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PLANT RESPONSE TO SOIL WATERLOGGING: PHYSIOLOGICAL, MORPHOLOGICAL AND BIOCHEMICAL ADAPTATIONS – A REVIEW

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Abstract

The phenomenon of global climate change, largely driven by human activities and associated with rising air temperatures, not only leads to intensified and longer-lasting droughts, but also increases the likelihood of extreme precipitation events that may trigger flooding concerns. The stress caused by soil waterlogging is intricate, leading to several concurrent challenges that disrupt normal plant functioning. A key challenge is the oxygen deficiency, which arises from the considerably reduced diffusion rates in floodwater relative to those in the atmosphere. The ability of plants to adapt to waterlogging stress is quite limited primarily because of the partial or complete absence of oxygen in the growth medium. However, certain plant species have evolved specific mechanisms through evolution that allow them to survive for a certain duration in hypoxic or anoxic environments. These mechanisms can be classified into two broad categories: plant morpho-anatomical adaptations to waterlogging stress and the biochemical and physiological responses of plants to such stress. These adaptations are interconnected rather than acting in isolation. Instead, they are intricately connected. This review explores: (i) the impact of soil waterlogging on plant development and function; (ii) current insights into the signal transduction pathways involved in stress recognition and response; and (iii) the key morpho-anatomical and physiological strategies plants use to cope with waterlogged conditions.

***Key words**: waterlogging, plant stress, oxygen deficiency, ethylene, adventitious roots, aerenchyma, flooding adaptation.*

INTRODUCTION

Soil waterlogging is a severe abiotic stress that occurs when water saturates the spaces between soil particles, severely limiting oxygen availability to plant roots and leading to hypoxic or anoxic conditions (Walne & Reddy, 2021). Under these conditions, the oxygen diffusion rate is up to ten thousand times lower than in well-drained soils, significantly impairing root function (Manghwar et al., 2024).

When soil becomes waterlogged, oxygen supply to the roots drops sharply, which stunts their growth and reduces the plant's ability to absorb water and nutrients (Abuarab et al., 2019). Excess water also disrupts the metabolism of aerobic soil microorganisms (Siebielec et al., 2020). Without oxygen, these microbes either die off or shift to anaerobic metabolism, producing organic acids that lower soil pH (Abdul Rahman et al., 2021). This acidification encourages harmful microbial activity and accelerates nutrient leaching from the soil's adsorptive complex, further limiting root nutrient uptake (Husson, 2013).

The accumulation of excess water also alters the soil's hydraulic conductivity, reducing water movement and impeding root penetration. In saturated or nearly saturated conditions, the soil's capacity to transmit water is greatly diminished, hindering root penetration through the compacted layer of soil (Jitsuyama, 2017; Luo et al., 2024). Collectively, these effects slow plant metabolism and, if prolonged, may cause wilting.

Although drought stress is more common, waterlogging remains a significant threat - particularly to crops. Poor drainage and excessive rainfall can quickly create oxygen-deficient soil conditions that impair root function (Topali et al., 2024).

Moreover, global climate change - driven by human activities and marked by rising air temperatures - intensifies both droughts and heavy rainfall. Over the last few decades, scientists studying this topic have persistently raised awareness about the problems associated with global climate change (Furtak & Wolińska, 2023; Bolane et al., 2024). The growing frequency of alternating drought and flooding events confirms their predictions and suggests that crops will face increasing vulnerability to both types of stress in the future.

EFFECTS OF WATERLOGGING STRESS ON PLANTS

Waterlogging stress occurs when oxygen is partially or completely absented from the growth medium, triggering several interconnected challenges that disrupt plant functioning. The primary concern is the impaired respiration, which consequently affects all metabolic processes in the plant that require energy, i.e., adenosine triphosphate (ATP) molecules (Aslam et al., 2023). The negative impact on the plant's metabolism due to low oxygen levels in the growth medium (soil) also leads to competition between the plant's roots and beneficial aerobic microflora. As a result, roots must compete with soil microflora for scarce oxygen, which weakens beneficial microbial nitrification and reduces nutrient uptake (Martínez-Arias et al., 2023). These circumstances pose significant challenges to all aspects of plant development, especially regarding the transition from the vegetative to the generative phase. Prolonged exposure of roots to anaerobic conditions caused by waterlogging prevents flowering, pollination, fertilization, and seed maturation (Insausti & Gorjón, 2013).

Roots are the first to encounter oxygen deprivation and are highly sensitive to it. Numerous studies show that root growth declines significantly when soil oxygen concentration drops below 20% (Tete et al., 2015; Fukao et al., 2019). As oxygen decreases, carbon dioxide (CO_2) concentrations rise, which further hinders root development. For instance, elevated CO_2 in the rhizosphere has been shown to suppress cell division in the root apical meristem (Ben-Noah and Friedman, 2018).

Greenway et al. (2006) have reported that increased soil CO_2 levels adversely affected the growth of the root apical meristem by restricting cell division. This finding agrees with He et al. (2019).

Above-ground symptoms of waterlogging resemble those caused by drought. Although it may seem counterintuitive, waterlogged plants often show signs of water stress. This happens because roots damaged by hypoxia cannot absorb water, prompting the plant to close its stomata to conserve internal moisture (Olorunwa et al., 2022). However, stomatal closure also restricts carbon dioxide uptake, reducing photosynthesis and leading to visible leaf chlorosis (Liu et al., 2022). This deficiency is visually evident through leaf chlorosis, which becomes more pronounced as the anaerobic conditions in the soil last longer.

If the closure of stomata is insufficient in effectively reducing transpiration, the plant may shed its lower leaves to reduce the surface area for transpiration, thereby limiting water loss. However, shedding leaves reduces the plant's ability to produce assimilates, which in turn lowers ATP levels and limits the synthesis of key stress-related metabolites (Chada et al., 2023).

The inability of plants to efficiently perform photosynthesis and respiration during anaerobic stress conditions results in a dysfunction in the mitochondrial electron transport chain and oxidative phosphorylation (Jethva et al., 2022). This, in turn, leads to an increased production of reactive oxygen species (ROS), resulting in oxidative stress. Oxidative stress is a common occurrence in all forms of stress, including waterlogging stress, and it poses a significant threat to plant organisms.

Overproduction of ROS causes severe damage to lipids, proteins and other biomolecules present in cells (Sachdev et al., 2021). Exposure to flooding stress can also lead to osmotic stress in plants, which disrupts all metabolic and physiological processes within plant cells (Li et al., 2025).

Due to the combined effects of oxygen deficiency, nutrient loss, oxidative damage, and metabolic disruption, most plants can only tolerate waterlogging for a limited time. Only those species with specific adaptive strategies can survive extended periods under hypoxic or anoxic conditions.

WATERLOGGING STRESS SIGNAL TRANSMISSION

Roots are the primary plant organs to encounter waterlogging stress, due to their direct exposure to the saturated soil environment. The precise mechanisms by which roots perceive anaerobic stress and initiate signal transduction remain under active scientific investigation.

