

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).

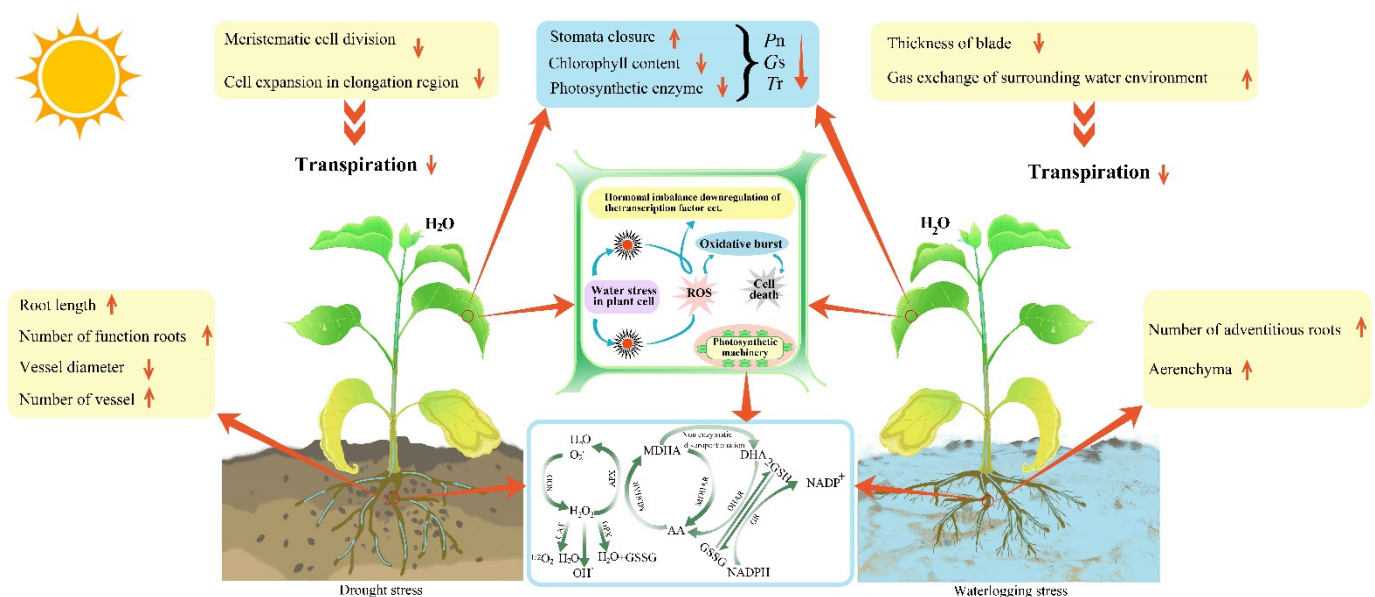


Figure 1. Changes to the morphological and anatomical structure of plant leaves and roots due to water stress. P_n : net photosynthetic rate; G_s : stomatal conductance; T_r : transpiration rate; ROS: reactive oxygen species; SOD: superoxide dismutase; CAT: catalase; APX: ascorbic peroxidase; GPX: peroxidase; 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.

