



Warmer nights predominantly alter yield and biomass in wheat experiencing heat waves at the terminal growth stage

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Received: 15 October 2023 / Revised: 13 January 2024 / Accepted: 8 February 2024 / Published online: 6 March 2024

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Abstract

Heat waves at the regional level could be devastating if they coincide with the sensitive growth stage of the crop. The sensitivity of wheat (*Triticum aestivum* L.) to heat stress is a major constraint limiting wheat production. Nevertheless, there are limited field studies where the impact of heat waves has been systematically studied and quantified. We phenotyped a mini panel of thirty diverse wheat genotypes under optimum and low planting densities. Staggered sowing was done to expose the late-sown genotypes to a higher temperature at the terminal growth stage. Heat wave occurred during March–April, 2022, resulting in late sown genotypes being exposed to a staggering 6.6 °C/4 °C higher day/night temperature during flowering and early grain filling stage, as compared to normal sown genotypes. Heat stress caused significant loss in biomass (34.46%), grains spike⁻¹ (22.34%), test weight (15.52%), and grain yield (28.67%) in late-sown genotypes as compared to normal-sown genotypes. Conversely, genotypes grown under low planting density showed substantial variations in growth parameters including plant height, tillering, thicker leaves, and canopy cover. Interestingly, genotypes with denser canopy and thicker leaves could avoid high day temperature-induced losses by maintaining lower canopy and spike temperatures, which eventually resulted in higher grains spike⁻¹. However, the impact of higher night temperature on biomass and seed weight was not affected by denser canopy and lower spike temperature. Hence, yield loss was majorly confined to high night temperature. The study suggests that higher night temperature could be a major determinant of yield under naturally occurring heat waves.

Keywords High day temperature · High night temperature · Heat waves · Phenotypic plasticity · Yield · Wheat

Introduction

The mean global temperature is increasing at a rapid pace due to the release of greenhouse gases, majorly from anthropogenic practices (Masson-Delmotte et al. 2022). According to the IPCC special report on global warming, the global temperature may rise beyond 1.5 °C above the pre-industrial level by the year 2040 (Masson-Delmotte et al. 2022).

Communicated by M. Labudda.

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Besides the rise in the mean temperature, heat waves at the regional level have become more prevalent and intense during the past decades. For example, the average number of heat waves and average duration of heat wave season recorded across the US in the 2020s were > 6 and > 70 days, respectively (NOAA 2022). An intense heat wave during mid-to-late April 2022 brought temperatures 4.5 to 8 °C above normal particularly in Northern and Central parts of India (<https://earthobservatory.nasa.gov>). The sudden rise in temperature during the heat wave could be devastating for crop plants particularly when it coincides with critical growth stages such as flowering and grain filling (Templ and Calanca 2020). Heat stress is well documented to impact spikelet fertility, seed set, grain filling duration, and sink strength, which ultimately leads to yield penalty (Jagadish et al. 2007, 2010; Bahuguna et al. 2015, 2017). Interestingly, a differential impact of high day temperature (HDT) and high night temperature (HNT) has been documented on plant growth and development where HDT mainly impacts pollen development, photosynthetic machinery, reactive oxygen species generation, and membrane damage (Djanaguiraman et al. 2020). Moreover, spikelet fertility and seed set are considered the key yield-determining traits affected by HDT (Jagadish et al. 2007; Bahuguna et al. 2015). On the contrary, reduced biomass and thousand-grain weight have been well documented under HNT in rice (Bahuguna et al. 2017; Shi et al. 2018), wheat (Impa et al. 2019), and soybean (Yang et al. 2023a, b), which was attributed to the augmented respiratory carbon losses and reduced activity of sink enzymes due to HNT (Bahuguna et al. 2017, 2022; Impa et al. 2019). The ability of plants to alter their phenotype in response to the changing environmental conditions or availability of resources such as light, space, and nutrients is termed as ‘phenotypic plasticity’ (Kumagai et al. 2015; Arnold et al. 2019; Bahuguna et al. 2022). Phenotypic plasticity could be helpful in acclimating to the changing environment. Interestingly, it has been demonstrated that efficient utilization of resources such as light, space, CO₂, and nutrients may provide extra benefits to resource-responsive plants under optimum and stress conditions (Shimono et al. 2014; Kumagai et al. 2015; Bahuguna et al. 2022). Nevertheless, a positive interaction between phenotypic plasticity and the acclimation potential of a genotype under stress needs further investigation.

Wheat is the second most important cereal crop, cultivated in more than 218 million ha of land, globally (Giraldo et al. 2019), and the total consumption recorded was around 791 million metric tons in 2022–23 (Shahbandeh 2023). Wheat is highly susceptible to heat stress particularly during flowering and early grain-filling stages (Farooq et al. 2011). Heat stress exposure during the anthesis and grain filling stage has been reported to cause up to 29 and 44% grain yield loss, respectively, in wheat at individual plant

levels (Djanaguiraman et al. 2020). Temperature higher than 22 °C disrupts the process of grain filling in wheat (Farooq et al. 2011; Schittenhelm et al. 2020). With every 1 °C increase in the global mean temperature, the grain filling duration in wheat is reduced by 2.8 days (Streck 2005), consequently decreasing wheat production by 6% (Asseng et al. 2015; Djanaguiraman et al. 2020). Hence, the occurrence of heat waves particularly during the terminal phase of wheat growth could be detrimental to wheat yield and grain quality (Zampieri et al. 2017).

