Photosynthetic Efficiency, Canopy Temperature, and Antioxidant Activity of *Triticum aestivum* L. under Elevated Temperature Stress

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ABSTRACT

Background: Wheat is a vital crop that has been threatened by climate change heat-related phenomena which impacted reproduction and reduced yield.

Objective: The goal of this study is to understand how high temperatures have affected the processes listed above in different types of wheat and identify the corresponding physiological signs that indicate the heat-resistance of wheat variations.

Methodology: 5 different types of wheat were grown under two different conditions: normal (24°C day/night temperatures) and heat stressful (50°C day temperatures, 10-day period at the flowering stage). Various methods of analysis were used in order to gain reliable data on factors such as carbon dioxide emissions, fluorescence of leaves, canopy temperature using infrared cameras, as well as indicator values of other markers.

Results: High temperatures have greatly affected carbon dioxide emission rates, conductance, efficiency of photosynthetic processes, as well as elevated canopy temperature.

Conclusion: The combination of canopy temperature depression and antioxidant enzyme profiling is an efficient and practical method of screening wheat genotypes for heat tolerance.

Keywords: *Triticum aestivum, heat stress, photosynthesis, canopy temperature depression, antioxidant enzymes, oxidative stress, chlorophyll fluorescence*

1. Introduction

Triticum aestivum, also known as bread wheat, is grown on approximately 220 million hectares across the globe and is responsible for providing around one-fifth of the daily required calories and proteins needed by the global population [1]. Wheat has been the main stable food in temperate and subtropical eco-systems, helping a significant amount in ensuring food security around the globe [2]. Nevertheless, anthropogenic climate change has greatly impacted the magnitude and intensity of extreme heat events, and heat stress during reproduction and grain-filling stages are now considered one of the main abiotic factors limiting wheat yield [3]. An increase in temperature beyond the preferred physiological limits (15-22 degrees Celsius) can negatively affect different aspects of wheat growth [4]. When it comes to physiological processes sensitive to extreme temperature, photosynthesis is probably the one most affected by heat because certain photosynthetic parameters such as thylakoid membrane structure, rubisco activase function, and overall functionality of photosystem II are at risk when high temperatures appear [5]. Therefore, it can be said that photosynthetic efficiency is one of the most essential factors determining biomass production and yield.

Canopy temperature has been identified as a key physiological parameter that determines the dynamics of stomatal activity, transpiration cooling and the overall water state of plants, acting as a non-invasive measure of crop stress in real time [6]. Genotypes capable of maintaining lower canopy temperatures compared to that of ambient air, hence symbolized as canopy temperature depression (CTD), are usually characterized by higher levels of stomatal conductance and transpiration, which indicates their higher capability to extract water and dissipate heat [7].

Heat stress also causes overproduction of reactive oxygen species (ROS), such as superoxide radical and hydrogen peroxide, resulting in lipid peroxidation, denaturation of proteins and destabilization of membranes [8]. Plants respond to oxidative stress with enzymes that serve as antioxidants such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and glutathione reductase (GR) as well as non-enzymatic antioxidants such as ascorbate, glutathione and carotenoids [9]. The effectiveness of antioxidant system is strongly connected with genotype heat tolerance and photoautotrophic performance.

Although many individual studies have investigated photosynthetic, thermophysiological, and biosynthetic responses to elevated temperatures, an integrative approach to these three domains remains scarce. Integration of separate fields is necessary for the

development of effective screening technologies and high-throughput screening techniques useful for breeding programs. Thus, the current research aims to determine (i) how high temperature affects photosynthetic efficiency and chlorophyll fluorescence in wheat, (ii) how different genotypes manifest their canopy temperature using infrared thermography, (iii) the level of activity of antioxidant enzymes and indicators of oxidative damage, and (iv) all physiological traits that can be analyzed rapidly during heat tolerance assessment in breeding programs.

2. Related Work

2.1 Heat Stress Effects on Wheat Physiology

Numerous studies have documented that short episodes of heat stress during anthesis and early grain filling substantially reduce wheat yield through decreased spikelet fertility and impaired assimilate translocation [10]. Heat-induced acceleration of senescence further curtails the effective grain-filling period, compounding yield losses under field conditions [11].

