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REVIEW

Physiological and Biochemical Mechanisms of Waterlogging Tolerance in Plants

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ABSTRACT

Waterlogging is a growing environmental challenge that significantly affects plant health and agricultural productivity by lowering soil oxygen levels, which creates hypoxic and anoxic conditions. This review consolidates the current knowledge of the physiological and biochemical mechanisms behind waterlogging tolerance in plants. Key physiological adaptations include alterations in energy metabolism, where anaerobic respiration pathways, such as glycolysis and fermentation, are activated to sustain ATP production in low-oxygen environments. Increased glycolytic and fermentation activities facilitate NAD^+ regeneration, crucial for continuous energy production. Furthermore, antioxidant defense mechanisms are activated to mitigate oxidative stress from elevated reactive oxygen species (ROS) during waterlogging, emphasizing the role of enzyme-based antioxidants in protecting cellular integrity. The review also explores the significance of osmoprotective compounds, such as proline and soluble sugars, which contribute to osmotic balance and protein stabilization under stress. Moreover, the roles of phytohormones, particularly ethylene and abscisic acid (ABA), serve as signaling molecules that regulate adaptive physiological changes. These hormones influence critical processes such as stomatal closure to conserve water, leaf senescence to allocate resources efficiently, and the induction of root adaptations to improve gas exchange. By elucidating these complex adaptive mechanisms, this review provides a comprehensive overview of the multifaceted strategies that contribute to plant resilience under waterlogged conditions, ultimately enhancing the understanding of plant survival in fluctuating environmental conditions.

1 | Introduction

Water is a vital component in plants, constituting a significant part of cell volume, and is essential for their growth and development. However, excessive water can cause various harmful effects. Under ideal conditions, roots in well-drained, structured soils depend on a proper balance of solid, liquid, and gas phases to obtain enough oxygen (O_2) for aerobic respiration from the air-filled soil pores. Nonetheless, natural events like flooding, combined with human activities such as improper irrigation and soil management, can greatly alter soil properties (Garcia-Vila et al. 2025). These changes often lead to soil compaction and complete saturation of pore spaces, decreasing the availability of gaseous oxygen (Jiménez-Ballesta et al. 2025). Oxygen deficiency is the primary consequence of excess water on plants, resulting in significant disruptions to cellular metabolism and causing serious biochemical and physiological imbalances (Zhang, Chen, et al. 2025). The resulting anoxic conditions lead to the obstruction of gas exchange between soil and roots, as well as between the soil and atmosphere, drastically reducing the rate of oxygen diffusion (Pedersen et al. 2021). Specifically, the diffusion rate of oxygen in saturated soil can decrease to as low as 1/10,000 of that in air. Moreover, oxygen, being a non-polar molecule, has a low solubility in water (with a maximum concentration of approximately 10 mg L^{-1} compared to about 300 mg L^{-1} in air), further exacerbated by rising temperatures (Stolzy and Letey 1964; Gibbs and Greenway 2003). This situation can lead to hypoxic conditions (oxygen concentrations below 2 mg L^{-1}) or complete asphyxiation within 24 h (Liang et al. 2024).

With climate change projected to increase the frequency and severity of soil flooding, especially in irrigated areas experiencing unpredictable rainfall, the sensitivity of soils with poor drainage, such as those with high clay content or those compacted by heavy machinery, will likely intensify (Tian et al. 2021). Consequently, waterlogging represents an increasingly significant abiotic stressor, adversely affecting agricultural yields and ecosystem health (Manghwar et al. 2024). In this context, it is essential to understand the main metabolic, biochemical, and physiological alterations and adaptations that plants put in place to cope with waterlogging. Plants have evolved a range of adaptive responses to survive waterlogging stress, including mechanisms such as aerenchyma formation for improved oxygen transport, alterations in root architecture for enhanced drainage, and adaptations in anaerobic metabolism to sustain energy levels. However, the degree of tolerance to waterlogging varies significantly among different crop species and varieties (Daniel and Hartman 2024; Manghwar et al. 2024). Particularly susceptible species exhibit a limited ability to manage soil oxygen deficiency, resulting in reduced growth, diminished yields, and ultimately plant death in extreme cases (Bhattarai et al. 2005). Therefore, identifying the critical physiological and metabolic processes in these sensitive species can help develop innovative solutions, such as the application of exogenous products and targeted agronomic practices (Manghwar et al. 2024). These strategies can enhance plant resilience against waterlogging and diminish the adverse effects of sudden extreme events. Such approaches serve as effective alternatives or complements to genetic improvement, particularly when the introduction of new, more tolerant genotypes is impractical or prohibited by regulations concerning genetically modified organisms (GMOs) (Babar et al. 2015). Furthermore, these strategies are vital for preserving native plant varieties linked to local agricultural practices and cultural heritage, ensuring their resilience amid changing climatic conditions while maintaining agricultural biodiversity and traditions.

The main goal of this review article is to compile current knowledge on the physiological and biochemical methods contributing to plant tolerance to waterlogging, highlighting the various adaptive responses that allow species to survive in low-oxygen conditions. This review aims to shed light on the key physiological adaptations, such as changes in root structure, gas exchange processes, and the activation of biochemical pathways like shifts in energy metabolism and the management of oxidative stress through reactive oxygen species (ROS) and antioxidant defenses. Additionally, we will highlight the differences in waterlogging tolerance among different plant types and varieties, while also considering how human activities influence waterlogging susceptibility and plant responses. To achieve these goals, the review gives up-to-date knowledge about important scientific questions:

- Which biochemical pathways are essential for plant reactions to waterlogging?
- How do modifications in energy metabolism, antioxidant activity, and osmoprotective compounds impact waterlogging tolerance?
- Which roles do carbohydrates and changes in root hydraulic conductivity play in strengthening plant resilience?
- How do endogenous hormones affect physiological adaptations to waterlogging stress?
- How can understanding these mechanisms assist in developing agricultural practices to boost crop resilience in the face of climate change?

By exploring these questions, this review aims to deepen our understanding of waterlogging tolerance mechanisms, ultimately guiding future research and practical strategies in agriculture and ecological management.

2 | Biochemical Changes in Plants Under Waterlogging Stress

2.1 | Changes in Energy Metabolism

Oxygen is a fundamental gas for aerobic respiration, a metabolic process fundamental to cellular life. This process is crucial for the energetic demands involved in growth, development, nutrient absorption, and overall biological activity. Respiration is characterized by three main metabolic processes: (1) glycolysis, which occurs in the cytoplasm; (2) the Krebs cycle (also known as the tricarboxylic acid cycle or citric acid cycle), taking place in the mitochondrial matrix; and (3) oxidative phosphorylation, which occurs in the inner mitochondrial membrane (Zheng et al. 2025). The complete oxidation of one molecule of glucose through aerobic respiration yields approximately 32 molecules of ATP, with 3 generated during glycolysis, 2 from the Krebs cycle, and 28 via oxidative phosphorylation (Melkonian and Schury 2019; Alabduladhem and Bordoni 2022).

Under waterlogging conditions, soil oxygen availability is significantly reduced. Hypoxia results in a low partial pressure of O_2, limiting ATP production through respiration, while anoxia leads to negligible mitochondrial ATP synthesis, consequently suppressing mitochondrial respiration and impairing root activity, thereby causing an energy deficit (Zahra et al. 2021). O_2 deficiency further inhibits oxidative phosphorylation by obstructing the electron transport chain (ETC) due to the lack of a final electron acceptor (Zhao et al. 2019). This saturation prevents the reoxidation of reduced electron carriers, NADH (nicotinamide adenine dinucleotide) and $FADH_2$ (flavin adenine dinucleotide), leading to a subsequent blockage of the Krebs cycle as the incapacity to oxidize these electron donors hampers citric acid cycle activity (Nantes et al. 2012). Moreover, hypoxia instigates an increase in nitric oxide (NO) production, which is a potent inhibitor of aconitase, an enzyme crucial for the conversion of citrate to isocitrate in the Krebs cycle (Cui et al. 2019; Lothier et al. 2020). In addition, NO-mediated inhibition of cytochrome oxidase, the terminal enzyme complex of the mitochondrial ETC in oxidative phosphorylation, further disrupts mitochondrial energy metabolism (Blokhina and Fagerstedt 2010). In response to these energy constraints, plants activate anaerobic respiration, which includes glycolysis and anaerobic fermentation to generate the requisite ATP (van Veen et al. 2025). Importantly, while aerobic respiration can yield approximately 32 molecules of ATP per molecule of glucose, glycolysis alone produces only 2 ATP (Melkonian and Schury 2019). The lower energy yield of anaerobic pathways necessitates an upregulation of glycolytic activity in various plant species such as *Sorghum bicolor*, *Melaleuca Cajuputi* and *Glycine max*, under waterlogging conditions, indicating the fundamental role of glycolysis for plant survival (Singla et al. 2003; Yamanoshita et al. 2005; Nakamura et al. 2012). This increased glycolytic activity observed in response to low oxygen availability is a significant adaptation in plants. A comparative trial between *S. bicolor* genotypes with varying tolerances to waterlogging stress revealed that the less sensitive genotypes exhibited higher root-level glycolytic activity than their more sensitive counterparts, suggesting a metabolic adaptation to maintain energy production under low O_2 conditions (Singla et al. 2003). A pronounced increase in glycolytic activity was reported in response to waterlogging, as indicated by measurements of final and intermediate glycolytic products (Bashar et al. 2020).

The oxidation of NADH to NAD^+ is essential to allow the glycolytic cycle to continue (Dumont and Rivoal 2019). In aerobic respiration, reduced NADH is oxidized during oxidative phosphorylation, allowing its reuse in glycolysis (Wilson and Matschinsky 2018). When oxidative phosphorylation is inhibited under hypoxia/anoxia, the regeneration of glycolytic NAD^+ is restricted (Nakamura and Noguchi 2020). As NAD^+ serves as an essential cofactor for the glycolytic enzyme glyceraldehyde 3-phosphate dehydrogenase (GAPDH), any failure to regenerate NAD^+ would hinder glycolysis altogether (Xiao et al. 2018). To address this metabolic challenge, cells increase the rates of lactic and alcoholic fermentation, which, although they do not directly produce energy, are vital for regenerating NAD^+ to support glycolytic processes (Luengo et al. 2021). As shown in Figure 1, the glycolytic pathway plays a crucial role in sustaining ATP production under anaerobic conditions by facilitating the conversion of glucose to pyruvate.

