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Md. Mehedi Hasan[1, 2], M A Baset Mia[1], Jalal Uddin Ahmed[1], M. Abdul Karim[3], A. K. M. Aminul Islam[4] and Mohammed Mohi-Ud-Din[1]

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WHEAT GENOTYPES SUSTAIN YIELD BY MAINTAINING BETTER CANOPY TEMPERATURE DEPRESSION, SPAD AND DRY MATTER PARTITIONING POTENTIAL UNDER TERMINAL HEAT STRESS CONDITION

Md. Mehedi Hasan[1, 2], M A Baset Mia[1], Jalal Uddin Ahmed[1], M. Abdul Karim[3], A. K. M. Aminul Islam[4] and Mohammed Mohi-Ud-Din[1]

[1] Department of Crop Botany, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur 1706, Bangladesh

[2] Department of Crop Botany & Tea Production Technology, Sylhet Agricultural University, Sylhet 3100, Bangladesh

[3] Department of Agronomy, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur 1706, Bangladesh

[4] Department of Genetics & Plant Breeding, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur 1706, Bangladesh

*Corresponding author(s)

Md. Mehedi Hasan, Email: mehedi.cbot@sau.ac.bd

M A Baset Mia, Email: miabaset@bsmrau.edu.bd

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ABSTRACT

Heat stress is one of the bottlenecks for global wheat production. The in-depth investigation of wheat genotypes based on canopy temperature depression, SPAD, and dry matter allocation attributes could assist in understanding the reasons for yield sensitivity under terminal heat stress condition. Four relatively heat-tolerant genotypes, namely AS-10636, BD-594, BD-674, and BARI Gom-33 (BG-33), and two heat-sensitive genotypes (BD-675 and Pavon-76), were grown under two temperature conditions, viz., “control” (optimum sowing on 30th November) and “heat stress” (late sowing on 30th December) to evaluate their yield performance as affected by varied temperatures. During the grain-filling period, late-sown heat-stressed wheat genotypes received about 4.7 ºC greater mean air temperature than the control conditions, and a 4% decrease in the grain yield was recorded for every 1 ºC rise in temperature. Heat stress significantly reduced the number of days required for heading and anthesis compared to the control. The upper exposed peduncle length increased under late-sown heat-stressed conditions, with a greater significant impact on the susceptible BD-675 genotype. Canopy temperature depression (CTD) was reduced to about 65% in susceptible genotypes and 40% in tolerant genotypes under heat stress, implying the tolerant genotypes could keep their leaves cooler than susceptible ones under high temperatures. The SPAD value was also severely decreased in the susceptible genotype Pavon-76 compared to the tolerant ones under heat stress. While dry matter distribution in the culm, flag leaf, husk, and grain decreased under heat stress conditions compared to the control, the tolerant genotypes maintained higher grain dry weight by prioritizing dry matter allocation to the grain, principally by reducing it in the culm. Our results concluded that genotypes that can tolerate terminal heat stress by maintaining better CTD, SPAD, and dry matter partitioning potential to grain, along with a relatively greater grain filling duration, can sustain a higher grain yield under heat stress conditions. Moreover, the proper dissection of underlying biochemical and molecular mechanisms associated with yield sustainability in tolerant genotypes is encouraged before adopting them for upcoming breeding programs.

1. INTRODUCTION

The wheat plant, *Triticum aestivum* L., is highly susceptible to high temperatures (Lal et al., 2022). The major wheat-producing regions have already shown signs of rising growing season temperatures (IPCC, 2014). It is estimated that every one-degree rise in temperature may reduce the wheat production by 6% (Akter & Islam, 2017). Heat stress adversely affects the vital biological processes and thus results in poor growth and development in plant (Fahad et al., 2017). Different phenological stages of wheat experience heat stress to variable degrees; however, because heat stress directly affects grain number and dry weight during the reproductive phase, it is more detrimental than during the vegetative phase (Djanaguiraman et al., 2020). Between 12 and 22 ^{o}C is the ideal temperature range for wheat anthesis and grain filling (Tomás et al., 2020). Due to pollen sterility, tissue dryness, decreased CO_2 absorption, and increased photorespiration, exposure to temperatures above optimum can drastically diminish grain output (Akter & Islam, 2017). Nonetheless, during floret production, temperatures exceeding 30 ^{o}C may result in total sterility (Farhad et al., 2023).

High temperatures speed up growth, but they also cause phenology to decrease by the early occurrence of flowering and maturity than usual, which is not offset by the faster growth rate (Gray & Brady, 2016). Another significant impact of heat stress is the reduction in photosynthesis brought on by reduced leaf area expansion, compromised photosynthetic machinery, early leaf senescence, and the corresponding decrease in wheat yield (Lal et al., 2022). In addition, heat stress also lowers photosynthesize capability in wheat due to metabolic restrictions and oxidative damage to chloroplasts, which also lowers grain yield and dry matter buildup (Farhad et al., 2023). Increased daily minimum temperature appears to have greater impact on wheat production as grain yield is more strongly negatively correlated with increasing minimum temperatures than maximum temperatures (Hatfield & Dold, 2018).

Phenotypic or morphological traits are the oldest and very important selection criteria for the breeding programs. Right trait selection and precise phenotypic data collection is very important for study the effect of any biotic or abiotic stress on plant as it clearly shows the response of plant to the stress (Mohanta et al., 2017). Among the potential traits, peduncle length is less explored but an important morphological trait. The upper exposed peduncle length has significant influence on plant morphology and inheritance of major yield contributing factors and hence important in late generation selection of cultivar selection (Farooq et al., 2018). Moreover, the peduncle length can be utilized in understanding the plant response and its adaptability to tolerate heat stress and maintain good yield (Paul & Duhan, 2021). Canopy temperature depression (CTD), the difference between air temperature and plant canopy temperature, is a potential physiological trait not only used for abiotic stress screening in plants but also adopted to identify stress-tolerant cultivars due to its correlation with yield (Sofi et al., 2020). The SPAD value measures chlorophyll content in plant leaves, assessing photosynthetic capacity and stress tolerance, providing a non-destructive and rapid method for plant health evaluation (Ge et al., 2019). In addition to helping to establish crop varieties that are more resilient to environmental stress conditions, the SPAD value can be used to identify plants that are more tolerant of abiotic stress causes (Shah et al., 2017).