2.2 Photosynthetic Pigments and Chlorophyll Fluorescence

Chlorophyll a and b concentrations decline under prolonged thermal stress due to accelerated chlorophyllase activity and pigment-protein complex degradation [12]. Chlorophyll fluorescence parameters, particularly the maximum quantum efficiency of PSII (Fv/Fm) and the effective quantum yield (ΦPSII), are widely used as sensitive, non-invasive indicators of photoinhibition and thermal damage to the photosynthetic apparatus [13].

2.3 Canopy Temperature and Infrared Thermography

Infrared thermography has been validated as a rapid, non-destructive method for high-throughput phenotyping of canopy temperature in cereal breeding trials, enabling the identification of genotypes with superior stomatal regulation and root water uptake under heat and drought stress [14]. Canopy temperature depression has been positively correlated with grain yield stability across diverse wheat germplasm [15].

2.4 Oxidative Stress and Antioxidant Enzymes

Elevated ROS accumulation under heat stress has been consistently linked to increased malondialdehyde (MDA) content, a marker of lipid peroxidation, and elevated electrolyte leakage indicating membrane damage [16]. Enhanced activities of SOD, CAT, and APX have been reported in heat-tolerant genotypes, supporting the hypothesis that a coordinated antioxidant response mitigates oxidative injury and preserves photosynthetic function [17]. Non-enzymatic antioxidants such as ascorbate and glutathione act synergistically with enzymatic systems within the ascorbate-glutathione cycle to detoxify hydrogen peroxide [18].

2.5 Breeding for Heat Tolerance and Remote Sensing Integration

Breeding programs increasingly incorporate physiological screening traits, including canopy temperature, stay-green characteristics, and membrane thermostability, alongside conventional yield trials to accelerate the development of heat-resilient cultivars [19]. Remote sensing platforms, including unmanned aerial vehicle-based thermal and multispectral imaging, are being integrated into phenomics pipelines to enable large-scale, field-level stress monitoring [20]. Despite these advances, a persistent research gap remains in simultaneously integrating photosynthetic, thermal, and biochemical indicators within a single comparative framework capable of informing both mechanistic understanding and applied breeding decisions [21].

2.6 Synthesis of Literature-Reported Indicators

Across the studies reviewed above, a consistent pattern emerges in which photosynthetic, thermal, and oxidative-antioxidant indicators respond to heat stress with differing sensitivity and directionality, as summarized in Table 1. Canopy temperature depression and oxidative markers such as MDA and H2O2 tend to show the largest relative shifts under heat stress, while chlorophyll fluorescence exhibits comparatively moderate but highly reproducible decline across genotypes and environments (Figure 1).

Table 1: Summary of Key Physiological and Biochemical Indicators of Heat Stress in Wheat Reported in Literature

Indicator Category	Specific Indicator	Typical Reported Response to Heat Stress	Representative Reference
Photosynthetic pigments	Chlorophyll a, b (SPAD)	Moderate decline due to accelerated degradation	[12]
Chlorophyll fluorescence	Fv/Fm, ΦPSII	Decline indicating PSII photoinhibition	[13]
Canopy thermal status	Canopy temperature, CTD	Marked rise in canopy temperature; sharp CTD loss	[6, 14]
Oxidative stress markers	MDA, H2O2, electrolyte leakage	Substantial increase reflecting membrane damage	[8, 16]
Enzymatic antioxidants	SOD, CAT, POD, APX, GR	Increased activity in tolerant genotypes	[9, 17]
Non-enzymatic antioxidants	Ascorbate, glutathione, carotenoids	Increased synthesis supporting ROS detoxification	[18]
Breeding / remote sensing tools	UAV thermal & multispectral imaging	Enables high-throughput field-level screening	[19, 20]