Lactic fermentation converts pyruvate to lactic acid using NADH and lactate dehydrogenase (LDH), while alcoholic fermentation decarboxylates pyruvate to acetaldehyde and then reduces it to ethanol using NADH, aided by pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH). The balance between these processes is regulated by cellular pH: LDH works best in alkaline conditions, whereas PDC is most active in acidic conditions. Changes in pH can modulate the activity of these enzymes accordingly (Peng et al. 2020; Bai et al. 2022; Gao et al. 2023).

The adaptive metabolic responses of plants under oxygen-limited conditions are critical for their survival. As previously discussed, plants engage in various fermentation processes to mitigate energy crises resulting from waterlogging and anaerobic conditions. Specifically, increased fermentation activity in hypoxia/asphyxia serves as a key indicator of tolerance to waterlogging conditions. For instance, research by Peng et al. (2020) demonstrated that grafted *Momordica charantia* exhibits a greater tolerance to waterlogging stress compared to self-rooted individuals, attributed to enhanced activity of PDC, ADH and LDH. This finding underscores the importance of enzymatic activity in conferring resilience to waterlogging. As illustrated in Figure 2, the enzymatic pathways of lactic and alcoholic fermentation emphasize the conversion of pyruvate into lactate or ethanol, highlighting the significance of NAD^+ regeneration and the regulatory balance under oxygen-limited conditions.

Although both alcoholic and lactic fermentation play a pivotal role in the regeneration of NAD^+, plants tend to favor alcoholic fermentation under these stressful conditions (Andreev and Vartapetian 1992). A persistent increase in LDH activity may result in excessive lactate accumulation, leading to cytoplasmic acidification and subsequent cellular imbalances (Du et al. 2018). Therefore, while lactic fermentation represents an initial stress response, a decrease in pH acts to slow lactate formation and simultaneously stimulates alcoholic fermentation. This shift redirects the glycolytic pyruvate towards ethanol production, a process believed to be less detrimental than lactic acid accumulation, which exacerbates cytoplasmic acidity (Gout et al. 2001; Vartapetian 2005).

In controlled experiments involving two wheat (*Triticum aestivum*) varieties, a hypoxia-tolerant genotype showed greater ADH activity and ethanol accumulation, while the susceptible cultivar showed greater LDH activity and significant lactate accumulation, ultimately resulting in a more rapid decline under hypoxic conditions (Du et al. 2018). The critical role of alcoholic fermentation is further supported by studies employing exogenous inhibitors, such as methylglyoxyl-bis-guanylhydrazone (MGBG). In these experiments, the application of MGBG on wheat plants inhibited PDC and ADH, leading to a shift towards lactic fermentation. This shift exacerbated the accumulation of lactate and aggravated the stress-induced damage to seedlings (Du et al. 2018). Moreover, a study on a mutated variety of maize (*Zea mays*) plants unable to perform alcoholic fermentation revealed a significant decline in ATP levels and an inability to maintain cytoplasmic pH under hypoxia. Prolonged lactic fermentation resulted in a continuous decrease in pH, contributing to a more accelerated deterioration of these mutant plants (Roberts et al. 1984).

As highlighted above, the ability of plants to switch to alcoholic fermentation during hypoxic conditions is a critical factor influencing their survival and resilience to waterlogging. Multiple studies have indicated that higher levels of alcoholic fermentation activity serve as a key indicator of waterlogging stress. For instance, investigations into various *Actinidia* genotypes revealed that the most waterlogging-tolerant individuals not only exhibited significantly higher activities of PDC and ADH but also showed increased expression of the ADH1 and ADH2 genes. In contrast, a drastic reduction in these enzymatic activities in sensitive genotypes was linked to plant mortality (Li et al. 2021; Bai et al. 2022; Gao et al. 2023). This trend was also observed in different genotypes of *Cajanus cajan*, where higher ADH activity correlated with better survival rates in tolerant genotypes (Bansal and Srivastava 2015). Moreover, a higher value of ADH activity compared to PDC serves as an additional mechanism of tolerance against the accumulation of acetaldehyde, a highly toxic and reactive byproduct. Due to the toxic effects of acetaldehyde, it is critical that plants rapidly convert it to ethanol

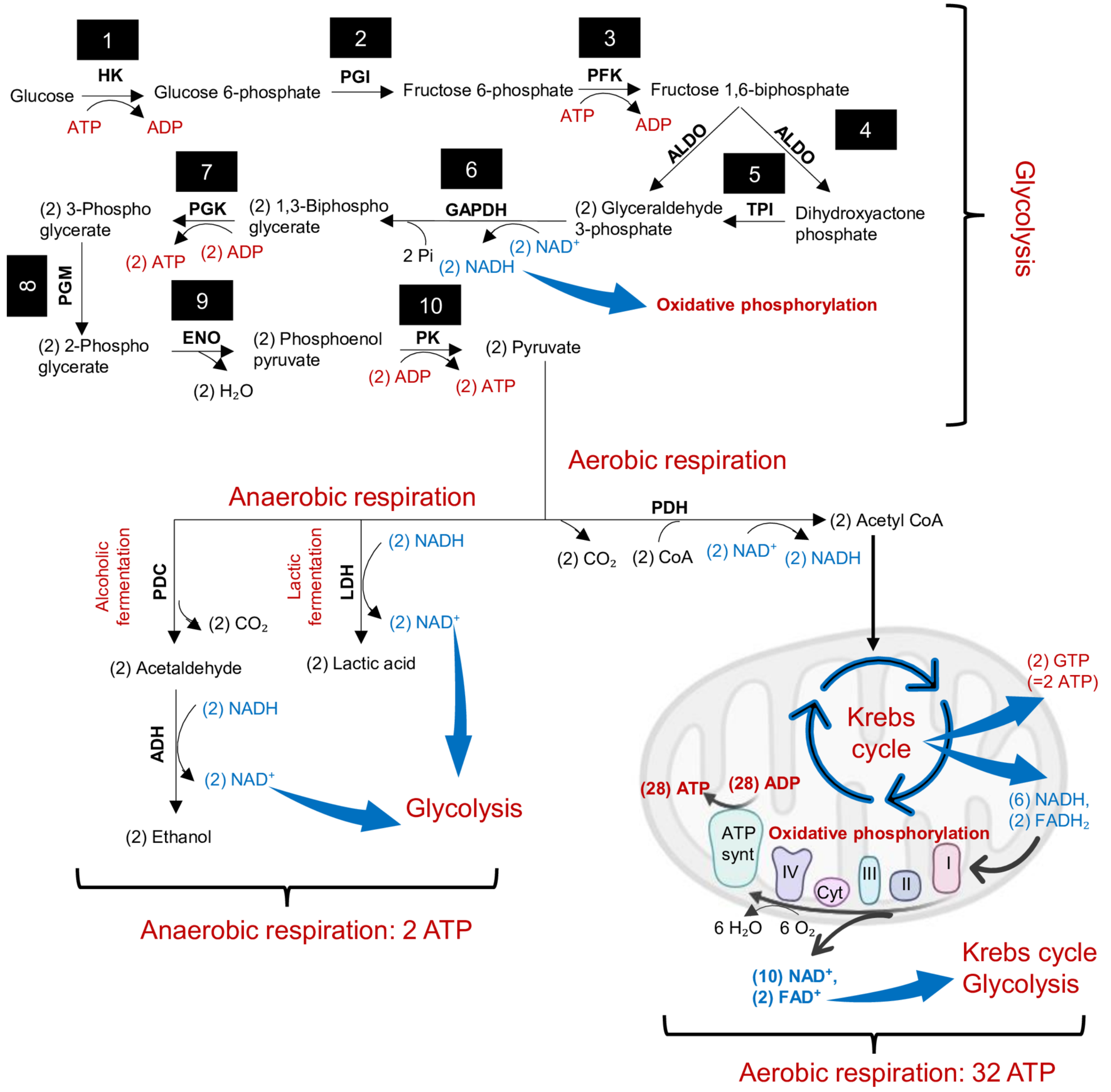

FIGURE 1 | Overview of glycolytic processes and aerobic versus anaerobic respiration. Glycolysis, occurring in the cytoplasm, degrades glucose (C6) into two pyruvate molecules (C3), yielding a net production of 2 ATP and 2 NADH. Under aerobic conditions, pyruvate enters the mitochondria as acetyl-CoA for the Krebs cycle, producing 2 GTP (equivalent to 2 ATP), 6 NADH, and 2 $FADH_2$. These reduced cofactors are then oxidized during oxidative phosphorylation, generating an additional 32 ATP. In contrast, under hypoxic or anaerobic conditions, pyruvate undergoes fermentation processes (lactic or alcoholic), allowing the oxidation of NADH to NAD$^+$ and enabling glycolysis to continue, but only yielding a net of 2 ATP.

via ADH; although ethanol can also be toxic (Xu et al. 2016), its concentrations in plants generally remain below harmful levels, and its lipid solubility allows for efficient diffusion out of the cell membrane (Drew 1997).

