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Review article

Waterlogging stress in plants: Unraveling the mechanisms and impacts on growth, development, and productivity

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ABSTRACT

Global climate change is closely related to changes in precipitation and flood events. In recent decades, waterlogging stress has become a greater threat to major crops and plants, ultimately affecting plant growth, development, and productivity. When plants are subjected to waterlogging, the oxygen supply in their roots is diminished, leading to hypoxic or anoxic conditions. To adapt to these conditions, plants go through a variety of physiological, morphological, and biochemical changes. This may involve the development of adventitious roots (ARs) and aerenchyma tissue, changes in the regulations of hormones, and shifts in metabolism. Specific genes and signaling pathways are essential for the coordination of these adaptive responses. Studies at the molecular level have significantly improved our understanding of the mechanisms by which plants respond to waterlogging stress. Identifying metabolic pathways and potential target genes is key to improving waterlogging tolerance in crops. Priority should be given to further research to uncover the gene regulatory networks and functional characterization of important genes involved in waterlogging tolerance. Furthermore, novel techniques, such as gene editing and breeding, can develop more resilient crop varieties to waterlogging stress. This review article discusses the current understanding of the molecular mechanisms underlying plant responses to waterlogging stress, as well as its effects on plant growth, development, and productivity. Furthermore, it discusses the potential future research challenges.

1. Introduction

The occurrence of adverse environmental conditions, such as extreme temperatures and irregular water supply have become more intense and unpredictable due to climate change, which can hinder the growth and survival of plants (Yeung et al., 2018). To withstand such conditions, different mechanisms have been developed by plants to adjust their metabolism to adapt to changing environments for maintaining growth and development. Plants must adapt to the stress and recover once it is removed. This is specifically apparent in the case of plants that recover from flooding. Flooding is an abiotic stress, which has been increasing globally, significantly affecting crop yields and plant biodiversity (Bailey-Serres et al., 2012b; Hirabayashi et al., 2013; Voesenek and Bailey-Serres, 2015). Most of the terrestrial plants, including almost all important crops, are vulnerable to partial to total submersion of their aboveground organs. When plants are subjected to waterlogging, their aerial organs are affected, causing a significant decrease in gas diffusion rates, and ultimately hindering respiration and photosynthesis. Moreover, the muddy floodwaters block light access, thereby inhibiting the ability of plants to carry out photosynthesis. Finally, plants are retorted in their growth due to the carbon and energy crisis (Yeung et al., 2018). As floodwaters recede, plants that have adapted to low oxygen and light levels in murky waters suddenly encounter aerial conditions. This sudden transition to a highly illuminated and oxygen-rich environment imposes further stresses on the plant, such as oxidative stress and paradoxical dehydration due to root

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malfunction, often leading to plant desiccation (Maurel et al., 2010; Yeung et al., 2018).

Floods or waterlogging have been increasing recently all over the world due to inadequate drainage systems, accelerated land degradation, and climate change (van Veen et al., 2013). In general, flooding stress involves submergence stress, where the plant is completely submerged or underwater, and waterlogging stress, where the leaves and stems of the plant are partially submerged (Nishiuchi et al., 2012). In submerged states, plants experience harsh environmental conditions like low light intensity, limited gas exchange, increased vulnerability to fungal diseases, and impaired soil nutrient uptake (Nishiuchi et al., 2012; Ram et al., 1999). In anaerobic conditions, plant cells convert to anaerobic respiration and ethanol fermentation pathways (Ricard et al., 1994). The reduction in adenosine triphosphate (ATP) production and resulting energy deficiency caused by transformation can lead to cell death or limit energy-intensive processes, including photosynthesis and growth (Malik et al., 2011) and nutrient absorption (Colmer and Greenway, 2011). Plants have developed diverse mechanisms to deal with the stress caused by waterlogging. One of the primary adaptations is the development of distinct root structures, including adventitious roots (ARs), aerenchyma, and hypertrophic lenticels (Eysholdt-Derzsó and Sauter, 2019). Furthermore, plants show physiological responses like the activation of anaerobic metabolic pathways for generating energy in oxygen-deprived conditions. Additionally, they have a role in the regulation of hormone levels in coordinating adaptive responses to waterlogging stress. Moreover, it has been shown that plants have the potential to alter their growth patterns, slow down vertical growth, and invest resources in lateral expansion in order to improve stability and nutrient uptake (Pan et al., 2021). Plants use these mechanisms to withstand the diverse effects of waterlogging stress, thereby demonstrating their ability to adapt to challenging environmental circumstances (Zhou et al., 2020). This review elucidates recent progress in our understanding of the mechanism by which plants respond to waterlogging. The molecular and physiological mechanisms that allow plants to survive in waterlogged environments have been discussed. Finally, research directions in this field are provided.

2. Effects of waterlogging stress on plant development and productivity

Water is essential for plant survival, but an excessive amount of water due to waterlogging or flooding can cause stress and hinders the exchange of gases between the soil and the atmosphere. This leads to adverse effects on various developmental stages of plants during their entire lifecycle, ultimately leading to reduced crop yield (Striker and Colmer, 2017; Wang et al., 2017) (Fig. 1). Globally, floods were the cause of nearly two-thirds of crop losses between 2006 and 2016, worth billions of dollars (FAO, 2018).

Waterlogging causes the closure of leaf stomata, leading to reduced photosynthetic activity due to the degradation of chlorophyll and leaf senescence (Yan et al., 2018). Submergence, waterlogging, or flooding has a direct effect on oxygen diffusion in plant tissues. This causes a hindrance in the exchange of oxygen and mitochondrial respiration between cells, ultimately disrupting the usual physiological and biochemical activities of plants (Liu et al., 2012; Voesenek and Bailey-Serres, 2013). Restricted gaseous exchange can also affect plant waterlogging tolerance by causing rapid accumulation or degradation of plant hormones (Kuroha et al., 2018).

