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Physiological and Anatomy Responses of Plants to Various Abiotic Stresses: A Comprehensive Review

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ABSTRACT

Global climate change increases abiotic stress (drought, waterlogging, extreme temperatures, acid rain) that threatens food security. This stress disrupts photosynthesis, hormone balance, and cell membranes in plants, thereby reducing crop yields and causing adaptation failure. This study analyzes the physiological and anatomical responses of plants to abiotic stress. The results indicate that plants possess complex defense mechanisms, such as stomatal modulation, root structure, cytoskeletal reorganization, osmo-protectant synthesis, and antioxidant system activation. These stresses also affect the phytochemical composition and nutritional value of crop yields, raising concerns about food quality. This review contributes by integrating various findings from the literature to present a comprehensive overview of physiological and anatomical responses in plants due to abiotic stress. By synthesizing existing data, the authors highlight the importance of developing sustainable agricultural strategies through integrated approaches, such as plant breeding to create stress-tolerant varieties and the application of biotechnology to enhance plant resilience. These efforts form a vital foundation for ensuring food availability that is not only sufficient but also nutritious amid increasingly extreme global environmental challenges.

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1. INTRODUCTION

The occurrence of global climate change has implications for plant resilience to abiotic stress, which is crucial to ensuring food security and agricultural sustainability. Extreme climate phenomena, such as prolonged droughts, floods caused by changes in rainfall patterns, heatwaves and cold snaps, exposure to acid rain and heavy metals, are becoming more intense and frequent, directly affecting plant growth, development, and productivity. These abiotic stresses trigger various negative responses in plants, ranging from oxidative stress, hormonal imbalances, to cellular damage, ultimately leading to significant reductions in crop yields.

Global climate change causes precipitation anomalies and increased abiotic stress. This has a significant impact on wildlife, with plant species showing high sensitivity to global climate change due to difficulties in adapting to increased pressure [1]. Global climate change, including extreme temperature changes, water scarcity, increased salinity, UV-B radiation, and increased concentrations of ozone and CO2, certainly has the potential to impact the nutritional quality and bioactive compounds in plant-based foods [2]. Plants have been an important part of human existence for thousands of years, serving as the foundation for nutrition, health, and survival by providing a wide variety of essential nutrients that are vital for human development and overall health [3]. Variations in temperature, rainfall, and atmospheric CO2 levels can affect the nutritional composition of plants and cause significant changes in their phytochemical composition. For example, higher temperatures can increase the levels of certain antioxidants but also lead to a decrease in the levels of others,

which has implications for the health benefits of food [4]. In addition to their nutritional value, plants are a rich source of bioactive compounds, including antioxidants and phytochemicals, which play an important role in preventing chronic diseases and promoting long-term health [5].

The functional traits of plants can effectively modulate plant responses and adaptations to environmental changes, and are therefore often used to discuss patterns and mechanisms of plant environmental adaptation [6]. Environmental temperature affects plant growth, reproduction, and material accumulation by influencing photosynthetic function. High temperatures are the main abiotic factor limiting plant growth and production [7]. On a global scale, annual average temperature is significantly negatively correlated with plant nitrogen (N) and phosphorus (P) content. The significant correlation between plant functional traits and temperature fully reflects the plant's response strategy to temperature changes. Temperature is the main factor affecting plant functional traits and adaptability [8]. Increases in temperature and CO2 levels do not support the photosynthetic activity of S. tabernaemontani. The rate of photosynthesis, stomatal density and size, vein density, epidermal structure size, and vascular bundle size play an important role in the adaptation of this species to changes in temperature and CO2 concentration. In the adaptation process, hydraulic properties are not isolated from one another, and there are functional relationships between them [6].

Climate change will result in an increase in average temperatures, particularly in the amount and distribution of rainfall. This will be reflected in changes to the climate zone classifications assigned to each land parcel. Climate change will cause changes in growing conditions, changes in the yields of conventional crops and energy crops, and changes in the allocation of energy crops to land in the region [9]. The agricultural sector is crucial to food security and is greatly affected by climate change. Rising temperatures and precipitation oscillations cause disturbances in the hydrological balance, making productive lowlands more vulnerable to extreme drought. This has the potential to significantly reduce crop yields and hamper adaptation and mitigation efforts in the face of climate change. In addition to exposure to drought, global climate change also has implications for rainfall patterns and has the potential to cause flooding on cultivated land.

Extreme flooding, which is projected to increase in frequency, requires better management. The potential for flooding on cultivated land is certainly not suitable for agricultural systems. Plant damage caused by flooding is likely to be greater in future climate conditions, meaning that the impact of flooding on agriculture is expected to pose even more challenges [10]. Unpredictable rainfall often causes field crops to be regularly exposed to waterlogging. This is a highly stressful factor that can lead to reduced crop yields and even total crop failure. Plant responses to waterlogging vary, with some species exhibiting complex morphological, anatomical, biochemical, and physiological adaptations, including photosynthesis, stomatal conductance, and gas exchange, as well as biochemical adaptations, such as increased fermentation enzyme activity, energy crises, and enhanced glycolysis supply [11].

Acid rain (AR) caused by industrial activity, transportation, and volcanic eruptions can damage plants and inhibit photosynthesis. Repeated exposure to AR causes necrotic damage to leaves, indicating cell and tissue death. This has the potential to disrupt the physiological functions of plants. Another significant impact is the reduction in photosynthetic pigments such as chlorophyll a, chlorophyll b, total chlorophyll, the chlorophyll a/b ratio, and total carotenoids, which directly inhibit the photosynthesis process. AR can cause structural changes in leaves, disrupt stomatal development, lead to the loss of the cuticle layer, and damage the overall anatomy of the leaf [12]. Research shows that AR can damage the physical form of tea plants, causing necrosis spots and corrosion on the leaf surface. Treatment with acid rain at a pH of 3.5 reduced the photosynthetic pigments chlorophyll a, chlorophyll b, and carotenoids by 6.6%, 8.5%, and 10.9%, respectively. Meanwhile, treatment with a more acidic pH of 2.5 resulted in a much more significant decrease in these pigments, with chlorophyll a decreasing by 38.4%, chlorophyll b decreasing by 55.3%, and carotenoids decreasing by 57.7% [13]. AR at pH 2.5 damages the wax layer and cuticle, destroys the shape of trichomes, and causes the loss of chloroplasts and severe damage to the palisade parenchyma, especially in the intercostal area and leaf margins [14]. Acid rain triggers a reaction with cadmium (Cd) in the soil. The composition of anions and the pH of acid rain are two important factors that influence the effects of Cd formation [15]. Cd causes significant changes in membrane function by inducing lipid peroxidation and disrupting chloroplast metabolism by inhibiting chlorophyll biosynthesis and reducing the activity of enzymes involved in CO2 fixation.

The presence of heavy metals in soil poses a serious challenge to global food security. Cereal crops, as a major source of nutrition, are vulnerable to heavy metal contamination resulting from anthropogenic activities. The effects of this contamination trigger physiological symptoms such as chlorosis and growth inhibition [16]. Heavy metals that contaminate soil have high persistence levels due to their low mobility and degradation. This causes long-term accumulation, posing a continuous threat to agricultural productivity [17]. Plants absorb heavy metals from contaminated soil through their root systems. Metals such as cadmium and lead have a high affinity for roots, making them easy to absorb even in low concentrations [18]. Heavy metals can interfere with

physiological processes in plants, triggering growth inhibition, chlorosis or yellowing of leaves, and nutritional imbalances [19].

The impact of global climate change on agriculture and food crops poses a serious threat to food security and human health. Climate change causes rainfall anomalies, increased abiotic stress such as drought and flooding, and increased extreme temperatures. These factors significantly affect the nutritional quality and bioactive compounds in food crops, as climate change can alter phytochemical composition and disrupt photosynthesis. Additionally, increased frequency of acid rain and heavy metal contamination in soil also damage plant physiology, hinder growth, and reduce nutrient content.

