

# Combined Heat and Drought Stress in Crops: Physiological Responses and Adaptation Mechanisms

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## Abstract

Climate change has intensified the frequency and severity of abiotic stresses, particularly heat and drought, posing significant threats to agricultural productivity worldwide. Although individual effects of heat and water deficit have been extensively investigated, crops in natural environments are often exposed to simultaneous heat and drought stress, which induces unique physiological, biochemical, molecular, and metabolic responses distinct from those triggered by either stress alone. Combined heat and drought stress adversely affects photosynthesis, water relations, nutrient uptake, reproductive development, membrane stability, and crop yield. Plants have evolved complex adaptive mechanisms involving osmotic adjustment, antioxidant defense systems, hormonal signaling, stress-responsive gene expression, and metabolic reprogramming to mitigate stress-induced damage. Advances in genomics, transcriptomics, metabolomics, and phenomics have improved our understanding of stress adaptation pathways and facilitated the development of climate-resilient crop varieties. Emerging technologies, including genome editing, marker-assisted breeding, genomic selection, and artificial intelligence-based phenotyping, are revolutionizing crop improvement strategies under multiple stress environments. This review summarizes the physiological, biochemical, and molecular responses of crops to combined heat and drought stress and discusses recent advances in breeding and biotechnological approaches aimed at enhancing stress tolerance and ensuring sustainable agricultural production under changing climatic conditions.

**Keywords:** Climate change; Heat stress; Drought stress; Abiotic stress; Photosynthesis; Antioxidants; Phytohormones.

## 1. Introduction

Global agriculture is increasingly threatened by climate change-induced abiotic stresses, among which heat and drought are considered the most detrimental factors limiting crop productivity. Rising temperatures and erratic rainfall patterns have increased the occurrence of prolonged dry periods accompanied by heat waves, resulting in severe reductions in crop growth, development, and yield. According to recent projections, global temperatures are expected to rise by 1.5–4.5°C by the end of the twenty-first century, with substantial implications for food security and agricultural sustainability. Heat stress and water scarcity frequently occur simultaneously in field environments, leading to complex interactions that impose greater damage than individual stresses alone [1]. Combined heat and drought stress negatively affects several physiological processes, including photosynthesis, transpiration, respiration, membrane stability, nutrient acquisition, and reproductive development. Elevated temperatures accelerate evapotranspiration, while drought reduces water availability and disrupts stomatal conductance, causing severe metabolic disturbances.

These stresses enhance the production of reactive oxygen species (ROS), resulting in oxidative damage to proteins, lipids, nucleic acids, and cellular membranes [2]. Consequently, significant yield losses have been reported in major crops such as wheat, rice, maize, soybean, chickpea, and sorghum.

Plants possess sophisticated defense mechanisms that enable them to perceive stress signals and initiate adaptive responses involving antioxidant enzymes, osmoprotectants, stress-responsive proteins, hormonal signaling pathways, and gene regulation networks. Recent advances in molecular biology and omics technologies have provided valuable insights into the mechanisms governing stress tolerance. Furthermore, modern breeding approaches, including genomic selection, marker-assisted breeding, speed breeding, and CRISPR/Cas-mediated genome editing, are facilitating the development of climate-resilient crop cultivars capable of withstanding multiple environmental stresses. Understanding the physiological and molecular basis of plant adaptation to combined heat and drought stress is essential for improving crop resilience and maintaining global food security [3-4].

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Therefore, this review aims to provide a comprehensive overview of the effects of simultaneous heat and drought stress on crop plants, the underlying physiological and biochemical responses, molecular adaptation mechanisms, and recent advances in breeding and biotechnology for stress tolerance enhancement.

## 2. Heat and Drought Stress under Climate Change

Climate change has emerged as one of the most significant threats to global agriculture, with increasing temperatures and irregular precipitation patterns intensifying the occurrence of multiple abiotic stresses. Among these, heat stress and drought stress frequently occur simultaneously and exert synergistic effects on plant growth and productivity. Global warming has led to a rise in the frequency and duration of heat waves, while changes in rainfall distribution have resulted in prolonged periods of water scarcity [5]. These environmental changes have significantly altered agroecosystems and have adversely affected the productivity of major crops worldwide. The combined occurrence of high temperature and water deficit is more detrimental than either stress individually because the interaction between these stresses triggers unique physiological and molecular responses that cannot be predicted from single-stress studies.

