Review
Molecular Aspects of MicroRNAs and Phytohormonal Signaling in Response to Drought Stress: A Review

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Abstract: Phytohormones play an essential role in plant growth and development in response to environmental stresses. However, plant hormones require a complex signaling network combined with other signaling pathways to perform their proper functions. Thus, multiple phytohormonal signaling pathways are a prerequisite for understanding plant defense mechanism against stressful conditions. MicroRNAs (miRNAs) are master regulators of eukaryotic gene expression and are also influenced by a wide range of plant development events by suppressing their target genes. In recent decades, the mechanisms of phytohormone biosynthesis, signaling, pathways of miRNA biosynthesis and regulation were profoundly characterized. Recent findings have shown that miRNAs and plant hormones are integrated with the regulation of environmental stress. miRNAs target several components of phytohormone pathways, and plant hormones also regulate the expression of miRNAs or their target genes inversely. In this article, recent developments related to molecular linkages between miRNAs and phytohormones were reviewed, focusing on drought stress.

Keywords: drought stress; microRNA; phytohormones; gene expression; stress regulation

1. Introduction

Abiotic stresses are common problems of every ecosystem and rely on various environmental factors [1,2]. Drought is among the most hazardous stresses among all other abiotic stresses that affect crop plants throughout the world [3,4]. A recent study has revealed that the total yield loss triggered by drought is approximately 7% worldwide [5,6]. It was estimated that by 2050, water stress will severely affect cultivated land and ultimately affect the two-thirds of the global population [7,8]. Drought affects crops in different ways, and even crops with the same drought tolerance might have different gene expression and metabolism. As a result, identification of drought-tolerant genetic resources and determining the best technique to avoid crop loss are critical [9]. Adverse effects of drought can be eliminated by post-transcriptional regulation of genes associated with signal transduction, protein biosynthesis, energy metabolism, photosynthetic activity, and membrane trafficking [8,10].

Phytohormones are key signaling molecules responsible for all biological and metabolic regulators in the plant’s life cycle [11]. Critical phytohormones include ethylene (Et), abscisic acid (ABA), salicylic acid (SA), cytokinin (CK), gibberellic acid (GA), auxin (Aux), indole acetic acid (IAA), brassinosteroids (BR), jasmonic acid (JA), and strigolactones (SL) [11,12]. Among these plant hormones, five hormones (ABA, IAA, CK, GA and ET) are classical hormones, whereas the rest (JA, SA, BR and SL) are recognized as putative or growing phytohormones. In plants, phytohormones are synthesized via various pathways and are perceived by specific receptors, triggering intracellular signal transduction [12].
Phytohormones work together to alter multiple cellular processes, such as elongation of cells, vascular root patterning, and management of abiotic and biotic stress response.

Intracellular phytohormones are important growth regulators, but they have significant functions in plant drought stress tolerance by regulating physiological processes and molecular interactions [13]. Drought stress has an impact on phytohormone generation, accumulation, and distribution throughout the plant body [13]. After signal perception, ABA is the most critical phytohormone and the most important hormone produced in response to water scarcity [14,15]. Jasmonates have a key function in fruit ripening, root growth, and reproduction. This hormone also plays an important function in regulating plant water stress reactions [13]. Salicylic acid (SA) was established by several researchers to play a significant function in plant under drought stress [13]. Low amounts of SA boost plant antioxidant capability, but greater levels can kill cells or make plants more vulnerable to abiotic stress [11]. SA stimulates genes with roles in the production of secondary metabolites, chaperones, organic acids, and heat shock proteins [16,17]. Cell elongation, vascular tissue improvement, and apical dominance are all known impacts of indole-3-acetic acid on plant elongation and development [18]. During drought conditions, IAA appears to assimilate plant development and upregulate gene expression linked with root meristem initiation, enhancing root branching, and increasing plant stress tolerance [13,18].

Plant microRNAs (miRNAs) are 20–24 nucleotide-long post-transcriptional regulatory molecules [19,20]. These highly conserved molecules play a function in various systems of mature plants, including plant growth, development, and stress tolerance. miRNA is a small RNA that control the expression of different genes involved in biological and metabolic processes. Because it induces divergence in the expressed gene, the interaction between miRNA and its mRNA target is particularly significant [21]. A single miRNA can target various additional genes in the same cell signaling pathway. Through endonucleolytic cleavage or translational inhibition of mRNA cognate targets, miRNAs operate as a negative gene expression regulator [19,22].

Stress response modulation via the miRNA pathway was found in several plant species [23,24]. To combat with severe environmental conditions, plants have evolved many strategies for modifying the expression of genes that regulate physiological processes. Drought stress was demonstrated to boost plant miRNA expression [25]. It has an impact on several biological processes, including stem, root, leaf, and flower production. In response to miRNA regulation, plants are affected by biotic and abiotic stress, hormone signaling, and nutritional balance [26].

Plants naturally have different processes to acclimatize to changes in harsh conditions, including pathways in which miRNAs play a vital role in biotic and abiotic stress conditions. miRNA genes are up- or downregulated in a variety of species, including soyabean (Glycine max), sugarcane (Saccharum officinarum), rice (Oryza sativa), and maize (Zea mays), under different stresses [24,27,28]. Multiple evidences are available in literature that indicate the expression or accumulation of these miRNAs to further explain the regulatory networks connected with stress defense mechanisms [23]. Several miRNAs have critical role in the morphological development of the fruit. miR164, miR156/miR157, miR396, and miR160 expression, for example, can cause abnormal fruit, such as fused carp and reduced fruit size and morphology [29,30].

This review focused on the recent knowledge about phytohormones, miRNAs, and their involvement in responses to drought stress in crop plants. We have tried to outline the impacts of miRNAs and phytohormones on the expression of drought-related genes. Another section addresses the crosstalk among miRNAs and plant hormones during drought conditions. At the end, we discuss about the potential of miRNAs to improve abiotic stress, such as drought, tolerance in crop plants.

2. Drought-Responsive Genes Are Regulated by Plant Hormones

Plant hormones are chemical messengers that control growth, development, and metabolic activities in plants under different biotic and abiotic stimuli [31]. Plant survival is
strongly linked to hormone-mediated main regulatory mechanisms, which is a complicated process involving multiple interactions at the transcriptional, translational, and cellular levels [10,16]. Plant hormones and miRNA-mediated gene regulation are critical regulators of gene expression in both normal and stressful situations [32]. Plants response to environmental stress differs due to variations in phytohormone levels.

Plant hormones, such as abscisic acid (ABA), auxins (IAA), gibberellin (GA), cytokinin (CTK), salicylic acid (SA), and jasmonic acid (JA), regulate the drought stress in plants [10,33,34]. However, the mode of action of various phytohormones to eliminate/escape the drought stress is diverse, depending upon the developmental stage, plant tissues and drought prevailing conditions. During drought stress, some plant hormones help modify the root architecture of plants, influence the photosynthetic machinery, modulate the water balance, enhance the antioxidant defense system and control the drought-related gene expression in plants [10].

Abscisic acid (ABA) is a crucial phytohormone that have a significant role in regulating different signaling pathways under environmental stresses [35,36]. During drought stress, ABA accumulates in guard cells via ABA biosynthesis pathway. ABA synthesis reduces turgor pressure and causes the closure of stomata, decreasing the transpirational water loss [37]. ABA is absorbed in plant leaves at the morphological level, improving cell wall extensibility, tissue turgidity, and root hydraulic transmission [36]. ABA content enhances drought resistance by improving total chlorophyll contents, more stem dry weight and high regulation of drought-tolerant genes such as RD22, RD29B and bZIP [33]. ABA regulates root growth to reach the deep water in the soil during osmotic stress. Interaction of ABA with other plants hormones leads to developing the lateral roots in plants necessary to tolerate dehydration stress [33]. Accumulation of ABA during drought conditions was observed in wheat, rice, sorghum, barley, and soybean [35,38].

ABA influences and controls the regulation of several genes by forming osmoprotectants and defensive proteins [35]. Upregulation of rice guard cell genes (SNAC1) enhances ABA sensitivity, drought stress tolerance, and closure of stomata [39]. Overexpression of Os-bZIP72 and OsbZIP46, which boosted the expression of ABA sensitive genes, improved rice drought tolerance considerably [40]. In rice plants, upregulation of OsMYB48–1 boosted the expression of genes produce ABA such as OsNCED4 and OsNCED5 [41]. GmHP08 improves drought tolerance in soybeans via ABA-dependent pathways [42]. Drought resistance in Arabidopsis thaliana is improved by overexpression of the AtSAUR32 gene, which accumulates ABA and IAA hormones [43]. By inducing ABA and ROS scavenging, Arabidopsis ascorbic acid peroxide genes such AtAPX2 increased water usage efficiency and drought resistance [44,45].

Auxin/Indole 3-acetic acid (IAA) was the first phytohormone discovered to have important functions for plant growth and development through cell elongation, tissue differentiation, axial elongation, and apical dominance [36]. Auxin regulates all aspects of plant life, from embryogenesis through senescence [32] although an increase in auxin levels was linked to a decrease in growth, indicating that a change in hormonal balance is to blame for a decrease in growth under stress [32,37]. Auxin also promote roots branching, potentially significant for increasing drought tolerance [46]. Studies proved that miRNAs could control the auxin signal transduction, and on the other hand, various auxin signaling genes were observed to target the miRNAs. In addition to genes, some auxin-responsive factors (ARFs) were reported as miRNA targets, i.e., ARF10, ARF16 and ARF 17 were upregulated by miRNA160 and miRNA167 where they were downregulated by ARF2, ARF3, ARF6 and ARF8 [47]. Activation of the OsGH3-2 gene encoding the IAA inactivation enzyme decreases free IAA content and various changes in the pattern of drought resistance in transgenic white clover (Trifolium repens) [33]. Drought stress was observed to upregulate two OsPIN rice genes, OsPIN2 and OsPIN5b [48]. TLD1/OsGH3 overexpression enhances the expression of LEA genes, resulting in greater drought tolerance in Oryza sativa plants, suggesting that auxins activate a number of interrelated metabolic pathways [49].
According to previous study, miRNAs could be a suitable pathway for incorporating auxin. Auxin genes such as OsIAA6 were found to be induced by drought stress and are involved in dehydration stress resistance [50]. In white clover, upregulation of auxin and drought-responsive genes such as bZIP11, MYB14, MYB48, DREB2, GH3.1, GH3.9, IAA8, WRKY2, WRKY56, WRKY108715, and RD22 was found [33]. OsGH3-2, an auxin and ABA regulating gene, was implicated in rice drought stress regulation [51].

