



RESEARCH ARTICLE

Genetic analysis of combining ability, heritability and genetic advance for morphological and biochemical traits in bread wheat (*Triticum aestivum* L.)

Anand Kumar^{1,2}, Laxmidas Verma³, Sagar¹, Prashant Kaushik⁴, D S Mishra⁵, Vikas Yadav^{6*}, Prakashbhai Ravat⁵, Prakash Yadav³, Aina Yadav⁷ & Ayush Yadav⁸

¹Faculty of Agricultural Sciences, GLA University, Mathura 281 406, Uttar Pradesh, India

²Chandra Shekhar Azad University of Agriculture and Technology, Kanpur 208 002, Uttar Pradesh, India

³Acharya Narendra Dev University of Agriculture and Technology, Kumarganj, Ayodhya 224 229, Uttar Pradesh, India

⁴Chaudhary Charan Singh Haryana Agricultural University, Hisar 125 001, Haryana, India

⁵ICAR-Central Institute of Agricultural Engineering (CIAH), Central Horticultural Experiment Station (CHES), Godhra 389 001, Gujarat, India

⁶ICAR-Central Institute for Arid Horticulture, Bichhwal, Bikaner 334 006, Rajasthan, India

⁷Department of Biotechnology, Shri Venkateshwara University, Gajraula 244 235, Uttar Pradesh, India

⁸Bundelkhand University, Jhansi 284 128, Uttar Pradesh, India

*Correspondence email - vikasyadav.hot@gmail.com

Received: 14 October 2025; Accepted: 11 March 2026; Available online: Version 1.0: 14 May 2026

Cite this article: Anand K, Laxmidas V, Sagar, Prashant K, Mishra DS, Vikas Y, Prakashbhai R, Prakash Y, Aina Y, Ayush Y. Genetic analysis of combining ability, heritability and genetic advance for morphological and biochemical traits in bread wheat (*Triticum aestivum* L.). Plant Science Today. 2026;13(sp2):01–11. <https://doi.org/10.14719/pst.12261>

Abstract

A total of 15 genetically diverse wheat genotypes (10 lines and 5 testers) and their fifty F₁ hybrids were evaluated for 15 traits under normal conditions at the Agricultural Research Farm of Chandra Shekhar Azad University of Agriculture and Technology in Kanpur, India. Analysis of variance showed highly significant mean squares for general combining ability (GCA) and specific combining ability (SCA), indicating both additive and non-additive gene actions. Parental genotypes PBW-343, DBW-39, K-402, K-1317, KRL-210 and K-68 exhibited strong GCA effects, identifying them as good general combiners. Significant positive SCA effects for grain yield were observed in hybrids HD-3086 × HD-3171, K-402 × K-9107, K-1317 × K-9107, HD-2967 × K-0307 and K-402 × K-68, indicating the contribution of non-additive genetic effects in these specific cross combinations. In contrast, moderate to high heritability estimates for plant height (77.32 %), biological yield (59.52 %) and grain yield (68.76 %), together with moderate genetic advance for harvest index (11.72 %) and grain yield (13.15 %), suggest a substantial additive genetic component. Collectively, these findings indicate that both additive and non-additive gene actions influence yield-related traits, supporting the use of integrated breeding approaches that combine heterosis exploitation with selection-based improvement.

Keywords: bread wheat; genetic advance; general combining ability; heritability; specific combining ability

Introduction

Bread wheat (*Triticum aestivum* L.) is a major cereal crop that contributes substantially to global food and nutritional security. It provides a significant proportion of daily caloric and protein intake and serves as an important component of livestock feed. With the global population projected to approach 10 billion by 2050, sustainable increases in wheat productivity are essential, particularly in developing countries where food demand is rapidly rising (1). With consideration of the global population reaching 10 billion by 2050, efficient and sustainable intensification of wheat yields and productivity is essential to fulfil the empty stomachs of the global population, with major consideration to poor, underdeveloped countries. To fulfil the global demand, well-established, sustainable demands-oriented intensive researches are needed which will improve the agronomic practices through intensive breeding programmes (2, 3). Moreover, mono-cultivation of some elite

varieties has reduced genetic load and diversity due to only production-based strategy and selective breeding, which provides a path to enhancing vulnerability to biological diseases (4). In the current scenario, sustaining genetic variability is critical for long-term productivity and adaptability (5). When sufficient variability exists, simple selection can achieve genetic improvement; however, under limited variability, hybridisation becomes indispensable to generate diversity (6, 7). The success of such breeding programmes depends on the identification of appropriate parental lines, which can be evaluated using biometrical approaches such as diallel and line × tester analyses (8). Among these, the line × tester design remains a robust method for assessing general and specific combining ability, gene action and genotype interactions, thereby facilitating the identification of superior parents and hybrids (9). Enhancing inter-population diversity through genetically divergent parental groups has also been reported to improve hybrid

performance (10).

Understanding the inheritance of yield and its component traits requires the estimation of quantitative genetic parameters. Heritability measures the proportion of phenotypic variation attributable to genetic factors and provides insight into the predictability of trait transmission across generations (11). It is classified as broad-sense and narrow-sense, with narrow-sense heritability being particularly relevant for selection in segregating populations (12). However, heritability estimates may vary depending on environmental conditions, population structure and analytical approaches. Therefore, interpretation of heritability in conjunction with genetic advance provides a more reliable estimate of expected genetic gain (13, 14). Genetic advance serves as an indicator of selection efficiency and reflects the potential improvement achievable through selection (15). The combined assessment of heritability and genetic advance also helps infer the relative importance of additive and non-additive gene effects in trait expression (16, 17). Several studies have examined the genetic control of grain yield and related traits in wheat using such approaches (18). In this context, the present study was undertaken to estimate combining ability, gene action, heritability and genetic advance for grain yield and its component traits in bread wheat using a line $\times$ tester mating design, to identify suitable parental combinations and guide effective breeding strategies (19).

Materials and Methods

Parental genotypes and crossing

The experiment involved 15 genetically diverse wheat (*T. aestivum*) genotypes, comprising 10 female lines and 5 male testers. Crosses were made during the rabi season of 2018–2019 at the Cereals Section, Nawabganj Farm, Chandra Shekhar Azad University of Agriculture and Technology (CSAUA&T), Kanpur, following the line $\times$ tester design. The weather parameters (monthly minimum and maximum temperature ($^{\circ}\text{C}$) under the study period were recorded (Fig. 1) for better implementation of the results of the trial. Each of the 10 lines was crossed with all 5 testers, producing fifty F_1 hybrids that generated sufficient seed for subsequent evaluation. The parental genotypes included HD-2733, K-1317, DBW-88, K-402, HD-3086, WR-544, HD-2967, KRL-210, PBW-343 and DBW-39 as female lines, originating mainly from IARI (New Delhi), CSAUA&T

(Kanpur), IIWBR (Karnal), CSSRI (Karnal) and PAU (Ludhiana). The 5 male testers K-8962, K-9107, K-68, K-0307 (CSAUA&T, Kanpur) and HD-3171 (from IARI), New Delhi, were used to generate the hybrids. The parental lines, F_1 hybrids and their corresponding F_2 populations were evaluated during the rabi season of 2019–2020 under field conditions at the same location.

Development of F_1 and F_2 seeds, experimental site and agronomic practices

All 15 genotypes, comprising 10 female lines and 5 male testers, were sown during the rabi season of 2018–2019 to generate 50 F_1 hybrids using the line $\times$ tester mating design. The harvested F_1 seeds were sown during the rabi season of 2019–2020 for further evaluation. Half of the F_1 seeds from each cross were sent to the IIWBR Regional Station, India, for advancement of the generation for off-season nursery advancement to produce F_2 seeds, while the remaining half of the population was used to raise the F_1 generation. A total of 115 genotypes, including fifteen parents, 50 F_1 hybrids and 50 F_2 populations, were evaluated at the Agricultural Research Farm, CSAUA&T, Kanpur, India (2019–2020). The experiment was carried out in a randomised complete block design (RCBD) and 3 replications were established. Each parent and F_1 hybrid was planted in a single 3 m row, while the F_2 populations were sown in paired 3 m rows, with a spacing of 22.5 cm between rows and 10 cm between plants. The soil of the experimental field ranged from sandy loam to loam with a pH of 7.1. Uniform and recommended agronomic practices were followed during the study, including the application of 80 kg N, 60 kg P_2O_5 and 60 kg K_2O per hectare, along with 15 kg Zn and 8 kg B, supplemented by appropriate disease and weed management to ensure optimal crop growth and performance.

