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Physiological basis of heat tolerance in late-planted wheat genotypes under terminal heat stress

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Abstract
Nearly 40% of the global wheat area faces terminal heat stress, yet physiological screening criteria for heat tolerance remain poorly standardized. This research assessed eight wheat genotypes planted late (December 15) at Rajshahi Agricultural University, Bangladesh, during rabi 2022–23 and 2023–24 to identify reliable physiological markers of heat tolerance under field conditions. A randomized complete block design with three replications was used. Membrane stability index (MSI), chlorophyll content index (CCI), canopy temperature depression (CTD), proline accumulation, and grain filling rate (GFR) were measured at anthesis and 15 days post-anthesis. Maximum temperatures during grain filling exceeded 35 °C on 23 days in 2023 and 27 days in 2024. Genotypes DBW-187 and HD-3226 consistently recorded the highest MSI (72.8% and 71.3%), CTD (6.7 and 6.2 °C), and GFR (1.91 and 1.83 mg day^{-1}). MSI showed the strongest correlation ($r = 0.89$) with grain yield under stress. A composite heat tolerance index combining MSI, CTD, and GFR explained 83.7% of yield variability. These results suggest that MSI-CTD-GFR screening can accelerate identification of heat-tolerant wheat lines for late-sown environments.

Keywords: Heat tolerance, wheat genotypes, terminal heat stress, membrane stability, canopy temperature depression, grain filling rate, proline, chlorophyll content, late planting, physiological screening.

Introduction

About 36% of irrigated wheat in South Asia is planted after the optimal sowing window, exposing the crop to temperatures above 35 °C during grain filling [1]. In Bangladesh, where wheat occupies roughly 0.35 million hectares, delayed planting after harvest of transplanted aman rice is a persistent agronomic constraint [2]. Terminal heat stress shortens the grain filling period, accelerates leaf senescence, and reduces test weight—collectively cutting yields by 15–25% in susceptible cultivars [3,4].

Plants cope with high temperatures through a combination of avoidance and tolerance mechanisms. Canopy temperature depression, driven by transpirational cooling, allows some genotypes to maintain leaf temperatures 4–7 °C below ambient air [5]. Membrane stability, measured as electrolyte leakage under controlled heating, reflects the integrity of cellular membranes and has been linked to stress survival in wheat and rice [6]. Proline accumulates as a compatible osmolyte and protein stabilizer under heat and drought [7], while sustained chlorophyll content supports continued photosynthesis during grain fill [8].

Despite the availability of individual trait data, few investigations have assessed how well combinations of these physiological parameters predict yield under field-level terminal heat stress, particularly in the Gangetic plain environment. Most screening protocols rely on single traits, yet heat tolerance is polygenic and multi-mechanistic [9,10]. A composite index that weights the most informative traits could accelerate breeding progress and reduce the cost of large-scale germplasm screening [11]. This research aimed to (a) quantify the physiological responses of eight wheat genotypes to terminal heat stress under late-planted field conditions at Rajshahi, Bangladesh, and (b) identify a trait combination with the highest predictive value for grain yield under heat.

Climatic Conditions During the Research

Rajshahi lies in the semi-arid western zone of Bangladesh (24°22′N, 88°36′E, 18 m a.s.l.) with

with a subtropical monsoon climate. During rabi 2022–23, mean maximum temperature rose from 26.4 °C in January to 38.1 °C in March; in 2023–24, the corresponding values were 25.8 and 39.3 °C. Maximum temperature exceeded 35 °C on 23 days (2023) and 27 days (2024) between heading and maturity. Total rainfall during the crop period was 18.6 mm (2023) and 12.4 mm (2024). Relative humidity at noon ranged from 38% to 62%. Weather data were recorded from the university's agrometeorological observatory, 200 m from the trial field.

Materials and Methods

Materials

Eight bread wheat (Triticum aestivum L.) genotypes—HD-3226, PBW-752, WH-1270, DBW-187, RAJ-4238, K-1317, NW-5054, and HUW-838—were obtained from the Wheat Research Centre, Rajshahi. These included released varieties and advanced lines representing diverse heat-response backgrounds. Seeds were treated with carbendazim (2 g kg^{-1}) before sowing. Basal fertilizer was applied at 120:60:40 kg $N:P_2O_5:K_2O$ ha^{-1}, with N split in three doses.

