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Effect of combined drought and high temperature stress on wheat (*Triticum aestivum*): Insights into grain yield and quality dynamics

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ABSTRACT

The experiment was conducted during winter (*rabi*) season of 2020–21 and 2021–22 at ICAR-Indian Agricultural Research Institute, New Delhi to assess the individual and combined effects of drought and heat stresses on bread wheat (*Triticum aestivum* L.), focusing on yield, yield-contributing parameters, and grain nutritional quality in four contrasting wheat genotypes (C306, HD2967, Raj3765 and WL711). The experiment was laid out in completely randomized design (CRD) with 15 replications of each genotype. The results revealed that combined drought and heat stress had a more severe impact on yield-related traits compared to individual stresses. Yield losses under drought stress ranged from 17.7–32.24%, while heat stress alone caused reductions of 29.98–46.55%. However, the combined stress led to the highest yield loss (42.13–61.06%), emphasizing the additive detrimental effects of both stresses. Similarly, 1000-kernel weight (TKW) declined significantly under combined stress conditions, with reductions ranging from 33.22–52.23%, due to impaired starch synthesis and reduced enzymatic activity. Genotype Raj3765 exhibited the highest tolerance, followed by C306, HD2967, and WL711, as indicated by the Stress Susceptibility Index (SSI) and Yield Stability Ratio (YSR). Additionally, nutritional quality assessments showed a decline in zinc (Zn) and iron (Fe) concentrations under drought and combined stresses, with Raj3765 exhibiting the least reduction and WL711 the highest. Despite reductions in starch content, protein content increased under heat stress, suggesting differential regulation of nitrogen metabolism. These findings highlight the necessity of breeding wheat varieties with enhanced resilience to multiple stress factors to sustain grain yield and nutritional quality under climate change scenarios.

Keywords: Abiotic stress, Combined effects, Grain yield, Grain quality, Nutritional composition

Water deficit stress (drought) and high temperature (heat) significantly impede crop growth, development and yield (Wahid *et al.* 2007, Barnabas *et al.* 2008), triggering biochemical and physiological changes at cellular level and also at whole plant levels, thereby influencing crop yield (Fahad *et al.* 2017) and its quality (Velu *et al.* 2016). Climate-induced abiotic stresses pose challenges exacerbated by the expanding global population and shifting food habits, particularly impacting spring wheat-growing regions (FAO 2015). With the global population predicted to be 9.7 billion, primarily in developing countries, there's a pressing need to bolster annual cereal production to meet rising food demand (FAO 2015, Ray *et al.* 2015). Wheat (*Triticum aestivum* L.), cultivated worldwide and thrives in temperatures between 15 and 25ºC, is critical for human nutrition, serving as a staple food and playing a pivotal role in meeting calorie needs (Paudel *et al.* 2021). Despite its importance, wheat, particularly *rabi* crops, is extremely susceptible to the adverse effects of drought and increasing temperatures during its reproductive phases, impacting various growth aspects and grain quality (Gonzalez-Navarro *et al.* 2015). Drought and High Temperature Stress (HTS) impact wheat development, particularly in its reproductive stages (Boyer and Westgate 2004), with combined stresses significantly reducing crop productivity (Shah and Paulsen 2005). Protein synthesis is hindered by both stresses, leading to decreased photosynthesis, shoot, and grain weight under high temperatures (Shah and Paulsen 2005). High temperatures at maturity can elevate grain nitrogen content, while global concerns persist over zinc and iron deficiency in wheat (Velu *et al.* 2016). Climate change compounds these issues, impacting both wheat grain nutrition and yield (Trnka *et al.* 2014).

Limited research has addressed the interactive effects of drought and increased temperature on crop productivity, with few studies comprehensively examining the full spectrum of physiological, growth, and yield traits (Barnabas *et al.* 2008). Understanding the combined impacts of these stresses is imperative, particularly in light of projected climate

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scenarios foreseeing seasonal shifts in temperature and drought stress (IPCC 2014). Therefore, the purpose of this study was to examine the impacts of drought stress and high temperatures, both alone and in combination, on different yield-related indices and grain quality components across four genotypes of wheat, from heading to till maturity. The study seeks to provide insights into the effects of these stresses on grain yield and quality components.

