

Physiological Response Characteristics of Plants under Extreme Climatic Conditions

Han Ruolin

Qingdao Technical College, Qingdao 266555, Shandong, China

Abstract: High temperature, drought, low temperature, and extreme precipitation can alter plant water balance, photosynthesis, membrane-system stability, and primary metabolism. Plants mitigate stress-induced damage through stomatal regulation, osmolyte accumulation, antioxidant defense, hormonal signaling, and metabolic reprogramming. This paper analyzes the similarities and differences in plant physiological responses to different climatic stresses, discusses the effects of stress intensity, duration, and developmental stage on response outcomes, and proposes future directions that include establishing a multi-indicator system for stress-resistance evaluation and strengthening research on combined stresses and post-stress recovery.

Keywords: extreme climate; plant physiology; antioxidant system; osmotic adjustment; stress response

Introduction

Extreme heat, prolonged drought, cold waves, frost, and short-duration heavy precipitation can rapidly exceed the environmental limits within which plants can maintain normal growth. Compared with gradual changes in mean climatic conditions, extreme events are characterized by their sudden onset, high intensity, and uncertain recovery periods. Because plants cannot relocate in response to unfavorable conditions, their growth depends on their structural characteristics, metabolic regulatory capacity, and the availability of environmental resources. When changes in external temperature or water availability exceed their physiological regulatory capacity, cellular membranes, photosynthetic organs, and enzyme systems are among the first components to be affected. Visible symptoms subsequently include leaf wilting, chlorosis, growth arrest, reduced pollen viability, and organ necrosis.

Plant responses to extreme climatic conditions cannot be represented by a change in any single indicator. Stomatal closure reduces water loss but also restricts the entry of carbon dioxide into leaves. Increased antioxidant-enzyme activity contributes to the removal of reactive oxygen species, yet excessively intense or prolonged stress may still cause oxidative damage. Some plants survive by adjusting their root-to-shoot ratio, changing leaf orientation, accelerating senescence, or entering a state of metabolic quiescence. An accurate understanding of the sequence and interrelationships of these responses provides an essential foundation for evaluating plant stress resistance, screening stress-tolerant germplasm, and optimizing agricultural management.

1. Extreme Climatic Stress and Physiological Injury in Plants

1.1 Principal Types of Extreme Climatic Stress

Extreme climatic stresses affecting plants primarily

include temperature and water anomalies. High temperature increases leaf transpirational demand, accelerates respiratory consumption, and disrupts protein and biological-membrane structures. Low temperature reduces membrane-lipid fluidity and the rates of enzymatic reactions. Under freezing conditions, extracellular ice formation additionally causes cellular dehydration. Drought is principally characterized by declining soil water potential, greater resistance to root water uptake, and reduced leaf turgor. Short-duration rainstorms and prolonged waterlogging compress the air-filled pore space in soil and rapidly reduce oxygen availability in the rhizosphere.

Strong interactions also exist among different extreme events. High temperature frequently occurs simultaneously with drought, and a high vapor pressure deficit accelerates water loss from leaves. Following heavy rainfall, soil hypoxia, root injury, and pathogen infection may occur sequentially. When low temperature is accompanied by strong winds, transpirational water loss and insufficient root water uptake may also intensify simultaneously. Experimental results obtained under a single environmental factor therefore cannot fully explain plant responses under natural conditions.

1.2 Fundamental Processes of Plant Physiological Responses

Following exposure to climatic stress, plant cells first perceive changes in temperature, membrane status, water potential, and oxygen concentration. Calcium ions, reactive oxygen species, and hormones participate in signal transduction, and the resulting signals regulate stomatal movement, gene expression, and enzyme activity. Short-term responses commonly include changes in stomatal aperture, reduced photosynthetic rates, osmolyte accumulation, and altered antioxidant-enzyme activity. As stress persists, leaf area, root distribution, biomass allocation, and reproductive

growth may also change.

Physiological responses can reflect both protection and injury. Stomatal closure is a water-conservation response, but prolonged closure reduces carbon assimilation. Reactive oxygen species can act as signaling molecules that activate defense processes, whereas their excessive accumulation oxidizes membrane lipids, proteins, and nucleic acids. Plant tolerance should therefore not be evaluated solely on the basis of an increase or decrease in a single indicator. Biomass, leaf water status, photosystem activity, and the extent of recovery after stress relief must also be considered.