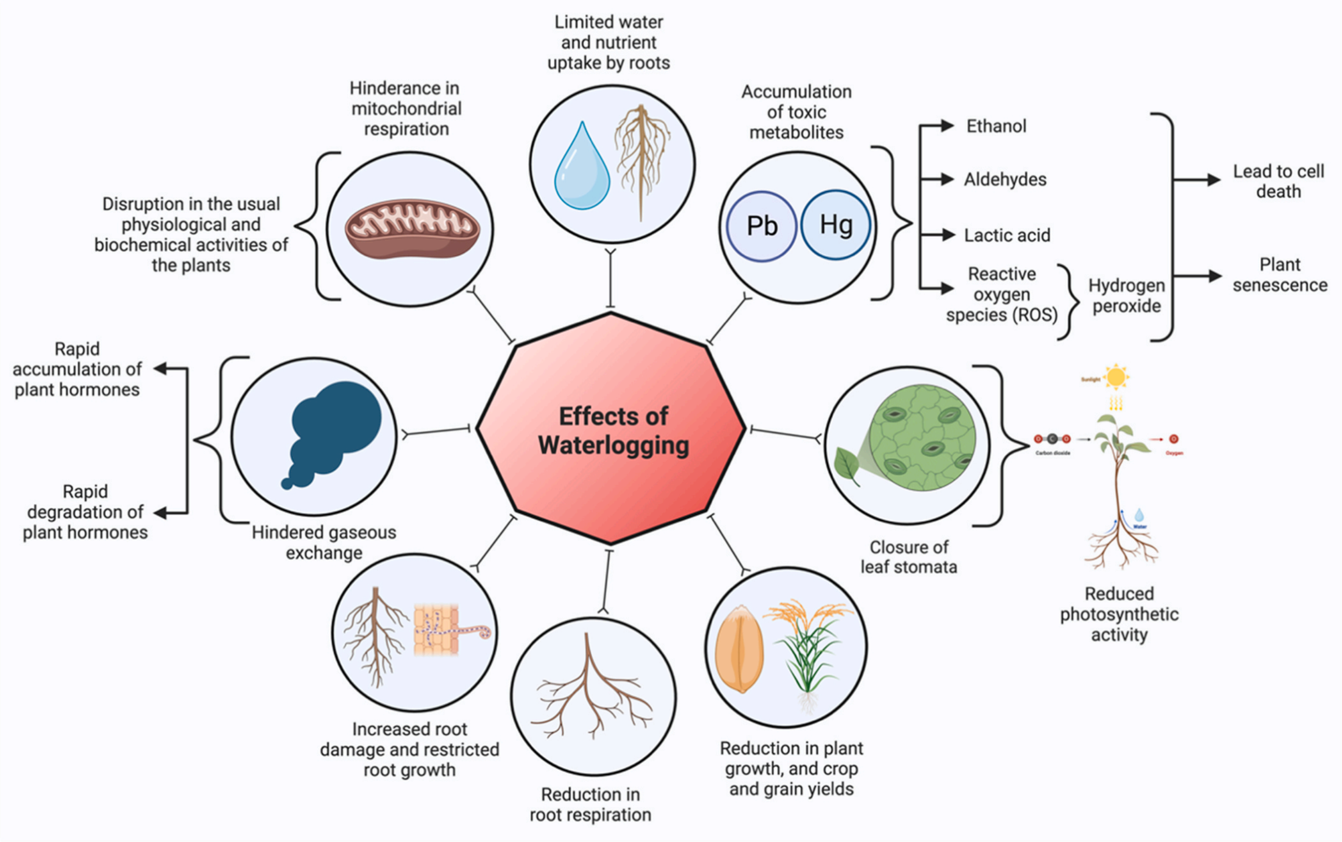

Fig. 1. Effects of waterlogging on plants/crops. Waterlogging causes the closure of leaf stomata, resulting in reduced photosynthetic activity due to chlorophyll degradation and leaf senescence. Prolonged waterlogging can result in the accumulation of toxic metabolites like ethanol, aldehydes, and lactic acid and an increase in ROS, such as hydrogen peroxide. These toxic substances can cause cell death and plant senescence. Waterlogging can also affect root and plant growth, resulting in reduced grain yield. Moreover, waterlogging affects mitochondrial respiration, which in turn disrupts the usual physiological and biochemical activities of plants. Furthermore, waterlogging hinders the gaseous exchange, which then degrades the plant hormones.

In a waterlogged environment, roots may not be able to grow properly due to the lack of oxygen, which can lead to root death. As a result, the ability of plants to absorb water and nutrients and then transport them to other parts of the plant is restricted, which can negatively impact its growth and development (Herzog et al., 2016) and final yield (Zheng et al., 2009). In addition, it causes a reduction in leaf water potential, leaf nitrogen content, CO_2 assimilation rate, stomatal conductance, and photosynthesis rate. It may also cause accelerated leaf senescence and chlorosis (Zheng et al., 2009). Waterlogging-sensitive plants experience a decrease in their photosynthetic machinery, which leads to the overproduction of reactive oxygen species (ROS). This can result in the degradation of cellular structures and severe oxidative damage, which in turn interferes with normal metabolism (Herzog et al., 2016). ROS cause lipoperoxidation phenomena, which causes damage to cell membrane, enzymes, nucleic acids, and proteins, resulting in cell death (Bali and Sidhu, 2019; Pais et al., 2023).

A study was conducted to check the impacts of waterlogging stress on yield and leaf physiology in two soybean varieties: Kenfeng 14, which is tolerant to waterlogging, and Kenfeng 16, which is sensitive to it. The study also aimed to investigate whether uniconazole (S3307) could alleviate the detrimental effects of waterlogging stress on growth and productivity. The results demonstrated that waterlogging stress increased the activity of antioxidant enzymes while simultaneously decreasing the levels of non-enzymatic antioxidants, including ascorbic acid (AA) and glutathione (GSH). Overall, S3307 improved the physiological characteristics of soybean leaves and increased yield by enhancing antioxidant defense mechanisms, which prevented lipid peroxidation caused by waterlogging stress. Therefore, S3307 may have the potential to alleviate some of the damages caused by waterlogging stress (Wang et al., 2022).

In another study in two spring maize (*Zea maize* L.) hybrids (Demeiya1 and Keyu16), the effects of waterlogging stress were investigated on grain yield, photosynthetic characteristics, and dry matter accumulation. Subsurface waterlogging and waterlogging treatments were applied at various growth stages (V3, V6, and VT) for varying durations (3, 6, and 9 days for waterlogging and 5, 10, and 15 days for subsurface waterlogging). The findings revealed that the severity of waterlogging stress was influenced by waterlogging duration and the growth stage. The most significant impact of waterlogging stress was recorded at the V3 stage, followed by the V6 and VT stages. The study found that an increase in waterlogging duration resulted in a decrease in the activities of PEP carboxylase and RuBP carboxylase, as well as the rates of photosynthesis (Pn), transpiration (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (Ci). This ultimately led to a decrease in the total dry matter weight and spring maize grain yield reduction. These findings highlight the importance of managing waterlogging stress in order to maximize maize crop yield (Tian et al., 2019). However, despite the adverse effects of waterlogging, plants have the ability to adapt to the damage caused by this stress through a variety of strategies (Yin et al., 2019).