MATERIALS AND METHODS

Experimental material and growth conditions: The experiment was conducted during winter (*rabi*) seasons of 2020–21 and 2021–22 at ICAR-Indian Agricultural Research Institute, New Delhi. The experiment involved four sets of wheat genotypes, C306 (drought tolerant), HD2967 (drought sensitive), Raj3765 (heat tolerant), and WL711 (heat sensitive). Various conditions were assessed, including timely irrigation (control), heat stress, drought stress, and combined heat and drought stress (without irrigation). Each genotype had 15 replications with each pot having four plants after thinning, grown under normal conditions until heading, following standard agronomic practices. From heading until maturity, treatments were applied. One set of genotypes experienced high temperature stress (H) in a controlled facility with a day/night temperature of 36/30ºC and normal irrigation. Another set faced a combination of both heat and drought stress (HD) in a controlled facility with a day/night temperature of 36/30ºC and moisture content at 50% field capacity was maintained. The non-stress/control treatment was maintained with normal irrigation and a day/night temperature of 21/15ºC. Drought stress was managed by maintaining pot moisture at 50% of field capacity, with re-watering whenever moisture dropped below 50%. The stress was maintained from heading to till maturity stage. The humidity of the chambers was raised in order to prevent drought stress caused by fast evapotranspiration under high air temperatures. Pots were randomly rearranged every alternate day to avoid positional effects. The experiment followed a completely randomized design (CRD) with 15 replications in each condition. Ten replications were used for physio-biochemical and destructive analysis, while five pots were used for yield analysis. The wheat was sown on November 19th and 20th, 2021 and 2022, respectively, following standard agronomic practices for irrigated conditions. Throughout the wheat development period, recorded minimum and maximum temperatures (ºC) along with precipitation (mm) showed considerable variation (Supplementary Fig. 1).

Soil moisture measurements: Soil moisture content (SMC) was assessed during the anthesis stage employing a gravimetric technique (Black 1965). Samples were obtained from a depth of 20 cm in the middle of the earthen pots using a tube auger. SMC readings were recorded as follows, 24.4% under control conditions; 18.99% during drought stress; 22.05% during heat stress, and 12.14% during combined heat and drought stress (Supplementary Fig. 2) (Meena *et al.* 2023).

Parameters for grain yield analysis: At harvest, when grain moisture content was approximately 8–10% (Velu *et al.* 2016), various yield-related attributes were measured, including plant height (PH) (cm/plant), ear weight (EW) (g/plant), total grain yield (TGY) (g/plant), 1000 kernel weight (TKW) (g), shoot biomass (SB) (g/plant DW), yield stability ratio (YSR) and stress susceptibility index (SSI).

To calculate the stress susceptibility index (SSI), yield per plant was taken down under both normal and stress conditions, following the formula by Fischer and Maurer (1978):

$$SSI = (1 - Y/Yp)/D$$

$$\text{Stress Intensity } (D) = 1 - X/Xp$$

Where Y, Mean yield or yield component of a genotype in a stress environment;Yp, Mean yield or yield component of a genotype in a stress-free environment; X, Mean Y of all genotypes; Xp, Mean Yp of all genotypes.

The SSI value was used to distinguish the relative stress tolerance of different genotypes. A value of $S \leq 0.50$ indicated high stress tolerance, $S > 0.50 \leq 1.00$ indicated moderate stress tolerance, and $S > 1.00$ indicated susceptibility to stress.

