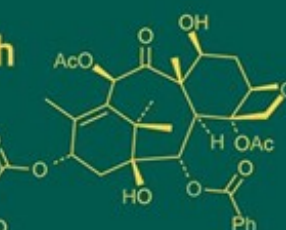
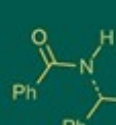


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Genetic variability, heritability and genetic advance for yield and yield attributing traits in wheat (*Triticum aestivum* L.)

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ABSTRACT

This present investigation was aimed at estimating the genetic variability, heritability, genetic advance (GA) and genetic advance as percentage of mean (GAM) in the F1 and F2 generations of wheat consisting of 14 lines and 5 testers (70 F1 and 70 F2 population) under normal sowing and late sowing conditions. In both generations, phenotypic coefficient of variation (PCV) was observed to be higher than genotypic coefficient of variation (GCV) for almost all the traits and the difference between the two increased for several traits under late sowing, indicating the increase of environment effect under heat stress. The majority of the traits in both generations had a high heritability (above 60%), while higher genetic advance was observed for some traits with low heritability and low genetic advance was observed for some traits with a high heritability. The proline content, flag leaf area, stress tolerance index and grain yield per plant had high heritability and high GAM (generally > 20%) in the F1 and F2 generations, suggesting that variation in these traits was primarily heritable and dominated by additive gene effects, thus providing good prospects for direct selection. Days to 50% heading, days to maturity and pollen viability had high heritability and low GAM indicating that non-additive gene action or a narrow genetic base restricts the response that can be achieved from direct selection for these traits. Heritability decreased from F1 to F2, especially under normal conditions, for protein content, number of spikelets/ear and chlorophyll content, which is consistent with the genetic variability released and sensitivity to environment that is characteristic of a segregating generation. These results suggest that grain yield/plant, biological yield/plant, flag leaf area, productive and total tillers/plant, proline content and the stress-tolerance index are good traits for direct selection in early segregating generations of wheat to develop heat tolerance and caution that heritability estimates would have inflated the selection potentials in some of the traits without considering genetic advance.

Keywords: Wheat, Heat stress, Genetic variability, Heritability, Genetic advance, GCV, PCV

Introduction

Wheat (*Triticum aestivum* L.) plays a significant role in global food security and an increase in the growing-season temperature has an immediate effect on its productivity. Potential abiotic stresses on the crop include terminal heat stress during grain-filling and during the anthesis period; this is a specific stress response as it results in a reduction in grain-filling time, a reduction in pollen viability and fertilisation, premature leaf senescence and a reduced grain number and test weight. Such stress is expected to increase with climate change and tolerance has therefore become a major breeding goal and achieving this requires the identification of traits with enough heritable variation to be responsive to selection.

Efficiency of selection for a quantitative trait is not solely determined by its phenotypic variation, but also by the heritability of its variation, and the genetic gain to be expected from the selection process. Genotypic and phenotypic coefficients of variation (GCV and PCV) measure the relative magnitude of genetic and total phenotypic variability for a trait, heritability (h^2) is the proportion of the phenotypic variance associated with genotypic differences, and genetic advance (GA) in particular as percentage of mean (GAM) can be estimated as the expected gain from selection at a specified selection intensity (Burton, 1952; Johnson *et al.*, 1955; Robinson *et al.*, 1949) [1, 2, 3]. However, the heritability estimated alone can be misleading because traits which have high non-additive gene action or limited genetic variability tend to have high heritability and the combined evaluation of heritability with genetic advance is a more reliable basis for predicting the effectiveness of selection (Johnson *et al.*, 1955) [2].

In wheat, a few recent studies have reported the genetic variability, heritability, and genetic advance for physio-morphological traits in timely and late sown conditions, generally concluding that PCV exceeds GCV, heritability is high for several phenological and morphological traits, and traits such as grain yield, bi

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ological yield, tillers per plant, and stress-tolerance index are highly heritable and have appreciable GA, making them useful selection criteria under heat stress (Hossain *et al.*, 2021; Thakur *et al.*, 2020; Karla *et al.*, 2023; Khan *et al.*, 2022; Das *et al.*, 2024) [5, 6, 7, 8, 4].

In this view, the present study was undertaken to estimate the genetic variability, heritability, genetic advance and genetic advance as percentage of mean for F₁ and F₂ wheat generations for both normal and late sown situations to identify traits and generations with the maximum potential for effective selection for heat tolerance.

2. Materials and methods

The experiment was conducted at the Rabi Cereals, Nawabganj Farm, Section of Rabi cereals, CS Azad University of Agriculture and Technology, Kanpur - 208002 (U.P.) during the Rabi 2023-2024 and 2024-2025. The experimental material for this study comprised 14 diverse wheat lines (DBW-316, DBW-187, PBW-373, HD-3388, HD-3386, PBW-833, HI-1612, HD-3293, DBW-252, DBW-173, DBW-222, PBW-644, HD-2967 and HI-1654) and 5 testers viz. K-424, K-9465, K-9423, K-1006 and K-607 which were crossed in a Line × Tester mating design (Kemphorne, 1957) [9] to generate 70 F₁ hybrid combinations (14 × 5). Individual F₁ plants of each of the 70 crosses were then self-pollinated to create 70 F₂ populations.