2. Physiological Responses under Different Extreme Climatic Conditions

2.1 Photosynthetic Inhibition and Membrane-System Damage under Heat Stress

High temperature alters thylakoid membrane structure and the stability of photosystem reaction centers. Photosystem II is particularly sensitive to heat stress. Once it is damaged, electron transport is impaired, and absorbed light energy cannot be used efficiently in normal photochemical reactions. Declining chlorophyll fluorescence parameters, reductions in the net photosynthetic rate, and loss of chlorophyll are commonly used indicators of heat injury. High temperature also affects the activation state of enzymes involved in carbon dioxide fixation and increases the rate of dark respiration, thereby reducing carbohydrate accumulation.

Cellular membranes become more fluid at high temperatures, resulting in greater electrolyte leakage. Changes in protein structure interfere with enzymatic reactions and organelle function. Plants can synthesize heat-shock proteins that assist in the refolding of damaged proteins and can activate antioxidant systems to restrict oxidative reactions. When heat stress persists for an extended period, however, the rate of damage exceeds the plant's protective capacity, and leaves exhibit chlorosis, scorching, and premature senescence. Previous research has indicated that heat tolerance involves responses at the organelle, cellular, and whole-plant levels, with antioxidant defense and heat-shock-protein regulation serving as important protective mechanisms^[1].

2.2 Water Regulation and Stomatal Responses under Drought Stress

As soil water content declines, resistance to root water uptake increases, followed by reductions in leaf water potential and relative water content. Stomatal closure is an important early response to drought because it limits transpirational water loss. However, declining stomatal

conductance also reduces the supply of carbon dioxide and inhibits the net photosynthetic rate. During mild drought, reduced photosynthesis may be attributable primarily to stomatal limitation. As stress intensifies, damage to chloroplast structure, photosynthetic-enzyme activity, and electron transport becomes more pronounced, and non-stomatal limitations gradually increase.

Plants may also allocate more resources to root growth, restrict leaf expansion, and reduce radiation loading through leaf rolling. The accumulation of proline, soluble sugars, betaine, and other compounds contributes to the regulation of cellular osmotic potential. Drought-resistance strategies vary among plant species. Deep-rooted plants rely primarily on access to water in deeper soil layers, whereas some species avoid prolonged drought by completing their life cycles rapidly. Chaves et al. indicated that phenology, root-system size and depth, hydraulic conductivity, and stored reserves are all involved in plant adaptation to drought^[2].

2.3 Membrane-Lipid Changes and Metabolic Imbalance under Low-Temperature Stress

Low temperature initially reduces biological-membrane fluidity, thereby restricting membrane-protein function and material transport. In chilling-sensitive plants, electrolyte leakage increases, chloroplast membrane structure is damaged, and both photosynthetic-pigment synthesis and photosynthetic electron transport are weakened. Carbon-assimilation rates decline under low-temperature conditions, producing an imbalance between light-energy absorption and utilization. The resulting excess energy increases the generation of reactive oxygen species.

Plants exposed to nonfreezing low temperatures for a certain period may develop cold acclimation. This process is generally accompanied by an increase in membrane-lipid unsaturation, the accumulation of soluble sugars and proline, changes in antioxidant-enzyme activity, and the expression of cold-responsive genes. Under freezing stress, extracellular ice formation lowers extracellular water potential, causing water to migrate out of cells and, in severe cases, resulting in dehydration and membrane rupture. Low-temperature responses are jointly affected by plant species, developmental stage, cooling rate, and stress duration. A single temperature threshold therefore cannot be used to define injury in all plant species^[3].

3. Physiological Changes Induced by Extreme Precipitation

3.1 Hypoxic Metabolism under Waterlogging Stress

Soil waterlogging reduces the rate of oxygen diffusion. As rhizospheric oxygen concentration declines,

mitochondrial aerobic respiration is inhibited. The tricarboxylic acid cycle and oxidative phosphorylation cannot proceed normally, resulting in a reduced supply of adenosine triphosphate. Plants consequently increase glycolytic and fermentative metabolism and maintain a limited energy supply through alcoholic or lactic acid fermentation. However, these pathways produce far less energy than aerobic respiration, and their prolonged operation consumes substantial quantities of soluble sugars.