To adapt new crop varieties to the elevated climate, we need to understand how crops respond to elevated temperatures and how tolerance to heat can be improved (Akter & Islam, 2017). Choosing and cultivating wheat genotypes with heat resistance can increase tolerance to heat. Secondary qualities such grain weight under heat stress, photosynthetic rate, and membrane stability may be used as markers for wheat pre- and breeding decisions (Khadka et al., 2020). To increase grain yield under heat stress, however, genotypes for grain size and filling rate must be chosen (Li et al., 2022; Yang et al., 2016). The assessment of dry matter distribution among culm, flag leaf, husk, and grain at different growth stages provides valuable insights into resource allocation under stress. Identifying genotypes that maintained better CTD, SPAD, and showed efficient stem remobilization under heat stress is crucial. These genotypes demonstrating superior stress tolerance and resilience might offer potential candidates for breeding programs or agronomic strategies to enhance wheat yield stability in heat-prone environments. To test this hypothesis, therefore, the present piece of research work was undertaken to assess the performance of wheat genotypes in two sowing times. Additionally, we evaluated the physiological and dry matter distribution pattern in wheat genotypes during the grain filling period in order to identify suitable genotypes prone to heat stress.

2. MATERIALS AND METHODS

2.1 Experimental Site

The experiment was conducted in the field laboratory of the Department of Crop Botany, Bangabandhu Sheikh Mujibur Rahman Agricultural University (24.038°N latitude, 90.397°E longitude), Gazipur, Bangladesh. The experimental soil was silt loam in texture (sand 26%, silt 50%, and clay 24%), having the full field capacity at 30.6% volumetric soil water content. The daily maximum, minimum, mean air temperatures, and rainfall at the reproductive stages of control (A) and heat stress (B) conditions are presented in Fig. 1. Under the heat stress condition, wheat varieties received 27.0 °C mean air temperature throughout the reproductive stages, which was higher than the optimum temperature required for the anthesis (23 °C) and grain filling phases (21.3 °C) (Farooq et al., 2011).

2.2 Experimental Materials, Treatments and Design

Two wheat varieties, namely BARI Gom 33 (‘BG-33’) and ‘Pavon-76’, developed by Bangladesh Wheat and Maize Research Institute (BAMRI); one mutant genotype namely ‘AS-10636’ collected from ACI seed; and three genotypes under accession category namely ‘BD-594’, ‘BD-674’, and ‘BD-675’, were collected from Plant Genetic Resource Center (PGRC) of Bangladesh Agricultural Research Institute (BARI) were used in this experiment. The BG-33 is a popular heat tolerant high yielding variety which is fortified with zinc and in addition carrying a $2N^{v}S$ chromosome translocation for blast resistance (Mohi-Ud-Din et al., 2023; Mottaleb et al., 2019). ‘Pavon-76’ is widely used as heat-susceptible check variety in different experiments (Khatun et al., 2018; Mohi-ud-din et al., 2021). The experiment was laid out in a split-plot design with three replications. The two growing conditions — “control” (optimum sowing on November 30) and “heat stress” (late sowing on December 30) — were placed in the main plots, whereas wheat genotypes were placed randomly in the sub-plots. Healthy seeds were sown in a plot of 4 m^2 area (2m × 2m), and all agronomic practices were performed as per the recommendation.

2.3 Days to heading and anthesis

The wheat plants in a plot were observed for the appearance of head or spike. A plot was considered as flowered when more than 50% of the total plant population visibly showed spike. Days to heading was recorded as days required to emerge at least half of the spike (GS55) in more than half of the plant population in a particular plot from days of sowing, as described by (Zadoks et al., 1974). Days to anthesis was recorded when the mid-anthesis stage (GS65) attain at 50% of completely emerged head in a plot. Mid-Anthesis (GS65) stage was characterized by the composition of both newly extruded yellow anthers, and older white anthers (Zadoks et al., 1974). Before the appearance of head, the main tiller was tagged by colored woolen threads for subsequent data collection.

2.4 Canopy temperature depression (CTD) and SPAD

Canopy temperature (CT) was recorded on every four days after anthesis up to the physiological maturity using a hand-held infrared thermometer (Model-IR-720, Amprobe, USA; distance-spot ratio of 20:1) between 11.30 a.m. and 12.30 p.m. At a distance of 1 m from the spotted canopy, measurements were taken at an angle of approximately 30° to the horizontal line. Six temperature readings were taken from different areas of each plot and averaged. Canopy temperature depression (CTD) was determined according to the procedure of (Mohi-Ud-Din et al., 2021) as ambient temperature minus leaf temperature. Like CTD, the SPAD was also recorded on every four days after anthesis with a Chlorophyll Meter (Model: SPAD-502, Minolta Co., Ltd., Tokyo, Japan). Six readings of SPAD value were taken from six flag leaves of main tiller and continued up to the physiological maturity (GS91) (Zadoks et al., 1974).

2.5 Dry matter distribution pattern in plant parts

From four days after anthesis, four main tillers from a plot were harvested from just above the soil surface and collected plant samples were transported into the laboratory and allowed them for two days for normal air drying. Then the plant samples were cut to separate the harvested plant into four parts. The culm portion, comprised of the total stem, all leaf sheaths and all leaf blades except the flag leaf, was placed into a brown envelope. The flag leaf was separated from the plant and placed into another brown paper envelope. The spike was separated from the plant and divided into the husk materials comprised of all empty glumes and associated parts except the wheat grains. Then the husk materials and grains were placed into separated brown envelopes. All the four plant parts were over dried (Model :DSO-300D, Digisystem Laboratory Instruments Inc., New Taipei City, Taiwan) at 80 ˚C for constant weight. After that, the dry weights of individual plant parts were measured using a digital weighing balance (Model: AJ-620E, Shinko Denshi Co. Ltd., Yushima, Bunkyo-ku, and Tokyo, Japan).

2.6 Grain filling duration (GFD)

During the separation of grains from spike at different days after sowing, the grains were observed carefully. When the grains attained the hardness i.e. difficult to divide by thumb-nail, that particular time was recognized at the physiological maturity stage (GS91) (Zadoks et al., 1974). GFD was recorded from the days of anthesis to the days of physiological maturity.

