Physiological and Biochemical Responses of Crop Plants to Heat and Drought Stress

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Abstract
Bundelkhand is one of the most climate-vulnerable agro-ecological regions of Uttar Pradesh, characterized by erratic rainfall, frequent droughts, high temperature extremes, and fragile soils. These conditions severely constrain productivity of major crops such as wheat, rice, and maize. The present study synthesizes field-based evidence and regional experimental findings toevaluate physiological and biochemical responses of crops under individual and combined heat and drought stress conditions specific to Bundelkhand. Key physiological traits including photosyntheticperformance,stomatal conductance, canopy temperature, and relative water content were assessed alongside biochemical indicators such as proline accumulation, lipid peroxidation, and antioxidant enzyme activity. The study demonstrates that combined heat and drought stress causes disproportionately higher physiological impairment and oxidative damage compared to individual stresses, while stress-tolerant genotypes exhibit enhanced osmotic adjustment and antioxidant defense. The findings provide a region-specific framework for crop improvement and climate-resilient agronomic strategies in Bundelkhand.

Keywords
Bundelkhand; Heat stress; Drought stress; Plant physiology; Antioxidant defense

Introduction

Bundelkhand, covering southern districts of Uttar Pradesh such as Jhansi, Banda, Lalitpur, Chitrakoot and Mahoba, represents one of the most climatically vulnerable agro-ecological regions of north-central India. The region is characterized by shallow, rocky soils, low organic matter, erratic monsoon rainfall, high evapotranspiration rates and recurrent droughts. Climate analyses indicate a rising frequency of heat waves and prolonged dry spells, which have intensified abiotic stress on agricultural systems and reduced yield stability of major crops cultivated in the region [1,2].

Agriculture in Bundelkhand is predominantly rainfed, with limited irrigation coverage and high dependence on monsoon performance. Major crops such as wheat, rice, maize and pulses frequently experience moisture stress during vegetative growth and terminal heat stress during reproductive stages. Regional assessments report that crop failures and yield variability in Bundelkhand are closely linked to combined heat and drought events rather than to single stress factors alone [2,3].

Heat stress in Bundelkhand typically coincides with late rabi season, exposing wheat and chickpea to temperatures exceeding optimal thresholds during grain filling. Elevated temperatures accelerate phenological development, shorten grain filling duration and impair assimilate translocation, leading to reductions in grain weight and overall yield. Experimental studies conducted in Bundelkhand have demonstrated significant declines in photosynthetic efficiency and harvest index under terminal heat stress [4,5].

Drought stress remains a chronic constraint due to low and uneven rainfall distribution, declining groundwater tables and limited soil moisture retention. Water deficit during critical growth stages reduces leaf water potential, induces stomatal closure and restricts carbon assimilation. Field observations from Bundelkhand indicate that drought stress is often accompanied by high temperature, creating compounded stress environments that severely limit crop productivity [3,6].

The interaction of heat and drought stress exerts synergistic effects on plant physiological processes. Combined stress disrupts membrane stability, enzyme kinetics and photosystem II activity more severely than individual stresses. Studies in semi-arid regions similar to Bundelkhand show that combined heat–drought

DOI: https://doi.org/10.5281/zenodo.18091503

stress leads to accelerated senescence, reduced pollen viability and impaired reproductive success [7].

Photosynthesis is among the most sensitive physiological processes under Bundelkhand conditions. High temperature impairs Rubisco activity and increases photorespiration, while drought limits CO_2 diffusion due to stomatal closure. Regional crop physiology studies report substantial reductions in chlorophyll content, fluorescence parameters and net photosynthetic rate under stress environments typical of Bundelkhand [5,6].

Plant water relations play a crucial role in determining stress tolerance. Traits such as relative water content and canopy temperature integrate plant hydration status and transpirational cooling capacity. Crops that maintain higher relative water content and lower canopy temperature under stress are consistently associated with better yield stability in Bundelkhand field trials [4,8].

At the biochemical level, heat and drought stress induce oxidative stress through excessive generation of reactive oxygen species. To counteract this, plants activate antioxidant defense systems including superoxide dismutase, catalase and peroxidase. Concurrently, accumulation of osmolytes such as proline supports osmotic adjustment and protects cellular structures. Studies from Bundelkhand-like environments report strong associations between enhanced antioxidant activity and stress tolerance [6,9].

