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RELATIONSHIPS BETWEEN PHYSIOLOGY, GROWTH, AND YIELD OF CEREAL CROPS UNDER WATERLOGGING STRESS

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ABSTRACT

Global food security is increasingly threatened by abiotic stresses, particularly waterlogging, which poses significant challenges to cereal crop production. Waterlogging is one of the primary abiotic stresses that significantly influence the interrelationships among plant physiology, growth, and yield. This review aims to examine the relationships among these three aspects in cereal crops, with an emphasis on the response mechanisms to waterlogging stress. Findings from the reviewed literature indicate that waterlogged conditions induce hypoxia in the root zone, leading to reduced photosynthetic rates, impaired nutrient uptake, and increased production of reactive oxygen species (ROS), which trigger cellular damage. These effects result in reduced plant growth and yield. Nevertheless, plants exhibit various adaptive mechanisms, such as aerenchyma formation, adventitious root development, and proline accumulation, which enhance tolerance to stress. Variations in tolerance levels among cereal species also influence the extent of yield reduction. Overall, improving plant tolerance to waterlogging stress requires an integrated approach through physiological understanding, genetic improvement, and the application of appropriate agronomic management.

Key words: Aerenchyma; Hypoxia; Reactive Oxygen Species

INTRODUCTION

A combination of rapid population growth, stagnating crop yields, declining soil fertility, and the accelerating impacts of climate change increasingly threatens global food security. Cereal crops are the backbone of human nutrition worldwide, providing more than 50% of daily caloric intake, particularly in tropical regions of Asia, Africa, and Latin America (Chaudhary *et al.,* 2023). In tropical countries such as Indonesia, staple food crops, including rice (*Oryza sativa* L.) and maize (*Zea mays* L.), are under significant socioeconomic pressure, driving growing interest in diversifying the range of cultivated cereals. Cereal crops such as sorghum (*Sorghum bicolor* L.) and job's tears (*Coix lacryma-jobi* L.) are underutilized but highly nutritious crops with significant potential as alternative food sources (Rodriguez *et al.,* 2020; Juhaeti *et al.,* 2024).

Despite their ecological adaptability, cereal crops face constraints caused by abiotic stresses, of which waterlogging is one of the most damaging. Waterlogging is one of the major abiotic stresses restricting crop productivity globally. Approximately 16% of arable lands worldwide are affected by waterlogging/flooding stress (Zhou *et al.,* 2020). The development of waterlogging-tolerant varieties is important to maintain crop production in areas prone to flooding and submergence due to high rainfall and poor drainage, because waterlogging is one of the main factors affecting plant growth and productivity globally (Yang *et al.,* 2023).

Waterlogging stress significantly affects the relations among plant physiology, growth, and yield. Under waterlogging conditions, oxygen deficiency in the root zone causes hypoxia, forcing plants to switch from aerobic to anaerobic respiration, which reduces energy production and disrupts nutrient uptake (Zhang *et al.,* 2025). Prolonged hypoxic stress increases the accumulation of reactive oxygen species (ROS) and other toxic compounds, which causes oxidative damage, inhibits root respiration, and disrupts nutrient storage (Ma *et al.,* 2022). These conditions directly impact plant growth and development, reducing yields and even causing crop failure under extreme conditions. In particular, the relationships between physiological, growth, and yield under waterlogging stress have not been comprehensively reviewed in the context of cereals. Therefore, this review aims to examine the relationships between physiology, growth, and yield of cereal crops under waterlogging stress, based on evidence from reputable international journals.