2.7 Grain yield

When the plants reached the physiological maturity stage, they were chopped at ground level four linear meters from the plot's center. Spikes were extracted from the harvested samples, gathered in a cotton bag, and let too dry in the sun. The spikes were manually cleaned and threshed. The grain weight was then adjusted to 12% moisture grain yield was expressed in kg m^{-2}.

2.8 Statistical analysis

Statistical analyses were performed using R-4.1.0 for win (http://CRAN.R-project.org/) (accessed on November 15, 2023). Upper exposed peduncle length, CTD, SPAD and dry matter distribution pattern data were subjected to 3-factor (genotypes × treatment × days after anthesis) and days to heading and anthesis, GFD and yield were subjected to 2-factor (genotypes × treatment) analysis of variance (ANOVA), respectively, in the general linear model using the package lme4 (Bates et al., 2015) and Tukey's HSD test was used to compare mean differences using the library agricolae (Puigvert et al., 2019). Differences at $p \leq 0.05$ were deemed significant. As different genotypes had different grain filling duration days, for convenience, the days after anthesis factor made distinctive for all genotypes and after that, the 3-factor ANOVA was computed. For easy recognition of the treatment effect for a particular genotype in case of traits like upper exposed peduncle length, CTD, SPAD and dry matter distribution pattern, repeated measures ANOVA was adopted following the type bonferroni (Hoffmann et al., 2010).

3. RESULTS

3.1 Appearance of terminal heat stress under late sown condition

The wheat genotypes sown under two different times, received differential air temperature during their life cycle. The mean air temperature of timely sowing (November 30) genotypes ranged from heading days to physiological maturity was 22.3 ^{o}C while the late sown (December 30) genotypes received about 4.7 ^{o}C greater amount of air temperature with an average of 27.0 ^{o}C (Figure 1). Among the studied genotypes sown under late condition, Pavon-76 received the highest mean air temperature during its reproductive stage (28.27 ^{o}C) followed by genotypes AS-10636 (27.96 ^{o}C), BD-594 (27.46 ^{o}C), BD-675 (26.72 ^{o}C), BD-674 (27.23 ^{o}C), and BG-33 (26.88 ^{o}C) (Figure 1). The recorded data clearly recognized the appearance of terminal heat stress in wheat under late sown condition as reported earlier (Khan et al 2020). Apart from the mean temperature, the greater amount of daily minimum temperature was noticed than the daily maximum temperature (Figure 1). Under control sowing condition, the mean daily minimum and maximum temperature were 15.0 and 29.5 ^{o}C, respectively; while for late sowing condition, the average daily minimum and maximum temperature were 20.2 and 33.9 ^{o}C, respectively.

3.2 Effect of genotypes, growing condition, and days after anthesis on the studied parameters

The main effect of genotypes (G), treatment (T), and days after anthesis (D) in the general linear model (GLM) was highly significant for almost all studied parameters except FLDW (Table 1). Except for FLDW, the G × T, G × D, T × D and G × T × D effects were significant for all of the studied traits. Days to heading and anthesis, grain filling duration and grain yield were estimated and subjected to two-factor analysis of variance and found that the main effects (G and T) for DTH, DTA, GFD and GY were highly significant, while interactions (G × T) were not significant in the GFD (Table 1).

3.3 Days to heading

Ear emergence or heading is a particular phenological stage of wheat which is characterized by the partial or full appearance of the spike or ear from its enclosing sheath. The highest mean number of days to heading (63) was observed from optimum sowing, while the fewest days to heading (59) was found in late sowing (Figure 2A). Under timely sowing condition, the Pavon-76 required the maximum days (72) to emerge its head while rest of the genotypes took an average of 61 days to heading (Figure 2A). Under late sown condition, again the sensitive genotype Pavon-76 took the maximum days to heading (65) followed by AS-10636 (61 days), BD-594 and BD-674 (an average of 59 days). BD-675 and BG-33 required the fewest days to emerge their heads (with a mean of 56 days) under late sown condition (Figure 2B).

3.4 Days to anthesis

The highest mean number of days to anthesis (68) was observed from optimum sowing, while the fewest days to anthesis (63) was found in late sowing (Figure 2B). Under timely sowing condition, the Pavon-76 required the maximum days (76) to anthesis followed by AS-10636 abd BD-594 (an average of 69 days), and BD-674 (66 days). BD-675 and BG-33 required the fewest days to anthesis (with a mean of 63 days) under optimum sowning condition (Figure 2B). Under late sown condition, the sensitive genotype Pavon-76 took the maximum days to anthesis (68) followed by AS-10636 (65 days), BD-594 and BD-674 (an average of 63 days), and BG-33 (60 days). BD-675 required the fewest days to anthesis (58 days) under late sown condition (Figure 2B). The days required from heading to anthesis is dependent on genotypes and environmental conditions and it can be related with the genotypic sensitivity towards terminal heat stress as well. In our study, the mean days required from heading to anthesis under timely sown condition was about 4.5 days while it reduced to 3.6 days under late sown condition and eventually recognizing the direct influence of elevated temperature during the reproductive stage. BD-675 took the lowest days (3) to anthesis from heading under late sown condition followed by BD-594 and Pavon-76 (an average of 3.3 days) while AS-10636, BD-674 and BG-33 extended the duration from heading to anthesis with maximum value (4 days).

3.5 Upper exposed peduncle length

Significant variations exist regarding the upper exposed part of peduncle among the wheat genotypes at two sowing times through the grain filling period. The mean peduncle length under timely sowing condition was 21.48 cm while it declined to 20.74 cm under late sown condition. In all genotypes and under both sowing times, the peduncle length increases gradually from anthesis to physiological maturity period but the increment rate was greater under late sown condition (Figure 3). According to repeated measured anova approach, the genotypes AS-10636 and BG-33 showed non-significant relationship under both sowing times implying their potentiality to mobilize the photo assimilates towards grain. BD-675 was severely affected under elevated temperature as it increased its peduncle length under late sown condition by 9.15% compared to control condition. BD-594, BD-674 and Pavon-76 also showed an increment in peduncle length under late sown condition compared to control by 4.58, 3.63 and 2.92%, respectively (Figure 3).