2.1 Experimental design

The 70 F₁ and 70 F₂ entries were tested under a Randomized Block Design, with three replications for each of the 2 sowing environments. The F₂ populations were grown in two rows while the F₁ cross and each parent was grown in single row configuration. The experimental arrangement used was the same as outlined in the source material for the final trial.

2.2 Traits recorded

Observations were taken on each plant/plots of each replications separately under normal (N) and late (L) environments on the following 18 traits viz. days to 50% heading, days to maturity, plant height (cm), flag leaf area (cm²), number of productive tillers per plant, total number of tillers per plant, number of spikelets per ear, number of grains per spike, biological yield per plant (g), harvest index (%), 1000-grain weight (g), protein content (%), canopy temperature depression (°C), pollen viability (%), proline content (µg/500 mg fresh wt.), heat injury (%), chlorophyll content, grain yield per plant (g). In addition, stress tolerance index (STI) was analysed as a derived index of performance under both sowing conditions and was evaluated separately.

3. Results and discussion

3.1 Analysis of variance

Significant genetic variation in the experimental material was demonstrated by the combined analysis of variance, which showed highly significant differences between the treatments for every character examined in both environments. Table 1(a,b,c) displays the combined analysis of variance for the characteristics under study. For every attribute, the treatment mean squares were significant at the 1% level. For most of the features, the research also revealed significant variation between parents and within both the F₁ and F₂ generations, indicating that there is enough variation for additional genetic investigation and selection. However, the stress tolerance index is a derived index calculated from yield performance across two sowing conditions was not included in . Table 1(a,b,c) presents the analysis of variance for the Parents, F₁, and F₂ generations, confirming significant variation among the assessed populations. The present study's significant treatment effects suggest that the parental combinations produced substantial variation in the segregating populations.

3.2 Genetic variability for physio-morphological traits

The data for mean, range, genotypic variance (σ^2_g), phenotypic variance (σ^2_p), heritability, genetic advance (GA), genetic advance as percentage of mean (GAM), GCV and PCV are given in Table 2 and

Table 3 for the two generations (F₁ and F₂) under the two sowing dates (normal and late) for the different characteristics studied. For days to 50% heading, the mean was 76.74 days for F₁ and 78.25 days for F₂ under normal sowing while under late sowing the means obtained were 72.23 days and 73.10 days respectively for F₁ and F₂. GCV and PCV were close to each other in both generations. Under normal sowing, GCV and PCV were 4.55% and 5.01% in F₁, and 3.87% and 4.39% in F₂. Under late sowing, GCV and PCV were 4.79% and 5.26% in F₁, and 3.16% and 3.92% in F₂. This suggested that heading time was not greatly influenced by the environment. Heritability for days to 50% heading was 82.43% in F₁ and 77.46% in F₂ under normal sowing, and 83.03% in F₁ and 64.86% in F₂ under late sowing, with a corresponding GAM of 8.50% in F₁ and 7.01% in F₂ under normal sowing, and 8.99% in F₁ and 5.24% in F₂ under late sowing.

Days to maturity followed the same pattern: the mean was 120.04 days in F₁ and 121.76 days in F₂ under normal sowing, and 117.11 days in F₁ and 118.68 days in F₂ under late sowing, with GCV and PCV of 3.58% and 3.83% in F₁ under normal sowing, and 3.59% and 3.85% in F₁ under late sowing, and 2.71% and 3.10% in F₂ under normal sowing, and 2.51% and 3.11% in F₂ under late sowing. Heritability for maturity was 87.33% in F₁ and 76.57% in F₂ under normal sowing, and 87.19% in F₁ and 65.38% in F₂ under late sowing, with a corresponding GAM of 6.89% in F₁ and 4.89% in F₂ under normal sowing, and 6.91% in F₁ and 4.19% in F₂ under late sowing. The high heritability coupled with low GAM for both the phenological traits indicated that the genotypic differences contribute largely to the phenotypic differences of both the traits, but the absolute genetic variation available among the available lines and testers was small, resulting in low gain possible through direct selection; similarly, the low GCV, PCV and GA for days to heading and days to maturity have been reported in other heat stress studies of wheat (Hossain *et al.*, 2021; Karla *et al.*, 2023) [5, 7].

Plant height showed considerably greater variability than the phenological traits. The mean was 96.00 cm in F₁ and 91.76 cm in F₂ under normal sowing, and 86.65 cm in F₁ and 83.15 cm in F₂ under late sowing. GCV and PCV were closely matched in F₁ i.e. 7.46% and 8.68% under normal sowing while 8.46% and 9.61% under late sowing, with high heritability (73.96% N; 77.44% L) and moderate GAM (13.22% N; 15.34% L) in F₁ indicating an increase in the environmental variance contribution. In F₂, heritability declined under both environments (63.88% N; 54.64% L) while GAM remained broadly similar (11.35% N; 9.92% L), pointing to an increase in the relative contribution of environmental variance to plant height after segregation. The decrease in heritability between generations, coupled with no genetic advance change, was similar to the results reported for segregating wheat populations under heat stress (Kiranakumara *et al.*, 2024) [10] for morphological traits.