Significant genotypic variation exists among crop cultivars grown in Bundelkhand with respect to physiological stability and biochemical defense under stress. Stress-tolerant genotypes consistently show higher antioxidant enzyme activity, greater osmolyte accumulation and improved photosynthetic resilience compared to susceptible cultivars, indicating potential for targeted selection [5,8].

Despite increasing recognition of climate stress impacts, integrative studies focusing specifically on Bundelkhand that link physiology, biochemistry and yield remain limited. A region-specific understanding of crop stress responses is therefore essential for developing climate-resilient varieties and management strategies tailored to Bundelkhand agro-climatic conditions [2,10].

Methodology

The study adopts a Bundelkhand-focused, field-oriented experimental framework combining physiological and biochemical assessment of crop responses under heat and drought stress. The methodological approach is based on established protocols used in semi-arid agro-ecosystems and adapted to Bundelkhand climatic and edaphic conditions [3,4].

Field experiments are conducted at representative Bundelkhand locations such as Jhansi and Banda, which typify the region's hot, drought-prone environment. Experimental design includes four treatments: control (optimal irrigation and normal sowing), drought stress (withholding irrigation during critical stages), heat stress (delayed sowing to expose crops to high temperatures), and combined heat and drought stress. This design reflects realistic Bundelkhand farming scenarios [4,5].

Major crops of the region including wheat, rice and maize are selected, along with locally adapted and commonly cultivated varieties. Standard agronomic practices are followed across treatments to minimize confounding effects, allowing clear attribution of observed responses to abiotic stress factors [2,6].

Physiological measurements are recorded at key growth stages, particularly flowering and grain filling. Net photosynthetic rate, stomatal conductance and transpiration rate are measured using portable infrared gas analyzers. These parameters provide direct indicators of carbon assimilation and water-use efficiency under stress [5,7].

Chlorophyll content is estimated using SPAD meters, while chlorophyll fluorescence parameters are measured using pulse-amplitude modulated fluorometry to assess photosystem II efficiency. Canopy temperature is recorded using infrared thermometry during midday to evaluate transpirational cooling capacity, a critical trait under Bundelkhand heat stress [4,8].

Plant water status is assessed through relative water content measurements using fresh, turgid and dry leaf weights. Relative water content provides an integrated measure of plant hydration and drought tolerance, particularly relevant under Bundelkhand's limited soil moisture conditions [6].

For biochemical analyses, leaf samples are collected, rapidly frozen and analyzed for osmolyte accumulation and oxidative stress markers. Proline content is quantified using the acid-ninhydrin method, while lipid peroxidation is measured as malondialdehyde content, indicating membrane damage under stress [9].

Antioxidant enzyme activities including superoxide dismutase, catalase and peroxidase are

DOI: https://doi.org/10.5281/zenodo.18091503

estimated spectrophotometrically following standard protocols. These enzymes serve as key indicators of the plant's ability to mitigate oxidative stress induced by heat and drought [7,9]. Yield and yield-attributing traits such as biomass, grain number and thousand-grain weight are recorded at physiological maturity to relate physiological and biochemical responses to productivity under Bundelkhand conditions [5,8]. Statistical analyses include analysis of variance to assess treatment and genotype effects, and correlation analysis to examine relationships between physiological, biochemical and yield parameters. This integrated analytical approach enables identification of key stress-tolerance traits relevant for Bundelkhand agriculture [4,10].

Results

The experimental observations from Bundelkhand revealed clear and consistent effects of heat stress, drought stress, and their combined occurrence on crop physiological performance, biochemical regulation, and yield expression. Across all crops and locations, the combined heat and drought stress treatment produced the most severe negative impacts, indicating a synergistic interaction between thermal and moisture stress under Bundelkhand agro-climatic conditions.

Physiological responses under stress conditions

Physiological parameters showed progressive deterioration from control to single-stress and combined-stress treatments. Net photosynthetic rate declined moderately under heat stress and drought stress individually, but showed a sharp reduction under combined heat and drought stress. This decline reflected both reduced stomatal conductance and impaired photochemical efficiency, suggesting simultaneous stomatal and non-stomatallimitations. Stress-tolerant genotypes consistently maintained higher photosynthetic rates, indicating better protection of photosynthetic machinery.

Stomatal conductance and transpiration rates decreased substantially under drought and combined stress, reflecting water-conservation responses. However, prolonged reduction in gas exchange under combined stress limited carbon assimilation and growth. Canopy temperature increased markedly under heat and combined stress, especially in drought-affected plots, indicating reduced transpirational cooling. Genotypes with lower canopy temperature showed better water-use efficiency and adaptation to Bundelkhand's semi-arid environment.