3.6 Canopy temperature depression (CTD)

In our study, canopy temperature depression (CTD) was the most affected trait. Within the grain filling period, the CTD gradually decreased from anthesis to physiological maturity (Figure 4). The mean CTD under timely sowing condition was 2.74 ^{o}C while it declined to 2.01 ^{o}C under late sown condition. Pavon-76 and BD-675 showed the minimum CTD value at their maturity stage (−0.53 and

−0.43 ºC, respectively) and their overall CTDs were also minimum among the genotypes during the total grain filling period at late sowing condition compared to control (−71.44 and −58.23%, respectively). However, BD-594 and BG-33 maintained relatively lower change in CTD (−34.32 and −37.47%, respectively as compared to control) followed by AS-10636 (−43.81%), BD-674 (−49.38%) further implying their better cooling system at elevated temperature condition that assist in efficient portioning of assimilates.

3.7 SPAD

The SPAD value, a non-destructive chlorophyll index, decreased under late sown condition (28.77) compared to unstressed control condition (30.77) in all genotypes and the relationship was highly significant between the sowing times (Figure 5). SPAD value decreased gradually under control condition but a sharp decrement was noticed in late sown condition. Genotypes like AS-10636, BD-674 and BD-675 showed greater SPAD value at initial anthesis period while the declining trend was noticed at later grain filling stages. Pavon-76 was severely affected under terminal heat stress condition in terms of SPAD value (about 37% decrement over control) while rest of the genotypes showed a similar trend of decrement of about 27% compared to timely sown condition (Figure 5).

3.8 Dry matter distribution pattern

The pattern of dry matter portioning in the above ground plant parts (culm, flag leaf, husk and grain) were studied in two sowing times ranged from anthesis up to physiological maturity. In all genotypes, as grain filling proceeds, the declining trend of dry matter deposition was noticed except the grain part (Figure 6). A typical sigmoid growth curve was noticed in the dry matter partitioning in wheat grain at different days after sowing under timely sowing condition while grain dry weight trend under late sown condition varied in the studied genotypes. As per findings from repeated measured anova approach, the dry matter partitioning in various plant parts significantly differed between two sowing times in all genotypes except the flag leaf dry weight in BG-33 and husk dry weight in Pavon-76 (Figure 6). In AS-10636, the dry weight in flag leaf and husk increased (on percentage basis) under late sown condition compared to control but a declining trend in culm dry weight at later growth stage under late sown condition might be its efficient remobilization capacity under terminal heat stress followed by sustaining grain weight (Figure 6A-D). BD-594 showed the similar dry matter partitioning pattern like AS-10636 with an exception of inferior culm reserve remobilization efficiency under late sown condition (Figure 6E-H). Like BD-594, the BD-674 had similar culm dry weight pattern but a gradual decline in husk dry weight under terminal heat stress condition could assisted in better grain weight deposition (Figure 6I-L). The sensitivity of BD-675 genotype was better recognized in terms of dry matter partitioning under heat stress condition. The relatively greater amount of dry weight deposition in culm and husk even at later grain filling stages was associated with inferior grain weight (Figure 6M-O). The husk dry weight was lower in later grain filling stage of BG-33 but this potential genotype still retained greater culm dry weight under late sown condition (Figure 6Q-T). Pavon-76 showed similar dry matter deposition like BD-675 with an exception of relatively lower culm dry weight under terminal heat stress condition (Figure 6U-X).

3.9 Grain filling duration

Statistically significant decrement was noticed regarding grain filling duration under late sowing condition (30 days) compared to control sowing (42 days) (Figure 7). Pavon-76 took the minimum 24 days (35% decreased compared to control) to reach the physiological maturity stage followed by BD-675 (29 days with a decrement of 29% over control). Under late sown condition, AS-10636, BD-594, BD-674 and BG-33 took almost similar days (32) to complete the grain filling with a decrement of 28, 27, 26 and 27% compared to control sowing (Figure 7).

3.10 Grain yield

The elevated temperature significantly decreased the grain yield (0.38 kg m^{-2}) in wheat in all genotypes and the decrement was almost 19% over control (Figure 8). The maximum yield reduction was noticed in Pavon-76 (26% over control) followed by BD-674 (24%), BD-675 (20%), BG-33 (18%). AS-10636 and BD-594 showed sustainability in grain yield under terminal heat stress condition (decrement of 13 and 15%, respectively compared to timely sowing condition) (Figure 8).

4. DISCUSSION

Grain yield eventually decreases as a result of heat stress in wheat at any stage of growth (Balla et al., 2019). In our study, the yields of all genotypes evaluated under terminal heat stress condition were lower than those under optimal environment, in accordance with (Chileshe et al., 2023). Grain yield is lowered at high temperatures because there is less time for the grain to absorb nutrients between anthesis and maturity. (Farooq et al., 2011). Growth environment and genotype genetic makeup determine how long it takes for a spike or ear to emerge from its enclosing sheath. Due to a rise in temperature, delayed seeding of wheat modified the physiological and biochemical processes of the plant, reducing the length of each developmental phase (Hossain et al., 2021). Accordingly, the sensitive genotypes, Pavon-76, took the highest days to flower even at timely sowing condition, allowing it to experience high temperature under control stage. Apart from daily mean temperature, daily minimum temperature was greater than daily maximum temperature under heat stress condition (Figure 1). When wheat genotypes are exposed to temperatures above 20 °C at night, they exhibit lower spikelet fertility, decreasing grain size and quantity, and a linear reduction in grain filling duration (Mamrutha et al., 2020). Heat stress shortens the grain-filling period and reduces the accumulation of starch and protein during grain formation (Arshad et al., 2017). This is because it lowers the activity of enzymes involved in grain biosynthesis, impairs the assimilatory efficiency of the flag leaf, and mobilizes the stem reserve (Riaz et al., 2021). This statement is relevant for sensitive genotypes, BD-675, with highest exposed peduncle length under terminal heat stress condition, although peduncle is pivotal for photosynthesis, food storage and mobilization, and grain filling, particularly under hot conditions (Gare et al., 2018).