Some researchers propose that oxygen deficiency itself is the primary signal (Sasidharan et al., 2018), while others suggest that alterations in the physical or chemical properties of the soil under hypoxic conditions are responsible for triggering the stress response (Setter & Waters, 2003; Rupngam & Messiga, 2024).

Likewise, there is ongoing debate regarding the nature of the primary abiotic stress sensors that detect such signals within plant cells. One school of thought posits that plant cells contain specific oxygen-sensing molecules capable of detecting sharp declines in intracellular oxygen concentrations (Sewelam et al., 2016; León et al., 2021; Selinski et al., 2024). A notable example is Class-1 hemoglobin (Hb), a molecule with high oxygen affinity that allows it to bind oxygen even at extremely low intracellular concentrations (Cochrane et al., 2017).

Conversely, other researchers argue that no dedicated oxygen sensor exists. Instead, they propose that plant cells detect anaerobic stress through disturbances in cellular homeostasis resulting from oxygen deprivation (Schmidt et al., 2018; Kosová et al., 2018; Safavi-Rizi et al., 2020). These disturbances may manifest as changes in cytosolic pH, shifts from aerobic to anaerobic metabolism, fluctuations in the reduced-to-oxidized glutathione ratio, calcium ion (Ca^{2+}) fluxes, or broader disruptions in the cellular redox balance (Rathore et al., 2015).

When plant cells detect anaerobic stress - either directly or through disrupted homeostasis - they activate signaling pathways that produce second messengers, including ethylene, reactive oxygen species (ROS), calcium ions (Ca^{2+}), and nitric oxide (NO). These substances function as essential regulatory components of signaling pathways that transmit signals to transcription factors by activating a series of downstream cascades (Farnese et al., 2016). Ethylene or ROS trigger stress signaling cascades, primarily through MAPKs or calcium-dependent protein kinases. Ultimately, they stimulate the expression of specific defense genes, leading to a comprehensive defensive response (Jagodzik et al., 2018).

Under anaerobic conditions, ethylene serves as a key regulator of plant adaptation by activating ethylene response factors (ERFs). These transcription factors upregulate genes involved in several key adaptive responses, including:

1. the development of aerenchyma in roots,
2. the growth and development of adventitious roots,
3. stem elongation,
4. various morphological or physiological alterations that ultimately improve the plant's ability to adapt to anaerobic stress.

Figure 1 illustrates the general pathway by which plants detect flooding stress and initiate adaptive responses.

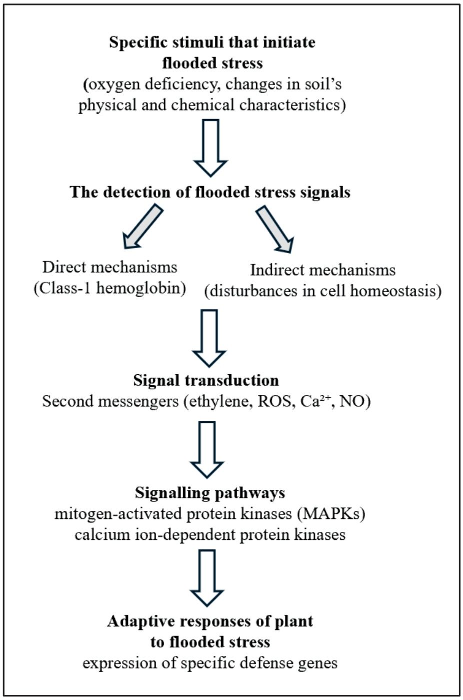

Figure 1. A simple diagram illustrating the pathway from recognizing flooded stress to the plant's response

PLANT MORPHO-ANATOMICAL AND PHYSIOLOGICAL ADAPTIONS TO WATERLOGGING STRESS

The ability of plants to adapt to anaerobic stress, caused by soil waterlogging, is quite limited because of the partial or complete absence of oxygen in the growth medium.

Nevertheless, certain plant species have evolved specific strategies that enable them to tolerate hypoxic or anoxic environments for limited periods. These strategies fall into two major categories: (1) morphological and anatomical adaptations, and (2) physiological modifications (Jia et al., 2021). These categories often operate in parallel; morpho-anatomical adaptations are typically accompanied by physiological changes, together forming an integrated response that enhances plant resilience under flooding stress.

Plant morpho-anatomical adaptations to waterlogging stress

Morphological and anatomical changes resulting from waterlogging primarily affect the root system, which is the first to detect anaerobic conditions in the soil (Lin et al., 2024). Common structural responses include: (1) the growth and development of adventitious roots, (2) the development of hypertrophic lenticels, (3) the formation of aerenchyma within the primary root cortex, and (4) the elongation of stem internodes (Leeggangers et al., 2023).

Growth and development of adventitious roots under soil waterlogging

In response to waterlogging, the plant activates a mechanism for the growth and development of adventitious roots, mainly occurring in the upper part of the root or in the lower part of the stem (Steffens & Rasmussen, 2016). These postembryonic roots are observed in several plant species, including rice, tomato and bittersweet (Sasidharan et al., 2018). When triggered by soil waterlogging, the formation of adventitious roots helps the plant escape hypoxic conditions in the root zone by improving oxygen uptake and increasing its chances of survival.

A plant's ability to promote the formation of adventitious roots is mainly based on the function of the hormone ethylene (Bai et al., 2020). Ethylene plays a significant role as a stress signal in plants affected by flooding, initiating various morphological and metabolic changes that facilitate their adaptation and survival in these challenging conditions. When plants face anaerobic stress, ethylene accumulates in plants underground parts at high levels because its diffusion and consequently its exit from the plant's roots are considerably hindered in these circumstances. During flooding, plant roots synthesize 1-aminocyclopropane-1-carboxylic acid (ACC), the direct precursor of ethylene. ACC is then transported to the stem—an aerobic region—where the enzyme ACC oxidase (ACO) converts it into ethylene, increasing ethylene concentrations in the stem. This rise in ethylene triggers adaptive responses in the submerged stem, initiating the plant's reaction to flooding stress (Khan et al., 2024). This response involves the activation of ethylene-responsive transcription factors (ERFs), which play a key role in regulating plant adaptation to flooding stress. Under anaerobic conditions, ethylene binds to membrane receptors, triggering a conformational change that releases ERFs into the cytosol. These transcription factors then move to the nucleus, where they activate stress-responsive genes essential for the plant's survival under hypoxic conditions (Wang et al., 2025) (Figure 2).

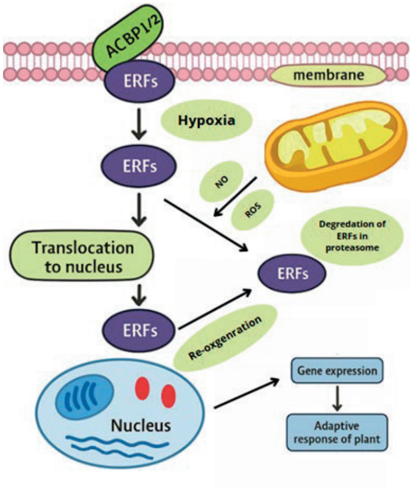

Figure 2. Diagram showing the ethylene-induced signaling pathway in plants facing waterlogging stress

In the context of adventitious root formation, ERF-activated genes are believed to encode enzymes that degrade cells adjacent to meristematic tissue in the root pericycle. This cell breakdown creates the necessary space for root meristem cells to divide and grow, ultimately leading to the emergence of adventitious roots (Roussos, 2023). While ethylene often promotes cell degradation or death, in this case, the process is beneficial, enabling structural adaptation under stress.