Ethylene is a methionine-derived metabolite that is sensitive to biotic and abiotic stressors. Stage ethylene controls shoot growth, stem thickness, root elongation, stomatal density, and leaf abscission at the seedling level [52]. It has, however, been extensively researched in the process of plant senescence, although it is less well understood in drought-induced senescence [53]. Under drought stress, ethylene was proven to cause leaf abscission, which reduces water loss [54]. Water stress stimulates the de novo synthesis of 1-aminocyclopropane-1-carboxylate (ACC) synthase, an ethylene biosynthesis rate-controlling enzyme [53]. Furthermore, ethylene and its metabolic process induce plant responses to flooding and water scarcity, and it is involved in a variety of abiotic stress-related plant metabolic activities [55]. Drought stress tolerance/resistance mediated by ethylene was seen in (Glycine max), rice (Oryza sativa), and maize (Zea mays), potato (Solanum tuberosum), and Arabidopsis plants [56]. Rice proline synthesis and drought tolerance have both been linked to OsEBP89, a member of the AP2/ERF family [55]. The gene SIERF36 was found to play a role in stomatal density, plant growth, and photosynthetic activities in potato (Solanum tuberosum) plants [57].

The phytohormone ethylene has a regulatory role in root elongation under drought conditions by interacting with auxin. During the seedling stage in rice plants, ethylene interacts with the auxin biosynthesis gene OsELI1 to inhibit the enlargement of roots [58]. A mutant eto1 was identified in Arabidopsis and rice, which accumulates more ethylene and affect the stomatal closure and ROS production in guard cells [59].

The plant hormone cytokinin (CK) was first found in maize crop. Plants produce CKs in their root tips, which are then transferred to the xylem. Cell division, vascular and shoot differentiation, nutrient mobilization, anthocynin production, photomorphogenic development, and leaf senescence are all pathways in which CK is required [60,61]. CK was reported to trigger in response to drought stress and exert positively or negatively on drought regulation, depending on stress interval and frequency in plants [10].

CKs are considered a crucial regulator of root length, root branching; hence it plays a significant role for elongation of primary roots and branching in response to drought stress [62]. Transgenic cotton (Gossypium hirsutum) enriched isopentenyl transferase (IPT) expression has resulted in higher endogenous CK levels, deferred plant senescence and enhanced drought tolerance [63]. CK improved drought tolerance in the transgenic barley lines through overexpressing the CK dehydrogenase gene [64].

The transgenic roots of barley also demonstrated significantly greater auxin productivity. Functional analyzes of CK receptor mutants revealed that certain Arabidopsis and Brassica napus CK receptors, namely AHK2, AHK3, CRE1/AHK4, BnCHK1 and BnCHK3, and BnCHK5 perform as negative osmotic stress regulators [65]. ARRI, ARRI0, and AARR12, Arabidopsis type B CK response regulators, were shown to promote drought stress tolerance by improving cell membrane integrity, ABA hypersensitivity, anthocynin production, and stomatal aperture reduction [66]. Similarly, type A CK response regulators (AHK2, AHK3 and AHK4) expressed higher ABA sensitivity and drought stress tolerance [67,68]. The higher expression of CKs from type B triple mutants arr1, arr10, and arr12 suggested that they play a role in ABA–CK crosstalk and were triggered by water stress [44,66].

Plants produce salicylic acid (SA), a phenolic molecule that works as a growth regulator and controls plant maturity, and abiotic interactions [69,70]. According to current research, SA plays a critical role in plants under different abiotic stresses such as drought stress [34,71]. SA improves drought resistance through influencing plant physiological systems such as photosynthetic activity, the production of antioxidants, and stress tolerance genes [70].
SA application in Arabidopsis regulates the ICS1 gene and confirms the drought tolerance. Many WRKY TFs such as WRKY70 and WRKY54 are widely distributed among plant species and are governed by SA application [72,73]. Overexpression of WRKY70 TFs regulates HD-zip-I genes under limited water conditions [72]. WRKY70 and WRKY54 cooperate as a negative regulator of osmotic stress tolerance and stomatal closure in Arabidopsis, showing their importance in abiotic stress signaling [73,74]. Drought resistance in rice, tomato, wheat, and bean (Phaseolus sp.) plants was confirmed by exogenous SA treatment [75,76]. A putative method for maintaining the water content in plant leaves was suggested: SA-induced stomatal closure [75]. AP2/ERFs, leucine zipper, Zn fingers, and other transcription factors, according to gene expression profiling studies, have responded to SA and drought stress, showing that this phytohormone plays a substantial role in drought stress response. In Arabidopsis, SA-dependent miRNA167 influenced flower and root growth as well as osmotic stress resistance [77].

Jasmonic acid (JA) is an important phytohormone produced in the chloroplast, cytoplasm, and peroxisomes. JA and its derivatives are known as jasmonates with significant roles in biotic and abiotic stresses in plants [2]. JAs are widely found in plant blooms [34,69]. This plant hormone regulates development and is involved in flowering, fertilization, and main root growth [34]. During drought stress JA enhances water uptaking capacity of plants by altering root hydraulic conductivity [78]. JA moderate the effect of low moisture conditions by regulating the signaling of secondary metabolites. Moreover, JA improves antioxidant activities by enhancing the production of osmoprotectants and compatible solutes [79]. The first ever response of JA against dehydration stress was reported in barley, where it was noted that an increased level of JA enhanced the transpiration induction of relevant downstream genes [80].

Drought tolerance mediated by JA has since been found in wheat [79], rice [81], maize [82], and chickpea (Cicer arietinum) [83]. The major precursor of JA, 12-OPDA, is involved in stomatal closure regulation in a model plant [84]. The gene OsbHLH148 interacts with OsJAZ in rice plants under drought stress, and high levels of OsDREB1 expression promote drought tolerance [37]. Another study found that upregulation of the OsbHLH148 gene makes rice plants more resistant to desiccation stress [85]. According to the findings, JA is involved in plant defense not only during injury and pathogen attack, but also during drought. Despite a lot of research on the role of JA in drought tolerance, more research is needed to fully understand drought tolerance in plants [37].

Gibberellic acids (GA) are important plant hormones which are involved to control the growth-related traits, i.e., cell expansion, cell elongation, leaf, stem, root and fruit growth [71]. Plants synthesize various GAs but GA1 and GA4 are the most active types of these hormones [37]. These phytohormones respond to drought stress by affecting photosynthetic enzymes, nutrient use efficiency, leaf area index and stomatal conductance [71]. GAs are synthesized in cytoplasm, plastids and endoplasmic reticulum [53]. Application of GAs to improve low moisture stress tolerance was observed in maize [71,86], wheat [87] and sunflower [88]. The Arabidopsis methyl transferase gene 1 AtGAMT1 was overexpressed in tomato plants to create drought-resistant transgenic tomatoes [37]. It was also found in another study that the GA 2-Oxidase gene (OsGA2ox) was found to improve rice drought resistance [89]. In a recent study, soybean TF GmTGA15 was shown to be overexpressed in plants with low moisture content [17].

Brassinosteroids (BRs) belong to a novel group of steroidal plant hormones that play role in morphological and physiological changes of plant by altering their growth and development [90,91]. Plant BRs are synthesized in immature seeds, pollens, flowers and roots and play indirect role to modulate the drought by stimulating the H$_2$O$_2$ level of plants [92,93]. In Arabidopsis, wheat, clover, tomato, and brassica, BRs have depicted positive functions under drought stress [94,95]. BRs interact with other plant hormones, such as ABA, to reduce the severity of drought stress in tomato plants [91]. BR precursor’s 24-Epibrassinosteroid and 28-homobrassinolide include favorable modifications in Arabidopsis, brassica, purple mustard, and pepper (Capsicum annuum) plants’ photosyn-
thetic antioxidant system during restricted water stress [90,96]. Overexpression of the Arabidopsis BR biosynthesis gene AtDWF4 in canola boosted growth, yield, and water stress tolerance, according to research [97]. Furthermore, whereas RNA interference improved drought stress tolerance in Brachypodium [98], overexpression of the SIBRII gene reduces drought tolerance in tomato plants, suggesting that drought tolerance is reliant on defective BRs production pathways. [91,95]. The genes AtDREBD2A and AINCE3 were elevated in Arabidopsis plants after exogenous BR treatment [90]. Various phytohormones that regulate drought responsive genes are listed in Table 1.

The BR-related gene OsLAC, which is connected to grain yield during osmotic stress, is inhibited by upregulation of miR397 in O. sativa and Arabidopsis. [99,100]. Strigolactones (SLs), which are generated from carotenoids, are a recent addition to the phytohormones family [101]. SL, a carotenoid-derived terpene lactone, was isolated from a G. hirsutum root culture solution in the 1960s [102]. Under environmental limits, SLs are biosynthesized at the plant root and induce the production of lateral roots and root hairs to increase the absorption of restricted inorganic nutrients by the roots [101]. Simultaneously, these SLs are transported to above-ground plant sections, limiting the growth of lateral buds or branches and lowering the branches’ inorganic nutritional requirements. Because they are generated in plant roots and transported to the rhizospheric zone, these plant hormones are best known for their role in the rhizospheric zone. The primary types of SLs analogues that are chemically produced are GR5, GR7, and GR24 [93,101]. Recently, the functions of SLs in reducing the negative effects of abiotic stressors were documented [93]. In Arabidopsis exogenous GR24 has several regulatory functions for drought tolerance. When drought stress was applied to SL depleted Arabidopsis and tomato mutants, plants revealed alterations in stomata and ABA levels. When lettuce plants were drought stressed, the Arbuscular mycorrhiza symbiosis changed the level of SLs in the root systems, according to other studies [103]. SLs were found to initiate and control stomatal closure in response to stressors, and the corresponding molecular mechanism for controlling stomatal closure was also elucidated [104]. Drought tolerance in Arabidopsis was proven to be positively regulated by strigolactone DWARF14, which modulates abscisic acid response, cell membrane integrity, accumulation of epicuticular waxes, stomatal closure and biosynthesis of anthocyanin [105].