Focusing on the late sown heat stress environment revealed that, AS-10636 wheat genotypes provided highest yield followed by BD-674, BD-594 and BG-33 (a heat tolerant variety) (Figure 8) which is associated with larger grain filling duration and requirement of moderate days to initiate flower. These features might be coping mechanisms against heat stress (Kazan & Lyons, 2016). The ability of tolerant genotypes to remobilize effectively under heat stress conditions—primarily from culm to grain—also helped this prospective genotype to sustain yield (Shirdelmoghanloo et al., 2016). Moreover, the preservation of a higher canopy temperature depression value under conditions of heat stress might be considered as an important component to enable adequate grain filling (Sarkar et al., 2021).

Canopy temperature is influenced by many factors, including leaf thickness and size (Konrad et al., 2021). Heat-tolerant genotypes are cooler than heat susceptible genotypes. Due to their greater thermal stability, genotypes with broader leaves are more resistant to heat damage than those with thinner leaves (Deva et al., 2020). Moreover, through transpiration-driven evaporative cooling, stomatal conductivity control in thicker leaves modulates leaf temperature. (Tricker et al., 2018). The SPAD was also greater in tolerant genotypes, indicating its potentiality to sustain stomatal opening under elevated temperatures

(Reynolds-Henne et al., 2010). This attribute probably led to enhanced gaseous exchange and stomatal conductance, and thus improved photosynthesis (Chileshe et al., 2023). The characteristics measured, when used in specific circumstances with constrained resources, can be acknowledged as useful tools for identifying genotypes that are tolerant of heat and have higher yields, as chosen in this study.

5. CONCLUSION

Elevated temperature, undoubtedly, affects the physiological and grain filling process in wheat along with shortening of flowering time. Dry matter partitioning can be a valuable approach to evaluate genotypes under limited resource condition but potentially provide important insight about the internal physiological processes. Our results conclude that, CTD, SPAD, and dry matter partitioning can be regarded as key indicators of terminal heat stress tolerance in wheat genotypes, as the tolerant genotypes showed superior yield by possessing these features along with relatively greater grain filling duration. The identified genotypes in our study could be a candidate in breeding for future heat tolerant and high yielding wheat varieties. Furthermore, identification of genes that initiate heat tolerance in tolerant genotypes in future could improve breeding of wheat to minimize the yield loss.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest.

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Table 1: Variance components (%) of days to heading (DTH) and anthesis (DTA), grain filling duration (GFD), grain yield (GY), upper exposed peduncle length (UEPL), canopy temperature depression (CTD), SPAD, and dry matter partitioning traits in the context of wheat genotypes × treatment × days after anthesis using the general linear model.

Trait	Genotypes (G)	Treatment (T)	Days after anthesis (D)	G × T	G × D	T × D	G × T × D	Residual
df	5	1	5	5	25	5	25	144
DTH	42.061***	54.989***	-	2.174*	-	-	-	0.776†
DTA	33.031***	64.671***	-	1.694*	-	-	-	0.604†
GFD	4.957***	94.999***	-	0.022	-	-	-	0.022†
GY	27.245***	71.645***	-	1.009***	-	-	-	0.101†
UEPL	34.030***	10.862***	53.180***	0.878***	0.546***	0.285***	0.186***	0.034
CTD	5.286***	65.037***	28.443***	0.863***	0.132***	0.156***	0.054*	0.030
SPAD	6.988***	33.160***	53.414***	1.085***	0.333***	4.847***	0.174***	0.000
CDW	92.002***	1.088***	1.334***	1.129***	1.092***	3.124***	0.226***	0.004
FLDW	73.243***	0.317	4.399	5.488	3.719	3.039	4.762	5.034
HDW	72.085***	20.339***	2.708***	3.238***	0.383***	1.030***	0.206***	0.012
GDW	11.191***	24.959***	61.229***	0.457***	0.794***	1.251***	0.109***	0.011

CDW = Culm dry weight, FLDW = Flag leaf dry weight, HDW = Husk dry weight, GDW = Grain dry weight.

***, and * indicate significant at $p \leq 0.001$, and $p \leq 0.05$, respectively. †df of residual was 24.

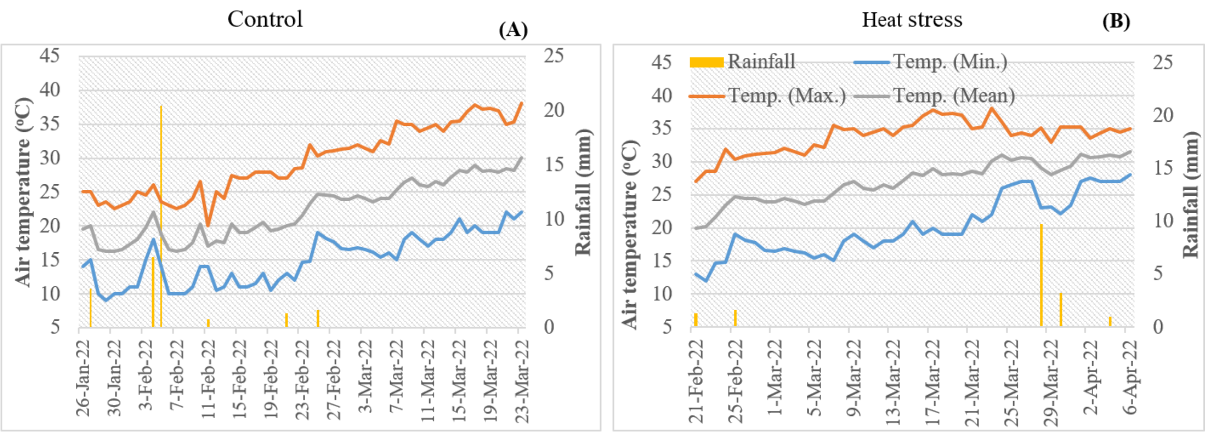

Fig. 1 Daily maximum (Max), minimum (Min), mean air temperatures, and rainfall data recorded at the reproductive growth stages for control (A) and heat stress (B) conditions, respectively.