As our understanding improves, complementary theories have emerged, suggesting additional metabolic pathways that plants may employ under hypoxia/asphyxia conditions to enhance their tolerance to waterlogging. One such theory posits the production of malate, succinate and nitrogen respiration in nitric form as alternative pathways to fermentation (Zhao et al. 2022; Samant et al. 2024). It has been reported that plants grown under anaerobic or hypoxic conditions could partially utilize the Krebs cycle to facilitate succinate production (Yemelyanov et al. 2023). This metabolic pathway not only enables NADH oxidation and ATP synthesis but also allows for the accumulation of less toxic compounds, thereby improving root tolerance to waterlogging conditions (Vanlerberghe et al. 1989; Bouillaud 2023). This explains the significant accumulation of succinate observed in oxygen-deficient

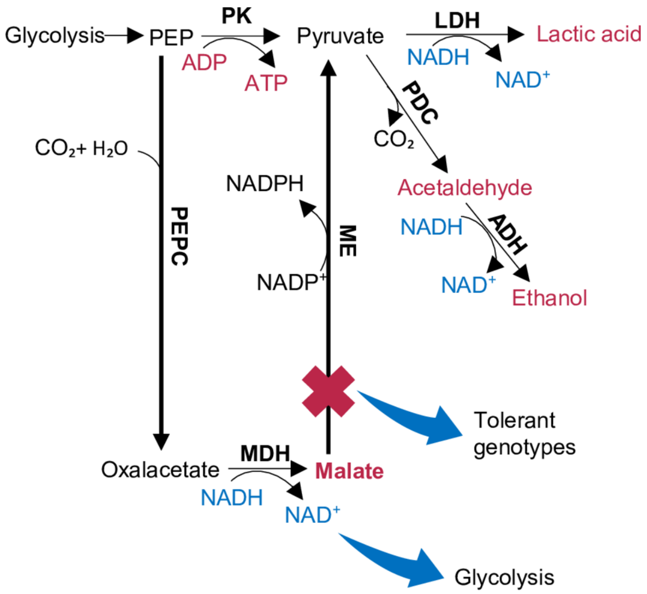

FIGURE 2 | Alternative pathway of malate under hypoxic/asphyxial conditions. In oxygen deficiency, fermentative processes (lactic and alcoholic) are activated to regenerate NAD^+ from NADH, enabling glycolysis but leading to the accumulation of toxic byproducts such as lactic acid, acetaldehyde, and ethanol. An alternative metabolic strategy diverts part of the phosphoenolpyruvate (PEP) pathway towards malate synthesis, which helps oxidize NADH and regenerate NAD^+ while producing malate, a less toxic compound. Tolerant genotypes exhibit low malic enzyme (ME) activity, promoting malate accumulation and minimizing harmful fermentation byproducts. In contrast, intolerant genotypes have high ME activity, converting malate to pyruvate and increasing the accumulation of toxic compounds.

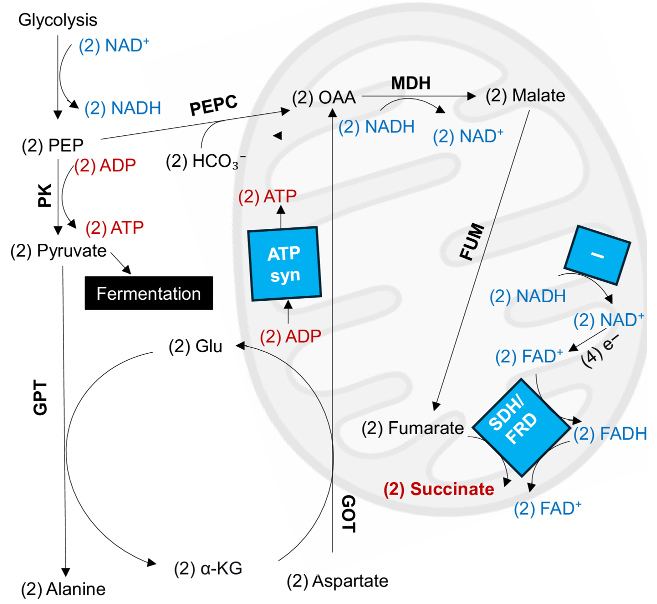

FIGURE 3 | Overview of the alternative pathway for succinate metabolism under hypoxic conditions. In oxygen-deprived environments, cells initiate glycolysis to generate ATP and pyruvate, which can be fermented to recycle NADH into NAD^+, producing toxic byproducts like lactate and ethanol. Some pyruvate is diverted to form succinate via the conversion of aspartate to oxaloacetate (OAA) and alanine. Additionally, OAA can be produced from phosphoenolpyruvate (PEP) through the action of phosphoenolpyruvate carboxylase (PEPC). In the mitochondria, OAA undergoes a reverse Krebs cycle, reducing NADH and transforming OAA into malate, which is further oxidized to fumarate. Complex I utilizes NADH, while complex II (succinate dehydrogenase/fumarate reductase) reduces fumarate to succinate, generating an electrochemical gradient for ATP synthesis via ATP synthase. The net ATP production is 4 per glucose when starting from pyruvate and 2 when starting from PEP, facilitating ATP generation and minimizing harmful fermentative byproducts.

conditions in higher plants (Figure 3) (Yemelyanov et al. 2023). Conversely, McManmon and Crawford (1971) proposed a mechanism whereby plants minimize ethanol production by redirecting metabolic flow towards malate synthesis, a less toxic byproduct than those resulting from fermentative pathways. This strategy not only aids in the oxidation of surplus NADH but potentially confers additional resilience to oxygen deficiency (McManmon and Crawford 1971).

Moreover, several studies have underlined the potential role of "nitrogen respiration" in conditions of hypoxia or anoxia (Gupta et al. 2020; Timilsina et al. 2022). This response promotes the recycling of NADH, aids in ATP production in the mitochondria, and helps avoid excessive reduction in the ETC, which can result in the generation of ROS (Napolitano et al. 2021). According to this theory, the surplus NADH produced during hypoxia can be oxidized by dehydrogenases found in the inner mitochondrial membrane. This process aids in the transfer of electrons to the ETC, starting at Complex III (cytochrome bc_1) and continuing to cytochrome c oxidase (COX) (Padilla et al. 2023; Chammakhi et al. 2025). Under conditions of oxygen deficiency, COX can shift its electron acceptor preference from oxygen to nitrite (NO_2^-), thereby mitigating full anoxia and enabling the reduction of nitrite to NO using electrons derived from the ETC (Gupta et al. 2020). During this electron transfer, protons (H^+) are pumped from the mitochondrial matrix into the intermembrane space, facilitating ATP synthesis despite O_2 deficiency (Tabassum et al. 2020). Although NO is a highly reactive and potentially cytotoxic gas that can diffuse easily across cellular membranes, plants possess mechanisms to neutralize its harmful effects (Mandal et al. 2022). These mechanisms involve non-symbiotic hemoglobin (Hb) and nitrate reductase (NR) present in the cytoplasm (Cong et al. 2024). Hb binds to NO through its heme group, forming the Hb-NO complex, which limits free NO concentration in tissues (Verde et al. 2023). The Hb-NO complex can reduce NO by oxidizing NADH/NADPH, resulting in the formation of the less toxic NO_3^- and NAD^+ (Sainz et al. 2013). In turn, NO_3^- can be reduced to NO_2^- by NR (Chamizo-Ampudia et al. 2017), facilitating its reuse in mitochondria as a substitute for deficient oxygen. Through the cooperative action of NR and Hb, plants can effectively recycle NO, enhancing their ability to survive under hypoxic conditions (del Castello et al. 2020). As shown in Figure 4, the interplay between NO metabolism, non-symbiotic Hb, and NR emphasizes the adaptive metabolic pathways plants utilize to sustain energy production during hypoxic conditions.

Studies on *Nicotiana tabacum* (Stoimenova et al. 2003) provided compelling evidence supporting the theory of "nitrogen respiration" in the complex responses of plants to hypoxic conditions. This mechanism suggests that NO can act as a

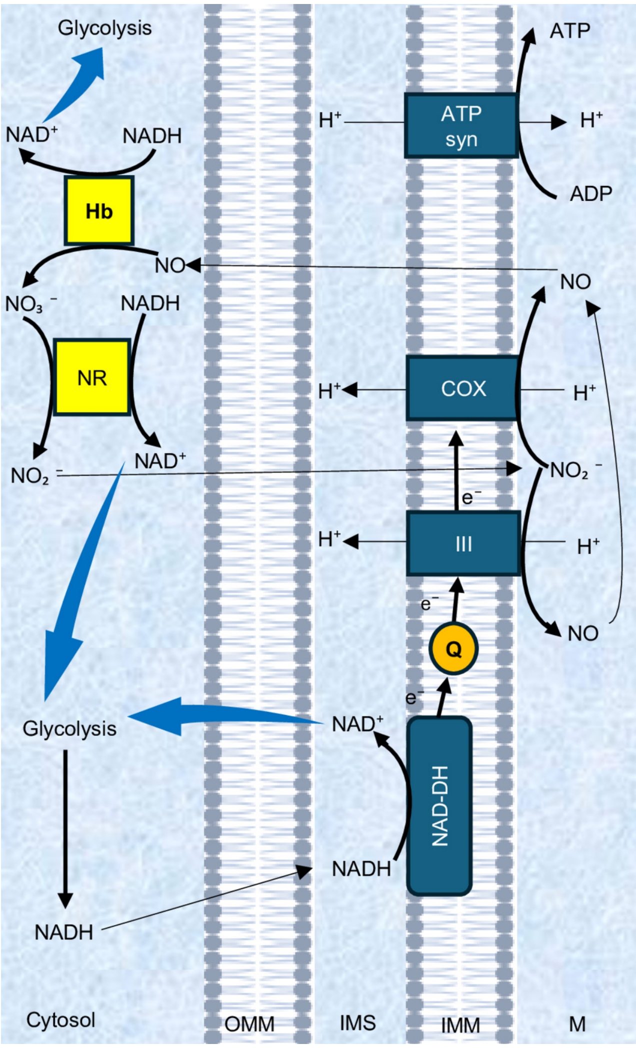

FIGURE 4 | Overview of anaerobic respiration of nitrite coupled to ATP synthesis and NADH oxidation. Under asphyxial or hypoxic conditions, the oxidation of glycolytic NADH to NAD^+ is restricted due to low oxygen availability, inhibiting oxidative phosphorylation. In this scenario, NADH is oxidized by NADH dehydrogenase located on the outer mitochondrial membrane (OMM), with electrons transferred to ubiquinone (Q). Nitrite (NO_2^-) serves as an alternative electron acceptor in complexes III and IV, enabling its reduction to nitric oxide (NO) and generating an electron flow that facilitates ATP synthesis. The produced NO is subsequently converted back to nitrate (NO_3^-) by non-symbiotic hemoglobin (Hb), allowing for further oxidation of NADH. Nitrate is then reduced by nitrate reductase (NR) back to NO_2^-, oxidizing further NADH oxidation to NAD^+, which can be reused in cellular metabolism, including glycolysis.

