PUBLIC HEALTH
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Interactive Effects of Heat and Drought Stress on Crop Growth and Yield Formation

Abhijit Debnath[1], Bashir A Alie[2], Ganesh Chandra Malik[3], L.Chanu Langlentombi[4]
[1]Krishi Vigyan Kendra, Dhalai-799278, Tripura, India
[2]Division of Agronomy SKUAST-Kashmir-193201, J&K, India
[3]Dept of Agronomy, Institute of Agriculture, PSB, Visva Bharati, Sriniketan, Bolpur-731236, West Bengal, India
[4]ICAR Research Complex for NEH Region, Manipur Centre, Lamphelpat 795004, Imphal West, Manipur, India
Corresponding Author
L.Chanu Langlentombi
Email: lclanglentombi@gmail.com

Article Information:
Received: 02 November 2025 | Revised: 04 December 2025 | Accepted: 03 January 2026 | Published: February 01, 2026

Cite this article:
Abhijit Debnath, Bashir A Alie, Ganesh Chandra Malik and L.Chanu Langlentombi. Interactive Effects of Heat and Drought Stress on Crop Growth and Yield Formation. *Public Health Open Journal*. 11(1):75–79.
https://doi.org/10.17140/PHOJ.11.01.75

Abstract
Heat and drought stresses are among the most dominant environmental constraints limiting crop productivity worldwide, particularly under the current scenario of climate variability. While individual stress responses have been widely documented, their simultaneous occurrence presents a more severe and complex challenge to crop systems. Heat stress accelerates plant metabolism and phenological development, whereas drought stress restricts water availability, leading to reduced turgor pressure and impaired physiological functioning. When these stresses occur together, they intensify cellular damage, disrupt metabolic pathways, and significantly reduce crop yield.
The combined stress adversely affects photosynthesis, nutrient uptake, reproductive development, and grain formation. It also enhances oxidative stress and alters hormonal balance, ultimately leading to premature senescence and yield loss. This review provides a comprehensive understanding of the physiological, biochemical, and molecular mechanisms underlying heat–drought interactions and discusses adaptive strategies for improving crop resilience.

Keywords: *Heat stress; Drought stress; Stress interaction; Crop physiology; Yield loss; Climate change.*

ISSN: 2472-3878 | Vol 11 | Issue 1 | 2026

Highlights

- Combined heat and drought stress exerts synergistic negative effects on crop growth,physiology, and yield formation.
- Photosynthesis, water relations, and reproductive processes are the most severely affected under stress interaction.
- Oxidative stress and hormonal imbalance play a key role in mediating plant responses to combined stress conditions.
- Integrated approaches involving breeding, agronomic management, and biotechnology are essential for improving crop resilience.

1. Introduction

Climate change has resulted in a marked increase in the frequency of extreme weather events, including prolonged droughts and heat waves. These stresses rarely occur in isolation under field conditions, making their combined impact highly relevant for modern agriculture(1). Heat stress, defined as temperatures exceeding optimal thresholds for plant growth, directly affects enzyme activity, membrane stability, and metabolic processes. On the other hand, drought stress limits soil water availability, affecting plant water relations and nutrient transport (2,3). When these stresses occur simultaneously, their effects are not merely additive but often synergistic. For example, drought-induced stomatal closure reduces transpiration cooling, which further elevates leaf temperature under heat stress conditions. This interaction amplifies physiological damage and reduces crop productivity more severely than individual stresses (–6). Several studies have reported that combined heat and drought stress can cause yield reductions exceeding 50% in major crops such as wheat and maize (7,8,9). Understanding these interactions is therefore essential for developing climate-resilient agricultural systems.

2. Physiological Mechanisms Under Combined Stress

2.1 Impact on Photosynthesis

Photosynthesis is one of the most sensitive processes affected by heat and drought stress. Under heat stress, the stability of photosystem II is compromised, and enzymatic reactions involved in carbon fixation are disrupted. Drought stress further limits CO_2 availability due to stomatal closure (10). When both stresses occur together, there is a drastic reduction in chlorophyll content, electron transport efficiency, and Rubisco activity. This leads to a sharp decline in photosynthetic rate and carbon assimilation (11,12). In addition, heat stress increases photorespiration, while drought reduces internal CO_2 concentration, further aggravating the inefficiency of carbon fixation. These combined effects significantly reduce biomass production and ultimately impact yield (13–15).

2.2 Water Relations and Transpiration

Water balance in plants is severely disrupted under drought stress due to reduced soil moisture availability. This leads to decreased leaf water potential and loss of cell turgidity (16,17). Heat stress, on the other hand, increases evapotranspiration demand, accelerating water loss from plant tissues. Under combined stress, plants experience severe dehydration, forcing stomatal closure to conserve water (18). While stomatal closure helps reduce water loss, it also limits CO_2 entry into leaves, reducing photosynthesis. This tradeoff significantly lowers water-use efficiency and growth (19–21).