Table 1. Phytohormones regulate the drought-responsive genes in various plant species.

| Plant Hormone | Gene Regulation | Crop Name | Reference |
|---------------|-----------------|-----------|-----------|
| IAA, ABA, GA, BR | Upregulation of drought-resistant TFs and genes | White clover | [33] |
| IAA | Upregulation of drought-responsive genes | Tea | [106] |
| CK | Overexpression of cytokinin oxidase genes | Tobacco | [31] |
| ET, ABA | Overexpression of ethylene-responsive factors (ERF9) | Tobacco | [107] |
| CK | Overexpression of cytokinin dehydrogenase genes | Barley | [108] |
| CK | Cytokinin biosynthesis gene IPT | Cotton | [63] |
| Aux, ABA, ET | Ectopic expression of GAWOX4 | Cotton | [109] |
| ABA | Overexpression of GsABF2 | Cotton | [110] |
| ABA | Overexpression of drought resistance genes OsbZIP72 | Rice | [111] |
| ABA | Overexpression of drought resistance genes OsbZIP46 | Rice | [40] |
| ABA, JA | Overexpression of OsJAZ1 | Rice | [81] |
| ABA, JA | Overexpressing of OsbZIP42 | Rice | [112] |
| ABA, GA, JA, IAA | Overexpressing of OsSAP | Rice | [113] |
| GA | Expression of GA2-specific mutants | Rice | [89] |
| ET | Expression of OsERF109 | Rice | [114] |
| ABA | Ectopic expression of OsSAPK2 | Rice | [115] |
| ET | Overexpression of ethylene response factors (ERFs) | Tomato | [116] |
| GA, ET | Downregulate the expression of SIDREB | Tomato | [117] |
| ABA | Upregulation of SGRAS4 | Tomato | [118] |
| BR | Upregulation of brassinosteroid biosynthetic gene DWF4 | Brassica | [97] |
| ABA | Uprogregation of LOSS5/ABA3 | Soybean | [119] |
| SA, ABA, GA | Overexpression of GmTGA15 TFs | Soybean | [17] |
| ABA | Ectopic expression of CaCal | Chickpea | [120] |
| ABA, BR | Expression of AtCAMTA1 | Arabidopsis | [121] |
3. Drought Stress Regulation by miRNAs in Diverse Crop Species

Physiological, molecular and transcription levels of drought tolerance were well characterized in crop plants [3,122]; however, miRNA mediation has not yet been properly explained [11]. In addition to plant development, miRNAs also regulate abiotic stress-responsive genes in plant species [123]. So, by understanding the mechanism through which miRNAs respond to stress-responsive genes and which genes are the targets of miRNAs will help to develop more resistant plants [124,125]. As an important regulator of the plant regulatory network, prior importance was given to miRNAs for post-transcriptional regulation of drought tolerance [125]. Due to their salient features, drought-responsive miRNAs were characterized in Arabidopsis, cereals and oil seed crops [126–130]. Role of various miRNAs to overcome the drought tolerance traits has been shown in Figure 1. A study about the miRNA transcriptome using high-throughput sequencing technologies in wild barley may be an effective way to determine the drought resistance attributes of miRNAs and their target genes [9]. When maize plants were subjected to drought stress, various miRNAs were upregulated, and some miRNAs were downregulated [131]. Drought stress also upregulated the expression of miRNAs in wheat [132] and rice [133,134]. In Arabidopsis, the gene expression of miR393, miR397, and miR402 increased, while the expression of miR319c and miR389a decreased under dehydration stress [99]. miR398 and miR408 are thought to induce drought tolerance in pea (Pisum sativum) [135] and clover [136]. In tomato plants, miR159, miR169, miR160, miR167, miR393 are associated with dehydration stress tolerance, by controlling hormonal signal transduction, stomatal closure and auxin-responsive genes [137,138]. miR164 was expressed in the leaf and roots of orchard grass when these plants were exposed to dehydration treatments [139]. A significant decrease in the expressions of miR530a, miR1445, and miR1447 in Populus trichocarpa was observed in plants under limited water stress, which varies from the expression pattern of miR1450 under drought conditions [140]. Similarly, when sugarcane plants were subjected to drought, several miRNAs showed higher expression and some were downregulated [141]. Further, it was observed that the expression pattern of miRNAs is also plant tissue growth stage and cultivars dependent. ABA treatment in rice downregulates the expression of miR167 [142]; however, drought stress upregulates it in Arabidopsis [143]. miR169 was downregulated in Arabidopsis and clover during drought, while it was upregulated in rice [144]. Drought stress reduced the expression of miR398 in maize [130], whereas its expression increased in clover [144].

Figure 1. Functions of miRNAs in response to drought stress in crop plants.
4. Crosstalk between Plant Hormones and miRNAs during Drought Stress

Hormone signaling and gene expression possess probabilistic roles in plant growth under miRNA control [145]. The first link between miRNAs and phytohormones (ABA, IAA and CK) was observed in the Arabidopsis plant [146]. After that, it was also confirmed that GA controls miR159 during anther development [147]. In addition, during Arabidopsis seed germination, it was revealed that miR160 promotes the production of the auxin response transcription factor ARF17 [148] and that miR159 induces ABA to bind to MYB (MYB33 and MYB101) mRNAs [149]. Many mRNAs involved in hormonal reactions, such as TIR1 and negative auxin signaling, are likely targets for miRNAs, and recent research has shown that TCP (TEOSINTE BRANCHED/CYCLOIDEA/PCF), the miR319 target, regulates the biosynthesis of the hormone jasmonic acid [150]. Despite the fact that the expression of miRNAs in plant hormone signaling is still poorly understood, no miRNAs were linked to cytokinin or ethylene signaling [142]. Three miRNAs, miR162, miR167, and miR413, are controlled by ABA during environmental stress and are responsible for stress tolerance and stress-related gene expression [142]. Furthermore, GA signaling downregulates two miRNAs, miR166 and miR319, which confer drought stress tolerance in plants [142]. According to available research, ABA regulates miRNA expression and influences the expression of some miRNA. For example, ABA regulates the expression of miR159, miR169, and miR172 in the embryonic callus of the Japanese larch (Larix kaempferi) [125].

In Arabidopsis, the higher gene expression of miR160 reduces ABA sensitivity during germination and tends to cause unusual root morphology, leading to the promotion of adventitious roots and lack of gravitropic responses [151]. During osmotic stress overexpression of miR172b reduces leaf water loss, increased ABA sensitivity and increase survival rate in soybean and Arabidopsis [152]. Researchers suggested that miR394 is implicated in ABA or ABA-dependent drought reactions in Arabidopsis [153]. Drought resulted in the miR393-dependent regulation of AUX signaling by the downregulation of AtTIR1 and AtAFB2 genes, which are growth inhibitors and associated with increasing ABA levels [154]. The overexpression of miR393, which inhibits the expression of OsTIR1 and OsAFB2, causes alterations in rice root development and drought tolerance [155].

Some miRNA expression is also affected by exogenous ABA, with miRNA controlling the downstream genes of ABA. ABA hypersensitivity and drought tolerance increase on the overexpression of miR168a, while hyposensitivity and dry hypersensitivity are observed in knockout miR168a-2 [156]. In Arabidopsis, ABA promotes the expression of mature miR394 and precursor miR394a/b [156]. This is also linked to the overexpression of miR396 in plants, which is responsible for reduced root length [157]. It has also been suggested that miR396 expression influences root expansion via the ABA/ET pathway. Because it was demonstrated to influence the expression of numerous ethylene response factor (ERF)- and ABA-related genes, miR396-GRF regulation of the ET and ABA pathways may have persisted [156]. Drought tolerance has also been enhanced by AtmiR396a and AtmiR396b by influencing morphology of leaf [142]. Draught conditions in plants are thought to be influenced by miR396 in ABA-mediated plant adaptation. Overall, the findings revealed that miR396 has a key role for control of cell propagation by ABA and ET in response to abiotic and biotic stresses [157].

Transgenic plants expressing the miR160-resistant AtARF10 form demonstrate the higher expression of several ABA-regulated genes as well as dose-dependent hypersensitivity to ABA, pointing to AUX as a possible ABA response modulator. ABA reduces the expression of miR167 in rice seedlings [142]. When this regulation occurs during germination, the production of miR167 is increased due to miR160's suppression of the ABA pathway, which promotes lateral root formation by IAR3 depression caused by AUX [53]. When rice seedlings were exposed to ABA treatment, the expression of miR167 was significantly reduced [142]. Similar regulation during the germination stage may restrict the ABA pathway, causing miRNA160 and miR167 production to increase. Despite the fact that ABA inhibits LCR (LEAF CURLING RESPONSIVENESS), which is a target of miR394a/b, and overexpression of miR394a/b results in ABA hypersensitivity and ABA-related phenotypes,
overexpression of LCR results in ABA-resistant phenotypes [153]. Role of miRNAs via plant hormones to control the drought related genes/trait in various plant species is listed in Table 2.

Furthermore, wild-type and LCR overexpressing plants collect more ABA-induced hydrogen peroxide and superoxide anion radicals than miR394a/b-expressing plants [153]. Drought-responsive miRNAs were found in barley [142]. Under dehydration stress, Arabidopsis showed upregulation of miR393, miR397b, and miR402, but downregulation of miR319c and miR389a [99]. It was discovered in another study that during dehydration stress in rice seedlings, 17 miRNAs were downregulated, including miR164c, miR319b, and miR1861d, while 16 miRNAs (miR166h, miR172d, miR408, and others) were upregulated [128]. MiR398 and MiR408 are downregulated in pea under restricted water stress [135].