Root hypoxia also restricts the absorption of water and mineral nutrients. Leaves may exhibit drought-like wilting under waterlogged conditions because root activity has declined, rather than because the soil lacks water. Stomatal conductance, chlorophyll content, and the net photosynthetic rate progressively decrease. After flooding subsides, the re-entry of oxygen into plant tissues may cause a rapid increase in reactive oxygen species and result in reoxygenation injury.

3.2 Morphological and Energy Regulation during Flooding Adaptation

Flood-tolerant plants can form aerenchyma, thereby enhancing oxygen transport from aboveground organs to the roots. Some plants develop adventitious roots, which shorten the oxygen-transport distance. Under complete submergence, plants generally adopt one of two major strategies: escape through elongation or metabolic quiescence. The escape strategy involves rapid petiole or stem elongation toward the water surface, facilitating the restoration of gas exchange but consuming substantial carbohydrate reserves. By contrast, metabolic quiescence suppresses growth and energy consumption and is suited to relatively deep flooding of limited duration.

Ethylene diffuses slowly under water and therefore readily accumulates within plant tissues. It participates in aerenchyma formation, stem and leaf elongation, and the regulation of senescence. Bailey-Serres and Voesenek identified low-oxygen escape and quiescence-based tolerance as two major adaptive strategies through which plants respond to flooding ^[4].

Table 1. Principal Physiological Response Characteristics of Plants under Extreme Climatic Conditions

Stress type	Initial effect	Principal physiological changes	Protective regulation
High temperature	Increased leaf temperature and transpirational demand	Reduced photosynthesis, enhanced respiration, and increased membrane permeability	Heat-shock-protein synthesis and antioxidant-enzyme activation
		Stomatal closure, reduced leaf water potential, and restricted carbon assimilation	Osmotic adjustment, root extension, and reduced leaf area
Drought	Reduced soil water potential	Decreased enzyme activity, photochemical imbalance, and dehydration caused by extracellular ice formation	Membrane-lipid adjustment, soluble-sugar accumulation, and cold acclimation
Low temperature	Reduced membrane fluidity	Inhibition of aerobic respiration, enhanced fermentation, and reduced root activity	Aerenchyma formation, adventitious-root development, and metabolic quiescence
Waterlogging	Reduced rhizospheric oxygen concentration		

4. Physiological Regulatory Mechanisms Underlying Plant Responses to Extreme Climate

4.1 Osmotic Adjustment and Water Maintenance

Osmotic adjustment is an important mechanism through which plants respond to drought, low temperature, and certain combined stresses. Following the accumulation of proline, soluble sugars, betaine, and selected inorganic ions, cellular osmotic potential decreases, enabling cells to maintain a certain degree of turgor when external water

potential declines. These compounds also stabilize proteins and biological membranes and buffer oxidative damage.

An increase in osmolyte concentration does not, by itself, demonstrate strong stress resistance. Stress-tolerant plants may actively accumulate these compounds to maintain cellular function, whereas sensitive plants may also exhibit high concentrations as a consequence of severe tissue injury. Osmolyte concentrations must therefore be evaluated in conjunction with leaf relative water content, post-stress growth recovery, and changes in biomass.

4.2 Antioxidant Defense and Reactive-Oxygen-Species Scavenging

Extreme climatic conditions disrupt the balance between the production and removal of reactive oxygen species. The accumulation of superoxide anions, hydrogen peroxide, and hydroxyl radicals causes membrane-lipid peroxidation, protein oxidation, and pigment degradation. Superoxide dismutase converts superoxide anions into hydrogen peroxide, while catalase and peroxidases contribute to the subsequent removal of hydrogen peroxide. Ascorbate, glutathione, carotenoids, and phenolic compounds constitute the nonenzymatic antioxidant system.

Malondialdehyde concentration and electrolyte leakage are frequently used as indicators of membrane-lipid peroxidation and membrane-system injury. Stress-tolerant plant materials can generally activate antioxidant responses at an earlier stage and restore redox homeostasis more rapidly after stress relief. A single measurement cannot adequately characterize the defensive process. Continuous monitoring is more effective for distinguishing active regulation from the progressive accumulation of damage.