3. Physiological mechanisms involved in waterlogging stress response

3.1. Oxygen deprivation and energy crisis

Flooding has a significant impact on agricultural production areas around the world. Waterlogging is often caused by external environmental factors, including heavy rainfall, river flooding, storms, over-irrigation, and poor soil drainage (Sundgren et al., 2018) (Fig. 2). Excessive oxygen deficiency caused by waterlogging negatively affects root and shoot growth, nutrient uptake, hydraulic conductivity, and photosynthesis. Oxygen depletion is a major source of harm, as the oxygen diffusion rate in waterlogged soils is 10,000 times lower than in well-drained soils (Hossain and Uddin, 2011). When oxygen levels are low, the respiration rate and ATP production in plants decrease, leading to a reduction in root growth (Bailey-Serres and Voesenek, 2010). When plant roots are waterlogged, they experience decreased respiration and a loss of ATP synthesis, which can cause a wilting (Tong et al., 2021). In oxygen-deprived conditions, plants suffer from an energy crisis, leading

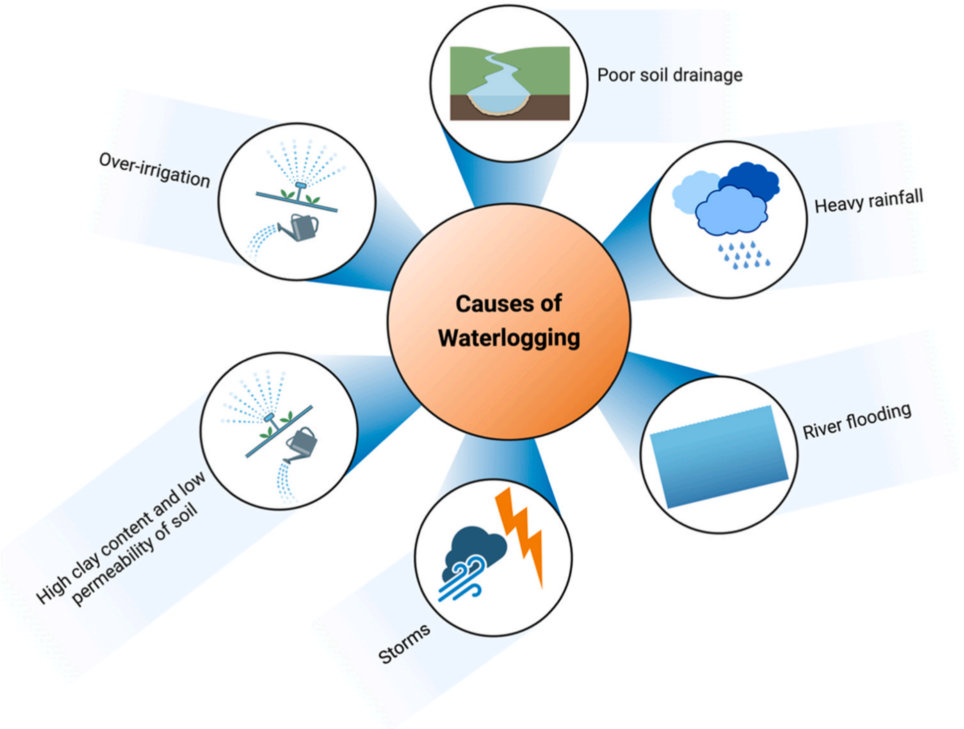

Fig. 2. Causes of waterlogging. Waterlogging is often caused by external environmental factors, including storms, river flooding, heavy rainfall, poor soil drainage, over-irrigation, and high clay content and low soil permeability.

to the overproduction of ROS that includes hydrogen peroxide (H_2O_2) and superoxide (Sun et al., 2018). Due to oxygen demand and limited gas exchange, plants are subjected to reduced O_2 during flooding. The concentration of oxygen in the atmosphere is close to 20.95%. However, due to the low diffusion coefficient in water, consequently, the supply of oxygen to underwater tissues is severely restricted (Pedersen et al., 2013), which results in decreased root activity, restricted root respiration, and energy shortage (van Veen et al., 2014).

Waterlogging is primarily caused by a deficiency of oxygen in the rhizosphere. It occurs when the soil pore space is filled with water, which causes either complete oxygen absence (anoxia) or partial oxygen absence (hypoxia) (Ricard et al., 1994). Hypoxia occurs in soil when the oxygen level falls below the optimal level, whereas anoxia typically refers to a total lack of oxygen (Ahmed et al., 2013; Hossain and Uddin, 2011). The anaerobic environment caused by hypoxia in the rhizosphere inhibits oxygen uptake, ultimately resulting in plant death (Fukao et al., 2019). Low oxygen levels substantially affect most developmental stages of plants and convert metabolic pathways related to energy from aerobic respiration to anaerobic fermentation (Xuewen et al., 2014). Glycolysis and ethanol fermentation can help maintain the production of energy to some extent during hypoxia caused by waterlogging stress. However, prolonged waterlogging can result in accumulating toxic metabolites, such as ethanol, aldehydes, and lactic acid, as well as an increase in ROS like hydrogen peroxide. These toxic substances can lead to plant senescence and cell death (Zhang et al., 2017a).

3.2. *Reactive oxygen species (ROS) and oxidative stress*

During normal physiological activities, plants generate ROS, including hydroxyl radicals (·OH), superoxide anion radicals (O_2^-), singlet oxygen (O_2), and H_2O_2. These serve as signal transmitters for regulating the expression of proteins and genes in plant cells. The elimination and production of ROS are constantly balanced, maintaining a dynamic equilibrium (Waszczak et al., 2018). When a plant is under stress, its balance is disrupted, which results in the disruption of the physiological and biochemical mechanisms of the plant cell membrane and an increase in ROS production (Polle, 2001; Wu et al., 2022). In order to prevent cell damage, plants activate their antioxidant defense system in response to waterlogging stress. The antioxidant defense system consists of enzymatic and non-enzymatic antioxidants. The enzymatic antioxidants include peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), dehydroascorbate reductase glutathione (DHAR), monodehydroascorbic acid reductase (MDHAR), and glutathione reductase (GR). The nonenzymatic antioxidants include AA, glutathione (GSH), tocopherols (lipid soluble), and carotenoids (Laxa et al., 2019; Wu et al., 2022).

Plants recovering from flooding encounter oxidative stress (Yeung et al., 2018) and need to remobilize nutrients to restore their normal homeostatic conditions (Tsai et al., 2016). A number of traits have evolved in flooding-tolerant species to enhance the oxygen supply and metabolic changes for compensating the limited oxidative ATP synthesis via ATP synthesis at the substrate level and recovery of NAD^+ in the fermentation (Mustroph et al., 2014). In a study, the barley (*Hordeum vulgare*) cultivar Naso Nijo, which is sensitive to waterlogging, showed a lower uptake of potassium in the mature zone than the tolerant cultivars TX9425 and CM72. However, after hypoxia treatment, the amount of potassium efflux in sensitive cultivars was higher than in tolerant cultivars in the elongation zone (Gill et al., 2018), indicating the ability of the root to retain more potassium is dependent on its tolerance to hypoxia.