Ethylene's role in enhancing plant adaptation to waterlogging becomes evident under low-oxygen conditions.

In well-aerated environments, ethylene-responsive transcription factors (ERFs) remain inactive. Under these normal conditions, cysteine oxidases - together with reactive oxygen species (ROS) and nitric oxide (NO) - oxidize ERFs, marking them for degradation via the proteasome pathway. ERF activation is therefore tightly regulated and occurs only under stress, with ethylene acting as the primary hormonal trigger (Giuntoli & Perata, 2018).

Formation of hypertrophic lenticels at the stem base

A significant adaptive mechanism that plants utilize to cope with waterlogging stress is the formation of hypertrophic lenticels at the stem base, situated slightly above the water surface (Shimamura et al., 2010). These lenticels function to improve oxygen intake while simultaneously allowing the release of ethanol, methane, and other toxic byproducts that arise from anaerobic metabolic activity. Many scientists note that the formation of hypertrophic lenticels occurs alongside the development of aerenchyma in roots (Thomas et al., 2005; Sou et al., 2021). This is quite reasonable, as it allows the plant to secure a constant influx of oxygen from the atmosphere to its roots.

Although the formation of large cracks (i.e., hypertrophic lenticels) at the stem base is not fully understood, it is generally accepted that the hypertrophy of secondary aerenchyma is responsible for their development. This aerenchyma is formed through successive divisions of the phellogen and is characterized by its white, porous (spongy) tissue. Being of secondary origin, it differs in both morphology and anatomy from the primary cortical aerenchyma (Jackson et al., 2009).

Aerenchyma formation in the root

The typical response of a plant to waterlogging is the development of aerenchyma in its roots. This formation, along with the connection to hypertrophied lenticels, creates a pathway for the roots to interact with the atmosphere. As a result, the plant can supply oxygen from the atmosphere to all root cells, despite being in anaerobic conditions (Evans, 2004). It is important to highlight that a certain amount of oxygen transported to the root aerenchyma is released into the rhizosphere, creating a distinct small zone of aerobic rhizosphere near the roots. This environment promotes the functioning of beneficial aerobic microflora, which greatly improves the roots' survival and, consequently, the plant's ability to withstand flooding (Björn et al., 2022).

Ethylene, a plant hormone, serves as the main mediator in the development of aerenchyma in the primary root cortex. The process through which ethylene promotes aerenchyma formation closely resembles its role in inducing the development of new adventitious roots when faced with anaerobic conditions. Essentially, a higher concentration of ethylene in the root, resulting from the roots' exposure to waterlogging stress, acts as a signal that activates a signaling pathway leading to the disintegration and programmed cell death of certain cells in the primary root cortex (Mergemann & Sauter, 2000). This leads to the formation of a specialized empty space in the primary root cortex i.e., aerenchyma, which serves to store and subsequently distribute oxygen throughout the root.

Recent studies have demonstrated that ethylene is not the only mediator in aerenchyma formation; nitric oxide (NO) and some other reactive oxygen species also fulfill this role (Wany & Gupta, 2018; Basu et al., 2020). The formation of aerenchyma in plant roots experiencing anaerobic stress is further influenced by the activity of certain enzymes that are responsible for the production and deposition of suberin in the cell walls of the root exodermis (Abiko et al., 2012).

Many agricultural species, including corn, tomato, soybean, wheat, and barley, have the ability to develop root aerenchyma under anaerobic stress conditions. Rice also has the capacity to form root cortical aerenchyma, but this process occurs independently of external environmental factors (Yamauchi et al., 2013).

Stem elongation

To cope with soil waterlogging, the plant initiates the development of adventitious roots, hypertrophied lenticels, and root aerenchyma, while also facilitating the elongation of submerged stem internodes (Jing et al., 2024). The mediator of stem elongation is also ethylene; however, in this instance, its activity will not result in programmed cell death. Instead, it will promote the synthesis of gibberellins, resulting in the stem elongation (Sasidharan & Voesenek, 2015). Thus, the signaling pathways triggered by ethylene can vary significantly depending on the plant species, its demands, and the surrounding environments.

The ethylene-induced signaling pathway that results in the elongation of stem internodes, especially those underwater, consists of the following phases:

(1) ethylene, which accumulates highly in cells under anaerobic stress, binds to a membrane protein receptor associated with an ethylene-responsive factor that contains an APETALA2 (AP2) DNA-binding domain;

(2) the binding of ethylene to the receptor results in a conformational change in the receptor, leading to the release of ethylene-responsive factor, which subsequently initiates the expression of the SK1/SK2 genes in the nucleus;

(3) the expression of the SK1/SK2 gene leads to the production of an enzyme essential for gibberellin synthesis;

(4) the resulting gibberellins subsequently activate signaling pathways that ultimately lead to the elongation of cells, and consequently, the internodes of the submerged stem (Patil et al., 2019) (Figure 3).

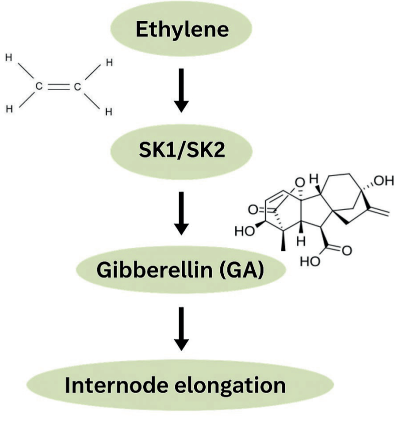

Figure 3. Diagram showing the ethylene-induced signaling pathway that results in the elongation of stem internodes

Plant physiological adaptations to waterlogging stress

In addition to mechanisms based on morpho-anatomical changes, plants strive to adapt to waterlogging stress by altering their metabolic processes. Key adaptations include shifts in respiration, adjustments in photosynthesis, and the synthesis of specific metabolites that enhance the plant's defense against flooding stress (Kato-Noguchi et al., 2003).

Plant respiration under oxygen deficiency

In the absence of oxygen, whether partially or fully, the capacity of plant cells to produce ATP in mitochondria through the Krebs cycle (aerobic metabolism) is limited, necessitating a switch to anaerobic metabolism, where ATP is generated via anaerobic respiration (Meng et al., 2020). From the standpoint of plant life, the greatest challenge of anaerobic respiration lies in its production of an extremely low amount of ATP. During anaerobic respiration, plant cells generate just two ATP molecules for every glucose molecule broken down, indicating that this process is much less efficient than aerobic respiration (2 ATP in glycolysis compared with 36 ATP in the Krebs cycle from one glucose molecule). For these reasons, the plant aims to enhance anaerobic metabolism by intensively producing the enzymes pyruvate decarboxylase and alcohol dehydrogenase within its cells.