Methods

The trial was sown on December 15 in both years at the research farm of Rajshahi Agricultural University in a randomized complete block design with three replications. Plot size was 3 m × 2 m with 20 cm row spacing. Five irrigations were scheduled at crown root initiation, tillering, booting, anthesis, and dough stages. MSI was determined by the dual-temperature electrolyte leakage method [6] at anthesis and 15 days post-anthesis. CCI was measured using a SPAD-502 chlorophyll meter on the flag leaf (mean of 10 readings per plot). CTD was recorded with a handheld infrared thermometer at solar noon on clear days. Proline was quantified by the acid-ninhydrin method [12]. GFR was calculated as the ratio of final grain weight to the duration from anthesis to physiological maturity. A composite heat tolerance index (HTI) was computed as the standardized sum of MSI, CTD, and GFR. Data were analyzed with ANOVA and Pearson correlation (STAR v.2.0.1). Stepwise regression identified the best trait combination for yield prediction.

Crop Growth Stage Documentation

Phenological stages were recorded on the Zadoks decimal scale [13]. Flag leaf emergence (Z37–39) occurred between 58 and 64 DAS, anthesis (Z60–65) between 68 and 76 DAS, and physiological maturity (Z92) between 98 and 112 DAS depending on genotype. The grain filling window (anthesis to maturity) coincided with the peak heat period (late February to mid-March), ensuring that genotypic differences in heat response were expressed under natural field stress.

Results

Table 1: Physiological parameters of wheat genotypes at 15 days post-anthesis under terminal heat stress (pooled means)

Genotype	MSI (%)	CCI	CTD (°C)	Proline (µmol/g)	GFR (mg/d)	TGW (g)	Yield (t/ha)
HD-3226	71.3	42.8	6.2	18.4	1.83	38.7	3.42
PBW-752	68.7	40.1	5.8	17.1	1.71	36.4	3.18
WH-1270	64.2	37.6	5.1	15.8	1.58	33.9	2.87
DBW-187	72.8	44.3	6.7	19.2	1.91	40.1	3.61
RAJ-4238	59.4	34.2	4.3	13.6	1.42	31.2	2.48
K-1317	66.1	38.9	5.4	16.3	1.64	35.1	3.04
NW-5054	61.8	35.7	4.8	14.7	1.49	32.6	2.69
HUW-838	57.3	32.8	3.9	12.4	1.34	29.8	2.31
CD (p=0.05)	3.6	2.4	0.7	1.8	0.12	2.1	0.22

Genotype DBW-187 recorded the highest values for MSI (72.8%), CCI (44.3 SPAD), CTD (6.7 °C), proline (19.2 µmol g^{-1}), GFR (1.91 mg day^{-1}), and grain yield (3.61 t ha^{-1}), followed closely by HD-3226 (Table 1). HUW-838 was the most susceptible, with the lowest scores across all parameters and a yield of 2.31 t ha^{-1}. Differences among genotypes were significant ($p < 0.05$) for every trait measured.

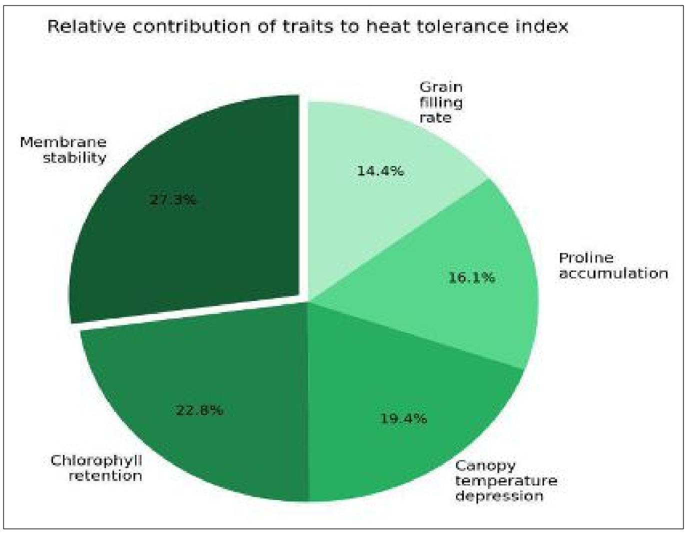

Fig 1: Relative contribution of physiological traits to the composite heat tolerance index based on stepwise regression weights (pooled data)

Stepwise regression identified MSI as the strongest single predictor of grain yield ($r^2 = 0.79$), followed by CTD and GFR (Figure 1). The three-trait composite index (MSI + CTD + GFR) explained 83.7% of yield variability under terminal heat stress. Proline and CCI added only marginal improvement when included as fourth and fifth variables.