The yield stability ratio (YSR) was calculated according to Lewis (1954):

$$YSR = (\text{Seed yield under stress condition/Seed yield under normal}) \times 100$$

Parameters for grain quality analysis: At full maturity, with grain moisture content at 8–10%, plant materials were harvested, and grain samples from each genotype were meticulously cleaned to eliminate foreign materials and broken grains. These samples were then subjected to micronutrient analysis. Zinc (Zn) and iron (Fe) concentrations were determined using the diacid digestion method with a double beam atomic absorption spectrophotometer (ECIL Model No. 4141). Grain nitrogen content was estimated via the Kjeldahl method, and the calculated nitrogen percentage was utilized to derive protein content in the wheat grains. Furthermore, total starch and sugar content in the grains were measured. Starch content determination followed the method outlined by McCready *et al.* (1950), while sugar content determination utilized the procedures described by Dubois *et al.* (1951) and Yemm and Willis (1954).

Statiscal analysis: The standard error (SE) as the mean of the standard deviations of the replicates was used to calculate the variability of the experimental data, which were acquired as the average mean of at least three separate biological replicates. Differences between treatments were analyzed for significance using analysis of variance (ANOVA) techniques suitable for factorial design based on a completely randomized design (CRD). The "R" statistical package version 4.1.2 was employed for statistical analysis, utilizing the "lm" function for ANOVA. Pairwise comparisons were conducted using the Duncan Multiple Range Test (DMRT), facilitated by the agricolae package in R. Data visualization was carried out using the ggplot2 package in R, renowned for its versatility and comprehensive tools for creating graphs.

RESULTS AND DISCUSSION

The pot experiment conducted during the reproductive period under stressful conditions underscores the significant influence of water scarcity and high temperatures on both quality and quantity of wheat grains. Prior researches by Gibson and Paulsen (1999), Bencze *et al.* (2004) and Zhao *et al.* (2009) has also emphasized the impact of extreme weather, particularly high temperature and water deficiency, on grain quantity and quality. These findings corroborate that adverse environmental conditions can adversely affect wheat grains, impacting both yield and nutritional composition. The research by Mahrookashani *et al.* (2017) highlights the consequences of combined stress, specifically high temperature and drought stress, on wheat growth, development, and quality of the grain. The study observed that the application of heat, drought, and combination of both the stresses during or near the anthesis had significant effects on various traits related to growth and yield, with a particular emphasis on TKW and TGY. The findings indicated that the additive effects of heat and drought stress were noticably higher than the individual effects of those stresses. However, the intensity of these effects varied depending on the specific yield traits being analyzed. It suggested that the simultaneous occurrence of drought and heat stress has a more harmful impacts on grain yield than experiencing either stress alone.

Impact of individual and combined stress on grain yield and related parameters: The present analysis revealed that high temperature, particularly in combination with drought stress, has a more profound impact on the quantity and quality of wheat grains compared to drought stress alone. The study found that the yield losses caused by drought stress ranged from 17.7–32.24%, while the combined stress of drought and heat stress resulted in more significant losses ranging from 42.13–61.06%. Heat stress alone led to a yield loss of 29.98–46.55%. A similar pattern was observed for the TKW, with drought stress reducing it by 9.39–29.27%, and the combined stress causing a more substantial reduction of 33.22–52.23%. High temperature during the grain-filling stage is known to negatively affect grain weight and yeild, primarily due to a reduction in starch content. The decrease in kernel weight and starch accumulation under heat stress can be attributed to the impairment of starch synthesis and the reduced activity of key enzymes involved in this process. Enzymes responsible for starch synthesis lose their activity at high temperatures, leading to a slowdown or cessation of starch production (Liu *et al.* 2020). Reduced source strength and carbon availability during the grain-filling stage will undoubtedly result in smaller seeds and reduced yield (Liu *et al.* 2020). Recent research showed that in conditions of high temperature or water stress, the activity of the enzymes involved in starch production decreased. Thus, it is evident that the additive effects of both the stress lead to reduction in the rate and duration of starch accumulation and starch content (Lu *et al.* 2019). In lentil seeds, under drought and HTS significant reduction in starch content was noticed by Sehgal *et al.* (2018).

Mean values with capped bars indicate ± SEM of three replicates. Statistically significant differences ($p< 0.05$) between genotypes were determined by the Duncan multiple range test. Mean values with the same alphabets on top are not statistically significant ($p<0.05$) at a specific measurement time.