Combined heat and drought stress has become increasingly common in many agricultural regions, particularly in arid and semi-arid environments.

Elevated temperatures accelerate evapotranspiration and soil moisture depletion, further intensifying drought conditions. Heat stress impairs enzymatic activities and cellular metabolism, whereas drought reduces water availability and limits nutrient uptake. Together, these stresses disrupt plant-water relations, photosynthesis, and reproductive processes, leading to severe reductions in biomass accumulation and grain yield. Major cereal crops such as wheat, rice, maize, and barley have exhibited significant yield losses under concurrent heat and drought conditions [6]. Climate models predict that these stresses will become more frequent and severe in the future, posing serious challenges to global food security and agricultural sustainability.

The economic consequences of combined heat and drought stress are substantial, affecting crop productivity, food availability, and farmer livelihoods. Reduced yields lead to increased food prices and threaten the stability of agricultural systems, particularly in developing countries where farming is highly dependent on climatic conditions. Furthermore, stress-induced reductions in crop quality and nutritional value have implications for human health and nutrition. Therefore, understanding plant responses to combined stress conditions is essential for developing climate-resilient agricultural systems capable of sustaining food production under changing environmental conditions.

**Table 1: Major Physiological and Biochemical Responses of Crops to Combined Heat and Drought Stress**

Plant Process	Effects of Combined Heat and Drought Stress	Adaptive Responses
Water relations	Reduced relative water content and leaf water potential	Stomatal closure and osmotic adjustment
Photosynthesis	Decreased chlorophyll content and CO <sub>2</sub> assimilation	Increased water-use efficiency and photoprotection
Membrane stability	Lipid peroxidation and electrolyte leakage	Enhanced membrane stabilization mechanisms
Reactive oxygen species (ROS)	Excessive accumulation causing oxidative damage	Activation of antioxidant defense systems
Antioxidant enzymes	Increased oxidative stress	Enhanced activity of SOD, CAT, APX, POD, and GR
Osmolyte accumulation	Cellular dehydration	Accumulation of proline, glycine betaine, trehalose, and soluble sugars
Nutrient uptake	Reduced mineral absorption and translocation	Improved root architecture and nutrient remobilization
Reproductive development	Reduced pollen viability and grain filling	Alteration in flowering time and stress acclimation
Growth and biomass	Decreased plant height and biomass accumulation	Resource allocation and metabolic adjustment
Yield	Reduced grain number, fruit set, and harvest index	Development of stress-tolerant genotypes

**Table 2: Molecular Mechanisms and Crop Improvement Strategies for Combined Heat and Drought Stress Tolerance**

Mechanism/Approach	Components	Function in Stress Tolerance
Signal transduction	Calcium signaling, MAPK cascades	Stress perception and activation of defense pathways
Heat shock proteins	HSP70, HSP90, HSP101	Protein folding and cellular protection
Transcription factors	DREB, WRKY, NAC, MYB, bZIP, HSF	Regulation of stress-responsive genes
Hormonal regulation	ABA, ethylene, salicylic acid, jasmonic acid, brassinosteroids	Coordination of physiological responses
Antioxidant defense	SOD, CAT, APX, POD, glutathione	Detoxification of reactive oxygen species
Genomics and QTL mapping	Stress-associated loci and candidate genes	Identification of tolerance-related traits
Marker-assisted selection	Molecular markers	Accelerated breeding for stress tolerance
Genomic selection	Genome-wide prediction models	Improvement of complex quantitative traits
Genome editing	CRISPR/Cas systems	Precise modification of stress-responsive genes
Speed breeding	Controlled environment-assisted breeding	Reduction in breeding cycle duration
Biostimulants and PGPR	Beneficial microbes and plant growth regulators	Improved nutrient uptake and stress resistance
Precision agriculture	Remote sensing, AI, phenomics	Real-time monitoring and stress management

**Abbreviations:** SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; POD, peroxidase; ABA, abscisic acid; MAPK, mitogen-activated protein kinase; QTL, quantitative trait locus; PGPR, plant growth-promoting rhizobacteria.