The increased activity of these enzymes accelerates anaerobic metabolism, specifically the breakdown of pyruvate generated from glycolysis, leading to a faster production of ATP (Tougou et al., 2012).

Under oxygen deficiency, plant cells switch to anaerobic metabolism via two main pathways. The first pathway is characterized by the activity of the lactate dehydrogenase enzyme (LDH) which catalyzes the conversion of pyruvate into lactate, accompanied by the transformation of NADH into NAD^+. This pathway is referred to as lactic fermentation, enabling plant cells to transform one glucose molecule into two lactate molecules and produce two ATP molecules. Nonetheless, a negative aspect of lactic fermentation is the acidification of the cytoplasm, which adversely influences the metabolic reactions occurring in the cell (Peetermans et al., 2021). The second pathway is marked by the action of the pyruvate decarboxylase enzyme (PDC), which transforms pyruvate into acetaldehyde. This acetaldehyde is then converted into ethanol by the alcohol dehydrogenase enzyme (ADH). This anaerobic fermentation process, known as alcoholic fermentation, also results in the generation of two ATP molecules.

A visual representation of anaerobic metabolism in plant cells is shown in Figure 4.

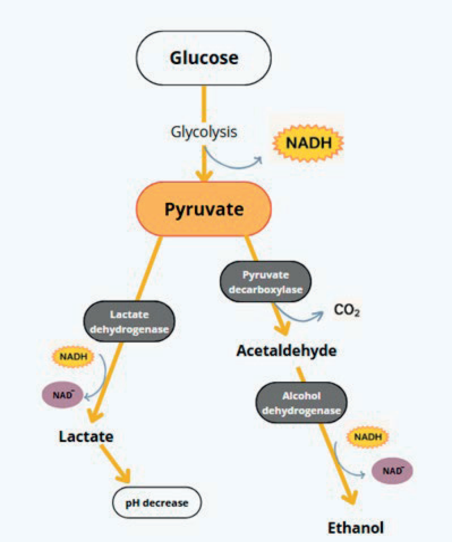

Figure 4. Diagram showing the process of anaerobic respiration in plant cell

Although ATP produced via anaerobic metabolism can offer temporary energy essential for a plant's existence, it is crucial to recognize that this process also generates toxic byproducts like lactate (lactic acid), ethanol, and aldehydes, which can severely disrupt cellular metabolism (Jain et al., 2020). Through anaerobic respiration, the plant cell can temporarily survive without oxygen; however, it cannot serve as a permanent alternative to aerobic metabolism. This means that a plant cell cannot survive for an extended time without oxygen.

Dynamics of photosynthesis under oxygen deficiency

In waterlogging stress conditions, plants cannot take up water through their root systems. Therefore, to maintain their existing water reserves, they must initiate mechanisms that result in stomatal closure. By closing their stomata, plants reduce transpiration but also limit CO_2 intake, which is essential for photosynthesis (Else et al., 2009). Waterlogging stress also negatively affects photosynthesis by limiting the distribution of nutrients, particularly nitrogen, throughout the plant (Zayed et al., 2023). This limitation obstructs chlorophyll synthesis, consequently threatening the plant's ability to absorb photosynthetically active light required for photosynthesis. Waterlogging stress adversely impacts the function of enzymes essential for photosynthesis and disrupts leaf development. This clearly demonstrates that performing photosynthesis under waterlogging stress is highly difficult (Zheng et al., 2009; Muhammad et al., 2021).

To overcome or at least reduce the negative effects of waterlogging stress on photosynthesis, plant cells in the early stages of flooding stress synthesize enzymes essential for converting starch into sucrose, which is then transported to other parts of the plant, particularly to the roots. By relocating assimilates to the roots, the plant aims to enhance root growth, helping it to escape the anaerobic zone of the growth medium and regain its ability to absorb the water and nutrients necessary for photosynthesis (Gangana Gowdra et al., 2025). Nevertheless, prolonged exposure to waterlogging stress can greatly diminish a plant's capacity to generate and transport assimilates to its roots, thereby restricting root growth. Under these conditions, the plant's chances of survival are considerably decreased.

Anaerobic stress-induced metabolites

Multiple studies have shown that plant cells subjected to waterlogging stress tend to either activate or produce significant quantities of specific metabolites, including non-symbiotic hemoglobin (Class-1 Hb) and nitric oxide (NO) (Igamberdiev et al., 2005; Zhao et al., 2008).

A key characteristic of Class-1 Hb is its strong affinity for oxygen, enabling it to effectively bind oxygen in conditions where its concentration in the cell is very low (Singh & Bhatla, 2019). The role of Class-1 Hb in plant cells subjected to anaerobic stress is highly significant: (1) it acts as a signaling molecule that transmits stress signals to target points, i.e., transcription factors; (2) it binds oxygen necessary for cellular aerobic respiration, thus slowing down the transition of plant cells from aerobic to anaerobic metabolism; and (3) it helps maintain glycolysis in cells facing oxygen deficiency (Riquelme & Hinrichsen, 2015). The research by Hebelstrup et al. (2007) indicates that the synthesis of Class-1 hemoglobin happens whenever the respiratory chain is inhibited, regardless of the oxygen concentration within the cell. This implies that the signal for increased Class-1 Hb production is not solely due to oxygen deficiency in plant cells but also encompasses any situation that results in a significant decrease in ATP synthesis.

Nitric oxide (NO) serves as a vital signaling molecule that regulates plant growth and development under stress conditions such as flooding. It plays a crucial role in enhancing plant resistance to flooding stress through several mechanisms: (1) it interacts with reactive oxygen species (ROS) to control their levels, thereby reducing the harmful effects of oxidative stress on plants; (2) it serves as the mediator in the development of aerenchyma in the primary root cortex; (3) it enhances plant immunity and stress tolerance through the post-translational modification of proteins; (4) it interacts with various plant hormones, playing a significant role in the regulation of plant growth and development under stress conditions (Khan et al., 2023).

It is important to highlight that these two metabolites, Class-1 Hb and NO, work together to alleviate the negative effects of anaerobic stress. In this regard, these metabolites assist in regenerating the enzymatic cofactor NAD^+ from NADH during hypoxia, which is crucial for maintaining glycolysis in plant cells under anaerobic conditions. This synergistic relationship between Class-1 Hb and NO is recognized in scientific literature as the Hb/NO cycle (Dordas et al., 2003) (Figure 5).

Hb/NO cycle initiates with activity of nitrate reductase (NR), which catalyzes the reduction of nitrate (NO_3^-) into nitrite (NO_2^-). Subsequently, NO_2^- is oxidized to nitric oxide (NO) through the activity of nitrite-NO reductase (NiNOR). NO is than reduced to NO3- by oxyhemoglobin ($Hb(Fe^{2+})O_2$), which transforms into methemoglobin ($HbFe^{3+}$), consuming NAD(P)H in the process. In essence, hemoglobin in plant cells helps reduce nitric oxide (NO) levels generated from nitrate during hypoxia. Through the Hb/NO cycle, the plant oxidizes approximately 2.5 moles of NADH for every mole of nitrate (NO_3^-) recycled in the reaction. This cycle is crucial for sustaining redox and energy equilibrium during hypoxia, which in turn reduces the production of ethanol and lactic acid (van Veen et al., 2024).