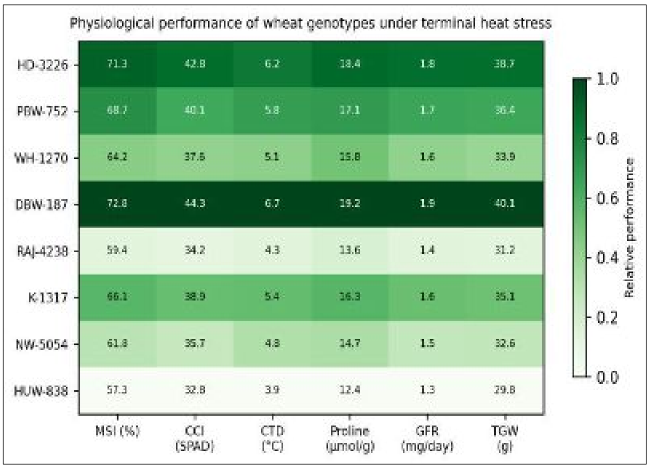

Fig 2: Heatmap showing performance of eight wheat genotypes across six physiological parameters under terminal heat stress. Darker shading indicates higher relative performance

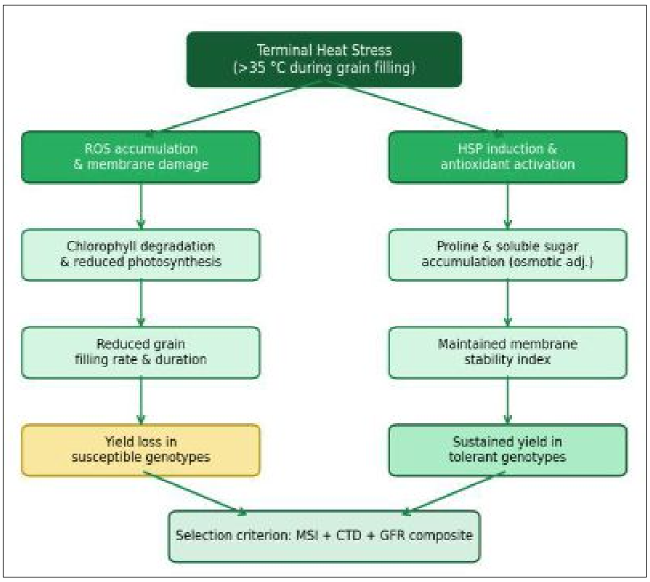

Fig 3: Conceptual pathway showing heat stress signaling, physiological responses, and their linkage to yield outcomes in tolerant versus susceptible wheat genotypes

Comprehensive Interpretation

The heatmap (Figure 2) clearly separates the tolerant group (DBW-187, HD-3226, PBW-752) from the susceptible group (HUW-838, RAJ-4238). The pathway diagram (Figure 3) outlines how heat triggers both damage and defense cascades, with tolerant genotypes maintaining membrane integrity and sustaining grain fill while susceptible ones lose yield.

Discussion

The strong correlation between MSI and grain yield ($r = 0.89$) agrees with reports from the Indo-Gangetic plains where membrane thermostability was the most consistent predictor of heat tolerance in wheat [6,14]. MSI reflects cellular membrane integrity, which directly controls ion homeostasis and enzyme function during heat episodes. The finding that CTD ranked second aligns with the physiological logic that genotypes capable of maintaining transpirational cooling can delay leaf senescence and extend the photosynthetically active period [5].

GFR emerged as the third contributor to the composite index, which makes sense because grain filling is the yield-forming process most sensitive to high temperature [3]. Together, MSI, CTD, and GFR captured 83.7% of yield variation—a level of predictive power that exceeds the 60–70% reported for single-trait models in earlier wheat screening trials [9,10]. This three-trait index could serve as a practical field-level tool, since all three measurements are non-destructive and can be completed within a few hours per genotype.

Proline accumulation was positively correlated with heat tolerance but added little predictive value beyond the three-trait index. This may be because proline serves more as a general stress marker than a direct yield determinant [7]. The relatively low contribution of CCI was unexpected but could reflect compensatory photosynthetic adjustments in some genotypes that maintained yield despite moderate chlorophyll loss. Future work should validate this index across multiple locations and sowing dates.

Conclusion

This research identified DBW-187 and HD-3226 as the most heat-tolerant genotypes among eight wheat lines evaluated under late-sown terminal heat stress at Rajshahi, Bangladesh. Membrane stability index showed the strongest association with grain yield and appears to be the single best physiological screening trait. A composite index combining MSI, CTD, and GFR explained over 83% of yield variation under stress and offers a rapid, non-destructive screening approach for breeding programs. Proline and chlorophyll content, while informative, didn't add meaningful predictive power beyond the three-trait model. These findings can be applied directly in wheat improvement programs targeting late-sown environments across the Indo-Gangetic region.

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Contributions Not Qualifying for Authorship

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