Data acquisition and analysis

Data of 15 traits were collected for both morphological and biochemical parameters. Morphological observations include days to 75 % flowering, plant height (cm), days to maturity, number of productive tillers per plant, flag leaf area (cm^2), spike length (cm), number of spikelets per spike, number of grains per spike, biological yield per plant (g), grain yield per plant (g), test weight (1000-grain weight, g) and harvest index (%). Harvest index was estimated as the ratio of grain yield to biological yield per plant $\times$ 100. Biochemical traits included seed hardness and phenol colour reaction, while protein content (%) was estimated using a

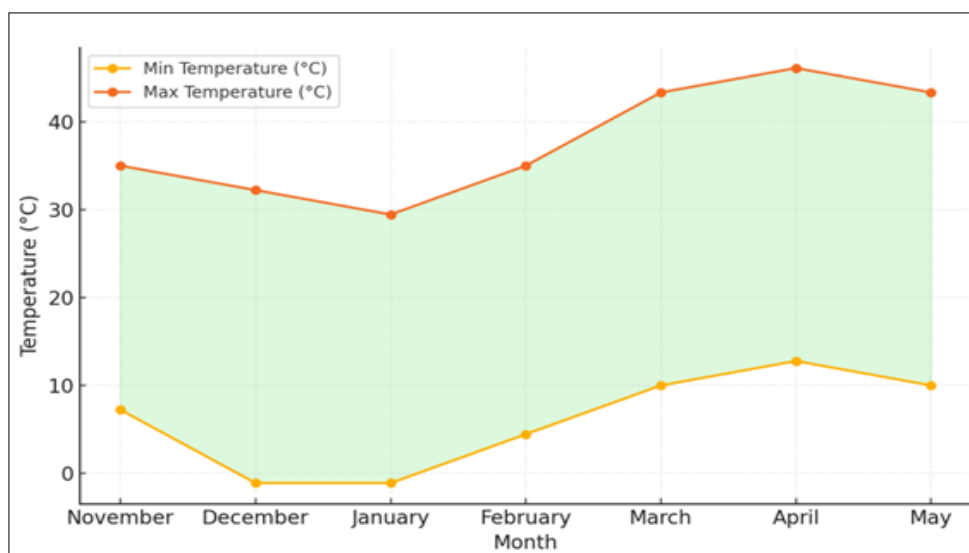


Fig. 1. Monthly minimum and maximum temperature ($^{\circ}\text{C}$) during the experimental period.

near-infrared spectroscope (NIRS DS-2500; Metrohm India Pvt. Ltd.) at CSAUA&T, Kanpur. Seed hardness was measured with an O.S.K. 20 seed hardness tester (Type E, 50 kg capacity) using the mean crushing pressure of 320 grains per treatment. The phenol colour reaction was determined by soaking seeds in water for 16–20 hr, followed by treatment with 1 % phenol solution and observing colour development after 3–4 hr. Crosses were carried out during the rabi season of 2018–2019 using standard emasculation and hand-pollination techniques. Female spikes were emasculated in the evening (16:00–18:00 hr) before anthesis and immediately bagged to prevent contamination. Pollination was performed the following morning (08:00–11:00 hr) using fresh pollen from the respective male testers. Pollinated spikes were re-bagged and labelled and approximately 20–25 spikes were crossed per combination to ensure sufficient F_1 seed set. Data were subjected to analysis of variance (ANOVA) using R software to assess variability among treatments. Combining ability analysis followed Sprague and Tatum and heritability (broad-sense and narrow-sense) was estimated using methods suggested by previous researchers (20, 21). The significance of treatment differences was tested using the least significant difference (LSD) at the 5 % level ($p < 0.05$), accounting for environmental effects such as temperature, soil and topography.

Results and Discussion

Analysis of variance for combining ability

The analysis of variance for combining ability (Fig. 2) revealed highly significant differences among crosses for all the studied traits, indicating the presence of substantial genetic variability among the parental genotypes and their hybrids. Significant mean squares due to lines, testers and line $\times$ tester interactions for most of the traits confirm the involvement of both additive and non-additive gene actions in the inheritance of yield and its related attributes. Across the evaluated traits, plant height, grain yield per plant, biological yield per plant and harvest index exhibited highly significant variation attributable to both line and tester effects, confirming that these traits are governed by a mixture of additive and dominant gene effects. Traits like days to flowering, number of productive tillers, spike length, number of grains per spike and flag leaf area

also showed notable line $\times$ tester interactions, emphasising the role of specific gene combinations contributing to hybrid performance.

The heatmap (Fig. 3) demonstrates the relative magnitude of mean squares, where higher intensity (blue-green gradient) indicates stronger genetic control. It showed that the tester effect was highest for biological yield/plant (2.63), grain yield/plant (2.17) and plant height (2.16), indicating strong tester influence. The line effect was prominent for harvest index (2.50), biological yield/plant (2.30) and grain yield/plant (2.20), reflecting additive gene action. Crosses showed higher effects for plant height (2.05) and harvest index (1.95), while line $\times$ tester interaction was comparatively low (0.25–1.75). Phenol colour reaction (0.34–0.63) and protein content (0.00–0.01) were observed with minimal variation, pointing out limited genetic influence. Traits such as biological yield per plant, grain yield per plant and harvest index showed the highest mean squares, suggesting their quantitative and polygenic inheritance, whereas phenol colour reaction and protein content exhibited lower values, reflecting limited genetic variability and greater environmental influence. The heatmap provides a clear depiction of genetic variance patterns, reflecting that yield-related and morphological traits are largely governed by both additive and dominance effects, while biochemical traits are less affected.

The significant line effects estimated for important agronomic traits like grain yield, test weight and plant height point out the importance of selecting genetically superior parents to exploit additive variance. The significant line $\times$ tester effects recorded for yield components indicate a predominant role of non-additive gene action, which can be effectively utilised in heterosis breeding programs and in boosting grain yield. This can be accomplished through better agronomic practices and thoughtfully designed hybridisation programs (22). When genetic variability is scarce within a crop, breeders primarily focus on creating that variability through a hybridisation programme (23). In this study, ANOVA showed significant differences between the parents and their crosses. This variability was especially evident in the hybrids, which displayed notable differences across all traits evaluated. The presence of such genetic diversity indicates that both the parental lines and their combinations hold great promise for future genetic enhancements (24).

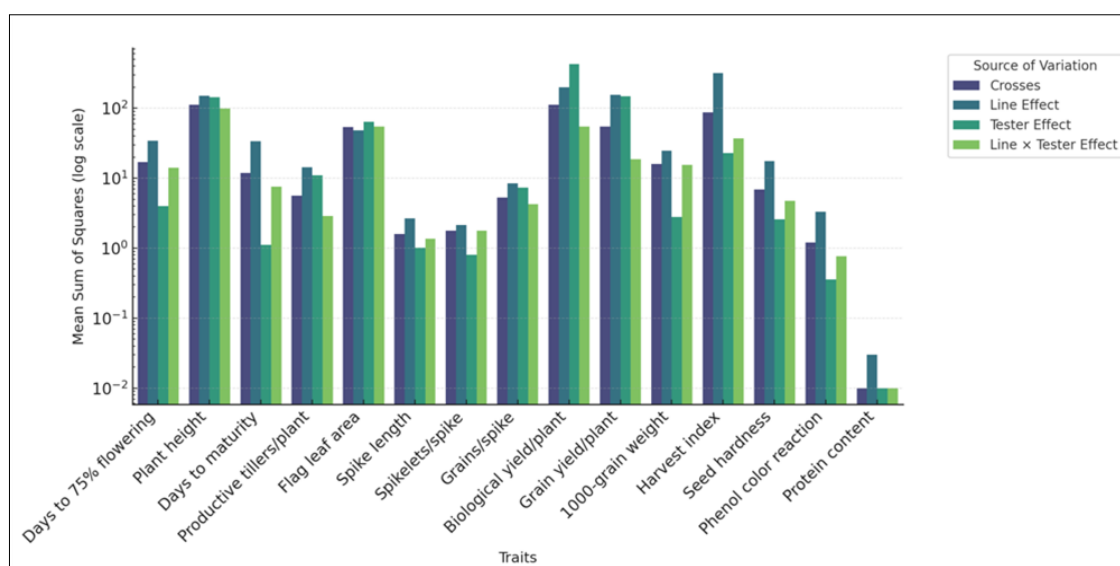


Fig. 2. Analysis of variance (ANOVA) of combining ability effects for 15 characters in F_1 of line $\times$ tester cross-analysis.

