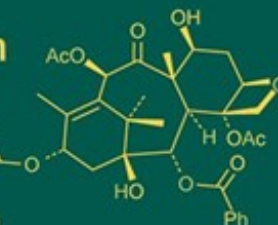
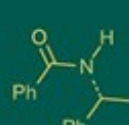
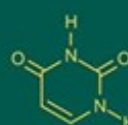


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Genetic analysis of yield and component traits in F1 and F2 generations of bread wheat (*Triticum aestivum* L.)

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ABSTRACT

The present investigation was undertaken to elucidate the genetic basis of inheritance and identify appropriate selection strategies for yield and yield-attributing traits in bread wheat (*Triticum aestivum* L. em. Thell.) during rabi 2025–26 at three experimental sites of C. S. Azad University of Agriculture and Technology, Kanpur, India. The experimental material comprised ten diverse parents, namely K8434, K1006, K65, DBW107, DBW252, HD2967, DBW316, K9351, HI1612 and DBW173, along with their derived F1 hybrids and F2 populations. Combined analysis of variance revealed highly significant differences among treatments, parents, F1 hybrids and F2 populations for all thirteen characters, demonstrating substantial genetic variability. Significant parent versus F1 and parent versus F2 contrasts were observed for all traits except harvest index, indicating pronounced generation-dependent differences and the presence of heterotic effects. Hayman's diallel analysis revealed that both additive and dominance components contributed to trait inheritance, although their relative magnitude varied considerably among traits and generations. Days to 50% flowering and days to maturity were predominantly governed by non-additive gene action, with over-dominance and indications that alleles conferring earliness were predominantly dominant. Plant height exhibited a significant additive component in both generations, with partial dominance in the F1, suggesting scope for effective early-generation selection for reduced stature. Flag leaf area, productive tillers per plant, spike length and number of spikelets per spike showed significant additive and dominance components in the F1, with partial to near-complete dominance and comparatively high narrow-sense heritability (65.28–76.32%). However, additive effects were reduced or became non-significant in most traits in the F2, accompanied by a marked decline in narrow-sense heritability. The results indicate that traits associated with plant stature and spike architecture possess greater prospects for early-generation selection, whereas phenological traits, being predominantly influenced by non-additive effects, may benefit from selection in later generations or exploitation of heterosis. Overall, the study demonstrates substantial exploitable genetic variation and generation-specific gene action, providing a basis for designing efficient breeding strategies for improving productivity and adaptive traits in bread wheat.

Keywords: Gene action, Hayman diallel analysis, Additive variance, Dominance variance, Heterosis, Narrow-sense heritability, Genetic variability

Introduction

Wheat (*Triticum aestivum* L.) is one of the world's major food crops and holds a prominent position among cultivated cereal crops. Its cultivation has played a significant role in the success of the Green Revolution, which contributed substantially to transforming India from a food-deficit country into a food-surplus nation. Wheat belongs to the family Poaceae and is predominantly a self-pollinated crop. India's wheat production is estimated to have increased from 109.52 million tonnes in 2022–2023 to 111.32 million tonnes in 2023–2024, representing a compound annual growth rate (CAGR) of approximately 1.64%. Wheat serves as an important source of nutrition for both humans and livestock and contributes substantially to meeting the food requirements of the rapidly increasing population in India as well as worldwide (Patil *et al.*, 2024) [1]. Common wheat (*Triticum aestivum* L.), owing to its suitability for chapatti, bread, and various bakery products, is widely cultivated across North India and is also grown in several regions of Central and South India. Durum wheat is particularly suitable for the preparation of products such as 'suji', 'semya', 'spaghetti', and 'macaroni' and is predominantly cultivated in the central and southern regions of India, mainly under rainfed conditions. Similarly, dicoccum wheat is well suited for the preparation of the traditional South Indian dish 'Uppumav' (Singh *et al.*, 2018) [2]. Durum wheat (*Triticum turgidum* L.) is the principal tetraploid wheat species, characterized by its large and exceptionally hard grains. The grain produces a low-gluten flour that serves as the primary source of semolina, which is widely used in the preparation of pasta, couscous, burghul, and various other traditional wheat-based products (Nachit *et al.*, 1995) [3]. Wheat is cultivated

