Plants in Response to Waterlogging Stress

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With the frequent occurrence of extreme weather such as typhoons and rainstorms, waterlogging has become one of the most important threats to global crop growth and production. Waterlogging limits plants' access to oxygen and light, leading to disadvantageous changes in metabolism to disturb plant growth and development. To escape the damage of hypoxia or promote the diffusion of oxygen to submerged organs, plants respond to waterlogging stress by regulating their morphological structure, photosynthesis, respiration, energy metabolism, and endogenous plant hormone biosynthesis/signal transduction. The adventitious roots (AR), aerenchyma, and stem internode are the major target structure for waterlogging adaptation.

molecular mechanism regulatory interaction signal transduction

1. Introduction

At the cellular level, waterlogging stress mainly affects internal metabolism, internal material flow out, cell membrane destruction, and photosynthetic rate [1]. Hypoxic immobility means that some crops can grow slowly underwater to conserve energy, and cells maintain their intact structure and essential functions through metabolic regulation. In addition, plants can retain a certain number of green leaves and generate new leaves to restore growth after submergence, which has a relatively lower impact on crop agronomic traits [2].

2. Hypoxic Response of Plants to Waterlogging Stress

Waterlogging stress causes anoxia in plant tissues, and the diffusion rate of atmospheric gas to roots is cut by 10^4 times, limiting the tricarboxylic acid (TCA) cycle and the oxygen demand on the mitochondrial electron transport chain. Anaerobic respiration becomes an important source of ATP in plants [3]. Some cells strongly increase metabolic flux through glycolysis, while others consume more conserved carbohydrates. Pyruvic acid accumulation during glycolysis can be used in anaerobic fermentation. Glyceraldehyde phosphate dehydrogenase (GAPDH), ethanol dehydrogenase (ADH), and pyruvate decarboxylase (PDC) in plant roots play a key role in the ethanol fermentation pathway, whose activities are generally considered as one of the important indicators of plant waterlogging resistance [4][5]. The *GmADH2* gene is induced during glycolysis and ethanol fermentation and enhanced the germination ability of transgenic *GmADH2* soybean seeds under waterlogged conditions [4]. Lactate dehydrogenase (LDH) is also involved in waterlogging resistance together with PDC. The overexpression of LDH significantly enhances the PDC activity and hypoxia-resistance of Arabidopsis [6]. In addition, the overexpression of *AdRAP2.3* in tobacco can increase the activity of PDC and ADH enzymes in the root system, as well as the expression levels of waterlogging marker genes [6]. Nevertheless, the intermediate product acetaldehyde and the final product ethanol produced by anaerobic respiration also accumulate correspondingly [7], and the high concentration of toxic anaerobic substances destroy the metabolic balance of plants [8]. Studies on the protein profiles of maize seedlings under anaerobic conditions showed that the synthesis of most proteins decreased sharply [9]. Hypoxia also affects the survival of bacteria in the soil, and the death of bacteria leads to the reduction in nitrate in plants, resulting in a decrease in plant yield [10].

The way plant cells perceive O_2 levels is largely dependent on the control of the stability of ERFVIIs transcription factors. Polyunsaturated long-chain acyl-coA is mainly dynamically involved in the activation of hypoxia signals in plants by regulating ACBP-ERF-VII [11]. As a member of the Arabidopsis CDPK family, *CPK12* is activated by calcium-dependent phosphorylation, then *CPK12* is transported from the cytoplasm to the nucleus, interacts and phosphorylates a regulator of the plant hypoxic sensing core *ERF-VII*, to improve hypoxia tolerance [12]. The ability of plants to maintain high levels of non-structural carbohydrates is also an important phenotypic characteristic of tolerant varieties. Amylase gene plays a central role in the degradation of endosperm starch during aerobic germination of cereal seeds [13]. *Amy3* subfamily gene expression is upregulated under hypoxic conditions. The rice *CIPK15* gene is the main positive and upstream regulatory gene of *SnRK1A*, which can induce the expression of *Amy3D* encoding α-amylase and actively regulate carbohydrate catabolism under hypoxia conditions [14][15]. Moreover, the *trehalose 6-phosphatase* gene is the main QTL for the anaerobic germination tolerance of rice [16]. *OsTPP7* induces transcription of α-amylase related genes, leading to the decomposability of starch to provide energy for seed germination [16]. In summary, genes related to sugar and energy metabolism are activated by flood stress to regulate the plant's response to hypoxia stress. The stratum corneum is the first barrier to gas exchange in plants, especially when the stomata are tightly closed under water flooding conditions. The increase in stratum corneum permeability induced by flooding is closely related to the down-regulation of genes involved in epidermal lipid synthesis in Arabidopsis under hypoxia stress [17]. Previous studies show that carbon dioxide (CO_2) and oxygen (O_2) can enter plant cells directly through the stratum corneum when the stomata are closed, and the thinner stratum corneum helps more CO_2 and O_2 flow in and stimulate photosynthesis. Long-chain acyl-CoA synthetase (*LACS2*) regulates the submergence tolerance by regulating the permeability of the stratum corneum in Arabidopsis cells, which is physiologically related to chlorophyll exudation, ion leakage, and gas exchange [18]. In addition, changes in cellular ion homeostasis and membrane transporters induced by hypoxia may be crucial for cell fate determination and formation of the lysigenous aerenchyma in plant roots, as well as the formation of root structure and adventitious root development [19].

3. Osmotic Regulation of Plants in Response to Waterlogging Stress

Waterlogging can affect the osmotic regulation process of plants. An important physiological response for plants to adapt to waterlogging stress is that during short-term waterlogging, osmoregulatory factors (such as soluble protein, sugar, and free proline) are mainly involved in regulating osmotic pressure of plant cells and can be stimulated to accumulate rapidly, which can protect plants under waterlogging conditions by optimizing cell environmental protection enzymes and membrane systems, but the contents of soluble protein, sugar, and free proline decreased gradually with prolonged waterlogging [9][20][21][22][23]. The decreased profiles of osmoregulatory factors in waterlogged grains is related to the growth stage. The loss of total protein (protein, albumin, and gluten) of waxy maize at the jointing stage is the most severe, and the starch content of grains increased but the soluble sugar content decreased at the V6 stage and heading stage, the amylopectin and amylose content increased, while the starch content decreased at maturity [9]. Waterlogging at flowering period or after flowering period can increase starch content and decrease total protein content [24], and plants with different genotypes showed different contents of osmoregulatory factors [25]. Therefore, paying attention to the changes and the internal regulation mechanism of total protein, sugar, and free proline contents in plants with different genotypes at different stages under waterlogging conditions is significantly crucial.

The expression of genes involved in osmotic stress can ameliorate plant cell damage caused by osmotic potential imbalance between plants and the environment. Notably, recent studies have shown that osmotic stress gene expression was influenced by inhibiting Arabidopsis PLANT U-BOX44 (*PUB44*) mediated calc-dependent protein kinase (*CPK4*) responding to osmotic stress [26]. The overexpression of maize transcription factor *ZmNAC2* in Arabidopsis upregulates the expression of many osmotic stress related genes and plant hormone signaling genes [27]. Therefore, these genes can serve as target genes for improving osmotic stress resistance in crop breeding.