Although a plethora of research studies are available emphasizing the impacts and mitigation strategies of heat stress on plants, the primary drawback of these studies is that almost all of these have been conducted in pots under controlled conditions and facilities such as growth chambers and glasshouses (Schrader et al. 2004; Jagadish et al. 2010; Bheemanahalli et al. 2019; Dusenge et al. 2020; Mukhtar et al. 2020; Qu et al. 2021; Jha et al. 2022), field-based tents (Bergkamp et al. 2018; Shi et al. 2013, 2023), and heaters (Ruiz-Vera et al. 2013, 2015). Facts and statistics acquired from such experiments help boost knowledge of the plant responses to stress conditions but it does not effectively relate to the realistic field conditions (Jagadish 2020). This study gave us the opportunity to evaluate the impact of a natural heat wave on wheat yield components. The heat wave resulted in a substantial increase in both HDT and HNT at the flowering and grain-filling stages. Therefore, our major objectives were to explore (i) the differential impact of natural heat wave on key traits associated with HDT and HNT, and (ii) the interaction of phenotypic plasticity with the acclimation potential of wheat under HDT and HNT, using a diverse panel of 30 wheat genotypes.

Material and methods

Experimental site and materials

The present study was conducted at the Crop Research Farm, Dr Rajendra Prasad Central Agricultural University (RPCAU), Pusa, Bihar (India), located at 25.98° N latitude and 85.67° E longitude and altitude of 52.0 m above the mean sea level. The experimental field comes under a subtropical climatic zone with hot and humid summers, and it was uniform in terms of soil fertility, topography, and texture and was well-connected with irrigation channels. The soil of the trial area was alluvial majorly calcareous and of khadar type with medium-to-hard texture, while pH, EC, organic carbon, available N, P, and K were 8.03, 0.46 ds/m, 0.47%, 241, 12.18 and 135.62 kg/ha, respectively. A mini-panel of twenty-nine diverse wheat genotypes along with a check HD2967 (recommended for high yield under late sowing conditions) were selected for the study. Selected

genotypes were previously screened for their response under low planting density and showed better response to late sown conditions.

Experimental details

The field experiment was conducted in a 22.6 m × 30 m area. Vermicompost, 1.25 kg m⁻² and N-P-K (urea, 35 g m⁻²; diammonium phosphate, 21.7 g m⁻²; muriate of potash, 8 g m⁻²) were mixed with the upper layer of soil to give adequate nutrient supply to the crop. The experiment was carried out with three treatments; each treatment had 90 plots (in total 270 plots), and each plot had an area of 1.8 m² (3 m × 0.6 m). In each treatment block, 30 genotypes (details of genotypes used in the study are provided in Supplementary Table S1) were accommodated with three replicates in a randomized complete block design (RCBD). The thirty wheat genotypes were sown on 26th November 2021 (normal date of sowing) and 15th December 2021 (late sowing). Staggered sowing of the genotypes was done under varying planting densities viz. optimum (line spacing of 20 cm) and low density (line spacing of 40 cm). The treatments are described as (i) control (C), normal date of sowing + optimum planting density, (ii) late sowing + optimum planting density (HT), and (iii) late sowing + low planting density (LD + HT). A general response observed under LD was higher growth due to more space, nutrients and light per unit area. We hypothesize that better growth and canopy cover under LD can help in sustaining HT. Hence, the comparison of the treatments was kept between HT and LD + HT.

Observations

Canopy and spike temperature

Canopy temperature (CT) was measured with an infra-red sensor-based thermometer (Apogee, USA, Model no: MI-210). Measurements were recorded by placing the sensor approximately at an angle of 45° from the horizontal plane near the canopy (Bahuguna et al. 2015). While spike temperature was recorded with the same instrument by placing the sensor directly on the surface of an individual spike. All the readings were taken during the flowering stage only on clear sunny days between 1130 to 1430 h when the day temperature was relatively stable without major fluctuation. The canopy and spike temperature readings were recorded in degree Celsius.

Specific leaf weight

Specific leaf weight was measured as a surrogate measurement for leaf thickness by calculating leaf dry weight per

unit area for each genotype across the treatments. Three flag leaves were taken from each treatment and cut at a fixed 5 cm length from the middle, and the width was measured. Length and width were used to calculate the area in cm². Thereafter, leaf pieces were kept in an oven (iGENE LAB-SERVE, India) at 70 °C for 72 h. The dry weight of the samples was recorded in mg after the complete removal of moisture. The leaf thickness was calculated using the formula below, and the final values were recorded in mg/cm².

$$\text{Specific leaf weight} = \frac{\text{Dry weight (mg)}}{\text{Leaf area (cm}^2\text{)}}$$

Greenness index (SPAD value)

The Greenness index of the plants was measured in SPAD values by SPAD-502 chlorophyll meter (Konica Monica Sensing Inc., Tokyo, Japan). Observations were recorded on one side of the midrib of the flag leaf of the plants in three replicates for each genotype for each treatment between 0900 to 1130 h to get an average value for a single observation (Bahuguna et al. 2022).

Relative water content (RWC)

Fresh flag leaf samples were collected from the field in small polythene zip bags from each genotype from each treatment in three replicates. The leaf samples were brought to the laboratory and immediately weighed with the help of an electronic digital weighing balance (iGENE Labserve, India) to record fresh weight. Once weighed, leaf samples were cut into 3–4 pieces, placed in petri plates filled with ¾th water and left undisturbed for four hours. After four hours, the leaf samples were removed from the water, gently wiped with tissue paper, and weighed again to record the turgid weight of the samples. Thereafter, the samples were placed into the oven (iGENE Labserve, India) for 72 h at 70 °C. After the complete drying of leaf samples, the dry weight was recorded. RWC was calculated using the following formula and expressed in percentage.

$$\text{RWC} = \frac{\text{Fresh weight} - \text{Dry Weight}}{\text{Turgid Weight} - \text{Dry Weight}} \times 100$$

Green seeker

Green seeker, a handheld Normalized Difference Vegetation Index (NDVI) crop sensor (Trimble, California) was used to measure the crop vigour and canopy cover (Bagherpour and Monavar 2017). Measurements were recorded by moving the instrument at a horizontal plane at 50–60 cm over the canopy. The sensor displayed the measured value in terms

of an NDVI (Normalized Difference Vegetation Index) reading (ranging from 0.00 to 0.99) on its LCD display screen. For observation, a middle row of the individual plot was selected, and the sensor was moved from one side to another, continuously pressing the trigger. As the trigger was relaxed, the average value for the entire row was displayed on the sensor display.