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across a diverse range of agro-climatic conditions, extending from the mountainous regions of Kashmir to semi-arid areas characterized by mild to severe winter conditions (Yadav *et al.*, 2021) [4]. Since ancient times, wheat has played a significant role in supporting the agricultural economy and food systems of several countries, making it an important crop from both economic and nutritional perspectives (Singh *et al.*, 2010) [5]. Several biometrical approaches are widely employed for the genetic evaluation of crop plants. Among these, diallel, partial diallel, and line $\times$ tester analyses are commonly used by plant breeders to investigate the genetic architecture of quantitative traits, as these methods provide valuable information on the genetic constitution and inheritance patterns of the materials under study. The diallel mating design is widely used to evaluate breeding materials by estimating their combining ability variances and effects, thereby providing insights into their genetic potential for the inheritance of quantitative traits. The diallel mating design provides estimates of general combining ability (GCA) and specific combining ability (SCA), including their respective variances and effects. It also enables the assessment of additive (D) and dominance (H) components of genetic variance, thereby providing valuable insights into the genetic control of the traits under investigation. Diallel analysis is an effective tool for identifying suitable parents for hybridization programmes and for determining appropriate breeding strategies for the genetic improvement of quantitative traits in crop species.

Materials and Methods

The present study was conducted during the Rabi season of 2025 at three locations, namely the Crop Research Farm, Kalai, Aligarh; the Crop Research Farm, Saini, Kaushambi; and the Student Instruction Farm, CSAUAT, Kanpur. A total of 100 treatments, comprising 10 parents, 45 F_1 hybrids, and 45 F_2 populations, were evaluated using a Randomized Block Design (RBD). The experimental material consisted of ten parental lines, namely K8434, K1006, K65, DBW107, DBW252, HD2967, DBW316, K9351, HI1612, and DBW173. These 100 treatments were evaluated for the genetic analysis of nine quantitative traits in wheat. A half-diallel mating design was employed, and the combining ability analysis was carried out following the method proposed by Griffing (1956) [6, 7]. The genetic variance was further partitioned into additive, dominance, and epistatic components following the approach of Fisher.

Results and Discussion

Combined analysis of variance

The combined analysis of variance for parents, F_1 and F_2 (Table 1) revealed highly significant mean squares due to treatments for all thirteen characters, indicating substantial genetic variability in the material. The mean squares due to replications were non-significant for every character, which shows that the experimental area was uniform. The variation among parents, among F_1 hybrids and among F_2 populations was highly significant for all characters. This is in accordance with Afridi *et al.* (2017) [8] and Bentouati *et al.* (2026) [9], who reported significant genotypic differences for all traits in both the F_1 and F_2 generations of wheat diallels. The mean squares of the F_2 populations exceeded those of the F_1 hybrids for twelve of the thirteen characters, number of grains per ear being the only exception (262.50 in the F_2 against 280.96 in the F_1). This reflects the additional variability released by segregation in the F_2 generation.

The parents versus F_1 and parents versus F_2 contrasts were significant for all characters except harvest index (0.019 and 2.599, respectively), which indicates that the mean performance of the F_1 hybrids and of the F_2 populations differed from that of the parents for every other character, the basis of heterosis. The parents versus F_1 mean squares were particularly large for days to maturity (3937.35), plant height (2082.65) and days to 50% flowering (1648.50), suggesting that heterosis was most pronounced for phenology and stature. Bentouati *et al.* (2026) [9], in contrast, found the parents versus F_1 contrast significant only for spike weight, number of spikes per plant

and biomass in durum wheat, so the extent of average heterosis clearly depends on the parental material. The direction of the differences cannot be judged from mean squares alone and should be read from the mean performance of the parents and hybrids.

Genetic components of variation in the F_1 and F_2 generations

The genetic components of variation for days to 50% flowering, days to maturity, plant height, flag leaf area, productive tillers per plant, spike length and number of spikelets per spike were estimated separately for the F_1 and F_2 generations (Table 2) by the approach of Hayman (1954) [7]. This approach assumes diploid segregation, homozygous parents, absence of reciprocal and maternal effects, epistasis and multiple allelism, and independent distribution of genes among the parents (Hayman, 1954; Mather *et al.*, 1982) [7, 10]. As wheat is a hexaploid, these assumptions are met only approximately, and the estimates are best taken as a description of apparent gene action, as in earlier wheat diallels (Afridi *et al.*, 2017; Bentouati *et al.*, 2026) [8, 9].

The additive component (D) was significant in the F_1 for all characters except days to maturity, whereas in the F_2 it was significant only for plant height and spike length. Its value was almost identical in the two generations for every character (for example, 79.65 and 79.97 for plant height and 1.55 and 1.55 for spike length). The dominance components (H_1 and H_2) were significant for all characters in the F_1 , and in the F_2 they were significant for all characters except H_1 of spike length. The dominance components in the F_2 were, however, many times larger than in the F_1 (for example, H_1 of days to maturity was 1676.44 against 150.94), and the standard errors of the F_2 estimates were large. The F_2 estimates are therefore indicative of the direction of gene action rather than of its exact magnitude.