Through a comprehensive analysis of various studies, the author integrates information on the impact of global climate change on plants, particularly in the context of abiotic stress. The author synthesizes data from relevant literature to highlight how drought, flooding, extreme temperatures, and exposure to acid rain influence the physiological and anatomical responses of plants. This review emphasizes the urgency of gaining a deep understanding of plant adaptation mechanisms as a crucial foundation for developing sustainable and innovative agricultural strategies.

Therefore, in-depth research on plant adaptation responses to various environmental stresses is crucial for developing effective mitigation strategies and ensuring the availability of safe and nutritious food. Mastering this information is a crucial foundation for maintaining food security and ensuring nutritional quality for the global population in the future.

2. METHODS

The literature review research methodology is a systematic approach to analyzing, synthesizing, and summarizing findings from relevant scientific literature on a particular topic. Its purpose is to identify trends, gaps, and contradictions in existing research, thereby providing a comprehensive overview of the current state of knowledge. This process begins with the formulation of clear research questions, followed by a comprehensive literature search using scientific databases such as PubMed, Scopus, and Web of Science. Once the literature has been collected, the next step is to screen and extract data from each selected article for analysis. Review procedure flowchart shown in Fig. 1.

The articles are original research published in reputable peer-reviewed journals to ensure the reliability of the data. The articles specifically discuss one or more types of abiotic stresses, including drought, waterlogging, extreme temperatures, acid rain exposure, and heavy metals, ensuring that the review covers the latest findings. By applying these strict selection criteria, the literature review we present is expected to provide an in-depth and accurate synthesis of how plants adapt under various environmental stresses.

The ability to compile a strong literature review is an important foundation for producing high-quality scientific works, such as scientific articles. An effective literature review requires critical evaluation of previous research in order to identify gaps in knowledge and formulate a research agenda for the future. A literature review is a systematic process that involves searching for, identifying, reading, analyzing, and interpreting scientific works carefully, and contributes significantly to scientific progress [20]. A scientific review is a scientific approach used to analyze bibliographic data quantitatively. This methodology is very useful for identifying trends, patterns, and conclusions from published research findings on a particular subject or discipline [21].

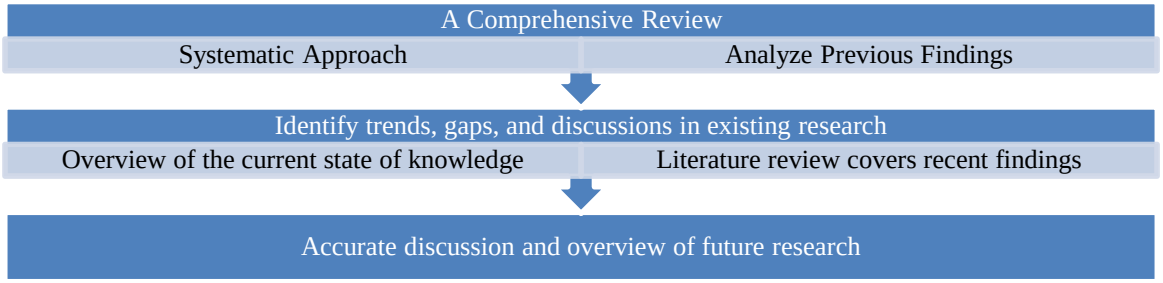


Fig. 1. Review procedure flowchart

The article search strategy was conducted systematically using relevant keywords such as plant abiotic stress, drought tolerance, waterlogging, extreme temperature adaptation, and acid rain effects on plants. Inclusion criteria included original research articles published in reputable journals, with a focus on articles published in the last 10 years to ensure the relevance and recency of the information. The article selection process was based on titles and abstracts to identify relevant articles, followed by reading the full text of the selected articles to ensure their suitability for the purpose of this review and to extract the necessary data.

3. RESULTS AND DISCUSSION

Global climate change has become one of the greatest threats to food security and agricultural sustainability. The frequency and intensity of abiotic stresses, such as prolonged droughts, floods caused by rainfall anomalies, heat waves, acid rain exposure, and heavy metal contamination, continue to increase. These phenomena directly disrupt plant growth, development, and productivity. The physiological response of plants to this stress is highly complex, involving a series of changes at the cellular and molecular levels that affect critical processes such as photosynthesis, hormonal balance, and cell membrane integrity. As a result, plants experience significant reductions in crop yields and, ultimately, fail to adapt to extreme environmental pressures. Table 1 shown about physiological and anatomy responses of plants to various abiotic stresses.

Table 1. Physiological and anatomy responses of plants to various abiotic stresses

Stress type	Physiological effect	Anatomical responses	Adaptive strategies
Drought stress	• Osmotic stress and dehydration, • Loss of cellular membrane integrity, • Disruption of photosynthesis (in both PSII and PSI), • Oxidative stress (increase in ROS), • Loss of cellular turgor, • Cellular energy depletion.	• Thick cuticles, • High glandular trichome and stomatal density, • Fewer but larger xylem vessels, • Formation of larger cortical aerenchyma and thicker nodal roots	• Stomatal modulation (movement and density), • Low leaf fall rate, • Osmotic adjustment (accumulation of proline and glycine betaine), • High water use efficiency.
Waterlogging stress	• Oxygen deficiency (anoxia/hypoxia), • Decreased photosynthesis, • Oxidative stress, • Hormonal imbalance, • Growth inhibition, • Chlorosis, • Metabolic disruption.	• Aerenchyma formation, • Adventitious root formation	• Genetic modification, • Agricultural management, • Antioxidant defense mechanisms, • Physiological adjustments.
Heat stress	• Protein damage, • Decreased photosynthesis and water use efficiency, • Oxidative stress (excessive ROS accumulation), • Nutrient reduction. • Cell membrane damage (increased electrolyte leakage), • Hormonal modulation. • Decreased growth and productivity.	• Changes in leaf structure and anatomy, • Damage to chloroplast ultrastructure, • Impaired root growth, • Maintained integrity of xylem vessels in tolerant plants.	• Cell membrane stability, • Increased antioxidant capacity, • Osmotic adjustment, • Stomatal regulation. • Production of Heat Shock Proteins (HSPs), • Metabolic reprogramming.
Cold stress	• Decreased plasma membrane fluidity, • Reduced photosynthesis and water use efficiency, • Increased oxidative stress, • Damaged productivity • Biochemical changes (increased cytosolic calcium), • Disrupted reproductive development	• Cytoskeleton reorganization, • Cell membranes become stiffer and less fluid, • Increase the ratio of polyunsaturated fatty acids for membrane flexibility, • Produce glycerolipids rich in polyunsaturated fatty acids to maintain fluidity.	• Membrane composition modification (increased unsaturated fatty acids), • Cold acclimation. • Molecular signaling, • Genetic regulation, • Internal protection (e.g., glycerolipid production)
Acid Rain Stress	• Decreased photosynthesis and water use efficiency, • Chlorophyll and carotenoid degradation, • Oxidative stress (ROS and MDA accumulation), • Reduced nutrient and water mobility, • Inhibited overall growth and biomass.	• Cuticle and epidermal erosion, • Stomatal damage, • Chloroplast and thylakoid structure damage, • Tissue necrosis.	• Antioxidant defense system activation (often insufficient), • Changes in chlorophyll fluorescence (as an indicator of stress).

In addition to affecting production quantities, climate change also impacts the nutritional quality and bioactive compounds in food crops. As environmental conditions change, the phytochemical composition of plants can shift substantially. For example, fluctuations in temperature and atmospheric CO_2 levels can affect the synthesis of antioxidants, vitamins, and minerals. This raises serious concerns about the nutritional value of plant-based foods, which are a primary source of nutrition for humans. Therefore, in-depth research into the physiological adaptation mechanisms of plants to various abiotic stresses is of utmost importance. This knowledge is not only crucial for developing more resilient plant varieties but also for designing sustainable agricultural strategies that can ensure a food supply that is not only sufficient but also nutritious amid global climate challenges.