Yield and yield components

At physiological maturity, five representative plants were harvested from each replicate for each genotype across the treatments to analyse the yield components. Plant height was measured manually by a metric scale from the root-shoot junction to the tip of a spike of the main tiller and expressed in cm, while the main spike length was also recorded with the help of a metric scale from the base of the rachis to the top of the glume of the tip spikelet and expressed in cm. The total number of grains in each spike was counted manually and expressed as grains per spike. Moreover, spike weight and total biomass of plants were recorded using an electronic weighing balance (iGENE, Labserve, India). Test weight (thousand-grain weight) was also measured by counting seeds manually and weighing using an electronic digital weighing balance (iGENE Labserve, India), and expressed in grams. The harvested plants from each plot for each genotype across the treatments were threshed to measure grain yield per plot for each genotype across the treatments.

Statistical analysis

Data retrieved across the treatments were analyzed using two-way analysis of variance (ANOVA) with treatments and genotypes as major factors with three replicated trait values for each treatment using GENSTAT 15Ed (Rothamsted Experimental Station). Correlation analysis was done to obtain the significant relationship between the fourteen traits targeted using R software (version 4.2.2). Significant genetic response across the treatments was given with Fisher's LSD value with P value indicating the level of significance, where $P < 0.001$, $P < 0.01$, $P < 0.05$ were denoted by ***, **, and *, respectively.

Results

Heatwave exposed late-sown plants to HDT and HNT

Day (T_{\max})/night (T_{\min}) temperature and relative humidity (RH) were recorded during the entire cropping season for timely (26th November, 2021 to 4th April, 2022) and late sown (15th December, 2021 to 16th April, 2022) conditions. Average T_{\max} , T_{\min} , and RH during the entire

timely sown cropping condition were 25.1 °C (SD ± 5.39), 12.6 °C (SD ± 4.22), and 77.7% (SD ± 6.37), respectively, whereas average T_{\max} , T_{\min} , and RH during the entire late sown cropping condition were 25.9 °C (SD ± 6.41), 13.6 °C (SD ± 5.12), and 76.8% (SD ± 7.11), respectively. During flowering, the genotypes grown under late sowing condition faced a higher mean T_{\max} of 27.8 °C (SD ± 0.75) as compared to the mean T_{\max} under timely shown [mean T_{\max} of 21.2 °C (SD ± 2.55)] resulting in 6.6 °C (SD ± 0.46) higher T_{\max} compared to the timely sown condition. Conversely, the average night temperature (T_{\min}) was 2.7 °C (SD ± 0.51) higher for late sown genotypes as compared to the timely sown genotypes at the flowering stage (Fig. 1). Similarly, the late sown genotypes experienced higher average T_{\max} (33.0 °C, SD ± 2.08) and average T_{\min} (18.0 °C, SD ± 2.81) during the early grain filling stage resulting in 4.5 °C (SD ± 0.50) and 4 °C (SD ± 0.55) higher day and night temperature as compared to timely sown condition (Fig. 1). In addition, the active grain filling period was reduced by 7 days under late sown condition. The total rainfall recorded throughout the cropping season was 41.9 mm (Fig. 1).

Impact of HT on physiological traits under varying planting density

Significant ($P < 0.001$) genotype (G), treatment (T), and genotypes and treatment ($G \times T$) interaction effects were observed for all the physiological traits targeted (Table 1, Supplemental Table S2–S3). Canopy and spike temperature were increased by 3.7–6.9 °C and 4.6–6.8 °C, respectively, under HT condition as compared to control, whereas under LD + HT condition, the temperature was increased by 2.9–6.6 °C and 2.3–6.0 °C, at canopy and tissue level, respectively, compared to control (Fig. 2A, B; Table 1). A decrease in canopy cover (CC) (6.9–33.3%), SPAD value (0.2–45.9%), and relative water content (RWC) (0.2–40.5%) was observed under HT condition as compared to control. However, the impact of HT on CC, SPAD value, and RWC was lower under LD + HT with a percent decline of 2.7–29.8%, 0.6–12.2%, and 1.3–30.6%, respectively, as compared to control (Fig. 2C–E; Table 1). Furthermore, the SPAD value was higher (0.5–83.6%) under LD + HT condition than HT across the genotypes. Conversely, the specific leaf weight (SLW) was decreased by 0.3–35.6% and 2.3–22.4% under HT and LD + HT condition, respectively (Fig. 2F; Table 1), hence, a higher SLW (2.9–59.1%) was recorded under LD + HT as compared to HT.

Comparative response of growth and yield-related traits under HT

A significant genotype and treatment interaction ($G \times T$) effect ($P < 0.001$) was observed for test weight and grain