metabolic regulator, modulating plants' response to anoxia and influencing critical processes such as fermentation, cytoplasmic acidification, and overall stress tolerance. In low-oxygen environments, the intracellular pH often decreases, resulting in a more acidic setting. This change increases the binding affinity of COX for nitrite. As a result, the conversion of NO_2^- to NO becomes more efficient, making this metabolic process particularly effective under conditions where oxygen is scarce (Capitanio et al. 2006). In experiments comparing the wild-type (WT) tobacco plants, which can synthesize NR, with the mutated genotype (LNR) that lacks this capability, significant differences in metabolic responses were observed. In the absence of NR, the LNR plants exhibited excessively high fermentation activity to compensate for ATP production. However, this compensatory mechanism led to an accumulation of lactate, resulting in considerable cytosolic acidification and causing these plants to wilt prematurely compared to their WT counterparts. In contrast, the WT plants demonstrated a more regulated anaerobic metabolism by employing nitrate reduction as an alternative to fermentation. This approach enabled the recycling of NADH and helped maintain a stable cytoplasmic pH, thereby minimizing cellular damage (Stoimenova et al. 2003). This distinction in metabolic strategies underscores the critical role of nitrogen respiration in enhancing plant resilience under oxygen-limited conditions, promoting sustained physiological functions and better overall plant health.

2.2 | Oxidative Damage and Antioxidant Defense Mechanisms

ROS is a normal byproduct of plant cell metabolism (Kathpalia and Agnihotri 2025). However, excessive ROS production can cause oxidative damage that affects major cellular macromolecules, resulting in impaired cellular functions and, eventually, cell death (Chandimali et al. 2025). Among the various forms of damage caused by ROS, lipid peroxidation plays a pivotal role, as it compromises membrane integrity, alters membrane permeability, results in the loss of electrolytes, and deactivates enzymes and receptors. ROS can also damage nucleic acids, leading to mutations and disruptions in protein synthesis (Blokhina et al. 2003; Sharma et al. 2012; Das and Roychoudhury 2014; Anjum et al. 2015). Stress conditions such as waterlogging have been shown to stimulate ROS formation, leading to oxidative damage within plant tissues. Key ROS include superoxide ion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH) and malondialdehyde (MDA), the latter serving as an indicator of lipid peroxidation (Blokhina et al. 2003; Sairam et al. 2009; Anee et al. 2019; Sachdev et al. 2021). In studies on *Actinidia* species, waterlogged plants showed a significant increase in ROS levels in both leaves and roots when compared to control plants (Li et al. 2021; Bai et al. 2022; Gao et al. 2023). Moreover, *Sesamum indicum* plants subjected to waterlogging showed a significant increase in MDA and H_2O_2 levels as early as the second day of stress exposure, with these increases correlating positively with the duration of stress (Anee et al. 2019). Similarly, experiments on different corn genotypes revealed that waterlogging damaged biological membranes and mitochondria, leading to increased MDA content (Ren et al. 2016).

It has been reported that the primary cellular organelles responsible for ROS production include mitochondria, peroxisomes, and chloroplasts. Mitochondria are the main source of O_2^-, H_2O_2, and OH, particularly when oxygen serves as the final electron acceptor of mitochondrial ETC. In situations where electron acceptors like oxygen are absent, excessive accumulation of electrons occurs, resulting in their reaction with residual oxygen to generate ROS. This oxidative damage becomes particularly severe when anaerobic conditions are followed by re-exposure to aerobic conditions. In such instances, a sudden influx of oxygen coupled with a fully reduced mitochondrial ETC can lead to increased ROS formation (Ito et al. 1999; Blokhina et al. 2003; Jayawardhane et al. 2020).

Chloroplasts also serve as additional sources of ROS. Waterlogging often reduces stomatal opening, thereby limiting CO_2 entry into plant cells, an essential gas for photosynthetic activity. This deficiency can excessively reduce the ETC in chloroplasts, resulting in the loss of electrons that subsequently react with O_2 to form ROS (Sharma et al. 2012; Pospíšil 2016). Moreover, during stress conditions such as waterlogging, reduced stomatal opening favors photorespiration processes in peroxisomes. In photorespiration, RuBisCO, the first enzyme of the Calvin cycle, binds to O_2 instead of CO_2, producing glycolate, a non-viable byproduct that hampers the Calvin cycle's progression. Glycolate is subsequently eliminated by peroxisomes through the action of glycolate oxidase (GOX), resulting in H_2O_2 generation as a byproduct. Thus, peroxisome-produced photorespiration directly increases ROS levels (Ogren and Chollet 1982; Sachdev et al. 2021).

To mitigate ROS accumulation, plant cells utilize a range of defense systems, classified into enzymatic antioxidants and non-enzymatic antioxidants (AbdElgawad et al. 2023; Albqmi, Selim, et al. 2023). Enzymatic antioxidants include catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), glutathione peroxidase (GPX), and enzymes involved in the glutathione-ascorbate cycle, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). These enzymes are essential for regenerating important non-enzymatic antioxidants, which include ascorbate (AsA), reduced glutathione (GSH), phenolic compounds and tocopherols (Albqmi, Yaghoubi Khanghahi, et al. 2023).

Under waterlogging conditions, robust antioxidant activity is crucial for protecting plant tissues from oxidative damage. Plants typically activate their antioxidant systems in response to oxidative stress resulting from waterlogging; however, the extent of this activation varies among plant species and genotypes. Waterlogging-tolerant species/genotypes often show greater antioxidant activity compared to sensitive ones, effectively reducing ROS levels. Experimental studies comparing two corn genotypes (*Z. mays*), HZ32 (tolerant) and K12 (sensitive), confirmed that the tolerant genotype exhibited higher activities of antioxidant enzymes (including SOD, APX, GR, CAT and POD), which helped limit oxidative damage (Bin et al. 2010). Conversely, the sensitive genotype showed significantly higher oxidative damage, characterized by increased lipid peroxidation (Bin et al. 2010). Similarly, in *C. cajan*, stress increased CAT, APX and SOD activities in both sensitive and waterlogging-tolerant lines; however, the enzymatic activity of the tolerant lines was significantly higher than their waterlogging-sensitive counterparts (Bansal and Srivastava 2012). In an experiment involving two *Actinidia* genotypes, the tolerant genotype showed significantly higher activities of SOD, CAT and APX than the sensitive genotype, resulting in reduced ROS accumulation and less oxidative damage (Gao et al. 2023). Comparable findings have been observed in other species, including *Oryza sativa* (Damanik et al. 2010) and *Hordeum vulgare* (Zhang et al. 2007), emphasizing the crucial role of enzymatic antioxidants in safeguarding against oxidative damage induced by waterlogging.

2.3 | Osmoprotective Compounds

As discussed previously, plants face osmotic stress and disruptions to ion homeostasis due to excessive water accumulation in the root zone. The production of ATP is critical for the absorption and transport of solutes through energy-dependent channels. Efficient solute absorption is important for meeting the plant's nutrient requirements, regulating water flow within tissues and maintaining optimal cellular water potential for effective water absorption from the soil (Huang et al. 2003; Zivcak et al. 2016; Hao et al. 2021).

Under hypoxic conditions, such as those induced by waterlogging, a significant decline in turgor and root pressure has been observed, highlighting the inability of the roots to effectively absorb and accumulate solutes and water (Bramley et al. 2010). To mitigate these adverse effects, plants often accumulate osmoprotectant compounds in both submerged organs, such as roots, and non-submerged organs, like leaves, as these solutes can decrease the osmotic potential (Cotrozzi et al. 2021). The accumulation of osmoprotectors represents a sustainable strategy, since these compatible solutes are organic compounds that can reach high intracellular concentrations without compromising cellular functions (Yang et al. 2023).

One of the most important osmoprotectants is proline, recognized for its beneficial effects in mitigating damage from various environmental stressors, including waterlogging. Proline acts by stabilizing cellular structures and maintaining osmotic balance within plant cells. It has been shown to scavenge reactive oxygen species (ROS) and other free radicals, thereby reducing oxidative stress (AbdElgawad et al. 2024; Alsherif et al. 2024). Furthermore, proline enhances the activity of antioxidant enzymes, preserving tissue from oxidative damage (Hoque et al. 2007; Ghaffari et al. 2019; Sehar et al. 2023). It also stabilizes protein structure and contributes to cytosolic pH buffering (Hossain et al. 2014; Barot et al. 2025). Increased levels of proline are often observed as a biochemical adaptation mechanism that helps plants cope with waterlogging stress. For instance, research on peach trees (*Prunus persica*), which are particularly susceptible to such conditions, showed that proline accumulation induced by the arbuscular mycorrhizal fungus *Funneliformis mosseae* improved their resistance to waterlogging. However, the capacity to activate this protective response varies among plant genotypes, being notably more pronounced in those that exhibit greater tolerance (Tuo et al. 2015).

Research on *Actinidia* rootstocks showing different waterlogging tolerances indicated that, after 5 days of waterlogging, the tolerant genotype showed a significantly higher proline level in the roots compared to control plants and the sensitive genotype, which showed lower proline content relative to both its control and the tolerant genotype (Bai et al. 2022). Similarly, an experiment involving five *Capsicum* species showed that while all species experienced increased proline levels under waterlogging, the more tolerant species exhibited higher concentrations (Ou et al. 2011), supporting the role of proline in waterlogging tolerance.