Flag leaf area recorded the widest genetic variability among the growth traits. GCV and PCV were 20.90% and 22.45% in F₁ under normal sowing, 21.63% and 23.92% in F₁ under late sowing, 16.28% and 17.60% in F₂ under normal sowing, and 14.37% and 15.88% in F₂ under late sowing. The heritability values for flag leaf area were 86.69% in the F₁ and 85.61% in the F₂ for normal sowing and 81.81% in F₁ and 81.90% in F₂ for late sowing while the heritability for GAM under normal sowing was 40.09% in the F₁ and 31.03% in the F₂ and under late sowing was 40.31% in the F₁ and 26.79% in the F₂; the highest values were recorded in flag leaf area and the GAM for normal sowing which were retained almost undiminished from F₁ to F₂.

Productive tillers per plant showed heritability of 90.88% and GAM of 40.17% in F₁ under normal sowing, and 83.87% and 32.36% under late sowing; in F₂, heritability was 83.81% and GAM 31.04% under normal sowing, and 78.78% and 26.68% under late sowing. GCV and PCV for productive tillers per plant were 20.45% and 21.46% in F₁ under normal sowing, and 17.15% and 18.73% under late sowing; in F₂, GCV and PCV were 16.46% and 17.98% under normal sowing, and 14.59% and 16.44% under late sowing.

Total tillers per plant showed heritability of 92.12% and GAM 41.00% in F₁ under normal sowing, and 84.15% and 32.60% under late sowing; in F₂, heritability was 83.42% and GAM 31.51% under normal sowing, and 79.84% and 29.06% under late sowing. GCV and PCV for total tillers per plant were 20.74% and 21.61% in F₁ under normal sowing, and 17.25% and 18.81% under late sowing. In F₂, GCV and PCV were 16.74% and 18.33% under normal sowing, and 15.79% and 17.67% under late sowing, although the absolute means for both tillering traits were markedly lower under late sowing (e.g., productive tillers per plant fell from 6.75 to 4.78 in F₁ and from 6.43 to 4.58 in F₂). High heritability coupled with high genetic advance for flag leaf area and tillering traits has similarly been reported as evidence of substantial additively inherited variation and good selection potential in wheat evaluated under terminal heat stress (Hossain *et al.*, 2021; Das *et al.*, 2024) [5, 4].

Number of spikelets per ear showed high heritability and moderate to high GAM in F₁ i.e. 83.06% and 25.77% under normal sowing while 72.16% and 19.92% under late sowing. GCV and PCV for spikelets per ear were 13.73% and 15.06% in F₁ under normal sowing while 11.38% and 13.40% in F₁ under late sowing. In F₂, GCV and PCV were 7.60% and 10.96% under normal sowing, and 9.96% and 12.78% under late sowing. In F₂, however, heritability and GAM declined markedly, particularly under normal sowing, where heritability fell to 48.11% (moderate) and GAM to 10.86%.

Number of grains per spike showed an increase in both heritability and GAM in F₁ i.e. from 53.61% and 16.75% under normal sowing to 68.87% and 22.11% under late sowing. While in F₂, heritability and GAM was 61.07% and 13.89% under normal sowing and 69.48% and 19.67% under late sowing. GCV and PCV for grains per spike were 12.93% and 15.58% in F₁ under normal sowing, and 11.10% and 15.17% in F₁ under late sowing. In F₂, GCV and PCV were 8.63% and 11.04% under normal sowing, and 11.45% and 13.74% under late sowing. This separation of the two ear-component traits: the variance for spikelets per ear decreased in F₂ but remained or increased under heat stress conditions, while the variance for grains per spike did not. This suggests that genetic variation for spike-related traits was not uniformly lost because of terminal heat stress in this material, and is generally consistent with reports that genetic variation for individual yield-component traits can vary because of terminal heat stress even within the same trial. (Karla *et al.*, 2023; Das *et al.*, 2024) [7, 4].

Biological yield per plant combined high heritability with high GAM in both generations and environments: in F₁, heritability was 92.87% and GAM 38.58% under normal sowing, and 89.43% and 36.82% under late sowing. In F₂, heritability was 88.19% and GAM 27.30% under normal sowing, and 91.03% and 34.68% under late sowing, making it one of the most consistently reliable traits identified in this study. GCV and PCV for biological yield were 19.43% and 20.17% in F₁ under normal sowing, and 18.90% and 19.99% in F₁ under late sowing; in F₂, GCV and PCV were 14.11% and 15.03% under normal sowing, and 17.64% and 18.49% under late sowing.

Harvest index also showed high heritability but only moderate GAM: 83.68% and 17.42% in F₁ under normal sowing, 79.13% and 16.64% in F₁ under late sowing, 79.96% and 13.72% in F₂ under normal sowing, and 77.98% and 16.26% in F₂ under late sowing. This indicates that although harvest index is strongly under genetic control, the expected gain from direct selection on the ratio itself is smaller than that expected from selection on biological yield. GCV and PCV for harvest index were 9.24% and 10.11% in F₁ under normal sowing, and 9.08% and 10.21% in F₁ under late sowing; in F₂, GCV and PCV were 7.45% and 8.33% under normal sowing, and 8.94% and 10.12% under late sowing.