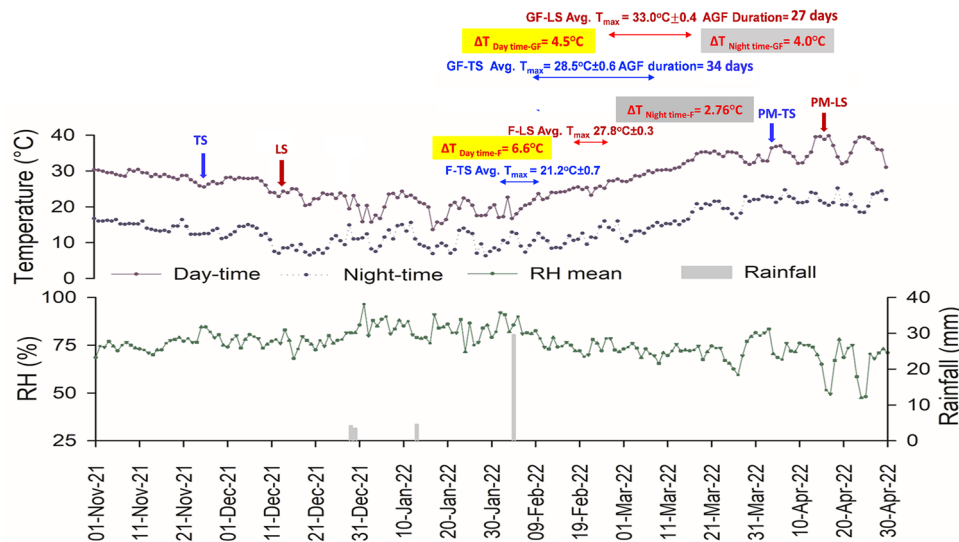


Fig. 1 Meteorological observations were recorded for the entire crop cycle (26th November 2021 to 16th April 2022). Graphs represent day/night temperature, relative humidity, and rainfall data. Blue and red horizontal arrows depict the calculated average day temperature during flowering and critical grain filling periods under timely and late sowing conditions, respectively. Vertical downside blue and red coloured arrows indicate the date of sowing and physiological maturity of timely and late sowing conditions, respectively. [T_{max} maximum temperature, RH relative humidity, TS timely sowing date, LS late sowing date, $PM-TS$ and $PM-LS$ date of physiological maturity of the timely and late sown crop, AGF active grain filling, $F-TS$ the

flowering period of timely sowing condition, $F-LS$ the flowering period of late sowing condition, $GF-TS$ grain filling period of timely sowing condition, $GF-LS$ grain filling period of late sowing condition, $\Delta T_{Day\ time-F}$ difference in mean day temperature of timely and late sown condition during flowering, $\Delta T_{Night\ time-F}$ difference in mean night temperature of timely and late sown condition during flowering, $\Delta T_{Day\ time-GF}$ difference in mean day temperature of timely and late sown condition during grain filling stage, $\Delta T_{Night\ time-GF}$ difference in mean night temperature of timely and late sown conditions during grain filling stage]

yield plot⁻¹ (Table 1), whereas a significant treatment effect ($P < 0.05$ to < 0.001) was recorded for all the growth and yield related traits (Table 1; Supplemental Table S4–S6). Grains spike⁻¹ (GPS), spike length (SL), and spike weight (SW) were decreased under HT by 5.5–27.0%, 0.6–21.8%, and 11.5–58.4%, respectively, as compared to control (Table 1; Fig. 3A–C). On the other hand, GPS, SL, and SW were reduced by 0.8–38.3%, 2.0–17.8%, and 15.8–62.5%, respectively under LD+HT condition with respect to control (Table 1; Fig. 3A–C). Interestingly, GPS and SL were increased by 5.2–45.6% and 1.6–23.3%, respectively under LD+HT condition as compared to HT (Table 1; Fig. 3A, B). Moreover, test weight (TW), total biomass plant⁻¹ (TB), and grain yield plot⁻¹ (GY) were decreased by 6.2–36.4%, 3.7–55.2%, and 1.6–58.6%, respectively under HT condition. (Fig. 3D–F; Table 1).

Association of yield component traits with spike and canopy temperature

A strong positive correlation ($r = 0.98$) was observed among CT and ST. CT showed a strong negative correlation with SW, TB, and GPS ($r = -0.79$, -0.79 , and -0.73 , respectively). Moreover, ST exhibited a negative correlation with

SW, TB, and GPS ($r = -0.78$, -0.77 , and -0.73 , respectively). In addition, GY was found negatively correlated with ST and CT ($r = -0.56$ and -0.60 , respectively). CC was negatively correlated with ST ($r = -0.81$) and CT ($r = -0.81$) (Fig. 4).

Discussion

An elevated level of emission of greenhouse gases due to anthropogenic practices as well as natural calamities led to an increase in global mean temperature. According to NASA Goddard Institute for Space Studies (2023), global mean temperature has increased by 1.1 °C since 1980. Furthermore, heat waves have become more prevalent and intense, and reports have explained that environmental co-variables particularly, high relative humidity intensify the impact of heat waves. In the year 2022, India recorded the warmest February with the maximum temperature rising up to 29.5 °C across the country (<https://www.india.today.in/>). Moreover, intense heat waves that occurred from 11th March to 18th May 2022 across India (Supplementary Figure S1) severely affected wheat yield in most of the northern India regions causing a 10–15% decline in

Table 1 Descriptive statistics and the significance (Fischer's test summary) for genotype (G), treatment (T), and their interactions (G × T) for different growth, yield, and physiological traits in a set of 29 diverse wheat genotypes along with check, HD2967 grown under C, HT, and LD+HT condition