2.4 | The Role of Carbohydrates

In addition to proline, soluble sugars serve as important osmoprotectants and play a fundamental role in survival under waterlogging conditions. Beyond their osmoprotective functions, soluble sugars are critical for various physiological processes, including signaling, turgor maintenance, phloem transport, xylem repair, and overall plant growth (Martínez-Vilalta et al. 2016; Alagoz et al. 2023). Sugar accumulation is recognized as a defensive response to a range of abiotic stresses (Morsy et al. 2007; Sami et al. 2016; Kopecká et al. 2023; Varshney et al. 2023). Furthermore, like proline, soluble sugars are vital for the antioxidant response of plants. Huang et al. (2013) observed that the higher levels of soluble sugars (e.g., glucose) in stressed plants increased the activity of antioxidant enzymes, thereby reducing the oxidative damage from ROS. This is particularly relevant considering that soluble sugars serve as the principal substrate for the pentose phosphate pathway, which is essential for generating NADPH, a critical component for maintaining robust antioxidants like GSH in an active state (Bolouri-Moghaddam et al. 2010; Huang et al. 2013).

As discussed earlier, one significant impact of waterlogging is the induction of the Pasteur Effect, which accelerates the consumption of soluble sugars. The availability of these sugars is vital as they support the continuation of glycolysis, ensuring the production of energy (ATP) under waterlogging stress, enabling cells to maintain active metabolism and survive adverse conditions (Gibbs and Greenway 2003; Bailey-Serres and Voesenek 2008; Cho et al. 2021). Waterlogging-tolerant genotypes can maintain an adequate supply of soluble sugars in the roots, ensuring glycolytic pathways remain operational. Conversely, sensitive genotypes experience a significant decline in soluble sugar levels, leading to an energy crisis.

In experiments with two *Actinidia* rootstocks under waterlogging, one tolerant genotype maintained stable soluble sugar levels and increased significantly by day five. The other sensitive genotype, however, initially experienced a rise in sugar content but then declined sharply, ending up with lower sugar levels than the more resilient type (Bai et al. 2022). Similar findings were reported by Li et al. (2021), which emphasized the importance of soluble sugar availability (e.g., sucrose) in the roots of tolerant genotypes for maintaining anaerobic metabolism. Comparative experiments on flood-tolerant *Quercus robur* and more sensitive *Fagus sylvatica* revealed that *Q. robur* preserved its root sugar content, while *F. sylvatica* showed a steady decline in soluble sugar levels under waterlogging (Ferner et al. 2012). In *Citrus* rootstocks, while both genotypes showed a decline in the soluble sugar content under waterlogging, the sensitive rootstock showed a more pronounced decline (Vu and Yelenosky 1991). Moreover, starch catabolism represents a fundamental strategy against waterlogging, serving as the primary reservoir for soluble sugars necessary for glycolysis (Loreti et al. 2018). Plants attempt to minimize the depletion of soluble sugars by mobilizing starch reserves, which are primarily a storage form of simple sugars (Martínez-Vilalta et al. 2016). In this regard, in a waterlogging experiment involving three tolerant *Actinidia* rootstocks, starch mobilization in the roots played a pivotal role in supporting soluble sugar production under stress. In fact, a significant reduction in starch concentration was observed, accompanying an increase in soluble sugars, such as glucose, fructose and sucrose, which are essential for energy metabolism (Li et al. 2020). *Citrus* plants of *Citrange Carizo* showed a significant decrease in starch levels, by 35%, in roots at day 36 of waterlogging, accompanied by a significant increase of 37%–56% in soluble sugars (Martínez-Alcántara et al. 2012). In gray poplar (*Populus* × *canescens*), under root hypoxia, an increase in starch degradation has been observed, accompanied by an accumulation of soluble sugars such as glucose and fructose in the roots (Kreuzwieser et al. 2009). Similarly, in an experiment assessing *Citrus* rootstocks' waterlogging tolerance, both sensitive and tolerant types experienced significant decreases in root starch (45% by day 24 and 51% by day 40) compared to controls, along with increases in soluble sugars (Vu and Yelenosky 1991).

Additionally, high consumption of soluble sugars in roots subjected to hypoxia stress could also be compensated in tolerant genotypes through the effective transport of photoassimilates from photosynthetic organs to the roots via the phloem. Waterlogging primarily inhibits phloem transport in susceptible genotypes, leading to starch and sugar accumulation in leaves and the phloem, while resulting in the rapid depletion of starch reserves in roots. This dynamic underscores the reliance on starch reserves within roots to sustain soluble sugar levels, ultimately leading to progressive depletion under prolonged stress. This phenomenon has been observed in various species, including *Helianthus annuus* (Wample and Davis 1983), *Citrus* (Martínez-Alcántara et al. 2012), several oak species (Gravatt and Kirby 1998), *Syzygium samarangense* (Hsu et al. 1999), *Quercus robur* (Ferner et al. 2012), *Fagus sylvatica* (Ferner et al. 2012), *Medicago truncatula* (Lothier et al. 2020), *Ricinus communis* (Peuke et al. 2015), *Solanum lycopersicum* (Mignolli et al. 2021), different *Prunus* rootstocks (McGee et al. 2022) and *M. charantia* (Su et al. 1998). Nonetheless, some tolerant genotypes demonstrate the ability to maintain phloem transport during waterlogging, thereby supporting the carbon demand of organs in hypoxia/asphyxia. Studies on various *Fraxinus* species revealed that tolerant species store carbohydrates in their roots by breaking down starch and enhancing phloem transport of mannitol and sucrose from the leaves. This buildup was characterized by the accumulation of these soluble sugars in the phloem and less buildup in the leaves. In contrast, sensitive genotypes showed an accumulation of starch and soluble sugars in the leaves and phloem, alongside a general reduction in sugars in the roots, indicative of ineffective phloem transport and discharge under waterlogging (Jaeger et al. 2009). Similarly, another research study indicated that tolerant tree species of *Nyssa sylvatica* could accumulate starch in their roots and maintain stable soluble sugar levels during waterlogging, while sensitive species experienced significant reductions in starch and sugars, resulting in higher mortality rates, highlighting the importance of nutrient translocation for survival under such conditions (Angelov et al. 1996). In the tolerant species of *Populus x canescens*, enhanced phloem transport from leaves to roots was evidenced by increased sucrose transport, coupled with elevated soluble sugar concentrations in the roots and maintenance of starch reserves, despite reductions in starch content in the leaves. This improvement was vital for sustaining fermentative metabolism at the root level (Kreuzwieser et al. 2009). In *G. max* (Takahashi et al. 2018) and *Cucumis sativus* (Qi et al. 2020), the transport of sugars from the leaves to submerged organs via the phloem proved essential for triggering adaptive responses to hypoxic stress caused by waterlogging.

Overall, these studies highlight the critical role of carbohydrate metabolism in waterlogging tolerance. The maintenance and mobilization of starch and sugar in submerged organs are pivotal characteristics of flood-resistant plants (Gérard et al. 2009; Calvo-Polanco et al. 2012), while the decline of starch and sugar reserves in sensitive plants severely restricts metabolic activity in hypoxia, culminating in plant mortality (Angelov et al. 1996; Loreti et al. 2016; Loreti et al. 2018; Nurrahma et al. 2021; Ding et al. 2019). Additionally, the starch and sugar concentration in the submerged organs appears to be essential for facilitating morphological adaptations to stress, such as the development of adventitious roots, further enhancing plants' tolerance to waterlogging (Li and Leung 2000; Liu and van Staden 2001; Qi et al. 2020; Takahashi et al. 2018; Yan et al. 2024; Zhang et al. 2017).

In addition to the metabolic adaptations involving carbohydrates, it is crucial to consider the role of energy-sensing mechanisms, particularly the TARGET OF RAPAMYCIN (TOR) complex and SUCROSE NON-FERMENTING 1-RELATED PROTEIN KINASE-1 (SnRK1), in mediating plant responses to waterlogging stress. The TOR complex is crucial in regulating cell growth and metabolism in response to nutrient availability, including carbohydrate levels during stress conditions. It serves as a central hub that modulates metabolic processes based on energy status, which becomes essential when plants confront anaerobic environments caused by waterlogging (Wang et al. 2025; Liu et al. 2025). Conversely, the SnRK1 pathway acts as an energy sensor that activates survival mechanisms when energy levels drop, including the promotion of catabolic processes and the inhibition of growth (Mesejo et al. 2019; Ramon et al. 2019). In waterlogging-tolerant genotypes, the interplay between these energy-sensing pathways and carbohydrate metabolism may facilitate the maintenance of soluble sugar and starch reserves, thus supporting continued ATP production necessary for survival. Therefore, understanding these regulatory mechanisms may provide insights into the physiological and biochemical responses under waterlogging stress, ultimately highlighting the importance of integrating metabolic and signaling pathways in developing resilient crops.

2.5 | Methylglyoxal Accumulation and Glyoxalase System

Building on the discussion of physiological responses to waterlogging, it is essential to consider the role of methylglyoxal (MG), a compound that has emerged as a significant focus in plant stress responses. MG is an α,ß-dicarbonyl aldehyde widely studied in animal systems and increasingly recognized for its implications in plants. It acts as a signaling molecule in stress response conditions; however, its excessive accumulation can be toxic to plants, impairing cellular function (Yadav et al. 2005; Hoque et al. 2012; Kaur, Kushwaha, et al. 2015; Mano et al. 2009; Hasanuzzaman et al. 2017).

In plants, both biotic stresses (e.g., fungal infections) (Chen et al. 2004; Melvin et al. 2017) and abiotic stresses (e.g., salinity, drought and low temperatures) (Yadav et al. 2005; Yadav et al. 2008; Talaat et al. 2023; Batth et al. 2020; Parvin et al. 2024; Kaya et al. 2023) have been shown to increase the MG content. A study of *S. indicum* plants indicated that waterlogging induced a significant increase in MG levels, up to 60%, 42%, 46% and 47% at 2, 4, 6 and 8 days, respectively, compared to control plants. This finding highlights the previously unrecognized link between waterlogging stress and MG accumulation in plant tissues (Anee et al. 2019).