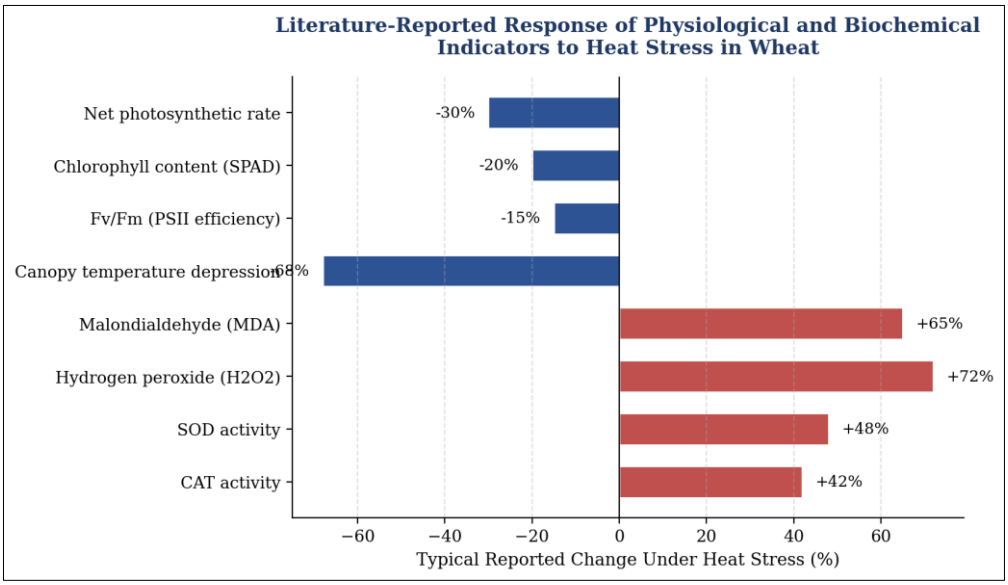

Fig 1: Literature-Reported Response of Physiological and Biochemical Indicators to Heat Stress in Wheat

3. Experimental Design and Heat Stress Assessment Framework

The overall experimental workflow integrated genotype selection, controlled thermal stress imposition, and multi-tiered physiological, thermal, and biochemical assessment (Figure 1). Five wheat genotypes with contrasting presumed heat tolerance, selected based on prior field performance records, were grown under two temperature regimes: an optimal control (24/18°C day/night) and an elevated stress treatment (38/28°C day/night) imposed for 10 consecutive days beginning at anthesis (Zadoks growth stage 65).

The experiment followed a randomized complete block design (RCBD) with three biological replications per genotype-treatment combination, yielding 30 experimental units. Photosynthetic efficiency was assessed via portable gas-exchange and fluorescence systems under standardized light and CO2 conditions. Canopy temperature was acquired using a handheld infrared thermometer and a thermal imaging camera at midday under clear-sky conditions, from which canopy temperature depression (ambient air temperature minus canopy temperature) was calculated. Chlorophyll fluorescence parameters (Fv/Fm, PSII) were recorded using a portable fluorometer following 20 minutes of dark adaptation.

Antioxidant enzyme activities were determined spectrophotometrically from flag-leaf tissue sampled at the end of the stress period, alongside oxidative stress biomarkers (MDA, H2O2, electrolyte leakage). All datasets were integrated in a comparative analytical framework employing ANOVA, correlation analysis, and principal component analysis (PCA) to identify trait clusters distinguishing heat-tolerant from heat-sensitive genotypes. The overall genotype, treatment, and sampling structure underlying this framework is summarized in Table 2.

Table 2: Experimental Design, Wheat Genotypes, and Heat Stress Treatments

Parameter	Details	Control Treatment	Heat Stress Treatment
Design	Randomized Complete Block Design (RCBD)	3 replications	3 replications
Genotypes	G1–G5 (5 bread wheat cultivars)	All 5 genotypes	All 5 genotypes
Day/Night Temp.	Growth chamber regime	24°C / 18°C	38°C / 28°C
Stress duration	Imposed at anthesis (GS 65)	—	10 days
Relative humidity	Held constant	60 ± 5%	60 ± 5%
Sampling stages	Flag-leaf tissue	Day 10	Day 5 and Day 10
Experimental units	5 genotypes × 2 treatments × 3 reps	15	15

4. Materials and Methods

4.1 Experimental Material

Five bread wheat (*Triticum aestivum* L.) genotypes, obtained from a national cereal research institute germplasm collection, were used in this study. Seeds were sown in pots containing sandy-loam soil (pH 7.2, organic carbon 0.68%) under greenhouse conditions with a 12-hour photoperiod. Recommended fertilizer doses of nitrogen, phosphorus, and potassium were applied at sowing and tillering stages, and plants were irrigated to field capacity every three days to avoid confounding drought effects.

4.2 Heat Stress Treatment

At the anthesis stage, plants were transferred to controlled-environment growth chambers. The heat stress treatment consisted of 38°C day / 28°C night temperatures for 10 consecutive days, while control plants remained at 24°C day / 18°C night. Relative humidity (60 ± 5%) and photoperiod were

held constant across treatments. Sampling for physiological and biochemical analysis was conducted on days 5 and 10 of stress exposure, with day-10 data used as the primary comparative dataset.