4. Active Oxygen Scavenging Mechanism of Plants in Response to Waterlogging Stress

During waterlogging stress, ROS such as hydroxyl radical (OH^-), superoxide anion radical (O^{2-}), and hydrogen peroxide (H_2O_2) accumulate excessively, leading to irreversible oxidation of membrane lipids and proteins, and severely damaging protective barriers of cell membranes and plants [28][29][30]. As the product of lipid peroxidation, MDA is an important physiological index to measure plant tolerance and sensitivity to abiotic stress [31]. MDA can bind to proteins and enzymes on the cell membrane and denature or inactivate them, thereby destroying the biofilm structure and function and affecting cell substances metabolism [32]. For example, MDA accumulation leads to an increase in cell membrane selective permeability and electrolyte exosmosis, further affecting other physiological and biochemical metabolic activities [33]. In addition, the activities of protective enzymes such as SOD and POD in plant tissues are increased in response to waterlogging, and plants maintain the normal level of ROS by coordinating the content of SOD, POD, and catalase (CAT), [34][35][36]. Under waterlogging stress, the antioxidant enzyme activity patterns of different crops vary greatly. For instance, POD activity in cotton first increases and then decreases with the prolongation of flooding time, while SOD activity first decreases and then increases [37]. The activities of SOD and CAT in rapeseed leaves decreases first and then increases, while POD activity always increases with the prolongation of waterlogging time [38][39], which suggests that the mechanism of the plant antioxidant enzyme system is not always same, and there may be different regulatory networks responsible for the antioxidant enzyme system in response to different types of waterlogging in different plants. In plant cells, the expression of some antioxidant genes can maintain the redox balance of cells by increasing the enzymatic antioxidants such as SOD and POD, as well as non-enzymatic antioxidants including ascorbic acid and glutathione. For example, the induced expression of ethylene response factor *BnERF2.4* in *Brassica napus* is involved in regulating the antioxidant system against waterlogging stress [40]. The overexpression of the barley *Phytoglobin 1* (*HvPgb1*) gene is involved in central carbon metabolism, carbon assimilation, and ethylene synthesis, thus improving the tolerance of plant roots to waterlogging [41]. The interaction between the *CmRCD1* gene and *CmSOS1* in chrysanthemums enhances the enzyme activities of SOD, POD, and CAT to regulate the waterlogging tolerance [42]. Furthermore, exogenous growth regulatory substances application also improve the antioxidant capacity of flooded crops [43]. The exogenous administration of glutathione (GSH) [44] and glycine betaine (GB) [45] in the field can significantly improve the transcription level and enzyme activity of antioxidant defense-related genes to reduce oxidative stress. The utilization of gamma-aminobutyric acid (GABA) can activate the activity of maize antioxidant enzymes, improve the ultrastructure of chloroplasts, enhance photosynthetic characteristics, and promote the growth of maize seedlings under flooded conditions [46].

Mitochondria are the main source of ROS in plants under hypoxic conditions. Chang et al. [47] demonstrated that mitochondrial electron transport chain (mETC) inhibitors can stimulate mitochondria to produce ROS in Arabidopsis seedlings. Under hypoxia conditions, damaged mitochondria can significantly destroy the dynamic equilibrium of cell metabolism, then accumulate excessive ROS and activate hypoxia-inducible factor *HIF*-1α, to initiate signaling transduction and regulate mitochondrial autophagy processes. There are many studies on the process of autophagy induced by hypoxia in animal cells, but few studies on the molecular process of hypoxia-induced autophagy in plant cells. Meanwhile, the concentration of free Ca^{2+} in the cytoplasm under waterlogging is increased, thus encoding calcium signals to activate NADPH oxidase and produce excessive ROS, which damages plant cell activity, physiological metabolism, and development [48].

5. Photosynthetic Signal Transduction in Response to Waterlogging Stress in Plants

The first response of plants to waterlogging stress is the closure of the leaf stomata. The decrease in gas exchange rate leads to a decrease in photosynthetic performance, and the reduction in water absorption leads to a decrease in transpiration [49][50]. Sucrose and starch are the main end products of photosynthesis in most plants, while flooding reduces the photosynthesis rate and affects the transportation of photosynthetic products from source tissues (leaves) to sink tissues (roots). Waterlogging-resistant plants maintain respiration and growth in the absence of photosynthesis, resulting in the accumulation of more carbohydrates in the roots, while waterlogging-sensitive plants reduce their demand for sucrose due to the obstruction of phloem transport and lead to more starch accumulation in the chloroplasts of leaves [50][51]. Therefore, maintaining low leaf starch concentration, high root tissue starch concentration, and high photosynthetic rate are important characteristics for plant survival in submerged environments [50].

Photochrome is a signal molecule acting as a photoreceptor in response to changes in the ambient light quality and level that regulates plant metabolic pathways and growth and development [52]. The degradation of phytochrome in a waterlogged environment is a common feature of plants. Flooding leads to decreased light intensity and the ratio of red to far-red light (R: FR). The specific transcriptional regulatory factor *WRKY6* in Arabidopsis is regulated by phytochrome and directly combines with the promoter of the *senescence-induced receptor-like protein kinase*

(*SIRK*) gene to induce leaf senescence [53]. This result was confirmed in another literature that *WRKY6* positively regulates leaf senescence by up-regulating the expression of senescence-related gene *SAG* [54]. The expression of photopigment-interacting factor-like protein (*OsPIL1*) in rice under waterlogging was relatively down-regulated compared with normal light exposure, resulting in a decrease in total chlorophyll (Chl) and Chlb contents, an increase in Chla/b ratio, and a decrease in light-trapping capacity, leading to a decrease in leaf biomass and grain yield [55].

Waterlogging causes stomatal closure and intercellular carbon dioxide cannot be fully absorbed and transformed by plants. Mitochondrial respiration decreases and the activities of photosynthetic-related proteins in plants are significantly down-regulated, resulting in the decomposition of photopigments, which directly affects the photosynthetic rate of plants by disrupting light signal recognition [56][57]. Moreover, the activities of the key carbon assimilation enzymes ribulose-1, 5-diphosphate carboxylase (Rubisco), and phosphoenolpyruvate (PEP) carboxylase decrease, which negatively affect the carbon dioxide assimilation and photosynthesis rate [58]. The reduction in carbohydrate allocation caused by low photosynthetic performance under waterlogging conditions leads to poor spike differentiation and development of plants and reduces plant yield and quality [59]. Moreover, such adverse effects involve different growth stages of plants which increase with the prolongation of waterlogging, and seedlings are usually more sensitive than older plants [60][61][62]. Plants maintain internal ventilation and photosynthesis of leaves by forming air film. A rice gene LEAF *GAS FILM 1* (*LGF1/OsHSD1*) controls the retention of air film in leaves to contribute to internal ventilation by regulating the synthesis of primary alcohol under waterlogging [63]. In addition, the exogenous application of glutathione can protect photosynthetic pigments for photosynthesis [64].