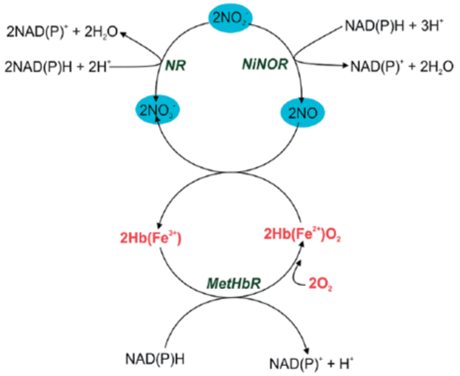

Figure 5. A simple diagram outlining the Hb/NO cycle

In addition to Class-1 Hb and NO, plant cells produce several additional metabolites that serve to strengthen the plant's ability to withstand the negative impacts of this stress. For instance, in response to osmotic stress caused by an excess of water in the growth medium, the plant cells intensively synthesize small organic metabolites (collectively called compatible solutes or osmolytes). Due to their small molecular weight and non-toxic nature, even at elevated concentrations, osmolytes are widely used by plants to alleviate osmotic stress. Among the most prevalent osmolytes in plant cells are amino acids like proline, sugars including mannitol, trehalose, and sorbitol, along with polyamines. This accumulation is beneficial as it enhances tolerance to osmotic stress without disrupting cellular processes. Plant species exhibit varying degrees of tolerance to osmotic stress, which depends on the type and level of osmolyte accumulation during osmotic stress caused by flooding or other stress factors (Chen et al., 2022).

To protect themselves from oxidative damage caused by flooding, plant cells strive to maintain a balance between the production of reactive oxygen species (ROS) and their neutralization.

An imbalance between ROS production and elimination can degrade essential structural and functional biomolecules, ultimately threatening the plant's overall integrity. To counteract these effects, plants deploy a broad array of enzymatic and non-enzymatic antioxidants that play a vital role in neutralizing excess ROS. Among the most prevalent non-enzymatic antioxidants in plant cells are ascorbic acid, tocopherol, glutathione, isoprenoids, carotenoids, flavonoids, ubiquinone and plastoquinone (Rudenko et al., 2023). These antioxidants typically serve as a secondary defense mechanism for plants, protecting them from the harmful effects of reactive oxygen species (ROS). While the mechanisms of action differ among these compounds, they generally function by providing an electron to free radicals, thereby neutralizing their harmful effects (Zandi & Schnug, 2022).

CONCLUSIONS

To address the escalating challenges posed by climate change, it is essential to deepen our understanding of how plants respond to waterlogging stress. This review highlights the complex physiological, morphological, and biochemical responses that plants employ to survive hypoxic conditions caused by soil saturation. Oxygen deprivation disrupts respiration, nutrient uptake, and photosynthesis, severely limiting plant productivity. However, certain species have evolved adaptive traits - such as adventitious root formation, aerenchyma development, and metabolic reprogramming - that enhance their survival under such conditions.

Recognizing these adaptive mechanisms holds significant value for improving agricultural resilience. As climate models predict more frequent and intense rainfall events, crop species will increasingly face alternating periods of drought and flooding. Integrating waterlogging-tolerant traits into breeding programs, particularly for staple crops, can help stabilize yields in flood-prone areas. Moreover, understanding root-zone adaptations can guide the design of land reclamation strategies on poorly drained or flood-affected soils.

In addition, these insights support the development of sustainable land and water management practices, which encompass improving drainage systems, altering planting schedules, and selecting or engineering robust crop varieties.

Ultimately, translating this knowledge into applied practices can help secure food production and maintain soil health in the face of accelerating climate variability.

REFERENCES

Abdul Rahman, N. S. N., & Abdul Hamid, N. W., & Nadarajah K. (2021). Effects of Abiotic Stress on Soil Microbiome. *International Journal of Molecular Sciences, 22*(16), 9036. https://doi.org/10.3390/ijms22169036

Abiko, T., Kotula, L., Shiono, K., Malik, A. I., & Colmer, T. D., & Nakazono, M. (2012). Enhanced formation of aerenchyma and induction of a barrier to radial oxygen loss in adventitious roots of *Zea nicaraguensis* contribute to its waterlogging tolerance as compared with maize (*Zea mays* ssp. mays). *Plant, Cell & Environment, 35*(9), 1618–30. https://doi.org/10.1111/j.1365-3040.2012.02513 .x

Abuarab, M. E., El-Mogy, M. M., Hassan, A. M., Abdeldaym, E. A., Abdelkader, N. H., & El-Sawy, M. B. I. (2019). The Effects of Root Aeration and Different Soil Conditioners on the Nutritional Values, Yield, and Water Productivity of Potato in Clay Loam Soil. *Agronomy, 9*(8), 418. https://doi.org/10.3390/agronomy9080418

Aslam, A., Mahmood, A., Ur-Rehman, H., Li, C., Liang, X., Shao, J., Negm, S., Moustafa, M., Aamer, M., & Hassan, M. U. (2023). Plant Adaptation to Flooding Stress under Changing Climate Conditions: Ongoing Breakthroughs and Future Challenges. *Plants (Basel), 12*(22), 3824. https://doi.org/10.3390/plants12223824

Bai, T., Dong, Z., Zheng, X., Song, S., Jiao, J., Wang, M., & Song, C. (2020). Auxin and Its Interaction with Ethylene Control Adventitious Root Formation and Development in Apple Rootstock. *Frontiers in Plant Science, 11,* 574881. https://doi.org/10.3389/fpls.2020.574881

Basu, S., Kumar, G., Kumari, N., Kumari, S., Shekhar, S., Kumar, S., & Rajwanshi, R. (2020). Reactive oxygen species and reactive nitrogen species induce lysigenous aerenchyma formation through programmed cell death in rice roots under submergence. *Environmental and Experimental Botany, 177,* 104–118. https://doi.org/10.1016/j.envexpbot.2020.104118

Ben-Noah, I., & Friedman, S. P. (2018). Review and evaluation of root respiration and of natural and agricultural processes of soil aeration. *Vadose Zone Journal, 17*, 170119. https://doi.org/10.2136/vzj2017.06.0119

Björn, L. O., Middleton, B. A., Germ, M., & Gaberščik, A. (2022). Ventilation Systems in Wetland Plant Species. *Diversity, 14*(7), 517. https://doi.org/10.3390/d14070517

Bolan, S., Padhye, L. P., Jasemizad, T., Govarthanan, M., Karmegam, N., Wijesekara, H., Amarasiri, D., Hou, D., Zhou, P., Biswal, B. K., Balasubramanian, R., Wang, H., Siddique, K. H. M., Rinklebe, J., Kirkham, M. B., & Bolan N. (2024). Impacts of climate change on the fate of contaminants through extreme weather events. *Science of the Total Environment, 909*, 168388. https://doi.org/10.1016/j.scitotenv.2023.168388