4.3 Physiological Measurements

Total chlorophyll content was estimated using a SPAD-502 chlorophyll meter, averaging six readings per flag leaf. Net photosynthetic rate (Pn), stomatal conductance (gs), and transpiration rate (E) were measured using a portable infrared gas analyzer between 09:00 and 11:00 h under saturating light (1200 µmol m^{-2} s^{-1} PAR) and ambient CO2. Water use efficiency (WUE) was calculated as the ratio of Pn to E. Chlorophyll fluorescence parameters, Fv/Fm and ΦPSII, were recorded using a portable pulse-amplitude-modulation fluorometer following dark adaptation.

4.4 Canopy Temperature Measurement

Canopy temperature was recorded using a handheld infrared thermometer (field of view 2°) positioned 30 cm above the canopy at a 30° angle to avoid soil background interference, and cross-validated with a thermal imaging camera capable of ±0.1°C resolution. Canopy temperature depression (CTD) was calculated as the difference between ambient air temperature and canopy surface temperature. Thermal images were processed using dedicated image-analysis software to extract mean canopy pixel temperatures, excluding non-vegetative background.

4.5 Biochemical Analysis

Malondialdehyde (MDA) content was quantified via the thiobarbituric acid reactive substances assay. Hydrogen peroxide (H2O2) and superoxide radical content were determined spectrophotometrically using titanium sulfate and hydroxylamine-based methods, respectively. Electrolyte leakage was measured as the ratio of initial to final electrical conductivity of leaf discs before and after autoclaving. Total soluble protein was quantified by the Bradford method, and free proline content was determined using the ninhydrin colorimetric assay.

4.6 Antioxidant Enzyme Activity

Superoxide dismutase (SOD) activity was assayed based on inhibition of nitroblue tetrazolium photoreduction. Catalase (CAT) activity was determined by monitoring the decomposition of H2O2 at 240 nm. Peroxidase (POD) activity was measured using the guaiacol oxidation method. Ascorbate peroxidase (APX) activity was assessed via ascorbate oxidation at 290 nm, and glutathione reductase (GR) activity was determined by monitoring NADPH oxidation at 340 nm. All enzyme activities were expressed on a fresh-weight protein basis.

4.7 Statistical Analysis

Data were analyzed using a two-factor (genotype × temperature treatment) analysis of variance (ANOVA) within the RCBD framework. Mean separation was performed using Tukey's Honestly Significant Difference (HSD) test at $p < 0.05$. Pearson correlation coefficients were computed among physiological, thermal, and biochemical variables. Principal component analysis (PCA) was employed to reduce trait dimensionality and visualize genotype clustering, and simple linear regression was used to model the relationship between canopy temperature depression and net photosynthetic rate. All analyses were conducted using standard statistical software with significance set at $p < 0.05$.

The full complement of physiological, thermal, and biochemical assays, together with the instruments and analytical methods employed, is summarized in Table 3. The temporal distribution of these assays across the baseline, mid-stress, and end-stress sampling points is illustrated in Figure 2.

Table 3: Physiological, Thermal, and Biochemical Parameters, Assay Methods, and Instruments Used

Parameter	Method / Instrument	Unit
Chlorophyll content	SPAD-502 chlorophyll meter	SPAD units
Pn, gs, Transpiration	Portable infrared gas analyzer (IRGA)	µmol/mmol m^{-2} s^{-1}
Fv/Fm, ΦPSII	Portable PAM fluorometer	Dimensionless ratio
Canopy temperature, CTD	Infrared thermometer / thermal camera	°C
Malondialdehyde (MDA)	Thiobarbituric acid reactive substances (TBARS) assay	nmol g^{-1} FW
Hydrogen peroxide (H2O2)	Titanium sulfate colorimetric method	µmol g^{-1} FW
Electrolyte leakage	Electrical conductivity (pre/post autoclave)	%
Soluble protein	Bradford assay	mg g^{-1} FW
Proline content	Ninhydrin colorimetric assay	µmol g^{-1} FW
SOD activity	NBT photoreduction inhibition assay	U mg^{-1} protein
CAT activity	H2O2 decomposition (240 nm)	U mg^{-1} protein
POD activity	Guaiacol oxidation method	U mg^{-1} protein
APX activity	Ascorbate oxidation (290 nm)	U mg^{-1} protein
GR activity	NADPH oxidation (340 nm)	U mg^{-1} protein