6. Changes of Plant Hormone and Signal Molecules-Mediated Pathways under Waterlogging Stress

Ethylene has been proven to play an important role in controlling rapid hypoxia stress responses and help plants adapt to hypoxic environments [65]. The ethylene signaling pathway is involved in various cellular reactions during hypoxia, including enhancing the vitality of apical hypoxic cells, maintaining ROS homeostasis and antioxidant activity [66][67], promoting the callus formation of auxin-induced xylem sheath cells [68], as well as controlling hypoxia induction [65]. In plants, cysteine oxidase (*PCOs*) acts as an oxygen sensor, mediating the abundance of three *ERF-VII* protein members [69]. Under hypoxic conditions, *PCO* cannot oxidize *ERF-VII* proteins and these proteins are stabilized and enter the nucleus, activating hypoxic response genes and triggering plant hypoxia response [69][70]. During hypoxia, ethylene regulates protein abundance through transcription. The overexpression of the Arabidopsis root tip ethylene regulatory proteins *PGB1*, *HUP26*, and *HUP36* genes can enhance root tip cells' hypoxia tolerance [67]. Ethylene enhances nitric oxide (NO) scavenger PHYTOGLOBIN1 (*PGB1*) and inhibits *MetCys2* (MC)-activated *ERFVII* protein NO-dependent proteolysis through *PRT6* N-degron pathway to promote ERFVII accumulation before hypoxia, and this process is involved in an increase in *RAP2.2* and *RAP2.12* genes expression, which allows plants to preadapt to the impending hypoxia [71][72][73]. *RAP2.2* is an important ethylene reaction factor, which regulates the alcohol dehydrogenase gene *ADH1*, pyruvic acid decarboxylase *PDC1*, and ethylene synthesis-related genes to counteract hypoxia stress in Arabidopsis [74][75]. *RAP2.12* affects the direction of root growth by limiting the flux of IAA from the root tip to the elongation zone [76]. Other *ERF* factors, including *PhERF2*, *HvERF2.11*, *ZmEREB180*, and *OsSublA*, have also been shown to play important roles in waterlogging tolerance, supporting the important functions of ethylene and related genes in waterlogging tolerance [77][78][79][80][81]. In addition, ethylene promotes the transcription of rice *SUB1A* and the overexpression of *SUB1A* enhances the transcription of *ADH1* in transgenic rice, leading to more ATP production [82]. The *SUB1A* gene also inhibits stem elongation by increasing the accumulation of DELLA protein SLENDER rice-1 (*SLR1*) and non-DELLA protein SLR1-like-1 (*SLRL1*) and internode elongation by up-regulating the expression of BR biosynthesis genes [2].

Under submerged conditions, ethylene contributes to promoting branch elongation, aerenchyma formation and adventitial root growth during submergence by coordinating the biosynthesis and signaling pathways of GA, ABA and IAA [83][84]. Rice *SD1* protein is a key factor in the gibberellin synthesis pathway and is transcriptionally activated by ethylene transcription factor *OsEIL1a*, which mainly catalyzes the biosynthesis of GA and significantly stimulates internode elongation in deep-water rice under flooding conditions [85]. Flooding leads to the accumulation of ethylene in the lower part of the stem, resulting in the decrease in the ABA level in the stem and AR primordium tissues and the induced expression of the auxin polar transporter *PIN2*, thereby increasing the cell activity in AR primordium [84]. Under ABA treatment, the overexpression of *AdPDC1* in Arabidopsis inhibited seed germination and root length [86]. Ethylene interception under waterlogging stimulates the transport of auxin to the submerged part, and the accumulation of auxin in the roots induces the division of meristem cells in AR primordium and promotes AR production [87]. Notably, flooded tomato plants do not produce AR after being treated with the auxin transport inhibitor *NPA*, which confirmed that ethylene-mediated auxin transport is necessary for AR formation [87].

Scientists from different geographical regions of the world are actively involved in the use of exogenous nutrients and plant hormones to make plants tolerant to flood stress. Exogenous plant growth regulators can alleviate waterlogging stress in many ways, including increasing leaf water content and cell viability, regulating canopy temperature and stomatal opening, and promoting root detoxification and wound healing [37][62][88][89]. An exogenous gas hydrogen sulfide (H_2S) application can enhance the function of endogenous H_2S in plants, and is involved in plant responses to waterlogging stress by increasing the expression of alternative oxidase genes and inducing Ca^{2+} influx to activate the expression of intracellular Ca^{2+}-sensing-related genes [90][91]. Moreover, the synergistic application of plant hormones and biochar can enhance the resilience and survival ability of plants under flood conditions [92].

7. Energy Metabolism of Plants in Response to Waterlogging Stress

The process of energy metabolism is closely related to seed germination, and plant development. Previous studies have shown that hypoxic concentration caused by flooding changes the energy metabolism pattern, and the aerobic respiration pathways such as tricarboxylic acid cycle (TCA cycle) and oxidative phosphorylation are damaged. Anaerobic respiration dominates but only provides limited energy for seed germination and plant growth under flooding conditions, thus affecting plant growth and the reproduction process. In many submerged plants, genes involved in β-oxidation and tricarboxylic acid cycles, as well as most genes involved in sucrose to acetyl-CoA are down-regulated [93]. On the contrary, hypoxia induces up-regulation of *ADH* and *PDC* genes related to ethanol fermentation, resulting in the formation of physiologically toxic substances such as ethanol and acetaldehyde [93]. The plants' responses to waterlogging are coordinated by regulating interconnected signal pathways in different metabolic networks. The upregulated activities of alanine aminotransferase, ubiquitin-activating enzyme E1, mitogen-activated protein kinase, and pyruvate kinase in waterlogging-resistant maize indicate that genes involved in protein degradation, signal transduction, and carbon metabolism are involved in the adaptive mechanisms under waterlogging conditions [94]. *PsERF/PsCIPK* genes in cherries regulate glucose metabolism to resist waterlogging stress by enhancing the activities of sucrose synthetase (SUS), α-amylase, ADH, and PDC in leaves [95]. The overexpression of *MaRAP2-4* of Mentha showed enhanced flooding tolerance and oxidative stress tolerance and regulated the bidirectional sugar transporter *AtSWEET10* to meet the sugar supply of transgenic plants [96].

Lipids are widely involved in regulating plant responses to hypoxia. The Arabidopsis CoA-binding protein *ACBP3* is involved in plant response to hypoxia by regulating ultra-long chain fatty acids metabolism [97]. The polyunsaturated long-chain acyl-CoA regulates hypoxic perception in plants by regulating the kinetics of the acyl-CoA-binding protein-Group VII ethylene reaction factor [98]. In addition, unsaturated ultra-long chain ceramide species protect plants from hypoxia-induced cell damage by modulating the kinase activity of the assembled triple RESPONSE1 in the ethylene signaling pathway. Jasmonic acid oxylipin specifically regulates plant response to reoxygenation stress through the transcriptional regulation of the antioxidant biotin [98]. Hypoxia reduces the membrane barrier function and induces changes in lipid composition [97]. Phosphatidyl acid (PA) is an important lipid required for plant growth and development and response to biotic and abiotic stresses. In Arabidopsis, PA regulates plant tolerance to flooding by regulating membrane integrity and *MPK3/6*-mediated hypoxia signaling pathway [99].