Traits	C				HT				LD+HT				% Change				P Value (Fischer's test)			
	Mean ± SEM		Minimum	Maximum	Mean ± SEM		Minimum	Maximum	Mean ± SEM		Minimum	Maximum	LD+HT		LD+HT		G × T			
													HT	HT	G	T	G × T			
Growth and yield traits																				
Plant height (cm)	94.35 ± 0.80	82.0	100.1	89.70 ± 0.86	81.2	98.3	87.63 ± 0.58	82.6	93.5	-4.93	-7.12	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.206		
No of tillers plant ⁻¹	2.72 ± 0.05	2.0	3.3	2.58 ± 0.05	2.0	3.0	2.45 ± 0.05	2.0	3.1	-4.99	-9.93	0.913	0.024	0.998				0.998		
Spike length (cm)	9.65 ± 0.10	8.7	10.8	9.10 ± 0.14	7.9	10.7	9.28 ± 0.11	8.0	10.5	-5.69	-3.81	0.029	0.002	0.734				0.734		
Spike weight (g)	5.80 ± 0.17	4.2	7.6	3.68 ± 0.11	2.5	4.9	3.73 ± 0.11	2.7	4.9	-36.59	-35.67	0.18	< 0.001	0.51				0.51		
Grains spike ⁻¹	48.69 ± 0.86	38.3	57.1	37.81 ± 0.76	28.7	45.8	40.79 ± 0.68	33.7	49.0	-22.34	-16.22	0.226	< 0.001	0.107				0.107		
Test weight (g)	43.72 ± 0.71	36.6	50.5	36.93 ± 0.87	27.6	45.5	36.78 ± 0.86	27.3	44.2	-15.52	-15.87	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Total biomass plant ⁻¹ (g)	9.87 ± 0.28	7.0	13.1	6.47 ± 0.21	4.2	8.6	6.51 ± 0.17	5.0	8.3	-34.46	-33.99	0.182	< 0.001	0.434				0.434		
Grain yield plot ⁻¹ (g)	564.40 ± 18.67	383.0	848.0	406.30 ± 17.48	222.0	584.0	333.97 ± 16.57	178.0	541.0	-28.01	-40.83	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Physiological traits																				
Canopy temperature (°C)	21.07 ± 0.14	19.3	22.2	26.50 ± 0.10	25.4	28.0	25.21 ± 0.29	24.3	26.7	25.80	19.70	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Spike temperature (°C)	22.35 ± 0.14	20.6	23.7	27.86 ± 0.07	27.2	28.7	26.00 ± 0.12	24.9	27.4	24.64	16.33	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Canopy cover	0.77 ± 0.00	0.7	0.8	0.65 ± 0.01	0.50	0.71	0.67 ± 0.01	0.6	0.7	-15.21	-13.70	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
SPAD Value	50.20 ± 0.49	44.8	56.0	45.47 ± 0.86	27.4	52.5	48.83 ± 0.53	42.9	54.5	-9.43	-2.73	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Relative water content (%)	76.59 ± 1.11	64.9	87.7	69.54 ± 1.18	44.2	81.7	71.31 ± 1.36	55.8	89.3	-9.21	-6.90	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		
Specific leaf weight (mg cm ⁻²)	5.34 ± 0.13	3.93	6.9	4.60 ± 0.08	3.81	5.34	5.46 ± 0.09	4.7	6.4	-13.77	2.23	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		

The level of significance for genotype (G), treatment (T), and their interaction (G × T) effects was given from analysis of variance (ANOVA) with Fischer's least significant difference (LSD) value ($P < 0.05$). (Significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$)

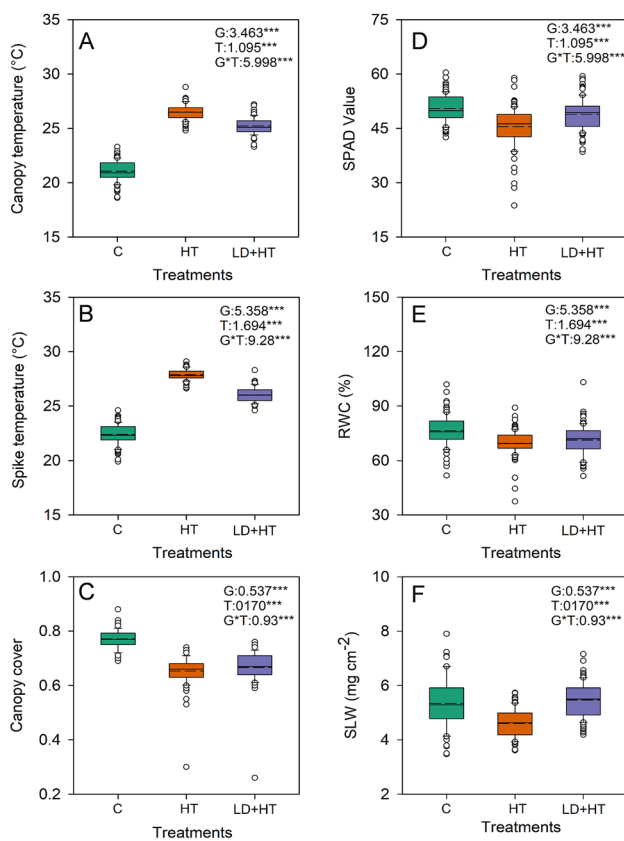


Fig. 2 Box plot depicts variation in physiological traits viz, canopy temperature (A), spike temperature (B), canopy cover (C), SPAD value (D), RWC (E), and SLW (F) in a diverse set of thirty wheat genotypes at flowering stage under control (C), heat (HT), and low planting density + heat stress (LD+HT) condition. Inside the box-plot, the solid and dotted lines represent the median and mean values of the population under respective treatments. Outliers are shown as open circles. The arrows represent trait plasticity under low-density condition under heat stress. The level of significance for genotype, treatment, and genotype × treatment effects from ANOVA are given with Fisher's LSD value ($P < 0.05$) (significance *** < 0.001)

overall wheat production in the 2022/23 marketing year. This study was conducted during the rabi season (from 26th November 2021 to 16th April 2022) using a mini-core set of diverse wheat genotypes selected for their high yield potential under late sown conditions. A staggered planting was done to expose late-sown genotypes to terminal heat stress. Coincidentally, besides the usually higher temperature expected than the normal sown window, late-sown genotypes encountered the impact of an unprecedented heat wave during the flowering and active grain-filling stage (extended from 26th February to 1st April 2022; Fig. 1). The key findings of our study are discussed below.