The formation and elimination of MG become critical under waterlogging conditions because it poses risks as a toxic compound. MG interacts with the main cellular macromolecules, such as proteins and nucleic acids. It can induce cellular damage directly through protein glycation, forming advanced glycation end products (AGEs) (Thornalley 2008; Rabbani and Thornalley 2012; Rabbani and Thornalley 2014) and inhibiting important mitochondrial enzymes (Kun 1950; Seo et al. 2014; de Souza Prestes et al. 2022; Kalapos and de Bari 2023), glycolytic enzymes (Leoncini et al. 1980), and various transport and defense proteins (Ferguson et al. 1998). Additionally, MG can disrupt nucleic acids, inhibiting protein synthesis and causing harmful mutations (Krymkiewicz 1973; Thornalley 2008; Rabbani and Thornalley 2012; Rabbani and Thornalley 2014). Moreover, the primary source of MG stems from triosophosphate intermediates of glycolysis, including dihydroxyacetone phosphate (DHA-P) and glyceraldehyde-3-phosphate (GA-3P) (Kalapos 1999; Yadav et al. 2005; Kaur, Kushwaha, et al. 2015; Kaur, Sharma, et al. 2015). This relationship between waterlogging and MG accumulation is further illustrated in Figure 5.

Consequently, enhanced glycolytic processes observed under waterlogging conditions can lead to increased MG formation, which may not merely be a byproduct but rather an active participant in the plant's stress response. Specifically, elevated glycolytic flux can result in the accumulation of intermediates such as dihydroxyacetone phosphate (DHA-P) and glyceraldehyde-3-phosphate (GA-3P), ultimately facilitating the buildup of MG (Richard 1993; Yadav et al. 2005; Kaur, Kushwaha, et al. 2015; Kaur, Sharma, et al. 2015). Furthermore, the reduced functionality of key enzymes, such as glyceraldehyde-3-phosphate dehydrogenase, may exacerbate this accumulation due to decreased availability of NAD^+, which is crucial for optimal glycolytic function and is often limited during intense fermentation activity. In contrast, a well-coordinated glycolytic and fermentative enzyme activity could play a protective role in mitigating MG accumulation, thereby suggesting that MG formation should not be viewed solely as a detrimental byproduct but rather as an integral component of stress response mechanisms (Richard 1993; Beisswenger et al. 2003; Barinova et al. 2023). Therefore, reducing MG through genetic manipulation should be approached with caution, as it may pose additional risks to plant health by impairing the plant's ability to effectively manage stress responses.

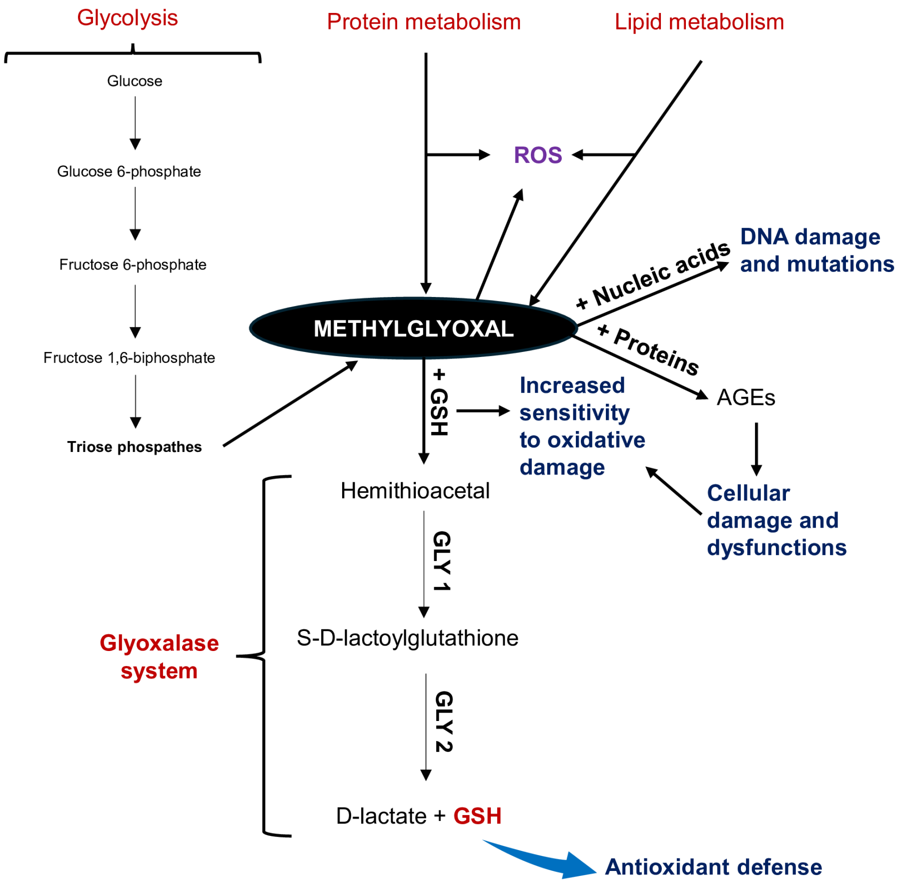

FIGURE 5 | Schematic representation of methylglyoxal (MG) formation and the glyoxalase system. Methylglyoxal is produced during both protein and lipid metabolism, with glycolysis serving as a significant source through spontaneous reactions involving triose phosphates. The synthesis of MG is associated with increased reactive oxygen species (ROS) production, which can lead to nucleic acid damage, resulting in potential mutations, and the formation of advanced glycation end products (AGEs) that are toxic to cells. MG also modifies proteins, altering their structure and affecting enzymatic activity, including that of antioxidant enzymes, thus compromising cellular defense against oxidative stress. Additionally, MG sequesters glutathione (GSH), a key non-enzymatic antioxidant, to form a hemithioacetal, further weakening antioxidant defenses. To detoxify MG and liberate GSH, cells activate the glyoxalase system, which converts MG to D-lactate while releasing GSH.

To combat the MG stress that arises under adverse conditions, plants have developed the glyoxalase system, comprising two critical enzymes: GLYOXALASE 1 and 2 (GLY1 and GLY2). The pathway initiated by GLY1 involves the isomerization of the hemithioacetal formed through the spontaneous reaction of MG and GSH into S-D lactoylglutathione (Racker 1951; Kaur et al. 2014). The second enzyme, GLY2, catalyzes the hydrolysis of S-D lactoylglutathione into D-lactate, regenerating GSH in the process (Racker 1951; Kaur et al. 2014).

Research on the glyoxalase system is valuable, as it plays a fundamental role in improving plant tolerance to adverse environmental conditions by maintaining low levels of MG and preventing excessive accumulation resulting from biotic and abiotic stresses. For instance, transgenic tobacco plants engineered to overexpress the genes encoding these enzymes demonstrated improved survival rates under heavy metal stress, resulting in reduced MG accumulation compared to their wild-type counterparts (Singla-Pareek et al. 2006). Similarly, transgenic rice lines showed a higher tolerance to toxic concentrations of MG compared to non-transgenic plants, correlating with the heightened activity of the glyoxalase system during stress (Singla-Pareek et al. 2008).

Additionally, several studies have indicated that enhancing the activity of the glyoxalase system promotes higher tolerance to various stresses (Hossain et al. 2010; Hasanuzzaman and Fujita 2011; Hasanuzzaman et al. 2018; Rahman et al. 2016; Mostofa et al. 2015; Alam et al. 2022). While research specific to the glyoxalase system under waterlogging conditions is still limited, Anee et al. (2019) showed that this enzyme system plays a key role in improving plant tolerance to waterlogging stress. Their findings showed that sesame plants subjected to waterlogging exhibited increased activity of both GLY1 and GLY2, facilitating the limitation of MG accumulation in response to stress (Anee et al. 2019).

3 | Physiological Changes and Impact of Endogenous Hormones

3.1 | Influence of Waterlogging on Root Hydraulic Conductivity and Photosynthetic Performance

Waterlogging profoundly affects plant physiology, primarily by altering root hydraulic conductivity and consequently influencing the overall water status and photosynthetic efficiency of the plant canopy. One significant consequence of waterlogging is the reduction in hydraulic conductivity of roots, which limits their ability to absorb water from saturated soils despite the presence of near-zero water potentials. This decline is primarily due to the inhibition of water transport mediated by aquaporins, which are transmembrane proteins essential for facilitating water movement across cell membranes and significantly influence water absorption within the root system (Bramley et al. 2007; Gambetta et al. 2017) (Figure 6).

Under hypoxic and asphyxic conditions induced by waterlogging, the activity of aquaporins is negatively affected. The associated reduction in cellular ATP content hinders the phosphorylation of aquaporins, impairing effective water absorption (Kamaluddin and Zwiazek 2001; Kapilan et al. 2018). Additionally, the initiation of fermentative metabolism, particularly lactic fermentation, leads to increased lactic acid production, resulting in an acidic cellular environment that further inhibits aquaporin activity (Tournaire-Roux et al. 2003; Kudoyarova et al. 2022; McGaughey et al. 2018). The ensuing deficiency of ATP also disrupts the active transport of H^+ ions from the cytoplasm into the vacuole, which exacerbates the acidification caused by the transition from aerobic to anaerobic respiration (Ratajczak 2000).

Conversely, waterlogging-tolerant genotypes exhibit more efficient energy metabolism under hypoxic conditions by regulating cellular pH through a balance of lactic and alcoholic fermentation, thereby mitigating lactate accumulation and preserving aquaporin functionality. For instance, studies on wild and mutated *Z. mays* plants that cannot initiate alcoholic fermentation reveal a significant drop in ATP levels and an inability to stabilize cytoplasmic pH, leading to continuous acidity due to prolonged lactic fermentation (Roberts et al. 1984). Comparative research between sensitive and tolerant species of *Actinidia* following 11 days of waterlogging supports this, demonstrating that the tolerant genotype effectively maintained tissue water status through alcoholic fermentation, in contrast to the sensitive genotype that experienced significant lactate accumulation and moisture loss (Li et al. 2021).