8. Nitrogen Uptake and Utilization under Waterlogging Stress

Nitrogen is an essential nutrient for plant growth and development, and nitrogen metabolism has also been proven to help cells adapt to hypoxic stress. Under waterlogging stress, the assimilation of ammonium nitrogen in rice and soybean requires less energy than nitrate nitrogen, and the utilization efficiency of ammonium nitrogen is higher than that of nitrate nitrogen [100]. There is a 30% reduction in ammonium uptake of nitrogen-deficient roots in *AtAMT1* (NH_4^+ translocator) Arabidopsis mutant, and the function of these genes showed additive effects [101]. Evidence show that the accumulation of NO and nitrate/nitrite plays an important and multifaceted role in plant adaptation to a hypoxic environment, such as morphological changes, hypotonia, mitochondrial structure protection, ATP production, and ROS clearance [102][103]. Nitrate fertilization increases NO accumulation and partially restores ATP levels in submerged plants, while reducing the content of reactive oxygen species and toxic products such as lactic acid and ethanol [104]. An important mechanism of plant survival in anoxic environments is the circulation of non-symbiotic hemoglobin and nitric oxide generated by nitrate supply. Nitrate is converted to nitrite by nitrate reductase (NR) to produce NO in the cytoplasm, and nitrite acts as an electron transport chain acceptor in mitochondria to promote proton pumping and ATP production under hypoxic conditions [102][105]. NO signaling by nitrite can inhibit CAT and maintain ROS levels under hypoxia conditions, on the other hand, NO signaling interacts with hypoxia-induced hemoglobin during NADH regeneration cycle to regulate ATP homeostasis [106].

NO is involved in plants response to abiotic stress in many ways, including promoting root aerenchyma formation [107], ethylene biosynthesis, mitochondrial electron transfer, antioxidant enzyme activity, antioxidant production, and regulating ROS content [102][108][109]. In Arabidopsis, changes in oxygen and nitric oxide (NO) control the stability of *ERFVII* transcription factors. *ERFVII* protein hydrolysis is regulated by the N-degron pathway and mediates adaptation to flood-induced hypoxia [71]. The application of NO donor sodium nitroprusside on leaves can increase NO concentration in plant tissues, reduce membrane lipid peroxidation and hypoxia damage caused by waterlogging, induce the expression of hormone metabolism-related genes, and reduce plant yield loss under waterlogging [110]. Exogenous spermidine application can maintain the integrity of root cells and the normal morphology and function of roots [111]. Nitrogen application changed the enzyme activity of nitrogen metabolism after alternating drought and flood and increased nitrogen accumulation in organs, as well as improving the microbial environment of rice rhizosphere soil [112]. There is evidence that the increase in rhizosphere anaerobic microorganisms under flooding may have potential negative effects on plants due to their pathogenic behavior or soil denitrification capacity [113]. At present, the positive effects of nitrogen application on flooded plant roots are well known, but the effects of the interaction between hypoxia with carbon and nitrogen metabolism are still not fully illustrated.

References

1. Bailey-Serres, J.; Colmer, T.D. Plant tolerance of flooding stress—Recent advances. Plant Cell Environ. 2014, 37, 2211–2215.
2. Hattori, Y.; Nagai, K.; Furukawa, S.; Song, X.J.; Kawano, R.; Sakakibara, H.; Wu, J.; Matsumoto, T.; Yoshimura, A.; Kitano, H.; et al. The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 2009, 460, 1026–1030.
3. Van Veen, H.; Akman, M.; Jamar, D.C.; Vreugdenhil, D.; Kooiker, M.; Van Tienderen, P.; Voesenek, L.A.; Schranz, M.E.; Sasidharan, R. Group VII ethylene response factor diversification and regulation in four species from flood-prone environments. Plant Cell Environ. 2014, 37, 2421–2432.
4. Tougou, M.; Hashiguchi, A.; Yukawa, K.; Nanjo, Y.; Hiraga, S.; Nakamura, T.; Nishizawa, K.; Komatsu, S. Responses to flooding stress in soybean seedlings with the alcohol dehydrogenase transgene. Plant Biotechnol. 2012, 29, 301–305.
5. Xuewen, X.; Huihui, W.; Xiaohua, Q.; Qiang, X.; Xuehao, C. Waterlogging-induced increase in fermentation and related gene expression in the root of cucumber (Cucumis sativus L.). Sci.

Hortic. 2014, 179, 388–395.

6. 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.
7. Atkinson, C.J.; Harrison-Murray, R.S.; Taylor, J.M. Rapid flood-induced stomatal closure accompanies xylem sap transportation of root-derived acetaldehyde and ethanol in Forsythia. Environ. Exp. Bot. 2008, 64, 196–205.
8. Zhou, W.; Chen, F.; Meng, Y.; Chandrasekaran, U.; Luo, X.; Yang, W.; Shu, K. Plant waterlogging/flooding stress responses: From seed germination to maturation. Plant Physiol. Biochem. 2020, 148, 228–236.
9. Ning, D.F.; Zheng, H.J.; Liu, Z.D. Effects of waterlogging at different stages on growth and ear quality of waxy maize. Agric. Water Manag. 2022, 266, 107603.
10. Chang, W.W.; Huang, L.; Shen, M.; Webster, C.; Burlingame, A.L.; Roberts, J.K. Patterns of protein synthesis and tolerance of anoxia in root tips of maize seedlings acclimated to a low-oxygen environment, and identification of proteins by mass spectrometry. Plant Physiol. 2000, 122, 295–317.
11. Zhou, Y.; Tan, W.J.; Xie, L.J.; Qi, H.; Yang, Y.C.; Huang, L.P.; Lai, Y.X.; Tan, Y.F.; Zhou, D.M.; Yu, L.J.; et al. Polyunsaturated linolenoyl-CoA modulates ERF-VII-mediated hypoxia signaling in Arabidopsis. J. Integr. Plant Biol. 2020, 62, 330–348.
12. Fan, B.; Liao, K.; Wang, L.N.; Shi, L.L.; Zhang, Y.; Xu, L.J.; Zhou, Y.; Li, J.F.; Chen, Y.Q.; Chen, Q.F.; et al. Calcium-dependent activation of CPK12 facilitates its cytoplasm-to-nucleus translocation to potentiate plant hypoxia sensing by phosphorylating ERF-VII transcription factors. Mol. Plant 2023, 16, 979–998.
13. Whan, A.; Dielen, A.-S.; Mieog, J.; Bowerman, A.F.; Robinson, H.M.; Byrne, K.; Colgrave, M.; Larkin, P.J.; Howitt, C.A.; Morell, M.K.; et al. Engineering alpha-amylase levels in wheat grain suggests a highly sophisticated level of carbohydrate regulation during development. J. Exp. Bot. 2014, 65, 5443–5457.
14. Park, M.; Yim, H.K.; Park, H.G.; Lim, J.; Kim, S.H.; Hwang, Y.S. Interference with oxidative phosphorylation enhances anoxic expression of rice alpha-amylase genes through abolishing sugar regulation. J. Exp. Bot. 2010, 61, 3235–3244.
15. Lee, K.W.; Chen, P.W.; Lu, C.A.; Chen, S.; Ho, T.H.D.; Yu, S.M. Coordinated responses to oxygen and sugar deficiency allow rice seedlings to tolerate flooding. Plant Biol. 2009, 2, 61.
16. Kretzschmar, T.; Pelayo, M.A.; Trijatmiko, K.R.; Gabunada, L.F.; Alam, R.; Jimenez, R.; Mendioro, M.S.; Slamet-Loedin, I.H.; Sreenivasulu, N.; Bailey-Serres, J.; et al. A trehalose-6-phosphate

phosphatase enhances anaerobic germination tolerance in rice. Nat. Plants 2015, 1, 15124.