1000-grain weight showed high heritability with moderate GAM in F₁ i.e. 75.13% and 19.20% under normal sowing, and 62.03% and 13.45% under late sowing. In F₂, heritability was 70.52% and GAM 17.33% under normal sowing, and heritability fell to 56.93% and GAM to 12.45% under late sowing while the lowest heritability among the yield-component traits, recorded under the combined stress of late sowing and segregation, suggesting that grain-filling under

heat stress became progressively more environment-sensitive in the F₂ generation. GCV and PCV for 1000-grain weight were 10.75% and 12.40% in F₁ under normal sowing, and 8.29% and 10.53% in F₁ under late sowing; in F₂, GCV and PCV were 10.02% and 11.93% under normal sowing, and 8.01% and 10.61% under late sowing. High heritability with appreciable genetic advance for biological yield, harvest index and 1000-grain weight has similarly been documented as favourable for selection in wheat breeding populations evaluated under heat stress (Hossain *et al.*, 2021; Kiranakumara *et al.*, 2024) [5, 10].

Grain yield per plant, the principal economic trait, combined high heritability with high GAM in both generations and under both sowing conditions: in F₁, heritability was 95.33% and GAM 47.78% under normal sowing, and 93.05% and 41.46% under late sowing; in F₂, heritability was 89.01% and GAM 31.68% under normal sowing, and 87.99% and 34.53% under late sowing, thus the most favourable and stable combination recorded for any single trait in this study. GCV and PCV for grain yield per plant were 23.76% and 24.33% in F₁ under normal sowing, and 20.86% and 21.63% in F₁ under late sowing; in F₂, GCV and PCV were 16.30% and 17.28% under normal sowing, and 17.87% and 19.05% under late sowing. Its mean fell from 16.62 g to 10.52 g (F₁) and 15.57 g to 10.42 g (F₂) between normal and late sowing, confirming the substantial yield penalty imposed by terminal heat stress even in the higher-performing crosses. The heritability and genetic advance for grain yield under non-stress (NS) and heat-stress (HS) conditions are very similar in this test of wheat genetic variability, and closely parallel the results from other wheat genetic-variability tests in which the grain yield has been found to have the highest and most consistent response to direct selection. (Thakur *et al.*, 2020; Karla *et al.*, 2023; Das *et al.*, 2024) [6, 7, 4].

Protein content showed moderate heritability with moderate GAM in F₁ i.e. 68.95% and 12.79% under normal sowing while 70.08% and 14.56% under late sowing. This declined markedly in F₂ i.e. 45.68% and 8.51% under normal sowing and 53.43% and 9.54% under late sowing, indicating that genetic variance for grain protein content, while appreciable in the F₁ hybrids, was substantially reduced in the segregating F₂ population and should not be assumed to respond strongly to direct selection at this generation. GCV and PCV for protein content were 7.48% and 9.00% in F₁ under normal sowing, and 8.44% and 10.08% in F₁ under late sowing; in F₂, GCV and PCV were 6.12% and 9.05% under normal sowing, and 6.34% and 8.67% under late sowing. This contrasts with the very high, stably inherited protein-content heritability reported in some other legume and cereal variability studies, and instead more closely resembles cases where quality traits show a narrowing of exploitable genetic variance upon segregation (Kiranakumara *et al.*, 2024) [10].

Among the physiological heat-tolerance indicators, canopy temperature depression showed high heritability throughout: 90.65% in F₁ and 91.46% in F₂ under normal sowing, and 75.55% in F₁ and 85.68% in F₂ under late sowing, together with high GAM under normal sowing (33.21% in F₁; 34.97% in F₂) and moderate GAM under late sowing (17.37% in F₁; 26.36% in F₂), indicating substantial additively inherited variation for canopy cooling capacity. GCV and PCV for canopy temperature depression were 16.93% and 17.78% in F₁ under normal sowing, and 9.70% and 11.16% in F₁ under late sowing; in F₂, GCV and PCV were 17.75% and 18.56% under normal sowing, and 13.83% and 14.94% under late sowing.

Pollen viability, despite its direct relevance to fertility under heat stress, showed the same high heritability and low GAM pattern observed for the phenological traits. Heritability was 63.61% in F₁ and 73.39% in F₂ under normal sowing while 61.50% in F₁ and 51.98% in F₂ under late sowing, with GAM of only 4.85% in F₁ and 6.38% in F₂ under normal sowing, and 6.33% in F₁ and 5.74% in F₂ under late sowing, suggesting a comparatively narrow range of genetic variation among these crosses for pollen thermotolerance despite its biological importance; a similarly limited genetic advance for pollen viability relative to its heritability has been reported in heat-stress screening of wheat, where pollen-viability-based indices were nonetheless found

useful as an indirect, rather than a direct, selection criterion (Khan *et al.*, 2022; Khan *et al.*, 2026) [11, 8]. GCV and PCV for pollen viability were 2.95% and 3.70% in F₁ under normal sowing, and 3.92% and 5.00% in F₁ under late sowing; in F₂, GCV and PCV were 3.62% and 4.22% under normal sowing, and 3.87% and 5.37% under late sowing.