Table 2. miRNAs response to drought stress via phytohormonal signaling.

| miRNA   | Gene/Trait Effected                   | Hormone Involved | Plant Species | Reference |
|---------|---------------------------------------|------------------|---------------|-----------|
| miR165  | Drought tolerance                     | ABA              | Arabidopsis   | [160]     |
| miR166  | Drought stress tolerance              | ABA              | Arabidopsis   | [160]     |
| miR160  | Leaf development                      | Aux              | Arabidopsis   | [160]     |
| miR167  | ARF6, ARF8                            | Aux              | Arabidopsis   | [77]      |
| miR398  | Upregulation                          | Aux              | Tomato        | [134]     |
| miR952  | Overexpression                        | Aux              | Tomato        | [134]     |
| miR115  | ROS homeostasis                       | ABA              | Millet        | [21]      |
| miR156  | Antioxidant enzymatic activities      | ABA              | Millet        | [21]      |
| miR399  | 9-cis-epoxy-carotenoid dioxygenase1 proteins | ABA              | Millet        | [21]      |
| miR164  | 9-cis-epoxy-carotenoid dioxygenase1 proteins | ABA              | Millet        | [21]      |
| miR444d | IF3 genes                             | ABA              | Wheat         | [161]     |
| miR169d | ABA-responsive TFs                    | ABA              | Wheat         | [161]     |
| miR156  | Biosynthesis of anthocyanin genes     | ABA              | wheat         | [162]     |
| miR172  | Upregulate AP2 TFs                    | Saflower         | Safflower     | [19]      |
| miR398  | Detoxification of ROS                 | ABA              | Maize         | [163]     |
| miR164-MYB | Module drought stress                | ABA              | Maize         | [163]     |
| miR164-NAC | Module drought stress                | ABA              | Maize         | [163]     |
| miR159  | Proline accumulation                  | ABA              | Tomato        | [164]     |
| miR167  | Downregulated                         | ABA              | Rice          | [142]     |
| miR162  | Slightly downregulated                | ABA              | Rice          | [142]     |
| miR413  | Upregulated                           | ABA              | Rice          | [142]     |
| miR166  | Downregulated                         | GA               | Rice          | [142]     |
| miR319  | Downregulated                         | GA               | Rice          | [142]     |

5. Conclusions

miRNAs are a type of small non-coding RNA of 22 nucleotides in length and are considered critical gene expression regulators at the post-transcriptional stage. Various plant miRNAs are conserved across species. Such observations suggest that genetic changes based on miRNA in important crops can change environmental stress. The major function of miRNAs is the regulation of plant hormones. A complex network operates between...
protein-coding genes, phytohormones and miRNAs, regulating various plant development processes. They are significant key regulators for the proper development and growth of plants under both optimal and stress conditions, through phytohormone and miRNA-mediated gene expression regulation. In this review article, we compared the available miRNA literature with six phytohormone classes in crop development through genetic modulation of abiotic stress tolerance, including cytokinin (CK), gibberellic acid (GA), abscisic acid (ABA), ethylene (ET), auxin (AUX), and jasmonic acid (JA).

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**References**

1. Javed, I.; Awan, S.; Ahmad, H.; Rao, A. Assessment of Genetic Diversity in Wheat Synthetic Double Haploids for Yield and Drought Related Traits Through Factor and Cluster Analyses. *Plant Gene Trait* 2016, 7, 1–9. [CrossRef]

2. Tiwari, M.; Sharma, D.; Trivedi, P.K. Artificial microRNA mediated gene silencing in plants: Progress and perspectives. *Plant Mol. Biol.* 2014, 86, 1–18. [CrossRef] [PubMed]

3. Ahmad, H.M.; Wang, X.; Mahmood-Ur-Rahman; Fiaz, S.; Azeem, F.; Shaheen, T. Morphological and Physiological Response of Helianthus annuus L. to Drought Stress and Correlation of Wax Contents for Drought Tolerance Traits. *Arab. J. Sci. Eng.* 2021, 47, 6747–6761. [CrossRef]

4. Li, H.; Li, Y.; Ke, Q.; Kwak, S.-S.; Zhang, S.; Deng, X. Physiological and Differential Proteomic Analyses of Imitation Drought Stress Response in Sorghum bicolor Root at the Seedling Stage. *Int. J. Mol. Sci.* 2020, 21, 9174. [CrossRef] [PubMed]

5. Lesk, C.; Rowhani, P.; Ramankutty, N. Influence of extreme weather disasters on global crop production. *Nature* 2016, 529, 84–87. [CrossRef]

6. Ahmad, H.M.; Mahmood-Ur-Rahman; Azeem, F.; Shaheen, T.; Irshad, M.A. Genome-Wide analysis of long chain Acyl-CoA synthetase (LACS) genes in sunflower (*Helianthus annuus*) suggests their role in drought stress. *Int. J. Agric. Biol.* 2020, 24, 863–870.

7. Naumann, G.; Alfieri, L.; Wyser, K.; Mentaschi, L.; Betts, R.A.; Carrao, H.; Spinnori, J.; Vogt, J.; Feyen, L. Global Changes in Drought Conditions Under Different Levels of Warming. *Geophys. Res. Lett.* 2018, 45, 3285–3296. [CrossRef] [PubMed]

8. Ahmad, H.M.; Mahmood-Ur-Rahman; Azeem, F.; Tahir, N.; Iqbal, M.S. QTL mapping for crop improvement against abiotic stresses in cereals. *J. Anim. Plant Sci.* 2018, 28, 1558–1573.

9. Qiu, C.-W.; Liu, L.; Feng, X.; Hao, P.-F.; He, X.; Cao, F.; Wu, F. Genome-Wide Identification and Characterization of Drought Stress Responsive microRNAs in Tibetan Wild Barley. *Int. J. Mol. Sci.* 2020, 21, 2795. [CrossRef]

10. Hai, N.N.; Chuong, N.N.; Tu, N.H.C.; Kisiala, A.; Hoang, X.L.T.; Thao, N.P. Role and regulation of cytokinins in plant response to drought stress. *Plants* 2020, 9, 422. [CrossRef]

11. Li, T.; Gonzalez, N.; Inzé, D.; Dubois, M. Emerging Connections between Small RNAs and Phytohormones. *Trends Plant Sci.* 2020, 25, 912–929. [CrossRef]

12. Foo, E.; Plett, J.M.; Lopez-Raez, J.A.; Reid, D. Editorial: The Role of Plant Hormones in Plant-Microbe Symbioses. *Front. Plant Sci.* 2019, 10, 1391. [CrossRef]

13. Ma, Y.; Dias, M.C.; Freitas, H. Drought and Salinity Stress Responses and Microbe-Induced Tolerance in Plants. *Front. Plant Sci.* 2020, 11, 591911. [CrossRef]

14. Chen, C.; Chen, H.; Zhang, Y.; Thomas, H.R.; Frank, M.H.; He, Y.; Xia, R. TBtools: An Integrative Toolkit Developed for Interactive Analyses of Big Biological Data. *Mol. Plant* 2020, 13, 1194–1202. [CrossRef]

15. Ku, Y.-S.; Sintaha, M.; Cheung, M.-Y.; Lam, H.-M. Plant Hormone Signaling Crosstalks between Biotic and Abiotic Stress Responses. *Int. J. Mol. Sci.* 2018, 19, 3206. [CrossRef]
16. Siddiqi, K.S.; Husen, A. Plant response to jasmonates: Current developments and their role in changing environment. Bull. Natl. Res. Cent. 2019, 43, 153. [CrossRef]
17. Chen, Z.; Fang, X.; Yuan, X.; Zhang, Y.; Li, H.; Zhou, Y.; Cui, X. Overexpression of Transcription Factor GmTGA15 Enhances Drought Tolerance in Transgenic Soybean Hairy Roots and Arabidopsis Plants. Agronomy 2021, 11, 170. [CrossRef]
18. Göre-Sağlam, N.; Harrison, E.; Breeze, E.; Oz, G.; Buchanan-Wollaston, V. Analysis of the impact of indole-3-acetic acid (IAA) on gene expression during leaf senescence in Arabidopsis thaliana. Physiol. Mol. Biol. Plants 2020, 26, 733–745. [CrossRef]
19. Koufi, F.; Sorkheh, K.; Ercisl, S. MicroRNA expression patterns unveil differential expression of conserved miRNAs and target genes against abiotic stress in safflower. PLoS ONE 2020, 15, e0228850. [CrossRef]
20. Parmar, S.; Gharat, S.A.; Tagirasa, R.; Chandra, T.; Behera, L.; Dash, S.K.; Shaw, B.P. Identification and expression analysis of miRNAs and elucidation of their role in salt tolerance in rice varieties susceptible and tolerant to salinity. PLoS ONE 2020, 15, e0230958. [CrossRef]
21. Chakraborthy, A.; Viswanath, A.; Malipatil, R.; Rathore, A.; Thirunavukkarasu, N. Structural and Functional Characteristics of miRNAs in Five Strategic Millet Species and Their Utility in Drought Tolerance. Front. Genet. 2020, 11, 608421. [CrossRef]
22. Guleria, P.; Mahajan, M.; Bhardwaj, J.; Yadav, S.K. Plant Small RNAs: Biogenesis, Mode of Action and Their Roles in Abiotic Stresses. Genom. Proteom. Bioinform. 2011, 9, 183–199. [CrossRef]
23. Basso, M.F.; Ferreira, P.C.G.; Kobayashi, A.K.; Harmon, F.G.; Nepomuceno, A.L.; Molinari, H.B.C.; Grossi-de-Sa, M.F. MicroRNAs and new biotechnological tools for its modulation and improving stress tolerance in plants. Plant Biotechnol. J. 2019, 17, 1482–1500. [CrossRef]
24. Millar, A.A.; Lohe, A.; Wong, G. Biology and Function of miR159 in Plants. Plants 2019, 8, 255. [CrossRef]
25. Fang, Y.; Xie, K.; Xiong, L. Conserved miR164-targeted NAC genes negatively regulate drought resistance in rice. J. Exp. Bot. 2014, 65, 2119–2135. [CrossRef]
26. Balyan, S.; Kumar, M.; Mutum, R.D.; Raghuvanshi, U.; Agarwal, P.; Mathur, S.; Raghuvanshi, S. Identification of miRNA-mediated drought responsive multiple tiered regulatory network in drought tolerant rice, Nagina. Sci. Rep. 2017, 7, 15446. [CrossRef]
27. Ahmed, W.; Xia, Y.; Li, R.; Bai, G.; Siddique, K.H.M.; Guo, P. Non-coding RNAs: Functional roles in the regulation of stress response in Brassica crops. Genomics 2020, 112, 1419–1424. [CrossRef]
28. Huang, X.; Wang, Y.; Xu, J.; Wang, N. Development of multiplex genome editing toolkits for citrus with high efficacy in biallelic and homozygous mutations. Plant Mol. Biol. 2020, 104, 297–307. [CrossRef]
29. Bai, S.; Tian, Y.; Tan, C.; Bai, S.; Hao, J.; Hasi, A. Genome-wide identification of microRNAs involved in the regulation of fruit ripening and climacteric stages inmelon (Cucumis melo). Hortic. Res. 2020, 7, 106. [CrossRef]
30. Silva, G.F.F.; Silva, E.M.; Correa, J.P.O.; Vicente, M.H.; Jiang, N.; Notini, M.M.; Junior, A.C.; De Jesus, F.A.; Castilho, P.; Carrera, E.; et al. Tomato floral induction and flower development are orchestrated by the interplay between gibberellin and two unrelated microRNA-controlled modules. New Phytol. 2019, 221, 1328–1344. [CrossRef]
31. Lubovská, Z.; Dobrá, J.; Štorcová, H.; Šmilová, N.; Vanková, R. Cytokinins oxidase/dehydrogenase overexpression modifies antioxidant defense against heat, drought and their combination in Nicotiana tabacum plants. J. Plant Physiol. 2014, 171, 1625–1633. [CrossRef] [PubMed]
32. Aslam, M.; Sugita, K.; Qin, Y.; Rahman, A. Aux/IAA14 Regulates microRNA-Mediated Cold Stress Response in Arabidopsis Roots. Int. J. Mol. Sci. 2020, 21, 8441. [CrossRef] [PubMed]
33. Zhang, Y.; Li, Y.; Hassan, M.J.; Li, Z.; Peng, Y. Indole-3-acetic acid improves drought tolerance of white clover via activating auxin, abscisic acid and jasmonic acid related genes and inhibiting senescence genes. BMC Plant Biol. 2020, 20, 150. [CrossRef] [PubMed]
34. Chhaya; Yadav, B.; Jogawat, A.; Gnanasekaran, P.; Kumari, P.; Lakra, N.; Lal, S.K.; Pawar, J.; Narayan, O.P. An overview of recent advancement in phytohormones-mediated stress management and drought tolerance in crop plants. Plant Gene 2020, 25, 100264.
35. Sah, S.K.; Reddy, K.R.; Li, J. Abscisic Acid and Abiotic Stress Tolerance in Crop Plants. Front. Plant Sci. 2016, 7, 571. [CrossRef]
36. Rowe, J.H.; Topping, J.F.; Liu, J.; Lindsey, K. Abscisic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. New Phytol. 2016, 211, 225–239. [CrossRef]
37. Ullah, A.; Manghwar, H.; Shaban, M.; Khan, A.H.; Akbar, A.; Ali, U.; Ali, E.; Fahad, S. Phytohormones enhanced drought tolerance in plants: A coping strategy. Environ. Sci. Pollut. Res. 2018, 25, 33103–33118. [CrossRef]
38. Guóth, A.; Tari, L.; Gallé, Á.; Csiszár, J.; Pécsváradí, A.; Cseuz, L.; Erdei, L. Comparison of the Drought Stress Responses of Tolerant and Sensitive Wheat Cultivars During Grain Filling: Changes in Flag Leaf Photosynthetic Activity, ABA Levels, and Grain Yield. J. Plant Growth Regul. 2009, 28, 167–176. [CrossRef]
39. Hu, H.; Dai, M.; Yao, J.; Xiao, B.; Li, X.; Zhang, Q.; Xiong, L. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. Proc. Natl. Acad. Sci. USA 2006, 103, 12987–12992. [CrossRef]
40. Tang, N.; Zhang, H.; Li, X.; Xiao, J.; Xiong, L. Constitutive Activation of Transcription Factor OsbZIP46 Improves Drought Tolerance in Rice. Plant Physiol. 2012, 158, 1755–1768. [CrossRef]
41. Xiong, H.; Li, J.; Liu, P.; Duan, J.; Zhao, Y.; Guo, X.; Li, Y.; Zhang, H.; Ali, J.; Li, Z. Overexpression of OsMYB48-1, a Novel MYB-Related Transcription Factor, Enhances Drought and Salinity Tolerance in Rice. PLoS ONE 2014, 9, e92913.
42. Chuong, N.N.; Hoang, X.L.T.; Nghia, D.H.T.; Nguyen, N.C.; Thao, D.T.T.; Tran, T.B.; Ngoc, T.T.M.; Thu, N.B.A.; Nguyen, Q.T.; Thao, N.P. Ectopic expression of GmHP08 enhances resistance of transgenic Arabidopsis to drought stress. Plant Cell Rep. 2021, 40, 819–834. [CrossRef]
43. He, Y.; Liu, Y.; Li, M.; Lamin-Samu, A.T.; Yang, D.; Yu, X.; Izhar, M.; Jan, I.; Ali, M.; Lu, G. The Arabidopsis SMALL AUXIN UP RNA32 Protein Regulates ABA-Mediated Responses to Drought Stress. *Front. Plant Sci.* 2021, 12, 625493. [CrossRef]