17. Kim, H.; Choi, D.; Suh, M.C. Cuticle ultrastructure, cuticular lipid composition, and gene expression in hypoxia-stressed Arabidopsis stems and leaves. Plant Cell Rep. 2017, 36, 815–827.
18. Xie, L.J.; Tan, W.J.; Yang, Y.C.; Tan, Y.F.; Zhou, Y.; Zhou, D.M.; Xiao, S.; Chen, Q.F. Long-Chain acyl-CoA Synthetase LACS2 Contributes to Submergence Tolerance by Modulating Cuticle Permeability in Arabidopsis. Plants 2020, 9, 262.
19. Huang, X.; Shabala, L.; Zhang, X.; Zhou, M.; Voesenek, L.A.C.J.; Hartman, S.; Yu, M.; Shabala, S. Cation transporters in cell fate determination and plant adaptive responses to a low-oxygen environment. J. Exp. Bot. 2022, 73, 636–645.
20. Phukan, U.J.; Mishra, S.; Shukla, R.K. Waterlogging and submergence stress: Affects and acclimation. Crit. Rev. Biotechnol. 2016, 36, 956–966.
21. Xu, J.; Qiao, X.; Tian, Z.; Zhang, X.; Zou, X.; Cheng, Y.; Lu, G.; Zeng, L.; Fu, G.; Ding, X.; et al. Proteomic analysis of rapeseed root response to waterlogging stress. Plants 2018, 7, 71.
22. Barickman, T.C.; Simpson, C.R.; Sams, C.E. Waterlogging causes early modification in the physiological performance, carotenoids, chlorophylls, proline, and soluble sugars of cucumber plants. Plants 2019, 8, 160.
23. Ghosh, U.K.; Islam, M.N.; Siddiqui, M.N.; Cao, X.; Khan, A.R. Proline, a multifaceted signalling molecule in plant responses to abiotic stress: Understanding the physiological mechanisms. Plant Biol. 2021, 24, 227–239.
24. Yang, H.; Huang, T.; Ding, M.; Lu, D.; Lu, W. Effects of waterlogging around flowering stage on the grain yield and eating properties of fresh waxy maize. Cereal Chem. 2016, 93, 605–611.
25. Habibullah, M.; Sarkar, S.; Islam, M.M.; Ahmed, K.U.; Rahman, M.Z.; Awad, M.F.; Elsayed, A.I.; Mansour, E.; Hossain, M.S. Assessing the response of diverse sesame genotypes to waterlogging durations at different plant growth stages. Plants 2021, 10, 2294.
26. Fan, W.; Liao, X.L.; Tan, Y.Q.; Wang, X.R.; Schroeder, J.; Li, Z.X. Arabidopsis PLANT U-BOX44 down-regulates osmotic stress signaling by mediating Ca2+-DEPENDENT PROTEIN KINASE4 degradation. Plant Cell 2023, 35, 3870–3888.
27. Chen, Y.Y.; Li, X.L.; Xie, X.; Liu, L.J.; Fu, J.Y.; Wang, Q. Maize transcription factor ZmNAC2 enhances osmotic stress tolerance in transgenic Arabidopsis. J. Plant Physiol. 2023, 282, 153948.
28. Cheng, C.; Che, Q.; Su, S.; Liu, Y.; Wang, Y.; Xu, X. Genome-wide identification and characterization of Respiratory Burst Oxidase Homolog genes in six Rosaceae species and an analysis of their effects on adventitious rooting in apple. PLoS ONE 2020, 15, e0239705.

29. Carvalho, P.A.D.; Oliveira, L.E.M.D.; Domiciano, D.; Carvalho, J.N.D.; Prudente, D.D.O.; Guimarães, R.J. Effect of nitrogen source and oxygen deficiency on carbon metabolism and antioxidant system of rubber tree plants (Hevea spp.). Aust. J. Crop Sci. 2018, 12, 116–125.
30. Basu, S.; Kumar, G.; Kumari, N.; Kumari, S.; Shekhar, S.; Kumar, S.; Rajwanshi, R. Reactive oxygen species and reactive nitrogen species induce lysigenous aerenchyma formation through programmed cell death in rice roots under submergence. Environ. Exp. Bot. 2020, 177, 104118.
31. Dantas, B.; Silva, R.; Ribeiro, R.; Aragão, C. Respiration and antioxidant enzymes activity in watermelon seeds and seedlings subjected to salt and temperature stresses. Am. J. Exp. Agric. 2015, 7, 70–77.
32. Ayala, A.; Munoz, M.F.; Arguelles, S. Lipid peroxidation: Production, metabolism, and signaling mechanisms of malondialdehyde and 4-hydroxy-2-nonenal. Oxid. Med. Cell Longev. 2014, 2014, 360438.
33. Ahmed, A.R.; Farris, F.F.; Ray, S.D. Lipid peroxidation. Biomed. Sci. 2023.
34. Hodges, D.M.; Andrews, C.J.; Johnson, D.A.; Hamilton, R.I. Antioxidant enzyme responses to chilling stress in differentially sensitive inbred maize lines. J. Exp. Bot. 1997, 48, 1105–1113.
35. Ekmekçi, Y.; Tanyolaç, D.; Ayhan, B. Effects of cadmium on antioxidant enzyme and photosynthetic activities in leaves of two maize cultivars. J. Plant Physiol. 2008, 165, 600–611.
36. Abedi, T.; Pakniyat, H. Antioxidant enzymes changes in response to drought stress in ten cultivars of oilseed rape (Brassica napus L.). Czech J. Genet. Plant Breed. 2010, 46, 27–34.
37. Li, M.-F.; Zhu, J.-Q.; Jiang, Z.-H. Plant growth regulators and nutrition applied to cotton after waterlogging. In Proceedings of the Third International Conference on Intelligent System Design and Engineering Applications, Hong Kong, China, 16–18 January 2013; pp. 1045–1048.
38. Das, K.K.; Panda, D.; Sarkar, R.K.; Reddy, J.N.; Ismail, A.M. Submergence tolerance in relation to variable floodwater conditions in rice. Environ. Exp. Bot. 2009, 66, 425–434.
39. Rich, S.M.; Ludwig, M.; Colmer, T.D. Photosynthesis in aquatic adventitious roots of the halophytic stem-succulent Tecticornia pergranulata (formerly Halosarcia pergranulata). Plant Cell Environ. 2008, 31, 1007–1016.
40. Lv, Y.; Fu, S.; Chen, S.; Zhang, W.; Qi, C. Ethylene response factor BnERF2-like (ERF2.4) from Brassica napus L. enhances submergence tolerance and alleviates oxidative damage caused by submergence in Arabidopsis thaliana. Crop J. 2016, 4, 199–211.
41. Hill, R.D.; De Castro, J.; Mira, M.M.; Igamberdiev, A.U.; Hebelstrup, K.H.; Renault, S.; Xu, W.; Badea, A.; Stasolla, C. Over-expression of the barley Phytoglobin 1 (HvPgb1) evokes leaf-specific transcriptional responses during root waterlogging. J. Plant Physiol. 2023, 283, 153944.