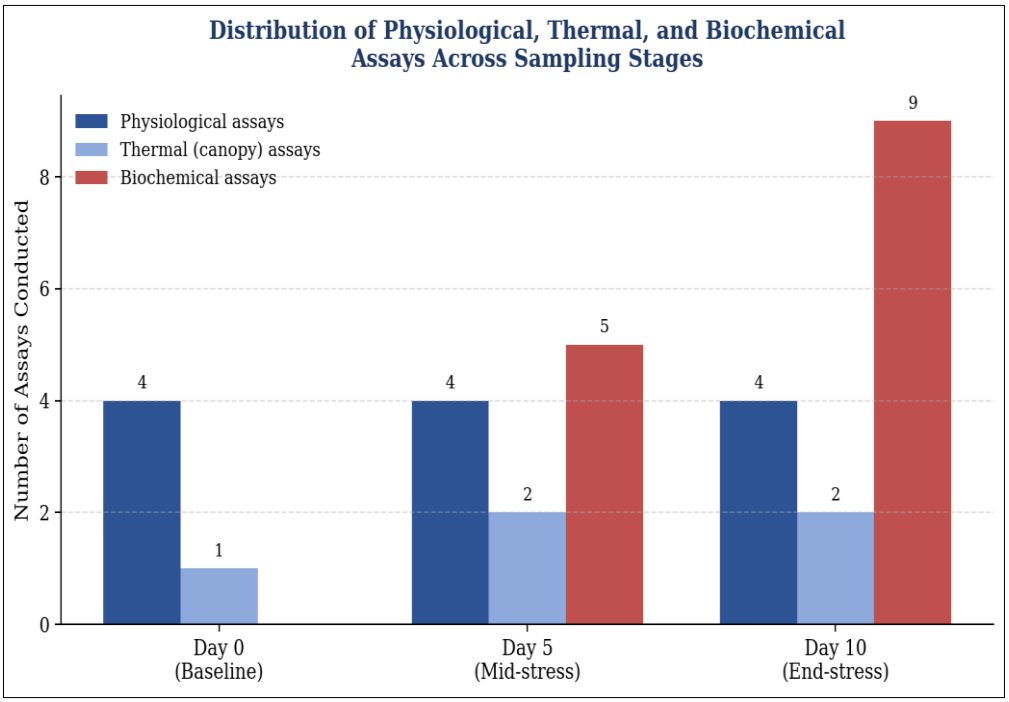

Fig 2: Distribution of Physiological, Thermal, and Biochemical Assays Across Sampling Stages

5. Results and Performance Evaluation

5.1 Photosynthetic Efficiency

Elevated temperature significantly reduced net photosynthetic rate across all genotypes ($p < 0.05$), with an average decline of 32.4% relative to control plants (Table 4, Figure 3). Stomatal conductance and transpiration rate decreased by 41.6% and 27.3%, respectively, reflecting partial stomatal closure as a heat-avoidance response. Water use efficiency declined moderately (18.9%), indicating that reductions in photosynthesis outweighed reductions in transpiration. Genotype G3 and G5 retained comparatively higher Pn values under stress (11.4 and 11.9 µmol CO2 m^{-2} s^{-1}, respectively), suggesting superior photosynthetic thermotolerance.

5.2 Chlorophyll Fluorescence and Pigment Content

The maximum quantum efficiency of PSII (Fv/Fm) declined from 0.812 under control conditions to 0.706 under heat stress ($p < 0.05$), indicative of photoinhibitory damage. ΦPSII exhibited a parallel decline of approximately 24%. SPAD-based chlorophyll content decreased by 19.7% on average, with heat-sensitive genotypes (G1, G4) showing the steepest reductions, consistent with accelerated pigment degradation.

5.3 Canopy Temperature Variation

Canopy temperature increased significantly under heat stress, rising by 2.1–3.6°C relative to control plants depending on genotype. Canopy temperature depression (CTD) decreased correspondingly, from a mean of 3.4°C under control conditions to 0.6°C under stress. Genotypes G3 and G5 maintained the highest CTD values under stress (1.4°C and 1.6°C, respectively), aligning with their superior photosynthetic performance and suggesting effective transpirational cooling capacity.