3.1. Drought Stress in Plants

Drought stress has a significant impact on plant cells, causing various consequences such as osmotic stress, dehydration, and membrane dysfunction. Water deficiency leads to the loss of cellular turgor, disrupting photosynthesis and metabolite synthesis processes, and causing cellular energy depletion. One of the most fatal consequences is the loss of cellular membrane integrity, which is considered the primary cause of cell death due to severe drought stress. To address this, plant cells have defense mechanisms by expressing certain proteins. However, further research is still needed to deeply understand how these cellular effects function.

The most important consequences of drought stress are osmotic stress, dehydration stress, plasma membrane and endosome dysfunction, loss of cellular turgidity, inhibition of metabolite synthesis, depletion of cellular energy, disruption of photosynthesis, and oxidative stress. Oxidative stress triggers a chain reaction that begins with the influx of ions and an increase in Reactive Oxygen Species (ROS). This condition causes damage to lipids, nucleic acids, and proteins, which can lead to cell death. Because they are rich in lipids, mitochondrial membranes are the most vulnerable cellular components to damage caused by oxidative stress [22]. Dehydration due to water deficiency damages membranes and lipids. Drought stress drastically reduces the composition of galactolipids and major phospholipids, such as phosphatidylethanolamine (PE), phosphatidylcholine (PC), and phosphatidylglycerol (PG), which are essential for membrane fluidity and stability, including in chloroplasts [23].

Fig. 2 Dehydration due to water deficit in plants damages their membranes and lipids. Drought stress drastically reduces galactolipids and major phospholipids, such as PE, PC, and PG, which are crucial for maintaining membrane fluidity and stability, including in chloroplasts. These changes in lipid composition represent a significant response mechanism in the cell's efforts to survive drought stress conditions. The most important consequences of drought stress are osmotic stress, dehydration stress, plasma membrane and endosome dysfunction, loss of cellular turgidity, inhibition of metabolite synthesis, depletion of cellular energy, disruption of photosynthesis, and oxidative stress [22].

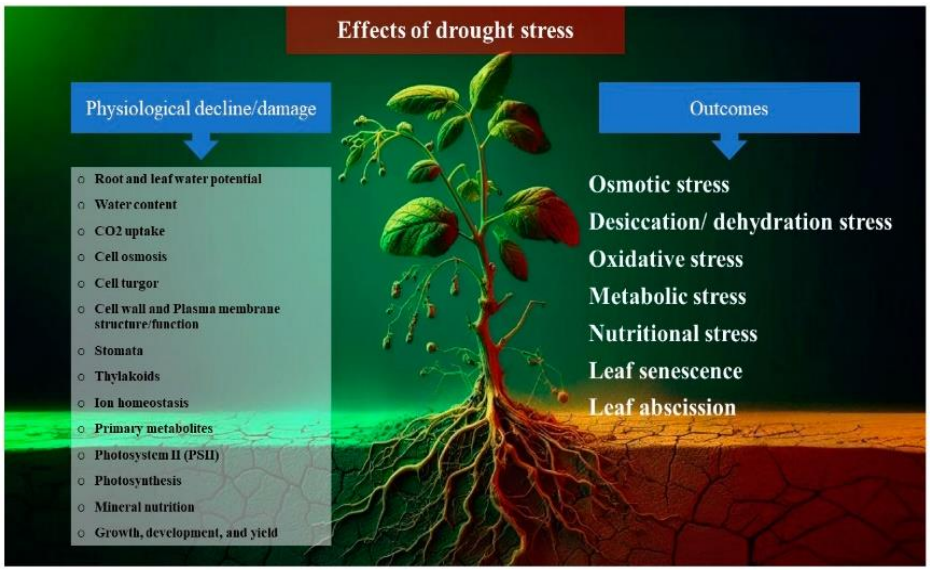


Fig. 2. Physiological effects of drought stress on plants and the outcomes that cause growth and yield reduction (reproduced from Haghpanah et al. 2024 under the term of CC-BY 4.0 License, copyright 2024 MDPI, Basel, Switzerland) [22]

The mechanism behind the decline in photosynthesis due to drought is still debated. In C3 plants, this decrease is largely caused by stomatal limitations under mild to moderate drought conditions. Meanwhile, in C4 plants, the decrease in photosynthesis is primarily caused by metabolic constraints in assimilating CO2. However, under severe drought conditions, non-stomatal factors also play an important role in reducing the rate of photosynthesis in C3 plants [24]. Drought disrupts photosynthesis by damaging the photosystem. In the early stages, photosystem II (PSII) disassembly and core degradation occur, although the light-harvesting complex (LHCII) remains intact. This causes LHCII to become a source of photo damage. In severe drought, photosystem I (PSI) is also affected, characterized by a reduction in antenna size and disassembly of the PSI-LHCI supercomplex, as well as the accumulation of non-functional PSI complexes. Based on these findings, the operational quantum efficiency of PSII can be used as an early indicator for detecting drought stress [25].

This study identified morphological, physiological, and anatomical characteristics correlated with drought tolerance in sesame plants. Well-adapted genotypes exhibited characteristics such as low leaf fall, high glandular trichome and stomatal density, thick cuticles, and substantial water use efficiency. They also have fewer xylem vessels but larger diameters to enhance water uptake and reduce water loss. These characteristics, along with high chlorophyll content and accumulation of osmoprotectants (such as proline and glycine betaine), can be used as selection indices in breeding programs to develop more drought-tolerant sesame varieties [26].

Stomatal modulation is a critical mechanism in plant tolerance to drought stress. Research shows that this adaptive ability depends not only on stomatal movement, stomatal closure to reduce water loss through transpiration, but also on stomatal density. Modifications to both of these characteristics enable food crops to maintain higher internal water levels. For example, plants that exhibit increased drought tolerance often have the ability to regulate stomatal closure more effectively, which ultimately limits water loss and maintains cellular hydraulic balance [27]. Drought-tolerant plants can adapt by increasing stomatal density and reducing stomatal size, allowing for faster stomatal opening, efficient CO2 absorption, prevention of excessive water loss, and maintenance of photosynthetic activity[28].

Based on the text, this study found that plant tolerance to drought is closely related to several key characteristics. Morphologically and anatomically, tolerant plants have low leaf fall rates, high trichome and stomatal density, thick cuticles, and fewer but larger xylem vessels. Physiologically, these plants exhibit high water use efficiency, high chlorophyll content, and accumulation of osmoprotectants such as proline and glycine betaine. Additionally, stomatal modulation plays a crucial role, tolerant plants can effectively regulate stomatal closure and have smaller but more numerous stomata. All these characteristics can be used as selection indices for developing more drought-tolerant varieties.

Faced with water deficits, plants respond to maintain cell turgor and prevent wilting. Turgor pressure, which is the main driving force for cell growth and expansion, decreases dramatically when cells lose water. This decrease directly disrupts various vital physiological processes, including photosynthesis and growth. To overcome this condition, plants activate an adaptive mechanism known as osmotic adjustment. Through this strategy, plants accumulate compatible solutes (such as proline, glycine betaine, and sugars) within the cell cytoplasm. The accumulation of these substances reduces the cell's osmotic potential, enabling it to absorb and retain more water from the dry environment. Thus, osmotic adjustment effectively maintains turgor pressure, preserves cellular function, and enhances plant survival under extreme drought conditions [29].

Root characteristics play an important role in water absorption and replenishment of water lost through transpiration. Adjustments to root structure under stress conditions have been linked to increased tolerance. Drought tolerance in corn is characterized by the formation of larger cortical aerenchyma, more numerous and narrower metaxylem vessels, and thicker nodal roots. These adaptations enable broader soil exploration, water conservation, and better penetration into dry soil. These phenotypes are proposed as breeding ideotypes for developing more drought-tolerant corn varieties [30].