Chada, S., Asiedu, S. K., Ofoe, R., & Abbey, L. (2023). An overview of plant morpho-physiology, biochemicals, and metabolic pathways under water stress. *Horticulture International Journal, 7*(4), 115–125. https://doi.org/10.15406/hij.2023.07.00285

Chen, D., Mubeen, B., Hasnain, A., Rizwan, M., Adrees, M., Naqvi, S. A. H., Iqbal, S., Kamran, M., El-Sabrout, A. M., Elansary, H. O., Mahmoud, E. A., Alaklabi, A., Sathish, M., & Din, G. M. U. (2022). Role of Promising Secondary Metabolites to Confer Resistance Against Environmental Stresses in Crop Plants: Current Scenario and Future Perspectives. *Frontiers in Plant Science, 13*, 881032. https://doi.org/10.3389/fpls.2022.881032

Cochrane, D. W., Shah, J. K., Hebelstrup, K. H., & Igamberdiev, A. U. (2017). Expression of phytoglobin affects nitric oxide metabolism and energy state of barley plants exposed to anoxia. *Plant Science, 265*, 124–130. https://doi.org/10.1016/j.plantsci.2017.10.001

Dordas, C., Hasinoff, B., Igamberdiev, A. U., Manac'h, N., Rivoal, J., & Hill, R. D. (2003). Expression of a stress-induced hemoglobin affects NO levels produced by alfalfa under hypoxic stress. *Plant Journal, 35,* 763–770. https://doi.org/10.1046/j.1365-313x.2003.01846.x

Else, M. A., Janowiak, F., Atkinson, C. J., & Jackson, M. B. (2009). Root signals and stomatal closure in relation to photosynthesis, chlorophyll a fluorescence and adventitious rooting of flooded tomato plants. *Annals in Botany, 103*(2), 313–23. https://doi.org/10.1093/aob/mcn208

Evans, D. E. (2004). Aerenchyma formation. *New Phytologist, 161,* 35–49. https://doi.org/10.1046/j.1469-8137.2003.00907.x

Farnese, F. S., Menezes-Silva, P. E., Gusman, G. S., & Oliveira, J. A. (2016). When Bad Guys Become Good Ones: The Key Role of Reactive Oxygen Species and Nitric Oxide in the Plant Responses to Abiotic Stress. *Frontiers in Plant Science, 7*, 471. https://doi.org/10.3389/fpls.2016.00471

Fukao, T., Barrera-Figueroa, B. E., Juntawong, P., & Peña-Castro, J. M. (2019). Submergence and Waterlogging Stress in Plants: A Review Highlighting Research Opportunities and Understudied Aspects. *Frontiers in Plant Science, 10*, 340. https://doi.org/10.3389/fpls.2019.00340

Furtak, K., & Wolińska, A. (2023). The impact of extreme weather events as a consequence of climate change on the soil moisture and on the quality of the soil environment and agriculture – A review. *Catena, 231*, 107378. https://doi.org/10.1016/j.catena.2023.107378

Gangana Gowdra, V. M., Lalitha, B. S., Halli, H. M., Senthamil, E., Negi, P., Jayadeva, H. M., Basavaraj, P. S., Harisha, C. B., Boraiah, K. M., Adavi, S. B., Suresha, P. G., Nargund, R., Mohite, G., & Sammi Reddy, K. (2025). Root growth, yield and stress tolerance of soybean to transient waterlogging under different climatic regimes. *Scientific Reports, 15*, 6968. https://doi.org/10.1038/s41598-025-91780-9

Giuntoli, B., & Perata, P. (2018). Group VII Ethylene Response Factors in Arabidopsis: Regulation and Physiological Roles. *Plant Physiology, 176*(2), 1143–1155. https://doi.org/10.1104/pp.17.01225

Greenway, H., Armstrong, W., & Colmer, T. D. (2006). Conditions leading to high CO_2 (>5 kPa) in waterlogged-flooded soils and possible effects on root growth and metabolism. *Annals of Botany, 98*(1), 9–32. https://doi.org/10.1093/aob/mcl076

He, W., Yoo, G., Moonis, M., Kim, Y., & Chen X. (2019) Impact assessment of high soil CO2 on plant growth and soil environment: a greenhouse study. *PeerJ, 7,* e6311. https://doi.org/10.7717/peerj.6311

Hebelstrup, K. H., Igamberdiev, A. U., & Hill, R. D. (2007). Metabolic effects of hemoglobin gene expression in plants. *Gene, 398*(1-2), 86–93. https://doi.org/10.1016/j.gene.2007.01.039

Husson, O. (2013). Redox potential (Eh) and pH as drivers of soil/plant/microorganism systems: a transdisciplinary overview pointing to integrative opportunities for agronomy. *Plant and Soil, 362,* 389–417. https://doi.org/10.1007/s11104-012-1429-7

Igamberdiev, A. U., Baron, K., Manac'h-Little, N., Stoimenova, M., & Hill, R. D. (2005). The haemoglobin/nitric oxide cycle: involvement in flooding stress and effects on hormone signalling. *Annals in Botany, 96*(4), 557–564. https://doi.org/10.1093/aob/mci210

Insausti, P., & Gorjón, S. (2013). Floods affect physiological and growth variables of peach trees (Prunus persica (L.) Batsch), as well as the postharvest behavior of fruits. *Scientia Horticulturae, 152,* 56–60. https://doi.org/10.1016/j.scienta.2013.01.005

Jackson, M. B., Ishizawa, K., & Osamu, I. (2009). Evolution and mechanisms of plant tolerance to flooding stress. *Annals of Botany, 103*, 137–142. https://doi.org/10.1093/aob/mcn242

Jagodzik, P., Tajdel-Zielinska, M., Ciesla, A., Marczak, M., & Ludwikow, A. (2018). Mitogen-Activated Protein Kinase Cascades in Plant Hormone Signaling. *Frontiers in Plant Science, 9*, 1387. https://doi.org/10.3389/fpls.2018.01387

Jain, M., Aggarwal, S., Nagar, P., Tiwari, R., & Mustafiz, A. (2020). A D-lactate dehydrogenase from rice is involved in conferring tolerance to multiple abiotic stresses by maintaining cellular homeostasis. *Scientific Reports, 10,* 12835. https://doi.org/10.1038/s41598-020-69742-0

Jethva, J., Schmidt, R. R., Sauter, M., & Selinski, J. (2022). Try or Die: Dynamics of Plant Respiration and How to Survive Low Oxygen Conditions. *Plants, 11*(2), 205. https://doi.org/10.3390/plants11020205

Jia, W., Ma, M., Chen, J., & Wu, S. (2021). Plant Morphological, Physiological and Anatomical Adaption to Flooding Stress and the Underlying Molecular Mechanisms. *International Journal of Molecular Sciences, 22*(3), 1088. https://doi.org/10.3390/ijms22031088

Jing, S., Ren, X., Lin, F., Niu, H., Ayi, Q., Wan, B., Zeng, B., & Zhang, X. (2024). Water depth-dependent stem elongation of completely submerged Alternanthera philoxeroides is mediated by intra-internodal growth variations. *Frontiers in Plant Science, 15,* 1323547. https://doi.org/10.3389/fpls.2024.1323547