RESULTS AND DISCUSSION

Cereal crops

a) Overview of Cereal Crops

Cereal crops play a crucial role in food security and nutrition, serving as the primary source of carbohydrates, protein, and micronutrients for billions of people, particularly in developing countries. Some of the major cereals in tropical regions include rice (*Oryza sativa* L.), maize (*Zea mays* L.), and sorghum (*Sorghum bicolor* L), all of which belong to the Poaceae family (Tong *et al.,* 2021). In addition, there are also cereal crops that are still underutilized (underutilized crops), such as job's tears (Coix lacryma-jobi L.), which have high nutritional value and great potential as an alternative food source and can be used as a substitute for rice (Juhaeti *et al.,* 2024).

b) Cereal Crops as C4 Plants

The main characteristic of C4 plants is the anatomical structure of their leaves, known as Kranz anatomy. In this anatomy, mesophyll cells are arranged around the vascular sheath cells, where sugar production occurs via the Calvin cycle (Sedelnikova *et al.,* 2018). Based on research results (Barupal & Kataria, 2024), Plants of the genus *Coix* have a distinctive anatomical form, demonstrating high activity of the enzyme phosphoenolpyruvate carboxylase (PEPC). The PEPC enzyme plays a role in capturing carbon dioxide in the early stages of photosynthesis. Due to this enzyme's ability, the job's tears can absorb CO_2 more efficiently and photosynthesize well in a hot environment with strong sunlight.

Waterlogging stress

a) Definition and types of waterlogging stress

Soil waterlogging can manifest in agricultural fields for various reasons, such as excessive rainfall or irrigation, inadequate soil drainage, rising or perched water tables, and lateral surface or subsurface flows. The availability of sufficient water can support optimal plant growth; however, when the soil becomes waterlogged, this condition can cause waterlogging stress in plants (Singhal *et al.,* 2022). Two types of flooding can occur in the field: (1) waterlogging, the saturation of the soil surface with the root system under water, and (2) submergence, where the plant is partially or entirely immersed in water (Tong *et al.,* 2021).

b) Effect of waterlogging stress on cereal crops

Water is essential for plant survival, but excessive waterlogging or flooding can cause stress and impede gas exchange between the soil and the atmosphere. This has detrimental effects on various stages of plant development throughout their life cycle, ultimately resulting in reduced crop yields. In waterlogged environments, roots may not grow properly due to oxygen deficiency, which can lead to root death. Consequently, the plant's ability to absorb water and nutrients and then transport them to other parts of the plant is limited, which can negatively impact its growth and development (Herzog *et al.,* 2016). C4 plants such as maize and sorghum require high energy, but under waterlogging stress, energy decreases drastically and becomes more serious than in other plants (Tong *et al.,* 2021)

Plants sensitive to waterlogging experience decreased photosynthesis, leading to excessive production of reactive oxygen species (ROS). This can lead to degradation of cell structures and severe oxidative damage, which in turn disrupts normal metabolism (Herzog *et al.,* 2016). ROS causes the phenomenon of lipoperoxidation, which causes damage to cell membranes, enzymes, nucleic acids, and proteins, resulting in cell death (Pais *et al.,* 2023).

The sensitivity of cereal crops to waterlogging varies considerably among species. Lowland rice varieties can tolerate waterlogging depths of 5-25 cm, although they remain susceptible to complete submergence. In contrast, crops such as maize and sorghum are much more sensitive to waterlogging, which can result in root damage, wilting of the upper part of the plant, and significant yield losses. Meanwhile, the job’s tears plant, given its hygrophytic characteristics, shows moderate sensitivity to waterlogging, which is generally consistent with the response of maize and sorghum (Feng *et al.,* 2020).

c) Plant tolerance mechanisms to waterlogging stress

Plants have undergone several adaptive morphological changes due to waterlogging stress (Manghwar *et al.,* 2024). First, plant stems or leaves rapidly elongate, allowing leaves to extend above the water surface, ensuring that the roots are replenished with oxygen and maintaining normal physiological activities (Yin & Komatsu, 2017). Then, waterlogging stress can form aerenchyma tissue and adventitious roots to facilitate oxygen diffusion towards the root tip, transmission of signal molecules, and removal of harmful substances (Sharma *et al.,* 2021). When waterlogging stress causes root damage or death, the rhizome will develop adventitious roots to mitigate the adverse effects of hypoxia. Additionally, plant stems or leaves can elongate rapidly, allowing the leaves to rise above the water surface, thereby ensuring that the roots reoxygenate and maintain normal life functions (Huawei *et al.,* 2022).