2.3 Oxidative Stress and Cellular Damage

One of the major consequences of combined heat and drought stress is the excessive accumulation of reactive oxygen species (ROS). These include superoxide radicals, hydrogen peroxide, and hydroxyl radicals, which damage cellular components (22). Under combined stress, ROS production increases beyond the detoxification capacity of antioxidant systems. This leads to lipid peroxidation, protein degradation, and damage to nucleic acids (23–25). Plants activate antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase to mitigate oxidative stress. However, under severe conditions, these defenses are insufficient,resulting in irreversible cellular injury (26).

3. Effects on Crop Growth and Development

3.1 Germination and Seedling Establishment

The early stages of crop growth are particularly vulnerable to environmental stresses. Drought stress reduces water availability for seed imbibition, which is essential for initiating germination (27). Heat stress can denature enzymes involved in metabolic activation during germination, further inhibiting seedling emergence. When both stresses occur together, germination rates decline sharply, and seedling vigor is significantly reduced (28,29). Poor establishment at this stage has long-term consequences on crop growth, as it reduces plant population and limits yield potential.

3.2 Vegetative Growth

During the vegetative stage, plant growth depends on cell division, elongation, and photosynthetic activity.

Drought stress reduces turgor pressure, limiting cell expansion, while heat stress accelerates developmental processes, shortening the vegetative phase (30). Combined stress results in reduced leaf area, decreased plant height, and lower biomass accumulation. The reduction in canopy size limits light interception and carbon assimilation, further affecting plant growth (31–33). Additionally, leaf senescence is accelerated under combined stress, reducing the duration of active photosynthesis.

3.3 Root Development and Function

Root systems play a critical role in stress adaptation by exploring deeper soil layers for water. Under moderate drought conditions, root growth may increase as an adaptive response (34). However, high soil temperatures under heat stress can impair root membrane stability and enzyme activity. Under combined stress, root growth is often restricted, reducing the plant's ability to absorb water and nutrients (35,36). This limitation further aggravates stress effects on above-ground plant parts.

4. Effects on Reproductive Development and Yield Formation

4.1 Flowering and Pollination

The reproductive stage is the most sensitive phase in crop growth. Heat stress during flowering can cause pollen sterility, reduce pollen viability, and impair fertilization (37,38). Drought stress limits assimilate supply to developing reproductive organs, leading to flower abortion. When both stresses occur together, spikelet sterility increases significantly in cereals, resulting in poor grain set (39–41). This stage largely determines final yield, making it highly critical under stress conditions.

4.2 Grain Filling and Yield Components

Grain filling is strongly affected by both heat and drought stress. Heat stress accelerates grain development but reduces its duration, leading to smaller grains (42). Drought stress limits the translocation of assimilates from leaves to grains, reducing grain weight. Under combined stress, both grain number and grain size are significantly reduced (43–45). These effects ultimately result in substantial yield losses, often exceeding those caused by individual stresses.

4.3 Biomass and Harvest Index

Total biomass production is reduced under combined stress due to impaired photosynthesis and nutrient uptake (46). The harvest index, which represents the proportion of economic yield to total biomass, also declines because plants allocate more resources toward survival rather than reproduction (47,48).

5. Molecular and Biochemical Responses

Plants respond to combined heat and drought stress through complex molecular mechanisms. Stress-responsive genes such as heat shock proteins (HSPs) are activated to protect cellular proteins from denaturation (49). Similarly, drought-responsive genes such as DREB regulate osmotic balance and stress signaling pathways. The interaction of these pathways creates unique gene expression patterns under combined stress (50–52). Hormonal regulation also plays a key role, with abscisic acid (ABA) levels increasing to induce stomatal closure and stress tolerance. Osmolytes such as proline accumulate to maintain cellular stability (53,54).

6. Adaptive and Mitigation Strategies

6.1 Breeding and Genetic Approaches

Developing crop varieties with improved tolerance to combined stress is a sustainable solution. Traits such as deep root systems, efficient water use, and heat tolerance are targeted in breeding programs (55–57).

6.2 Agronomic Management

Agronomic practices such as mulching, conservation tillage, and optimized irrigation can help reduce soil moisture loss and temperature stress (58). Adjusting sowing dates can also help crops escape peak stress periods (59,60).

6.3 Biotechnological Interventions

Biotechnological tools, including genetic engineering and microbial inoculants, can enhance stress tolerance by improving antioxidant capacity and nutrient uptake (61–63).