Proline content showed the largest stress-induced increase in genetic advance of any trait measured, with GAM rising from 31.86% (F₁, N) to 46.03% (F₁, L) and from 36.10% (F₂, N) to 51.19% (F₂, L). While heritability remained high throughout i.e. 92.16% in F₁ and 92.13% in F₂ under normal sowing, and 95.79% in F₁ and 95.74% in F₂ under late sowing. GCV and PCV for proline content were 16.11% and 16.78% in F₁ under normal sowing, and 22.83% and 23.33% in F₁ under late sowing; in F₂, GCV and PCV were 18.26% and 19.02% under normal sowing, and 25.40% and 25.96% under late sowing.

For heat injury, the pattern was similar: heritability was high (87.23% and 90.94% under normal sowing; and 90.18% and 87.45% under late sowing) and GAM was 34.20% and 31.99% under normal sowing and 42.41% and 32.53% under late sowing. GCV and PCV for heat injury were 17.77% and 19.03% in F₁ under normal sowing, and 21.68% and 22.83% in F₁ under late sowing; in F₂, GCV and PCV were 16.29% and 17.08% under normal sowing, and 16.89% and 18.06% under late sowing. Both are direct physiological responses to heat stress, and their increasing heritability and genetic advance with late sowing suggest that selection for the traits under heat stress, rather

than adding environmental variation, revealed and accentuated the genetic differences in these stress response mechanisms among the crosses as seen in screening under heat stress, where osmotic adjustment and tissue-damage traits were found to be important and highly discriminating under late-sown conditions (Thakur *et al.*, 2020; Lamba *et al.*, 2023) [6, 12].

Chlorophyll content, by contrast, showed high heritability with moderate to high GAM in F₁ i.e. 71.09% and 15.93% under normal sowing, and 76.20% and 20.40% under late sowing. Both parameters declined clearly in F₂ i.e. 51.28% and 10.82% under normal sowing and 46.94% and 10.04% under late sowing. GCV and PCV for chlorophyll content were 9.17% and 10.88% in F₁ under normal sowing, and 11.34% and 12.99% in F₁ under late sowing. In F₂, GCV and PCV were 7.34% and 10.25% under normal sowing, and 7.11% and 10.38% under late sowing.

Stress tolerance index showed very high heritability, 95.94% in F₁ and 91.56% in F₂, together with the highest GAM values recorded for any trait in this study, 78.54% in F₁ and 58.74% in F₂. GCV and PCV were 38.93% and 39.74% in F₁, and 29.80% and 31.14% in F₂. Because the underlying genotypic and phenotypic variances for both indices are very small in absolute terms (σ^2_g and σ^2_p on the order of 0.04-0.24), the derived percentage parameters are correspondingly sensitive to rounding in the source variance estimates, and the very high GAM values should be interpreted with this in mind rather than as evidence of an unusually large absolute genetic gain.

Table 1a. Combined analysis of variance for parent and hybrids of F₁ and F₂

Source	df	Days to 50% heading		Days to maturity		Plant height		Flag leaf area		Productive tillers/plant		Total tillers/plant	
		Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late
Replication	2	6.24	0.61	0.15	2.45	0.62	10.73	1.13	4.84	0.34	0.32	0.42	0.59
Treatment	158	41.36**	28.36**	52.93**	46.95**	171.52**	152.98**	135.39**	90.46**	4.56**	1.72**	6.10**	2.26**
PARENT	18	60.62**	23.54**	64.74**	59.66**	194.90**	144.07**	99.27**	63.91**	1.96**	0.89**	2.00**	0.41**
LINE(c)	13	44.38**	41.77**	80.43**	102.79**	356.58**	345.17**	353.01**	179.93**	5.41**	2.75**	6.88**	3.67**
TEST(c)	4	203.37**	208.51**	282.11**	174.82**	303.86**	270.05**	571.75**	247.04**	18.89**	8.70**	24.40**	11.01**
LXT (c)	52	25.16**	24.45**	35.26**	34.79**	115.76**	127.58**	100.95**	112.16**	5.04**	1.49**	6.75**	1.89**
F1s	69	39.11**	38.38**	58.08**	55.72**	172.03**	176.84**	175.73**	132.75**	5.91**	2.15**	7.80**	2.76**
F2s	69	30.11**	18.87**	36.01**	31.44**	142.57**	112.41**	106.73**	57.24**	3.58**	1.46**	4.92**	2.28**
P v F1s	1	606.53**	61.89**	601.75**	176.28**	262.20**	30.23	107.05**	11.74	28.23**	3.85**	50.58**	2.07**
P v F2s	1	211.78**	4.26	168.70**	7.59	147.55**	837.56**	97.88**	31.59	9.97**	0.38	28.99**	0.76
Error	316	2.64	2.75	3.16	3.71	19.49	18.53	7.01	6.71	0.20	0.12	0.26	0.17
Total	476	15.51	11.24	19.67	18.06	69.88	63.13	49.60	34.50	1.65	0.65	2.20	0.87