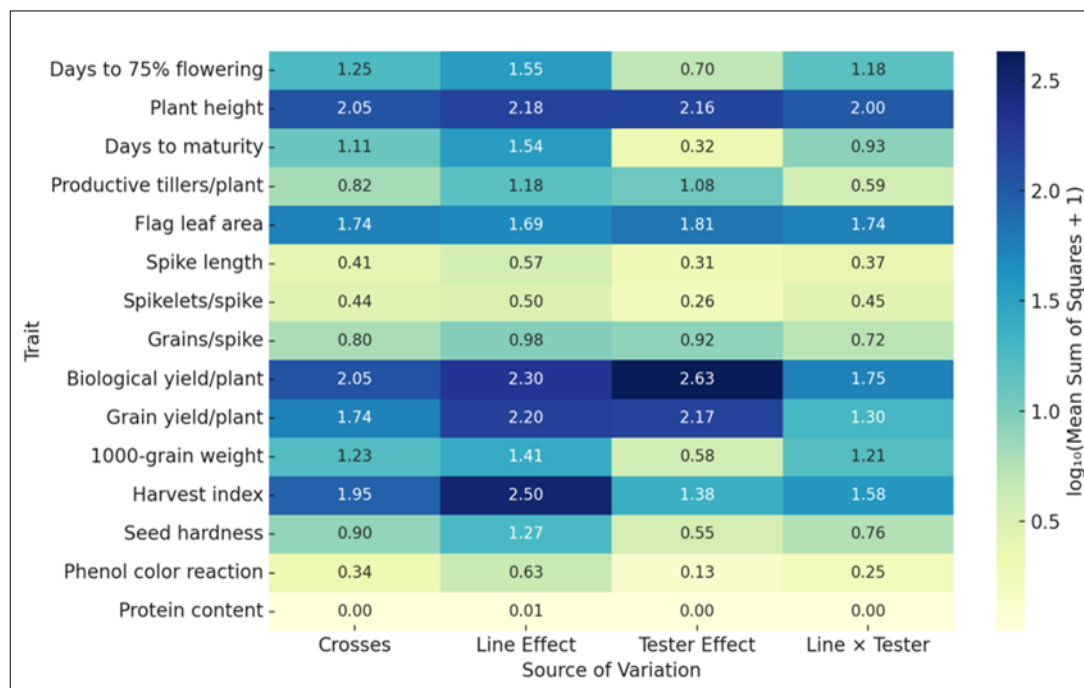


Fig. 3. Heatmap of combining ability effects for F_1 wheat.

Analysis of variance and gene action

Analysis of variance showed a significant genetic variation among wheat genotypes for grain yield and related traits, endorsing the presence of substantial variability. In the F_2 generation, combining ability variances were significant for all traits except protein content in crosses and line $\times$ tester interactions. Traits such as days to flowering, days to maturity, phenol colour reaction and protein content showed non-significant differences among testers, suggesting limited variability within male parents. In the F_1 generation, female parents had a greater influence on flag leaf area and test weight, while male parents significantly affected days to flowering. In the F_2 generation, the male component also contributed significantly to days to maturity and test weight, whereas both parental components were significant for most traits across generations. The phenol colour reaction was significant only in F_2 (Table 1). Estimates of genetic variance (δ^2g) were lower than specific variance (δ^2s) for all traits except flag leaf area and test

weight in F_1 , indicating a predominant role of non-additive gene action (Fig. 3). The δ^2g/δ^2s ratio being less than one and the average degree of dominance $[\delta^2s/\delta^2g]^{0.5} > 1$ across both generations, further confirmed the predominance of non-additive effects for most yield-related traits. These results are consistent with earlier studies that indicate both additive and non-additive gene actions play a role in the expression of complex traits (25). The differences in genetic estimates between the F_1 and F_2 generations, even when grown in similar conditions, could stem from a limited sampling of genetic variability in the F_2 generation or the effects of linkage (26). Repulsion phase linkage can increase non-additive variance by diminishing the expression of additive effects (27). However, in the F_2 generation, traits like days to flowering (75 %), seed hardness and phenol colour reaction showed a clear predominance of additive gene action.

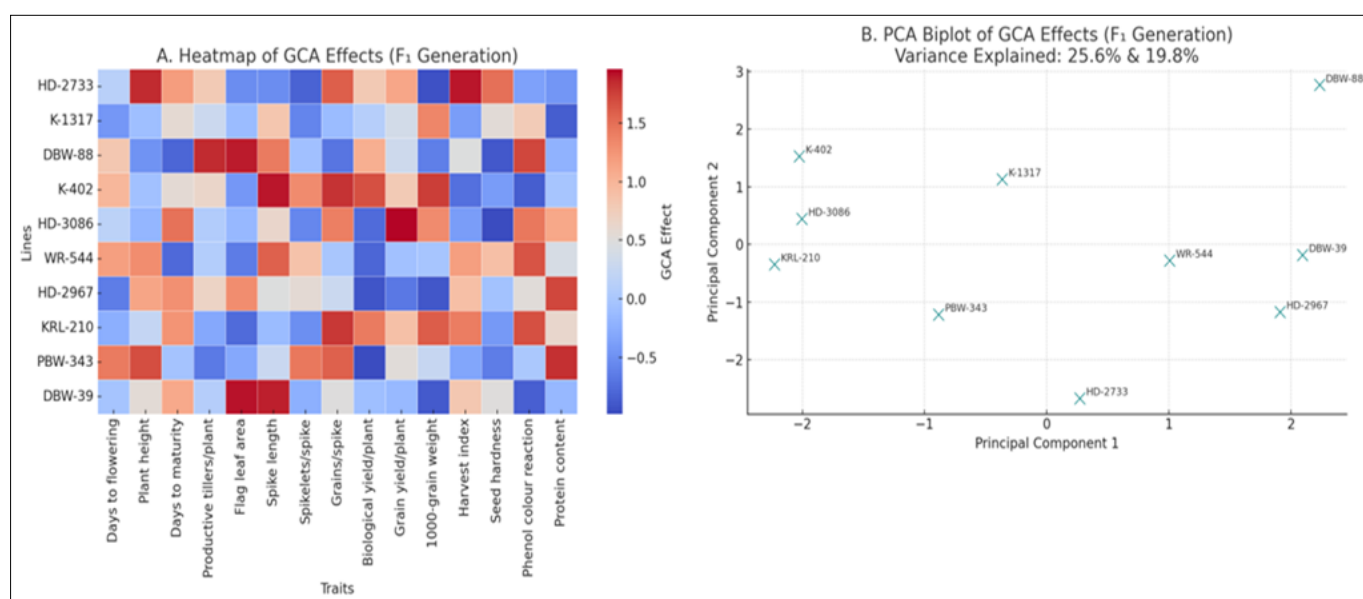


Fig. 4. The heatmap and principal component analysis (PCA) biplot of general combining ability (GCA) effects in F_1 among wheat parents for 15 traits.