Cereal crops exhibit various morphological and metabolic adaptations in response to waterlogging stress. among which, the formation of aerenchyma is one of the most important structural mechanisms (Sharma *et al.,* 2021). Aerenchyma consists of interconnected air-filled channels within the cortical tissues of roots and stems, facilitating the internal diffusion of oxygen from the aerial parts of the root zone. In particular, the formation of aerenchyma in adventitious roots has been strongly associated with increased tolerance to waterlogging (Liu *et al.,* 2023). Recent studies further demonstrate that an increased proportion of aerated root tissue enhances waterlogging tolerance in cereal crops such as rice and maize, with genotypes exhibiting greater aerenchyma formation capacity exhibiting increased biomass accumulation (Zhang *et al.,* 2025).

Effect of waterlogging on the physiology of cereal crops

a) Decline in photosynthetic rate and chlorophyll content

Inhibited oxygen is supplied beneath waterlogged soil, which can significantly impair chlorophyll and photosynthetic rate (Najeeb *et al.,* 2015). During waterlogging stress, plant stomata close, chlorophyll levels decrease, and leaf light capture declines, ultimately reducing the rate of photosynthesis (Wu *et al.,* 2022). In addition, the oxygen content in the soil decreases under hypoxic conditions, so plant roots lose oxygen, forcing them to switch to anaerobic respiration and thereby disrupting cellular gas exchange (Wang *et al.,* 2023).

Plants require CO_2 and light for photosynthesis to support their growth and development. However, prolonged waterlogging disrupts the activity of photosynthetic enzymes. This reduces leaves' ability to produce chlorophyll, causing them to age, turn yellow, and fall off. Furthermore, new leaf formation is inhibited, leading to a decrease in the rate of photosynthesis and ultimately, plant death.

b) Electrolyte leakage

Electrolyte leakage is the loss of essential ions, particularly potassium (K^+), from plant cells through damaged membranes, thus being a clear indicator of membrane damage due to waterlogging stress. This phenomenon is closely related to increased membrane permeability due to stress, which causes ion loss from within the cell and reflects impaired membrane integrity (Su *et al.,* 2025). Abiotic stresses such as waterlogging and low temperatures can both trigger physiological disorders in plants by increasing the production of reactive oxygen species (ROS) (Hasanuzzaman *et al.,* 2020; Ding *et al.,* 2019).

Under waterlogging conditions, hypoxia and anoxia disrupt mitochondrial respiration, resulting in electron leakage from the electron transport chain (Complex I/III), which increases the formation of ROS such as superoxide (O_2^-) and hydrogen peroxide (H_2O_2) through the activation of NADPH oxidase (RBOH) (Rao *et al.,* 2025). Low-temperature stress causes excessive production of reactive oxygen species (ROS) in plants through several mechanisms, including disruption of membrane fluidity, disruption of photosynthetic machinery function, and disruption of ROS homeostasis, ultimately resulting in cell membrane damage and electrolyte leakage (Fan *et al.,* 2023). These two conditions prevent the plant's antioxidant system from functioning optimally, leading to increased ROS accumulation and oxidative damage to cells.

c) Proline accumulation

Proline is an amino acid produced by plants as a form of "self-defense" when faced with stressful conditions. The greater the stress a plant experiences, the more proline it typically produces (Ghosh *et al.,* 2022). Increased proline accumulation is closely related to the plant's ability to maintain physiological balance and increase tolerance to environmental stress.

Physiologically, proline functions as an osmoprotectant, a compound that helps maintain the osmotic balance of cells. Under stressful conditions, particularly those related to water availability, such as waterlogging or drought, proline accumulates in the cytoplasm, reducing the cell's osmotic potential without disrupting metabolism (Zulfiqar & Ashraf, 2023). This mechanism aims to maintain turgor pressure and prevent excessive water loss, thus maintaining stable cell structure and function (Renzetti *et al.,* 2025).