Table 1b. Combined analysis of variance for parent and hybrids of F₁ and F₂

Source	df	Number of spikelets/ears		Number of grains/spike		Biological yield per plant		Harvest index		1000-grain weight		Protein content	
		Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late
Replication	2	1.94	0.86	5.28	6.17	3.09	0.96	6.83	3.72	12.47	17.68	0.09	0.16
Treatment	158	18.19**	10.48**	148.41**	92.16**	103.36**	56.03**	49.17**	53.47**	69.08**	34.61**	2.30**	2.58**
PARENT	18	5.19*	6.40**	67.38**	56.76**	68.73**	58.09**	18.56**	53.89**	40.22**	15.62**	1.56*	1.95**
LINE(c)	13	16.68**	11.21**	87.16**	117.52**	261.75**	97.05**	60.90**	55.25**	151.27**	63.97**	3.37**	7.98**
TEST(c)	4	130.79**	8.95**	940.05**	50.14**	403.82**	170.49**	317.44**	231.97**	208.94**	102.05**	11.26**	7.33**
LXT (c)	52	20.81**	12.76**	160.20**	100.18**	89.14**	42.71**	42.79**	41.79**	47.78**	26.22**	1.83**	1.82**
F1s	69	26.40**	12.24**	191.65**	100.55**	139.90**	60.35**	62.12**	55.35**	76.62**	37.73**	2.67**	3.30**
F2s	69	9.07**	9.26**	79.97**	87.28**	68.66**	52.77**	39.65**	52.44**	61.03**	34.18**	2.19**	2.08**
P v F1s	1	261.49**	17.82**	3245.19**	370.47**	642.34**	0.66	409.70**	14.53**	267.60**	3.03	0.40	0.08
P v F2s	1	55.94**	0.27	1230.26**	38.37	228.53**	0.00	221.10**	0.07	0.02	111.65**	0.08	0.58
Error	316	2.02	1.50	18.28	15.67	3.39	2.13	4.26	6.29	7.12	6.43	0.49	0.41
Total	476	7.39	4.48	61.42	41.02	36.57	20.01	19.18	21.94	27.71	15.83	1.09	1.13

Table 1c. Combined analysis of variance for parent and hybrids of F₁ and F₂

Source	df	Canopy temperature depression		Pollen viability		Proline content		Heat injury		Chlorophyll content		Grain yield/plant	
		Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late	Normal	Late
Replication	2	0.09	0.39	0.48	1.25	0.73	0.45	2.79	8.01	2.82	5.96	2.96	0.20
Treatment	158	0.94**	1.79**	36.03**	46.27**	22.47**	175.16**	84.82**	186.07**	54.07**	53.90**	33.50**	12.24**
PARENT	18	1.73**	2.47**	2.39**	30.10**	34.88**	32.01**	87.67**	135.87**	47.39**	48.66**	13.10**	8.86**
LINE(c)	13	2.72**	3.04**	17.57**	34.87**	56.47**	269.48**	207.93**	346.31**	61.96**	122.94**	79.84**	17.78**
TEST(c)	4	1.14**	2.66**	21.75**	35.31**	52.41**	586.67**	179.93**	1318.93**	258.71**	106.62**	141.28**	22.83**
LXT (c)	52	0.30**	0.54**	30.01**	46.02**	6.35**	92.62**	56.92**	132.55**	48.94**	59.98**	32.21**	13.47**
F1s	69	0.81**	1.13**	27.19**	43.29**	18.46**	154.58**	92.51**	241.60**	63.55**	74.54**	47.51**	14.82**
F2s	69	0.86**	1.89**	37.11**	43.45**	23.71**	154.46**	78.57**	148.58**	44.53**	35.90**	20.13**	10.87**
P v F1s	1	2.33**	20.67**	597.64**	80.93**	11.22**	5706.88**	0.17	27.99	121.47**	11.29**	367.57**	0.91
P v F2s	1	1.53**	2.83**	1198.60**	549.46**	11.33**	2952.12**	5.41	24.69	4.68	0.59	148.68**	0.06
Error	316	0.03	0.11	3.81	9.06	0.66	2.30	3.35	7.41	8.68	8.01	0.75	0.43
Total	476	0.33	0.67	14.49	21.38	7.90	59.67	30.39	66.72	23.72	23.23	11.63	4.35

*, ** significant at 5% and 1% level, respectively

Table 2. Mean, range and genetic variability parameters for different traits in the F₁ generation under normal (N) and late-sown (L) conditions.