Root characteristics play an important role in water absorption and replenishment of water lost through transpiration. Adjustments to root structure under stress conditions have been linked to increased tolerance. Drought tolerance in plants is characterized by the formation of larger cortical aerenchyma, more numerous and narrower metaxylem vessels, and thicker nodal roots. These adaptations enable broader soil exploration, water conservation, and better penetration into dry soil. These phenotypes are proposed as breeding ideotypes for developing more tolerant and resilient plants under drought conditions. Root anatomy and architecture can be a response to drought stress. Most root phenotypes are plastic and highly responsive to water deficiency, as indicated by shifts in mean values and their distribution, and are important factors to consider along with root traits in drought tolerance strategies.

Drought is a major challenge in modern agriculture, seriously impacting crop productivity by damaging cell membranes, disrupting photosynthesis, and causing osmotic stress. Based on available information, the role of agricultural science in addressing this issue is crucial, focusing on an integrated approach. One such approach is through plant breeding to develop varieties that are more drought-tolerant. Characteristics such as

low leaf shedding, high stomatal and trichome density, and fewer but larger xylem vessels can serve as selection indices in breeding programs. Additionally, stomatal modulation and the accumulation of osmoprotectants like proline and glycine betaine are important physiological mechanisms that can be enhanced. Structural root adaptations, such as the formation of larger cortical aerenchyma, also serve as breeding ideotypes to enhance water uptake. Through a deep understanding of plant responses at the morphological, anatomical, and physiological levels, agricultural science can proactively create superior varieties capable of adapting and maintaining productivity under extreme drought conditions.

3.2. Waterlogging Stress in Plants

Understanding the physiological and anatomical responses of plants to waterlogging stress is crucial in the context of global food security because waterlogging, or anoxia, drastically alters the root environment. When waterlogging occurs, oxygen supply to the roots is blocked, triggering oxygen deprivation that disrupts aerobic respiration, metabolism, and nutrient uptake. At the anatomical level, some flood-tolerant plants develop aerenchyma, a parenchyma tissue with large intercellular air spaces that facilitate gas diffusion from the canopy to the roots. By studying these deep adaptations, we can pave the way for breeding plant varieties that are more resistant to flooding stress, while also developing more effective agronomic strategies to address the impacts of climate change.

Climate change increases the threat of waterlogging to food crops, disrupting their growth and productivity. When roots are waterlogged, oxygen supply is reduced, triggering hypoxic or anoxic conditions. To adapt, plants undergo physiological and morphological changes, such as forming adventitious roots and aerenchyma tissue to channel air to the roots. These adaptations are regulated by specific gene and hormone signaling pathways. Understanding these molecular mechanisms, such as identifying key genes, is crucial for developing crop varieties that are more resistant to waterlogging [31]. The presence of water is crucial for plant life, but waterlogging or flooding causes harmful waterlogging stress. This condition inhibits the exchange of vital gases between the soil and the atmosphere, which ultimately has a negative impact on the entire plant life cycle. Plant responses to waterlogging stress vary greatly depending on the species. Flood-tolerant plants, such as rice, develop specialized adaptations, such as the formation of aerenchyma (air-filled tissue) to transport oxygen from the leaves to the roots. In contrast, flood-intolerant plants, such as corn, are more susceptible to severe damage and even death. Ultimately, waterlogging stress can lead to stunted plant growth, chlorosis (yellowing of leaves), flower and fruit drop, and a drastic reduction in productivity and crop yield [32].

Fig. 3 Under waterlogged conditions, roots lack oxygen, and plants focus on adapting for respiration. Normal root growth is inhibited, but plants form adventitious roots that grow upward toward surfaces richer in oxygen. In addition, aerenchyma, a specialized tissue with air spaces, forms within the roots to facilitate oxygen transport from the leaves to the submerged roots. Physiologically, these conditions also cause a decrease in photosynthesis and transpiration due to impaired root function [33].

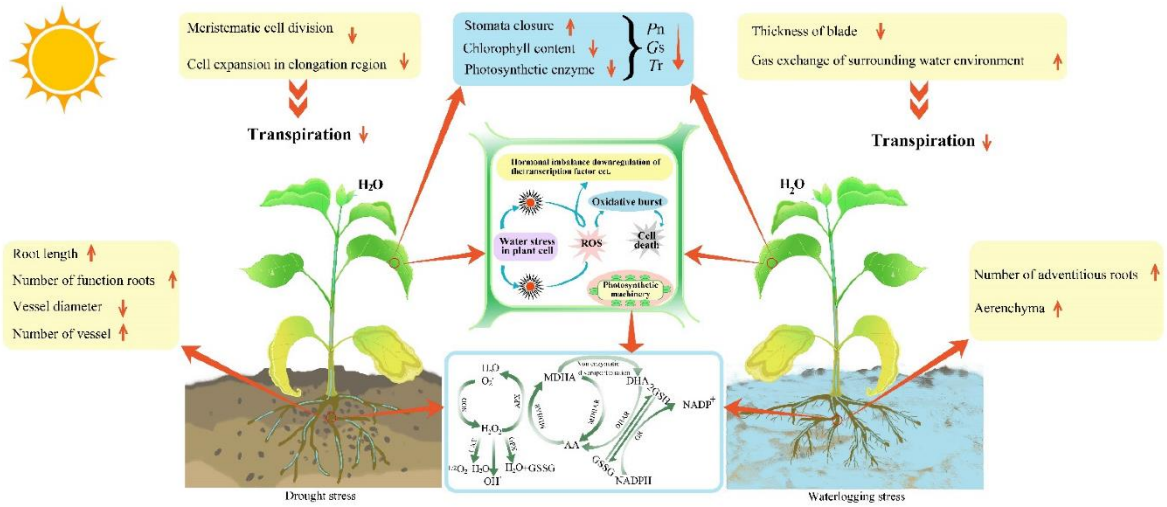


Fig. 3. Changes to the morphological and anatomical structure of plant leaves and roots due to water stress. (reproduced from Wu et al. 2022 under the term of CC-BY 4.0 License, copyright 2024 MDPI, Basel, Switzerland) [33]

Waterlogging triggers stomatal closure, which reduces the rate of photosynthesis due to chlorophyll degradation and leaf senescence. Oxygen deficiency in the root zone (anoxia) disrupts mitochondrial

respiration and triggers fermentation. This process results in the accumulation of toxic metabolites such as ethanol and ROS, which cause oxidative stress and cell death. Overall, waterlogging inhibits root and shoot growth, disrupts hormonal balance, and significantly reduces productivity and crop yield [31]. Waterlogging affects both tolerant (Kenfeng 14) and sensitive (Kenfeng 16) soybean varieties. Research shows that waterlogging stress increases antioxidant enzyme activity but decreases non-enzymatic antioxidants such as ascorbic acid (AA) and glutathione (GSH). The application of uniconazole (S3307) has been shown to alleviate these negative effects. S3307 improves leaf physiology, enhances antioxidant defense mechanisms, and prevents cell damage due to lipid peroxidation caused by waterlogging [34].

Waterlogging occurs when the soil becomes saturated with water, causing anaerobic conditions in the plant root zone. Climate change increases the frequency of waterlogging events, resulting in significant crop losses. When plant roots are waterlogged, they experience a decrease in respiration and a loss of ATP synthesis, which can cause wilting. Plants respond to waterlogging stress through adventitious root growth, aerenchyma formation, energy metabolism, and phytohormone signaling. Different genotypes vary in terms of biomass reduction, photosynthesis rate, adventitious root development, and aerenchyma formation in response to waterlogging. We reviewed the detrimental effects of waterlogging on physiological and genetic mechanisms in four major cereal crops (rice, maize, wheat, and barley) [35]. Glucose is the main source of energy for plants. Through the processes of glycolysis and respiration, glucose is broken down to produce the energy needed for all important processes, such as growth and reproduction [36].