Jitsuyama, Y. (2017). Hypoxia-Responsive Root Hydraulic Conductivity Influences Soybean Cultivar-Specific Waterlogging Tolerance. *American Journal of Plant Sciences, 8*, 770–790. https://doi.org/10.4236/ajps.2017.84054

Kato-Noguchi, H., Ohashi, C., & Sasaki, R. (2003). Metabolic adaptation to flooding stress in upland and lowland rice seedlings. *Acta Physiologiae Plantarum, 25,* 257–261. https://doi.org/10.1007/s11738-003-0006-3

Khan, M., Ali, S., Al Azzawi, T. N. I., & Yun, B. W. (2023). Nitric Oxide Acts as a Key Signalling Molecule in Plant Development under Stressful Conditions. *International Journal of Molecular Sciences, 24*(5), 4782. https://doi.org/10.3390/ijms24054782

Khan, S., Alvi, A. F., & Khan, N. A. (2024). Role of Ethylene in the Regulation of Plant Developmental Processes. *Stresses, 4*(1), 28–53. https://doi.org/10.3390/stresses4010003

Kosová, K., Vítámvás, P., Urban, M. O., Prášil, I. T., & Renaut, J. (2018). Plant Abiotic Stress Proteomics: The Major Factors Determining Alterations in Cellular Proteome. *Frontiers in Plant Science, 9,* 122. https://doi.org/10.3389/fpls.2018.00122

Leeggangers, H. A. C. F., Rodriguez-Granados, N. Y., Macias-Honti, M. G., & Sasidharan, R. (2023). A helping hand when drowning: The versatile role of ethylene in root flooding resilience. *Environmental and Experimental Botany, 213*, 105422. https://doi.org/10.1016/j.envexpbot.2023.105422

León, J., Castillo, M. C., & Gayubas, B. (2021). The hypoxia–reoxygenation stress in plants. *Journal of Experimental Botany, 72*(16), 5841–5856. https://doi.org/10.1093/jxb/eraa591

Li, Y-K., Zhang, Y-M., Dai, G-Y., Chen, Y-L., Chen, D-K., & Yao, N. (2025). Sphingolipid remodeling in the plasma membrane is essential for osmotic stress tolerance in Arabidopsis. *Plant Physiology, 197*(2), kiaf031. https://doi.org/10.1093/plphys/kiaf031

Lin, C., Zhang, Z., Shen, X., Liu, D., & Pedersen, O. (2024). Flooding-adaptive root and shoot traits in rice. *Functional Plant Biology, 51*, FP23226. https://doi.org/10.1071/FP23226

Liu, C., Wang, Q., Mäkelä, A., Hökkä, H., Peltoniemi, M., & Hölttä, T. (2022). A model bridging waterlogging, stomatal behavior and water use in trees in drained peatland. *Tree Physiology, 42*(9), 1736–1749. https://doi.org/10.1093/treephys/tpac037

Luo, H., Liu, S., Song, Y., Qin, T., Xiao, S., Li, W., Xu, L., & Zhou, X. (2024). Effects of Waterlogging Stress on Root Growth and Soil Nutrient Loss of Winter Wheat at Seedling Stage. *Agronomy, 14*(6), 1247. https://doi.org/10.3390/agronomy14061247

Manghwar, H., Hussain, A., Allam, I., Khoso, M. A., Ali, Q., & Liu, F. (2024). Waterlogging stress in plants: Unraveling the mechanisms and impacts on growth, development, and productivity. *Environmental and Experimental Botany, 224,* 105824. https://doi.org/10.1016/j.envexpbot.2024.105824

Martínez-Arias, C., Witzell, J., Solla, A., Martin, J. A., & Rodríguez-Calcerrada, J. (2022). Beneficial and pathogenic plant-microbe interactions during flooding stress. *Plant, Cell & Environment, 45*(10), 2875–2897. https://doi.org/10.1111/pce.14403

Meng, X., Li, L., Narsai, R., De Clercq, I., Whelan, J., & Berkowitz O. (2020). Mitochondrial signalling is critical for acclimation and adaptation to flooding in Arabidopsis thaliana. *Plant Journal, 103*(1), 227–247. https://doi.org/10.1111/tpj.14724

Mergemann, H., & Sauter, M. (2000). Ethylene induces epidermal cell death at the site of adventitious root emergence in rice. *Plant Physiology, 124*(2), 609–614. https://doi.org/10.1104/pp.124.2.609

Muhammad, I., Shalmani, A., Ali, M., Yang, Q. H., Ahmad, H., & Li, F. B. (2021). Mechanisms Regulating the Dynamics of Photosynthesis Under Abiotic Stresses. *Frontiers in Plant Science, 11,* 615942. https://doi.org/10.3389/fpls.2020.615942

Olorunwa, O. J., Adhikari, B., Brazel, S., Popescu, S. C., Popescu, G. V., & Barickman, T. C. (2022). Short waterlogging events differently affect morphology and photosynthesis of two cucumber (*Cucumis sativus* L.) cultivars. *Frontiers in Plant Science, 13*, 896244. https://doi.org/10.3389/fpls.2022.896244

Patil, V., McDermott, H. I., McAllister, T., Cummins, M., Silva, J. C., Mollison, E., Meikle, R., Morris, J., Hedley, P. E., Waugh, R., Dockter, C., Hansson, M., & McKim, S. M. (2019). APETALA2 control of barley internode elongation. *Development, 146*(11), dev170373. https://doi.org/10.1242/dev.170373

Peetermans, A., Foulquié-Moreno, M. R., & Thevelein, J. M. (2021). Mechanisms underlying lactic acid tolerance and its influence on lactic acid production in Saccharomyces cerevisiae. *Microbial Cell, 8*(6), 111–130. https://doi.org/10.15698/mic2021.06.751

Rathore, S., Datta, G., Kaur, I., Malhotra, P., & Mohmmed, A. (2015). Disruption of cellular homeostasis induces organelle stress and triggers apoptosis like cell-death pathways in malaria parasite. *Cell Death and Disease, 6*(7), e1803. https://doi.org/10.1038/cddis.2015.142

Riquelme, A., & Hinrichsen, P. (2015). Non-symbiotic hemoglobin and its relation with hypoxic stress. *Chilean journal of agricultural research, 75*(1), 80–89. https://doi.org/10.4067/S0718-58392015000300009

Roussos, P. A. (2023). Adventitious Root Formation in Plants: The Implication of Hydrogen Peroxide and Nitric Oxide. *Antioxidants,12*(4), 862. https://doi.org/10.3390/antiox12040862

Rudenko, N. N., Vetoshkina, D. V., Marenkova, T. V., & Borisova-Mubarakshina, M. M. (2023). Antioxidants of Non-Enzymatic Nature: Their Function in Higher Plant Cells and the Ways of Boosting Their Biosynthesis. *Antioxidants (Basel), 12*(11), 2014. https://doi.org/10.3390/antiox12112014

Rupngam, T., & Messiga, A. J. (2024). Unraveling the Interactions between Flooding Dynamics and Agricultural Productivity in a Changing Climate.