Characters	Envi	Mean	Min	Max	var (g)	var (p)	Heritability (%)	GA	GA% mean	GCV (%)	PCV (%)
Days to 50% heading	N	76.74	70.00	85.67	12.17	14.77	82.43	6.53	8.50	4.55	5.01
	L	72.23	65.33	81.67	11.98	14.43	83.03	6.50	8.99	4.79	5.26
Days to maturity	N	120.04	111.33	129.67	18.47	21.15	87.33	8.27	6.89	3.58	3.83
	L	117.11	108.67	126.67	17.70	20.31	87.19	8.09	6.91	3.59	3.85
Plant height	N	96.00	82.31	114.97	51.32	69.38	73.96	12.69	13.22	7.46	8.68
	L	86.65	70.53	103.68	53.73	69.38	77.44	13.29	15.34	8.46	9.61
Flag leaf area	N	35.72	19.08	53.64	55.73	64.28	86.69	14.32	40.09	20.90	22.45
	L	29.67	17.32	50.46	41.20	50.35	81.81	11.96	40.31	21.63	23.92
Productive tillers/plant	N	6.75	3.73	9.60	1.91	2.10	90.88	2.71	40.17	20.45	21.46
	L	4.78	3.00	6.93	0.67	0.80	83.87	1.55	32.36	17.15	18.73
Total tillers/plant	N	7.67	4.27	10.93	2.53	2.74	92.12	3.14	41.00	20.74	21.61
	L	5.39	3.20	7.47	0.86	1.03	84.15	1.76	32.60	17.25	18.81
Number of spikelets/ears	N	20.91	13.93	26.20	8.24	9.92	83.06	5.39	25.77	13.73	15.06
	L	16.71	11.73	21.47	3.62	5.01	72.16	3.33	19.92	11.38	13.40
Number of grains/spike	N	57.62	41.80	73.53	55.52	80.61	68.87	12.74	22.11	12.93	15.58
	L	45.93	32.53	59.27	26.01	48.52	53.61	7.69	16.75	11.10	15.17
Biological yield per plant	N	34.70	22.22	53.31	45.47	48.96	92.87	13.39	38.58	19.43	20.17
	L	23.27	11.09	33.16	19.36	21.64	89.43	8.57	36.82	18.90	19.99
Harvest index	N	47.70	34.41	53.45	19.45	23.24	83.68	8.31	17.42	9.24	10.11
	L	45.34	34.80	52.59	16.96	21.43	79.13	7.55	16.64	9.08	10.21
1000-grain weight	N	44.62	35.79	55.56	23.00	30.62	75.13	8.56	19.20	10.75	12.40
	L	38.98	32.01	49.90	10.44	16.84	62.03	5.24	13.45	8.29	10.53
Protein content	N	11.77	9.23	13.75	0.77	1.12	68.95	1.51	12.79	7.48	9.00
	L	11.63	9.02	15.07	0.96	1.38	70.08	1.69	14.56	8.44	10.08
Canopy temperature depression	N	3.01	1.77	3.80	0.26	0.29	90.65	1.00	33.21	16.93	17.78
	L	6.02	4.20	6.93	0.34	0.45	75.55	1.05	17.37	9.70	11.16
Pollen viability	N	93.34	86.85	98.31	7.60	11.96	63.61	4.53	4.85	2.95	3.70
	L	88.19	79.55	94.49	11.94	19.41	61.50	5.58	6.33	3.92	5.00
Proline content	N	15.19	10.16	20.93	5.98	6.49	92.16	4.84	31.86	16.11	16.78
	L	31.21	14.18	46.15	50.78	53.01	95.79	14.37	46.03	22.83	23.33
Heat injury	N	30.50	23.36	47.30	29.40	33.70	87.23	10.43	34.20	17.77	19.03
	L	40.66	26.73	63.33	77.71	86.18	90.18	17.25	42.41	21.68	22.83
Chlorophyll content	N	47.08	36.28	55.51	18.65	26.24	71.09	7.50	15.93	9.17	10.88
	L	41.83	31.64	52.19	22.51	29.53	76.20	8.53	20.40	11.34	12.99
Grain yield/plant	N	16.62	10.91	26.63	15.58	16.35	95.33	7.94	47.78	23.76	24.33
	L	10.52	5.30	16.39	4.82	5.18	93.05	4.36	41.46	20.86	21.63
Stress tolerance index		0.65	0.21	1.58	0.06	0.07	95.94	0.51	78.54	38.93	39.74

Table 3. Mean, range and genetic variability parameters for different traits in the F₂ generation under normal (N) and late-sown (L) conditions.

Characters	Envi.	Mean	Min	Max	var (g)	var (p)	Heritability (%)	GA	GA% mean	GCV (%)	PCV (%)
Days to 50% heading	N	78.25	72.00	85.00	9.15	11.81	77.46	5.48	7.01	3.87	4.39
	L	73.10	69.33	81.00	5.33	8.21	64.86	3.83	5.24	3.16	3.92
Days to maturity	N	121.76	116.33	131.33	10.89	14.23	76.57	5.95	4.89	2.71	3.10
	L	118.68	112.33	126.67	8.91	13.62	65.38	4.97	4.19	2.51	3.11
Plant height	N	91.76	75.79	107.29	39.99	62.60	63.88	10.41	11.35	6.89	8.62
	L	83.15	70.66	99.33	29.35	53.71	54.64	8.25	9.92	6.52	8.81
Flag leaf area	N	35.65	19.89	47.76	33.69	39.35	85.61	11.06	31.03	16.28	17.60
	L	29.34	16.81	39.61	17.77	21.70	81.90	7.86	26.79	14.37	15.88
Productive tillers/plant	N	6.43	4.13	8.93	1.12	1.34	83.81	2.00	31.04	16.46	17.98
	L	4.58	3.33	6.33	0.45	0.57	78.78	1.22	26.68	14.59	16.44