The stress susceptibility index, which provides an estimation of genotype susceptibility, indicates that the combined heat and drought stress has a higher impact than individual stress factors (Supplemenatry Fig. 3). This finding is consistent with previous research on combined drought and heat stress. The study highlights that the effects of combined stress are stronger and can have varying magnitudes on specific growth traits. Grain yield was reduced in all wheat genotypes under combined high

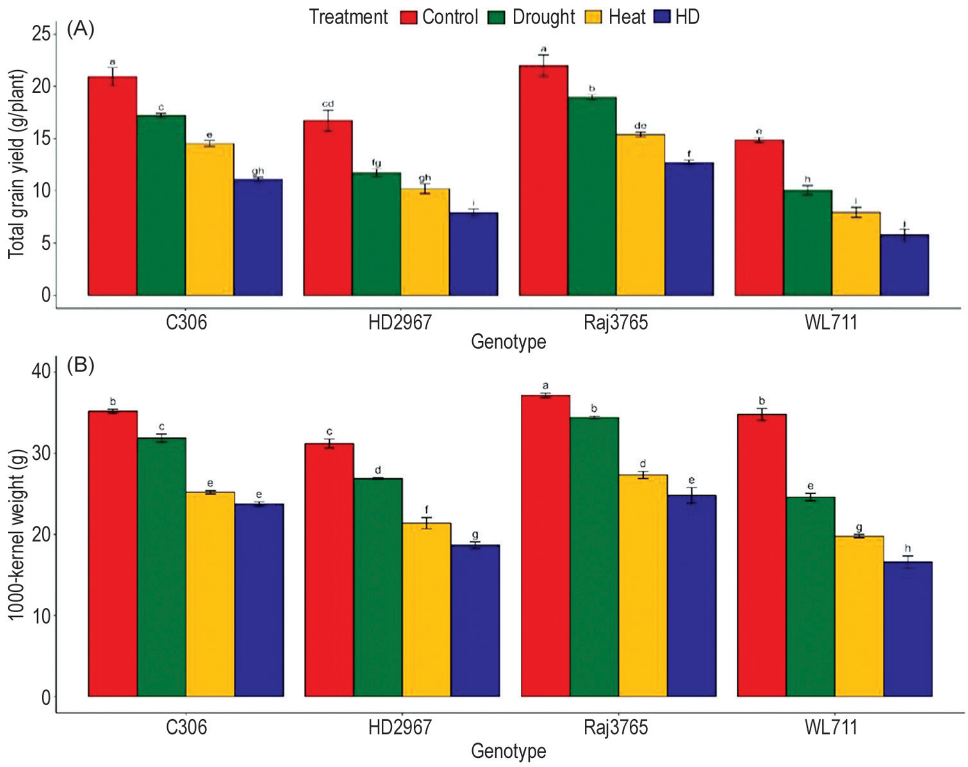

Fig. 1 The total grain yield (A) and 1000-kernel weight (B) were calculated in all the wheat genotypes under control, drought, heat and combined stress conditions.