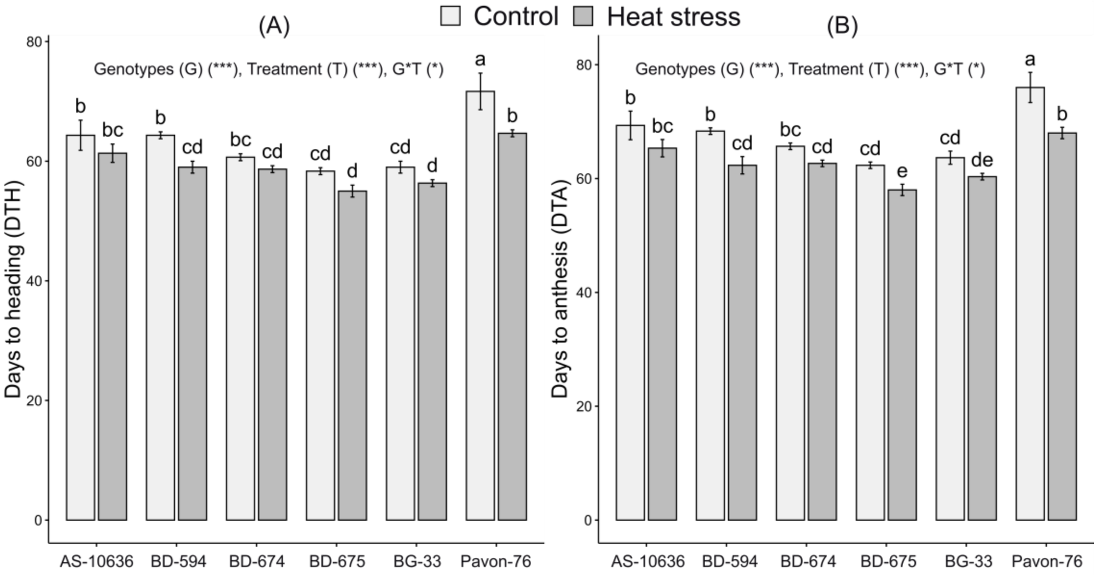

Fig. 2 Days to heading (A) and days to anthesis (B) of the wheat genotypes under control and heat stress conditions. Vertical bars represent ± SE values. Different letters indicate significant difference at p **≤0.05 by Tukey's HSD test.**

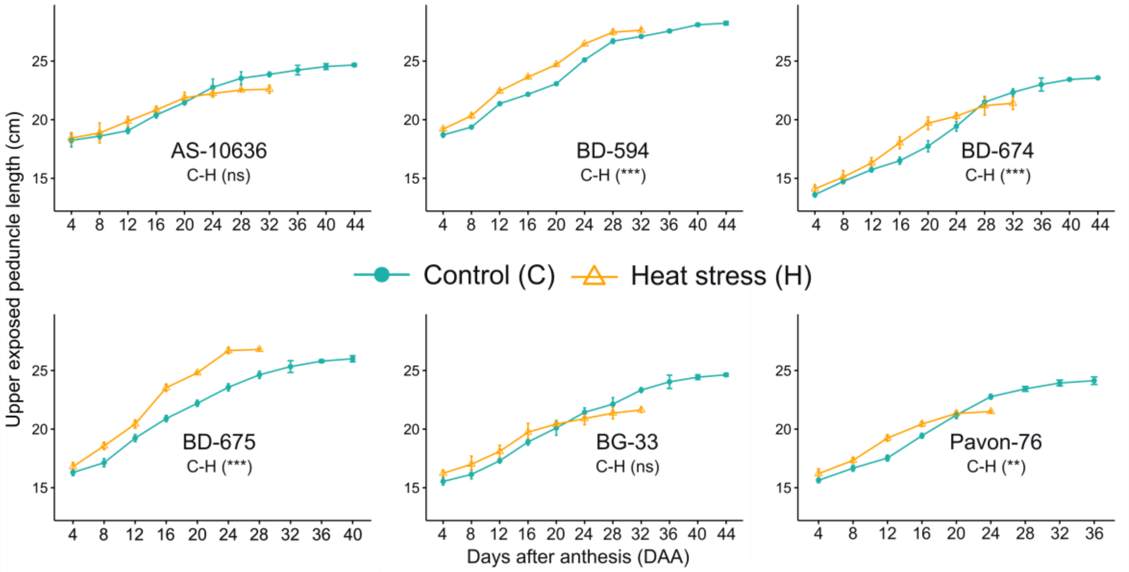

Fig. 3 Variation in upper exposed peduncle length (cm) in wheat genotypes at various days after anthesis under control and heat stress conditions. Vertical bars represent ± SE values. **Asterisk(s) within the parenthesis in a particular genotype indicate the significant difference between the treatment conditions according to repeated measured anova (type = bonferroni) by Tukey's HSD test.** *****, and** ** **indicate significant at** $p \leq 0.001$**, and** $p \leq 0.01$**, respectively. ns = non-significant.**

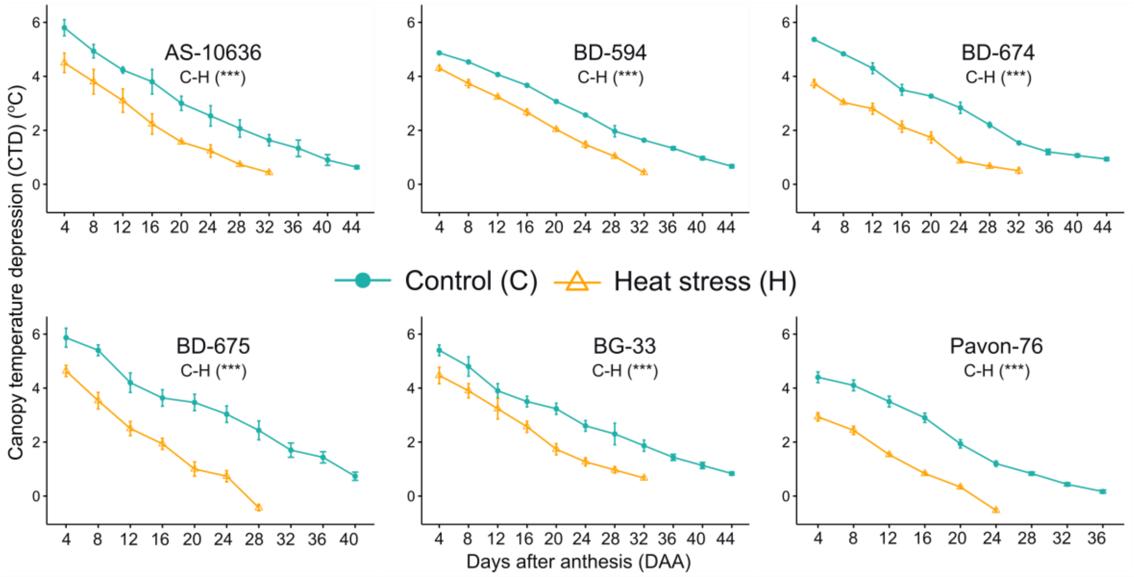

Fig. 4 Variation in canopy temperature depression (ºC) in wheat genotypes at various days after anthesis under control and heat stress conditions. Vertical bars represent ± SE values. Asterisk(s) within the parenthesis in a particular genotype indicate the significant difference between the treatment conditions according to repeated measured anova (type = bonferroni) by Tukey's HSD test. *** indicates significant at $p \leq 0.001$.