42. Wang, L.; Gao, J.; Zhang, Z.; Liu, W.; Cheng, P.; Mu, W.; Su, T.; Chen, S.; Chen, F.; Jiang, J. Overexpression of CmSOS1 confers waterlogging tolerance in Chrysanthemum. J. Integr. Plant Biol. 2020, 62, 1059–1064.
43. An, Y.Y.; Lin, Q.; Wang, L.J. ALA pretreatment improves waterlogging tolerance of fig plants. PLoS ONE 2016, 11, e0147202.
44. Keya, S.S.; Mostofa, M.G.; Mezanur Rahman, M.; Das, A.K.; Abiar Rahman, M.; Anik, T.R.; Sultana, S.; Arifur Rahman Khan, M.; Robyul Islam, M.; Watanabe, Y.; et al. Effects of glutathione on waterlogging-induced damage in sesame crop. Ind. Crops Prod. 2022, 185, 115092.
45. Rasheed, R.; Iqbal, M.; Ashraf, M.A.; Hussain, I.; Shafiq, F.; Yousaf, A.; Zaheer, A. Glycine betaine counteracts the inhibitory effects of waterlogging on growth, photosynthetic pigments, oxidative defence system, nutrient composition, and fruit quality in tomato. J. Hortic. Sci. Biotechnol. 2017, 93, 385–391.
46. Salah, A.; Zhan, M.; Cao, C.; Han, Y.; Ling, L.; Liu, Z.; Li, P.; Ye, M.; Jiang, Y. γ-Aminobutyric acid promotes chloroplast ultrastructure, antioxidant capacity, and growth of waterlogged maize seedlings. Sci. Rep. 2019, 9, 484.
47. Chang, R.; Jang, C.J.; Branco-Price, C.; Nghiem, P.; Bailey-Serres, J. Transient MPK6 activation in response to oxygen deprivation and reoxygenation is mediated by mitochondria and aids seedling survival in Arabidopsis. Plant Mol. Biol. 2012, 78, 109–122.
48. Wan, D. The Study of Calcium Signal Transduction Induced by Oxidative Stress (H2O2). Master’s Thesis, Hangzhou Normal University, Hangzhou, China, 2018.
49. Bansal, R.; Srivastava, J.P. Effect of waterlogging on photosynthetic and biochemical parameters in pigeonpea. Russ. J. Plant Physiol. 2015, 62, 322–327.
50. Gravarr, D.A.; Kirby, C.J. Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. Tree Physiol. 1998, 18, 411–417.
51. Sairam, R.K.; Dharmar, K.; Chinnusamy, V.; Meena, R.C. Waterlogging-induced increase in sugar mobilization, fermentation, and related gene expression in the roots of mung bean (Vigna radiata). J. Plant Physiol. 2009, 166, 602–616.
52. Distefano, G.; Cirilli, M.; Las Casas, G.; La Malfa, S.; Continella, A.; Rugini, E.; Thomas, B.; Long, G.; Gentile, A.; Muleo, R. Ectopic expression of Arabidopsis phytochrome B in Troyer citrange affects photosynthesis and plant morphology. Sci. Hortic. 2013, 159, 1–7.
53. Lim, J.; Park, J.H.; Jung, S.; Hwang, D.; Nam, H.G.; Hong, S. Antagonistic roles of PhyA and PhyB in far-red light-dependent Leaf senescence in Arabidopsis thaliana. Plant Cell Physiol. 2018, 59, 1753–1764.

54. Zhang, Y.; Liu, Z.; Wang, X.; Wang, J.; Fan, K.; Li, Z.; Lin, W. DELLA proteins negatively regulate dark-induced senescence and chlorophyll degradation in Arabidopsis through interaction with the transcription factor WRKY6. Plant Cell Rep. 2018, 37, 981–992.
55. Panda, D.; Dash, G.K.; Mohanty, S.; Sekhar, S.; Roy, A.; Tudu, C.; Behera, L.; Tripathy, B.C.; Baig, M.J. Phytochrome A mediated modulation of photosynthesis, development and yield in rice (Oryza sativa L.) in fluctuating light environment. Environ. Exp. Bot. 2023, 206, 105183.
56. Jackson, M.B. Long-distance signalling from roots to shoots assessed the flooding story. J. Exp. Bot. 2002, 53, 175–181.
57. Ren, B.; Zhang, J.; Dong, S.; Liu, P.; Zhao, B. Effects of waterlogging on leaf mesophyll cell ultrastructure and photosynthetic characteristics of summer maize. PLoS ONE 2016, 11, e0161424.
58. Liao, C.T.; Ho, L.C. Effect of flooding stress on photosynthetic activities of momordica charantia. Plant Physiol. Biochem. 1994, 32, 479–485.
59. Hu, J.; Ren, B.; Dong, S.; Liu, P.; Zhao, B.; Zhang, J. Poor development of spike differentiation triggered by lower photosynthesis and carbon partitioning reduces summer maize yield after waterlogging. Crop J. 2022, 10, 478–489.
60. Huang, C.; Gao, Y.; Qin, A.; Liu, Z.; Zhao, B.; Ning, D.; Ma, S.; Duan, A.; Liu, Z. Effects of waterlogging at different stages and durations on maize growth and grain yields. Agric. Water Manag. 2022, 261, 107334.
61. Tian, L.; Li, J.; Bi, W.; Zuo, S.; Li, L.; Li, W.; 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. Agric. Water Manag. 2019, 218, 250–258.
62. Wakchaure, G.C.; Minhas, P.S.; Kumar, S.; Khapte, P.S.; Rane, J.; Reddy, K.S. Bulb productivity and quality of monsoon onion (Allium cepa L.) as affected by transient waterlogging at different growth stages and its alleviation with plant growth regulators. Agric. Water Manag. 2023, 278, 108136.
63. Kurokawa, Y.; Nagai, K.; Huan, P.D.; Shimazaki, K.; Qu, H.; Mori, Y.; Toda, Y.; Kuroha, T.; Hayashi, N.; Aiga, S.; et al. Rice leaf hydrophobicity and gas films are conferred by a wax synthesis gene (LGF1) and contribute to flood tolerance. New Phytol. 2018, 218, 1558–1569.
64. Siddiqui, M.N.; Mostofa, M.G.; Rahman, M.M.; Tahjib-Ul-Arif, M.; Das, A.K.; Mohi-Ud-Din, M.; Rohman, M.M.; Hafiz, H.R.; Ansary, M.M.U.; Tran, L.P. Glutathione improves rice tolerance to submergence: Insights into its physiological and biochemical mechanisms. J. Biotechnol. 2021, 325, 109–118.
65. Perata, P. Ethylene signaling controls fast oxygen sensing in plants. Trends Plant Sci. 2020, 25, 3–6.