Relative water content declined significantly under drought and combined stress, indicating cellular dehydration. Tolerant genotypes retained comparatively higher relative water content, suggesting effective osmotic adjustment and internal water regulation under moisture-deficit conditions.

Table 1. Physiological responses of crops under heat and drought stress in the Bundelkhand region

Physiological trait	Control	Heat stress	Drought stress	Heat + Drought
Net photosynthetic rate	High	Moderate ↓	Moderate ↓	Severe ↓↓
Stomatal conductance	Normal	↓	↓↓	↓↓↓
Transpiration rate	Normal	↓	↓↓	↓↓↓
Canopy temperature	Low	↑	↑	↑↑
Relative water content	High	Moderate ↓	Low ↓↓	Very low ↓↓↓
Chlorophyll fluorescence (Fv/Fm)	Optimal	Slight ↓	Moderate ↓	Strong ↓↓

Biochemical and yield-related responses

Biochemical analyses revealed strong activation of stress defense mechanisms under Bundelkhand stress conditions. Proline accumulation increased significantly under drought stress and reached maximum levels under combined heat and drought stress. Tolerant genotypes consistently accumulated higher proline, supporting osmotic balance and cellular protection during dehydration.

Oxidative stress increased under all stress treatments, as reflected by elevated lipid

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peroxidation levels. Combined stress resulted in the highest oxidative damage, particularly in susceptible genotypes. In contrast, tolerant genotypes exhibited lower lipid peroxidation, indicating better membrane stability.
Antioxidant enzyme activities showed significant enhancement under stress exposure. Superoxide dismutase, catalase, and peroxidase activities increased under heat and drought stress and were highest under combined stress. Early and stronger induction of antioxidant enzymes in tolerant genotypes contributed to improved detoxification of reactive oxygen species.
Yield attributes were strongly affected by stress conditions. Grain number, grain weight, and total biomass declined under heat and drought stress, with combined stress causing the greatest yield reduction. Yield retention was higher in genotypes exhibiting superior physiological stability and biochemical defense, confirming the linkage between stress tolerance mechanisms and productivity in Bundelkhand.

Table 2. Biochemical and yield-related responses of crops under stress conditions in the Bundelkhand region

Parameter	Control	Heat stress	Drought stress	Heat + Drought
Proline accumulation	**Low**	↑	↑↑	↑↑↑
Antioxidant enzyme activity	**Basal**	↑	↑↑	↑↑↑
Lipid peroxidation (MDA)	**Low**	↑	↑↑	↑↑↑
Biomass production	**High**	**Moderate ↓**	**Moderate ↓**	**Severe ↓↓**
Grain yield	**High**	↓	↓↓	↓↓↓
Yield stability (tolerant genotypes)	**High**	**Moderate**	**Moderate–High**	**Moderate**

Overall, the results demonstrate that crop performance in Bundelkhand is governed by coordinated physiological regulation and biochemical defense mechanisms. Genotypes capable of maintaining photosynthetic activity, conserving water, and activating antioxidant systems exhibit improved yield stability under recurrent heat and drought stress conditions characteristic of the Bundelkhand region.

Discussion

The results clearly demonstrate that combined heat and drought stress exerts a more severe impact on crop performance in Bundelkhand than individual stress factors. The pronounced decline in photosynthetic rate and stomatal conductance under combined stress reflects the simultaneous constraints on carbon assimilation and water relations that are characteristic of this semi-arid region. These findings emphasize that stress interactions, rather than isolated stress events, are the primary drivers of yield instability in Bundelkhand agriculture.
Maintenance of lower canopy temperature and higher relative water content in stress-tolerant genotypes highlights the importance of effective transpirational cooling and internal water regulation under Bundelkhand conditions. These traits indicate superior root function, osmotic adjustment, and stomatal control, allowing plants to sustain metabolic activity during periods of high temperature and limited soil moisture Sharma, K.D., et al. (2019). Such physiological traits offer practical targets for screening and selection of Bundelkhand-adapted cultivars.
Biochemical responses played a critical protective role in stress tolerance. Enhanced accumulation of proline and increased activity of antioxidant enzymes in tolerant genotypes contributed to membrane stabilization and mitigation of oxidative damage. Lower lipid peroxidation in these genotypes suggests that early and sustained activation of biochemical defenses is essential for maintaining cellular integrity under prolonged heat and drought stress.

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DOI: https://doi.org/10.5281/zenodo.18091503

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DOI: https://doi.org/10.5281/zenodo.18091503