The physiological ramifications of these changes extend beyond the roots, as diminishing root hydraulic conductivity directly impacts the water status of canopy tissues. This deterioration leads to reduced physiological parameters related to gas exchange and the overall photosynthetic process. Hypoxia-induced stress in roots results in cell death and biochemical alterations, triggering a cascade of hormonal signals that affect the entire plant (Yiu et al. 2011; Olorunwa et al. 2023). Although soil remains saturated, hypoxic conditions in roots increase hydraulic resistance, thereby reducing water availability at the canopy level (Bramley et al. 2007; Haverroth et al. 2025). For example, *Actinidia chinensis* under waterlogged conditions exhibited a significant decline in root hydraulic conductivity, leading to negative osmotic and xylem potential values and a decrease in leaf turgor, which in turn contributed to leaf tissue dehydration (Jackson and Drew 1984).

The impairment of water uptake from roots results in water stress at the leaf level, leading to stomatal closure and reduced transpiration, which compromises photosynthetic activity (Kubota et al. 2024). A study on *Sesamum indicum* demonstrated a significant decline in relative water content of leaves following waterlogging, indicating progressive dehydration (Anee et al. 2019). In contrast, the waterlogging-tolerant species *A. valvata* utilized morphological adaptations such as adventitious roots to maintain physiological parameters and stabilize water balance, unlike the sensitive *A. chinensis*, which suffered early lactate accumulation and physiological impairment (Li et al. 2021).

Transpiration is critical for nutrient transport, cooling leaf tissue, and regulating leaf temperature. Waterlogging-induced impairment of transpiration elevates leaf temperatures, potentially leading to lethal stress for leaf tissues (Smith et al. 1989; Zhang, Zhu, et al. 2019; Zhang, Zhou, et al. 2019). Furthermore, waterlogging restricts chlorophyll synthesis, resulting in foliage senescence and yellowing, which adversely affects photosynthetic efficiency. Experiments on *S. indicum* illustrated lower levels of key photosynthetic pigments in waterlogged plants compared to controls (Anee et al. 2019). Similar results have been reported across various species, including Alfalfa (*Medicago sativa*) (Smethurst and Shabala 2003), sugarcane (*Saccharum officinarum*) (Jain et al. 2017), wheat (*Triticum aestivum*) (Tiryakioğlu et al. 2015), tomato (*Solanum lycopersicum*) (Rasheed et al. 2018), rapeseed (*Brassica napus*) (Lee et al. 2014), and sorghum (*Sorghum bicolor*) (Zhang, Zhu, et al. 2019; Zhang, Zhou, et al. 2019), highlighting the extensive impact of waterlogging on photosynthetic activity.

Moreover, numerous studies have documented a decline in the activity of RuBisCO, the crucial enzyme for CO_2 fixation, due to oxidative stress during waterlogging (Lee et al. 2014; Kuai et al. 2020). This oxidative damage, particularly pronounced in chloroplasts, severely limits photosynthesis, as evidenced by research on two *S. bicolor* cultivars subjected to waterlogging, where the sensitive genotype displayed a 62% reduction in photosynthesis compared to 39% in the tolerant genotype (Zhang, Zhu, et al. 2019; Zhang, Zhou, et al. 2019). Increased antioxidant enzyme activity in the tolerant genotype indicates a capacity to mitigate oxidative damage and preserve photosynthetic function, underscoring the vital role of metabolic regulation in sustaining hydraulic conductivity and physiological resilience during waterlogging.

3.2 | Hormonal Interactions and Responses

Studies suggest that roots can exert a significant influence on leaf physiology through the chemical signals transmitted to the foliage, particularly endogenous plant hormones (Smith et al. 1989; Zhao et al. 2021; Cantero-Navarro et al. 2016). Plant hormones play a central role in regulating and coordinating metabolism, growth, and physiological responses, allowing plants to adapt to waterlogging stress (Benschop et al. 2006; Wu et al. 2019). Under hypoxic conditions, roots can significantly influence leaf physiology by producing and transporting hormones such as ethylene. In roots, increased synthesis of the ethylene precursor ACC occurs, which is transported to the leaves through the xylem. In leaves, oxygen facilitates the conversion of ACC to ethylene, while the enzyme ACC oxidase modulates ethylene biosynthesis in response to flooding stress (English et al. 1995; Zhang, Zhu, et al. 2019; Zhang, Zhou, et al. 2019;

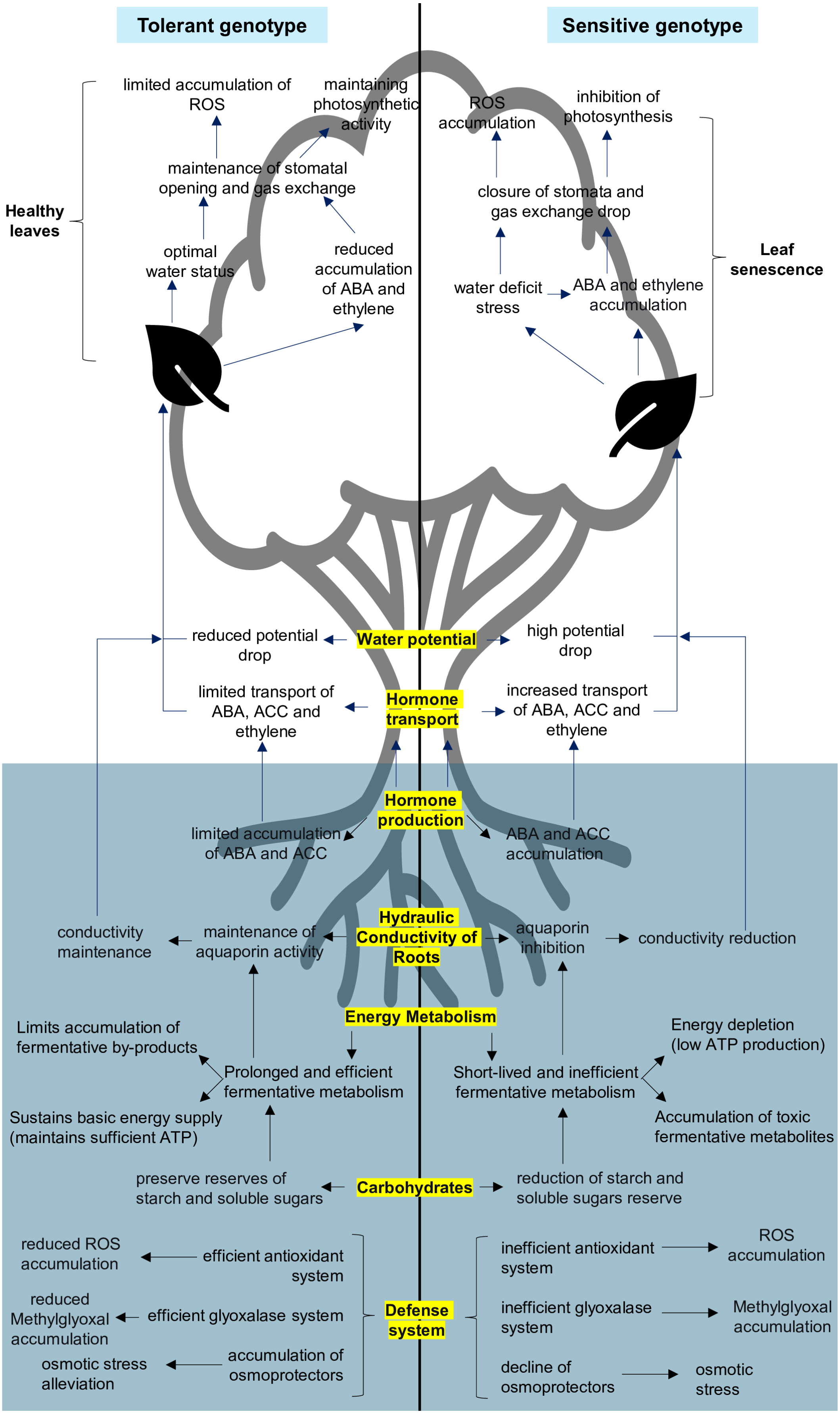

FIGURE 6 | Legend on next page.

FIGURE 6 | Overview of physiological, hormonal, and biochemical changes induced by waterlogging in sensitive and tolerant genotypes. This figure illustrates the responses initiated in submerged roots that subsequently affect non-submerged organs, including stems and leaves. The depicted changes encompass alterations in hormonal signaling, metabolic pathways, and physiological processes, highlighting the differential responses between waterlogging-sensitive and waterlogging-tolerant genotypes.

Sasidharan and Voesenek 2015). Excessive ethylene levels at the leaf level stimulate abscission and senescence processes, thus limiting plant growth while concurrently regulating water loss by reducing the transpirable surface area of the plant (Najeeb et al. 2015; Zhang, Zhu, et al. 2019; Zhang, Zhou, et al. 2019; Najeeb et al. 2017). Application of ethylene inhibitors, such as aminoethoxyvinylglycine (AVG), can mitigate leaf abscission and senescence and help maintain more stable photosynthetic rates during waterlogging, indicating the strong signaling role of ethylene from roots to leaves (Najeeb et al. 2015). Moreover, ethylene accumulation in leaf petioles encourages epinasty, the downward curvature of leaves due to faster growth of the upper (adaxial) side of the petiole compared to the lower side (abaxial). Experimental evidence from *S. lycopersicum* showed that genetically modified plants with reduced ethylene production exhibited less epinastic curvature under waterlogging conditions than wild-type plants, underlining ethylene's crucial role in inducing this response (English et al. 1995). Still in *S. lycopersicum* plants, an increase in ethylene levels was observed under waterlogging stress compared to the controls, and this increase was responsible for the induction of leaf epinasty (Geldhof, Pattyn, et al. 2022). In species such as *H. annuus* (Rawson 1979), *G. max* (Stevenson and Shaw 1971), *S. lycopersicum* (Mohorović et al. 2023) and *Vigna unguiculata* (Schakel and Hall 1979), leaf orientation shifts from horizontal to vertical, reducing the surface area for light interception while enhancing water use efficiency.