7. Discussion

The interaction of heat and drought stress represents a significant challenge to crop production systems worldwide. The combined stress leads to greater physiological disruption compared to individual stresses due to its synergistic effects (64–66). The interaction between heat and drought stress represents one of the most complex challenges in crop production systems, as these stresses rarely occur independently under field conditions. Unlike individual stresses, their combined occurrence triggers a cascade of physiological, biochemical, and molecular disruptions that often lead to disproportionately higher yield losses. This synergistic effect arises because drought-induced stomatal closure reduces transpirational cooling, thereby intensifying leaf temperature under heat stress conditions (3,16,40).

One of the central findings across studies is the severe impairment of photosynthesis under combined stress. Heat stress destabilizes thylakoid membranes and reduces the efficiency of photosystem II, while drought stress limits CO availability due to stomatal closure. When both stresses act simultaneously, both photochemical and biochemical processes are affected, leading to a drastic reduction in carbon assimilation (10,22). This dual limitation is particularly critical because photosynthesis serves as the primary source of assimilates required for growth and reproductive development. Another important aspect is the disruption of plant water relations. Drought stress reduces soil moisture availability, lowering plant water potential and cell turgor, while heat stress increases evaporative demand. Under combined stress, plants experience rapid dehydration, which accelerates leaf senescence and reduces canopy duration (16,18,23). This reduction in active photosynthetic area further compounds the decline in biomass accumulation. In many crops, this leads to a shortened crop cycle, reducing the time available for yield formation. Oxidative stress plays a crucial role in mediating the adverse effects of combined stress. The excessive production of reactive oxygen species under heat and drought conditions leads to oxidative damage to lipids, proteins, and nucleic acids. Although plants possess antioxidant defense systems, these mechanisms are often overwhelmed under severe stress combinations (34,35,37). This imbalance between ROS production and detoxification is a major factor contributing to cellular injury and metabolic dysfunction. The reproductive stage has been consistently identified as the most sensitive phase to combined stress. High temperatures can impair pollen viability and fertilization, while drought limits assimilate supply to developing reproductive organs. The simultaneous occurrence of these stresses results in high spikelet sterility in cereals and reduced fruit set in other crops (7,10,41). This explains why even short periods of stress during flowering can lead to substantial yield losses. Grain filling is another critical stage affected by stress interaction. Heat stress accelerates grain development but reduces its duration, while drought stress restricts assimilate translocation. Together, these stresses result in smaller grain size and reduced grain weight (19,42). The combined effect on both grain number and grain weight ultimately leads to significant reductions in overall yield. At the molecular level, plants exhibit unique responses to combined stress that differ from individual stress responses. Studies have shown that specific genes are differentially regulated under combined stress conditions, indicating the activation of distinct signaling pathways (17,40). This highlights the importance of studying stress combinations rather than extrapolating from single-stress responses. Hormonal interactions, particularly involving abscisic acid, also play a key role in regulating plant responses under combined stress conditions. The variability in crop responses to combined heat and drought stress suggests that tolerance mechanisms are highly species- and genotype-specific. Some genotypes exhibit better adaptive traits such as deeper root systems, efficient water use, and enhanced antioxidant capacity, which enable them to withstand stress conditions more effectively (51,55). This variability provides opportunities for breeding programs aimed at developing stress-resilient cultivars. From an agronomic perspective, management strategies such as adjusting sowing dates, improving soil moisture conservation, and adopting climate-smart practices can help mitigate the adverse effects of combined stress (44). However, these approaches alone may not be sufficient under extreme climate scenarios, highlighting the need for integrated solutions combining genetic improvement, agronomic management, and biotechnological interventions.

Overall, the evidence clearly indicates that the interaction of heat and drought stress poses a significant threat to crop productivity. Addressing this challenge requires a comprehensive understanding of plant responses at multiple levels, from physiological processes to molecular mechanisms. Future research should focus on identifying key traits and genes associated with stress tolerance and developing integrated strategies for sustainable crop production under changing climatic conditions (65,69). Photosynthesis, water relations, and reproductive processes are the most affected, resulting in reduced biomass and yield. The variability in crop response highlights the need for integrated approaches that combine physiological understanding with agronomic and genetic solutions (67–69).

8. Conclusion

Combined heat and drought stress significantly affects crop growth, physiological processes, and yield formation. Their interaction leads to severe reductions in photosynthesis, water-use efficiency, and reproductive success. To sustain agricultural productivity under climate change, it is essential to develop integrated strategies involving stress-tolerant varieties, improved agronomic practices, and advanced biotechnological tools. Future research should focus on understanding stress interactions at multiple levels and developing resilient cropping systems.

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