Table 1. Genetic parameters showing heritability stability, selection efficiency and genetic control classification for 15 traits in F_1 and F_2 generations of wheat (*Triticum aestivum*)

Traits	F_1 Heritability	F_2 Heritability	F_1GA	F_2GA	Heritability (F_2/F_1 %)	GA stability (F_2/F_1 %)	Selection efficiency (F_2/F_1 %)	F_1 (GA/H $\bar{A}^2$)	Selection efficiency (F_2/F_1 %)	F_2 (GA/H $\bar{A}^2$)	Genetic control F_1	Genetic control F_2
Days to flowering	2	9.97	2.38	3.45	498.5	144.96	1.19	0.346	1.19	0.346	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Plant height	77.32	27.97	10.72	13.68	36.17	127.61	0.139	0.489	0.139	0.489	High (Additive)	Low (Environmental/Non-additive)
Days to maturity	22.78	30.98	0.7	2.31	136	330	0.031	0.075	0.031	0.075	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Productive tillers/plant	54.25	53.84	4.02	3.42	99.24	85.07	0.074	0.064	0.074	0.064	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Flag leaf area	90.49	21.4	4.51	8.17	23.65	181.15	0.05	0.382	0.05	0.382	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Spike length	32.26	24.94	2.28	1.8	77.31	78.95	0.071	0.072	0.071	0.072	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Spikelets/spike	14.14	15.78	2.26	1.74	111.6	76.99	0.16	0.11	0.16	0.11	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Grains/spike	18.95	18.93	5.1	3.99	99.89	78.24	0.269	0.211	0.269	0.211	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Biological yield/plant	59.52	60.35	23.15	22.42	101.39	96.85	0.389	0.371	0.389	0.371	Low (Environmental/Non-additive)	High (Additive)
Grain yield/plant	68.76	68.37	13.15	12.51	99.43	95.13	0.191	0.183	0.191	0.183	High (Additive)	High (Additive)
1000-grain weight	94.34	19.27	4.76	5.28	20.43	110.92	0.05	0.274	0.05	0.274	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Harvest index	54.32	54.83	11.72	11.58	100.94	98.81	0.216	0.211	0.216	0.211	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Seed hardness	61.08	35.92	1.71	3.08	58.81	180.12	0.028	0.086	0.028	0.086	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Phenol colour reaction	18	31.86	0.57	0.63	177	110.53	0.032	0.02	0.032	0.02	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)
Protein content	3.5	5.04	1.21	1.23	144	101.65	0.346	0.244	0.346	0.244	Low (Environmental/Non-additive)	Low (Environmental/Non-additive)

The table presents comparative values of narrow-sense heritability (H^2) and genetic advance (GA) in F_1 and F_2 generations, along with derived parameters, including heritability stability ratio ($F_2/F_1 \times 100$), genetic advance stability ratio ($F_2/F_1 \times 100$) and selection efficiency (GA/ H^2). Traits were further classified based on the magnitude of heritability and genetic advance into high (additive), moderate (additive + non-additive), or low (environmental/non-additive) genetic control categories. High heritability with high GA indicates the predominance of additive gene action, whereas low heritability and GA reflect the influence of environmental or dominance effects.

General combining ability effects

The heatmap and principal component analysis (PCA) biplot (Fig. 4) revealed significant variation in GCA in F_1 effects among wheat parents for 15 traits. Line K-1317 showed the highest positive GCA for biological yield/plant (+7.8), grain yield/plant (+7.5) and harvest index (+7.5), indicating strong general combining ability. K-402 and DBW-39 exhibited positive GCA for plant height (+7.9), flag leaf area (+2.0) and grain yield/plant (+2.7), while WR-544 and HD-2733 recorded negative GCA for yield traits (-2.5 to -3.8). Traits such as phenol colour reaction (-0.58 to +0.42) and protein content (-0.09 to +0.08) showed minimal variation. The PCA explained 44.3 % of total variance (PC1 = 25.8 %, PC2 = 18.5 %), distinctly grouping K-1317, K-402 and DBW-39 as superior general combiners, while WR-544 and HD-2733 were identified as poor combiners. whereas heatmap and PCA biplot (Fig. 5) for the F_2 generation revealed substantial variation in general combining ability (GCA) effects among wheat parents across 15 traits. Line K-1317 exhibited the highest positive GCA for biological yield/plant (+7.82), grain yield/plant (+7.59) and harvest index (+7.81), indicating strong additive effects and its superiority as a general combiner. K-402 and DBW-39 also showed high GCA for grain yield (+2.74 and +3.32) and flag leaf area (+2.04 and +1.55), whereas WR-544 and HD-2733 displayed negative GCA for most yield traits (-2.03 to -3.88), identifying them as poor combiners. Traits such as protein content (-0.09 to +0.07) and phenol colour reaction (-0.58 to +0.74) showed low GCA variation, suggesting limited genetic diversity. The PCA analysis explained 46.2 % of the total variation (PC1 = 26.9 %, PC2 = 19.3 %), clearly separating K-1317, K-402 and DBW-39 on the positive axis as superior combiners, while WR-544 and HD-2733 clustered negatively, confirming their inferior performance across traits. In crops self-pollinated, like wheat, hybrids usually do not play a big role. Still, looking into segregating populations for specific combining ability (SCA) is very important. Grain yield is a complex trait because it is influenced by many different components, all of which affect how much yield can vary (28). Earlier studies pointed out that these promising parental lines could be useful for developing segregating populations and focused on improving these traits (29). However, relying on GCA might not be enough to boost grain yield, especially when the parent plants are genetically similar (30). That's why it's crucial to combine SCA analysis with GCA to pinpoint heterotic combinations and achieve better genetic improvements in yield and related traits.

Specific combining ability effects

The combined heatmap and PCA biplot (Fig. 6) for the F_1 generation revealed wide variation in SCA effects among wheat crosses for 15 traits. The cross K-402 $\times$ K-9107 showed the highest positive SCA for biological yield (+6.74) and grain yield (+4.44), followed by HD-3086 $\times$ HD-3171 with strong effects for biological yield (+8.36) and grain yield (+4.72), identifying them as superior specific combiners. Similarly, WR-544 $\times$ K-8962 exhibited high SCA for biological yield (+5.43) and grain yield (+2.84). In contrast, DBW-39 $\times$ K-68 and HD-2967 $\times$ K-68 recorded negative SCA values for harvest index (-6.75) and biological yield (-1.66), indicating poor specific combinations. The PCA analysis explained 49.8 % of the total variance (PC1 = 28.4 %, PC2 = 21.4 %), clearly separating high-performing crosses (K-402 $\times$ K-9107, HD-3086 $\times$ HD-3171) on the positive axis and low-performing crosses (DBW-39 $\times$ K-68, HD-2967 $\times$ K-68) on the negative axis, confirming their contrasting specific combining abilities for yield-related traits. Although SCA

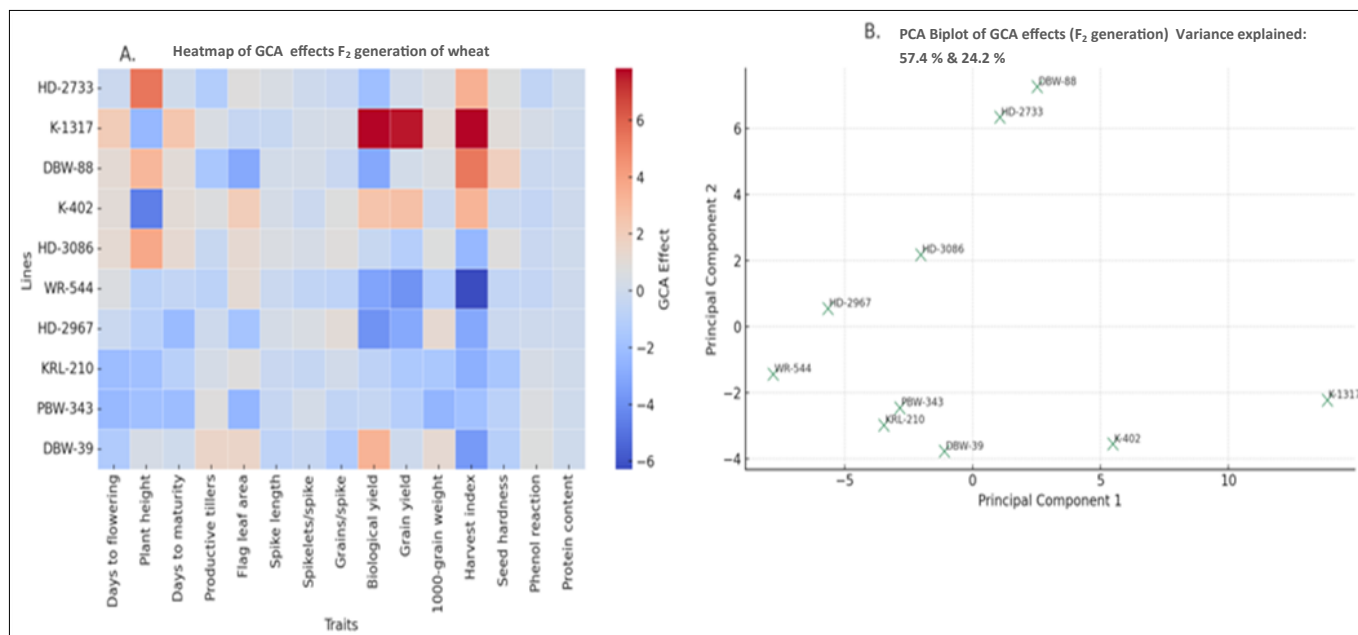


Fig. 5. The heatmap and principal component analysis (PCA) biplot of general combining ability (GCA) effects in F₂ among wheat parents for 15 traits.