temperature and water stress than under individual stresses due to the additive effects of both the stresses occuring at a same time (Fig. 1A). Our data corroborate the theory that the HTS and drought belonged to the category of potential negative interaction, as do those of Mittler (2006) and Prasad *et al.* (2011). Grain yield is decreased under drought and HTS, because it has shorten the grain filling duration and reduced the rate of grain filling too (Prasad *et al.* 2008). Grain yield is reduced by impaired starch, sugar, and metabolism as well as changes in photosynthate translocation during heat stress, according to study by Farooq *et al.* (2011). Thus, this might be a one reason among many for the reduction in grain yield under combined stress than under individual stresses. In the current experiment, drought and heat stress has reduced the plant height (cm /plant), shoot biomass (g/plant), the weight of ear (g/plant) (Supplemenatry Fig. 3), 1000-kernel weight (g/plant) and total grain yield (g/plant) (Fig. 1), ultimately reducing the yield and related attributes in all four wheat genotypes. However, compared to their individual impacts, the combined stresses had a more detrimental impact on all the traits in all wheat genotypes. These stress conditions had more serious effects on WL711 followed by HD2967, C306, and Raj3765. However, there was a significant increase in shoot biomass under heat stress in all wheat genotypes than under drought and combined stresses. This might be due to the availability of sufficient water under heat stress conditions which caused an increase in the number of non-effective tillers. The growth and yields of various cereal crops have previously been shown to be negatively impacted by heat and drought stressors (Rollins *et al.* 2013), although the degree of damage caused by these stresses varies depending on the stressor severity and the crop stage of growth (Fahad *et al.* 2017). Accordingly, the Stress Susceptibility Index (SSI) indicated that Raj3765 (0.891) is tolerant, C306 (0.937) is moderately tolerant, HD2967 (1.066) is a moderate type and WL711 (1.195) is a sensitive genotype (Supplementary Fig. 4). Similarly based on the Yield Stability Ratio (YSR), we found higher yield stability in Raj3765 (65.30%), followed by C306 (63.422%), HD2967 (58.43%), and WL711 (53.381%) under stress environments (Supplementary Fig. 5).

Our study showed a decrease in TKW due to drought and temperature stress, while combined temperature-drought stress magnified the impact (Fig. 1B). During stress conditions, like high temperatures, drought stress, or both, there will be less availability of carbohydrates for transporting into developing seeds. This is because, under stress, the photosynthetic rate and sucrose metabolism in leaves will be reduced during grain filling and maturity (Cohen *et al.* 2021). Previous studies revealed that the decreased rate of starch accumulation and change in endosperm cells during grain filling could result in decreased seed weight under high temperatures and/or drought stress (Nicolas *et al.* 1985, Balla *et al.* 2011). Overall, our findings unambiguously demonstrate that drought stress and high temperatures both reduced the TKW, and TGY. It's significant to note that the combined effects of heat and drought were more severe than the additive effects of heat and drought alone; as a result, interactions between the two stress factors were beneficial for all traits. According to this study, the interactions between drought and heat varied depending on the type of yield and the physiological processes that affect the yield. The TKW, grain yield, and biomass, on the other hand, were significantly reduced under both irrigated and dry conditions by HTS. Future studies should therefore place more emphasis on comparisons with cultivars resulting from breeding initiatives designed to create cultivars that can withstand both stresses (Barnabas *et al.* 2008, Prasad *et al.* 2017).

Impact of individual and combined stress on grain nutritional traits: A study by Velu *et al.* (2016) emphasized the significant impact of high temperatures on concentrations of zinc (Zn) and iron (Fe) in wheat grains, particularly when compounded by the concurrent stress of temperature and drought. The study revealed a marked reduction in Zn (Fig. 2A) and Fe concentrations (Fig. 2B) under combined drought and heat stress than control conditions. Notably, among the genotypes studied, Raj3765 shown least reduction, while WL711 showed the highest reduction. These findings suggest potential for improvement in genotypes with higher Zn and Fe concentrations, such as Raj3765 and C306, through targeted breeding programmes. Protein content in grains, assessed via percent nitrogen content, shown that protein synthesis is less sensitive to heat stress than starch accumulation, as reported by Zahedi *et al.* (2004) and Triboi *et al.* (2003). However, during grain development, even brief high temperatures can have a negative impact on grain quality. Both drought and heat stress were found to increase nitrogen content in all genotypes, with a notable increase observed under heat stress (Supplementary Fig. 6A). Grain nitrogen accumulation remained relatively stable under heat stress compared to starch accumulation. The rise in grain nitrogen content could be attributed to a decrease in starch accumulation or an increase in protein synthesis. Similarly, protein content in grains exhibited a significant enhancement under heat stress compared to drought stress (Supplementary Fig. 6B). However, the combined stress of drought and heat had a more detrimental impact on grain quality across all wheat genotypes, underscoring the necessity of considering the combined effects of multiple stresses when evaluating grain quality and the importance of targeted breeding efforts to enhance stress tolerance and grain quality in challenging environments. Furthermore, there was a statistically significant reduction in starch content under combined drought and high temperature stress (Fig. 2C) because under stress the activity of sucrose synthesizing enzyme (sucrose synthase) and starch synthesizing enzyme (starch synthase) get inhibited, which were previously found to have a correlated effect on chickpea seed size (Kumar *et al.* 2009).