(continued on next page)

Characters	Envi.	Mean	Min	Max	var (g)	var (p)	Heritability (%)	GA	GA% mean	GCV (%)	PCV (%)
Total tillers/plant	N	7.41	4.53	10.47	1.54	1.84	83.42	2.33	31.51	16.74	18.33
	L	5.31	3.67	7.53	0.70	0.88	79.84	1.54	29.06	15.79	17.67
Number of spikelets/ears	N	19.62	16.00	23.87	2.22	4.62	48.11	2.13	10.86	7.60	10.96
	L	16.00	12.33	20.20	2.54	4.18	60.74	2.56	15.99	9.96	12.78
Number of grains/spike	N	54.35	45.13	65.93	21.98	36.00	61.07	7.55	13.89	8.63	11.04
	L	43.98	30.40	59.60	25.38	36.53	69.48	8.65	19.67	11.45	13.74
Biological yield per plant	N	33.17	22.12	44.67	21.91	24.84	88.19	9.06	27.30	14.11	15.03
	L	23.39	13.41	33.96	17.03	18.71	91.03	8.11	34.68	17.64	18.49
Harvest index	N	46.90	35.71	52.29	12.20	15.26	79.96	6.43	13.72	7.45	8.33
	L	44.73	33.50	51.67	15.98	20.49	77.98	7.27	16.26	8.94	10.12
1000-grain weight	N	42.19	32.14	51.86	17.86	25.32	70.52	7.31	17.33	10.02	11.93
	L	37.67	29.73	45.57	9.10	15.98	56.93	4.69	12.45	8.01	10.61
Protein content	N	11.82	9.17	13.52	0.52	1.14	45.68	1.01	8.51	6.12	9.05
	L	11.56	9.30	13.54	0.54	1.00	53.43	1.10	9.54	6.34	8.67
Canopy temperature depression	N	2.97	1.40	3.70	0.28	0.30	91.46	1.04	34.97	17.75	18.56
	L	5.59	3.57	6.93	0.60	0.70	85.68	1.47	26.36	13.83	14.94
Pollen viability	N	91.82	84.01	98.64	11.04	15.04	73.39	5.86	6.38	3.62	4.22
	L	86.03	78.73	94.54	11.07	21.30	51.98	4.94	5.74	3.87	5.37
Proline content	N	15.18	8.80	22.24	7.69	8.34	92.13	5.48	36.10	18.26	19.02
	L	28.04	11.46	43.89	50.74	52.99	95.74	14.36	51.19	25.40	25.96
Heat injury	N	30.91	24.09	46.65	25.35	27.87	90.94	9.89	31.99	16.29	17.08
	L	40.71	29.69	61.07	47.27	54.05	87.45	13.24	32.53	16.89	18.06
Chlorophyll content	N	45.76	35.51	53.85	11.27	21.99	51.28	4.95	10.82	7.34	10.25
	L	41.44	32.61	49.16	8.69	18.51	46.94	4.16	10.04	7.11	10.38
Grain yield/plant	N	15.57	10.16	21.07	6.44	7.24	89.01	4.93	31.68	16.30	17.28
	L	10.42	5.80	14.83	3.47	3.94	87.99	3.60	34.53	17.87	19.05
Stress tolerance index		0.68	0.24	1.29	0.04	0.04	91.56	0.40	58.74	29.80	31.14

var (g)=genotypic variance; var (p)= phenotypic variance; GA = genetic advance; GAM = genetic advance as percentage of mean; GCV/PCV = genotypic/phenotypic coefficient of variation; N = normal-sown condition; L = late-sown.

5. Conclusion

The present study showed that there is high level of genetic variability among wheat populations evaluated in the F₁ and F₂ generation for physio-morphological traits. PCV always surpassed over GCV for all traits and the differences were greater under heat stress for some physiological traits; this means that there was a higher contribution of environment in the phenotypic expression under terminal heat stress. Traits like grain yield per plant, biological yield per plant, flag leaf area, productive and total tillers per plant, proline content, heat injury, canopy temperature depression and the stress tolerance index showed high heritability coupled with high genetic advance as percentage of mean in both F₁ and F₂, indicating potential for direct selection in breeding programs. Heritability was high and genetic advance was low for days to 50% heading, days to maturity and pollen viability, suggesting that heritability alone is not a good guide when choosing traits for selection. The heritability decreased from F₁ to F₂ in the number of spikelets per ear, protein content and chlorophyll content, especially in the case of normal sowing, which means that it is necessary to continue monitoring the genetic parameters from generation to generation. The results are used to make data-driven choices of parents and segregants for future generations in this breeding programme to help develop heat tolerance and yield.

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