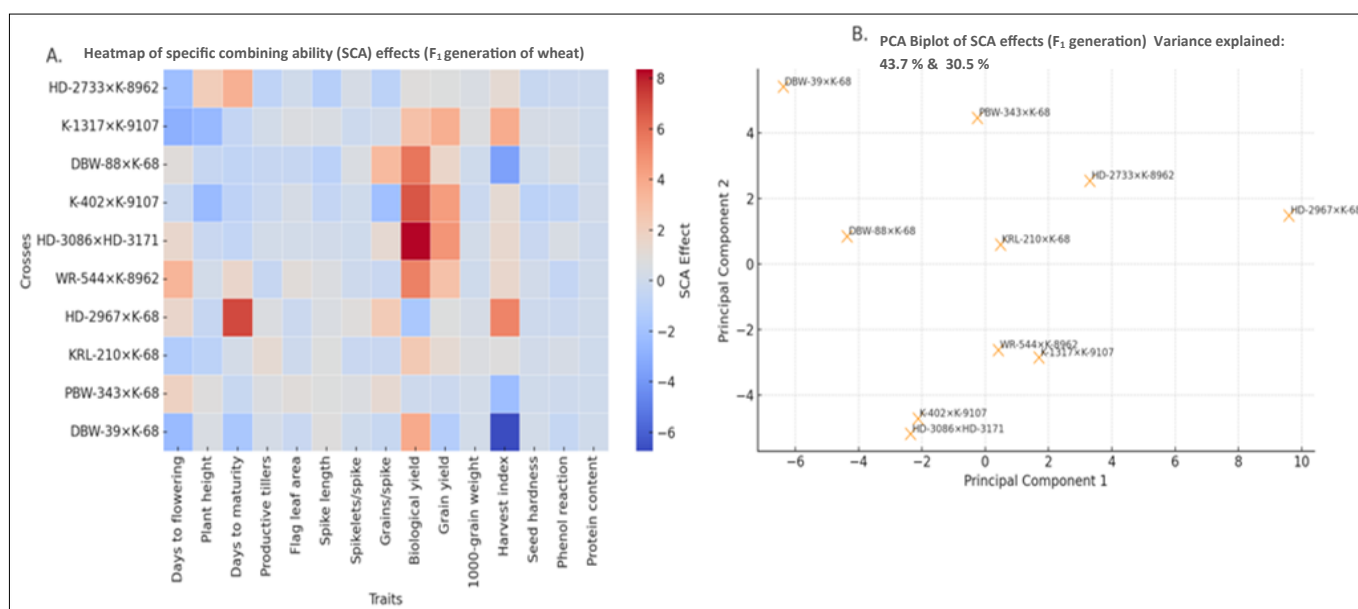


Fig. 6. The heatmap and principal component analysis (PCA) biplot of general combining ability (GCA) effects in F₁ among wheat parents for 15 traits.

alone may not directly enhance yield in self-pollinated crops like wheat, productive crosses can generate transgressive segregants, leading to promising homozygous lines in subsequent generations (31). In this study, the top-performing crosses for SCA effects on yield-related traits demonstrated the significance of non-additive gene action. Successful hybrids emerged from diverse parental combinations, high × high, high × low and low × low general combiners, indicating that superior hybrids do not always result from parents with strong GCA (32). These outcomes suggest the involvement of dominant and epistatic interactions, consistent with earlier findings (33). This finding reinforces that top-performing hybrids do not always arise from crosses between two strong general combiners. Such outcomes may result from dominant and epistatic gene interactions. Non-additive gene action has also been identified as a major factor governing key traits in wheat (34). The use of genetically diverse parents in this study facilitated a more effective assessment of variation among cross combinations (35). Furthermore, the low to moderate narrow-sense heritability values

observed for all traits highlight the role of non-additive gene action, indicating that direct selection may be less effective in early generations (36). Therefore, recurrent or pedigree selection in later generations would be more suitable for improving these traits (37).

Principal component analysis biplot

The PCA showed that the first two components exhibited 90.44 % of the total variation, with PC1 (79.12 %) and PC2 (11.32 %). Biological yield/plant (+4.0, -1.5) and plant height (+3.0, +0.8) showed the highest loadings on PC1, suggesting their major contribution to overall variability. Harvest index (+2.0) reflected a strong influence along PC2, signifying its distinct role in trait differentiation, whereas days to flowering, days to maturity, productive tillers/plant, seed hardness, phenol colour reaction and protein content clustered near the origin, contributing minimally to total variance. Flag leaf area, grain yield/plant and 1000-grain weight point out moderate association, revealing positive interrelationships among yield-related traits. Fig. 7 shows the multivariate variance structure,

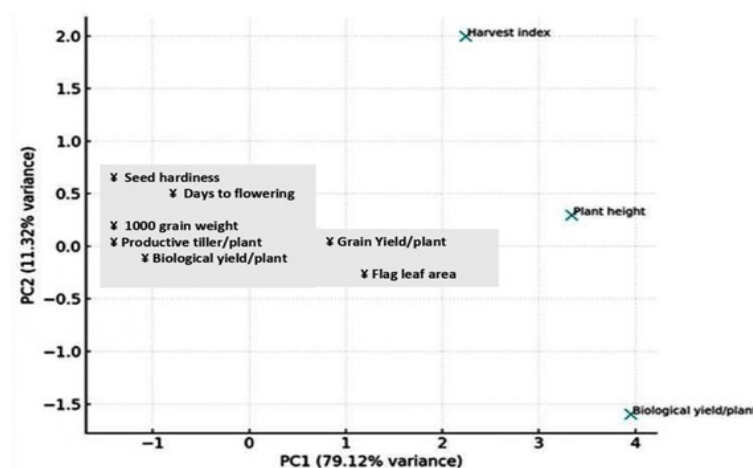


Fig. 7. Principal component analysis (PCA) biplot of combining ability effects in F_1 wheat crosses.

grouping traits with similar genetic behaviour. The first two principal components accounted for the majority of total variance, clearly separating high-yielding, morphologically dominant traits (e.g., plant height, biological yield, grain yield) from biochemical and physiological traits (e.g., protein content, phenol colour reaction) (38). This separation underscores the multidimensional nature of genetic control in bread wheat and supports the interpretation that yield and its components are strongly influenced by additive gene effects. Previous researchers reported that the first five principal components explained 78.4 % (well-watered) and 76.0 % (drought) of the variation among genotypes and biplot analysis showed clustering of yield and yield-component traits (39).

The clustered radar chart

The variance component analysis (Fig. 8) demonstrated that the line effect accounted for the maximum proportion (≈ 60 %) of the total variance, followed by the tester effect (≈ 45 %) and crosses (≈ 35 %).

