

Review

Physiology of Plant Responses to Water Stress and Related Genes: A Review

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Abstract: Drought and waterlogging seriously affect the growth of plants and are considered severe constraints on agricultural and forestry productivity; their frequency and degree have increased over time due to global climate change. The morphology, photosynthetic activity, antioxidant enzyme system and hormone levels of plants could change in response to water stress. The mechanisms of these changes are introduced in this review, along with research on key transcription factors and genes. Both drought and waterlogging stress similarly impact leaf morphology (such as wilting and crimping) and inhibit photosynthesis. The former affects the absorption and transportation mechanisms of plants, and the lack of water and nutrients inhibits the formation of chlorophyll, which leads to reduced photosynthetic capacity. Constitutive overexpression of 9-cis-epoxydioxygenase (NCED) and acetaldehyde dehydrogenase (ALDH), key enzymes in abscisic acid (ABA) biosynthesis, increases drought resistance. The latter forces leaf stomata to close in response to chemical signals, which are produced by the roots and transferred aboveground, affecting the absorption capacity of CO₂, and reducing photosynthetic substrates. The root system produces adventitious roots and forms aerenchymal to adapt the stresses. Ethylene (ETH) is the main response hormone of plants to waterlogging stress, and is a member of the ERFVII subfamily, which includes response factors involved in hypoxia-induced gene expression, and responds to energy expenditure through anaerobic respiration. There are two potential adaptation mechanisms of plants (“static” or “escape”) through ETH-mediated gibberellin (GA) dynamic equilibrium to waterlogging stress in the present studies. Plant signal transduction pathways, after receiving stress stimulus signals as well as the regulatory mechanism of the subsequent synthesis of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) enzymes to produce ethanol under a hypoxic environment caused by waterlogging, should be considered. This review provides a theoretical basis for plants to improve water stress tolerance and water-resistant breeding.

Keywords: drought stress; waterlogging stress; plant morphology; physiology and biochemistry; transcription factor



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1. Introduction

In recent years, drought and waterlogging stress have seriously affected the growth of plants due to extreme climate change; these stresses are an important limiting factor for global agricultural and forestry productivity [1]. Over the past decade, the total area of the world’s drylands has increased dramatically, with a clear upward trend in the scope, extent and frequency of drought, resulting in a total global loss of crop production of approximately \$30 billion [2,3]. Waterlogging is the second most important climate disaster after drought. Since the 1990s, the scope of waterlogging disasters has been expanding year by year, and the frequency has also been increasing [4,5]. Due to the frequency and severity of drought and waterlogging, the global vegetation loss caused by these stresses is equivalent. The response and adaptation mechanisms of plants have been the focus of

physiological and ecological research related to water stress (including drought stress and waterlogging stress), and are also very important for breeding water-tolerant varieties.

When plants are damaged by water stress, they will respond to adverse environments with changes to different morphological structures and physiological metabolisms, such as leaf and root morphology, photosynthesis, antioxidant enzyme systems and hormone levels [6,7]. A large number of stress response genes are activated through complex signal transduction networks and synthesize many functional proteins to improve the ability of plants to resist water stress [8,9]. To date, it is believed that drought stress mainly affects the absorption and transport of nutrients from roots to leaves [10–12], while waterlogging stress is an anaerobic respiratory metabolism caused by the environment around the roots [13–15]. Based on the research results, this review discusses and compares the changes to plant morphology, structure, physiology and molecular mechanisms under drought and waterlogging stress. These are important factors to understand plant regulatory mechanisms in response to drought and waterlogging stress, and to increase plant productivity in adverse environments.

2. Morphological Structure Responses to Water Stress in Plants

The response of plants to water stress is mainly reflected in leaves and roots, and their external morphological characteristics and internal anatomical structure can best reflect the adaptability to adverse environments [16–19] (Table 1). Leaves are the most variable organs in long-term adaptation to the environment. They react similarly under drought and waterlogging stress, showing signs of etiolation, atrophy, curling, senescence and even abscission [20,21]. In some cases, stress resulted in stunted leaf growth and reduced leaf number and area [22–24] (Figure 1).

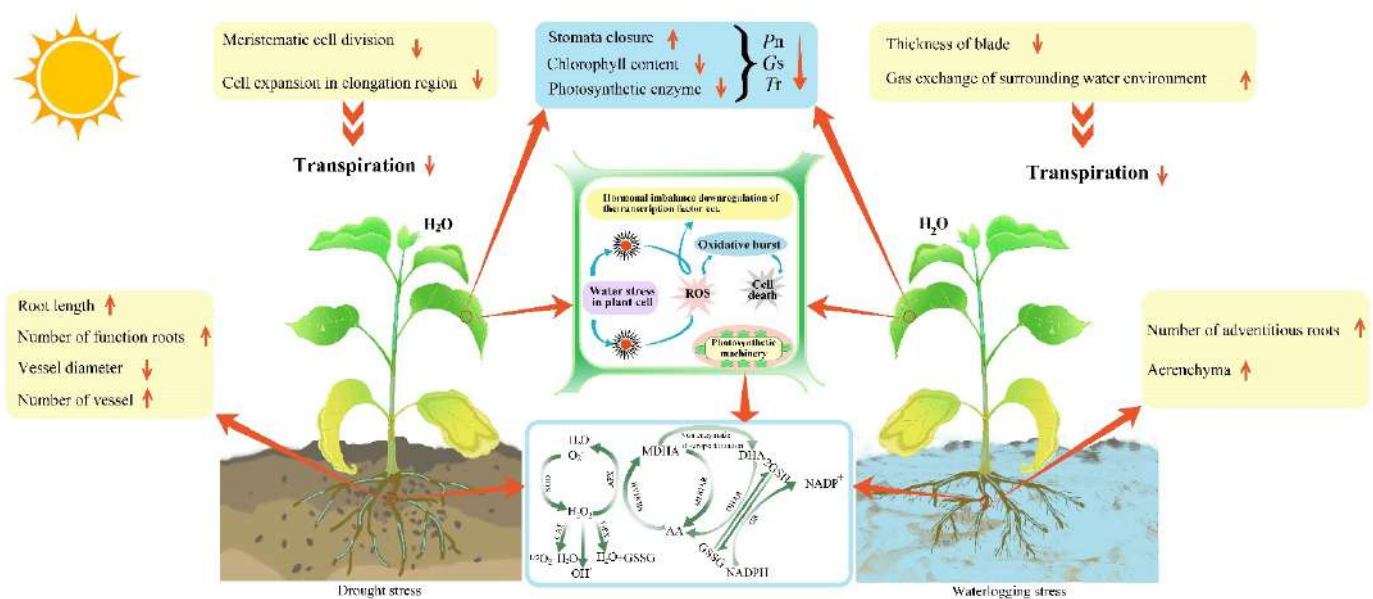


Figure 1. Changes to the morphological and anatomical structure of plant leaves and roots due to water stress. P_n : net photosynthetic rate; G_s : stomatal conductance; T_r : transpiration rate; ROS: reactive oxygen species; SOD: superoxide dismutase; CAT: catalase; APX: ascorbic peroxidase; GPX: peroxidase; GSSG: L-glutathione oxidized; MDHA: dehydroascorbic acid reductase; MDHAR: monodehydroascorbic acid reductase; DHAR: dehydroascorbate reductase glutathione; GR: glutathione reductase; GSH: glutathione peroxidase; AA: ascorbic acid.

2.1. Morphological Structure Responses to Drought Stress

Drought can limit plant growth by inhibiting the cell division of leaf meristematic tissue and cell expansion in elongation areas, as well as inducing complex changes in leaf thickness, palisade tissue and spongy tissue during adaptation [25–27]. Rueda et al. [28]

found that the conifers (water-holding capacity of plants) could be improved by increasing the thickness of leaves and decreasing the thickness of palisade tissue and spongy tissue in drought environments. However, Zheng et al. [29] found that *Lycium barbarum* increased the thickness of palisade tissue and reduced the thickness of spongy tissue, inhibiting transpiration and preventing tissue from excessive dehydration. The above results presented that the internal structure of the leaf changes resulted in transpiration reduction, as well as photosynthetic rate.

The root is an important organ for plants to fix and absorb substances from the soil. Drought stress reduces the stele area, vessel diameter and secondary root cortex cells and increases the number of vessels in the stele to facilitate water flow [30–32]. To improve water retention and drought resistance, plants not only extend the root system by increasing the number of functional roots, but also increase the water-absorbing capacity of the root sheath [33,34]. Furthermore, plants improve resistance by changing the root structure (such as root hair and root density) to influence root spatial distribution, soil fixation and nutrient absorption [35–37]. Therefore, plants could improve water absorption capacity by changing root length and internal structure under drought stress conditions.

2.2. Morphological Structure Responses to Waterlogging Stress

The main response symptoms of leaves to waterlogging stress are curling, yellowing, wilting, falling off, rotting, etc. Leaves have two kinds of adaptation to waterlogging stress: one is to increase the thickness, while the other is to reduce the thickness. For the former, the water loss is reduced and the water holding capacity of plants is improved by increasing palisade tissue and spongy tissue, as well as the decrease in leaf and stomata size [38–40]. The latter takes place because leaves cannot complete morphogenesis normally due to lack of water and nutrition [41]. Thereby, some plants thin their leaves or form special leaves to promote the infiltration ability of CO₂ and inorganic nutrients into the leaves [42,43], and improve gas exchange to restore and maintain respiration under waterlogging stress [44,45]. Therefore, the internal anatomy variation of the leaf is to adjust the stomata and improve transpiration under waterlogging stress, but the reason is uncertain and further study is needed.

Aerenchyma forming in the adventitious roots are the most obvious adaptation features under waterlogging stress. Meanwhile, the epithelial cell wall keratinizes gradually under a waterlogged environment to promote oxygen capture by underwater tissue, and enhance waterlogging tolerance [46,47]. Yamauchi et al. [48] found that there are a lot of root hairs in the adventitious roots, the surface area is large, and the cuticle of the adventitious root is thin, but the aerenchyma is well developed, which can improve the oxygen content of waterlogging-tolerant plants. Moreover, lignified and embolized vascular bundle cortical cells contribute to long-distance oxygen diffusion to the root tips, and block the entry of soil toxins into plants effectively. For instance, Ranathunge et al. [49] found that rice promoted the early formation and increased lignin deposition in both the internal and external epidermis of roots, and prevented ion penetration more effectively under waterlogged conditions. Abiko et al. [50] found that waterlogging-tolerant *teosinte* formed adventitious roots and produced larger aerenchyma, a stronger lignified vascular bundle cell barrier, and the transport of oxygen from stem base to root tip was better than normal maize under a waterlogging environment. Therefore, the ways of producing adventitious roots are diverse in different types of plants under waterlogging stress, and strong waterlogging-tolerant plants are more likely to have the ability to form adventitious roots. It has been indicated that roots could improve adaptability by creating air cavities in the aerenchyma to expand storage space, and block the entry of soil toxins into plants.

Table 1. Characteristics of plant roots and leaves under water stress.