## 3. Physiological Responses of Crops to Combined Heat and Drought Stress

Combined heat and drought stress induces profound physiological changes that influence plant growth, development, and productivity. One of the earliest responses involves alterations in plant water relations. Water deficit decreases leaf water potential and relative water content, resulting in reduced cell turgor and impaired cell expansion. Simultaneously, high temperatures enhance transpiration rates and increase evaporative demand, thereby aggravating water loss. Plants respond to these conditions by closing stomata to minimize transpiration; however, stomatal closure also restricts carbon dioxide uptake and limits photosynthetic efficiency. Consequently, reductions in photosynthesis lead to decreased carbohydrate synthesis and impaired growth [7]. Photosynthesis is highly sensitive to combined heat and drought stress.

High temperatures affect chlorophyll stability and damage photosystem II, while water deficit reduces stomatal conductance and carbon assimilation. The combined stress significantly decreases chlorophyll content, electron transport activity, and Rubisco enzyme efficiency, thereby reducing photosynthetic performance. Furthermore, membrane integrity is compromised due to lipid peroxidation and increased electrolyte leakage. Cellular dehydration and membrane instability adversely affect nutrient transport and metabolic activities, ultimately leading to growth inhibition and premature senescence [8]. Reproductive development is particularly vulnerable to simultaneous heat and drought stress. Elevated temperatures and water scarcity interfere with pollen viability, pollen germination, fertilization, and grain filling processes. In cereal crops, these stresses reduce the number of fertile florets and grains per spike, leading to considerable yield losses. Heat stress during anthesis has been shown to impair reproductive success and shorten the grain-filling period, whereas drought restricts assimilate translocation to developing seeds. Consequently, reductions in grain weight, fruit set, and biomass accumulation are frequently observed under combined stress conditions. These physiological alterations collectively contribute to decreased crop productivity and threaten food security in many regions of the world.

#### **4. Biochemical Responses and Antioxidant Defense Mechanisms**

Exposure to combined heat and drought stress leads to excessive production of reactive oxygen species (ROS), including superoxide radicals, hydrogen peroxide, and hydroxyl radicals. Although ROS serve as signaling molecules under normal physiological conditions, their excessive accumulation causes oxidative stress, resulting in damage to proteins, nucleic acids, lipids, and cellular membranes. Oxidative damage disrupts cellular homeostasis and accelerates senescence, thereby negatively affecting plant growth and survival. Lipid peroxidation caused by ROS is often associated with increased malondialdehyde accumulation and membrane instability, which are considered indicators of stress-induced cellular injury [9]. To mitigate oxidative damage, plants activate complex antioxidant defense systems consisting of enzymatic and non-enzymatic components. Enzymatic antioxidants such as superoxide dismutase, catalase, peroxidase, ascorbate peroxidase, and glutathione reductase play critical roles in detoxifying reactive oxygen species and maintaining cellular redox balance. Superoxide dismutase converts superoxide radicals into hydrogen peroxide, which is subsequently decomposed into water and oxygen by catalase and peroxidase enzymes. Increased activity of these antioxidant enzymes has been observed in many crops under combined heat and drought stress and is often associated with enhanced stress tolerance. In addition to enzymatic antioxidants, plants accumulate non-enzymatic antioxidant compounds such as ascorbic acid, glutathione, carotenoids, flavonoids, and tocopherols.

These compounds protect cellular components against oxidative injury by scavenging free radicals and stabilizing membranes. Furthermore, plants synthesize compatible solutes and osmoprotectants, including proline, glycine betaine, trehalose, and soluble sugars, which contribute to osmotic adjustment and maintain cellular hydration [10]. Proline accumulation is one of the most common responses to combined stress and functions in membrane stabilization, free radical scavenging, and protection of proteins and enzymes. The coordinated action of antioxidant systems and osmoprotectants enables plants to tolerate adverse environmental conditions and maintain metabolic functions under stress.

#### **5. Hormonal Regulation under Combined Heat and Drought Stress**

Plant hormones play pivotal roles in coordinating stress perception and adaptive responses under simultaneous heat and drought stress. Among these hormones, abscisic acid (ABA) serves as a key regulator of stress signaling. Water deficit stimulates ABA biosynthesis, leading to stomatal closure and reduced water loss through transpiration. ABA also activates stress-responsive genes involved in osmotic adjustment, antioxidant defense, and protective protein synthesis. Elevated ABA levels enhance the accumulation of compatible solutes and improve cellular tolerance under stress conditions. Therefore, ABA-mediated signaling pathways are considered central components of plant adaptation to combined abiotic stresses [11]. Ethylene is another important hormone involved in stress responses. Under severe stress conditions, increased ethylene production may accelerate leaf senescence and inhibit growth; however, ethylene also interacts with other hormones to regulate stress tolerance mechanisms. Cytokinins generally promote cell division and delay senescence, but their concentration often declines under drought stress, contributing to growth inhibition. Auxins influence root architecture and facilitate water uptake by promoting deeper root development. Jasmonic acid and salicylic acid participate in defense signaling and modulate antioxidant systems, while brassinosteroids enhance membrane stability and improve photosynthetic efficiency under stressful conditions.