The line $\times$ tester interaction contributed the least (≈ 20 %). The predominance of line variance suggests a strong additive genetic basis for the traits studied, while the moderate tester and cross effects highlight exploitable genetic diversity. The relatively lower interaction component indicates that non-additive effects were less influential, confirming the potential of direct selection based on line performance in subsequent breeding cycles. The comparatively lower contribution of crosses suggested that much of the variation was explained by parental and interaction components rather than environmental factors. The pattern indicated that additive genetic variance predominated, although non-additive effects were also evident, supporting the need for a combined selection and hybridisation strategy to increase the yield and related traits in bread wheat. The tested wheat genotypes exhibited considerable genetic diversity, endorsing that indirect selection for traits like the number of spikelets per spike, grains per spike, spikes per square meter and thousand-grain weight could effectively enhance grain



Fig. 8. Clustered radar chart showing overall genetic contribution profiles in F_1 crosses.

yield, as reported previously and highlight the utility of multivariate approaches, like principal component analysis, in identifying the most discriminating yield-attributing traits and revealed meaningful heritability and genetic gain estimates (40). These findings provide a useful base for interpreting trait groupings and the underlying genetic control mechanisms in wheat for the betterment of productivity.

Heritability and genetic advance

In the F_1 generation, the highest heritability were recorded for test weight (94.34 %) followed by flag leaf area (90.49 %), plant height (77.32 %), grain yield (68.76 %), seed hardness (61.08 %), biological yield (59.52 %), harvest index (54.32 %) and productive tillers per plant (54.25 %). whereas moderate heritability was estimated for spike length (32.26 %), days to maturity (22.78 %), spikelets per spike (14.14 %), grains per spike (18.95 %) and phenol colour reaction (18.00 %). In the F_2 generation, high heritability was observed for grain yield (68.37 %), biological yield (60.35 %), harvest index (54.83 %) and productive tillers (53.84 %), while seed hardness (35.92 %), days to maturity (30.98 %) and phenol colour reaction (31.86 %) exhibited moderate values. Notable genetic advance was estimated for plant height, biological yield, grain yield and harvest index in both generations, indicating the predominance of additive gene action and good potential for selection.

Heritability estimates and genetic advance provide insight into the effectiveness of selection for yield and related traits in the population. In both generations, heritability values ranged widely, indicating variable genetic control across traits (Fig. 9 and 10). High heritability coupled with moderate to high genetic advance in traits like grain yield per plant, biological yield, harvest index and test weight suggests the predominance of additive gene action, making these traits more amenable to improvement through direct selection, whereas, traits like phenol colour reaction and protein contents showed low heritability and genetic advance, reflecting greater environmental influence and the need for multi-environment evaluation. A decline in heritability from F_1 to F_2 for most traits reflected segregation and environmental effects in the subsequent generation. The results of the study highlight that yield-related traits can be effectively improved through selection,

while biochemical traits may require recurrent selection or hybridisation strategies to accumulate favourable alleles.

High heritability (h^2) values observed in this study indicate that the expression of these traits is predominantly governed by genetic factors, with minimal environmental influence. This suggests that phenotypic selection would be effective and desirable traits can be reliably transmitted to subsequent generations (41). The predominance of additive gene action further supports the potential for selection-based genetic improvement. Phenological traits such as days to heading (DTH) and days to anthesis (DTA) exhibited high h^2 coupled with moderate genetic advance, indicating that both genetic and environmental components contribute to their expression, thereby reducing the precision of direct genotypic selection (42). Conversely, days to maturity (DTM) showed high h^2 but low genetic advance, suggesting the influence of non-additive gene action, where direct selection would be less effective. Similar findings have been reported in wheat by previous researchers (43, 44). They noted that traits with high heritability and moderate genetic advance are primarily under additive control and respond well to selection, whereas traits exhibiting high heritability but low genetic advance are influenced by dominance and epistatic effects.

Correlation among heritability and genetic advance parameters

The correlation matrix (Fig. 11) summarises the relationships among heritability, genetic advance, stability indices and selection efficiency across the F_1 and F_2 generations. A strong positive association between F_1 and F_2 genetic advance ($r = 0.97$), along with a positive correlation between F_2 heritability and F_1 genetic advance ($r = 0.68$), indicates that traits with greater predicted improvement in F_1 generally maintained comparable response in F_2 , suggesting persistence of transmissible genetic variance across generations. The moderate correlation between F_1 and F_2 heritability ($r = 0.43$) further reflects the partial stability of genetic variance components despite segregation. Heritability stability (F_2/F_1 %) showed a negative correlation with F_1 heritability ($r = -0.65$), indicating that traits with initially high heritability may experience proportional reductions in F_2 , possibly due to recombination effects, altered dominance interactions and environmental influences. The positive relationship between F_2 genetic advance and selection efficiency

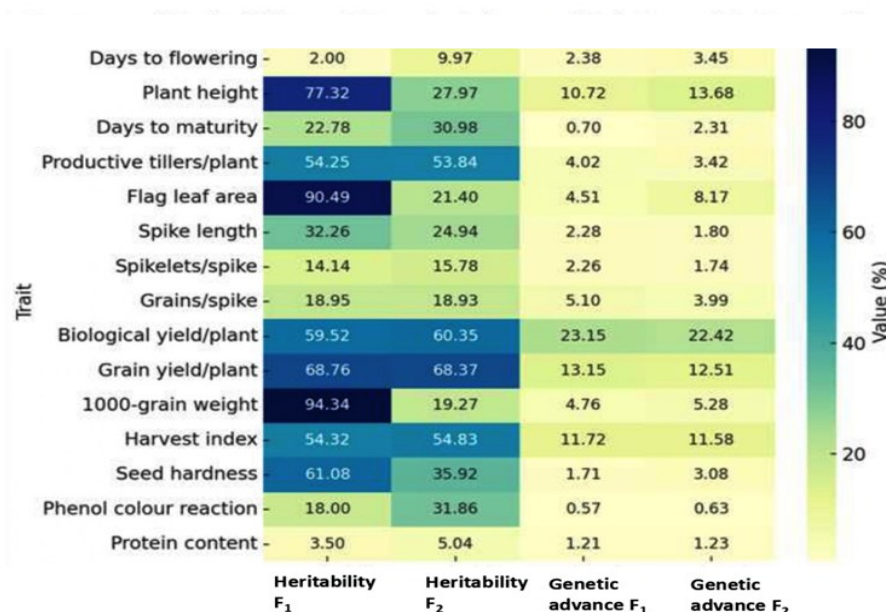


Fig. 9. Heatmap of heritability and genetic advance (%) in F_1 and F_2 generations.

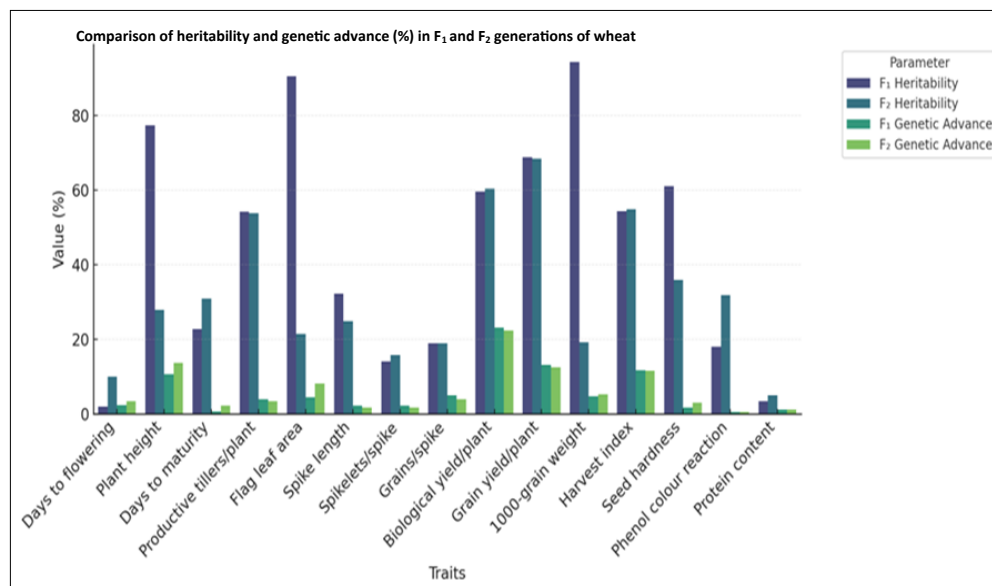


Fig. 10. Grouped bar chart comparing heritability and genetic advance in F_1 and F_2 generations.