Treatment	Root	Reference	Leaf	Reference
Drought stress	Root system lengthens; functional root number increases; distribution breadth increases.	[2,51]	Wilting; crimping; stomatal closure.	[52,53]
	Area of the stele reduces; number of vascular bundles increases but their diameter reduces.	[2,54,55]	Thickness of spongy tissue decreases; vascular bundles increase.	[56,57]
Waterlogging stress	Number of roots decreases; root activity decreases; adventitious roots are generated.	[58–61]	Etiolation; wilting; abscission; stomatal closure.	[62–64]
	Aerenchyma is formed in adventitious roots; size of the stele reduces.	[65–67]	Blade thickness is reduced; number and area of leaves decreases.	[62,68,69]

3. Photosynthetic Characteristics of Plant Responses to Water Stress

3.1. Photosynthetic Characteristics of Plant Responses to Drought Stress

To maintain photosynthesis, plants form a series of defense mechanisms to protect their photosynthetic organs from damage in the process of adapting to water stress [70,71]. For most plants, light water stress can control stomata and transpiration, directly regulate leaf water potential, and self-repair after a return to a normal water supply; some plants even increase photosynthesis [72,73]. For example, light drought stress usually leads to a stomatal conductance and transpiration increase, while moderate and severe drought stress results in a net photosynthetic rate (P_n), stomatal conductance (G_s) and transpiration rate (T_r) decrease. However, the intercellular carbon dioxide concentration (C_i) shows a different trend. C_i increases or decreases with the deepening of stress, while the stomatal limit (L_s) first increases and then decreases. These results indicate that the decrease in P_n under drought stress is mainly caused by nonstomatal factors [74,75]. Most nonstomatal factors, including chlorophyll content, photosynthetic enzyme activity and active oxygen metabolism, are induced by moderate and severe drought stress. Drought not only inhibits the formation of chlorophyll directly [76,77], but also causes difficulty in absorbing mineral elements from the soil, causing leaf nutrient deficiency (for example, leaf etiolation) [78,79] (Figure 1). The regulation of photosynthetic enzymes is a very complicated process. Light drought stress may slightly affect the photosynthetic carboxylation efficiency, but it can inhibit the activity of RuBPCase, which may result in a decrease in the photosynthetic carboxylation efficiency under severe drought stress [80].

3.2. Photosynthetic Characteristics of Plant Responses to Waterlogging Stress

Under waterlogging stress, both stomatal and nonstomatal factors inhibit photosynthesis. For stomatal factors, the chemical signals from roots are transferred to the ground, forcing the stomata of leaves to close, and reducing the photosynthetic rate by decreasing the absorption capacity of the photosynthetic substrate CO_2 [81–83]; Another aspect of stomatal conductance increasing is the supply of CO_2 , which increases the amount of assimilates to maintain growth under waterlogging. For non-stomatal factors, there is the anaerobic respiration of the plant under hypoxic surroundings. Lactic acid and ethanol are produced, which break the balance of active oxygen metabolism, degrade chlorophyll and damage the photosynthetic apparatus, producing excess excitation energy and causing photoinhibition [84,85]. For severe waterlogging-tolerant plants, the stomata closed quickly due to the stress reaction of plants at the initial stage. For poor waterlogging-tolerant plants, leaf carbohydrates may accumulate rapidly within a few days, because root anaerobic respiration restrains sugar transfer from the stem to the root by reducing sugar consumption in

the root, and the accumulation of photoassimilated products in leaves can form a negative feedback inhibition to the photosynthetic rate.

4. Antioxidant System of Plant Responses to Water Stress

Under normal physiological activities, plants produce reactive oxygen species (ROS), such as superoxide anion radicals (O_2^-), singlet oxygen (O_2), hydroxyl radicals ($\cdot OH$) and hydrogen peroxide (H_2O_2), as signal transmitters to regulate gene and protein expression in plant cells, and the production and elimination of ROS are always in a state of dynamic equilibrium [86]. When the plant is stressed, the balance will be broken, the physiological and biochemical functions of the plant cell membrane will be disturbed, and the production of reactive oxygen species will increase [87]. Plants have similar responses to drought and waterlogging, and both stresses activate the antioxidant defense system of plants to avoid cell damage. The components of the antioxidant defense system are enzymatic and nonenzymatic antioxidants. The enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), dehydroascorbate reductase glutathione (DHAR) and monodehydroascorbic acid reductase (MDHAR). The nonenzymatic antioxidants are glutathione (GSH), ascorbic acid (AA) (both water soluble), carotenoids and tocopherols (lipid soluble). Both components counteract the harm caused by reactive oxygen species [88–91].

The response of antioxidant enzymes in plants to water stress is mainly related to tolerance and the level of stress. The activity of SOD in leaves and roots of the same species increases with an increasing level of water stress. Furthermore, the disproportionation conversion of O_2^- to H_2O_2 increases and the content of O_2^- decreases. POD and CAT decompose H_2O_2 to H_2O , inhibit the accumulation of H_2O_2 effectively, protect plants from oxidative damage, and reduce the toxic effect on plants caused by water stress [92]. This mechanism has been demonstrated in mosses [93], trifoliolate orange seedlings [94], and tobacco [95]. There are different antioxidant enzyme activities in different tolerant varieties under the same water stress. The adaptive mechanism of plants is a very complicated process, and there are no fixed rules to follow. For example, the SOD activity of *Poa pratensis* and *Festuca arundinacea* increased briefly and then decreased, while the CAT activity of *F. arundinacea* decreased with increasing drought stress [96]. The SOD activity of the drought-sensitive cultivar *Trifolium repens* was inhibited under stress, but there was no significant change in the drought-tolerant cultivar Debut, which may be related to its higher ability to mitigate oxidative damage [97]. These results showed that plants could increase the activity of antioxidant enzymes to cope with adverse environments, but the dynamic changes across individuals and stress degrees.

5. Phytohormones and Related Genes in Plant Responses to Drought Stress

Phytohormones play a vital role in plant growth and metabolism, as well as the transport and distribution of nutrients, as their synthesis and signal transduction pathways are interrelated. The physiological function is changed to a specific antistress mechanism through regulating hormone metabolism and signal transduction [98–100]. Drought stimulates abscisic acid (ABA) production in different plant organs, especially in the root, which can reach leaf guard cells and send signals through xylem transport and transpiration. ABA combines cytokinin (CTK) and jasmonic acid (JA) to regulate stomatal movement. They reduce the leaf transpiration rate and guard cell turgor pressure, which causes stomatal closure to adapt to external environments stress [101–104], and ABA accumulation also activates downstream signal components and enhances root antioxidant capacity to improve stress resistance [105]. These results indicated that ABA could play an important role in plant cells receiving drought signals. Therefore, it is of great significance to understand the involvement of ABA in regulating cell metabolism, energy supply, growth, and the expression of functional genes at the transcriptional level under drought stress.

To avoid drought, plants have evolved complex mechanisms to adapt (such as strictly controlling stomatal opening and closing), and endogenous ABA plays an important role

in this process [106]. There are many ways to synthesize ABA under a drought environment. One is the involvement of key regulatory factors (such as 9-cis-epoxydioxygenase (*NCED*) and acetaldehyde dehydrogenase (*ALDH*)) in the last step of the ABA biosynthesis pathway, as the accumulation of ABA activates downstream signals and specifically binds to genes, which play an important role in drought environments [107] (Figure 2). We grouped them into drought adjustment (Table 2). Increased expression of the *TaNCED1* gene isolated from *Triticum aestivum*, significantly improved drought tolerance in tobacco transgenic plants [108]. Moreover, different levels of *OsALDH* expression were detected in rice seedlings under drought stress. Transgenic rice overexpressing *OsALDH* showed elevated stress tolerances and a down-regulation of *OsALDH* in the RNA interference (RNAi). Repression transgenic lines manifest a declined stress tolerance [109].

The second method plays an important role in the upstream enhancement of the expression of downstream genes to increase *NCED* enzyme activity, and promote ABA biosynthesis. The ABA-mediated signal transduction pathway leads to stomatal closure involved in ABA synthesis, including *NGA1*, *ATAF1*, *HAT1* and *ATX1* [110,111]. *NGA1* (a B3 transcription factor) binds directly to the *NCED3* promoter and activates its expression in vitro and in vivo under drought stress [112]. The regulatory target gene of *ATAF1* (a NAC protein) is *NCED3*, which binds specifically to the transcription factor NAC, regulates the ABA biosynthesis gene directly, and activates its expression. Drought-stimulated plants can enhance the expression of downstream genes by binding specific transcription factors (such as B3, NAC and MIKC) to cis-regulatory elements. Transcription factors such as MYB and WRKY bind specifically to cis-regulatory elements and induce the expression of drought-responsive genes to maintain osmotic balance [113–115]. Moreover, some genes can suppress ABA synthesis and signaling, such as *HAT1* (an HD-ZIP transcription factor) binding to their promoters and the ABA/drought-responsive genes *RD29A* and *RD22* directly, by down-regulating the expression of *ABA3* and *NCED3* [116]. *ATX1* not only upregulates *NCED3* transcription but also affects ABA production in response to drought stress directly [117].

The third method is changes in leaf stomatal density, leaf water loss rate and reactive oxygen species levels. *AGL16* (a MIKC transcription factor) plays an important role in the upstream of the *AAO3* gene (abscisic aldehyde oxidase 3, the gene encodes an aldehyde oxidase). *AGL16* binds to the CArG motif in the *AAO3* promoter, regulates transcription, and changes ABA levels and leaf stomatal density [118]. *GbMYB5* and *GhWRKY17* play an active role by regulating the expression of drought-related genes and the production of reactive oxygen species under drought stress [119,120].

In addition, ABA-independent signaling includes both the NAC and DREB2 pathways [121–123]. The former, *SINAC4*, plays a role as a transcription factor in the positive regulation of stress tolerance. Zhu et al. [9] found that the chlorophyll content and leaf water content of transgenic tomato with *SINAC4-RNAi* were lower than those of wild-type plants, and the leaf water loss rate was higher under drought stress. Drought also directly induces the binding of *HcDREB2* to the *DRE* cis-regulatory element and activates downstream gene expression to significantly improve the drought resistance of plants [124] (Figure 2). These results showed that genes can regulate signal transduction and induce the drought resistance gene expression under drought stress, and the functional genes can transcribe and synthesize proteins that play a direct role in stress tolerance. The activity of transcription factors was enhanced, and the interaction between transcription factors and cis-regulatory elements could further induce the expression of functional genes under drought stress.