66. Negi, S.; Sukumar, P.; Liu, X.; Cohen, J.D.; Muday, G.K. Genetic dissection of the role of ethylene in regulating auxin-dependent lateral and adventitious root formation in tomato. Plant J. 2010, 61, 3–15.
67. Liu, Z.; Hartman, S.; Van Veen, H.; Zhang, H.; Leeggangers, H.; Martopawiro, S.; Bosman, F.; De Deugd, F.; Su, P.; Hummel, M.; et al. Ethylene augments root hypoxia tolerance via growth cessation and reactive oxygen species amelioration. Plant Physiol. 2022, 190, 1365–1383.
68. Shin, S.Y.; Choi, Y.; Kim, S.G.; Park, S.J.; Park, J.S.; Moon, K.B.; Kim, H.S.; Jeon, J.H.; Cho, H.S.; Lee, H.J. Submergence promotes auxin-induced callus formation through ethylene-mediated post-transcriptional control of auxin receptors. Mol. Plant 2022, 15, 1947–1961.
69. White, M.D.; Kamps, J.; East, S.; Taylor Kearney, L.J.; Flashman, E. The plant cysteine oxidases from Arabidopsis thaliana are kinetically tailored to act as oxygen sensors. J. Biol. Chem. 2018, 293, 11786–11795.
70. Weits, D.A.; Giuntoli, B.; Kosmacz, M.; Parlanti, S.; Hubberten, H.M.; Riegler, H.; Hoefgen, R.; Perata, P.; Van Dongen, J.T.; Licausi, F. Plant cysteine oxidases control the oxygen-dependent branch of the N-end-rule pathway. Nat. Commun. 2014, 5, 3425.
71. Hartman, S.; Liu, Z.; Van Veen, H.; Vicente, J.; Reinen, E.; Martopawiro, S.; Zhang, H.; Van Dongen, N.; Bosman, F.; Bassel, G.W.; et al. Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. Nat. Commun. 2019, 10, 4020.
72. Gibbs, D.J.; Tedds, H.M.; Labandera, A.M.; Bailey, M.; White, M.D.; Hartman, S.; Sprigg, C.; Mogg, S.L.; Osborne, R.; Dambire, C.; et al. Oxygen-dependent proteolysis regulates the stability of angiosperm polycomb repressive complex 2 subunit VERNALIZATION 2. Nat. Commun. 2018, 9, 5438.
73. Gibbs, D.J.; Md Isa, N.; Movahedi, M.; Lozano-Juste, J.; Mendiondo, G.M.; Berckhan, S.; Marin-De La Rosa, N.; Vicente Conde, J.; Sousa Correia, C.; Pearce, S.P.; et al. Nitric oxide sensing in plants is mediated by proteolytic control of group VII ERF transcription factors. Mol. Cell 2014, 53, 369–379.
74. 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.
75. Peng, H.P.; Lin, T.Y.; Wang, N.N.; Shih, M.C. Differential expression of genes encoding 1-aminocyclopropane-1-carboxylate synthase in Arabidopsis during hypoxia. Plant Mol. Biol. 2005, 58, 15–25.
76. Nakano, T.; Suzuki, K.; Fujimura, T.; Shinshi, H. Genome-wide analysis of the ERF gene family in Arabidopsis and rice. Plant Physiol. 2006, 140, 411–432.

77. Xu, K.; Xu, X.; Fukao, T.; Canlas, P.; Maghirang-Rodriguez, R.; Heuer, S.; Ismail, A.M.; Bailey-Serres, J.; Ronald, P.C.; Mackill, D.J. Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 2006, 442, 705–708.
78. Yu, F.; Liang, K.; Fang, T.; Zhao, H.; Han, X.; Cai, M.; Qiu, F. A group VII ethylene response factor gene, ZmEREB180, coordinates waterlogging tolerance in maize seedlings. Plant Biotechnol. J. 2019, 17, 2286–2298.
79. Yin, D.; Sun, D.; Han, Z.; Ni, D.; Jiang, C.Z. PhERF2, an ethylene-responsive element binding factor, plays an essential role in waterlogging tolerance of petunia. Hortic. Res. 2019, 6, 83.
80. Luan, H.; Guo, B.; Shen, H.; Pan, Y.; Hong, Y.; Lv, C.; Xu, R. Overexpression of barley transcription factor HvERF2.11 in Arabidopsis enhances plant waterlogging tolerance. Int. J. Mol. Sci. 2020, 21, 1982.
81. Sun, D.; Nandety, R.S.; Zhang, Y.; Reid, M.S.; Niu, L.; Jiang, C.Z. A petunia ethylene-responsive element binding factor, PhERF2, plays an important role in antiviral RNA silencing. J. Exp. Bot. 2016, 67, 3353–3365.
82. 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.
83. Fukao, T.; Bailey-Serres, J. Ethylene—A key regulator of submergence responses in rice. Plant Sci. 2008, 175, 43–51.
84. Dawood, T.; Yang, X.; Visser, E.J.; Te Beek, T.A.; Kensche, P.R.; Cristescu, S.M.; Lee, S.; Flokova, K.; Nguyen, D.; Mariani, C.; et al. A Co-Opted hormonal cascade activates dormant adventitious root primordia upon flooding in solanum dulcamara. Plant Physiol. 2016, 170, 2351–2364.
85. Kuroha, T.; Nagai, K.; Gamuyao, R.; Wang, D.R.; Furuta, T.; Nakamori, M.; Kitaoka, T.; Adachi, K.; Minami, A.; Mori, Y.; et al. Ethylene-gibberellin signaling underlies adaptation of rice to periodic flooding. Science 2018, 361, 181–186.
86. Zhang, J.Y.; Huang, S.N.; Wang, G.; Xuan, J.P.; Guo, Z.R. Overexpression of Actinidia deliciosa pyruvate decarboxylase 1 gene enhances waterlogging stress in transgenic Arabidopsis thaliana. Plant Physiol. Biochem. 2016, 106, 244–252.
87. Vidoz, M.L.; Loreti, E.; Mensuali, A.; Alpi, A.; Perata, P. Hormonal interplay during adventitious root formation in flooded tomato plants. Plant J. 2010, 63, 551–562.
88. Wang, X.; Huang, M.; Zhou, Q.; Cai, J.; Dai, T.; Cao, W.; 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.