Further investigation into grain quality parameters, including total starch, sugars, protein, nitrogen content, Zn, and Fe concentrations, unveiled variations under both normal and stressful conditions. Consistent with previous findings, higher zinc concentrations were observed under heat stress compared to control, drought, and combined stresses. This increase under stress conditions may be attributed to a reduction in grain size, altering the aleurone to endosperm ratio. Similar trends were observed for iron content in grains. However, subjecting the reproductive stage to drought and heat stress significantly affected grain yield components and nutritional quality parameters across all genotypes studied (Velu *et al.* 2016). Combining drought with heat stress through limited irrigation had a more severe impact on plant growth, resulting in significantly lower grain yield and nutritional quality. These findings corroborate earlier studies confirming the negative influence of water limitation and high temperature in wheat. Comparable detrimental effects of combined stress were also observed in other crops such as lentil (Sehgal *et al.* 2018), chickpea (Awasthi *et al.* 2024), soybean (Poudel *et al.* 2024) and groundnut (Viswanathan and Khanna-Chopra 2001). Sucrose concentration in grains was substantially affected by drought and heat stress, with drought stress causing a more pronounced reduction (11.02–15.08%) compared to heat stress (7.11–14.84%). The combined stress further exacerbated the decrease, i.e. 15.18–31.90%. The activity of sucrose phosphate synthase, a key enzyme involved in sucrose synthesis, was significantly affected by drought stress, resulting in a decline in sucrose concentration (Sehgal *et al.* 2018, Choukri *et al.* 2020). Tolerant genotypes, exemplified by Raj3765, maintained higher sucrose concentrations in grains under stress conditions compared to other genotypes, potentially due to increased enzyme activity (Supplementary Fig. 6C). In conclusion, these findings highlight the intricate interactions between temperature, drought, and their combined effects on grain quality parameters in wheat. Understanding these interactions is pivotal for devising strategies to enhance stress tolerance and improve grain quality in challenging environment through targeted breeding efforts.

Mean values with capped bars indicate ±SEM of three replicates. Statistically significant differences ($p<0.05$) between genotypes were determined by the Duncan multiple range test. Mean values with the same alphabets on top are not statistically significant ($p<0.05$) at a specific measurement time.

Correlation between environments based on stress tolerance index: The study suggested a positive correlation between genotypes' stress tolerance under heat stress alone and their tolerance in combined drought and heat stress conditions. However, there were no significant relationships observed between stress tolerance under individual stressors.