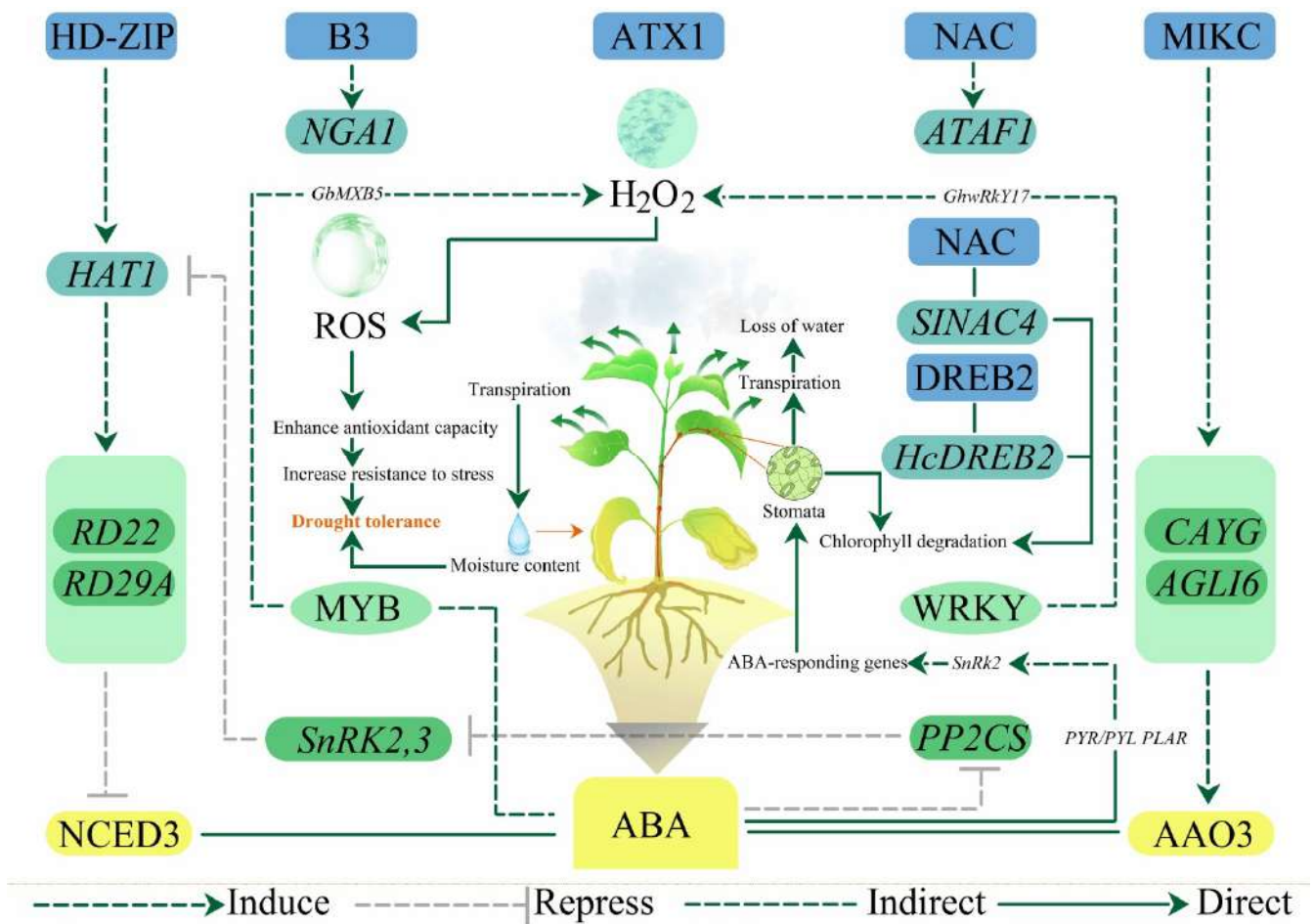


Figure 2. Regulatory mechanisms of abscisic acid (ABA) and related genes in response to drought stress in plants.

6. Phytohormones and Related Genes in Plant Responses to Waterlogging Stress

The root is the most sensitive and responsive organ, and its primary responsibility is to adapt to waterlogging by controlling growth [125,126]. Similar to drought stress, waterlogging stress induces ABA synthesis in the root system and adjusts stomatal movement to adapt to the external environment [127]. The difference is that ethylene (ETH) is one of the more sensitive hormones to waterlogging, and it is increased in an anoxic environment [128,129]. It has been reported that the regulatory mechanism of waterlogging in plants involves not only the production of ABA in the root system but also the regulation of stomatal opening and closing. First, plants respond to a lack of energy by increasing anaerobic respiration. Hypoxia stress caused by waterlogging leads to the inhibition of aerobic respiration to increase the ATP supply, and plants create energy through ethanol fermentation (mainly through pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH)) [130,131]. Second, plants adapt to waterlogging through a “static” strategy [132,133]. ETH can regulate gibberellin (GA) synthesis, inhibit internode elongation and reduce energy consumption [134–136]. Third, plants adapt to long-term waterlogging through an “escape” strategy [137]. ETH maintains the stability of GA and ABA in plants to increase the contact between plants and the air, and promotes stem elongation to the water surface for photosynthesis and rapid aerobic absorption to maintain growth [138,139] (Figure 3).

Ethylene response factor (ERFVII) subfamily members are response factors involved in hypoxia-induced gene expression [140,141]. Plant hypoxia-responsive genes are involved in fermentation and glycometabolism pathways and affect gene expression related to ethylene biosynthesis [142]. When breathing is restricted, lactate dehydrogenase converts the

pyruvate produced during glycolysis into lactic acid. The PDC and ADH genes can convert pyruvic acid into lactic acid and change it into ethanol; that is, PDC converts pyruvic acid into acetaldehyde, and ADH converts acetaldehyde into ethanol. Additionally, NAD^+ and a finite amount of ATP are produced [143,144]. At present, it has been shown that ADH and PDC activity are regulated by *SUB1*, *HRE1* and *HRE2* under waterlogging. We grouped them into waterlogging adjustment (Table 2), as waterlogging could increase the transcription level of *Sub1A* and *Sub1C* and affect PDC and ADH activity to inhibit the chlorophyll degradation and carbohydrate consumption of waterlogged plants [145]. *HRE1* overexpression increased the induction of anaerobic genes in a hypoxic environment. Compared with normal oxygen conditions, the overexpression of *HRE1* and *ATERF73/HRE1* has a positive regulatory role in the absence of oxygen, in which plants not only increase PDC enzyme activity, ADH enzyme activity, and ethanol content, but also induce elongated adventitious roots to adapt to waterlogging [146,147]. Moreover, amino-oxyacetic acid, an inhibitor of ethylene biosynthesis, can partially inhibit the anoxic induction of ADH, but this partial inhibition could be reversed by adding 1-aminocyclopropane-1-carboxylic acid, which is a direct precursor of ethylene [148,149]. *CgACO* (1-aminocyclopropane-1-carboxylate oxidase) expression in roots of the waterlogging-tolerant species (*Chrysanthemum zawadskii*) were higher than the sensitive species (*Chrysanthemum nankingense*) after 12 h waterlogging treatment. This indicated that higher *CgACO* expression possibly contributed to higher accumulation of ethylene in the waterlogging-tolerant species [150]. At present, research on this pathway mainly focuses on the enhancement of PDC and ADH enzyme activity after the overexpression of ERFVII subfamily members. The signal transduction mechanism of increased PDC and ADH activity in the synthesis of ethanol in an anoxic environment caused by waterlogging needs further study [151–154].

The waterlogging environment showed two opposite growth responses: “static” and “escape”. Both were mainly regulated by *SK* and *Sub1* transcription factors induced by ETH [155,156]. *Sub1A* inhibits ETH production and the expression of the related downstream genes of ETH to promote the synthesis of brassinosteroids (BRs), and activates *Ga2oxidase7* expression to inhibit the synthesis of gibberellin (GA) while increasing the expression of the suppressor of the GA signaling pathway *SLR1* [157,158]. This process is a “static” strategy to adapt to short-term waterlogging by inhibiting internode elongation and reducing energy consumption until the stress is relieved [159]. Rice *SK1*, *SK2* and *Sub1* upregulate ABA-inactivating enzyme genes *OsCYP707A5* or *OsABA8ox1* and GA anabolism genes (*OsGA20ox* and *OsGA3ox*) under deep water, which induces a decline in ABA in rice internodes and increases the accumulation of GA in the subaqueous internodes, eventually upregulating growth-related genes to rapidly elongate stems to the water surface. This process is an “escape” strategy for the long-term submergence of plants [139,160]. The ERFVII transcripts downstream genes in a cascade amplification mode, which converts extracellular signals into intracellular, and then induces a series of adaptive mechanisms, such as accelerated glycolysis, elongated stem, formation of aerenchyma and increased oxygen transport rate, etc., to adapt to the waterlogging environment (Figure 3).

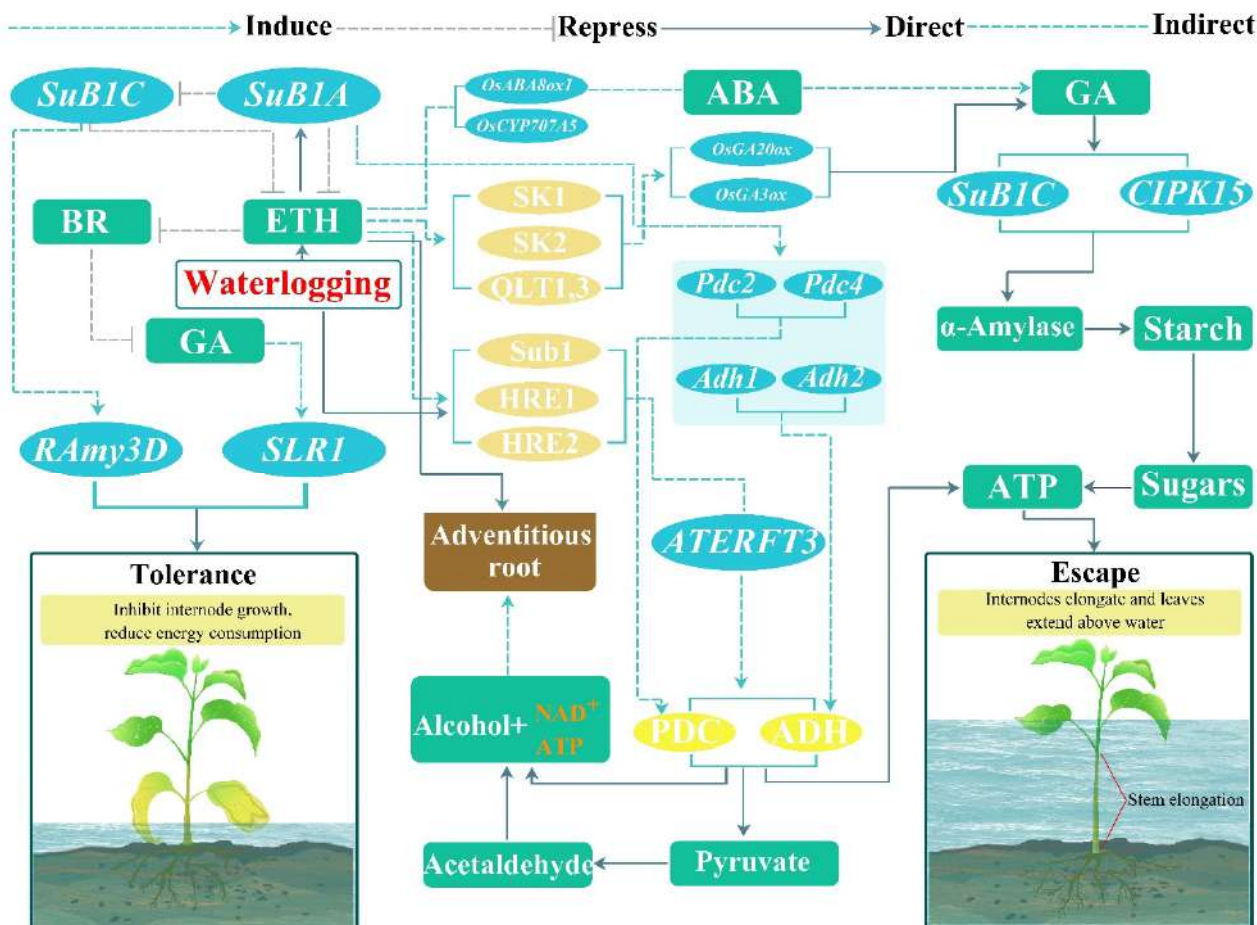


Figure 3. Regulatory mechanisms of phytohormones and related genes in response to waterlogging stress in plants.