44. Osakabe, Y.; Osakabe, K. Chapter Six-Genome Editing to Improve Abiotic Stress Responses in Plants. In *Gene Editing in Plants*; Weeks, D.P., Yang, B., Eds.; Academic Press: Cambridge, MA, USA, 2017; Volume 149, pp. 99–109, ISBN 1877-1173.

45. Rossel, J.B.; Walter, P.B.; Hendrickson, L.; Chow, W.S.; Poole, A.; Mullineaux, P.M.; Pogson, B.J. A mutation affecting ASCORBATE PEROXIDASE 2 gene expression reveals a link between responses to high light and drought tolerance. *Plant Cell Environ.* 2006, 29, 269–281. [CrossRef]

46. Wolters, H.; Jürgens, G. Survival of the flexible: Hormonal growth control and adaptation in plant development. *Nat. Rev. Genet.* 2009, 10, 305–317. [CrossRef]

47. Cui, J.; Sun, Z.; Li, J.; Cheng, D.; Luo, C.; Dai, C. Characterization of miRNA160/164 and Their Targets Expression of Beet (*Beta vulgaris*) Seedlings Under the Salt Tolerance. *Plant Mol. Biol. Report.* 2018, 36, 790–799. [CrossRef]

48. Lu, G.; Coneva, V.; Casaretto, J.A.; Ying, S.; Mahmood, K.; Liu, F.; Nambara, E.; Bi, Y.-M.; Rothstein, S.J. OsPIN5b modulates rice (*Oryza sativa*) plant architecture and yield by changing auxin homeostasis, transport and distribution. *Plant J.* 2015, 83, 913–925. [CrossRef]

49. Zhang, C.; Fei, S.; Warnke, S.; Li, L.; Hannapel, D. Identification of genes associated with cold acclimation in perennial ryegrass. *J. Plant Physiol.* 2009, 166, 1436–1445. [CrossRef]

50. Jung, H.; Lee, D.-K.; Choi, Y.D.; Kim, J.-K. OsIAA6, a member of the rice Aux/IAA gene family, is involved in drought tolerance and tiller outgrowth. *Plant Sci.* 2015, 236, 304–312. [CrossRef]

51. Du, H.; Wu, N.; Fu, J.; Wang, S.; Li, X.; Xiao, J.; Xiong, L. A GH3 family member, OsGH3-2, modulates auxin and abscisic acid levels and differentially affects drought and cold tolerance in rice. *J. Exp. Bot.* 2012, 63, 6467–6480. [CrossRef]

52. Hussain, A. Genome–Wide Analysis of Ethylene Responsive Factor in Maize: An In Silico Approach. *Appl. Ecol. Environ. Res.* 2016, 14, 177–200. [CrossRef]

53. Salvi, P.; Manna, M.; Kaur, H.; Thakur, T.; Gandass, N.; Bhatt, D.; Muthamilarasan, M. Phytohormone signaling and crosstalk in regulating drought stress response in plants. *Plant Cell Rep.* 2021, 40, 1305–1329. [CrossRef]

54. Habben, J.E.; Bao, X.; Bate, N.J.; DeBruin, J.L.; Dolan, D.; Hasegawa, D.; Helentjaris, T.G.; Lafitte, R.H.; Lovan, N.; Mo, H.; et al. Transgenic alteration of ethylene biosynthesis increases grain yield in maize under field drought-stress conditions. *Plant Biotechnol. J.* 2014, 12, 685–693. [CrossRef]

55. Zhang, Y.; Li, J.; Chen, S.; Ma, X.; Wei, H.; Chen, C.; Gao, N.; Zou, Y.; Kong, D.; Li, T.; et al. An APETALA2/ethylene responsive factor, OsEBP89 knockout enhances drought tolerance by regulating sugar and cytokinin metabolism. *J. Exp. Bot.* 2020, 295, 941–956. [CrossRef]

56. Ahmadzadeh, M.; Chen, J.-T.; Hasanzadeh, S.; Ahmar, S.; Heidari, P. Insights into the genes involved in the ethylene biosynthesis pathway in Arabidopsis thaliana and *Oryza sativa*. *J. Genet. Eng. Biotechnol.* 2020, 18, 62. [CrossRef]

57. Upadhuyay, R.K.; Soni, D.K.; Singh, R.; Dwivedi, U.N.; Pathre, U.V.; Nath, P.; Sane, A.P. SIERP36, an EAR-motif-containing ERF gene from tomato, alters stomatal density and modulates photosynthetic activity and growth. *J. Exp. Bot.* 2013, 64, 3237–3247. [CrossRef]

58. Qin, H.; Zhang, Z.; Wang, J.; Chen, X.; Wei, P.; Huang, R. The activation of OsEII1 on YUC8 transcription and auxin biosynthesis is required for ethylene-inhibited root elongation in rice early seedling development. *PloS Genet.* 2017, 13, e1006955. [CrossRef]

59. Tanaka, Y.; Sugano, S.S.; Shimada, T.; Hara-Nishimura, I. Enhancement of leaf photosynthetic capacity through increased stomatal density in Arabidopsis. *New Phytol.* 2013, 198, 757–764. [CrossRef] [PubMed]

60. Glanz-Idan, N.; Tarkowski, P.; Turečková, V.; Wolf, S. Root–shoot communication in tomato plants: Cytokinins as a signal molecule modulating leaf photosynthetic activity. *J. Exp. Bot.* 2020, 71, 247–257. [CrossRef] [PubMed]

61. Ming, M.; Ren, Q.; Pan, C.; He, Y.; Zhang, Y.; Liu, S.; Zhong, Z.; Wang, J.; Malzahn, A.A.; Wu, J.; et al. CRISPR-Cas12b enables efficient plant genome engineering. *Nat. Plants* 2020, 6, 202–208. [CrossRef] [PubMed]

62. Wang, M.; Le Gourrierec, J.; Jiao, F.; Demotes-Mainard, S.; Perez-Garcia, M.-D.; Ogé, L.; Hamama, L.; Crespel, L.; Bertheloot, J.; Chen, J.; et al. Convergence and Divergence of Sugar and Cytokinin Signaling in Plant Development. *Int. J. Mol. Sci.* 2021, 22, 1282. [CrossRef]

63. Kuppu, S.; Mishra, N.; Hu, R.; Sun, L.; Zhu, X.; Shen, G.; Blumwald, E.; Payton, P.; Zhang, H. Water-Deficit Inducible Expression of a Cytokinin Biosynthetic Gene IPT Improves Drought Tolerance in Cotton. *PLoS ONE* 2013, 8, e64190.