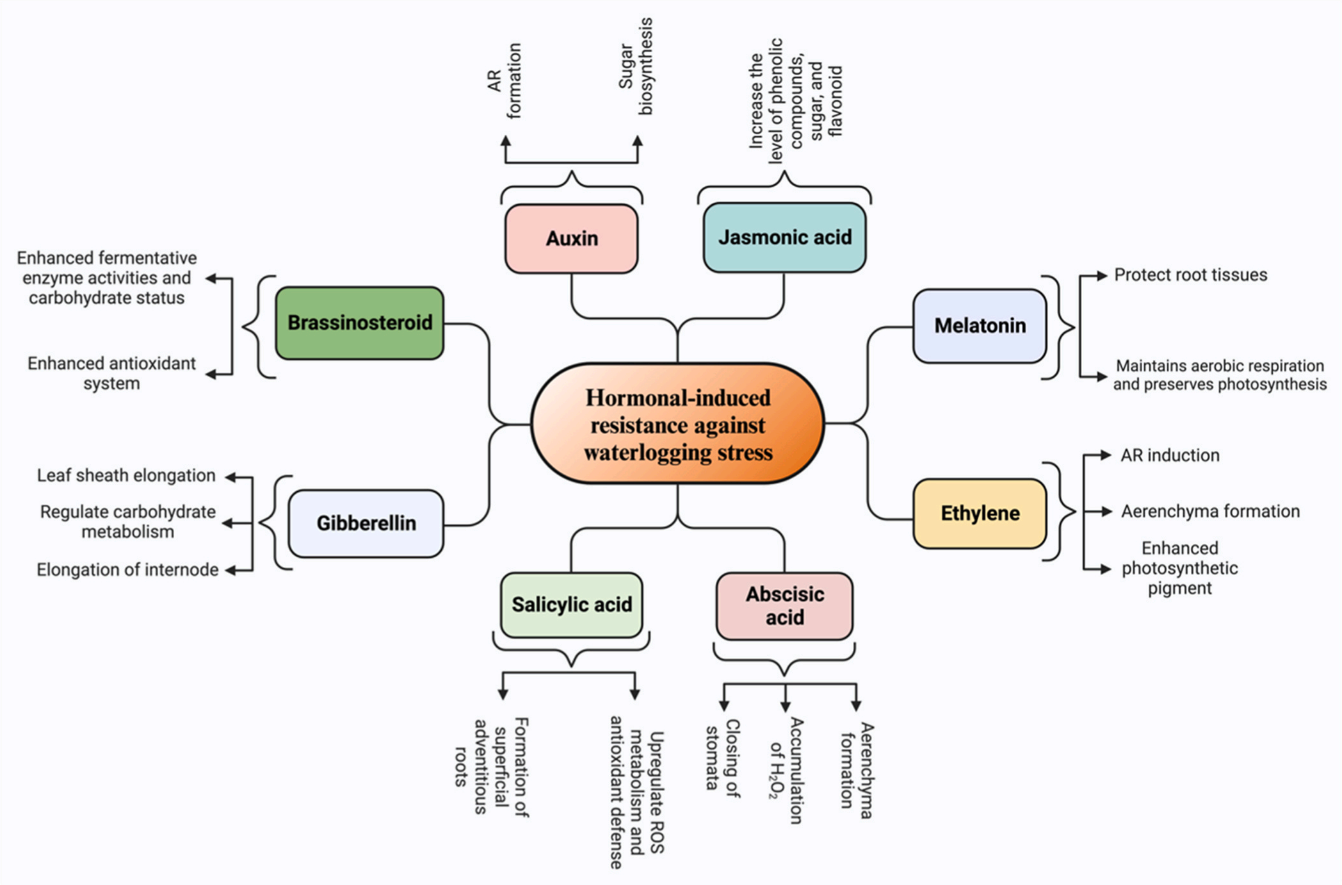

Fig. 3. Hormonal-induced resistance against waterlogging stress in plants.

4. Role of phytohormones in modulating waterlogging response

Phytohormones play an essential role in all molecular, morphological, biochemical, anatomical, and signaling mechanisms for plant survival under oxygen-deprived stress conditions (Bashar et al., 2019) (Fig. 3, Table 1). Plants regulate their response to waterlogging through a complex signaling process involving synthesizing and transporting plant hormones. These hormones are important endogenous signals that play crucial roles in the waterlogging stress tolerance mechanism (Yamauchi et al., 2020). When plants are waterlogged, their growth is affected in several ways. Waterlogging inhibits the exile root elongation and lateral root formation. However, exile promotion, surface ARs emergence, and aerenchyma formation are associated with increased expression levels of *ACS7* and *ACO2* genes, which are responsible for the production of ethylene in both the main root and lateral roots. The emergence of ARs from waterlogged stem nodes is linked with increased GA and IAA levels but decreased levels of abscisic acid (ABA) and cytokinin (Nguyen et al., 2018).

4.1. Jasmonic acid (JA)

Jasmonic acid (JA) is a substance that regulates endogenous growth, which was first identified as a hormone that responds to stress in higher plants (Wang et al., 2020a). In soybean, a study found that foliar application of MeJA on leaves increased tolerance to water stress. The application increased the levels of phenolic compounds, flavonoids, and sugars (Mohamed and Latif, 2017). Under water stress conditions, the proline accumulation is a response that does not depend on ABA. Two Arabidopsis (*Arabidopsis thaliana* L.) lines, including JA-deficient (*jar1–1*) and JA-insensitive (*jai1*) were found to accumulate similar amounts of proline (De Ollas et al., 2015), indicating that the JA and ABA signaling pathways work together for regulating each other's responses to a variety of abiotic stresses, such as water, cold, drought, and stress (Wang et al., 2020a). When Arabidopsis was under water stress, a specific transcription factor (TF) known as octadecanoid-responsive AP2/ERF-domain 47 (*ORA47*) functioned as a gene target in the biosynthesis of JA and ABA (Chen et al., 2016).

4.2. Salicylic acid (SA)

Salicylic acid (SA) is an endogenous plant hormone that regulates plant growth and development, disease resistance, photosynthesis, and plant tolerance to various abiotic stresses (Wang et al., 2021). A study was conducted in soybean (*Glycine max* cv. Sohag) to check the positive effects of foliar application of SA and kinetin (KN) in order to improve resistance against waterlogging stress by upregulation of antioxidant defense and ROS metabolism. The exogenous application of SA and KN reduced the proline, malondialdehyde (MDA), and H_2O_2 contents, and leaf electrolyte leakage under waterlogging stress conditions. Additionally, the application of SA and KN was observed to enhance the activities of MDHAR, DHAR, GR, POD, glutathione peroxidase (GPX), CAT, glyoxalase I (Gly I), and glyoxalase II (Gly II) under waterlogging stress conditions (Hasanuzzaman et al., 2022).

Another study investigated how SA regulates the morphological adaptive responses in wheat (*Triticum aestivum* L.) plants subjected to waterlogging stress conditions. Under the conditions of waterlogging stress, the application of SA to water plants promoted the formation of superficial ARs and axial roots but inhibited their elongation, resulting in the development of a shallow root system. SA was found to be involved in promoting the growth of superficial ARs and axial roots in wheat plants under waterlogged conditions in an ethylene-independent manner (Koramutla et al., 2022).

4.3. Brassinosteroids (BRs)

Brassinosteroids (BRs) are plant hormones that play an essential function in plant growth and development against various stresses (Vardhini, 2017). In a study, BRs supplementation increased the resistance against waterlogging stress in oilseed rape (*Brassica napus*) (Liang and Liang, 2009). (Lu et al., 2006) discovered that BL application enhanced seedling growth and resistance against the waterlogging stress in soybean. In another study on cucumber (*Cucumis sativus* L.) seedlings, BL treatment modulated ATPase activity, polyamines, and inorganic ion content in the roots under the conditions of hypoxia stress. In another study on cucumbers, the application of 24-epibrassinolide (24-epiBL) resulted in increased activities of the antioxidant system and anaerobic respiratory enzyme under hypoxia stress conditions in roots. Further studies also discovered that 24-epiBL application to the cucumber roots

Table 1
Role of phytohormones in mediating resistance to waterlogging stress conditions in plants.