Heat stress impact on canopy temperature, canopy cover, and leaf thickness

Heat stress tolerance is a complex trait governed by genotype by treatment interaction effect. Moreover, the interaction of heat with environmental co-variables such as solar radiation, humidity, and vapour pressure deficit (VPD) determines the impact of heat stress, which requires multiple levels of regulations at the cellular and tissue levels. Thus, the induction of heat stress tolerance through conventional breeding approaches is challenging. Nevertheless, environment-specific trait-based phenotyping has become one of the reliable approaches to introducing heat stress tolerance in crop plants (Djalovic et al. 2023). For instance, traits associated with canopy microclimate are important for heat tolerant studies. A comprehensive understanding of the canopy microclimate, modulated by canopy aerodynamics and stomatal conductance is essential to manage crops under heat stress. Canopy temperature is determined by the compound interaction of air temperature and soil moisture availability (Luan and Vico 2021; Djalovic et al. 2023). In our study, CT was increased significantly across the genotypes by an average of 25.8% under HT as compared to the control (Fig. 2A; Table 1). It has been reported that the increased rate of evaporation from plant and soil surfaces due to increased atmospheric temperature could subsequently lead to reduced soil moisture that ultimately limits the rate of transpirational cooling, resulting in higher CT (Yang et al. 2023a, b). Singh et al. (2022) reported an average of 2.8 °C higher CT due to terminal heat stress during the reproductive and early grain-filling stage of a diverse set of thirty wheat genotypes. It is well documented that organ (leaf and spike) temperature changes in response to changes in canopy temperature (Ayeneh et al. 2002). We observed a significant ($P < 0.001$) positive correlation ($r = 0.98$) between canopy and spike temperature (Fig. 4). Interestingly, canopy cover (CC) that represents the fraction of soil surface covered by green vegetation (Tenreiro et al. 2021) could influence canopy temperature, and be considered a promising avoidance trait under high day temperature stress (Burgess et al. 2017). We observed a significant reduction (15.2%) in canopy cover under HT (Fig. 3C; Table 1), which can be attributed to enhanced senescence rate in lower leaves resulting in a decrease in foliar density. However, a significant genetic variation was observed for canopy cover across the genotypes (Fig. 2C; Table 1). On the other hand, relative water content (RWC), is an important trait determining the water status of plants (Xie et al. 2020). RWC is sensitive to heat stress (Qaseem et al. 2019). We have observed a significant reduction (0.1–40.5%) in RWC under HT across the genotypes (Fig. 2E; Table 1). Heat stress could increase leaf temperature, which is reported to cause desiccation and drying of cells leading to a lower number of fully turgid cells (Lugojan and Ciulca 2011), which

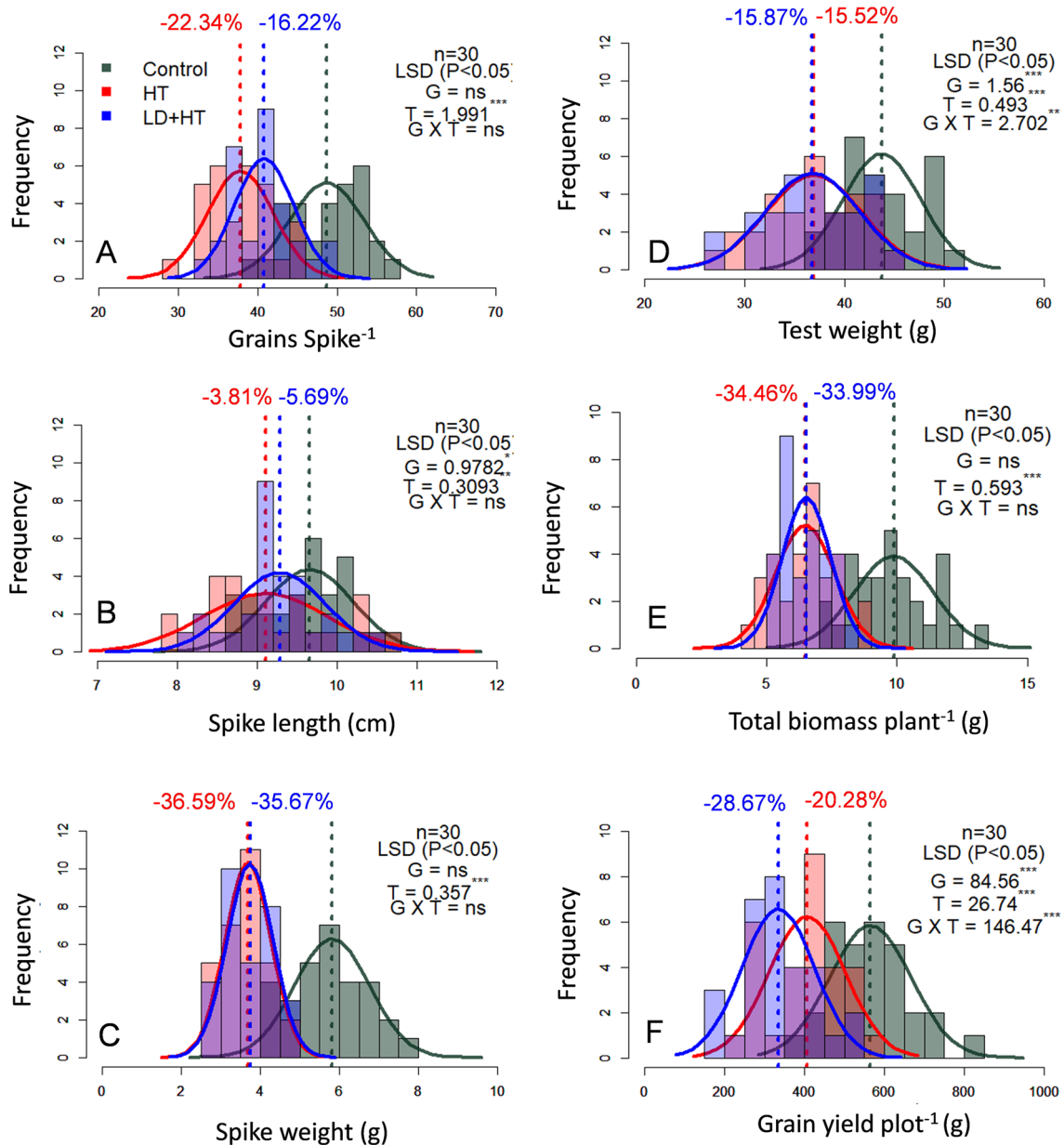


Fig. 3 Overlying histograms with normal distribution curves showing the phenotypic distribution of yield-related traits viz. grain spike⁻¹ (A), spike length (B), spike weight (C), test weight (D), total biomass plant⁻¹ (E), and grain yield plot⁻¹ (F) of thirty diverse wheat genotypes under control (C), heat (HT), and low planting density+heat stress (LD+HT) conditions. The vertical dotted lines depict the pop-