Hormonal crosstalk among ABA, ethylene, auxins, cytokinins, jasmonates, and salicylic acid creates a highly integrated signaling network that enables plants to coordinate growth and stress adaptation. These interactions regulate gene expression, antioxidant activities, osmotic adjustment, and cellular metabolism, thereby enhancing plant survival under adverse environments. Recent studies have demonstrated that manipulation of hormonal pathways through genetic engineering and exogenous application of plant growth regulators can improve crop tolerance to combined heat and drought stress [12]. Understanding these hormonal interactions provides valuable opportunities for developing climate-resilient crop varieties capable of sustaining productivity under changing environmental conditions.

## 6. Molecular and Genetic Mechanisms of Adaptation to Combined Heat and Drought Stress

Plants exposed to simultaneous heat and drought stress activate a complex network of molecular and genetic responses that enable them to perceive stress signals, regulate gene expression, and maintain cellular homeostasis. Stress perception begins at the cellular membrane, where changes in temperature and water status trigger signaling cascades involving calcium ions, reactive oxygen species (ROS), and protein kinases. These signaling molecules function as secondary messengers that transmit stress signals to the nucleus, leading to the activation of stress-responsive genes. Combined heat and drought stress often induces unique transcriptional responses that differ from those triggered by individual stresses, indicating the existence of specialized regulatory pathways for multiple-stress adaptation [13]. Calcium signaling plays a crucial role in stress sensing and signal transduction. Changes in cytosolic calcium concentration activate calcium-dependent protein kinases and calmodulin-mediated pathways, which regulate downstream stress responses. Mitogen-activated protein kinase (MAPK) cascades further amplify stress signals and coordinate cellular defense mechanisms. These pathways regulate antioxidant systems, osmoprotectant synthesis, and hormonal signaling, thereby enhancing stress tolerance. The activation of heat shock proteins (HSPs) is another important adaptive mechanism. HSPs function as molecular chaperones that stabilize proteins, prevent protein aggregation, and assist in protein refolding during stress conditions. Increased expression of HSPs has been widely associated with enhanced thermotolerance and improved plant survival under combined stress environments [14]. Transcription factors are central regulators of stress-responsive gene networks. Families such as DREB (Dehydration-Responsive Element Binding), WRKY, NAC, MYB, bZIP, and Heat Shock Factors (HSFs) regulate the expression of genes involved in osmotic adjustment, antioxidant defense, membrane protection, and cellular repair. These transcription factors coordinate the activation of multiple physiological and biochemical pathways that contribute to stress adaptation. Recent studies have also highlighted the role of epigenetic mechanisms, including DNA methylation, histone modifications, and small RNAs, in regulating stress memory and adaptive responses. Such epigenetic modifications enable plants to respond more effectively to recurring stress events and may contribute to the development of stress-resilient crop varieties.

## 7. Omics Approaches for Understanding Combined Stress Responses

Advances in omics technologies have significantly enhanced our understanding of plant responses to combined heat and drought stress. Genomics provides insights into the genetic architecture underlying stress tolerance by identifying quantitative trait loci (QTLs), stress-responsive genes, and genetic markers associated with adaptive traits.

The availability of whole-genome sequences for major crops has facilitated the discovery of candidate genes involved in stress resistance and has accelerated crop improvement programs through marker-assisted selection and genomic breeding approaches.

Transcriptomics enables the comprehensive analysis of gene expression patterns under stress conditions. High-throughput sequencing technologies such as RNA sequencing have revealed thousands of differentially expressed genes associated with signal transduction, hormone metabolism, antioxidant defense, and osmoprotection [15]. Proteomics complements transcriptomic studies by identifying stress-responsive proteins and post-translational modifications that regulate cellular functions. Proteomic analyses have demonstrated significant changes in enzymes involved in photosynthesis, energy metabolism, and ROS detoxification during combined stress exposure.