Phytohormone	Plant/crop species	Response	Reference
Jasmonic acid (JA)	Soybean (*Glycine max* L.)	Promoted plant growth under waterlogging stress through the activation of proteins related to stress	(Kamal and Komatsu, 2016)
Abscisic acid (ABA)	Bittersweet Nightshade (*Solanum dulcamara* L.)	ABA inhibited the development of AR, which results in enhanced sensitivity	(Dawood et al., 2016)
Methyl Jasmonate (MeJa)	Soybean (*G. max* L.)	Increased resistance to water stress. Increases the levels of flavonoids, sugars, and phenolic compounds, sugars	(Mohamed and Latif, 2017)
Melatonin (MT)	Apple (*Malus baccata* L.)	The plant exhibited enhanced aerobic respiration as a mechanism to mitigate the detrimental impacts of waterlogging stress	(Zheng et al., 2017)
Ethephon (ETP; donor source of ethylene)	Soybean (*G. max* L.)	Increased the contents of endogenous GA_s and enhanced the pigments involved in photosynthesis. ETP application induced the initiation of ARs, increased root surface area, and substantially increased glutathione transferases expressions and activity of relative glutathione	(Kim et al., 2018)
Melatonin (MT)	Alfalfa (*Medicago sativa* L.)	Increased the productions of AR and endogenous melatonin	(Zhang et al., 2019b)
1-Aminocyclopropane-1-carboxylic acid (ACC)	Cucumber (*Cucumis sativus* L.)	Enhance plant development under waterlogging stress and improved AR formation	(Qi et al., 2019)
Ethephon	Barley (*Hordeum vulgare* L.)	Improved the formation of aerenchyma at root tips and delayed wilting caused by waterlogging	(Shiono et al., 2019)
Melatonin (MT)	Wheat (*Triticum aestivum* L.)	Exhibited enhanced water status and less oxidative damage, which results in enhanced photosynthetic capacity and enhanced tolerance to the waterlogging stress	(Ma et al., 2022)
Salicylic acid (SA)	Wheat (*T. aestivum* L.)	Promotes the formation of ARs and aerenchyma	(Koramutla et al., 2022)
Salicylic acid (SA)	Soybean (*G. max* cv. Sohag)	Upregulated ROS metabolism and antioxidant defense	(Hasanuzzaman et al., 2022)
Brassinosteroids (BRs)	Maize (*Zea maize* L.)	Increased shoot dry matter, root dry matter, root volume, root length, net photosynthetic rate, and number of living cortical cells in seminal roots	(Salah et al., 2022)

enhanced the activities of fermentative enzyme and carbohydrate status under hypoxia conditions (Kang et al., 2009).

In a study, (Salah et al., 2022) investigated the impact of the application of exogenous brassinolide (BRs) and spermidine (Spd) on maize (Maize cultivar Xingken-6 (XK-6)) seedling adaptation against severe waterlogging stress. The treatments of BRs and Spd effectively alleviated the adverse effects of waterlogging by increasing shoot dry matter, root dry matter, root volume, root length net photosynthetic rate, and a number of living cortical cells in seminal roots. Additionally, BRs and Spd were found to decrease the area of root aerenchyma and the production of ROS throughout the growth stages.

4.4. Gibberellin (GA)

Gibberellin (GA) is a plant hormone that plays a vital role in plant growth and development and responds to various stresses. When plants experience flash floods, those tolerant to the submergence typically limit their growth by activating the GA signal (Fukao and Bailey-Serres, 2008; Jia et al., 2021). GA has been observed to play a crucial role in stem elongation of pants (Zhou et al., 2016). Under submergence stress, an increase of active GA (GA1) led to leaf sheath elongation in lowland rice (*Oryza sativa* L.) (Dubois et al., 2011). For deep-water rice, submergence was found to induce the expression of a GA biosynthesis gene, *SD1* (*SEMIDWARF1*), which is controlled by an ethylene-responsive TF known as *OsEIL1a*, and increased GA levels promoted internode elongation (Kuroha et al., 2018). In a study, two genes, *ACE1* and *DEC1*, were found to be involved in regulating the elongation of internode together with GA in an antagonistic manner. ACE1, as an unknown function protein, was found to regulate the elongation of internode along with GA. Both genes were found to be involved in acclimation to submergence stress in deep-water rice (Nagai et al., 2020). GA helps plants cope with flooding stress by regulating carbohydrate metabolism and internode regulation or elongation of other organs (Jia et al., 2021). Additionally, GA helps plants in coping with shade and flooding stress (Li et al., 2017).

4.5. Ethylene

Ethylene is a plant gaseous hormone that plays a crucial role in waterlogging stress. However, it diffuses at an extremely low rate in plants (Hartman et al., 2019). To produce ethylene, the plant first produces a large amount of 1-aminocyclopropane-1-carboxylic acid (ACC) under hypoxic conditions. This process is catalyzed by ACC synthase (ACS). The ACC oxidase (ACO) is involved in catalyzing the conversion of ACC to ethylene, but oxygen is needed for this process. Therefore, the ACC must be transferred from the root system environment to the lower part of the aerobic region of the plant, where it can undergo oxidation, resulting in the production of ethylene (Pan et al., 2021).

Studies have shown that ethylene induces the formation of aerenchyma in the root of maize and wheat when they are exposed to low oxygen conditions by increasing cortical cell death (Nguyen et al., 2018; Yamauchi et al., 2014). To prevent wilting in barley caused by waterlogging, ethephon; an ethylene-releasing agrochemical, has been discovered to improve the formation of aerenchyma at root tips and delayed wilting caused by waterlogging (Shiono et al., 2019).

A study was conducted to identify physiological mechanisms during waterlogging stress in soybean plants. The study applied various phytohormones, including ethephon, ABA, GAs, indole-3-acetic acid, JA, SA, and KN to plants. Compared to untreated plants, the application of ethephon mitigated waterlogging stress, enhanced the photosynthesis pigment, and increased endogenous GA_s contents. The application of ethephon had several positive effects on the plants. It increased root surface area, induced ARs initiation, and substantially enhanced the relative glutathione activity and expressions of glutathione transferases in comparison to non-ethephone-treated plants (Kim et al., 2018).

4.6. Abscisic acid (ABA)

ABA has a variety of roles in the regulation of stomata guard cell size. This helps to regulate the water potential in plants; therefore, ABA has been considered an important hormone in responses to water stress (He et al., 2018; Tong et al., 2021). Under the conditions of waterlogging stress, ABA is produced in the root system and regulates the stomatal opening and closing (Wu et al., 2022). ABA contributes to the formation of root aerenchyma under waterlogging. In wheat, gene expression levels in ABA biosynthesis and stem node ABA content were observed to be reduced in the ARs of waterlogged wheat (Nguyen et al., 2018). Similarly, in both resistant and susceptible barley varieties, ABA content was found to be reduced in the roots and leaves after 3-weeks of waterlogging treatment, with tolerant varieties exhibiting a greater reduction (Luan et al., 2018). A study on Arabidopsis discovered that the genes involved in ABA biosynthesis were upregulated in leaves and downregulated in the roots during waterlogging stress (Hsu et al., 2011). Additionally, the concentration of ABA in the xylem sap in flooded tomato roots was found to be reduced (Janowiak et al., 2010). It was hypothesized that ABA accumulates in the leaves of flooded plants due to reduced translocation of photoassimilates out of leaves. Additionally, the roots do not serve as a source of ABA because majority of them collapse rapidly and die within the first few days of flooding (JACKSON et al., 1988; Zhao et al., 2021).

