitive to ABA and play important roles in plant ABA rebuttal [167]. This discovery was made after reverse genetic experiments yielded

a triple knockout mutant of subclass III SnRK2s (SnRK2.2, 2.3, and 2.6, Srk2dei). Most ABA responses were hampered by srk2dei, including stomatal closure, seed dormancy, and ABA-responsive gene expression [168]. Based on the results, we can conclude that subclass III SnRK2s function as positive modulators in ABA signaling. The *Sln1* gene product, a membrane-spanning histidine kinase, regulates osmotic-stress-responsive gene expression by activating the MAPK cascade [169]. The Arabidopsis gene *AHK1 (AtHK1)* was identified as an osmosensor due to its connection with Sln1 in yeast [170]. The Arabidopsis gene *AHK1 (AtHK1)* was identified as an osmosensor due to its connection with Sln1 in yeast [171]. All SnRK2 classes respond to osmotic stress reversely through the ABA signaling pathway. SRK2C/SnRK2.8, a member of SnRK2 subclass II, is triggered by osmotic stress and impacts dehydration resistance in Arabidopsis [143]. *SRK2C* overexpression in Arabidopsis upregulates many dehydration stress-responsive genes, including the transcription factors DREB1A and CBF3 [172]. SnRK2s are triggered by ABA and osmotic stress, as previously stated. Even though the mechanism of ABA-dependent stimulation of SnRK2 has been identified [117], it is still unclear how osmotic-stress signals activate SnRK2s. Since osmotic-stress-dependent stimulation of SnRK2 is quicker than ABA-dependent activation, it is plausible that osmotic-stress signaling involves several activation pathways. Moreover, as previously stated, group A PP2Cs have a negative effect on subclass III SnRK2s, but subclasses I and II SnRK2s have no or weak interactions with PP2C [173].

5. Conclusions

Due to their sessile life cycle, plants have developed systems to react to and adapt to harmful environmental stimuli throughout their development and growth. Understanding the regulatory systems that govern and enhance how different plants react to stress is crucial for developing strategies to keep plants productive. In this study, we focused on the molecular mechanisms that underlie how plants respond to water stress. Ion transfer, signaling pathway activation, and the proteins involved in these pathways that protect against drought stress are a few of these processes. This review can help researchers to understand the complex and nuanced ways in which plants respond to signals of drought, as well as the role of drought-responsive pathways in these responses. Possible drought-resistance proteins have been identified via crosstalk pathways. This review addressed the potential functions of a drought-responsive pathway in dehydration tolerance and the relationships between phytohormone signaling pathways. Expression of one or more tolerance effector genes under constitutive or stress-inducible promoters enhances the genetic engineering of drought stress resistance. In addition, this review identified a signaling model for drought stress that considers the signaling components shared by all abiotic stresses and can thus be applied to develop stress tolerance in plants. The development of stable, abiotic-stress-resistant plant strains that are also amenable to being manipulated with phytohormones to fulfill individualized requirements will be one of the most challenging tasks in future decades. This review presents an intriguing opportunity for researchers to explore methods of engineering drought-resistant crop plants that are robust to various abiotic stresses.

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