64. Ramireddy, E.; Hosseini, S.A.; Eggert, K.; Gillandt, S.; Gnadt, H.; von Wirén, N.; Schmülling, T. Root Engineering in Barley: Increasing Cytokinin Degradation Produces a Larger Root System, Mineral Enrichment in the Shoot and Improved Drought Tolerance. *Plant Physiol.* 2018, 177, 1078–1095. [CrossRef]

65. Kuderová, A.; Gallyová, L.; Kuricová, K.; Nejedlá, E.; Cúrdová, A.; Michalová, L.; Pihlal, O.; Šmajs, D.; Spichal, L.; Hejátko, J. Identification of AHK2- and AHK3-like cytokinin receptors in Brassica napus reveals two subfamilies of AHK2 orthologues. *J. Exp. Bot.* 2015, 66, 339–353. [CrossRef]

66. Nguyen, K.H.; Van Ha, C.; Nishiyama, R.; Watanabe, Y.; Levyva-Gonzalez, M.A.; Fujita, Y.; Tran, U.T.; Li, W.; Tanaka, M.; Seki, M.; et al. Arabidopsis type B cytokinin response regulators ARR1, ARR10, and ARR12 negatively regulate plant responses to drought. *Proc. Natl. Acad. Sci. USA* 2016, 113, 3090–3095. [CrossRef]

67. Jeon, J.; Kim, N.Y.; Kim, S.; Kang, N.Y.; Novák, O.; Ku, S.-J.; Cho, C.; Lee, D.J.; Lee, E.-J.; Strnad, M.; et al. A Subset of Cytokinin Two-component Signaling System Plays a Role in Cold Temperature Stress Response in Arabidopsis. *J. Biol. Chem.* 2010, 285, 23371–23386. [CrossRef]
68. Osakabe, Y.; Osakabe, K.; Shinozaki, K.; Tran, L.-S.P. Response of plants to water stress. Front. Plant Sci. 2014, 5, 86. [CrossRef]

69. Jogawat, A.; Yadav, B.; Chhaya; Lakra, N.; Singh, A.K.; Narayan, O.P. Crosstalk between phytohormones and secondary metabolites in the drought stress tolerance of crop plants: A review. Physiol. Plant. 2021, 172, 1106–1132. [CrossRef]

70. Khan, M.I.R.; Fatma, M.; Per, T.S.; Anjum, N.A.; Khan, N.A. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front. Plant Sci. 2015, 6, 462. [CrossRef]

71. Bahramadi, E.; Tavakkol Afshari, R.; Mahallati, M.N.; Seyyedi, S.M. Abscisic, gibberellic, and salicylic acids effects on germination indices of corn under salinity and drought stresses. J. Crop Improv. 2021, 36, 73–89. [CrossRef]

72. Sek, S.; Chakraborty, J.; Ghosh, P.; Basu, D.; Das, S. Chickpea WRKY70 Regulates the Expression of a Homeodomain-Leucine Zipper (HD-Zip) I Transcription Factor CaHDZ12, which Confers Abiotic Stress Tolerance in Transgenic Tobacco and Chickpea. Plant Cell Physiol. 2017, 58, 1934–1952. [CrossRef]

73. Li, J.; Besseau, S.; Törönen, P.; Sipari, N.; Kollist, H.; Holm, L.; Palva, E.T. Defense-related transcription factors WRKY70 and WRKY54 modulate osmotic stress tolerance by regulating stomatal aperture in Arabidopsis. New Phytol. 2015, 200, 457–472. [CrossRef]

74. Besseau, S.; Li, J.; Palva, E.T. WRKY54 and WRKY70 co-operate as negative regulators of leaf senescence in Arabidopsis thaliana. J. Exp. Bot. 2012, 63, 2667–2679. [CrossRef]

75. Khalvandi, M.; Siosemardeh, A.; Roohi, E.; Keramati, S. Salicylic acid alleviated the effect of drought stress on photosynthetic characteristics and leaf protein pattern in winter wheat. Heligmon 2021, 7, e05908. [CrossRef]

76. Siosemardeh, A.M.; Tahjib-Ul-Arif, M.; Afrin, S.; Sakil, M.A.; Hossain, M.T.; Hossain, M.A.; Hossain, M.A. Exogenous salicylic acid and hydrogen peroxide attenuate drought stress in rice. Plant Soil Environ. 2020, 66, 7–13. [CrossRef]

77. Caruana, J.C.; Dhar, N.; Raina, R. Overexpression of Arabidopsis microRNA167 induces salicylic acid-dependent defense against Pseudomonas syringae through the regulation of its targets ARF6 and ARF8. Plant Direct 2020, 4, e00270. [CrossRef]

78. Sanchez-Romera, B.; Ruiz-Lozano, J.M.; Li, G.; Luu, D.-T.; Martinez-Ballesta, M.D.C.; Carvajal, M.; Zamarreño, A.M.; García-mina, J.M.; Maurel, C.; Arroca, R. Enhancement of root hydraulic conductivity by methyl jasmonate and the role of calcium and abscisic acid in this process. Plant Cell Environ. 2014, 37, 995–1008. [CrossRef]

79. Anjum, S.A.; Tanveer, M.; Hussain, S.; Tung, S.A.; Samad, R.A.; Wang, L.; Khan, I.; Rehman, N.U.; Shah, A.N.; Shahzad, B. Exogenously applied methyl jasmonate improves the drought tolerance of wheat imposed at early and late developmental stages. Acta Physiol. Plant. 2016, 38, 25. [CrossRef]

80. Kramell, R.; Miersch, O.; Atzorn, R.; Parthier, B.; Wasternack, C. Octodecanoid-Derived Alteration of Gene Expression and the “Oxylipin Signature” in Stressed Barley Leaves. Implications for Different Signaling Pathways. Plant Physiol. 2000, 123, 177–188. [CrossRef]

81. Fu, J.; Wu, H.; Ma, S.; Xiang, D.; Liu, R.; Xiong, L. OsJAZ1 Attenuates Drought Resistance by Regulating JA andABA Signaling in Rice. Front. Plant Sci. 2017, 8, 2108. [CrossRef]

82. Zhou, X.; Yang, S.; Sun, C.; Li, S.; Li, J.; Xu, M.; Liu, X.; Zhang, S.; Zhao, Q.; Li, Y.; et al. A Maize Jasmonate Zim-Domain Protein, ZmJAZ14, Associates with the JA, ABA, and GA Signaling Pathways in Transgenic Arabidopsis. PLoS ONE 2015, 10, e0121824. [CrossRef] [PubMed]

83. Zhou, X.; Li, L.; Xiang, J.; Gao, G.; Xu, F.; Liu, A.; Zhang, X.; Peng, Y.; Chen, X.; Wan, X. OsGL3-1 is involved in cuticular wax biosynthesis and tolerance to water deficit in rice. PLoS ONE 2015, 10, e0116676. [CrossRef] [PubMed]

84. Riemann, M.; Dhakeray, R.; Hazman, M.; Miro, B.; Kohli, A.; Nick, P. Exploring Jasmonates in the Hormonal Network of Drought and Salinity Responses. Front. Plant Sci. 2015, 6, 1077. [CrossRef] [PubMed]

85. Seo, P.J.; Lee, S.B.; Suh, M.C.M.C.; Park, M.-J.; Go, Y.S.; Park, C.-M.C.-M. The MYB96 transcription factor regulates cuticular wax biosynthesis under drought conditions in Arabidopsis. Plant Cell 2011, 23, 1138–1152. [CrossRef] [PubMed]

86. Sarwar, N.; Farooq, O.; Mubeen, K.; Wasaya, A.; Nouman, W.; Zafar Ali, M.; Shehzad, M. Exogenous Application of Gibberellic Acid Improves the Maize Crop Productivity Under Scarce and Sufficient Soil Moisture Condition. Cerec. Agron. Mold. 2017, 50, 65–73. [CrossRef]

87. Abbasi, A.; Maleki, A.; Babaei, F.; Safari, H.; Rangin, A. The role of gibberellic acid and zinc sulfate on biochemical performance relate to drought tolerance of white bean under water stress. Cell. Mol. Biol. 2019, 65, 1–10. [CrossRef] [PubMed]

88. Erdemli, H.; Kaya, M.D. Ayıcığı (Helianthus annuus L.)’nde Gibberellik Asit Dozlarının Verim ve Abiyotik Stres Köşullarında Çımlenen Uzerine Etikleri. Tarla Bitk. Merk. Araştırmaları Enstitüsü Derg. 2015, 24, 1–66. [CrossRef]

89. Lo, S.-F.; Ho, T.-H.D.; Liu, Y.-L.; Jiang, M.-J.; Hsieh, K.-T.; Chen, K.-T.; Yu, L.-C.; Lee, M.-H.; Chen, C.; Huang, T.-P.; et al. Ectopic expression of specific GA2 oxidase mutants promotes yield and stress tolerance in rice. Plant Biotechnol. J. 2017, 15, 850–864. [CrossRef]

90. Diaz, K.; Espinoza, L.; Carvajal, R.; Silva-Moreno, E.; Olea, A.F.; Rubio, J. Exogenous Application of Brassinosteroid 22(5S)-23-Dihydroxy Type Analogs to Enhance Water Deficit Stress Tolerance in Arabidopsis italiana. Int. J. Mol. Sci. 2021, 22, 1158.

91. Ahammed, G.J.; Li, X.; Liu, A.; Chen, S. Brassinosteroids in Plant Tolerance to Abiotic Stress. J. Plant Growth Regul. 2020, 39, 1451–1464. [CrossRef]

92. Tian, Y.; Fan, M.; Qin, Z.; Lv, H.; Wang, M.; Zhang, Z.; Zhou, W.; Zhao, N.; Li, X.; Han, C.; et al. Hydrogen peroxide positively regulates brassinosteroid signaling through oxidation of the BRASSINAZOLE-RESISTANT1 transcription factor. Nat. Commun. 2018, 9, 1063. [CrossRef]
93. Bhatt, D.; Sharma, M.; Nath, M.; Bhatt, M.D.; Badoni, S. Brassinosteroid Signaling and Complex Interplay of ROS, NADPH Oxidase, and MAPK Mediated Biotic and Abiotic Stress Acclimation in Plants. In *Plant Signaling Molecules*; Elsevier: Amsterdam, The Netherlands, 2019; pp. 407–416.