4.7. Auxin

The hormone Auxin (IAA) is crucial for plant growth and development (Lv et al., 2019). During waterlogging, ethylene production promotes the transport of auxin. In turn, the auxin accumulation can lead to the biosynthesis of ethylene, which further stimulates the transport of auxin to flooded plant parts. This accumulation of auxin has the ability to induce ARs through the initiation of cell division (Lv et al., 2019). The ARs growth was inhibited when auxin transport inhibitor 1-naphthylphthalamic acid (NPA) was exogenously applied after flooding in tobacco (McDonald and Visser, 2003), cucumber (Qi et al., 2019), and tomato (*Solanum lycopersicum* L.) (Vidoz et al., 2010).

4.8. Melatonin

Melatonin is an important plant hormone that has been discovered to play a crucial role in waterlogging stress (Moustafa-Farag et al., 2020). According to a study by (Zheng et al., 2017), melatonin helps apple seedlings to withstand waterlogging, which maintains aerobic respiration and preserves photosynthesis by repressing ROS burst and subsequent mitochondrial degradation. Another model in alfalfa (*Medicago sativa* L.) was suggested by the interaction with or direct regulation of metabolic pathways of polyamines (Pas) and ethylene. Melatonin reduces ethylene production by downregulating ethylene synthesis-associated genes and alleviating growth inhibition, premature senescence, and chlorosis caused by waterlogging (Zhang et al., 2019a). Melatonin then increases the levels of polyamines by enhancing the gene expression of the polyamine-metabolizing enzymes (Zhang et al., 2019a).

In another study, melatonin was found to protect growth and grain yield loss of wheat from waterlogging stress. Two wheat cultivars, namely Yangmai 18 and Yannong 19, were subjected to 7 days of soil waterlogging during flowering. The exogenously applied melatonin was found to protect the root tissues of wheat from oxidative damage induced by waterlogging through increasing antioxidant enzymes and maintaining leaf photosynthesis. Melatonin-treated plants exhibited less oxidative damage and improved water status, which contributed to maintaining a higher photosynthetic capacity, thus enhancing the wheat tolerance to the waterlogging (Ma et al., 2022).

In another study by (Ahmad et al., 2022), maize seedlings were treated with 100 μM melatonin and potassium nitrate (KNO_3) via seed soaking and foliar application. Melatonin with KNO_3 substantially enhanced biochemical parameters and plant growth under waterlogging stress conditions. Moreover, their applications enhanced chlorophyll content, plant growth characteristics, and the net photosynthetic rate at variable rates. Additionally, treatments of melatonin and KNO_3 decreased the accumulation of MDA and H_2O_2 and reduced the activity of alcohol dehydrogenase and pyruvate decarboxylase. However, their treatment increased the soluble protein content and enzymatic activities.

5. Physiological and biochemical adaptations by plants

Understanding how plants respond to unexpected flooding at a biochemical and physiological level is crucial for developing new flood-resistant crop varieties (Jia et al., 2021). The earlier investigations have highlighted the significance of enhancing crop yield by creating plants capable of withstanding flooding conditions (Komatsu et al., 2021). To improve gas exchange, the plants which are tolerant to flooding form gas films (Herzog et al., 2018), aerenchyma (Steffens et al., 2011; Yamauchi et al., 2013), and ARs (Lorbiecke and Sauter, 1999) or induce petiole elongation or stem (Millenaar et al., 2005) and hyponastic growth (Pierik et al., 2005) for raising leaves above the water surface. The development of ARs in response to flooding is a common adaptive mechanism observed in various plants, including deep-water rice (Lorbiecke and Sauter, 1999), tamarack (*Larix laricina*) (Calvo-Polanco et al., 2012), *Rumex palustris*, and tomato (Vidoz et al., 2010). During the post-submergence phase, ARs facilitate important functions, such as gas exchange, uptake of water, minerals, and $O_{2,}$ and plant anchoring. While nodal AR initiation is a normal developmental process in rice, AR formation is induced by environmental cues, specifically the trapping of ethylene during flooding, which triggers the emergence of AR primordia (Eysholdt-Derzsó and Sauter, 2019).

One of the most important adaptation responses is the activation of fermentative metabolism to generate ATP, which enhances the activity of alcohol dehydrogenase (ADH) and expression levels of ADH1 in Arabidopsis (Sun et al., 2018). A study was conducted to determine the anatomical and transcriptional differences between two different maize inbreds, I110 (susceptible) and I172 (tolerant). Under waterlogging stress, the I110 inbred was found to reduce dry matter translocations from leaves and stems to ears. This resulted in inadequate sink capacity and insufficient grain filling, resulting in a significant decrease in grain yield. Within 48 hours in I172, the formation of aerenchyma cells enabled hypoxia tolerance. In I172 inbred, increased expression of alanine-aminotransferase, pyruvate kinase, ubiquitin-activating enzyme E1, and putative mitogen-activated protein kinase indicated that genes involved in carbon metabolism, signal transduction, and protein degradation provided adaptive mechanisms in response to waterlogging (Kaur et al., 2021).

6. Genetic approaches and breeding for waterlogging tolerance

There are a growing number of flooding incidents all around the world due to climate change; hence, it is crucial to develop crop varieties with a greater tolerance to the conditions of low oxygen (Bailey-Serres et al., 2012a; Voesenek and Bailey-Serres, 2013). While aquatic flowering plants have the ability to show tolerance against submergence, a few cultivated crop species have been observed to exhibit low-oxygen tolerance mechanisms. Plants respond to waterlogging and other related stress factors by changing their gene expression, that are tightly regulated at multiple levels, ranging from the epigenetic modifications (Tsuji et al., 2006) to the translational (Juntawong et al., 2014) and transcriptional regulation (Lee et al., 2011; Mustroph et al., 2010). Research regarding waterlogging stress has been conducted in rice (Loreti et al., 2016), Arabidopsis (Sun et al., 2018), barley (Zhang et al., 2017b), rapeseed (Xu et al., 2016), and other plant species (Dossa et al., 2019). Many studies have shown that different genes significantly respond to waterlogging stress in plants (Table 2).