Waterlogging stress reduces the rate of photosynthesis in plants through several mechanisms. This condition causes stomatal closure and reduces mesophyll conductance, which inhibits CO2 uptake. In addition, waterlogging also triggers chlorophyll degradation and damage to Photosystem II (PS II), an essential component in the photosynthetic chain. Concurrently, the activity of enzymes involved in photosynthesis also decreases, collectively resulting in a drastic reduction in plant photosynthetic efficiency [37]. Waterlogging causes chlorosis, or yellowing of the leaves, which is a common visual sign. This chlorosis triggers premature leaf senescence, allowing the plant to transfer existing nitrogen (N) to younger leaves to maintain its growth. In addition, waterlogging disrupts nutrient uptake by the roots, resulting in lower nutrient concentrations in the upper parts of the plant (shoots) [38]. Waterlogging disrupts nitrogen (N) metabolism and assimilation in corn, which negatively impacts various stages of its growth [39].

The number of adventitious roots in tolerant barley genotypes was significantly higher after 21 days of waterlogging treatment than in sensitive genotypes [40]. It has been shown that aerenchyma occupies 20–22% and 19% of adventitious roots in wheat and barley, respectively [41]. Based on research, barley plants that are tolerant to waterlogging show a significant increase in the number of adventitious roots after 21 days of treatment, compared to sensitive varieties. The formation of adventitious roots is an important morphological response that allows plants to survive in anoxic conditions. Furthermore, analysis of the structure of adventitious roots in wheat and barley revealed the formation of aerenchyma, a tissue with large intercellular air spaces. This aerenchyma was reported to occupy 20–22% of the total volume of adventitious roots in wheat and 19% in barley, playing a crucial role in facilitating oxygen transfer from the upper parts of the plant to the submerged roots. This adaptation is key for plants to maintain normal respiration and metabolism in oxygen-deprived environments.

Plants respond to waterlogging stress by regulating their morphological structure, energy metabolism, endogenous hormone biosynthesis, and signaling processes. Efforts to improve plant tolerance to waterlogging can be done through two main approaches. First, by implementing better cultivation management, which is to minimize the impact of direct damage. Second, by utilizing modern molecular biology, through identifying important genes that control waterlogging tolerance responses and then using them to modify plants [42].

Based on this study, it is evident that waterlogging stress on plants will respond through various coordinated mechanisms. This response involves adjustments to morphological structure, energy metabolism, and regulation of endogenous hormone biosynthesis, as well as coordinated signaling pathways. Efforts to enhance plant tolerance to these conditions can be approached through two main strategies. First, by implementing better cultivation management practices to reduce direct physical and physiological damage. Second, by leveraging modern molecular biology technologies, this approach enables the identification of key genes controlling waterlogging tolerance, which can then be used to modify plants and produce more resilient varieties. The combination of these two approaches constitutes an effective strategy for enhancing plant resilience to waterlogging stress, particularly in the face of global climate change threats.

To ensure the sustainability of agriculture in the future, an integrated approach combining cultivation management and molecular biology innovation is needed. From a management perspective, the implementation of agricultural practices that reduce the direct impact of waterlogging is crucial, such as through improved drainage systems or efficient water management. Meanwhile, from a molecular biology perspective, priority should be given to in-depth research to identify key genes that control waterlogging tolerance. Findings that

tolerant plants form more aerenchyma and adventitious roots indicate the presence of genetic pathways that can be exploited. Modern technologies such as gene editing and plant breeding can be used to develop varieties with stronger adaptive responses, such as more efficient aerenchyma formation or more effective antioxidant defense mechanisms. Thus, the combination of these strategies will be key to building plant resilience to waterlogging stress while maintaining global food security in the future.

3.3. Effects of Heat Stress on Plants

Beyond the macro impact on crop yields, extreme temperature stress triggers a complex series of physiological, biochemical, and molecular responses within plants. Temperatures exceeding the optimal threshold, whether chronically or suddenly in the form of heat waves, can cause permanent damage to plant growth and development. One area that remains poorly understood is how long-term heat stress affects nutrient uptake and related physiological responses. Mineral nutrients, which are essential for optimal growth, have availability that is highly dependent on soil conditions, which in turn are influenced by temperature. The reduction in nutrient uptake due to heat stress, which may be mediated by damage to nutrient-absorbing proteins and the accumulation of ROS (reactive oxygen species), highlights the complex interactions between abiotic factors and internal plant mechanisms. This phenomenon not only highlights the vulnerability of our food systems but also underscores the importance of a deep understanding of how plants respond to environmental stress under extreme temperature conditions.

Fig. 4 Heat stress inhibits overall plant growth, both in the roots and shoots. This occurs because extreme temperatures damage the proteins responsible for absorbing nutrients in the roots, thereby reducing the roots' ability to extract nutrients from the soil. As a result, root mass and the amount of nutrients absorbed are reduced, which ultimately leads to a decrease in nutrient levels in the shoots of the plant. Global warming caused by heat waves damages plant function by inhibiting growth at various stages, reducing crop quality, and disrupting nitrogen metabolism enzymes. Although the widespread effects of heat stress have been extensively studied, there is still a lack of specific understanding of its impact on nutrient content and the genetic regulatory mechanisms of nutrient uptake. Heat stress is known to reduce plant nutrient concentrations through root cell damage, which decreases root growth and nutrient absorption proteins. Future research should focus on molecular analysis of nutrient absorption proteins and the role of cellular signaling pathways, such as peroxisomes, to develop plant adaptation strategies for climate change [43].

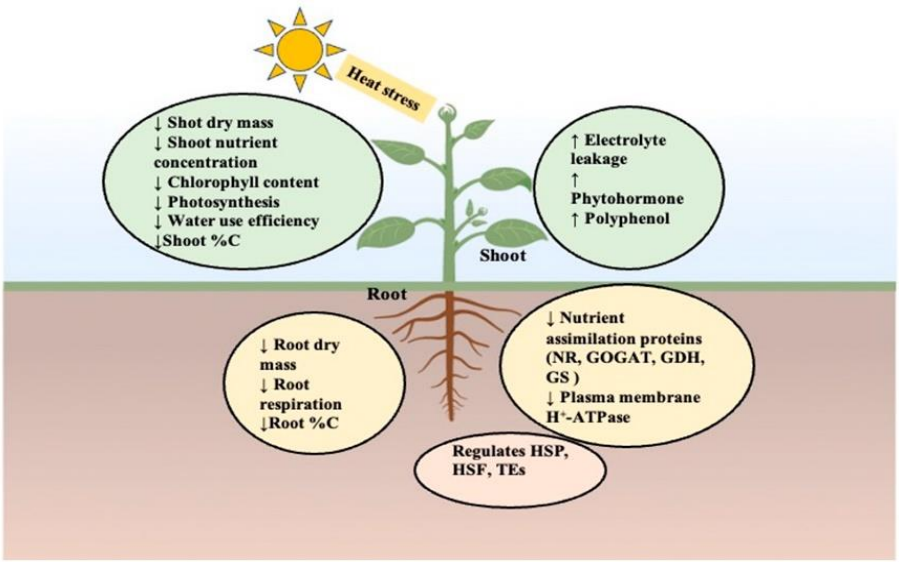


Fig. 4. The effects of heat stress on plants (reproduced from Mishra et al. 2023 under the term of CC-BY 4.0 License, copyright 2023 MDPI, Basel, Switzerland) [43]

Based on this, it shows that heat stress triggers complex and integrated physiological and biochemical responses in plants, starting from the molecular level to macroscopic manifestations. At the root level, high temperatures not only inhibit biomass growth but also critically disrupt nutrient uptake by inactivating key proteins involved in nutrient assimilation, such as NR, GOGAT, GDH, and GS, and impairing essential plasma membrane functions. This damage compromises cellular membrane integrity and reduces the availability of absorbed nutrients. The effects extend to the shoot, causing a reduction in nutrient supply from the roots, combined with direct heat damage to chlorophyll, drastically reducing photosynthesis rates and water use

efficiency. This reduction in photosynthesis leads to decreased carbohydrate synthesis, reflected in reduced shoot dry weight and carbon content. Additionally, heat stress triggers increased electrolyte leakage, an indicator of cellular membrane damage, and modulates phytohormone and polyphenol levels as a defensive response. Overall, these negative interactions create a domino effect that inhibits growth, reduces quality, and ultimately significantly lowers plant productivity.