94. Chen, J.; Yin, Y. WRKY transcription factors are involved in brassinosteroid signaling and mediate the crosstalk between plant growth and drought tolerance. *Plant Signal. Behav.* 2017, 12, e1365212. [CrossRef]

95. Nie, S.; Huang, S.; Wang, S.; Mao, Y.; Liu, J.; Ma, R.; Wang, X. Enhanced brassinosteroid signaling intensity via SIBRI1 overexpression negatively regulates drought resistance in a manner opposite of that via exogenous BR application in tomato. *Plant Physiol. Biochem.* 2019, 138, 36–47. [CrossRef]

96. Hu, W.; Yan, X.; Xiao, Y.; Zeng, J.; Qi, H.; Ogweno, J.O. 24-Epibrassinosteroid alleviate drought-induced inhibition of photosynthesis in Capsicum annuum. *Sci. Hortic.* 2013, 150, 232–237. [CrossRef]

97. Sahni, S.; Prasad, B.D.; Liu, Q.; Grbic, V.; Krishna, P. Overexpression of the brassinosteroid biosynthetic gene DWF4 in Brassica napus simultaneously increases seed yield and stress tolerance. *Sci. Rep.* 2016, 6, 28298. [CrossRef]

98. Feng, Y.; Yin, Y.; Fei, S. Down-regulation of BdBRI1, a putative brassinosteroid receptor gene produces a dwarf phenotype with enhanced drought tolerance in Brachypodium distachyon. *Plant Sci.* 2015, 234, 163–173. [CrossRef]

99. Sunkar, R.; Zhu, J.-K. Novel and Stress-Regulated MicroRNAs and Other Small RNAs from Arabidopsis. *Plant Cell* 2004, 16, 2001–2019. [CrossRef]

100. Zhang, C.; Bai, M.; Chong, K. Brassinosteroid-mediated regulation of agronomic traits in rice. *Plant Cell Rep.* 2014, 33, 683–696. [CrossRef]

101. Ling, F.; Su, Q.; Jiang, H.; Cui, J.; He, X.; Wu, Z.; Zhang, Z.; Liu, J.; Zhao, Y. Effects of strigolactone on photosynthetic and physiological characteristics in salt-stressed rice seedlings. *Sci. Rep.* 2020, 10, 6183. [CrossRef]

102. Cook, C.E.; Whichard, L.P.; Wall, M.; Egley, G.H.; Coggon, P.; Luhan, P.; McPhail, A.T. Germination stimulants. II. Structure of a-Mina, J.M.; Pozo, M.J.; López-Ráez, J.A. Arbuscular mycorrhizal symbiosis influences strigolactone production under salinity and alleviates salt stress in lettuce plants. *J. Plant Physiol.* 2013, 170, 47–55. [CrossRef]

103. Aroca, R.; Ruiz-Lozano, J.M.; Zamarreño, A.M.; Paz, J.A.; García-Mina, J.M.; Pozo, M.J.; López-Ráez, J.A. Arbuscular mycorrhizal symbiosis modulates the response to drought stress and the production of strigol, a potent seed germination stimulant for witchweed (*Striga lutea*). *J. Am. Chem. Soc.* 1972, 94, 6198–6199. [CrossRef]

104. Zhang, C.; Bai, M.; Chong, K. Brassinosteroid-mediated regulation of agronomic traits in rice. *Plant Cell Rep.* 2014, 33, 683–696. [CrossRef]

105. Li, W.; Gupta, A.; Tian, H.; Nguyen, K.H.; Tran, C.D.; Watanabe, Y.; Tian, C.; Li, K.; Yang, Y.; Guo, J.; et al. Different strategies of strigolactone and karrin signals in regulating the resistance of Arabidopsis thaliana to water-deficit stress. *Plant Signal. Behav.* 2020, 15, 1789321. [CrossRef]

106. Li, H.; Teng, R.M.; Liu, J.X.; Yang, R.Y.; Yang, Y.Z.; Lin, S.J.; Han, M.H.; Liu, J.Y.; Zhuang, J. Identification and Analysis of Genes Involved in Auxin, Abscisic Acid, Gibberellin, and Brassinosteroid Metabolisms Under Drought Stress in Tender Shoots of Tea Plants. *DNA Cell Biol.* 2019, 38, 1292–1302. [CrossRef]

107. Zhai, Y.; Shao, S.; Sha, W.; Zhao, Y.; Zhang, J.; Ren, W.; Zhang, C. Overexpression of soybean GmERF9 enhances the tolerance to drought and cold in the transgenic sugarcane. *Plant Cell Tissue Organ Cult.* 2017, 128, 607–618. [CrossRef]

108. Pospišilová, H.; Jiskrová, E.; Voja, P.; Mrizová, K.; Kokaš, F.; Čudejková, M.M.; Bergougnoux, V.; Pihal, O.; Klimesová, J.; Novák, O.; et al. Transgenic barley overexpressing a cytokinin dehydrogenase gene shows greater tolerance to drought stress. *New Biotechnol.* 2016, 33, 692–705. [CrossRef]

109. Sajjad, M.; Wei, X.; Liu, L.; Li, F.; Ge, X. Transcriptome Analysis Revealed GhWOX4 Intercedes Myriad Regulatory Pathways to Modulate Drought Tolerance and Vascular Growth in Cotton. *Int. J. Mol. Sci.* 2021, 22, 898. [CrossRef]

110. Liang, C.; Meng, Z.; Meng, Z.; Malik, W.; Yan, R.; Lwin, K.M.; Lin, F.; Wang, Y.; Sun, G.; Zhou, T.; et al. GhABF2, a bZIP transcription factor, confers drought and salinity tolerance in cotton (*Gossypium hirsutum* L.). *Sci. Rep.* 2016, 6, 35040. [CrossRef]

111. Lu, G.; Gao, C.; Zheng, X.; Han, B. Identification of OsbZIP72 as a positive regulator of ABA response and drought tolerance in rice. *Planta* 2009, 229, 605–615. [CrossRef]

112. Joo, J.; Lee, Y.H.; Song, S.I. OsbZIP42 is a positive regulator of ABA signaling and confers drought tolerance to rice. *Planta* 2019, 249, 1521–1533. [CrossRef]

113. Ubaidillah, M.; Saffriti, F.A.; Jo, J.-H.; Lee, S.-K.; Hussain, A.; Mun, B.-G.; Chung, I.K.; Yun, B.-W.; Kim, K.-M. Roles of plant hormones and anti-apoptosis genes during drought stress in rice (*Oryza sativa* L.). *3 Biotech* 2016, 6, 247. [CrossRef] [PubMed]

114. Yu, Y.; Yang, D.; Zhou, S.; Gu, J.; Wang, F.; Dong, J.; Huang, R. The ethylene response factor OsERF109 negatively affects ethylene biosynthesis and drought tolerance in rice. *Protoplasma* 2017, 254, 401–408. [CrossRef] [PubMed]

115. Lou, D.; Wang, H.; Liang, G.; Yu, D. OsSAPK2 Confers Abscisic Acid Sensitivity and Tolerance to Drought Stress in Rice. *Front. Plant Sci.* 2017, 8, 993. [CrossRef] [PubMed]

116. Pan, Y.; Seymour, G.B.; Lu, C.; Hu, Z.; Chen, X.; Chen, G. An ethylene response factor (ERF5) promoting adaptation to drought and salt tolerance in tomato. *Plant Cell Rep.* 2012, 31, 349–360. [CrossRef] [PubMed]

117. Li, J.; Sima, W.; Ouyang, B.; Wang, T.; Ziaf, K.; Luo, Z.; Liu, L.; Li, H.; Chen, M.; Huang, Y.; et al. Tomato SIDREB gene restricts leaf expansion and internode elongation by downregulating key genes for gibberellin biosynthesis. *J. Exp. Bot.* 2012, 63, 6407–6420. [CrossRef] [PubMed]
118. Liu, Y.; Wen, L.; Shi, Y.; Su, D.; Lu, W.; Cheng, Y.; Li, Z. Stress-responsive tomato gene SIGRA54 function in drought stress and abscisic acid signaling. *Plant Sci.* 2021, 304, 110804. [CrossRef] [PubMed]

119. Li, Y.; Zhang, J.; Zhang, J.; Hao, L.; Hua, J.; Duan, L.; Zhang, M.; Li, Z. Expression of an Arabidopsis molybdenum cofactor sulphurase gene in soybean enhances drought tolerance and increases yield under field conditions. *Plant Biotechnol. J.* 2013, 11, 747–758. [CrossRef] [PubMed]

120. Salvi, P.; Kamble, N.U.; Majee, M. Ectopic over-expression of ABA-responsive Chickpea galactinol synthase (CaGolS) gene results in improved tolerance to dehydration stress by modulating ROS scavenging. *Environ. Exp. Bot.* 2020, 171, 103957. [CrossRef]

121. Pandey, N.; Ranjan, A.; Pant, P.; Tripathi, R.K.; Ateeq, F.; Pandey, H.P.; Patre, U.V.; Sawant, S.V. CAMTA 1 regulates drought responses in Arabidopsis thaliana. *BMC Genom.* 2013, 14, 216. [CrossRef]

122. Awan, S.I.; Ahmad, S.D.; Ali, M.A.; Ahmed, M.S.; Rao, A. Use of Multivariate Analysis in Determining Characteristics for Grain Yield Selection in Wheat. *Sarhad J. Agric.* 2015, 31, 139–150. [CrossRef]

123. Farrokhi, N.; Hahieghrari, B. Chronicles of Dolos and Ape in Plant microRNAs. *Biologia* 2020, 75, 2441–2463. [CrossRef]

124. Hombach, S.; Kretz, M. Non-coding RNAs: Classification, biology and functioning. *Adv. Exp. Med. Biol.* 2016, 937, 3–17.