Rice is one of the few crops that can tolerate flooding, but extended periods of complete submergence can prevent seedling growth (Ma et al., 2020). Most plants are susceptible to flooding (BAILEY-SERRES and Colmer, 2014), and they have evolved various coping mechanisms to withstand such stressful conditions (Hattori et al., 2009a). Rice grown in semi-aquatic environments exhibits two opposing strategies, which are linked with flooding evasion, escape, or quiescence (Bailey-Serres et al., 2012a; Bailey-Serres and Voesenek, 2008). The SUBMERGENCE1A (SUB1A) locus controls a quiescence response that suppresses growth and induces fermentative metabolism until stress is alleviated (Bailey-Serres et al., 2010). Standard breeding lines lack the SUB1A locus, which was originally discovered in lowland rice varieties that were resistant to the submergence from the Indian subcontinent and is now commonly used in breeding programs (Bailey-Serres et al., 2010; Xu et al., 2006).

On the other hand, SNORKEL1 (SK1) and SK2 loci regulate the enhanced elongation of the internode that confers flood tolerance to rice varieties grown in deep water (Hattori et al., 2009a). Under the conditions of flooding stress, they are involved in promoting the elongation of the internode by stimulating the gibberellin biosynthesis in deep-water rice, which enables rice to grow upward to the water surface for air exchange (Hattori et al., 2009b). In barley, the group VII ethylene response factor (ERFVII) TF BERF1 serves as a substrate for the N-end rule pathway *in vitro*. Transgenic RNAi barley plants exhibited increased expression of genes related to hypoxia and changed the phenotypes of seed germination due to decreased expression of the N-end rule pathway N-recognin E3 ligase PROTEOLYSIS6 (HvPRT6). Moreover, transgenic plants exhibited prolonged sustained biomass, chlorophyll retention, enhanced activation of genes related to hypoxia, and improved yield in response to waterlogging (Mendiondo et al., 2016). The flooding stress led to an increase in cell death in the wild-type soybean, while the mutant soybean line exhibited a decrease in cell death. These findings indicate that cell death regulation through fermentation and glycoprotein folding systems may be critical in enhancing tolerance to the flooding in the mutant soybean line (Komatsu et al., 2021).

Soybean is a major agricultural crop, but it is very sensitive to flooding stress (Githiri et al., 2006). Plant growth and grain yield of soybean are observed to be reduced in flooded soil (Githiri et al., 2006). When exposed to flooding at the reproductive or vegetative growth stage, soybean experiences a decrease in plant growth, grain yield, and quality (Oosterhuis et al., 1990). In response to flooding, soybean forms secondary aerenchyma, which acts as an oxygen pathway (Shimamura et al., 2003). Moreover, flooding stress inhibits root elongation and reduces hypocotyl pigmentation, which impairs plant growth (Komatsu et al., 2012). Studies have shown that under flooding, soybean seedlings exhibit differential regulation of proteins involved in hormonal signaling, glucose degradation/sucrose accumulation, transcriptional control, signal transduction, gamma-aminobutyric acid shunt, alcohol fermentation, mitochondrial impairment, suppression of ROS scavenging, cell-wall loosening, and ubiquitin/proteasome-mediated proteolysis (Komatsu et al., 2015; Wang and Komatsu, 2018, 2020).In a study, the response of an ethylene-responsive factor, *HvERF2.11*, to waterlogging stress was examined in barley. It was observed that overexpression of *HvERF2.11* increased resistance to waterlogging stress. Under waterlogging stress, further analysis of transgenic plants showed rapid increases in the expression of *AtACO1*, *AtSOD1*, and *AtPOD1* genes, which did not occur in non-transgenic plants. Additionally, ADH and antioxidant enzymes were shown to have higher activities in the transgenic plants than non-transgenic plants. Based on the research conducted by Luan et al. (Luan et al., 2020), it can be concluded that *HvERF2.11* enhances plant resistance to waterlogging stress by regulating genes related to the waterlogging, which improves the activities of ADH and antioxidant enzymes. In another study, the waterlogging stress significantly inhibits the development of roots and shoots of a rapeseed cultivar Zhongshuang 11 (ZS11) (Guo et al., 2020).

Table 2
Involvement of different genes in response to waterlogging stress in plants.

Gene	Crop	Gene function	Reference
OsSUB1C	Rice (*Oryza sativa* L.)	*SUB1C* is responsible for positively regulating the downstream of the GA signaling pathway and promotes elongation of shoot	(Fukao and Bailey-Serres, 2008; Fukao et al., 2006)
OsSUB1A	Rice (*O. sativa* L.)	*SUB1A* limits the shoot elongation under conditions of submergence by accumulating DELLA protein SLR1 and non-DELLA protein SLRL1. By upregulating BR biosynthesis gene expression, the *SUB1A* also inhibits internode elongation	(Fukao and Bailey-Serres, 2008)
OsSK1 and *OsSK2*	Rice (*O. sativa* L.)	*SK1* and *SK2* promote elongation of the internode under submergence conditions by promoting the biosynthesis of GA in deep-water rice. *SK1* and *SK2* overexpression considerably enhances the resistance of non-deep-water rice to submergence	(Hattori et al., 2009a)
OsCIPK15	Rice (*O. sativa* L.)	In anoxic stress, *CIPK15* accumulates *SnRK1A*, which in turn induces *AMY3s* expression, and eventually regulates carbohydrate catabolism	(Lee et al., 2009; Park et al., 2010)
OsAMY3	Rice (*O. sativa* L.)	Hypoxic stress induces transcription of *AMY3s* subfamily genes, which encode α-amylase. The *AMY3s* are involved in positively regulating carbohydrate catabolism under the conditions of anoxia and increasing tolerance to flooding stress	(Park et al., 2010)
AtLDH	Arabidopsis (*Arabidopsis thaliana*)	Overexpression of *LDH* increases the activity of PDC and low oxygen tolerance	(Brownstein et al., 2013; Dolferus et al., 2008)
AtPCO1/ AtPCO2	Arabidopsis (*A. thaliana*)	Overexpression of *PCO1* and *PCO2* decreases the survival rate during flooding stress	(Licausi et al., 2011; Weits et al., 2014)
tRAP2.12	Arabidopsis (*A. thaliana*)	Under the conditions of low oxygen, the *RAP2.12* induces the expression of hypoxia-related genes, for example ADH and PDC	Eysholdt-Derzsó and Sauter, (2017); Paul et al., (2016))
GsADH	Cotton (*Gossypium hirsutum*)	*ADH* is responsible for reducing ethanol during hypoxic or flooding conditions. *ADH* expression can be induced by flooding stress	(Zhang et al., 2015)
AtPDC	Arabidopsis (*A. thaliana*)	The *Actinidia deliciosa PDC1* gene overexpression in Arabidopsis improves resistance against waterlogging stress	(Zhang et al., 2016)
OsSD1	Rice (*O. sativa* L.)	Under the conditions of submergence stress, the SD1 protein promotes the elongation of internode	(Kuroha et al., 2018)
OsEIL1a	Rice (*O. sativa* L.)	The *OsEIL1a* binds directly to the promoters of SD1 and SKs and promotes the elongation of the internode in response to submergence stress	(Kuroha et al., 2018)
AtRBOH I	Arabidopsis (*A. thaliana*)	Under conditions of limited oxygen availability (hypoxic stress), the expression of *AtRBOH I* expression is upregulated. When compared to WT plants, those with impaired *AtRBOH I* function exhibit reduced survival rates when submerged in water	(Lin et al., 2017)
MaRAP2–4	Mint (*Mentha arvensis*)	*MaRAP2–4* encodes for an ERF-I type TF. The overexpression of *MaRAP2–4* in Arabidopsis has been shown to improve the plant's ability to tolerate waterlogging and oxidative stress	(Phukan et al., 2018)
LGF1	Rice (*Oryza sativa* L.)	The expression of *LGF1* was found to have an impact on the development of gas films on leaves, as well as the production of C30 primary alcohol. These changes ultimately led to an improvement in the ability of rice plants to tolerate submergence, through an increase in underwater photosynthesis	(Kurokawa et al., 2018)
ACS7 and *ACO2*	Wheat (*Triticum aestivum*)	Promotes the formation of aerenchyma and emergence of axile root	(Nguyen et al., 2018)
OsARD1	Rice (*O. sativa* L.)	*OsARD1* overexpression leads to higher levels of internal ethylene production, which	(Liang et al., 2019)