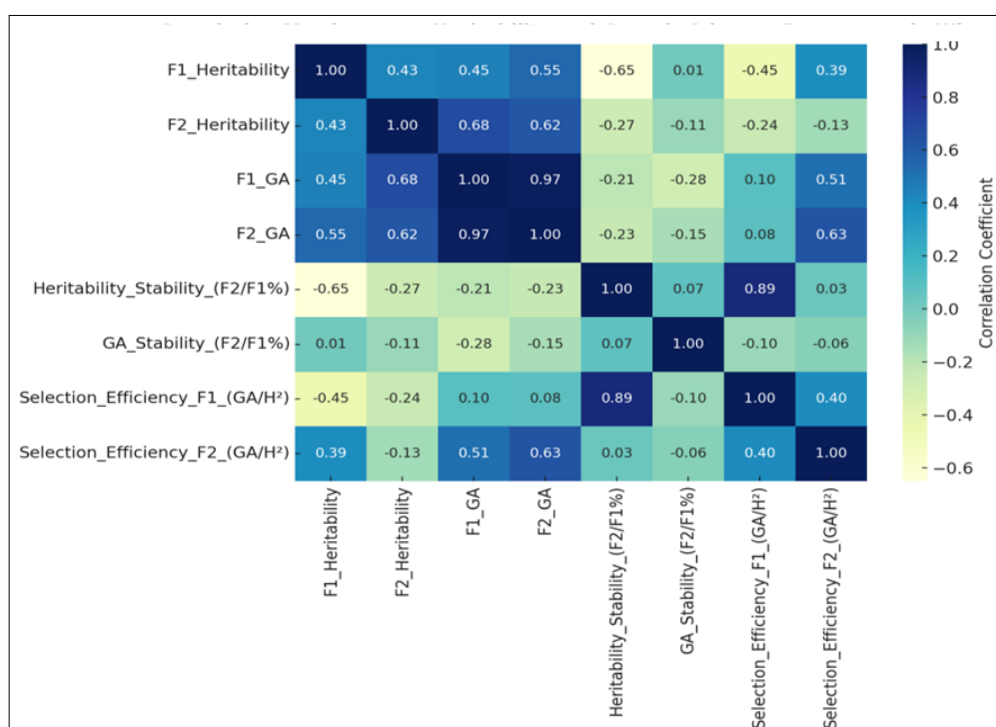


Fig. 11. Correlation matrix among heritability and genetic advance parameters in wheat.

($r = 0.63$) suggests that realised selection response is closely associated with the magnitude of transmissible genetic variance. In contrast, weak or negative associations between stability indices and selection efficiency indicate that statistical stability alone does not necessarily translate into accelerated genetic gain.

Overall, the correlation structure interpreted alongside variance component estimates suggests that grain yield, biological yield and harvest index, which consistently exhibited higher heritability and genetic advance across generations, represent reliable targets for selection. Conversely, phenol colour reaction and protein content displayed weaker associations, reflecting comparatively greater environmental influence and more complex inheritance patterns.

Conclusion

The present study revealed substantial genetic variability among wheat genotypes for yield and related traits, highlighting the importance of estimating gene effects, heritability and genetic advance in breeding programmes. Line $\times$ tester analysis indicated the involvement of both additive and non-additive gene actions. Grain yield, biological yield, harvest index and plant height exhibited high heritability coupled with moderate to high genetic advance, suggesting a predominant additive component and supporting the effectiveness of direct selection in early generations. In contrast, phenol colour reaction and protein content showed low heritability and genetic advance, indicating greater environmental influence and possible non-additive control. Superior general combiners (K-1317, K-402, HD-3171, WR-544 and DBW-88) were identified as valuable parents for accumulating favourable alleles through selection, while promising crosses (HD-3086 $\times$ HD-3171, K-402 $\times$ K-9107 and K-1317 $\times$ K-9107) may be exploited for heterosis

and for generating superior segregants. Overall, integrating additive-based selection with strategic hybridisation and recurrent selection approaches may facilitate the development of high-yielding and quality-improved wheat (*Triticum aestivum*) varieties.

Acknowledgements

The authors express their sincere gratitude to the professors of the Department of Agronomy, Chandra Shekhar Singh Haryana Agricultural University, Kanpur 208 002, Uttar Pradesh, India, for their invaluable support and contributions to this research project.

Authors' contributions

AK and S were responsible for the study design, while LV handled the data arrangement. PY, DSM and VY contributed to manuscript preparation. PR, PK, AY¹ and AY² edited the manuscript. All authors read and approved the final version of the manuscript [AY¹ stands for Aina Yadav and AY² stands for Ayush Yadav].

Compliance with ethical standards

Conflict of interest: Authors do not have any conflicts of interests to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT-5 to improve language clarity and readability. After using this tool, the authors carefully reviewed and edited the content as needed and take full responsibility for the accuracy and integrity of the publication.

References

1. Anbes T, Asredie S. Effects of lower seed rate and seed classes on seed quality yield and seed multiplication factors of bread wheat (*Triticum aestivum* L.) under irrigation in the Northwest Amhara region. *Discov Agric.* 2025;3:30. <https://doi.org/10.1007/s44279-025-00178-8>
2. Eze VH, Eze EC, Alaneme GU, BUBU PE, Nnadi EO, Okon MB. Integrating IoT sensors and machine learning for sustainable precision agroecology: enhancing crop resilience and resource efficiency through data-driven strategies, challenges and future prospects. *Discov Agric.* 2025;3:83. <https://doi.org/10.1007/s44279-025-00247-y>
3. Mohammadi M, Mirlohi A, Majidi MM, Soleimani Kartalaei E. Emmer wheat as a source for trait improvement in durum wheat: a study of general and specific combining ability. *Euphytica.* 2021;217:64. <https://doi.org/10.1007/s10681-021-02806-4>
4. Fu YB, Somers DJ. Genome-wide reduction of genetic diversity in wheat breeding. *Crop Sci.* 2009;49:161–8. <https://doi.org/10.2135/cropsci2008.03.0125>
5. Bassi FM, Nachit MM. Genetic gain for yield and allelic diversity over 35 years of durum wheat breeding at ICARDA. *Crop Breed Genet Genom.* 2019;3:1. <https://doi.org/10.20900/cbagg20190002>
6. Sarkar S, Barma NC, Ahmed JU, Waza SA, Islam AA. Morpho-physiological characterisation for identification of heat-tolerant wheat genotypes. *Discov Agric.* 2025;3:74. <https://doi.org/10.1007/s44279-025-00223-6>
7. Kamara MM, Ibrahim KM, Mansour E, Kheir AM. Combining ability and gene action controlling grain yield and its related traits in bread wheat under heat stress and normal conditions. *Agronomy.* 2021;11:1450. <https://doi.org/10.3390/agronomy11081450>
8. Hassan MZ, Hasanuzzaman M, Uddin MJ, Alomgir MB, Akter MS, Mohanto AC, et al. Assessing genetic diversity and population structure of F4:F5 wheat genotypes using morphological and microsatellite markers under heat stress. *Discov Agric.* 2025;3:14. <https://doi.org/10.1007/s44279-025-00161-3>
9. Ma H, Liu Y, Zhang S, Sha J, Sun Y, Hu Z, et al. Wheat resistance to Fusarium head blight and breeding strategies. *Crop Health.* 2025;3:9. <https://doi.org/10.1007/s44297-025-00048-1>
10. Lai X, Zhu Z, Zhang Y, Liu Y, Lu T, Qin J, et al. The selection and application of tiller number QTLs in modern wheat breeding. *Theor Appl Genet.* 2025;138:124. <https://doi.org/10.1007/s00122-025-04908-w>
11. Xiong W, Reynolds MP, Montes C, Crossa J, Snapp S, Akin B, et al. New wheat breeding paradigms for a warming climate. *Nat Clim Chang.* 2024;14:869–75. <https://doi.org/10.1038/s41558-024-02069-0>
12. Chowdhary MA, Sajad M, Ashraf MI. Analysis on combining ability of metric traits in bread wheat (*Triticum aestivum*). *J Agric Res.* 2007;45:11–7
13. Zencirci N, Altay F, Baloch FS, Nadeem MA, Ludidi N, editors. *Advances in wheat breeding: towards climate resilience and nutrient security.* 1st ed. Singapore: Springer Nature Singapore; 2024. <https://doi.org/10.1007/978-981-99-9478-6>
14. Karaoğlu C, Salantur A. Recent technologies in wheat breeding. In: Zencirci N, Altay F, Baloch FS, Nadeem MA, Ludidi N, editors. *Advances in wheat breeding.* Singapore: Springer; 2024. p. 13. https://doi.org/10.1007/978-981-99-9478-6_13
15. Zhao Y, Han G, Qie Y, Song J, Zi Y, Xiao B, et al. Characterisation of the powdery mildew resistance locus in wheat breeding line Jimai 809 and its breeding application. *Mol Breed.* 2024;44:28. <https://doi.org/10.1007/s11032-024-01467-8>
16. Nannuru VKR, Dieseth JA, Lillemo M. Evaluating genomic selection and speed breeding for Fusarium head blight resistance in wheat using stochastic simulations. *Mol Breed.* 2025;45:14. <https://doi.org/10.1007/s11032-024-01527-z>
17. Johnson HW, Robinson HF, Comstock RE. Estimates of genetic and environmental variability in soybeans. *Agron J.* 1955;47:314–8. <https://doi.org/10.2134/agronj1955.00021962004700070009x>
18. Ali S, Khan NU, Gul S, Goher R, Naz I, Khan SA, et al. Heterotic effects for yield-related attributes in F₁ populations of maize. *Pak J Bot.* 2019;51:1675–86. [https://doi.org/10.30848/PJB2019-5\(33\)](https://doi.org/10.30848/PJB2019-5(33))
19. Zhuang L, Liu H, Hou J, Jian C, Liu Y, Li H, et al. Genetic improvement of important agronomic traits in Chinese wheat breeding over the past 70 years. *BMC Plant Biol.* 2024;24:1151. <https://doi.org/10.1186/s12870-024-05841-8>
20. Sprague GH, Tatum LA. General versus specific combining ability in single crosses in corn. *J Am Soc Agron.* 1942;30:923–32. <https://doi.org/10.2134/agronj1942.00021962003400100008x>
21. Robinson HF, Comstock RE, Harvey PH. Estimate of heritability and degree of dominance in corn. *Agron J.* 1949;41:353–9. <https://doi.org/10.2134/agronj1949.00021962004100080005x>
22. Gimenez K, Blanc P, Argillier O, Pierre JB, Le Gouis J, Paux E, et al. Dissecting bread wheat heterosis through the integration of agronomic and physiological traits. *Biology (Basel).* 2021;10:907. <https://doi.org/10.3390/biology10090907>
23. Omara RI, Shahin AA, Ahmed SM, Mostafa YS, Alamri SA, Hashem M, et al. Wheat resistance to stripe and leaf rusts conferred by introgression of slow rusting resistance genes. *J Fungi (Basel).* 2021;7:622. <https://doi.org/10.3390/jof7080622>