ulation mean under respective treatments. The numerical indicates the relative change in trait value with respect to control. The level of significance for genotype (G), treatment (T), and their interaction (G×T) effects was given from analysis of variance (ANOVA) with Fischer's least significant difference (LSD) value ($P < 0.05$) (Significance: $***P < 0.001$, $**P < 0.01$, $*P < 0.05$, and ns: non-significant)

could alter leaf water status and RWC. On the other hand, specific leaf weight was decreased by 0.3–35.5% under HT across the genotypes (Fig. 2F; Table 1). Zhang et al. (2009) reported that the mesophyll cells in the leaves of the heat-sensitive wheat genotypes showed a tendency to reduce cell size, and the cells were loosely arranged which could lead to a reduction in SLW under HT. Carrera et al. (2021) also reported a decrease in leaf thickness under heat stress

conditions in soybean. Interestingly, we observed that a few genotypes for example 11th HPYT 425 showed an increase in SLW under HT (Supplementary Table S3). A higher thermal mass could help in reducing temperature-induced damage (Deva et al. 2020), for example, thicker leaves in the succulents help in thermal stability (Deva et al. 2020). However, further studies are warranted to explore the role of leaf thickness in heat stress avoidance particularly under

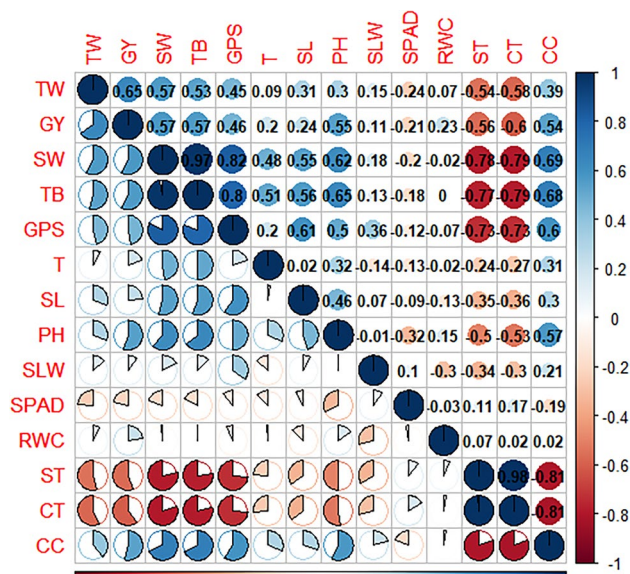


Fig. 4 Correlation matrix of physiological, growth, and yield related traits of the diverse set of thirty wheat genotypes across control, heat stress, and low density+heat stress condition. *TW* test weight, *GY* grain yield, *SW* spike weight, *TB* total biomass, *GPS* grain per spike, *T* number of tillers per plant, *SL* spike length, *PH* plant height, *SLW* specific leaf weight, *SF* spikelet fertility, *SPAD* soil plant analysis development value, *RWC* relative water content, *ST* spike temperature, *CT* canopy temperature, *CC* canopy cover

water-limited conditions. Heat stress showed a minor impact on SPAD value with a 9.43% reduction under HT across the genotypes as compared to the control (Fig. 2D; Table 1). It has been reported that desiccated and irregularly arranged mesophyll cells could lead to structural damage to chloroplasts, ultimately degrading leaf chlorophyll content under heat stress (Fu et al. 2022).

Heat stress reduced growth and yield-component traits

Anthesis is regarded as the most sensitive stage to heat stress and reproductive tissue viability is considered as a crucial factor under heat stress (Djanaguiraman et al. 2014; Jagadish 2020). The main physiological processes happening during anthesis are anther dehiscence, pollen perception by stigma, and pollen tube growth which eventually determines spikelet fertility (Prasad and Djanaguiraman 2014). In cereals, a reduction in spikelet fertility has been well documented after the imposition of heat stress during the flowering stage (Jagadish 2020). In our study, HT reduced spike length and grain spike⁻¹ by 3.8 and 22.3%, respectively (Fig. 3B, C; Table 1). SL reduction has been well documented when wheat plants were exposed to heat stress during the heading stage (Shenoda et al. 2021). Moreover, Djanaguiraman et al. (2020) observed up to 36% decline in grain spike⁻¹

when heat stress was imposed during anthesis in wheat. An increase in temperature in reproductive tissue could significantly decrease reproductive tissue biomass and increase spikelet abortion which ultimately results in a reduction in grains spike⁻¹. Interestingly, the relationships were confirmed from the results wherein GPS showed a strong negative correlation with ST ($R^2 = -0.73$) (Fig. 4).

Besides HDT, an increase in night temperature by 4 °C was recorded during the early grain filling stage under the late sowing condition (Fig. 1). HNT, particularly during the early grain-filling stage has been previously reported to limit the source-to-sink sugar translocation processes in rice and wheat (Bahuguna et al. 2017; Impa et al. 2019). Thus, HNT results in lower productivity particularly by limiting biomass and grain filling (Impa et al. 2021). In our study, significant reductions in spike weight, test weight, total biomass plant⁻¹, and grain yield plot⁻¹ were observed under HT (Fig. 3), and the traits are reported to be governed majorly by night temperature anomaly (Impa et al. 2020). Hein et al. 2020 experienced a reduction in grain weight and grain yield by 1.25 and 2.36%, respectively, for every 1 °C night temperature increase. Furthermore, HNT could alter the physical dimension of grains indicating limitations in assimilate supply due to altered functioning of key sugar metabolizing enzymes, i.e., sucrose synthase and invertases. In addition, carbon imbalance due to a higher rate of night respiration results in biomass and grain yield loss (Impa et al. 2019).