Days to 50% flowering and days to maturity

Both characters were governed mainly by dominance. In the F_1 , H_1 and H_2 were significant for days to 50% flowering (48.97* and 48.56*) and days to maturity (150.94** and 153.06**) and exceeded D (22.84* and 37.55, respectively). The mean degree of dominance, $\sqrt{H_1/D}$, was 1.46 and 2.00, indicating over-dominance. The dominance effect (h^2) was highly significant (216.23** and 515.68**), which points to unidirectional dominance, and the narrow-sense heritability was moderate to low (41.12% and 29.18%). The correlation between the covariance-variance sum and the parental mean (r) was positive (0.70 and 0.62), which indicates that the alleles increasing days to flowering and maturity were recessive, in other words that earliness was largely dominant (Bentouati *et al.*, 2026) [9]. This is a favourable situation for breeding early hybrids. The ratio of dominant to recessive alleles was close to unity (1.03 and 0.93) and $H_2/4H_1$ was 0.25 for both characters, so positive and negative alleles were symmetrically distributed among the parents.

In the F_2 , D was non-significant for both characters, whereas H_1 rose to 624.45** and 1676.44**, the mean degree of dominance to 5.49 and 6.90, and the covariance component F was positive (79.83 and 114.49), with dominant to recessive allele ratios of 2.08 and 1.62. The correlation r fell to near zero (0.05 and -0.06), so no consistent direction of dominance could be inferred. Predominantly non-additive control with over-dominance for earliness is in agreement with Afridi *et al.* (2017) [8] for days to heading in spring wheat. The dominance effect (h^2) was non-significant in the F_2 , and the narrow-sense heritability declined to 36.16% and 17.06%.

Plant height

Plant height and spike length were the only characters in which the additive component was significant in both generations (79.65** and 79.97** for plant height). In the F_1 the dominance components were also significant for plant height (H_1 51.42* and H_2 55.37*) but smaller than D , and the mean degree of dominance (0.80) indicated partial dominance. The ratio of dominant to recessive alleles (0.98) showed a balanced distribution, and the dominance effect was signifi-

cant (272.54**). The positive correlation r in both the F1 (0.69) and the F2 (0.86) indicates that alleles increasing height were recessive, so that reduced stature was dominant, a desirable feature in breeding semi-dwarf types. Narrow-sense heritability was high in the F1 (65.28%) but fell to 38.06% in the F2, where the dominance components were much larger (H_1 1013.45**), the mean degree of dominance was 3.56, and the covariance F (217.19*) was significant and positive, indicating an excess of dominant alleles (ratio 2.23). The combination of a stable additive component with partial dominance in the F1 agrees with Bentouati *et al.* (2026) [9], who found plant height to be under predominantly additive control with partial dominance in both generations, and it suggests that selection for stature can begin early.

Flag leaf area and productive tillers per plant

In the F1, both flag leaf area and productive tillers per plant showed significant additive components (14.85** and 0.45**) with dominance components of comparable size (H_1 12.77** and 0.43**), giving degrees of dominance of 0.93 and 0.98, that is, partial dominance approaching complete dominance. The covariance F was negative (−6.76** and −0.22*) and the ratio of dominant to recessive alleles was 0.61 for both characters, indicating an excess of recessive alleles among the parents. The negative correlation r for productive tillers per plant (−0.60) shows that alleles increasing tiller number were dominant, whereas for flag leaf area it was close to zero (−0.04) and no clear direction of dominance emerged. The ratio h^2/H_2 (5.60 and 6.35) indicated that five to six groups of genes exhibited dominance, and narrow-sense heritability was high (72.13% and 71.83%).

In the F2, D was non-significant for both characters, the dominance components were very large (H_1 567.63** and 14.94**), the degree of dominance exceeded unity (6.23 and 5.92), and narrow-sense heritability fell to 26.03% and 39.11%. The high heritability with partial dominance in the F1 suggests that both characters can be improved by selection in early generations. The apparent over-dominance in the F2 should be confirmed in later generations, because non-allelic interaction may contribute to it (Bentouati *et al.*, 2026) [9].