Metabolomics provides valuable information regarding changes in plant metabolites that contribute to stress adaptation. Accumulation of amino acids, sugars, organic acids, polyamines, and secondary metabolites has been linked to improved tolerance against heat and drought stress. Phenomics, which involves high-throughput assessment of plant traits using advanced imaging technologies, facilitates the rapid evaluation of stress responses under controlled and field conditions. The integration of genomics, transcriptomics, proteomics, metabolomics, and phenomics through systems biology approaches provides a comprehensive understanding of plant stress responses and enables the identification of key regulatory networks that can be targeted for crop improvement.

## 8. Crop Improvement Strategies for Combined Heat and Drought Stress Tolerance

Developing crop varieties capable of tolerating combined heat and drought stress is a major objective of modern agricultural research. Conventional breeding remains an important approach for improving stress tolerance by exploiting natural genetic variation within crop germplasm. Screening and selection of stress-tolerant genotypes have resulted in the development of several improved cultivars with enhanced resilience. However, the complex inheritance of stress tolerance traits and the influence of environmental factors often limit the efficiency of conventional breeding programs.

Molecular breeding approaches have significantly improved the precision and efficiency of crop improvement efforts. Marker-assisted selection enables breeders to identify and select desirable traits using molecular markers linked to stress-responsive genes and quantitative trait loci. Genomic selection further accelerates breeding progress by predicting the performance of breeding lines based on genome-wide marker information. These approaches reduce breeding cycles and facilitate the development of varieties adapted to multiple stress environments [2]. Recent advances in biotechnology have opened new opportunities for enhancing stress tolerance.

Genetic engineering has been employed to introduce genes encoding osmoprotectants, antioxidant enzymes, transcription factors, and heat shock proteins into crop plants. More recently, CRISPR/Cas genome editing technology has emerged as a powerful tool for precise modification of stress-responsive genes. Genome editing enables targeted manipulation of key regulatory pathways associated with heat and drought tolerance without introducing foreign DNA. Additionally, speed breeding techniques combined with genomic tools allow the rapid generation and evaluation of breeding populations, significantly accelerating the development of climate-resilient crop cultivars.

### 9. Agronomic and Management Strategies for Mitigating Combined Stress Effects

While genetic improvement plays a crucial role in enhancing crop resilience, agronomic management practices are equally important for minimizing the adverse impacts of combined heat and drought stress. Efficient irrigation management remains one of the most effective strategies for maintaining crop productivity under water-limited conditions. Advanced irrigation techniques such as drip irrigation, deficit irrigation, and precision water management improve water-use efficiency while ensuring adequate moisture availability during critical growth stages. Conservation agriculture practices, including minimum tillage, crop residue retention, and crop rotation, contribute to improved soil structure, enhanced water infiltration, and reduced evaporation losses [12]. Mulching with organic or synthetic materials helps conserve soil moisture, regulate soil temperature, and suppress weed growth. These practices collectively enhance the ability of crops to withstand environmental stresses. Improved nutrient management, particularly balanced application of nitrogen, phosphorus, potassium, and micronutrients, supports physiological functions and strengthens stress tolerance mechanisms.

The use of plant growth regulators, biofertilizers, biostimulants, and beneficial microorganisms has gained increasing attention as sustainable approaches to stress management. Exogenous application of compounds such as salicylic acid, jasmonic acid, brassinosteroids, and silicon has been shown to enhance antioxidant activity and improve stress tolerance. Beneficial microorganisms, including plant growth-promoting rhizobacteria and mycorrhizal fungi, improve nutrient uptake, water relations, and root development [6-7]. Furthermore, emerging technologies such as nanotechnology-based fertilizers and stress-protective formulations offer promising opportunities for enhancing crop performance under challenging environmental conditions.

### 10. Conclusion

Combined heat and drought stress represents one of the greatest challenges to global agricultural sustainability in the era of climate change. The simultaneous occurrence of these stresses causes profound physiological, biochemical, and molecular alterations that adversely affect crop productivity.

Plants employ complex defense mechanisms involving antioxidant systems, osmotic adjustment, hormonal signaling, and stress-responsive gene networks to counteract stress-induced damage. Advances in omics technologies, genome editing, genomic selection, and artificial intelligence are providing unprecedented opportunities for developing climate-resilient crop varieties. Integration of molecular breeding with sustainable agronomic practices will be essential to enhance crop adaptation and ensure food security under future climate scenarios.

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