Table 2. Genes involved in drought and waterlogging adjustment.

Type	Gene	Accession Nr.	Annotation	Function	References
Drought adjustment	<i>NCED1</i>	AT3G63520	9-cis-epoxycarotenoid dioxygenase	ABA biosynthesis	[109]
	<i>ALDH</i>	AT1G44170	Aldehyde dehydrogenase	ABA biosynthesis	[109]
	<i>ATAF1</i>	AT1G01720	Transcriptional activators with NAC domain	ABA signaling and synthesis	[110,111]
	<i>NCED3</i>	AT3G14440	9-cis-epoxycarotenoid dioxygenase	ABA biosynthesis	[112]
	<i>NGA1</i>	AT2G46870	DNA-binding proteins/contains B3 domain	Transcriptional regulation	[112]
	<i>HAT1</i>	AT4G17460	HD-ZIP transcription factor	Regulates meristematic	[116]
	<i>RD29A</i>	AT1G12610	DREB subfamily A-1 of ERF/AP2 transcription factor	Drought responsive gene	[116]
	<i>RD22</i>	AT5G25610	Dehydration 22 (RD22)-mediated	Responsive by ABA	[116]
	<i>ABA3</i>	AT1G16540	Molybdenum cofactor sulfurase	ABA biosynthesis	[116]
	<i>ATX1</i>	AT1G05830	Homolog of trithorax	Transcriptional regulation	[117]
	<i>AGL16</i>	AT3G57230	MIKC transcription factor	Transcriptional regulation	[118]
	<i>AAO3</i>	AT3G43600	Aldehyde oxidase	ABA biosynthesis	[118]
	<i>WRKY17</i>	AT2G24570	WRKY transcription factor	Transcriptional regulation	[119]
	<i>MYB5</i>	AT3G13540	MYB family of transcriptional regulators	Transcriptional regulation	[120]
	<i>DREB2</i>	AT1G75490	A-2 of ERF/AP2 transcription factor	Response to drought	[121–124]

Table 2. Cont.

Type	Gene	Accession Nr.	Annotation	Function	References
Waterlogging adjustment	<i>SLR1</i>	AT1G47440	S-locus related protein	Transcriptional regulation	[136]
	<i>GA20</i>	AT1G80330	Gibberellin 3-oxidase	Transcriptional regulation	[139]
	<i>HRE1</i>	AT1G72360	Ethylene response factor	Transcriptional regulation	[145,151]
	<i>HRE2</i>	AT2G47520	Ethylene response factor	Transcriptional regulation	[145,146]
	<i>ATERF73</i>	AT1G72360	Ethylene response factor	Transcriptional regulation	[146,147]
	<i>ACO</i>	AT1G12010	1-amino-cyclopropane-1-carboxylic acid oxidase	ETH biosynthesis	[150]
	<i>SK</i>	AT1G05180	RUB1-activating enzyme	Transcriptional regulation	[155]
	<i>SUB1</i>	AT4G08810	Calcium-binding protein	Transcriptional regulation	[156,158]
	<i>SK2</i>	AT3G62980	Auxin receptor	Transcriptional regulation	[160]
<i>SK1</i>	AT1G06390	GSK3/shaggy-like protein kinase	Transcriptional regulation	[160]	

7. A View to the Future

In recent years, more research has been devoted to the study of the harmful effects of extreme climate on plants, and some important progress has been made into the adaptability of different plants to drought and waterlogging. However, great differences were observed in the response mechanisms of different plants under water stress. To date, although scholars have proposed many mechanisms of plant tolerance, none of them have been universally accepted due to their complexity. Currently, gene cloning and genetic transformation are mainly focused on model plants and some crops, but these methods are still in their infancy in some species. On the one hand, the regulatory mechanism of plants under drought and waterlogging stress should be further compared to explore the gene expression regulation and functional identification of resistance genes. On the other hand, the response mechanism of roots and leaves to water stress and the generation and transformation of important regulatory factors should be further studied. In particular, the signal transduction pathway, after receiving a stimulus but before hormone production, should be focused on. In addition, the gene regulation mechanism of inducing PDC and ADH enzymes to create ethanol under an anoxic environment caused by waterlogging in order to improve the plant stress-resistance signaling network also needs further study.

Author Contributions: All authors contributed to the study conception and design. J.W. (Jiaojiao Wu) had the idea for the article; J.W. (Ji-aojiao Wu), P.W. and C.S. performed the literature search; F.Z. drew the pictures; J.W. (Jingyan Wang), W.H. and W.G. critically revised the work. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest. We confirm that neither the manuscript nor any parts of its content are currently under consideration or published in another journal.

References

1. Teshome, D.T.; Zharare, G.E.; Naidoo, S. The threat of the combined effect of biotic and abiotic stress factors in forestry under a changing climate. *Front. Plant Sci.* **2020**, *11*, 601009. [CrossRef]
2. Gupta, A.; Rico-Medina, A.; Cano-Delgado, A.I. The physiology of plant responses to drought. *Science* **2020**, *368*, 266–269. [CrossRef]
3. Lesk, C.; Rowhani, P.; Ramankutty, N. Influence of extreme weather disasters on global crop production. *Nature* **2016**, *529*, 84–87. [CrossRef] [PubMed]
4. Du, W.; FitzGerald, G.J.; Clark, M.; Hou, X.Y. Health impacts of floods. *Prehosp. Disaster Med.* **2010**, *25*, 265–272. [CrossRef] [PubMed]

5. Shi, W.; Wang, M.; Liu, Y. Crop yield and production responses to climate disasters in China. *Sci. Total Environ.* **2021**, *750*, 141147. [[CrossRef](#)] [[PubMed](#)]
6. Khaleghi, A.; Naderi, R.; Brunetti, C.; Maserti, B.E.; Salami, S.A.; Babalar, M. Morphological, physiochemical and antioxidant responses of *Maclura pomifera* to drought stress. *Sci. Rep.* **2019**, *9*, 19250. [[CrossRef](#)] [[PubMed](#)]
7. Ren, B.; Zhang, J.; Dong, S.; Liu, P.; Zhao, B. Responses of carbon metabolism and antioxidant system of summer maize to waterlogging at different stages. *J. Agron. Crop Sci.* **2018**, *204*, 505–514. [[CrossRef](#)]
8. Wang, X.; Huang, M.; Zhou, Q.; Cai, J.; Dai, T.B.; Cao, W.X.; Jiang, D. Physiological and proteomic mechanisms of waterlogging priming improves tolerance to waterlogging stress in wheat (*Triticum aestivum* L.). *Environ. Exp. Bot.* **2016**, *132*, 175–182. [[CrossRef](#)]
9. Zhu, M.K.; Chen, G.P.; Zhang, J.L.; Zhang, Y.J.; Xie, Q.L.; Zhao, Z.P.; Pan, Y.; Hu, Z.L. The abiotic stress-responsive NAC-type transcription factor *SINAC4* regulates salt and drought tolerance and stress-related genes in tomato (*Solanum lycopersicum*). *Plant Cell Rep.* **2014**, *33*, 1851–1863. [[CrossRef](#)]
10. Bista, D.R.; Heckathorn, S.A.; Jayawardena, D.M.; Boldt, J.K. Effect of drought and carbon dioxide on nutrient uptake and levels of nutrient-uptake proteins in roots of barley. *Am. J. Bot.* **2020**, *107*, 1401–1409. [[CrossRef](#)]
11. Jiao, P.P.; Wu, Z.H.; Wang, X.; Jiang, Z.B.; Wang, Y.Q.; Liu, H.; Qin, R.; Li, Z.J. Short-term transcriptomic responses of *Populus euphratica* roots and leaves to drought stress. *J. Forestry Res.* **2021**, *32*, 841–853. [[CrossRef](#)]
12. Zhao, Q.; Guo, J.; Shu, M.; Wang, P.; Hu, S. Impacts of drought and nitrogen enrichment on leaf nutrient resorption and root nutrient allocation in four Tibetan plant species. *Sci. Total Environ.* **2020**, *723*, 138106. [[CrossRef](#)]
13. Hartman, S.; Liu, Z.; van Veen, H.; Vicente, J.; Reinen, E.; Martopawiro, S.; Zhang, H.; van Dongen, N.; Bosman, F.; Bassel, G.W. Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. *Nat. Commun.* **2019**, *10*, 4020. [[CrossRef](#)] [[PubMed](#)]
14. Loreti, E.; van Veen, H.; Perata, P. Plant responses to flooding stress. *Curr. Opin. Plant Biol.* **2016**, *33*, 64–71. [[CrossRef](#)]
15. Coutinho, I.D.; Henning, L.M.; Dopp, S.A.; Nepomuceno, A.; Moraes, L.A.; Marcolino-Gomes, J.; Richter, C.; Schwalbe, H.; Colnago, L.A. Flooded soybean metabolomic analysis reveals important primary and secondary metabolites involved in the hypoxia stress response and tolerance. *Environ. Exp. Bot.* **2018**, *153*, 176–187. [[CrossRef](#)]
16. Cal, A.J.; Sanciangco, M.; Rebolledo, M.C.; Luquet, D.; Torres, R.O.; McNally, K.L.; Henry, A. Leaf morphology, rather than plant water status, underlies genetic variation of rice leaf rolling under drought. *Plant Cell Environ.* **2019**, *42*, 1532–1544. [[CrossRef](#)]
17. Liu, W.S.; Zheng, L.; Qi, D.H. Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. *Ecol. Evol.* **2020**, *10*, 8166–8175. [[CrossRef](#)]
18. Lozano, Y.M.; Aguilar-Trigueros, C.A.; Flaig, I.C.; Rillig, M.C. Root trait responses to drought are more heterogeneous than leaf trait responses. *Funct. Ecol.* **2020**, *34*, 2224–2235. [[CrossRef](#)]
19. Pedersen, O.; Sauter, M.; Colmer, T.D.; Nakazono, M. Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytol.* **2021**, *229*, 42–49. [[CrossRef](#)]
20. Patharkar, O.R.; Walker, J.C. Connections between abscission, dehiscence, pathogen defense, drought tolerance, and senescence. *Plant Sci.* **2019**, *284*, 25–29. [[CrossRef](#)]
21. Bhusal, N.; Kim, H.S.; Han, S.G.; Yoon, T.M. Photosynthetic traits and plant-water relations of two apple cultivars grown as bi-leader trees under long-term waterlogging conditions. *Environ. Exp. Bot.* **2020**, *176*, 104111. [[CrossRef](#)]
22. Wei, W.L.; Li, D.H.; Wang, L.H.; Ding, X.; Zhang, Y.X.; Gao, Y.; Zhang, X.R. Morpho-anatomical and physiological responses to waterlogging of sesame (*Sesamum indicum* L.). *Plant Sci.* **2013**, *208*, 102–111. [[CrossRef](#)] [[PubMed](#)]
23. Fang, Y.J.; Xiong, L.Z. General mechanisms of drought response and their application in drought resistance improvement in plants. *Cell Mol. Life Sci.* **2015**, *72*, 673–689. [[CrossRef](#)]
24. Nadal, M.; Roig-Oliver, M.; Bota, J.; Flexas, J. Leaf age-dependent elastic adjustment and photosynthetic performance under drought stress in *Arbutus unedo* seedlings. *Flora* **2020**, *271*, 151662. [[CrossRef](#)]
25. Nelissen, H.; Sun, X.H.; Rymen, B.; Jikumaru, Y.; Kojima, M.; Takebayashi, Y.; Abbeloos, R.; Demuyne, K.; Storme, V.; Vuylsteke, M. The reduction in maize leaf growth under mild drought affects the transition between cell division and cell expansion and cannot be restored by elevated gibberellic acid levels. *Plant Biotechnol. J.* **2018**, *16*, 615–627. [[CrossRef](#)]
26. Binks, O.; Meir, P.; Rowland, L.; Costa, A.C.; Vasconcelos, S.S.; Oliveira, A.A.R.; Ferreira, L.; Mencuccini, M. Limited acclimation in leaf anatomy to experimental drought in tropical rainforest trees. *Tree Physiol.* **2016**, *36*, 1550–1561. [[CrossRef](#)] [[PubMed](#)]
27. Meng, D.; Dong, B.; Niu, L.; Song, Z.; Wang, L.; Amin, R.; Cao, H.; Li, H.; Yang, Q.; Fu, Y. The pigeon pea CcCIPK14-CcCBL1 pair positively modulates drought tolerance by enhancing flavonoid biosynthesis. *Plant J.* **2021**, *106*, 1278–1297. [[CrossRef](#)]
28. Rueda, M.; Godoy, O.; Hawkins, B.A. Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States. *Global Ecol. Biogeogr.* **2017**, *26*, 31–42. [[CrossRef](#)]
29. Zheng, G.Q.; Zhang, L.; Zheng, G.B.; Zhang, Y.P.; Wang, J.; Hu, Z.H. Effects of irrigation amount on leaf structure, photosynthetic physiology, and fruit yield of *Lycium barbarum* in arid area. *Ying Yong Sheng Tai Xue Bao* **2010**, *21*, 2806–2813.
30. De Bauw, P.; Vandamme, E.; Lupembe, A.; Mwakasege, L.; Senthilkumar, K.; Drame, K.N.; Merckx, R. Anatomical root responses of rice to combined phosphorus and water stress-relations to tolerance and breeding opportunities. *Funct. Plant Biol.* **2019**, *46*, 1009–1022. [[CrossRef](#)]
31. Thangthong, N.; Jogloy, S.; Punjansing, T.; Kvien, C.K.; Kesmala, T.; Vorasoot, N. Changes in root anatomy of peanut (*Arachis hypogaea* L.) under different durations of early season drought. *Agronomy* **2019**, *9*, 215. [[CrossRef](#)]
32. Hazman, M.; Brown, K.M. Progressive drought alters architectural and anatomical traits of rice roots. *Rice* **2018**, *11*, 1–16. [[CrossRef](#)] [[PubMed](#)]