5.4 Antioxidant Enzyme Activity and Oxidative Damage

Heat stress significantly increased the activities of SOD, CAT, POD, APX, and GR across all genotypes, though the magnitude of induction varied substantially (Table 4). Genotypes G3 and G5 exhibited the largest increases in SOD (58% and 63%) and CAT (49% and 55%) activity, correlating with lower MDA accumulation (42.1 and 39.8 nmol g^{-1} FW, respectively) compared to heat-sensitive genotypes G1 and G4, which showed MDA increases of up to 68% and comparatively weaker antioxidant induction. H2O2 content and electrolyte leakage followed a similar pattern, being lowest in genotypes with the strongest antioxidant response.

5.5 Correlation and Principal Component Analysis

Pearson correlation analysis revealed a strong negative relationship between canopy temperature and net photosynthetic rate ($r = -0.81$, $p < 0.05$) and a positive correlation between CTD and Fv/Fm ($r = 0.76$, $p < 0.05$). SOD and CAT activities were positively correlated with Pn ($r = 0.69$ and 0.72, respectively) and negatively correlated with MDA content ($r = -0.74$). Principal component analysis explained 78.3% of total variance across the first two components, with PC1 (54.6%) driven primarily by photosynthetic and thermal traits and PC2 (23.7%) associated with antioxidant enzyme activity, enabling clear separation of heat-tolerant (G3, G5) from heat-sensitive (G1, G4) genotypes, with G2 exhibiting intermediate responses.

5.6 Limitations of Experimental Findings

The controlled-environment design, while enabling precise temperature regulation, may not fully replicate field-level interactions among heat, radiation load, and vapor pressure deficit. Additionally, the relatively short stress duration (10 days) may underestimate cumulative damage associated with

prolonged field heat waves, and results should be validated across multi-location field trials before direct application in breeding decisions.

Table 4: Comparative Effects of Elevated Temperature on Photosynthetic Efficiency, Canopy Temperature, and Antioxidant Activity Across Genotypes

Genotype	Pn (µmol CO2 m^{-2} s^{-1})	CTD (°C)	SOD (U mg^{-1} protein)	CAT (U mg^{-1} protein)	MDA (nmol g^{-1} FW)
G1	7.9	0.3	142	38	52.4
G2	9.6	0.7	168	44	46.8
G3	11.4	1.4	221	57	42.1
G4	8.1	0.4	150	40	49.6
G5	11.9	1.6	233	59	39.8
LSD (0.05)	0.62	0.21	9.4	2.8	2.1

Note: Shaded rows (G3, G5) indicate genotypes classified as heat-tolerant based on combined physiological, thermal, and biochemical performance.