In waterlogged maize plants, proline content along with peroxidase (POD) and catalase (CAT) activities increased significantly, indicating the activation of various protective responses (Zhou *et al.,* 2026)**.** Proline also plays a role as a signaling molecule in plant stress responses. Proline can regulate the expression of genes related to stress tolerance and interact with plant hormones such as abscisic acid (ABA), jasmonate, and auxin. This role suggests that proline functions not only as a cell protector but also as a regulator of plant adaptive responses to environmental changes (Bhardwaj *et al.,* 2025).

Effect of waterlogging on growth and yield of cereal crops

Waterlogging stress can have a direct impact on plant growth, primarily through disruption of the root system. In saturated soil conditions, oxygen availability decreases drastically, causing roots to experience hypoxia (Zhang *et al.,* 2025). Inhibition of aerobic respiration during waterlogging stress limits energy metabolism and inhibits growth and various developmental processes, from seed germination to vegetative and reproductive growth (Pan *et al.,* 2021).

From a morphological and growth perspective, waterlogging stress significantly impairs root and shoot development. Root systems become shorter, shallower, and more susceptible to rot as a direct consequence of the lack of oxygen in the root zone (Li *et al.,* 2025). The uptake of essential macronutrients, including nitrogen, phosphorus, and magnesium, is simultaneously reduced, resulting in nutrient deficiencies throughout the plant (Topali *et al.,* 2024). Collectively, these conditions manifest as a marked reduction in plant height, leaf area expansion, and overall biomass accumulation. In addition, plants respond to waterlogging stress through adventitious root growth, aerenchyma formation, and energy metabolism (Tong *et al.,* 2021).

Among the most critical consequences of waterlogging, reduced crop yields represent the most significant economic impact on agricultural production (Manik *et al.,* 2019). Different cereal crops show varying levels of sensitivity to stress, which leads to differences in yield reduction. In maize, waterlogging has been shown to cause progressive yield reductions of 22.43%, 39.77%, 52.72%, and 76.33% under stress durations of 0-3, 3-6, 6-9, and 9-15 days, respectively, indicating a strong duration effect (Tian *et al.,* 2021). Compared with maize, rice exhibits greater tolerance, with comparatively lower yield reductions under similar waterlogging conditions. Furthermore, sorghum also experiences substantial yield losses due to waterlogging, particularly during the reproductive stage, which is considered the most sensitive phase. Meanwhile, in job's tears, waterlogging stress was associated with a 30-40% decrease in grain yield, consistent with the general pattern in cereals sensitive to waterlogging. This decrease was closely related to a reduction in leaf area index, photosynthetic rate, and plant biomass accumulation (Tian *et al.,* 2021; Pan *et al.,* 2021).

Research applications and implications

The findings synthesized in this review provide important insights for both scientific advancement and practical applications in cereal crop production under waterlogging stress. One of the primary applications lies in crop improvement programs, where physiological traits such as maintenance of photosynthetic capacity, membrane stability (indicated by reduced electrolyte leakage), and osmoprotectant accumulation (proline) can serve as reliable selection criteria for developing waterlogging-tolerant genotypes. From an agronomic perspective, this review highlights the importance of optimizing crop management practices to reduce the adverse impact of waterlogging.

CONCLUSION

1. Waterlogging stress significantly disrupts plant physiological processes, causing decreased photosynthesis, oxidative damage, and impaired nutrient uptake. These impacts ultimately inhibit plant growth and result in substantial yield losses, especially in sensitive cereal crops.
2. Plants exhibit adaptive responses to waterlogging stress, including aerenchyma formation, adventitious root development, and proline accumulation, which contribute to enhanced stress tolerance under waterlogged conditions.
3. Improving waterlogging tolerance in cereal crops requires an integrated approach combining physiological understanding, genetic improvement, and appropriate agronomic management strategies.
4. Further research is needed to explore the molecular mechanisms and validate adaptive traits under field conditions to ensure sustainable cereal production.

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