Another vital hormone involved in the physiological response to waterlogging stress is abscisic acid (ABA), known as the stress hormone. Under abiotic stresses, ABA accumulation in leaves induces stomatal closure, thereby minimizing water loss, albeit at the expense of photosynthesis and thermoregulation (Lim et al. 2015; Zhao et al. 2017; Niu et al. 2018). Similarly, waterlogging induces ABA accumulation in leaves in various plant species, including *Pisum sativum* (Zhang and Zhang 1994), *N. tabacum* (Hurng et al. 1994), *S. lycopersicum* (Geldhof et al. 2024) and *Citrus* (Arbona and Gómez-Cadenas 2008). For instance, in *Vigna radiate*, after just 2 days of waterlogging, transpiration and stomatal conductance decreased significantly alongside a sharp increase in ABA level, confirming the role of ABA in regulating stomatal closure and minimizing water loss in response to waterlogging stress (Ahmed et al. 2006). Under waterlogging conditions, an increase in ABA levels was observed in *Malus domestica*, which contributed to a reduction in transpiration (Bhusal et al. 2023).

Much like ethylene, ABA serves as a signaling compound between the root and canopy. Under abiotic stress, one of the first sources of canopy ABA is often the pool synthesized by the roots and transported via the xylem (Schurr et al. 1992; Bhusal et al. 2023). A recent study complements this understanding by demonstrating that plant roots exhibit plasticity in their branching patterns, particularly through the xerobranching response, which systematically represses lateral root formation when roots lose contact with water. This response is regulated by the radial movement of the phloem-derived hormone abscisic acid (Mehra et al. 2022). It has been found that ABA disrupts intercellular communication between the inner and outer cell layers via plasmodesmata, leading to the closure of these intercellular pores and subsequently blocking the inward movement of the auxin signal essential for lateral root branching (Mehra et al. 2022). Interestingly, while research has shown that, under waterlogging conditions, root production of ABA diminishes due to hypoxic stress, we noted that once root tips regain contact with moisture, the ABA response rapidly attenuates (Zhang and Zhang 1994; Arbona and Gómez-Cadenas 2008). This is further supported by findings in *S. lycopersicum*, where a decline in ABA accumulation in the xylem coincided with increased levels in the leaves (Janowiak et al. 2010), and by research in Arabidopsis showing upregulation of ABA biosynthesis genes in leaves but downregulation in roots under flooding conditions, reflecting actual ABA concentrations (Hsu et al. 2011).

As shown by the study conducted by Zhang and Zhang (1994) on *P. sativum*, ABA accumulation in leaves seems to arise from a decrease in cellular turgor in leaf tissues due to the water stress induced by waterlogging. In fact, leaves exhibited reduced turgor, higher ABA content and lower stomatal conductance compared to more turgid leaves. In the latter, a decline in conductance only occurred following increased ABA levels (Zhang and Zhang 1994). In *Arabidopsis*, a decrease in leaf cell turgor rapidly induces ABA biosynthesis by stimulating the expression of *NCED3*, a key regulator of this process. A significant increase in ABA levels has been observed as early as 5 min after the reduction in leaf turgor (Sussmilch et al. 2017). Similar findings were reported by Else et al. (2001) in *Ricinus communis*, where ABA concentration in flooded roots decreased significantly, while ABA in the phloem increased, suggesting that the leaves initiated production in response to turgor loss caused by the poor hydraulic conductance of the root. Furthermore, the reduced hydraulic conductivity of roots under hypoxia leads to decreased water absorption, resulting in a rapid drop in leaf water potential and consequent deterioration of leaf tissue water status. Thus, initial stomatal closure likely results from a hydraulic signal (low root conductivity), with ABA further contributing to the maintenance of this response (Else et al. 2001; Sussmilch et al. 2017).

Hypoxia/asphyxia conditions can also limit the production and transport of hormones such as cytokinins. Root tips serve as the primary source of cytokinins, which are transported to the canopy through the xylem. This hormone inhibits leaf senescence and promotes growth. Numerous studies have shown that exogenous application of cytokinin can significantly delay plant senescence under stress conditions (Goicoechea et al. 1995; Zaheer et al. 2019; Mughal et al. 2024). In experiments conducted on several waterlogged species, including *Phaseolus* (Neuman et al. 1990), hybrid poplar (Neuman et al. 1990), *S. lycopersicum* (Geldhof, Novák, and van de Poel 2022), *P. persica* (Ateeq et al. 2023), *Z. mays* (Hu et al. 2022), *T. aestivum* (Nguyen et al. 2016) and *H. annuus* (Burrows and Carr 1969), the concentration of cytokinins in the plant dramatically decreased due to damage to the root tips thereby limiting the export of this critical hormone to the aerial part of the plant. Similarly, transgenic plants of *Arabidopsis* (Zhang et al. 2000) and *T. aestivum* (Tereshonok et al. 2011) engineered for high cytokinin production exhibited enhanced vitality and higher tolerance to flooding stress, maintaining greener leaves for prolonged periods and delaying leaf senescence compared to wild-type plants. These findings collectively underscore the crucial role that endogenous hormones play in the physiological responses of plants to waterlogging, influencing growth, senescence, and overall plant resilience.

3.3 | The Role of Group VII Ethylene Response Factors in Low Oxygen Perception and Signaling During Waterlogging in Plants

Group VII ERFVIIs are critical transcription factors that regulate plant responses to hypoxia, particularly during flooding or waterlogging events. These factors are uniquely characterized by their vulnerability to oxygen levels due to the oxidation of their N-terminal cysteine residue by Plant Cysteine Oxidases (PCOs) (Gibbs et al. 2011; Licausi et al. 2011). Under hypoxic conditions, PCO activity diminishes, leading to the stabilization of ERFVIIs, allowing them to translocate to the nucleus and activate hypoxia-responsive genes (HRGs). These genes facilitate metabolic adjustments necessary for anaerobic respiration, promoting survival during low oxygen availability (Kunkowska et al. 2023). The N-end rule pathway, which governs the stability of these ERFVIIs, relies upon the oxidation status of the N-terminal cysteine (Nt-Cys) residue (Gibbs et al. 2011). This pathway regulates protein degradation and facilitates rapid responses to changes in oxygen levels, where decreased PCO activity under hypoxic conditions protects ERFVIIs from degradation, thus enhancing their activity and allowing them to activate HRGs (Akter et al. 2024). Notably, the ectopic stabilization of these transcription factors leads to an adaptive response that primes the plant's physiological status for flooding tolerance.

Recent studies emphasize the interactions between oxygen and nitric oxide (NO) signaling during waterlogging. The stabilization of ERFVIIs is also mediated through ethylene signaling and NO, with ethylene enhancing the stability of ERFVIIs through mechanisms that involve phytohormonal crosstalk (Weits et al. 2014; Hartman et al. 2019). Ethylene acts as a signaling molecule that increases NO scavengers like PHYTOGLOBIN1, promoting the accumulation of ERFVIIs even prior to hypoxic conditions, which helps to preadapt plants for subsequent flooding stress (Hartman et al. 2019). This mechanism highlights the nuanced regulatory framework involving multiple gaseous signals in plant responses to low oxygen stress.

Another critical factor influencing the transcriptional response of ERFVIIs to hypoxia is the cellular energy status as regulated by the TOR pathway. Recent findings show that the activation of ERFVIIs requires optimal energy availability, implicating the TOR pathway in fine-tuning oxygen-sensing mechanisms. In hypoxic conditions, low ATP levels attenuate TOR activity, consequently dampening the induction of HRGs by ERFVIIs (Kunkowska et al. 2023). This convergence of energy sensing and oxygen perception underscores the importance of maintaining homeostasis in metabolic signaling to facilitate optimal adaptive responses during waterlogging.

The stabilization of ERFVIIs under low oxygen stress initiates significant physiological adaptations. For instance, the expression of genes such as *ALCOHOL DEHYDROGENASE* (ADH) and *PYRUVATE DECARBOXYLASE* (PDC) increases, promoting fermentative metabolism, which is essential for energy production in hypoxic environments (Kunkowska et al. 2023; Akter et al. 2024). Additionally, studies showed that mutants lacking functional N-end rule components exhibit enhanced expression levels of HRGs, improving their tolerance to hypoxia and waterlogging (Gibbs et al. 2011; Licausi et al. 2011). Furthermore, manipulating the expression of components in the N-end rule pathway, such as reducing the activity of the N-recognin E3 ligase PRT6, has led to sustained biomass and chlorophyll retention in transgenic plants under waterlogged conditions, signifying enhanced survival and growth during prolonged submergence (Mendiondo et al. 2016). These reports collectively emphasize the pivotal role of ERFVIIs in mediating both the perception and the downstream signaling necessary for plants to cope with low oxygen stress arising from waterlogging.

4 | Limitations and Future Perspectives

This review highlights the intricate adaptations employed by plants to cope with reduced oxygen availability, including anaerobic respiration, the activation of antioxidant systems, and the accumulation of osmoprotectants. Mechanisms such as the glyoxalase system, which detoxifies harmful methylglyoxal accumulation, underscore the importance of metabolic pathways in enhancing waterlogging resilience. Importantly, the differential responses among various species/genotypes demonstrate the potential to select for or engineer crop varieties with improved tolerance to waterlogging, thereby preserving agricultural productivity and ecosystem health in the face of environmental stressors.

However, despite the insights gained regarding plant responses to waterlogging, several limitations in the current research landscape warrant acknowledgment. Many studies focus on a limited range of species, which may restrict the generalizability of the findings. Furthermore, the complex interactions between waterlogging stress and other abiotic factors, such as salinity and temperature fluctuations, are often not adequately addressed. Future research should aim to explore these multifactorial interactions and employ a broader range of plant species to develop a more comprehensive understanding of waterlogging tolerance mechanisms. Additionally, integrating molecular and genetic approaches with physiological studies could uncover novel regulatory pathways and enhance the development of strategies for crop improvement, particularly in the context of sustainable agricultural practices in waterlogged regions.

Author Contributions

C.D., A.S. and R.A. conceived the idea. C.D. wrote the manuscript. M.Y.K., A.S., R.A. revised the manuscript. All authors read and approved the manuscript.

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In this manuscript, no generative AI has been employed.

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The authors declare no conflicts of interest.

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The authors have nothing to report.

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