(continued on next page)

Table 2 (*continued*)

Gene	Crop	Gene function	Reference
		results in enhanced tolerance to submergence in transgenic plants	
AdRAP2.3	Kiwi (*Actinidia deliciosa*)	*AdRAP2.3* is a TF belonging to the ERF-VII family, and it promotes resistance to waterlogging stress by controlling the expression of *PDC* and *ADH* genes. On the other hand, *SOS1* is responsible for encoding a Na+/H+ antiporter, and it might interact with *CmRCD1* to promote plant tolerance to waterlogging stress	(Pan et al., 2019)
HvERF2.11	Barley (*Hordeum vulgare* L.)	The *HvERF2.11* expression is upregulated in response to waterlogging stress, leading to enhanced tolerance to waterlogging in plants by increasing activities of various antioxidant and ADH enzymes	(Luan et al., 2020)
CmSOS1	Chrysanthemum (*Chrysanthemum morifolium* Ramat.)	The gene *SOS1* is responsible for encoding a type of transporter known as a Na+/H+ antiporter. It is believed that *SOS1* may have a role in facilitating the ability of plant to tolerate waterlogging stress, possibly through an interaction with *CmRCD1*	(Wang et al., 2020b)

Under waterlogging stress, maize gene expression analysis revealed differential expression of genes. These genes are responsible for generating or scavenging ROS, cell wall loosening degradation pathways, and Ca^{2+} signaling. *GRMZM2G300965* (RBOH) plays a role in generating ROS, and its expression level was 117-fold higher in stelar cells and cortical under waterlogging stress than under control conditions. Under waterlogged conditions, *GRMZM2G174855* (XET) also showed enhanced expression in stelar cells and cortical (Steffens et al., 2011). The gene *ZmERB180*, a member of ethylene response factors group VII, enhances the resistance against waterlogging stress. Its expression in maize and Arabidopsis increased survival rate under waterlogging stress through ROS homeostasis and the formation of ARs (Yu et al., 2019).

A study discovered that waterlogging stress induced *AtrbohD* expression, and mutations in *AtrbohD* resulted in increased sensitivity of Arabidopsis plants to waterlogging stress. Additionally, two mutant lines of *AtrbohD* showed decreased ADH activity, H_2O_2 accumulation, and expression of *ADH1* in response to the waterlogging stress. These results suggest that *AtrbohD* significantly contributes to resistance to waterlogging stress in Arabidopsis (Sun et al., 2018). Developing waterlogging-tolerant plants represents a critical endeavor in the face of mounting environmental challenges. With climate change leading to increased instances of heavy rainfall and waterlogged conditions, the significance of these plants cannot be overstated. They hold the key to ensuring global food security by safeguarding agricultural productivity in regions prone to waterlogging. Beyond food production, they help mitigate soil erosion, preserve soil health, and reduce the need for excessive chemical inputs, thereby promoting sustainable agriculture. Furthermore, they support the conservation of wetland ecosystems, which play pivotal roles in maintaining ecological balance. In essence, the development of waterlogging-tolerant plants not only addresses immediate agricultural concerns but also aligns with long-term sustainability goals, making it a vital pursuit for the well-being of both humanity and the planet.

7. Conclusions and future perspectives

Globally, flooding poses a significant threat that can lead to a considerable reduction in cereal crop yields and is predicted to become more severe in various regions due to anomalous climatic conditions in the forthcoming years. Plant growth and productivity are significantly impacted by waterlogging stress. When plants are subjected to waterlogged conditions, they undergo stress that affects their growth and nutrient uptake. This stress results in alteration in the roots, which then impacts the growth of leaves, flowers, and shoots of plants. In addition, the ability of plants to efficient photosynthesis and biomass production might be diminished, resulting in lower crop productivity. The regulation of hormones is also crucial to how plants respond to waterlogging stress.

Multiple mechanisms have been discovered in which plants respond to waterlogging stress, such as activation of signaling pathways, ROS accumulation, oxygen deprivation, and energy crisis. The interaction between signaling pathways of different phytohormones plays a key role in the complex response. Moreover, TFs and gene expression are involved in adaptation to waterlogging stress conditions.

To reduce the detrimental effects of waterlogging stress and enhance crop resilience, various strategies can be employed. Genetic breeding is one of the approaches that can create waterlogging-resistant cultivars. In addition, there are other strategies, such as biochemical and physiological adaptations, that can regulate hormonal balance and activate antioxidant systems. Agronomic practices and soil management techniques, including drainage enhancement and irrigation optimization, can also reduce the frequency and severity of waterlogging stress.

Although significant progress has been made in understanding the molecular mechanisms and effects of waterlogging stress, however, further research and investigation are needed. Here are some key considerations for future investigations:

1. Investigating new genes, signaling components, and proteins is essential to understanding the response of plants to waterlogging stress.
2. Modern molecular methods, such as omics approaches, can provide greater insight into the molecular aspect of how plants respond to waterlogging stress.
3. The knowledge acquired from molecular studies must be applied to practical applications in order to improve crops. This requires the development of breeding strategies that incorporate traits for waterlogging tolerance and the implementation of effective agronomic practices for managing waterlogging stress in a variety of cropping systems.
4. Extreme weather events, such as flooding and heavy rainfall, become more frequent and intense due to climate change. It is essential to investigate the effects of waterlogging stress on plants. By investigating how factors related to climate change interact with waterlogging stress, valuable insights can be obtained about future agricultural challenges.

In conclusion, it is crucial to understand the molecular mechanisms underlying waterlogging stress in plants and how it impacts their growth and productivity, which is vital for the development of strategies to enhance crop resilience. It is essential to continue ongoing research to find sustainable agricultural solutions.

Authors agreement

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CRediT authorship contribution statement

Hakim Manghwar: Conceptualization, Supervision, Validation, Writing – original draft, Writing – review & editing. **Amjad Hussain:** Writing – review & editing. **Intikhab Alam:** Software. **Muneer Ahmed Khoso:** Data curation, Methodology. **Qurban Ali:** Methodology, Software. **Fen Liu:** Funding acquisition.

Declaration of Competing Interest

The authors declare no potential conflict of interest.

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