Phenotypic plasticity could help in HDT resilience

Low planting density can reduce competition among plants by providing more nutrients, space, and light per unit area (Ainsworth and Long 2005; Bahuguna et al. 2022). Consequently, better availability of space could help genotypes to grow more profusely, which eventually improved canopy cover under LD+HT conditions. Increased canopy cover could help in improving transpirational cooling which eventually led to a reduction in CT and ST under LD+HT (Fig. 2). The lowered temperature at tissue and canopy levels could also help in maintaining reproductive tissue viability, which was evident with significantly higher GPS and SL under LD+HT as compared to HT (Figs. 2, 3). In addition, higher SLW under LD+HT might have helped in better thermostability of the genotypes as compared to HT (Fig. 3). However, the direct role of leaf thickness in thermal stability and reproductive success would need further investigation. Besides avoidance, plants may show escape and augmented tissue-level tolerance under heat stress. For example, dryland cereals are adaptive to flower opening during cooler early morning or late evening hours to escape heat exposure (Jagadish 2020). Moreover, the completion of the life cycle before the onset of heat stress by shortening the growth phases is another mechanism reported in plants

to escape terminal heat stress (Jha et al. 2014). Conversely, the cellular level of tolerance strategies includes elevated levels of expression of heat-responsive genes, antioxidant enzymes, and heat shock protein (Asthir 2015; Bahuguna et al. 2015) which is relatively well characterized across crop plants. However, our study demonstrated that phenotypic traits such as canopy cover and spike temperature are reliable traits that can help in screening for heat avoidance traits in a larger set of genotypes.

Genotypes could avoid HDT but not HNT

This study demonstrated that HDT-induced losses in traits such as GPS and SL were compensated to a significant extent under LD + HT for the responsive genotypes, which showed better canopy cover and lower spike temperature (Figs. 2A–C, 4; Table 1; Supplementary Table S4, S5). Moreover, higher RWC and SLW could contribute to maintaining the lower temperature at the canopy level and tissue level (Fig. 2) and avoided HDT-induced losses. On the contrary, the effect of denser canopy cover, higher SLW, and cooler ST observed under LD + HT did not help in compensating losses in traits that are mostly affected by HNT such as test weight, and total biomass plant⁻¹ (Bahuguna et al. 2017, 2022; Fig. 2D–F). It has been well documented that, unlike HDT, there is no escape and avoidance strategy reported in rice that can contribute to HNT resilience (Bahuguna et al. 2017; Sadok and Jagadish 2020). Hence, additional benefits in terms of resources such as light, space, and nutrients under LD, which were evident in terms of denser canopy and growth could help in mitigating the impact of HDT on GPS, but could not compensate for the effect of HNT on grain weight and grain yield. Further studies are warranted to explore traits that may contribute to escape, avoidance and tissue-level tolerance. Recently it has been reported that lower dark respiration at the post-flowering phase, and temperature-resilient sink (developing caryopsis) enzymes, and enhanced responsiveness to CO₂ may compensate HNT-induced losses in rice (Bahuguna et al. 2017, 2022) and wheat (Impa et al. 2020; Narayanan et al. 2016a,b). However, no traits were reported to be associated with escape and avoidance under HNT (Fig. 5).

Conclusion

The late sown genotypes were exposed to heat wave resulting in high day and night temperature during the reproductive and early grain-filling stages. Observations showed that genotypes with higher phenotypic plasticity to low planting density could maintain higher CC, which eventually lowered canopy and tissue temperature. This could avoid HDT-led reduction in grains per spike. On

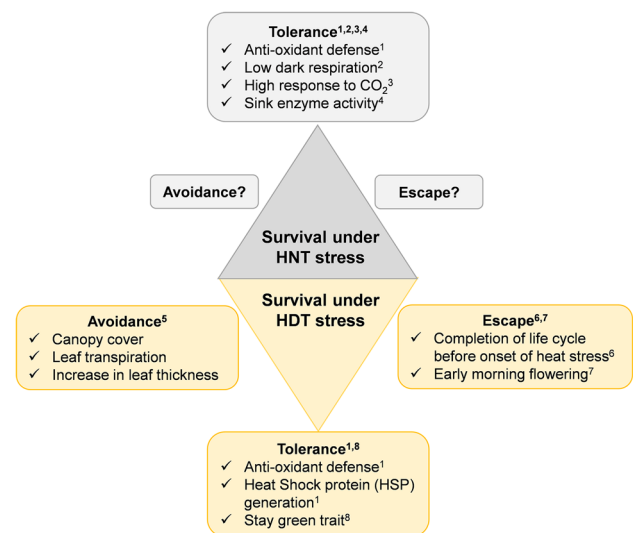


Fig. 5 Schematic diagram showing plant survival strategies under high day temperature (HDT) and high night temperature (HNT) stress. The escape, avoidance, and tolerance strategies are well documented in plants under HDT stress. Whereas, limited studies report traits contributing to HNT stress tolerance. Escape and avoidance traits are not well characterized under HNT [¹Asthir (2015); ²Bahuguna et al. (2017); ³Bahuguna et al. (2022); ⁴Chaturvedi et al. (2017); ⁵Leigh et al. (2012); ⁶Jha et al. (2014); ⁷Ishimaru et al. (2010); ⁸Abdelrahman et al. (2017)]

the contrary, genotypes showed significant reductions in HNT-influenced traits such as test weight and total biomass, which eventually contributed to lower grain yield. Therefore, the heat avoidance strategy effective for HDT was not beneficial for HNT. We conclude that the selection of traits for heat tolerance requires the inclusion of both the HDT and HNT scenarios as the occurrence of heat waves causes both the high day and night temperature increase. Furthermore, heat adaptive strategies such as heat escape and heat avoidance under HNT warrant further investigations (Fig. 5).

Author contribution statement Conceived and designed the experiments, R.N.B., S.K.S.; performed the experiments, G.P.P., S.K., B.P.M., data analysis and interpretation, S.K., G.P.P., B.P.M., drafted the manuscript, S.K., S.D., edited and finalized the manuscript, R.N.B., S.K.S.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11738-024-03670-8>.

Acknowledgements Department of Science and Technology, Government of India Research grants CRG/2020/001935 (2021–2024) to RNB is duly acknowledged.

Data availability All the data used for this experiment is given in the form of tables and figures after suitable statistical analyses.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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