4.3 Hormonal Signaling and the Regulation of Protective Proteins

Absciscic acid plays an important role in drought responses. As soil moisture declines, changes in abscisic acid concentrations in the roots and leaves contribute to stomatal closure, osmotic adjustment, and the expression of stress-related genes. Under waterlogging stress, ethylene participates in aerenchyma formation, leaf senescence, and elongation responses. Jasmonic acid, salicylic acid, and brassinosteroids can also contribute to signaling under temperature and water stresses.

Heat-shock proteins produced under high-temperature conditions can bind to improperly folded proteins and reduce the damage caused by protein aggregation. Cold-induced proteins contribute to membrane stabilization, ice-crystal control, and protection against cellular dehydration. Hormones and protective proteins do not function

independently; instead, they interact with calcium signaling, reactive oxygen species, and transcriptional regulation to form a multilevel response network.

5. Applications of Research on Plant Responses to Extreme Climate

5.1 Improvement of Indicators for Stress-Resistance Evaluation

Plant stress-resistance evaluation should consider the degree of injury, regulatory capacity, and recovery capacity. A basic set of indicators may include leaf relative water content, net photosynthetic rate, maximum photochemical efficiency, electrolyte leakage, malondialdehyde concentration, and antioxidant-enzyme activity. However, these indicators do not respond simultaneously. Stomatal conductance may change during the early stages of stress, whereas reductions in chlorophyll content and biomass generally occur later.

Evaluation protocols should clearly specify stress intensity, duration, developmental stage, and sampling time and should include observations of recovery following stress relief. Plant materials that maintain relatively high physiological activity during stress and recover rapidly afterward are more likely to possess stable tolerance. Principal component analysis and membership-function analysis can be used for comprehensive multi-indicator evaluation, but indicator weights must still be determined according to the particular plant species and production objectives.

5.2 Research on Multiple Stresses and Recovery Processes

Under natural conditions, extreme climatic events frequently occur in combined or sequential forms. When high temperature and drought occur simultaneously, plants must both restrict water loss and maintain transpirational cooling, creating a conflict between these physiological demands. Following flooding, high temperature and intense light may intensify reoxygenation injury and water-loss pressure in plants with damaged root systems. Prior exposure to mild stress may also generate physiological memory and alter the speed of the plant's response to subsequent stress.

Future experiments should reproduce the combinations, sequences, and intervals of actual climatic events and reduce reliance on constant single-factor treatments as substitutes for natural extremes. Continuous monitoring of leaf temperature, chlorophyll fluorescence, stomatal conductance, and rhizospheric oxygen concentration can help identify critical transition points in plant responses. Field experiments should also record soil moisture, air humidity, radiation, and wind speed to establish relationships

among meteorological conditions, physiological indicators, and yield formation.

Conclusion

The effects of extreme climatic conditions on plants are principally manifested as disrupted water balance, inhibited photosynthesis, reduced membrane-system stability, impaired energy metabolism, and the accumulation of reactive oxygen species. High temperature primarily affects photosystems, proteins, and membrane structures. Drought initially causes reductions in water potential and stomatal closure. Low temperature decreases membrane fluidity and produces photochemical imbalance, while waterlogging is characterized by rhizospheric hypoxia and insufficient energy supply.

Plants survive these stresses through osmotic adjustment, antioxidant defense, hormonal signaling, the synthesis of protective proteins, and morphological modification. These responses are constrained by species, developmental stage, stress intensity, and duration, and no single indicator can fully characterize stress resistance. Establishing a multi-indicator

evaluation system covering stress onset, persistence, and recovery and strengthening research on combined extreme events can provide a more reliable basis for screening stress-tolerant germplasm, regulating crop cultivation, and managing ecological vegetation.

References

- [1] Hasanuzzaman, M., Nahar, K., Alam, M. M., et al. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants [J]. *International Journal of Molecular Sciences*, 2013, 14(5), 9643–9684.
- [2] Chaves, M. M., Maroco, J. P., & Pereira, J. S. Understanding plant responses to drought: From genes to the whole plant [J]. *Functional Plant Biology*, 2003, 30(3), 239–264.
- [3] Theocharis, A., Clément, C., & Barka, E. A. Physiological and molecular changes in plants grown at low temperatures [J]. *Planta*, 2012, 235(6), 1091–1105.
- [4] Bailey-Serres, J., & Voesenek, L. A. C. J. Flooding stress: Acclimations and genetic diversity [J]. *Annual Review of Plant Biology*, 2008, 59, 313–339.