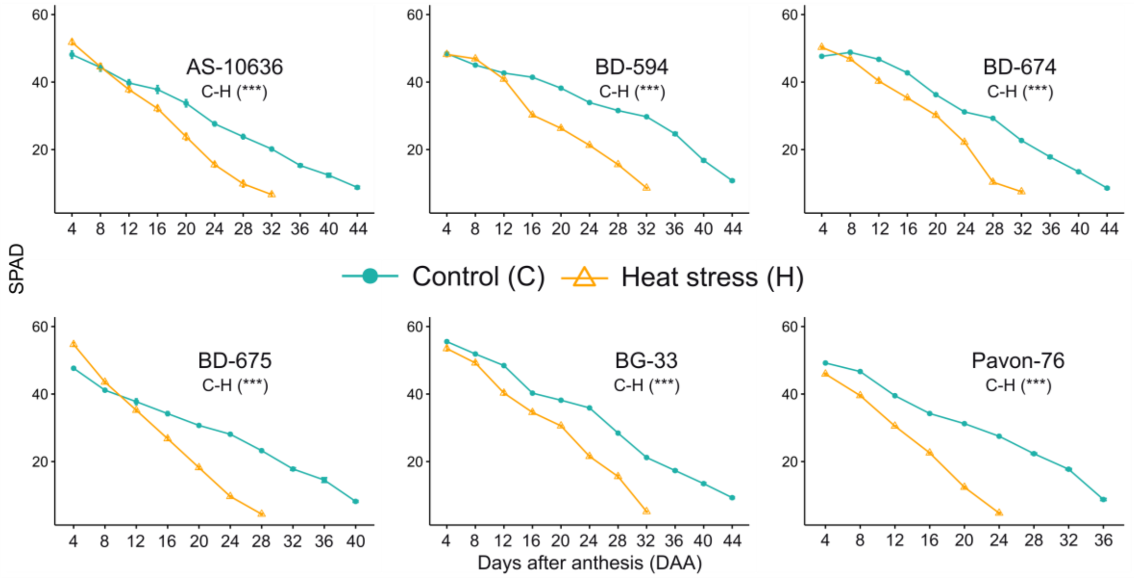

Fig. 5 Variation in SPAD value in wheat genotypes at various days after anthesis under control and heat stress conditions. Vertical bars represent ± SE values. Asterisk(s) within the parenthesis in a particular genotype indicate the significant difference between the treatment conditions according to repeated measured anova (type = bonferroni) by Tukey's HSD test. *** indicates significant at $p \leq 0.001$.