33. Lee, D.K.; Jung, H.; Jang, G.; Jeong, J.S.; Kim, Y.S.; Ha, S.H.; Do Choi, Y.; Kim, J.K. Overexpression of the *OsERF71* transcription factor alters rice root structure and drought resistance. *Plant Physiol.* **2016**, *172*, 575–588. [[CrossRef](#)]
34. Pierret, A.; Maeght, J.L.; Clement, C.; Montoroi, J.P.; Hartmann, C.; Gonkhamdee, S. Understanding deep roots and their functions in ecosystems: An advocacy for more unconventional research. *Ann. Bot.* **2016**, *118*, 621–635. [[CrossRef](#)]
35. Henry, A.; Gowda, V.R.P.; Torres, R.O.; McNally, K.L.; Serraj, R. Variation in root system architecture and drought response in rice (*Oryza sativa*): Phenotyping of the *OryzaSNP* panel in rainfed lowland fields. *Field Crop Res.* **2011**, *120*, 205–214. [[CrossRef](#)]
36. Tanaka, N.; Kato, M.; Tomioka, R.; Kurata, R.; Fukao, Y.; Aoyama, T.; Maeshima, M. Characteristics of a root hair-less line of *Arabidopsis thaliana* under physiological stresses. *J. Exp. Bot.* **2014**, *65*, 1497–1512. [[CrossRef](#)]
37. Strock, C.F.; Burridge, J.D.; Niemiec, M.D.; Brown, K.M.; Lynch, J.P. Root metaxylem and architecture phenotypes integrate to regulate water use under drought stress. *Plant Cell Environ.* **2021**, *44*, 49–67. [[CrossRef](#)]
38. Yin, D.M.; Luo, H.L. Anatomical responses to waterlogging in *Chrysanthemum zawadskii*. *Sci. Hort.* **2012**, *146*, 86–91. [[CrossRef](#)]
39. Tahira, M.H.; Muhammad, A.; Muhammad, S.A.A.; Riffat, B.; Sana, F. Anatomical and physiological adaptations in aquatic ecotypes of *Cyperus alopecuroides* Rottb. under saline and waterlogged conditions. *Aquat. Bot.* **2014**, *116*, 60–68.
40. Zuniga, F.A.; Bustos, S.A.; Alves, F.; Martinez, V.; Smith, R.C. Physiological and morphological responses to permanent and intermittent waterlogging in seedlings of four evergreen trees of temperate swamp forests. *Tree Physiol.* **2017**, *37*, 779–789. [[CrossRef](#)]
41. Fan, C.F.; Yang, Y.F. Water affects morphogenesis of growing aquatic plant leaves. *Phys. Rev. Lett.* **2020**, *124*, 038003.
42. Colmer, T.D.; Pedersen, O. Underwater photosynthesis and respiration in leaves of submerged wetland plants: Gas films improve CO₂ and O₂ exchange. *New Phytol.* **2008**, *177*, 918–926. [[CrossRef](#)] [[PubMed](#)]
43. Brodersen, K.E.; Hammer, K.J.; Schrammeyer, V.; Floytrup, A.; Rasheed, M.A.; Ralph, P.J.; Kuhl, M.; Pedersen, O. Sediment resuspension and deposition on seagrass leaves impedes internal plant aeration and promotes phytotoxic H₂S intrusion. *Front. Plant Sci.* **2017**, *8*, 657. [[CrossRef](#)] [[PubMed](#)]
44. Lawson, J.R.; Fryirs, K.A.; Leishman, M.R. Interactive effects of waterlogging and atmospheric CO₂ concentration on gas exchange, growth and functional traits of Australian riparian tree seedlings. *Ecohydrology* **2017**, *10*, e1803. [[CrossRef](#)]
45. Mommer, L.; Visser, E.J. Underwater photosynthesis in flooded terrestrial plants: A matter of leaf plasticity. *Ann Bot.* **2005**, *96*, 581–589. [[CrossRef](#)]
46. Ayi, Q.L.; Zeng, B.; Liu, J.H.; Li, S.Q.; Bodegom, P.M.; Cornelissen, J.H.C. Oxygen absorption by adventitious roots promotes the survival of completely submerged terrestrial plants. *Ann. Bot.* **2016**, *118*, 675–683. [[CrossRef](#)]
47. Pedersen, O.; Nakayama, Y.; Yasue, H.; Kurokawa, Y.; Takahashi, H.; Floytrup, A.H.; Omori, F.; Mano, Y.; Colmer, T.D.; Nakazono, M. Lateral roots, in addition to adventitious roots, form a barrier to radial oxygen loss in *Zea nicaraguensis* and a chromosome segment introgression line in maize. *New Phytol.* **2021**, *229*, 94–105. [[CrossRef](#)]
48. Yamauchi, T.; Abe, F.; Tsutsumi, N.; Nakazono, M. Root cortex provides a venue for gas-space formation and is essential for plant adaptation to waterlogging. *Front. Plant Sci.* **2019**, *10*, 259. [[CrossRef](#)]
49. Ranathunge, K.; Lin, J.; Steudle, E.; Schreiber, L. Stagnant deoxygenated growth enhances root suberization and lignifications, but differentially affects water and NaCl permeabilities in rice (*Oryza sativa* L.) roots. *Plant Cell Environ.* **2011**, *34*, 1223–1240. [[CrossRef](#)]
50. Abiko, T.; Kotula, L.; Shiono, K.; Malik, A.I.; Colmer, T.D.; Nakazono, M. Enhanced formation of aerenchyma and induction of a barrier to radial oxygen loss in adventitious roots of *Zea nicaraguensis* contribute to its waterlogging tolerance as compared with maize (*Zea mays* ssp. *mays*). *Plant Cell Environ.* **2012**, *35*, 1618–1630. [[CrossRef](#)]
51. Djanaguiraman, M.; Prasad, P.V.V.; Kumari, J.; Rengel, Z. Root length and root lipid composition contribute to drought tolerance of winter and spring wheat. *Plant Soil* **2019**, *439*, 57–73. [[CrossRef](#)]
52. Song, H.; Li, Y.B.; Zhou, L.; Xu, Z.Z.; Zhou, G.S. Maize leaf functional responses to drought episode and rewatering. *Agr. For. Meteorol.* **2018**, *249*, 57–70. [[CrossRef](#)]
53. Chen, M.J.; Zhu, X.F.; Zhang, Y.; Du, Z.H.; Chen, X.B.; Kong, X.R.; Sun, W.J.; Chen, C.S. Drought stress modify cuticle of tender tea leaf and mature leaf for transpiration barrier enhancement through common and distinct modes. *Sci. Rep.* **2020**, *10*, 6696. [[CrossRef](#)] [[PubMed](#)]
54. Canales, F.J.; Risipail, N.; Garcia, T.O.; Arbona, V.; Perez, L.A.; Prats, E. Drought resistance in oat involves ABA-mediated modulation of transpiration and root hydraulic conductivity. *Environ. Exp. Bot.* **2021**, *182*, 104333. [[CrossRef](#)]
55. Xiao, S.; Liu, L.T.; Zhang, Y.J.; Sun, H.C.; Zhang, K.; Bai, Z.Y.; Dong, H.Z.; Li, C.D. Fine root and root hair morphology of cotton under drought stress revealed with RhizoPot. *J. Agron. Crop Sci.* **2020**, *206*, 679–693. [[CrossRef](#)]
56. Zhang, J.S.; Zhang, H.; Srivastava, A.K.; Pan, Y.J.; Bai, J.J.; Fang, J.J.; Shi, H.Z.; Zhu, J.K. Knockdown of rice MicroRNA166 Confers drought resistance by causing leaf rolling and altering stem xylem development. *Plant Physiol.* **2018**, *176*, 2082–2094. [[CrossRef](#)]
57. Ouyang, W.J.; Struik, P.C.; Yin, X.Y.; Yang, J.C. Stomatal conductance, mesophyll conductance, and transpiration efficiency in relation to leaf anatomy in rice and wheat genotypes under drought. *J. Exp. Bot.* **2017**, *68*, 5191–5205. [[CrossRef](#)]
58. Palta, J.A.; Ganjeali, A.; Turner, N.C.; Siddique, K.H.M. Effects of transient subsurface waterlogging on root growth, plant biomass and yield of chickpea. *Agr. Water Manag.* **2010**, *97*, 1469–1476. [[CrossRef](#)]
59. Domisch, T.; Qian, J.; Sondej, I.; Martz, F.; Lehto, T.; Piirainen, S.; Finer, L.; Silvennoinen, R.; Repo, T. Here comes the flood! Stress effects of continuous and interval waterlogging periods during the growing season on Scots pine saplings. *Tree Physiol.* **2020**, *40*, 869–885. [[CrossRef](#)]