125. Ferdous, J.; Hussain, S.S.; Shi, B.J. Role of microRNAs in plant drought tolerance. *Plant Biotechnol. J.* 2015, 13, 293–305. [CrossRef]

126. Wang, M.; Wang, Q.; Zhang, B. Response of miRNAs and their targets to salt and drought stresses in cotton (*Gossypium hirsutum* L.). *Gene* 2013, 530, 26–32. [CrossRef]

127. Zhang, F.; Luo, X.; Zhou, Y.; Xie, J. Genome-wide identification of conserved microRNA and their response to drought stress in Dongxiang wild rice (*Oryza rufipogon* Griff.). *Biotechnol. Lett.* 2016, 38, 711–721. [CrossRef]

128. Zheng, Y.; Hivrale, V.; Zhang, X.; Valliyodan, B.; Lelandais-Brière, C.; Farmer, A.D.; May, G.D.; Crespi, M.; Nguyen, H.T.; Sunkar, R. Small RNA profiles in soybean primary root tips under water deficit. *BMC Syst. Biol.* 2016, 10, 126. [CrossRef]

129. Guo, C.; Xu, Y.; Shi, M.; Lai, Y.; Wu, X.; Wang, H.; Zhu, Z.; Poethig, R.S.; Wu, G. Repression of miR156 by miR159 regulates the timing of the juvenile-to-adult Transition in Arabidopsis. *Plant Cell* 2017, 29, 1293–1304. [CrossRef]

130. Wei, L.; Zhang, D.; Xiang, F.; Zhang, Z. Differentially expressed miRNAs potentially involved in the regulation of defense mechanism to drought stress in maize seedlings. *Int. J. Plant Sci.* 2009, 170, 979–989. [CrossRef]

131. Liu, S.; Xu, M.; Wu, L.; Qi, H. LncRNA/circRNA-miRNA-mRNA networks regulate the development of root and shoot meristems in Populus. *Ind. Crop. Prod.* 2019, 133, 333–347. [CrossRef]

132. Akdogan, G.; Tufekci, E.D.; Uranbey, S.; Unver, T. miRNA-based drought regulation in wheat. *Funct. Integr. Genom.* 2016, 16, 221–233. [CrossRef]

133. Cheah, B.H.; Nadarajah, K.; Divate, M.D.; Wickneswari, R. Identification of four functionally important microRNA families with contrasting differential expression profiles between drought-tolerant and susceptible rice leaf at vegetative stage. *BMC Genom.* 2015, 16, 692. [CrossRef]

134. Candar-Cakir, B.; Arican, E.; Zhang, B. Small RNA and degradation deep sequencing reveals drought-and tissue-specific micrornas and their important roles in drought-sensitive and drought-tolerant tomato genotypes. *Plant Biotechnol. J.* 2016, 14, 1727–1746. [CrossRef]

135. Jovanović, Ž.; Stanisavljević, N.; Mikić, A.; Radović, S.; Maksimović, V. Water deficit down-regulates miR398 and miR408 in pea (*Pisum sativum* L.). *Plant Physiol. Biochem.* 2014, 83, 26–31. [CrossRef]

136. Trindade, I.; Capitano, C.; Dalmat, Y.; Fevereiro, M.P.; Santos, D.M. dos miR398 and miR408 are up-regulated in response to water deficit in Medicago truncatula. *Planta* 2010, 214, 705–716. [CrossRef]

137. Zhou, R.; Yu, X.; Otto, C.-O.; Zhang, T.; Wu, Z.; Zhao, T. Unique miRNAs and their targets in tomato leaf responding to combined drought and heat stress. *BMC Plant Biol.* 2020, 20, 107. [CrossRef]

138. Rao, S.; Balyan, S.; Jha, S.; Mathur, S. Novel insights into expansion and functional diversification of MIR169 family in tomato. *Planta* 2020, 251, 55. [CrossRef]

139. Ji, Y.; Chen, P.; Chen, J.; Pennerman, K.; Liang, X.; Yan, H.; Zhou, S.; Feng, G.; Wang, C.; Yin, G.; et al. Combinations of Small RNA, RNA, and Degradation Sequencing Uncovers the Expression Pattern of microRNA–mRNA Pairs Adapting to Drought Stress in Leaf and Root of *Dactylis glomerata* L. *Int. J. Mol. Sci.* 2018, 19, 3114. [CrossRef]

140. Li, B.; Qin, Y.; Duan, H.; Yin, W.; Xia, X. Genome-wide characterization of new and drought stress responsive microRNAs in Populus euphratica. *J. Exp. Bot.* 2011, 62, 8–12. [CrossRef]

141. Gentile, A.; Dias, L.I.; Mattos, R.S.; Ferreira, T.H.; Menossi, M. MicroRNAs and drought responses in sugarcane. *Front. Plant Sci.* 2015, 6, 58. [CrossRef]

142. Liu, Q.; Zhang, Y.-C.; Wang, C.-Y.; Luo, Y.-C.; Huang, Q.-J.; Chen, S.-Y.; Zhou, H.; Qu, L.-H.; Chen, Y.-Q. Expression analysis of phytohormone-regulated microRNAs in rice, implying their regulation roles in plant hormone signaling. *FEBS Lett.* 2009, 583, 723–728. [CrossRef]

143. Liu, H.H.; Tian, X.; Li, Y.J.; Wu, C.A.; Zheng, C.C. Microarray-based analysis of stress-regulated microRNAs in Arabidopsis thaliana. *RNA* 2008, 14, 836–843. [CrossRef] [PubMed]

144. Ding, Y.; Tao, Y.; Zhu, C. Emerging roles of microRNAs in the mediation of drought stress response in plants. *J. Exp. Bot.* 2013, 64, 3077–3086. [CrossRef] [PubMed]

145. Yue, E.; Cao, H.; Liu, B. Osmir535, a potential genetic editing target for drought and salinity stress tolerance in *Oryza sativa*. *Plants* 2020, 9, 1337. [CrossRef] [PubMed]
146. Lu, C.; Fedoroff, N. A Mutation in the Arabidopsis HYL1 Gene Encoding a dsRNA Binding Protein Affects Responses to Abscisic Acid, Auxin, and Cytokinin. *Plant Cell* 2000, 12, 2351. [CrossRef]

147. Achard, P.; Herr, A.; Baulcombe, D.C.; Harberd, N.P. Modulation of floral development by a gibberellin-regulated microRNA. *Development* 2004, 131, 3357–3365. [CrossRef]

148. Mallory, A.C.; Bartel, D.P.; Bartel, B. MicroRNA-Directed Regulation of Arabidopsis AUXIN RESPONSE FACTOR17 Is Essential for Proper Development and Modulates Expression of Early Auxin Response Genes. *Plant Cell* 2005, 17, 1360–1375. [CrossRef]

149. Fujii, H.; Chiu, T.-J.; Lin, S.-I.; Aung, K.; Zhu, J.-K. A miRNA Involved in Phosphate-Starvation Response in Arabidopsis. *Curr. Biol.* 2005, 15, 2038–2043. [CrossRef]

150. Schommer, C.; Palatnik, J.F.; Aggarwal, P.; Chételat, A.; Cubas, P.; Farmer, E.E.; Nath, U.; Weigel, D. Control of Jasmonate Biosynthesis and Senescence by miR319 Targets. *PLoS Biol.* 2008, 6, e230. [CrossRef]

151. Nadarajah, K.; Kumar, I.S. Drought response in rice: The miRNA story. *Int. J. Mol. Sci.* 2019, 20, 3766. [CrossRef]

152. Li, W.; Wang, T.; Zhang, Y.; Li, Y. Overexpression of soybean miR172c confers tolerance to water deficit and salt stress, but increases ABA sensitivity in transgenic Arabidopsis thaliana. *J. Exp. Bot.* 2016, 67, 175–194. [CrossRef]

153. Song, J.; Gao, S.; Sun, D.; Li, H.; Shu, X.; Yang, Z. miR934 and LCR are involved in Arabidopsis salt and drought stress responses in an abscisic acid-dependent manner. *BMC Plant Biol.* 2013, 13, 210. [CrossRef]

154. Cai, Z.; Zeng, D.; Liao, J.; Cheng, C.; Sahito, Z.A.; Xiang, M.; Fu, M.; Chen, Y.; Wang, D. Genome-Wide Analysis of Auxin Receptor Family Genes in Brassica juncea var. tumida. *Genes* 2019, 10, 165. [CrossRef]

155. Yuan, Y.; Scheben, A.; Chan, C.K.K.; Edwards, D. Databases for wheat genomics and crop improvement. *Methods Mol. Biol.* 2017, 1679, 277–291.

156. Curaba, J.; Singh, M.B.; Bhalla, P.L. miRNAs in the crosstalk between phytohormone signalling pathways. *J. Exp. Bot.* 2014, 65, 1425–1438. [CrossRef]

157. Bazin, J.; Khan, G.A.; Combier, J.-P.; Bustos-Sanmamed, P.; Debernardi, J.M.; Rodriguez, R.; Sorin, C.; Palatnik, J.; Hartmann, C.; Crespi, M.; et al. miR396 affects mycorrhization and root meristem activity in the legume Medicago truncatula. *Plant J.* 2013, 74, 920–934. [CrossRef]

158. Zhou, L.; Liu, Y.; Liu, Z.; Kong, D.; Duan, M.; Luo, L. Genome-wide identification and analysis of drought-responsive microRNAs in *Oryza sativa*. *J. Exp. Bot.* 2010, 61, 4157–4168. [CrossRef]

159. Niu, Y.; Zhao, T.; Xu, X.; Li, J. Genome-wide identification and characterization of GRAS transcription factors in tomato (*Solanum lycopersicum*). *PeerJ* 2017, 5, e3955. [CrossRef]

160. Yang, T.; Wang, Y.; Teotia, S.; Wang, Z.; Shi, C.; Sun, H.; Gu, Y.; Zhang, Z.; Tang, G. The interaction between miR160 and miR165/166 in the control of leaf development and drought tolerance in Arabidopsis. *Sci. Rep.* 2019, 9, 2832. [CrossRef]

161. Ma, X.; Xin, Z.; Wang, Z.; Yang, Q.; Guo, S.; Guo, X.; Cao, L.; Lin, T. Identification and comparative analysis of differentially expressed miRNAs in leaves of two wheat (*Triticum aestivum*) genotypes during dehydration stress. *BMC Plant Biol.* 2015, 15, 21. [CrossRef]

162. González-Villagra, J.; Kurepin, L.V.; Reyes-Díaz, M.M. Evaluating the involvement and interaction of abscisic acid and miRNA156 in the induction of anthocyanin biosynthesis in drought-stressed plants. *Planta* 2017, 246, 299–312. [CrossRef]

163. Liu, J.; Hasanuzzaman, M.; Wen, H.; Zhang, J.; Peng, T.; Sun, H.; Zhao, Q. High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice. *Protozoa* 2019, 256, 1217–1227. [CrossRef]

164. López-Galiano, M.J.; García-Robles, I.; González-Hernández, A.I.; Camañes, G.; Vicedo, B.; Real, M.D.; Rausell, C. Expression of miR159 is altered in tomato plants undergoing drought stress. *Plants* 2018, 7, 201. [CrossRef]