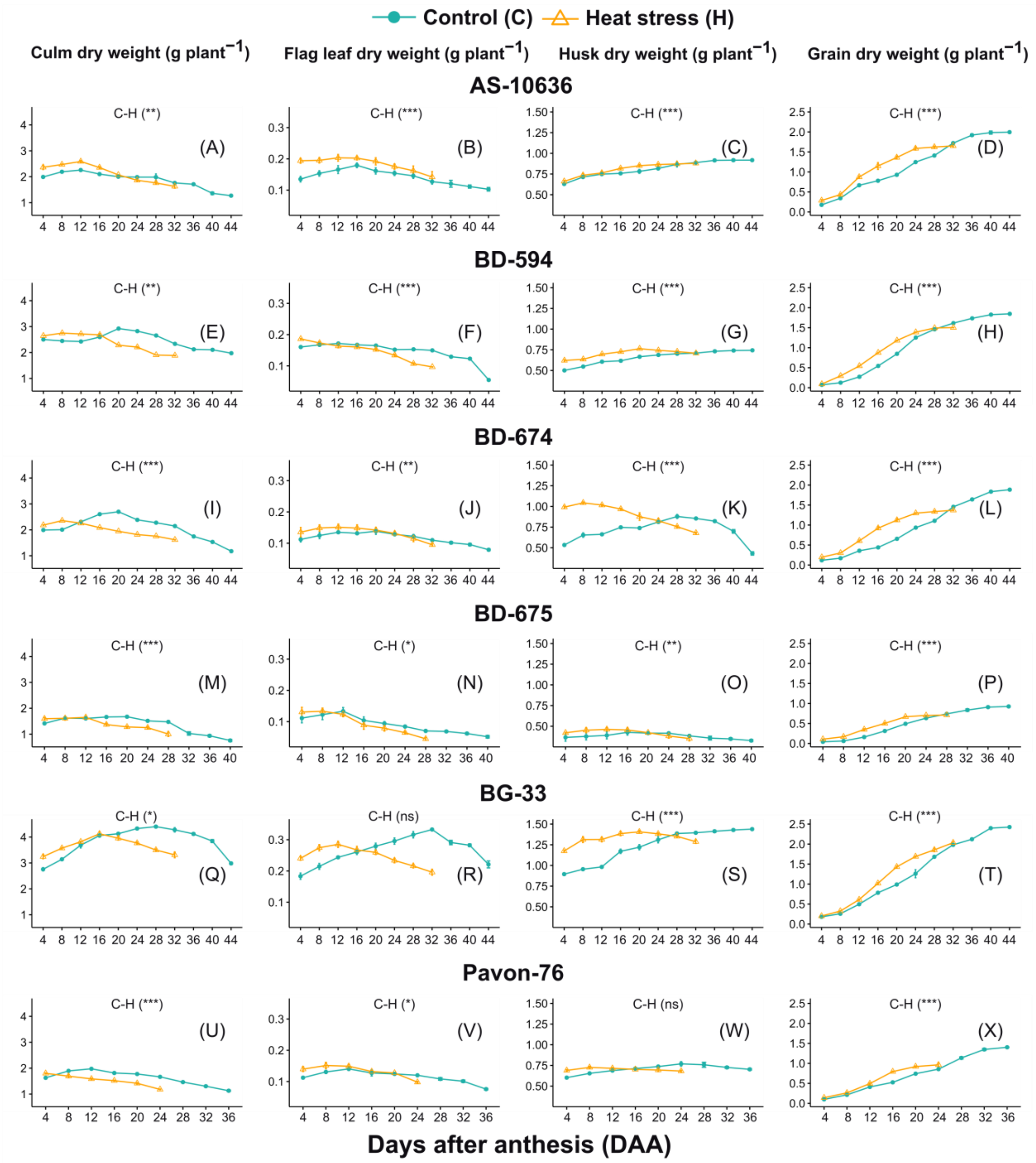

Fig. 6 Variation in partitioning of dry matter plant^{-1} in culm (A, E, I, M, Q, U); flag leaf (B, F, J, N, R, V); husk (C, G, K, O, S, W); and grain (D, H, L, P, T, X) in wheat genotypes at various days after anthesis under control and heat stress conditions. Vertical bars represent ± SE values. Asterisk(s) within the parenthesis in a particular genotype for specific dry matter trait indicate the significant difference between the treatment conditions according to repeated measured anova (type = bonferroni) by Tukey's HSD test. ***, **, and * indicate significant at $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$, respectively. ns = non-significant.

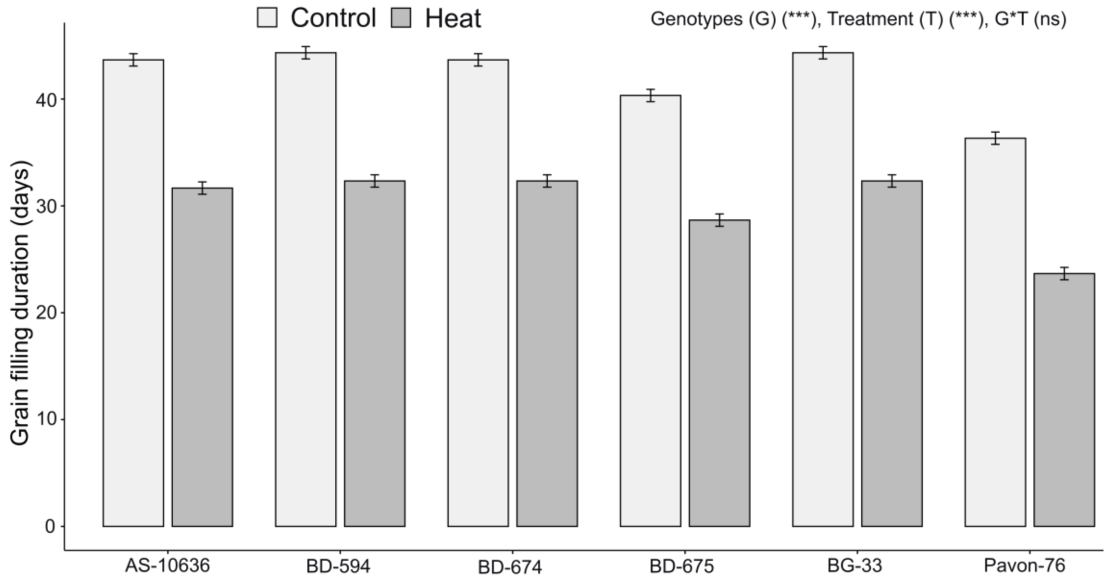

Fig. 7 Grain filling duration (days) of the wheat genotypes under control and heat stress conditions. Vertical bars represent ± SE values.

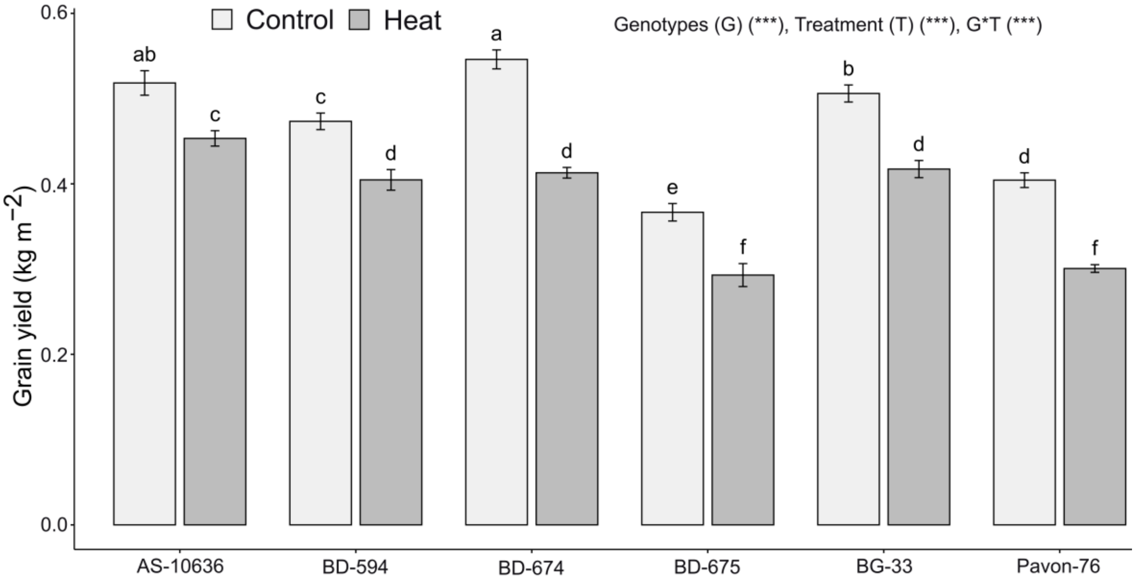

Fig. 8 Grain yield (kg m^{-2}) of the wheat genotypes under control and heat stress conditions. Vertical bars represent ± SE values. Different letters indicate significant difference at p **$\leq$0.05 by Tukey's HSD test.**