60. Dresboll, D.B.; Thorup, K.K. Spatial variation in root system activity of tomato (*Solanum lycopersicum* L.) in response to short and long-term waterlogging as determined by N-15 uptake. *Plant Soil* **2012**, *357*, 161–172. [[CrossRef](#)]
61. Pan, D.L.; Wang, G.; Wang, T.; Jia, Z.H.; Guo, Z.R.; Zhang, J.Y. *AdRAP2.3*, a novel ethylene response factor vii from *Actinidia deliciosa*, enhances waterlogging resistance in transgenic tobacco through improving expression levels of PDC and ADH genes. *Int. J. Mol. Sci.* **2019**, *20*, 1189. [[CrossRef](#)]
62. Yin, D.M.; Chen, S.M.; Chen, F.D.; Guan, Z.Y.; Fang, W.M. Morpho-anatomical and physiological responses of two *Dendranthema* species to waterlogging. *Environ. Exp. Bot.* **2010**, *68*, 122–130. [[CrossRef](#)]
63. Ploschuk, R.A.; Miralles, D.J.; Colmer, T.D.; Ploschuk, E.L.; Striker, G.G. Waterlogging of winter crops at early and late stages: Impacts on leaf physiology, growth and yield. *Front. Plant Sci.* **2018**, *9*, 1863. [[CrossRef](#)] [[PubMed](#)]
64. Fukao, T.; Xu, K.; Ronald, P.C.; Bailey-Serres, J. A variable cluster of ethylene response factor-like genes regulates metabolic and developmental acclimation responses to submergence in rice. *Plant Cell* **2006**, *18*, 2021–2034. [[CrossRef](#)] [[PubMed](#)]
65. Celedonio, R.P.D.; Abeledo, L.G.; Mantese, A.I.; Miralles, D.J. Differential root and shoot biomass recovery in wheat and barley with transient waterlogging during preflowering. *Plant Soil* **2017**, *417*, 481–498. [[CrossRef](#)]
66. Zhang, X.C.; Shabala, S.; Koutoulis, A.; Shabala, L.; Johnson, P.; Hayes, D.; Nichols, D.S.; Zhou, M.X. Waterlogging tolerance in barley is associated with faster aerenchyma formation in adventitious roots. *Plant Soil* **2015**, *394*, 355–372. [[CrossRef](#)]
67. Sundgren, T.K.; Uhlen, A.K.; Lillemo, M.; Briese, C.; Wojciechowski, T. Rapid seedling establishment and a narrow root stele promotes waterlogging tolerance in spring wheat. *J. Plant Physiol.* **2018**, *227*, 45–55. [[CrossRef](#)]
68. Mommer, L.; Pons, T.L.; Wolters-Arts, M.; Venema, J.H.; Visser, E.J. Submergence-induced morphological, anatomical, and biochemical responses in a terrestrial species affect gas diffusion resistance and photosynthetic performance. *Plant Physiol.* **2005**, *139*, 497–508. [[CrossRef](#)]
69. Challabathula, D.; Zhang, Q.; Bartels, D. Protection of photosynthesis in desiccation-tolerant resurrection plants. *J. Plant Physiol.* **2018**, *227*, 84–92. [[CrossRef](#)]
70. Yang, X.; Li, Y.; Chen, H.; Huang, J.; Zhang, Y.; Qi, M.; Liu, Y.; Li, T. Photosynthetic response mechanism of soil salinity-induced cross-tolerance to subsequent drought stress in tomato plants. *Plants* **2020**, *9*, 363. [[CrossRef](#)]
71. Sharma, A.; Kumar, V.; Shahzad, B.; Ramakrishnan, M.; Sidhu, G.P.S.; Bali, A.S.; Handa, N.; Kapoor, D.; Yadav, P.; Khanna, K. Photosynthetic response of plants under different abiotic stresses: A review. *J. Plant Growth Regul.* **2020**, *39*, 509–531. [[CrossRef](#)]
72. Ding, L.; Lu, Z.; Gao, L.; Guo, S.; Shen, Q. Is Nitrogen a key determinant of water transport and photosynthesis in higher plants upon drought stress? *Front. Plant Sci.* **2018**, *9*, 1143. [[CrossRef](#)] [[PubMed](#)]
73. Killi, D.; Haworth, M. Diffusive and metabolic constraints to photosynthesis in quinoa during drought and salt stress. *Plants* **2017**, *6*, 49. [[CrossRef](#)]
74. Li, P.D.; Zhu, Y.F.; Song, X.L.; Song, F.P. Negative effects of long-term moderate salinity and short-term drought stress on the photosynthetic performance of *Hybrid Pennisetum*. *Plant Physiol. Biochem.* **2020**, *155*, 93–104. [[CrossRef](#)]
75. Tian, L.X.; Li, J.; Bi, W.S.; Zuo, S.Y.; Li, L.J.; Li, W.L.; Sun, L. Effects of waterlogging stress at different growth stages on the photosynthetic characteristics and grain yield of spring maize (*Zea mays* L.) under field conditions. *Agr. Water Manag.* **2019**, *218*, 250–258. [[CrossRef](#)]
76. Shivakrishna, P.; Reddy, K.A.; Rao, D.M. Effect of PEG-6000 imposed drought stress on RNA content, relative water content (RWC), and chlorophyll content in peanut leaves and roots. *Saudi. J. Biol. Sci.* **2018**, *25*, 285–289.
77. Chen, Y.E.; Liu, W.J.; Su, Y.Q.; Cui, J.M.; Zhang, Z.W.; Yuan, M.; Zhang, H.Y.; Yuan, S. Different response of photosystem II to short and long-term drought stress in *Arabidopsis thaliana*. *Physiol. Plant.* **2016**, *158*, 225–235. [[CrossRef](#)]
78. Smirnov, N.; Colombe, S.V. Drought influences the activity of enzymes of the chloroplast hydrogen peroxide scavenging system. *J. Exp. Bot.* **1988**, *39*, 1097–1108. [[CrossRef](#)]
79. Bondada, B.R.; Oosterhuis, D.M. Canopy photosynthesis, specific leaf weight, and yield components of cotton under varying nitrogen supply. *J. Plant Nutr.* **2001**, *24*, 469–477. [[CrossRef](#)]
80. Parry, M.A.; Andralojc, P.J.; Khan, S.; Lea, P.J.; Keys, A.J. Rubisco activity: Effects of drought stress. *Ann Bot.* **2002**, *89*, 833–839. [[CrossRef](#)]
81. Pereira, T.S.; Lobato, A.K.S.; Alves, G.A.R.; Ferreira, R.N.; Silva, O.N.; Martins, A.P.; Pereira, E.S.; Sampaio, L.S. Tolerance to waterlogging in young *Euterpe oleracea* plants. *Photosynthetica* **2014**, *52*, 186–192. [[CrossRef](#)]
82. Horiguchi, G.; Nemoto, K.; Yokoyama, T.; Hirotsu, N. Photosynthetic acclimation of terrestrial and submerged leaves in the amphibious plant *Hygrophila difformis*. *AoB Plants* **2019**, *11*, plz009. [[CrossRef](#)] [[PubMed](#)]
83. De Pedro, L.F.; Mignolli, F.; Scartazza, A.; Colavita, J.P.M.; Bouzo, C.A.; Vidoz, M.L. Maintenance of photosynthetic capacity in flooded tomato plants with reduced ethylene sensitivity. *Physiol. Plant.* **2020**, *170*, 202–217. [[CrossRef](#)] [[PubMed](#)]
84. Hole, D.J.; Cobb, B.G.; Hole, P.S.; Drew, M.C. Enhancement of anaerobic respiration in root tips of *Zea mays* following low-oxygen (hypoxic) acclimation. *Plant Physiol.* **1992**, *99*, 213–218. [[CrossRef](#)]
85. Fan, X.; Zhang, Z.; Gao, H.; Yang, C.; Liu, M.; Li, Y.; Li, P. Photoinhibition-like damage to the photosynthetic apparatus in plant leaves induced by submergence treatment in the dark. *PLoS ONE* **2014**, *9*, e89067. [[CrossRef](#)] [[PubMed](#)]
86. Waszczak, C.; Carmody, M.; Kangasjarvi, J. Reactive oxygen species in plant signaling. *Annu. Rev. Plant Biol.* **2018**, *69*, 209–236. [[CrossRef](#)]
87. Polle, A. Dissecting the superoxide dismutase-ascorbate-glutathione-pathway in chloroplasts by metabolic modeling. Computer simulations as a step towards flux analysis. *Plant Physiol.* **2001**, *126*, 445–462. [[CrossRef](#)]