The response of plants to heat stress, both above ground (shoots) and below ground (roots), is very complex and varies depending on how the heat exposure occurs. However, in general, root growth is more susceptible to high temperatures than shoot growth. This is because roots have a lower optimal temperature range for growth, making them more sensitive to temperature increases [44]. The response of plants to heat stress in above-ground (shoots) and below-ground (roots) organ systems is a highly complex phenomenon, influenced by the duration and intensity of heat exposure. In general, root growth is more sensitive to high temperatures than shoots. This higher sensitivity is due to the lower optimal growth temperature range of roots, making them more susceptible to physiological and metabolic damage caused by increased environmental temperatures [45].

The increase in environmental temperature caused by climate change poses a serious threat to global crop production. Chloroplasts, as the center of metabolism, play an important role in physiological adaptation to heat stress. Under heat stress conditions, chloroplasts not only produce heat shock proteins to protect proteins from damage, but also undergo metabolic reprogramming. Heat stress directly inhibits photosynthetic activity by damaging key metabolic components, ultimately leading to a significant decline in biomass production and crop yields [46]. Numerous studies have shown that heat stress, both short-term and long-term, disrupts photosynthesis by causing changes in leaf structure and anatomy, as well as affecting the function of the photosynthetic apparatus itself.

Scientific studies on heat tolerance in Rhododendron indicate that physiologically, this plant is more effective in maintaining cell membrane stability, demonstrating higher antioxidant capacity to neutralize Reactive Oxygen Species (ROS), and performing osmotic adjustments to protect proteins and maintain cell turgor. From a morphological and anatomical perspective, the plants can regulate stomatal opening to reduce water loss and maintain the integrity of chloroplast ultrastructure and xylem vessels. The combination of these protective mechanisms enables the plants to survive and function more effectively under high-temperature conditions, providing valuable insights for breeding ornamental plants that are more resilient to climate change [47]. Plants cope with heat by maintaining cell membrane stability, increasing antioxidant capacity, and performing osmotic adjustments. Morphologically, these plants regulate stomata to reduce water loss and maintain the integrity of chloroplasts and xylem vessels. The combination of these protective mechanisms provides valuable insights for breeding ornamental plants that are more resistant to climate change.

Heat stress exposure affects nutrient concentrations in plants in varying ways, depending on which part of the plant is exposed (roots, shoots, or the entire plant) and the stage of growth. For example, when Chenopodium plants were exposed to heat stress at 30 °C and 35 °C for 11 days during the anthesis phase, there was a decrease in the concentration of As, Cd, Rb, and Sr in their main inflorescences [48]. The formation of reactive oxygen species (ROS) is a common response of plants to stress, and its regulation is essential for maintaining cellular balance. If ROS production is excessive, it can damage cells. In this case, peroxisomes, together with mitochondria and chloroplasts, function as an integrated center for maintaining ROS balance within cells [49]. Temperatures exceeding the optimal range accelerate the growth phase, resulting in a decrease in biomass, seed weight, and overall yield. In addition, high temperatures increase the water requirements of plants, leading to increased transpiration, reduced photosynthesis, and subsequently lower yields [50].

Based on this scientific study, it is evident that heat stress poses a serious threat to plant growth and productivity, including cultivated plants. Heat stress causes cascading effects, starting from the molecular level to the macroscopic level. At the root level, high temperatures damage nutrient absorption proteins, inhibit root growth, and disrupt nitrogen metabolism, which ultimately reduces nutrient availability throughout the plant. This damage also extends to the shoots, where heat directly damages chlorophyll, reduces photosynthesis rates, and decreases water use efficiency. This response, combined with cell membrane damage evident from increased electrolyte leakage, collectively inhibits growth, reduces quality, and significantly decreases yield.

For further development, future research is expected to focus on a more specific understanding of the molecular and genetic mechanisms regulating plant tolerance to heat. Although the broad effects of heat stress have been extensively studied, there remains a lack of understanding of how heat specifically affects nutrient content and the proteins involved in nutrient absorption. Therefore, research should be directed toward in-depth analysis of nutrient absorption proteins and the role of cellular signaling pathways, such as peroxisomes, in maintaining ROS balance. The goal is to develop more effective plant adaptation strategies, including through the breeding of crop varieties that are more resilient to climate change.

3.4. Effects of Cold Stress on Plants

Cold stress on plants causes the plasma membranes of plant cells to become less fluid and more rigid. This rigidity disrupts membrane functions, such as nutrient transport and intercellular signaling. Cold-tolerant plants overcome this problem by altering the composition of their membranes. They increase the ratio of polyunsaturated fatty acids, which have double bonds in their hydrocarbon chains. These double bonds create bends that prevent lipid molecules from packing too tightly. As a result, the membrane remains flexible or fluid even at low temperatures. This maintained membrane fluidity is crucial for enzyme function, protein transport, and cellular communication.

Additionally, the cytoskeleton, which is a network of protein filaments within the cell, also undergoes reorganization. The cytoskeleton functions as the cell's framework, determining its shape, the position of organelles, and movement within the cell. During cold stress, the cytoskeleton changes to stabilize the cell structure and prevent mechanical damage. For example, microtubules become more stable and ordered, helping to keep organelles like chloroplasts in optimal positions for photosynthesis. These changes ensure the structural integrity of the cell and the smooth operation of metabolic processes, which are crucial for the survival of plants in low-temperature conditions.

Cold stress is a major obstacle to plant growth, often causing a drastic reduction in crop yields.Cold stress is a major challenge for plant growth, especially for tropical plants such as rice, which can lead to reduced crop yields. To survive, plants have developed various strategies, including cold acclimation in temperate climate plants, as well as physiological, biochemical, and molecular mechanisms. These responses involve modifications to cell membranes, temporary increases in cytosolic calcium, activation of protein kinases, and epigenetic control to sense and cope with low temperatures. Overall, understanding these mechanisms is crucial for enhancing plant resilience to cold stress [51].

Fig. 5 Illustrates the plant response to cold stress, which is divided into three main pathways: signaling, phytohormones, and epigenetic control. The signaling pathway involves changes in the membrane and cytoskeleton, while the phytohormone pathway uses hormones such as ABA and auxin. Epigenetic control involves gene regulation through MicroRNAs and chromatin remodeling. All of these pathways ultimately lead to transcriptional regulation that determines whether plants will be tolerant or susceptible to cold stress. When faced with low temperatures, many plants undergo changes in their cell membranes as an essential physiological response to survive [51].