24. Elango D, Sandoya G, Chopra S. Techniques and tools of modern plant breeding. In: Plant biotechnology: experience and future prospects. 2021. p. 17–26. https://doi.org/10.1007/978-3-030-68345-0_2
25. Abbass DM, Al-Layla MG, Al-Hamdani ZB. Estimation of heritability and expected genetic improvement in durum wheat (*Triticum durum* Desf.). J Univ Shanghai Sci Technol. 2020;22:2192–200.
26. Hassan G, Mohammad F, Afridi SS, Khalil IH. Combining ability in the F₁ generations of diallel cross for yield and yield components in wheat. Sarhad J Agric. 2007;23:937–44.
27. Valério IP, de Carvalho FI, de Oliveira AC. Combining ability of wheat genotypes in two models of diallel analyses. Crop Breed Appl Biotechnol. 2009;9:1–7. <https://doi.org/10.12702/1984-7033.v09n02a01>
28. Mia MS, Liu H, Wang X, Lu Z, Yan G. Response of wheat to post-anthesis water stress and the nature of gene action as revealed by combining ability analysis. Crop Pasture Sci. 2017;68:534–43. <https://doi.org/10.1071/CP17112>
29. Griffing B. Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci. 1956;9:463–93. <https://doi.org/10.1071/BI9560463>
30. Fasahat P, Rajabi A, Rad JM, Derera J. Principles and utilisation of combining ability in plant breeding. Biom Biostat Int J. 2016;4:1–24. <https://doi.org/10.15406/bbij.2016.04.00085>
31. Fellahi ZE, Hannachi A, Bouzerzour H, Boutekrabt A. Line × tester mating design analysis for grain yield and yield-related traits in bread wheat (*Triticum aestivum* L.). Int J Agron. 2013;2013:1–8. <https://doi.org/10.1155/2013/201851>
32. Ahmad E, Akhtar M, Badoni S, Jaiswal JP. Combining ability studies for seed yield related attributes and quality parameters in bread wheat (*Triticum aestivum* L.). J Genet Genom Plant Breed. 2017;1:21–27.
33. Hama-Amin TN, Towfiq SI. Estimation of some genetic parameters using line × tester analysis of common wheat (*Triticum aestivum* L.). Appl Ecol Environ Res. 2019;17:9735–52. https://doi.org/10.15666/aeer/1704_97359752
34. Mwadzingeni L, Shimelis H, Tsilo TJ. Combining ability and gene action controlling yield and yield components in bread wheat (*Triticum aestivum* L.) under drought-stressed and non-stressed conditions. Plant Breed. 2018;137:502–13. <https://doi.org/10.1111/pbr.12609>
35. Akram Z, Ajmal SU, Khan KS, Qureshi R, Zubair M. Combining ability estimates of some yield and quality related traits in spring wheat (*Triticum aestivum* L.). Pak J Bot. 2011;43:221–31.
36. Delaney A. Investigating parental effects on end-use quality in hard winter wheat (*Triticum aestivum* L.) hybrids. [dissertation]. Lincoln (NE): University of Nebraska–Lincoln; 2019. p. 118. <https://digitalcommons.unl.edu/agronhortdiss/169>
37. Khan SA, Hassan G. Heritability and correlation studies of yield and yield-related traits in bread wheat. Sarhad J Agric. 2017;33:103–7. <https://doi.org/10.17582/journal.sja/2017.33.1.103.107>
38. Hulle A, Dubey N, Avinash H, Reddy JP, Chormule S, Sachan S. PCA-based multivariate statistical diversity analysis for grain yield and its components in wheat (*Triticum aestivum* L.). Ann Biol. 2023;39(2):386–91.
39. Sewore BM, Abe A. Genetic variability and trait associations in bread wheat (*Triticum aestivum* L.) genotypes under drought-stressed and well-watered conditions. CAB Int Biosci. 2024;5:64. <https://doi.org/10.1186/s43170-024-00259-6>
40. KC B, Pandit R, Maharjan B, Adhikari NR, Poudel MR, Thapa DB, et al. Genetic parameters, correlation and multivariate analysis of yield and yield components in 30 promising wheat (*Triticum aestivum* L.) genotypes. Int J Agron. 2025;2025:3774228. <https://doi.org/10.1155/2025/3774228>
41. Bartaula S, Panthi U, Timilsena K, Acharya SS, Shrestha J. Variability, heritability and genetic advance of maize (*Zea mays* L.) genotypes. Res Agric Livest Fish. 2019;6(2):163–9. <https://doi.org/10.3329/ralf.v6i2.42962>
42. Tiwari DN, Tripathi SR, Tripathi MP, Khatri N, Bastola BR. Genetic variability and correlation coefficients of major traits in early maturing rice under rainfed lowland environments of Nepal. Adv Agric. 2019;2019:5975901. <https://doi.org/10.1155/2019/5975901>
43. Reddy BR, Reddy DS, Reddaiah K, Sunil N. Studies on genetic variability, heritability and genetic advance for yield and quality traits in tomato (*Solanum lycopersicum* L.). Int J Curr Microbiol Appl Sci. 2013;2(9):238–44.
44. Regmi S, Poudel B, Ojha BR, Kharel R, Joshi P, Khanal S, et al. Estimation of genetic parameters of different wheat genotype traits in Chitwan, Nepal. Int J Agron. 2021;2021:6651325. <https://doi.org/10.1155/2021/6651325>

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonpublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc. See https://horizonpublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (<https://creativecommons.org/licenses/by/4.0/>)

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.