89. Jiang, Z.-H.; Zhua, J.-Q.; Yang, W.; Lia, M.-F.; Yua, Y. Effects of remedial measures implemented after waterlogging on cotton. In Proceedings of the Third International Conference on Intelligent System Design and Engineering Applications, Hong Kong, China, 16–18 January 2013; pp. 692–695.
90. Li, Y.; Sun, D.; Xu, K.; Jin, L.; Peng, R. Hydrogen sulfide enhances plant tolerance to waterlogging stress. Plants 2021, 10, 1928.
91. Zhong, Y.-H.; Guo, Z.-J.; Wei, M.-Y.; Wang, J.-C.; Song, S.-W.; Chi, B.-J.; Zhang, Y.-C.; Liu, J.-W.; Li, J.; Zhu, X.-Y.; et al. Hydrogen sulfide upregulates the alternative respiratory pathway in mangrove plant Avicennia marina to attenuate waterlogging-induced oxidative stress and mitochondrial damage in a calcium-dependent manner. Plant Cell Environ. 2023, 46, 1521–1539.
92. Hasnain, M.; Munir, N.; Abideen, Z.; Zulfiqar, F.; Koyro, H.W.; El-Naggar, A.; Caçador, I.; Duarte, B.; Rinklebe, J.; Yong, J.W.H. Biochar-plant interaction and detoxification strategies under abiotic stresses for achieving agricultural resilience: A critical review. Ecotoxicol. Environ. Saf. 2023, 249, 114408.
93. Zhou, W.; Yang, Y.; Zheng, C.; Luo, X.; Chandrasekaran, U.; Yin, H.; Chen, F.; Meng, Y.; Chen, L.; Shu, K. Flooding represses soybean seed germination by mediating anaerobic respiration, glycometabolism and phytohormones biosynthesis. Environ. Exp. Bot. 2021, 188, 104491.
94. Kaur, G.; Vikal, Y.; Kaur, L.; Kalia, A.; Mittal, A.; Kaur, D.; Yadav, I. Elucidating the morpho-physiological adaptations and molecular responses under long-term waterlogging stress in maize through gene expression analysis. Plant Sci. 2021, 304, 110823.
95. Sheng, L.; Meng, X.; Wang, M.; Zang, S.; Feng, L. Improvement in submergence tolerance of cherry through regulation of carbohydrate metabolism and pant growth by PsERF and PsCIPK. Appl. Biochem. Biotechnol. 2018, 184, 63–79.
96. Phukan, U.J.; Jeena, G.S.; Tripathi, V.; Shukla, R.K. MaRAP2-4, a waterlogging-responsive ERF from Mentha, regulates bidirectional sugar transporter AtSWEET10 to modulate stress response in Arabidopsis. Plant Biotechnol. J. 2018, 16, 221–233.
97. Xie, L.J.; Yu, L.J.; Chen, Q.F.; Wang, F.Z.; Huang, L.; Xia, F.N.; Zhu, T.R.; Wu, J.X.; Yin, J.; Liao, B.; et al. Arabidopsis acyl-CoA-binding protein ACBP3 participates in plant response to hypoxia by modulating very-long-chain fatty acid metabolism. Plant J. 2015, 81, 53–67.
98. Xie, L.J.; Zhou, Y.; Chen, Q.F.; Xiao, S. New insights into the role of lipids in plant hypoxia responses. Prog. Lipid Res. 2021, 81, 101072.
99. Zhou, Y.; Zhou, D.M.; Yu, W.W.; Shi, L.L.; Zhang, Y.; Lai, Y.X.; Huang, L.P.; Qi, H.; Chen, Q.F.; Yao, N.; et al. Phosphatidic acid modulates MPK3- and MPK6-mediated hypoxia signaling in Arabidopsis. Plant Cell 2022, 34, 889–909.

100. Bloom, A.J.; Sukrapanna, S.S.; Warner, R.L. Root respiration associated with ammonium and nitrate absorption and assimilation by barley. Plant Physiol. 1992, 99, 1294–1301.
101. Loque, D.; Ludewig, U.; Yuan, L.; Von Wiren, N. Tonoplast intrinsic proteins AtTIP2;1 and AtTIP2;3 facilitate NH3 transport into the vacuole. Plant Physiol. 2005, 137, 671–680.
102. Gupta, K.J.; Mur, L.A.J.; Wany, A.; Kumari, A.; Fernie, A.R.; Ratcliffe, R.G. The role of nitrite and nitric oxide under low oxygen conditions in plants. New Phytol. 2020, 225, 1143–1151.
103. Borella, J.; Becker, R.; Lima, M.C.; Oliveira, D.D.S.C.D.; Braga, E.J.B.; Oliveira, A.C.B.D.; Amarante, L.D. Nitrogen source influences the antioxidative system of soybean plants under hypoxia and re-oxygenation. Sci. Agric. 2019, 76, 51–62.
104. Da-Silva, C.J.; Do Amarante, L. Short-term nitrate supply decreases fermentation and oxidative stress caused by waterlogging in soybean plants. Environ. Exp. Bot. 2020, 176, 104078.
105. Pucciariello, C.; Perata, P. New insights into reactive oxygen species and nitric oxide signalling under low oxygen in plants. Plant Cell Environ. 2017, 40, 473–482.
106. Prakash, V.; Vishwakarma, K.; Singh, V.P.; Rai, P.; Ramawat, N.; Tripathi, D.K.; Sharma, S. NO and ROS implications in the organization of root system architecture. Physiol. Plant 2020, 168, 473–489.
107. Wany, A.; Kumari, A.; Gupta, K.J. Nitric oxide is essential for the development of aerenchyma in wheat roots under hypoxic stress. Plant Cell Environ. 2017, 40, 3002–3017.
108. Zottini, M.; Formentin, E.; Scattolin, M.; Carimi, F.; Lo Schiavo, F.; Terzi, M. Nitric oxide affects plant mitochondrial functionality in vivo. FEBS Lett. 2002, 515, 75–78.
109. Nabi, R.B.S.; Tayade, R.; Hussain, A.; Kulkarni, K.P.; Imran, Q.M.; Mun, B.-G.; Yun, B.-W. Nitric oxide regulates plant responses to drought, salinity, and heavy metal stress. Environ. Exp. Bot. 2019, 161, 120–133.
110. Zhang, Y.; Zhang, Y.; Liu, G.; Xu, S.; Dai, J.; Li, W.; Li, Z.; Zhang, D.; Li, C.; Dong, H. Nitric oxide increases the biomass and lint yield of field-grown cotton under temporary waterlogging through physiological and molecular regulation. Field Crops Res. 2021, 261, 107989.
111. Liu, C.; Lan, C.; Li, C.; Li, C.; Huang, J. Exogenous spermidine and calcium alleviate waterlogging stress in cherry tomato at the seedling stage. Sci. Hortic. 2023, 307, 111504.
112. Zhu, J.; Li, A.; Zhang, J.; Sun, C.; Tang, G.; Chen, L.; Hu, J.; Zhou, N.; Wang, S.; Zhou, Y.; et al. Effects of nitrogen application after abrupt drought-flood alternation on rice root nitrogen uptake and rhizosphere soil microbial diversity. Environ. Exp. Bot. 2022, 201, 105007.
113. Martínez-Arias, C.; Witzell, J.; Solla, A.; Martin, J.A.; Rodríguez-Calcerrada, J. Beneficial and pathogenic plant-microbe interactions during flooding stress. Plant Cell Environ. 2022, 45, 2875–2897.

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