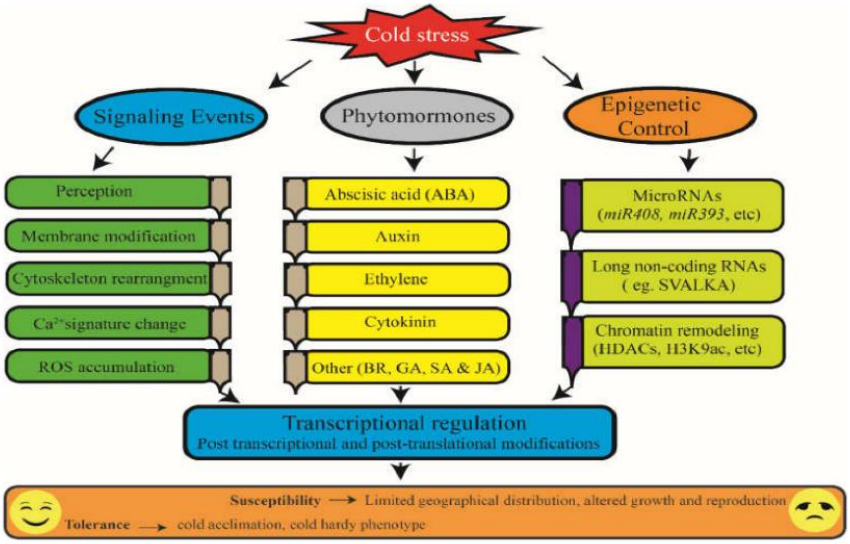


Fig. 5. Significant events during cold stress response in plants (reproduced from Aslam et al. 2022 under the term of CC-BY 4.0 License, copyright 2022 MDPI, Basel, Switzerland) [51]

The phenomenon of frost occurring in early spring can cause significant losses in tea harvest yields, but the underlying physiological mechanisms are still not fully understood. This study shows that exposure to varying freezing temperatures (−5 °C for 3, 6, and 12 hours) gradually reduces photosynthesis rates, water use efficiency, and photosystem II efficiency, while increasing oxidative stress in mature leaves. These conditions ultimately result in reduced yield and quality of young tea leaves, characterized by decreased water content and dry weight, as well as an increase in the polyphenol-to-amino acid ratio, which is detrimental [52].

Cold stress poses a serious threat to crop productivity, especially during the growth phase, and can affect the geographical distribution of crops. The most vulnerable stage is flowering, as cold stress can be fatal to reproductive success. Although pollen development and fertilization are considered most critical, female reproductive tissues are also vulnerable to cold stress [53]. Rice plants, as a model monocotyledonous cereal from tropical and subtropical regions, are highly susceptible to stress caused by cold temperatures [54]. In annual woody plants, internal systems such as photoreceptors and circadian clocks detect the shortening of days in autumn. These changes trigger the cessation of shoot growth and increase frost tolerance in tissues. Although low temperatures also help, the main trigger for this cold acclimation process is the shortening of days. For example, trees like Silver Birch and Populus begin to develop frost tolerance as days shorten, which becomes stronger as temperatures drop [55].

The endoplasmic reticulum (ER) plays an important role in helping plant cells adapt to cold stress. When temperatures drop, the ER acts as a functional part that produces stress-induced lipids, such as glycerolipids, which are rich in polyunsaturated fatty acids. These lipids are then sent to the cell membrane to maintain its fluidity, preventing stiffness that can damage cellular function. Interestingly, glycerolipids also serve a dual function as signaling molecules. Their fragments can trigger a series of signals that activate cold tolerance genes. Thus, the endoplasmic reticulum not only modifies the physical structure of the cell but also initiates a genetic response to ensure the survival of plants under low-temperature conditions [56].

Changes in the cytoskeleton are also an important part of the plant's response to cold stress. Within minutes, exposure to cold can alter the structure and organization of the cytoskeleton. To maintain structural integrity, the cytoskeleton will undergo reorganization or dismantling. This process of cytoskeletal depolymerization is believed to be the trigger needed to activate genes that are responsive to low temperatures [57]. When exposed to low temperatures, plants activate rapid and coordinated physiological responses at the cellular level. These responses involve crucial modifications to the cell membrane and cytoskeleton. In the membrane, plants increase the ratio of unsaturated fatty acids to maintain fluidity and prevent stiffness that can damage cell function. Concurrently, the cytoskeleton undergoes reorganization or depolymerization within minutes, which is not merely a passive response but an active process that generates molecular signals. This depolymerization process is believed to be a key trigger that induces the expression of cold-responsive genes, thereby ensuring the survival and adaptation of plants under cold stress conditions.

Based on this study, exposure to cold stress triggers a series of coordinated physiological responses in plants to ensure survival. At the cellular level, the initial response involves modifications to membrane composition, with the synthesis of glycerolipids rich in polyunsaturated fatty acids from the endoplasmic reticulum. These modifications are important for maintaining membrane fluidity and preventing stiffness that impairs cell function. Additionally, cold stress triggers cytoskeletal reorganization and increased intracellular Ca2+ signaling, which serves as a trigger to activate downstream signaling cascades. Overall, these responses demonstrate complex physiological adaptations in which plants rapidly alter cellular structure and biochemical composition to counteract the direct effects of low temperatures.

These physiological mechanisms ultimately translate into gene expression regulation that determines the plant's cold tolerance phenotype. Through the activation of cold-responsive genes, such as those regulated by phytohormone signals like ABA and epigenetic control via miRNAs and chromatin remodeling, plants can induce cold acclimation. This acclimation enables plants to withstand freezing temperatures and maintain the integrity of photosynthesis and carbon metabolism, which are crucial for sustaining growth and productivity. Therefore, a deep understanding of the interactions between initial physiological signals and long-term genetic responses is key to developing biotechnology strategies to enhance plant resistance to cold stress.

3.5. Exposure to Acid Rain in Plants

The phenomenon of acid rain (AR) is an ecological problem that has existed since the industrial revolution, caused by emissions of acidic gases such as sulfur dioxide (SOx) and nitrogen oxides (NOx) from human activities and natural sources. Rainfall with a pH below 5.6 causes widespread damage, including soil and water acidification, reduced crop yields, forest degradation, and corrosion of infrastructure. Plants, as the main component of terrestrial ecosystems, are direct receptors of these pollutants. Therefore, understanding how plants respond to acid rain is very important, not only to provide a scientific basis for mitigation efforts, but also to design effective ecosystem restoration strategies in affected areas.

Acid rain is one of the main environmental factors that hinders plant growth and productivity globally, posing a serious threat to the agricultural sector. To assess its impact, scientists use acid rain simulations (SAR) to observe how exposure to acid rain changes plant growth, development, and physiological and molecular activity, ultimately leading to a decline in crop yields [58].

Acid rain (AR) is one of the main threats to crop productivity because it significantly inhibits basic growth, including height, number of leaves, stem diameter, and root biomass. These negative effects are

primarily caused by disruption of the photosynthesis process, characterized by a decrease in photosynthesis rate, damage to chloroplast ultrastructure, and chlorophyll degradation. Additionally, exposure to AR triggers the accumulation of reactive oxygen species (ROS) and malondialdehyde (MDA) within cells. While plants can activate antioxidant defense systems to counteract oxidative stress at moderate levels, this detoxification capacity can plummet drastically under severe AR stress conditions, ultimately leading to greater cellular damage and disrupting overall plant growth and development.

Industrial development, transportation, volcanic activity, and the use of fossil fuels increase acid gas emissions, which exacerbate acid rain, directly damaging plants and inhibiting photosynthesis. Acid rain causes changes in the morphology, anatomy, and photosynthetic pigments of plants. Our previous findings indicate that the main impact of acid rain exposure is damage to stomata, which are pores on the surface of leaves that are important for gas exchange (CO2 and H2O). Damage to stomata disrupts vital processes such as photosynthesis, respiration, and transpiration. These disruptions, in turn, reduce CO2 assimilation, interfere with nutrient and water mobility, and indirectly inhibit plant growth and productivity. When stomata are damaged, photosynthetic efficiency decreases due to impaired CO2 uptake, and transpiration and respiration processes are also disrupted, all of which contribute to reduced growth rates [12]. Exposure to acid rain (AR) can cause chloroplast degradation and a decrease in water potential in plant cells. This triggers stomatal closure and reduces CO2 assimilation, which ultimately disrupts cell division [59]. Low pH levels in AR exposure can damage chloroplast and thylakoid structures, even causing the loss of starch granules. This damage inhibits photosynthetic transport within the leaves, which ultimately disrupts the entire photosynthetic process in plants [60].