Spike length and number of spikelets per spike

In the F1, spike length and number of spikelets per spike showed significant additive components (1.55** and 3.51**) and significant dominance components (H_1 0.82* and 2.57*; H_2 0.84** and 2.76**), with partial dominance (0.73 and 0.86). The covariance F was negative (−0.60 and −1.67) and the ratio of dominant to recessive alleles was 0.58 and 0.57, indicating an excess of recessive alleles. The negative correlations r (−0.56 and −0.62) show that the alleles increasing spike length and spikelet number were dominant. Narrow-sense heritability was high (76.32% and 68.41%), the highest recorded being that of spike length.

In the F2, spike length retained a significant additive component (1.55**) and its dominance component was comparatively small (H_1 7.32, non-significant), with a mean degree of dominance of 2.17, a ratio of dominant to recessive alleles near unity (0.96) and a correlation

r near zero (−0.03). For number of spikelets per spike, D was non-significant and dominance predominated (H_1 55.81**), with a degree of dominance of 3.97 and a ratio of 1.52. Narrow-sense heritability declined to 36.27% and 38.49%. Bentouati *et al.* (2026) [9] reported for spike length a shift from over-dominance in the F1 to partial dominance in the F2, the reverse of the present pattern, which indicates that the trend depends on the parental material.

Heritability and implications for selection

Narrow-sense heritability was lower in the F2 than in the F1 for all seven characters, the largest reductions being for flag leaf area (72.13% to 26.03%), productive tillers per plant (71.83% to 39.11%) and spike length (76.32% to 36.27%). Similarly, significant dominance effects in the F1 were not retained in the F2 for any character, as also observed by Bentouati *et al.* (2026) [9], which suggests that the dominance detected in the F1 arose largely from heterozygosity that was reduced by segregation and increasing homozygosity in the F2. Plant height, flag leaf area, productive tillers per plant, spike length and number of spikelets per spike had high narrow-sense heritability in the F1 (65.28% to 76.32%) and are therefore amenable to selection in early generations. Days to 50% flowering and days to maturity, with predominantly non-additive control and lower heritability, call for selection to be delayed to later, more homozygous generations or for exploitation of heterosis (Bentouati *et al.*, 2026) [9].

Conclusion

The combined analysis of variance established significant genetic variability among the parents, F1 hybrids and F2 populations for all characters, and significant differences between the parents and both filial generations for all characters except harvest index, indicating heterosis in the material. Hayman's analysis showed that both additive and dominance variation governed the inheritance of the characters studied, but their relative importance depended on the character and the generation. Days to 50% flowering and days to maturity were controlled chiefly by dominance, with dominant alleles favouring earliness. Plant height, flag leaf area, productive tillers per plant, spike length and number of spikelets per spike showed partial dominance with a significant additive component in the F1. Alleles reducing stature, flowering time and maturity time were predominantly dominant, as were those increasing productive tillers per plant, spike length and number of spikelets per spike. The significant dominance effects of the F1 were not retained in the F2, so heterozygosity was the principal basis of dominance, and the apparent over-dominance in the F2 must be interpreted with caution.

Narrow-sense heritability was high in the F1 for plant height, flag leaf area, productive tillers per plant, spike length and number of spikelets per spike, and declined in the F2. Selection for these characters can therefore begin in early segregating generations, whereas selection for phenology should be deferred to later homozygous generations or combined with the exploitation of heterosis in hybrids. These inferences rest on the assumptions of the Hayman analysis and should be validated in advanced generations.

Table 1. Combined Analysis of variance for parents, F1 and F2 for thirteen traits in half diallel cross of wheat genotypes

Source of variation	df	Days to 50% Flowering	Days to Maturity	Plant Height	Flag Leaf Area	Productive Tillers/Plant	Spike Length	Number of Spikelets/Spike	Number of Grains/Ear	1000 grain weight	Biological Yield/Plant	Harvest Index	Protein Content	Grain Yield/Plant
REP	2	13.35	21.36	1.123	1.173	0.005	0.023	0.375	1.993	2.437	0.544	0.489	0.187	0.064
Treat	99	116.69**	285.86**	194.30**	85.91**	2.420**	4.147**	13.13**	299.87**	57.98**	56.65**	45.97**	3.841**	13.07**
PAR	9	79.99**	146.39**	258.71**	47.54**	1.454**	4.997**	11.93**	459.76**	40.37**	46.27**	20.52**	2.089**	11.37**
F1	44	49.69**	136.51**	119.95**	33.16**	1.040**	3.193**	7.825**	280.96**	41.08**	41.07**	31.28**	2.391**	8.754**
PVF1	1	1648.50**	3937.35**	2082.65**	542.66**	19.79**	33.22**	127.24**	845.16**	649.54**	411.85**	0.019	40.71**	74.95**
F2	44	135.69**	352.79**	204.84**	134.39**	3.281**	3.801**	14.66**	262.50**	60.83**	60.83**	67.79**	4.267**	15.61**
PVF2	1	218.88**	838.20**	578.62**	137.34**	1.679**	3.480**	17.91**	57.80**	141.42**	44.87**	2.599	4.783**	10.45**
EROR	198	4.922	12.57	6.131	1.140	0.048	0.116	0.475	2.850	1.331	1.410	3.186	0.155	0.287
Total	299	41.98	103.12	68.40	29.21	0.833	1.450	4.663	101.19	20.10	19.70	17.33	1.376	4.519