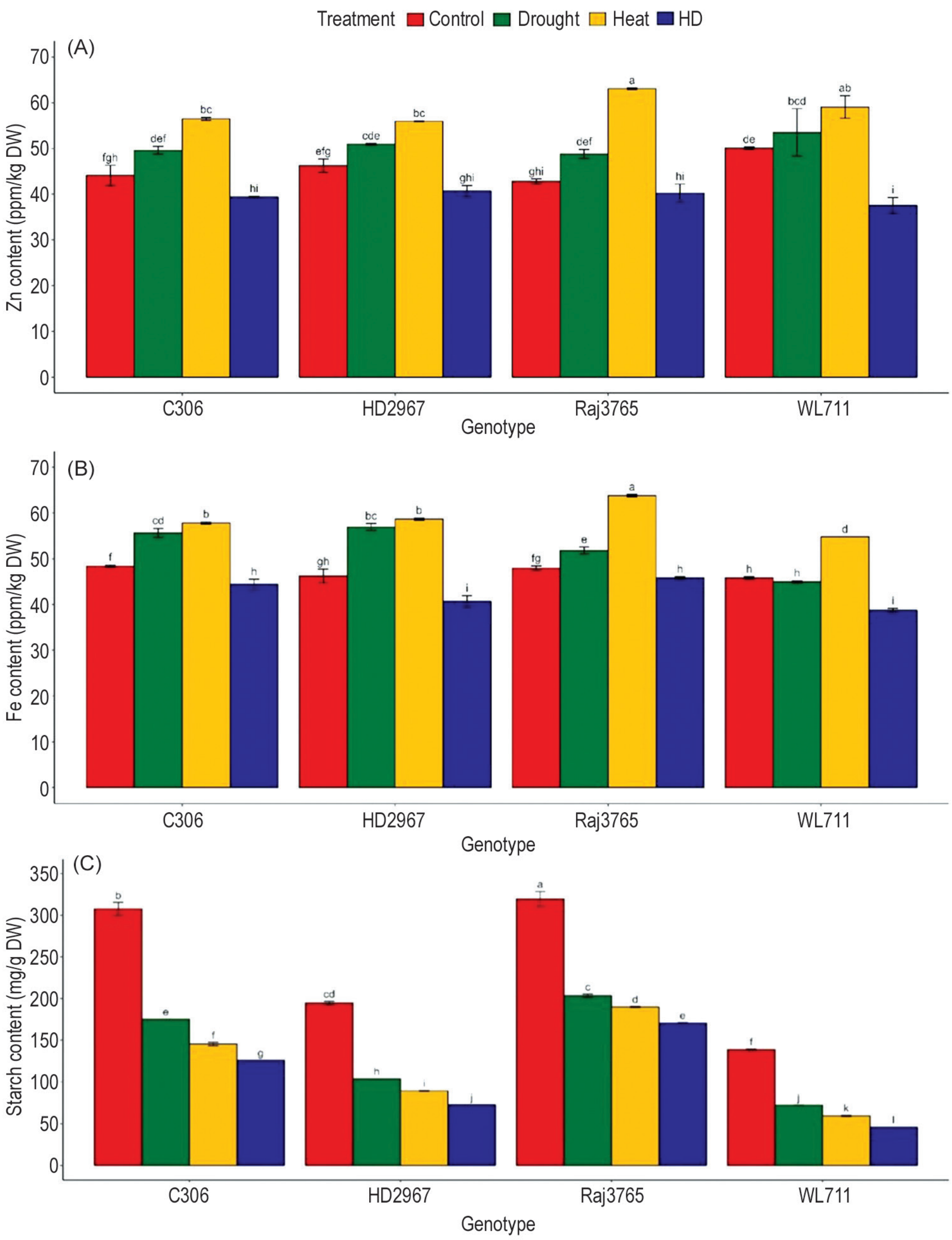

Fig. 2 The zinc (A), iron concentration (B) and starch content (C) were calculated in the grains of all the wheat genotypes at the time of harvesting under control, drought, heat and combined stress conditions.

This supports previous research (Cairns *et al.* 2013) indicating no significant correlation between grain yield under drought stress and combined heat and drought stress. Combined drought and heat stress had a more detrimental impact on TKW and TGY compared to either stressor alone, with heat stress causing a more pronounced decrease. The drop in shoot biomass was greatest under combined stress, then under drought stress alone, then under heat stress alone. Similarly, drought stress significantly affected ear weight compared to heat stress, while the combined stress had the most detrimental effect on yield traits. Understanding these distinct effects is crucial for developing targeted strategies to enhance stress tolerance and improve crop performance in challenging environments.

The study investigated the impact of drought, heat, and combined stress on wheat genotypes during the reproductive stage. Findings demonstrated that combined drought and heat stress exerted the most severe effects on yield and related traits. Heat stress predominantly affected seed yield reduction, while combined stress hindered both yield and quality traits, resulting in smaller, shriveled grains with impaired starch and sugar concentration. However, certain genotypes, like Raj3765, exhibited tolerance to combined stress, displaying increased zinc/iron content and protein ratio despite reduced yield and kernel weight. Yet, further confirmation is essential. The study also hints at partial cross-tolerance to drought and heat stress in specific genotypes, advocating for expanded research with a broader genotype pool to validate these findings.

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