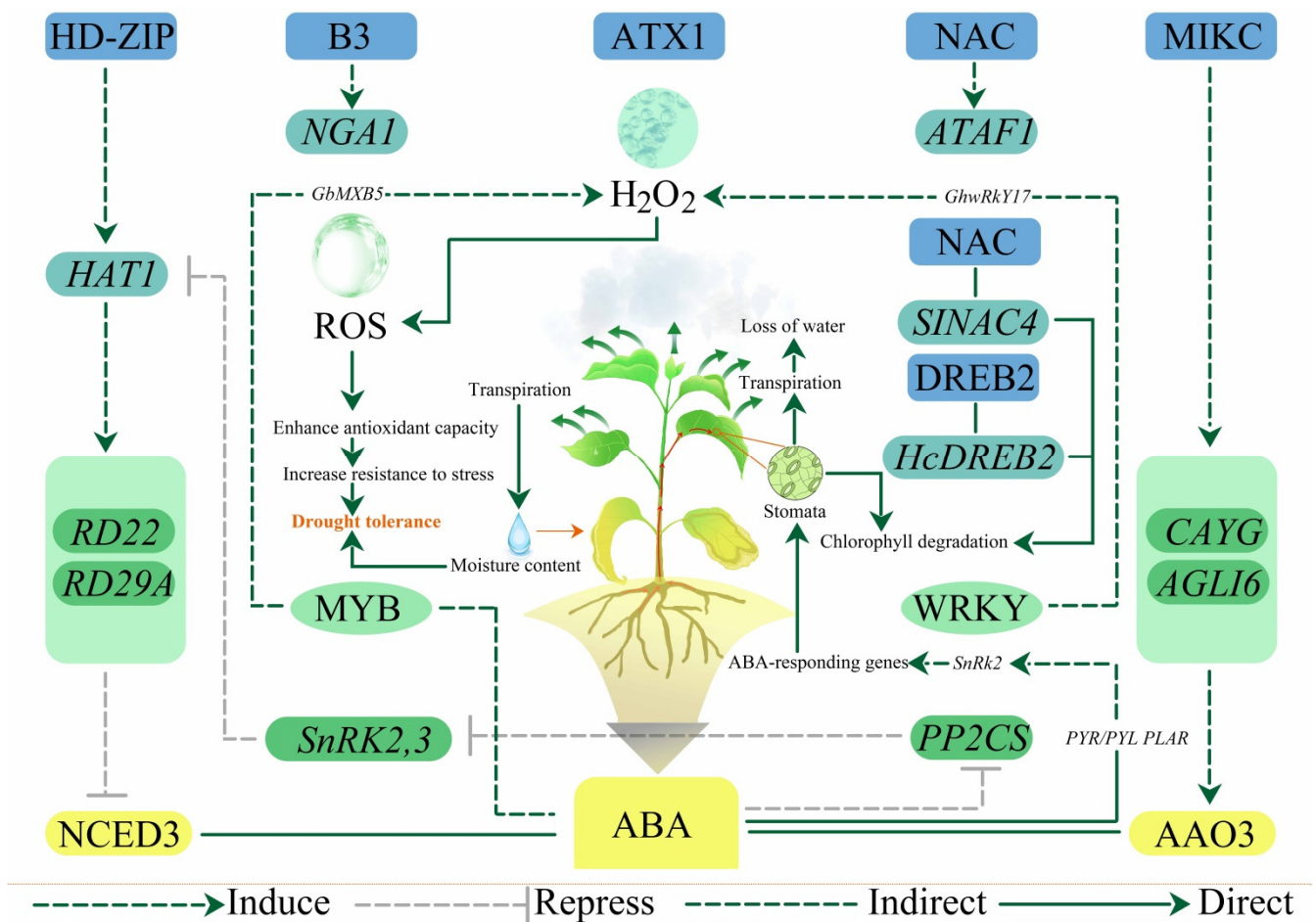


Figure 2. Regulatory mechanisms of abscisic acid (ABA) and related genes in response to drought stress in plants.

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).

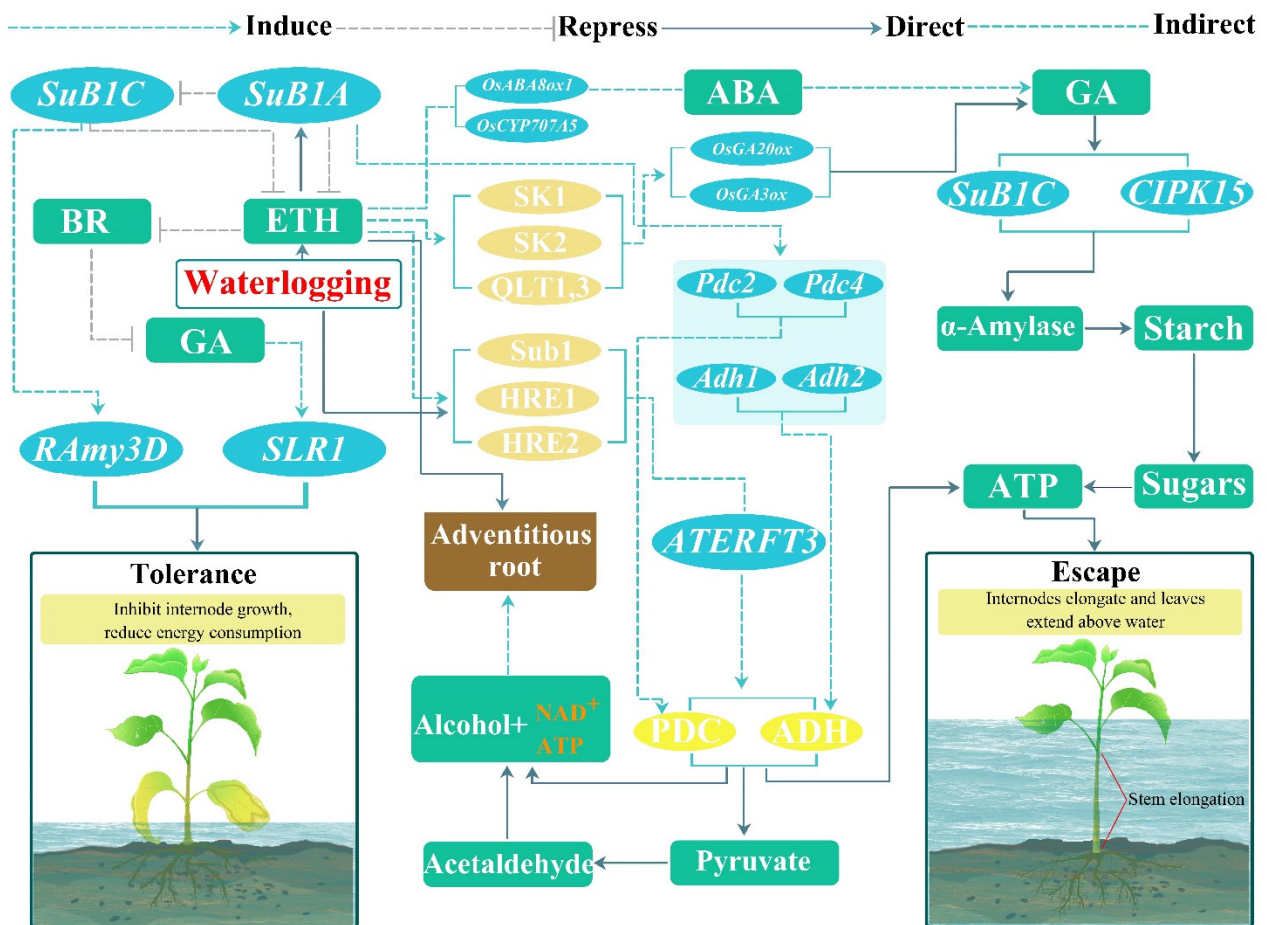


Figure 3. Regulatory mechanisms of phytohormones and related genes in response to waterlogging stress in plants.

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.

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