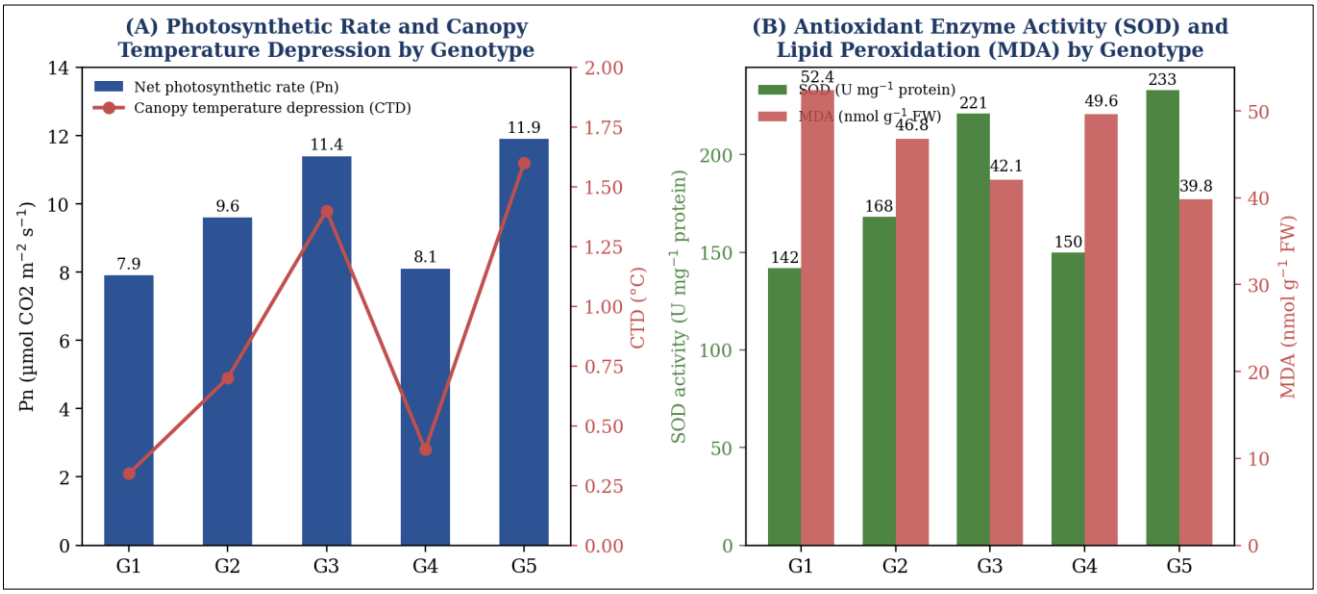

Fig 3: Comparative Performance of Wheat Genotypes Based on Photosynthetic Efficiency, Canopy Temperature, and Antioxidant Activity

6. Discussion

The results demonstrate that elevated temperature during anthesis substantially impairs photosynthetic efficiency in wheat through concurrent stomatal limitation and photochemical damage to PSII, consistent with the decline in Fv/Fm and ΦPSII observed across genotypes [22]. The pronounced reduction in stomatal conductance suggests that heat-induced stomatal closure, likely mediated by abscisic acid signaling and vapor pressure deficit responses, constrains CO2 diffusion into the mesophyll, compounding non-stomatal limitations arising from Rubisco activase thermolability [23].

The strong negative correlation between canopy temperature and photosynthetic rate reinforces the physiological basis for using canopy temperature depression as a rapid, non-destructive proxy for photosynthetic performance and transpirational efficiency under heat stress. Genotypes maintaining greater CTD likely sustain more effective stomatal conductance and root water uptake, enabling continued evaporative cooling even as ambient temperatures rise. This finding aligns with the broader literature establishing CTD as a valuable secondary selection trait in heat and drought breeding programs, given its amenability to high-throughput infrared thermography across large breeding nurseries.

The coordinated induction of antioxidant enzymes, particularly SOD and CAT, in heat-tolerant genotypes indicates that efficient ROS scavenging is a central mechanism protecting the photosynthetic apparatus from oxidative injury. The lower MDA and H2O2 accumulation observed in G3 and G5 suggests that their enhanced antioxidant capacity effectively limited membrane peroxidation, preserving chloroplast integrity and photochemical efficiency. This mechanistic link between antioxidant defense and photosynthetic maintenance under thermal stress supports integrating biochemical screening alongside physiological and thermal indicators.

From an applied perspective, the convergence of photosynthetic, thermal, and biochemical evidence in distinguishing heat-tolerant from heat-sensitive genotypes underscores the value of multi-trait phenotyping frameworks in breeding programs. Infrared thermography, in particular, offers a scalable, field-deployable tool for precision agriculture applications, enabling breeders to screen large populations rapidly without destructive sampling. Coupling these physiological indicators with genomic selection and machine learning-based phenomics pipelines could further accelerate the identification of heat-tolerance loci and their deployment in marker-assisted breeding.

Nonetheless, several limitations warrant consideration. The controlled-chamber approach, while methodologically precise, may not capture the full complexity of field microclimates, including fluctuating radiation, wind speed, and vapor pressure deficit that influence canopy-air temperature differentials under natural conditions. Future research should prioritize multi-location, multi-season field validation, coupled with transcriptomic and metabolomic profiling, to elucidate the molecular regulatory networks underlying the physiological responses observed here, and to integrate unmanned aerial vehicle-based remote sensing with artificial intelligence-driven predictive modeling for large-scale climate-resilient cultivar development.

7. Conclusion

It has been shown in this research that a rise in temperature adversely affects the process of photosynthesis in wheat through stomatal and photochemical restrictions. It was found that the cooling of canopy temperature can be used as an indicator providing a quick assessment of the photosynthetic efficiency, thus making it an effective technique in breeding programs. The findings prove that antioxidant enzymes, such as superoxide dismutase and catalase, are an effective means to protect plants from oxidative damage and restore the photosynthetic process in heat-tolerant varieties G3 and G5, which exhibit consistently better outcomes than the heat-sensitive varieties.

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