Fig. 6 Based on the scheme, acid rain causes a series of negative effects on plants through two main interconnected pathways. The first pathway begins with osmotic imbalance, which disrupts plant metabolism and directly inhibits growth and development. The second pathway is more complex, beginning with damage to chloroplasts and important macromolecules, which triggers chlorophyll degradation and oxidative stress. This condition causes excessive production of ROS (Reactive Oxygen Species) and an imbalance in the antioxidant system. These two pathways converge and exacerbate each other, collectively leading to a significant decrease in the rate of photosynthesis. This decrease in photosynthesis is the main cause of stunted growth, development, and overall plant productivity [61].

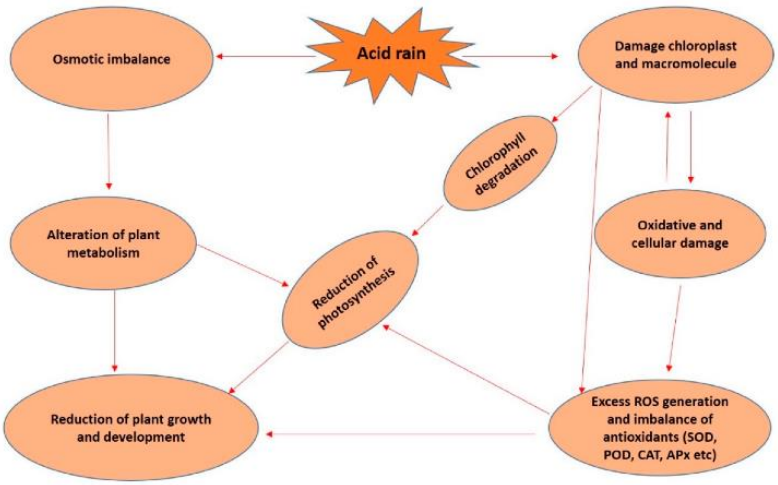


Fig. 6. The action of acid rain stress on photosynthesis, antioxidant system and growth in plants (reproduced from Debnath et al. 2021 under the term of CC-BY 4.0 License, copyright 2021 MDPI, Basel, Switzerland) [61]

Erosion of the cuticle disrupts gas exchange and cuticle biosynthesis. Hydrogen ion penetration into cells disrupts chloroplast function, leading to starch accumulation and inefficient carbohydrate metabolism. Increased absorption of heavy metals can trigger toxicity, disrupting cellular homeostasis. As a result, photosynthesis decreases, light utilization is reduced, and this series of structural and metabolic dysfunctions inhibits plant growth, development, and productivity [62]. Low pH levels in AR exposure can damage chloroplast and thylakoid structures, even causing the loss of starch granules.

Acid rain exposure induces leaf damage with necrotic symptoms indicating cell and tissue death, potentially disrupting physiological functions. Test results show that the percentage of tea leaf damage reached 82.73%. The high percentage of leaf damage is directly correlated with impaired photosynthesis due to a

reduction in the effective leaf surface area for capturing sunlight, thereby potentially significantly reducing plant productivity [12]. Acid rain increases the levels of reactive oxygen species (ROS) and malondialdehyde (MDA) by 30.1% and 41.9%, respectively, causing chlorosis in rice seedlings and disrupting the rate of photosynthesis. Genetic analysis shows that this disruption of the photosynthetic system occurs in the thylakoid membrane, indicating damage to key genes involved in chloroplast development [63].

Photosynthesis is a fundamental physiological and morphological process that enables plants to synthesize organic compounds using light energy, which is essential for their growth, development, and survival [64]. Chlorophyll and carotenoids, as photosynthetic pigments, are vital for plant growth and development. Due to their central role, these pigments are often used as sensitive indicators to assess the negative impacts of various environmental stresses, including exposure to acid rain [65]. Testing of photosynthetic pigments exposed to acid rain on tea seedlings showed a significant decrease in all pigments, with chlorophyll a, chlorophyll b, and total chlorophyll decreasing by 65.69%, 50.66%, and 58.69%, respectively. A similar decrease was also observed in the ratio of chlorophyll to total carotenoids, which decreased by 41.91% and 64.58% [12].

In addition to chlorophyll content, chlorophyll fluorescence testing is very important for predicting stress in plants because this method can non-destructively measure the efficiency of photosystem II (PSII). Chlorophyll fluorescence is the emission of light that is not used by chlorophyll after absorbing light energy, and its emission level is inversely proportional to photosynthetic efficiency. When plants experience stress, such as exposure to acid rain, PSII efficiency decreases due to damage to the reaction center, resulting in increased chlorophyll fluorescence emission. By measuring parameters such as the ratio of variable fluorescence to maximum fluorescence, researchers can assess the level of photosynthetic damage and the plant's capacity to adapt, making it a sensitive and accurate diagnostic tool for detecting stress at an early stage.

Chlorophyll fluorescence measurement is a fast and reliable method for assessing photosynthetic activity in plants under stress [65]. The high acidity level of acid rain can damage photosynthetic pigments and assimilation tissues, which could potentially be the main cause of its impact [66]. Exposure to AR on tomato seedlings increases the Fo value and decreases the Fv/Fm ratio. The increase in Fo indicates damage to the reaction center of photosystem II (PSII), while the decrease in the Fv/Fm ratio shows that the photochemical efficiency of the PSII photosynthetic apparatus has decreased significantly. This demonstrates that stress caused by acid rain can impair the photosynthetic capacity of tomato plants [67].

Physiologically and anatomically, AR exposure in plants is highly damaging, starting at the cellular level and extending to the organ level. AR exposure causes corrosion of the epidermal cuticle, which is the first protective layer, thereby disrupting gas exchange regulation through stomata and triggering necrotic tissue damage. At the cellular level, the influx of hydrogen ions damages the ultrastructure of chloroplasts and thylakoids, disrupting photosynthetic activity and significantly reducing photochemical efficiency, as evidenced by a decrease in chlorophyll fluorescence. This damage also causes degradation of photosynthetic pigments such as chlorophyll, hindering CO2 assimilation, and disrupting carbohydrate metabolism, ultimately limiting overall plant growth and development. The structural and physiological damage caused by acid rain has serious implications for agricultural productivity and sustainability. The reduction in photosynthesis rates due to damage to stomata, chloroplasts, and pigments directly results in decreased biomass, crop yields, and product quality. AR reduces the effective leaf surface area for photosynthesis, further reducing the plant's capacity to produce energy and biomass. In the long term, this not only threatens food security but also reduces the economic viability of farmers, especially in areas vulnerable to industrial pollution and acid rain.

4. CONCLUSION

The phenomenon of global climate change has increased the frequency and intensity of abiotic stresses, such as drought, flooding, extreme temperatures, and acid rain, which fundamentally threaten food security and agricultural sustainability. Physiologically, plants respond to these stresses through coordinated mechanisms, such as modifying cell membrane composition to maintain fluidity, reorganizing the cytoskeleton, and modulating stomata. However, excessive stress can damage photosynthesis, trigger oxidative stress, and disrupt hormonal balance, ultimately hindering plant growth and productivity. Therefore, a deep understanding of these adaptive mechanisms is a critically important scientific foundation.

To ensure the sustainability of agriculture in the future, further research must focus on more integrated approaches. The primary priority is to identify and characterize the key genes responsible for plant resilience to various abiotic stresses. This genetic knowledge, combined with modern breeding technologies and genetic engineering, can be used to develop plant varieties that are inherently more resilient and adaptive. Additionally, research should explore the role of symbiotic soil microorganisms and agronomic practices that can enhance plant defense responses, thereby creating agricultural systems that are not only productive but also resilient in the face of increasingly extreme global environmental challenges.

Author Contribution
All authors contributed equally to the main contributor to this paper. All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest
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