Sustainability, 16(14), 6141. https://doi.org/10.3390/su16146141

Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., & Hasanuzzaman, M. (2021). Abiotic Stress and Reactive Oxygen Species: Generation, Signaling, and Defense Mechanisms. *Antioxidants, 10*(2), 277. https://doi.org/10.3390/antiox10020277

Safavi-Rizi, V., Herde, M., & Stöhr, C. (2020). RNA-Seq reveals novel genes and pathways associated with hypoxia duration and tolerance in tomato root. *Scientific Reports, 10*, 1692. https://doi.org/10.1038/s41598-020-57884-0

Sasidharan, R., Hartman, S., Liu, Z., Martopawiro, S., Sajeev, N., van Veen, H., Yeung, E., & Voesenek, L. A. C. J. (2018). Signal Dynamics and Interactions during Flooding Stress. *Plant Physiology, 176*(2), 1106–1117. https://doi.org/10.1104/pp.17.01232

Sasidharan, R., & Voesenek, L. A. C. J. (2015). Ethylene-mediated acclimations to flooding stress. *Plant Physiology, 169*, 3–12. https://doi.org/10.1104/pp.15.00387

Schmidt, R. R., Weits, D. A., Feulner, C. F. J., & van Dongen, J. T. (2018). Oxygen Sensing and Integrative Stress Signaling in Plants. *Plant Physiology, 176*(2), 1131–1142. https://doi.org/10.1104/pp.17.01394

Selinski, J., Frings, S., & Schmidt-Schippers, R. (2024). Perception and processing of stress signals by plant mitochondria. *Plant Journal, 120*(6), 2337–2355. https://doi.org/10.1111/tpj.17133

Setter T. L., & Waters I. (2003). Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. *Plant and Soil, 253*, 1–34. https://doi.org/10.1023/A:1024573305997

Sewelam, N., Kazan, K., & Schenk, P. M. (2016). Global Plant Stress Signaling: Reactive Oxygen Species at the Cross-Road. *Frontiers in Plant Science, 7*, 187. https://doi.org/10.3389/fpls.2016.00187

Shimamura, S., Yamamoto, R., Nakamura, T., Shimada, S., & Komatsu, S. (2010). Stem hypertrophic lenticels and secondary aerenchyma enable oxygen transport to roots of soybean in flooded soil. *Annals of Botany, 106*(2), 277–284. https://doi.org/10.1093/aob/mcq123

Siebielec, S., Siebielec, G., Klimkowicz-Pawlas, A., Gałązka, A., Grządziel, J., & Stuczyński, T. (2020). Impact of Water Stress on Microbial Community and Activity in Sandy and Loamy Soils. *Agronomy, 10* (9), 1429. https://doi.org/10.3390/agronomy10091429

Singh, N., & Bhatla, S. C. (2019). Hemoglobin as a probe for estimation of nitric oxide emission from plant tissues. *Plant Methods, 15*, 39. https://doi.org/10.1186/s13007-019-0425-9

Sou, H. D., Masumori, M., Yamanoshita, T., & Tange, T. (2021). Primary and secondary aerenchyma oxygen transportation pathways of Syzygium kunstleri (King) Bahadur & R. C. Gaur adventitious roots in hypoxic conditions. *Scientific Reports, 11*, 4520. https://doi.org/10.1038/s41598-021-84183-z

Steffens, B., & Rasmussen, A. (2016). The Physiology of Adventitious Roots. *Plant Physiology, 170*(2), 603–617. https://doi.org/10.1104/pp.15.01360

Tete, E., Viaud, V., & Walter, C. (2015). Organic carbon and nitrogen mineralization in a poorly-drained mineral soil under transient waterlogged conditions: an incubation experiment. *European Journal of Soil Science, 66,* 427–437. https://doi.org/10.1111/ejss.12234

Thomas, A. L., Guerreiro, S. M., & Sodek, L. (2005). Aerenchyma formation and recovery from hypoxia of the flooded root system of nodulated soybean. *Annals of Botany, 96*(7), 1191–1198. https://doi.org/10.1093/aob/mci272

Topali, C., Antonopoulou, C., & Chatzissavvidis, C. (2024). Effect of Waterlogging on Growth and Productivity of Fruit Crops. *Horticulturae, 10*(6), 623. https://doi.org/10.3390/horticulturae10060623

Tougou, M., Hashiguchi, A., Yukawa, K., Nanjo, Y., Hiraga, S., Nakamura, T., Nishizawa, K., & Komatsu, S. (2012). Responses to flooding stress in soybean seedlings with the alcohol dehydrogenase transgene. *Plant Biotechnology, 29*, 301–305. https://doi.org/10.5511/plantbiotechnology.12.0301a

van Veen, H., Triozzi, P. M., & Loreti, E. (2024). Metabolic strategies in hypoxic plants. *Plant Physiology, 197*(1), kiae564. https://doi.org/10.1093/plphys/kiae564

Walne, C. H., & Reddy, K. R. (2021). Developing Functional Relationships between Soil Waterlogging and Corn Shoot and Root Growth and Development. *Plants, 10*(10), 2095. https://doi.org/10.3390/plants10102095

Wang, X., Wen, H., Suprun, A., & Zhu, H. (2025). Ethylene Signalling in Regulating Plant Growth, Development, and Stress Responses. *Plants, 14*(3), 309. https://doi.org/10.3390/plants14030309

Wany, A., & Gupta, K. J. (2018). Reactive oxygen species, nitric oxide production and antioxidant gene expression during development of aerenchyma formation in wheat. *Plant Signaling & Behavior, 13*(2), e1428515. https://doi.org/10.1080/15592324

Yamauchi, T., Shimamura, S., Nakazono, M., & Mochizuki, T. (2013). Aerenchyma formation in crop species: A review. *Field Crops Research, 152*, 8–16. https://doi.org/10.1016/j.fcr.2012.12.008

Zandi, P., & Schnug, E. (2022). Reactive Oxygen Species, Antioxidant Responses and Implications from a Microbial Modulation Perspective. *Biology (Basel), 11*(2), 155. https://doi.org/10.3390/biology11020155

Zayed, O., Hewedy, O. A., Abdelmoteleb, A., Ali, M., Youssef, M. S., Roumia, A. F., Seymour, D., & Yuan, Z. C. (2023). Nitrogen Journey in Plants: From Uptake to Metabolism, Stress Response, and Microbe Interaction. *Biomolecules, 13*(10), 1443. https://doi.org/10.3390/biom13101443

Zhao, L., Gu, R., Gao, P., & Wang, G. (2008). A nonsymbiotic hemoglobin gene from maize, ZmHb, is involved in response to submergence, high-salt and osmotic stresses. *Plant Cell, Tissue and Organ Culture, 95*, 227–237. https://doi.org/10.1007/s11240-008-9436-3

Zheng, C., Jiang, D., Liu, F., Dai, T., Jing, Q., & Cao, W. (2009). Effects of salt and waterlogging stresses and their combination on leaf photosynthesis, chloroplast ATP synthesis, and antioxidant capacity in wheat. *Plant Science, 176*, 575–582. https://doi.org/10.1016/j.plantsci.2009.01.015