88. Miller, G.; Suzuki, N.; Ciftci-Yilmaz, S.; Mittler, R. Reactive oxygen species homeostasis and signaling during drought and salinity stresses. *Plant Cell Environ.* **2010**, *33*, 453–467. [[CrossRef](#)]
89. Wu, S.W.; Hu, C.X.; Tan, Q.L.; Xu, S.J.; Sun, X.C. Nitric oxide mediates molybdenum-induced antioxidant defense in wheat under drought stress. *Front Plant Sci.* **2017**, *8*, 1085. [[CrossRef](#)]
90. Ahmad, S.; Kamran, M.; Ding, R.X.; Meng, X.P.; Wang, H.Q.; Ahmad, I.; Fahad, S.; Han, Q.F. Exogenous melatonin confers drought stress by promoting plant growth, photosynthetic capacity and antioxidant defense system of maize seedlings. *Peer J.* **2019**, *7*, e7793. [[CrossRef](#)]
91. Laxa, M.; Liebthal, M.; Telman, W.; Chibani, K.; Dietz, K.J. The role of the plant antioxidant system in drought tolerance. *Antioxidants* **2019**, *8*, 94. [[CrossRef](#)]
92. Wang, W.B.; Kim, Y.H.; Lee, H.S.; Kim, K.Y.; Deng, X.P.; Kwak, S.S. Analysis of antioxidant enzyme activity during germination of alfalfa under salt and drought stresses. *Plant Physiol. Biochem.* **2009**, *47*, 570–577. [[CrossRef](#)] [[PubMed](#)]
93. Rajinder SDhindsa, W.M. Drought tolerance in two mosses: Correlated with enzymatic defence against lipid peroxidation. *J. Exp. Bot.* **1981**, *32*, 79–91.
94. Huang, Y.M.; Zou, Y.N.; Wu, Q.S. Alleviation of drought stress by mycorrhizas is related to increased root H₂O₂ efflux in trifoliolate orange. *Sci. Rep.-UK* **2017**, *7*, 42335. [[CrossRef](#)] [[PubMed](#)]
95. Zhang, H.H.; Xu, N.; Teng, Z.Y.; Wang, J.R.; Ma, S.L.; Wu, X.Y.; Li, X.; Sun, G.Y. 2-Cys Prx plays a critical role in scavenging H₂O₂ and protecting photosynthetic function in leaves of tobacco seedlings under drought stress. *J. Plant Interact.* **2019**, *14*, 119–128. [[CrossRef](#)]
96. Jiang, Y.; Huang, B. Drought and heat stress injury to two cool-season turfgrasses in relation to antioxidant metabolism and lipid peroxidation. *Crop Sci.* **2001**, *41*, 436. [[CrossRef](#)]
97. Vaseva, I.; Akiscan, Y.; Simova-Stoilova, L.; Kostadinova, A.; Nenkova, R.; Anders, I.; Feller, U.; Demirevska, K. Antioxidant response to drought in red and white clover. *Acta Physiol. Plant.* **2012**, *34*, 1689–1699. [[CrossRef](#)]
98. Di, T.M.; Zhao, L.; Chen, H.M.; Qian, W.J.; Wang, P.Q.; Zhang, X.F.; Xia, T. Transcriptomic and metabolic insights into the distinctive effects of exogenous melatonin and gibberellin on terpenoid synthesis and plant hormone signal transduction pathway in camellia sinensis. *J. Agric. Food Chem.* **2019**, *67*, 4689–4699. [[CrossRef](#)]
99. Song, S.; Chang, J.; Ma, C.J.; Tan, Y.W. Single-molecule fluorescence methods to study plant hormone signal transduction pathways. *Front. Plant Sci.* **2017**, *8*, 1888. [[CrossRef](#)]
100. Takeuchi, J.; Fukui, K.; Seto, Y.; Takaoka, Y.; Okamoto, M. Ligand-receptor interactions in plant hormone signaling. *Plant J.* **2021**, *105*, 290–306. [[CrossRef](#)]
101. Goodger, J.Q.D.; Sharp, R.E.; Marsh, E.L.; Schachtman, D.P. Relationships between xylem sap constituents and leaf conductance of well-watered and water-stressed maize across three xylem sap sampling techniques. *J. Exp. Bot.* **2005**, *56*, 2389–2400. [[CrossRef](#)] [[PubMed](#)]
102. Fereres, E.; Soriano, M.A. Deficit irrigation for reducing agricultural water use. *J. Exp. Bot.* **2007**, *58*, 147–159. [[CrossRef](#)] [[PubMed](#)]
103. Schachtman, D.P.; Goodger, J.Q.D. Chemical root to shoot signaling under drought. *Trends Plant Sci.* **2008**, *13*, 281–287. [[CrossRef](#)]
104. Yin, D.M.; Chen, S.M.; Chen, F.D.; Guan, Z.Y.; Fang, W.M. Morphological and physiological responses of two chrysanthemum cultivars differing in their tolerance to waterlogging. *Environ. Exp. Bot.* **2009**, *67*, 87–93. [[CrossRef](#)]
105. Bulgakov, V.P.; Wu, H.C.; Jinn, T.L. Coordination of ABA and chaperone signaling in plant stress responses. *Trends Plant Sci.* **2019**, *24*, 636–651. [[CrossRef](#)] [[PubMed](#)]
106. Qian, D.; Zhang, Z.; He, J.X.; Zhang, P.; Ou, X.B.; Li, T.; Niu, L.P.; Nan, Q.; Niu, Y.; He, W.L. *Arabidopsis* ADF5 promotes stomatal closure by regulating actin cytoskeleton remodeling in response to ABA and drought stress. *J. Exp. Bot.* **2019**, *70*, 435–446. [[CrossRef](#)] [[PubMed](#)]
107. Gong, P.J.; Zhang, J.H.; Li, H.X.; Yang, C.X.; Zhang, C.J.; Zhang, X.H.; Khurram, Z.; Zhang, Y.Y.; Wang, T.T.; Fei, Z.J. Transcriptional profiles of drought-responsive genes in modulating transcription signal transduction, and biochemical pathways in tomato. *J. Exp. Bot.* **2010**, *61*, 3563–3575. [[CrossRef](#)]
108. Urbanavičiūtė, I.; Bonfiglioli, L.; Pagnotta, M.A. One hundred candidate genes and their roles in drought and salt tolerance in wheat. *Int. J. Mol. Sci.* **2021**, *22*, 6378. [[CrossRef](#)]
109. Sheng, H.Y.; Xiang, L.N.; Di, L.; Chang, D.; Chen, X.Y.; Wei, T.; Lu, B.R.; Liu, Y.S. Functional characterization of an aldehyde dehydrogenase homologue in rice. *J. Integr. Agr.* **2012**, *11*, 1434–1444.
110. Shang, X.G.; Yu, Y.J.; Zhu, L.J.; Liu, H.Q.; Chai, Q.C.; Guo, W.Z. A cotton NAC transcription factor *GhirNAC2* plays positive roles in drought tolerance via regulating ABA biosynthesis. *Plant Sci.* **2020**, *296*, 110498. [[CrossRef](#)]
111. Jensen, M.K.; Lindemose, S.; Masi, F.; Reimer, J.J.; Nielsen, M.; Perera, V.; Workman, C.T.; Turck, F.; Grant, M.R.; Mundy, J. *ATAF1* transcription factor directly regulates abscisic acid biosynthetic gene *NCED3* in *Arabidopsis thaliana*. *FEBS Open Bio* **2013**, *3*, 321–327. [[CrossRef](#)] [[PubMed](#)]
112. Sato, H.; Takasaki, H.; Takahashi, F.; Suzuki, T.; Iuchi, S.; Mitsuda, N.; Ohme-Takagi, M.; Ikeda, M.; Seo, M.; Yamaguchi-Shinozaki, K. *Arabidopsis thaliana* *NGATHA1* transcription factor induces ABA biosynthesis by activating *NCED3* gene during dehydration stress. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, E11178–E11187. [[CrossRef](#)] [[PubMed](#)]
113. Zhao, N.A.; He, M.J.; Li, L.; Cui, S.L.; Hou, M.Y.; Wang, L.; Mu, G.J.; Liu, L.F.; Yang, X.L. Identification and expression analysis of *WRKY* gene family under drought stress in peanut (*Arachis hypogaea* L.). *PLoS ONE* **2020**, *15*, e0231396. [[CrossRef](#)] [[PubMed](#)]

114. Wang, N.N.; Xu, S.W.; Sun, Y.L.; Liu, D.; Zhou, L.; Li, Y.; Li, X.B. The cotton *WRKY* transcription factor (*GhWRKY33*) reduces transgenic *Arabidopsis* resistance to drought stress. *Sci. Rep.* **2019**, *42*, 1471–1485. [[CrossRef](#)]
115. Zhang, L.; Song, Z.Q.; Li, F.F.; Li, X.X.; Ji, H.K.; Yang, S.S. The specific MYB binding sites bound by *TaMYB* in the *GAPCp2/3* promoters are involved in the drought stress response in wheat. *BMC Plant Biol.* **2020**, *20*, 366. [[CrossRef](#)]
116. Tan, W.; Zhang, D.; Zhou, H.; Zheng, T.; Yin, Y.; Lin, H. Transcription factor *HAT1* is a substrate of *SnRK2.3* kinase and negatively regulates ABA synthesis and signaling in *Arabidopsis* responding to drought. *PLoS Genet.* **2018**, *14*, e1007336. [[CrossRef](#)]
117. Ding, Y.; Avramova, Z.; Fromm, M. The *Arabidopsis trithorax*-like factor *ATX1* functions in dehydration stress responses via ABA-dependent and ABA-independent pathways. *Plant J.* **2011**, *66*, 735–744. [[CrossRef](#)]
118. Zhao, P.X.; Miao, Z.Q.; Zhang, J.; Chen, S.Y.; Liu, Q.Q.; Xiang, C.B. *Arabidopsis* MADS-box factor *AGL16* negatively regulates drought resistance via stomatal density and stomatal movement. *J. Exp. Bot.* **2020**, *71*, 6092–6106. [[CrossRef](#)]
119. Yan, H.R.; Jia, H.H.; Chen, X.B.; Hao, L.L.; An, H.L.; Guo, X.Q. The Cotton *WRKY* transcription factor *GhWRKY17* functions in drought and salt stress in transgenic *Nicotiana benthamiana* through ABA signaling and the modulation of reactive oxygen species production. *Plant Cell Physiol.* **2014**, *55*, 2060–2076. [[CrossRef](#)]
120. Chen, T.Z.; Li, W.J.; Hu, X.H.; Guo, J.R.; Liu, A.M.; Zhang, B.L. A Cotton MYB transcription factor, *GbMYB5*, is positively involved in plant adaptive response to drought stress. *Plant Cell Physiol.* **2015**, *56*, 917–929. [[CrossRef](#)]
121. Yang, W.; Liu, X.D.; Chi, X.J.; Wu, C.A.; Li, Y.Z.; Song, L.L.; Liu, X.M.; Wang, Y.F.; Wang, F.W.; Zhang, C.A. Dwarf apple *MbDREB1* enhances plant tolerance to low temperature, drought, and salt stress via both ABA-dependent and ABA-independent pathways. *Planta* **2011**, *233*, 219–229. [[CrossRef](#)] [[PubMed](#)]
122. Bandeppa, S.; Paul, S.; Thakur, J.K.; Chandrashekar, N.; Umesh, D.K.; Aggarwal, C.; Asha, A.D. Antioxidant, physiological and biochemical responses of drought susceptible and drought tolerant mustard (*Brassica juncea* L) genotypes to rhizobacterial inoculation under water deficit stress. *Plant Physiol. Bioch.* **2019**, *143*, 19–28. [[CrossRef](#)]
123. Thirumalaikumar, V.P.; Devkar, V.; Mehterov, N.; Ali, S.; Ozgur, R.; Turkan, I.; Mueller-Roeber, B.; Balazadeh, S. NAC transcription factor *JUNGBRUNNEN1* enhances drought tolerance in tomato. *Plant Biotechnol. J.* **2018**, *16*, 354–366. [[CrossRef](#)] [[PubMed](#)]
124. Chen, Y.X.; Huang, L.K.; Yan, H.D.; Zhang, X.; Xu, B.; Ma, X. Cloning and characterization of an ABA-independent DREB transcription factor gene, *HcDREB2*, in *Hemarthria compressa*. *Hereditas* **2016**, *153*, 3. [[CrossRef](#)] [[PubMed](#)]
125. Jimenez, J.D.; Cardoso, J.A.; Kotula, L.; Veneklaas, E.J.; Pedersen, O.; Colmer, T.D. Root length is proxy for high-throughput screening of waterlogging tolerance in *Urochloa* spp. grasses. *Funct. Plant Biol.* **2021**, *48*, 411–421. [[CrossRef](#)] [[PubMed](#)]
126. Ye, H.; Song, L.; Chen, H.T.; Valliyodan, B.; Cheng, P.; Ali, L.; Vuong, T.; Wu, C.J.; Orłowski, J.; Buckley, B. A major natural genetic variation associated with root system architecture and plasticity improves waterlogging tolerance and yield in soybean. *Plant Cell Environ.* **2018**, *41*, 2169–2182. [[CrossRef](#)]
127. Hu, B.; Cao, J.J.; Ge, K.; Li, L. The site of water stress governs the pattern of ABA synthesis and transport in peanut. *Sci. Rep.* **2016**, *6*, 32143. [[CrossRef](#)]
128. Najeeb, U.; Tan, D.K.Y.; Bange, M.P.; Atwell, B.J. Protecting cotton crops under elevated CO₂ from waterlogging by managing ethylene. *Funct. Plant Biol.* **2018**, *45*, 340–349. [[CrossRef](#)]
129. Zhang, Q.; Liu, X.F.; Zhang, Z.F.; Liu, N.F.; Li, D.Z.; Hu, L.X. Melatonin improved waterlogging tolerance in Alfalfa (*Medicago sativa*) by reprogramming polyamine and ethylene metabolism. *Front. Plant Sci.* **2019**, *10*, 44. [[CrossRef](#)]
130. Ismond, K.P.; Dolferus, R.; de Pauw, M.; Dennis, E.S.; Good, A.G. Enhanced low oxygen survival in *Arabidopsis* through increased metabolic flux in the fermentative pathway. *Plant Physiol.* **2003**, *132*, 1292–1302. [[CrossRef](#)]
131. Christianson, J.A.; Llewellyn, D.J.; Dennis, E.S.; Wilson, I.W. Comparisons of early transcriptome responses to low-oxygen environments in three dicotyledonous plant species. *Plant Signal Behav.* **2010**, *5*, 1006–1009. [[CrossRef](#)]
132. Yue, M.F.; Shen, H.; Li, W.H.; Chen, J.F.; Ye, W.H.; Tian, X.S.; Yin, A.G.; Cheng, S.M. Waterlogging tolerance of *Bidens pilosa* translates to increased competitiveness compared to native *Bidens biternata*. *Plant Soil* **2019**, *437*, 301–311. [[CrossRef](#)]
133. Zaman, M.S.U.; Malik, A.I.; Erskine, W.; Kaur, P. Changes in gene expression during germination reveal pea genotypes with either “quiescence” or “escape” mechanisms of waterlogging tolerance. *Plant Cell Environ.* **2019**, *42*, 245–258. [[CrossRef](#)] [[PubMed](#)]
134. Rzewuski, G.; Sauter, M. Ethylene biosynthesis and signaling in rice. *Plant Sci.* **2008**, *175*, 32–42. [[CrossRef](#)]
135. Zhou, X.; Zhang, Z.L.; Park, J.; Tyler, L.; Yusuke, J.; Qiu, K.; Nam, E.A.; Lumba, S.; Desveaux, D.; McCourt, P. The ERF11 transcription factor promotes internode elongation by activating gibberellin biosynthesis and signaling. *Plant Physiol.* **2016**, *171*, 2760–2770. [[CrossRef](#)]
136. Zhai, F.F.; Li, H.D.; Zhang, S.W.; Li, Z.J.; Liu, J.X.; Qian, Y.Q.; Ju, G.S.; Zhang, Y.X.; Liu, L.; Han, L. Male and female plants of *Salix viminalis* perform similarly to flooding in morphology, anatomy, and physiology. *Forests* **2020**, *11*, 321. [[CrossRef](#)]
137. Zhang, Y.; Liu, G.; Dong, H.; Li, C. Waterlogging stress in cotton: Damage, adaptability, alleviation strategies, and mechanisms. *Crop J.* **2021**, *9*, 257–270. [[CrossRef](#)]
138. Avila-Lovera, E.; Zerpa, A.J.; Santiago, L.S. Stem photosynthesis and hydraulics are coordinated in desert plant species. *New Phytol.* **2017**, *216*, 1119–1129. [[CrossRef](#)]
139. Choi, D. Molecular events underlying coordinated hormone action in submergence escape response of deepwater rice. *J. Plant Biol.* **2011**, *54*, 365–372. [[CrossRef](#)]
140. Yu, F.; Liang, K.; Fang, T.; Zhao, H.L.; Han, X.S.; Cai, M.J.; Qiu, F.Z. A group VII ethylene response factor gene, *ZmERE180*, coordinates waterlogging tolerance in maize seedlings. *Plant Biotechnol. J.* **2019**, *17*, 2286–2298. [[CrossRef](#)]

141. Wei, X.N.; Xu, H.J.; Rong, W.; Ye, X.G.; Zhang, Z.Y. Constitutive expression of a stabilized transcription factor group VII ethylene response factor enhances waterlogging tolerance in wheat without penalizing grain yield. *Plant Cell Environ.* **2019**, *42*, 1471–1485. [[CrossRef](#)]
142. Geisler-Lee, J.; Caldwell, C.; Gallie, D.R. Expression of the ethylene biosynthetic machinery in maize roots is regulated in response to hypoxia. *J. Exp. Bot.* **2010**, *61*, 857–871. [[CrossRef](#)]
143. Peng, Y.Q.; Zhu, J.; Li, W.J.; Gao, W.; Shen, R.Y.; Meng, L.J. Effects of grafting on root growth, anaerobic respiration enzyme activity and aerenchyma of bitter melon under waterlogging stress. *Sci. Hortic.* **2020**, *261*, 108977. [[CrossRef](#)]
144. Zhang, Y.J.; Chen, Y.Z.; Lu, H.Q.; Kong, X.Q.; Dai, J.L.; Li, Z.H.; Dong, H.Z. Growth, lint yield and changes in physiological attributes of cotton under temporal waterlogging. *Field Crop Res.* **2016**, *194*, 83–93. [[CrossRef](#)]
145. Licausi, F.; Dongen, J.T.; Giuntoli, B.; Novi, G.; Santaniello, A.; Geigenberger, P.; Perata, P. HRE1 and HRE2, two hypoxia-inducible ethylene response factors, affect anaerobic responses in *Arabidopsis thaliana*. *Plant J.* **2010**, *62*, 302–315. [[CrossRef](#)]
146. Eysholdt-Derzso, E.; Sauter, M. Hypoxia and the group VII ethylene response transcription factor HRE2 promote adventitious root elongation in *Arabidopsis*. *Plant Biol.* **2019**, *21*, 103–108. [[CrossRef](#)]
147. Peng, H.P.; Chan, C.S.; Shih, M.C.; Yang, S.F. Signaling events in the hypoxic induction of alcohol dehydrogenase gene in *Arabidopsis*. *Plant Physiol.* **2001**, *126*, 742–749. [[CrossRef](#)]
148. Min, T.; Yin, X.R.; Shi, Y.N.; Luo, Z.R.; Yao, Y.C.; Grierson, D.; Ferguson, I.B.; Chen, K.S. Ethylene-responsive transcription factors interact with promoters of ADH and PDC involved in persimmon (*Diospyros kaki*) fruit de-astringency. *J. Exp. Bot.* **2012**, *63*, 6393–6405. [[CrossRef](#)]
149. Zhang, Z.G.; Luan, D.T.; Chen, G.; Xiao, F.; Yin, D.M.; Ni, D.; Li, X.R.; Qi, L.H. Isolation and characterization of a waterlogging-responsive gene involved in ethylene biosynthesis in *Chrysanthemum*. *Acta Physiol. Plant* **2018**, *40*, 100. [[CrossRef](#)]
150. Hinz, M.; Wilson, I.W.; Yang, J.; Buerstenbinder, K.; Llewellyn, D.; Dennis, E.S.; Sauter, M.; Dolferus, R. Arabidopsis RAP2.2, An ethylene response transcription factor that is important for hypoxia survival. *Plant Physiol.* **2010**, *153*, 757–772. [[CrossRef](#)]
151. Yang, C.Y.; Hsu, F.C.; Li, J.P.; Wang, N.N.; Shih, M.C. The AP2/ERF transcription factor *AtERF73/HRE1* modulates ethylene responses during hypoxia in *Arabidopsis*. *Plant Physiol.* **2011**, *156*, 202–212. [[CrossRef](#)]
152. Juntawong, P.; Butsayawarapat, P.; Songserm, P.; Pimjan, R.; Vuttipongchaikij, S. Overexpression of *Jatropha curcas* ERFVII2 transcription factor confers low oxygen tolerance in transgenic *Arabidopsis* by modulating expression of metabolic enzymes and multiple stress-responsive genes. *Plants* **2020**, *9*, 1068. [[CrossRef](#)] [[PubMed](#)]
153. Kasparý, T.E.; Roma-Burgos, N.; Merotto, A. Snorkeling strategy: Tolerance to flooding in rice and potential application for weed management. *Genes* **2020**, *11*, 975. [[CrossRef](#)]
154. Fukao, T.; Xiong, L.Z. Genetic mechanisms conferring adaptation to submergence and drought in rice: Simple or complex? *Curr. Opin. Plant Biol.* **2013**, *16*, 196–204. [[CrossRef](#)]
155. Khan, M.I.R.; Trivellini, A.; Chhillar, H.; Chopra, P.; Ferrante, A.; Khan, N.A.; Ismail, A.M. The significance and functions of ethylene in flooding stress tolerance in plants. *Environ. Exp. Bot.* **2020**, *179*, 104188. [[CrossRef](#)]
156. Locke, A.M.; Barding, G.A.; Sathnur, S.; Larive, C.K.; Bailey-Serres, J. Rice *SUB1A* constrains remodelling of the transcriptome and metabolome during submergence to facilitate post-submergence recovery. *Plant Cell Environ.* **2018**, *41*, 721–736. [[CrossRef](#)] [[PubMed](#)]
157. Fukao, T.; Bailey-Serres, J. Submergence tolerance conferred by Sub1A is mediated by *SLR1* and *SLRL1* restriction of gibberellin responses in rice. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 16814–16819. [[CrossRef](#)]
158. Schmitz, A.J.; Folsom, J.J.; Jikamaru, Y.; Ronald, P.; Walia, H. *SUB1A*-mediated submergence tolerance response in rice involves differential regulation of the brassinosteroid pathway. *New Phytol.* **2013**, *198*, 1060–1070. [[CrossRef](#)]
159. Hattori, Y.; Nagai, K.; Furukawa, S.; Song, X.J.; Kawano, R.; Sakakibara, H.; Wu, J.Z.; Matsumoto, T.; Yoshimura, A.; Kitano, H. The ethylene response factors *SNORKEL1* and *SNORKEL2* allow rice to adapt to deep water. *Nature* **2009**, *460*, 1026–1116. [[CrossRef](#)]
160. Fukushima, A.; Kuroha, T.; Nagai, K.; Hattori, Y.; Kobayashi, M.; Nishizawa, T.; Kojima, M.; Utsumi, Y.; Oikawa, A.; Seki, M. Metabolite and phytohormone profiling illustrates metabolic reprogramming as an escape strategy of deepwater rice during partially submerged stress. *Metabolites* **2020**, *10*, 68. [[CrossRef](#)]