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

Table 2. Estimates of D, H1, H2, F, h2 and E component and related statistics for 13 attributes in 10 parent-diallel cross in F1 and F2 generation of wheat

Components	Days to 50% Flowering	Days to 50% Flowering F1	Days to 50% Flowering F2	Days to Maturity F1	Days to Maturity F2	Plant Height F1	Plant Height F2	Flag Leaf Area F1	Flag Leaf Area F2	Productive Tillers/Plant F1	Productive Tillers/Plant F2	Spike Length F1	Spike Length F2	Number of Spikelets/Spike F1	Number of Spikelets/Spike F2
D	22.84*	37.55	20.72	35.22	35.22	79.65**	79.97**	14.85**	14.61	0.45**	0.43	1.55**	1.55**	3.51**	3.55
SE±	8.51	20.43	17.03	29.99	29.99	9.33	19.93	0.80	8.77	0.03	0.42	0.14	0.38	0.39	1.69
F	0.96	-5.37	79.83	114.49	114.49	-1.11	217.19*	-6.76**	14.08	-0.22*	1.46	-0.60	-0.15	-1.67	5.79
SE±	19.63	47.14	78.50	138.27	138.27	21.53	91.86	1.84	40.41	0.08	1.93	0.31	1.75	0.90	7.78
H1	48.97*	150.94**	624.45**	1676.44**	1676.44**	51.42*	1013.45**	12.77**	567.63**	0.43**	14.94**	0.82*	7.32	2.57*	55.81**
SE±	18.11	43.49	144.99	255.38	255.38	19.86	169.66	1.70	74.63	0.07	3.56	0.29	3.23	0.83	14.37
H2	48.56*	153.06**	435.33**	1443.14**	1443.14**	55.37*	664.38**	12.73**	482.42**	0.41**	10.47**	0.84**	6.93*	2.76**	40.40*
SE±	15.39	36.96	123.23	217.05	217.05	16.88	144.19	1.45	63.43	0.06	3.02	0.25	2.74	0.71	12.21
h2	216.23**	515.68**	26.76	105.76	105.76	272.54**	74.12	71.27**	17.69	2.60**	0.20	4.34**	0.42	16.63**	2.21
SE±	10.30	24.74	82.48	145.28	145.28	11.30	96.52	0.97	42.46	0.04	2.02	0.16	1.84	0.47	8.17
E	3.82	11.24	5.94	13.57	13.57	6.59	6.27	1.00	1.23	0.03	0.06	0.12	0.11	0.46	0.43
SE±	2.57	6.16	5.13	9.04	9.04	2.81	6.01	0.24	2.64	0.01	0.13	0.04	0.11	0.12	0.51
$\sqrt{H1/D}$	1.46	2.00	5.49	6.90	6.90	0.80	3.56	0.93	6.23	0.98	5.92	0.73	2.17	0.86	3.97

(continued on next page)

Components	Days to 50% Flowering F1	Days to 50% Flowering F2	Days to Maturity F1	Days to Maturity F2	Plant Height F1	Plant Height F2	Flag Leaf Area F1	Flag Leaf Area F2	Productive Tillers/Plant F1	Productive Tillers/Plant F2	Spike Length F1	Spike Length F2	Number of Spikelets/Spike F1	Number of Spikelets/Spike F2
$H_2/4H_1$	0.25	0.17	0.25	0.22	0.27	0.16	0.25	0.21	0.24	0.18	0.26	0.24	0.27	0.18
$\frac{(4DH_1)^{0.5} + F}{(4DH_1)^{0.5} - F}$	1.03	2.08	0.93	1.62	0.98	2.23	0.61	1.17	0.61	1.82	0.58	0.96	0.57	1.52
h^2/H_2	4.45	0.06	3.37	0.07	4.92	0.11	5.60	0.04	6.35	0.02	5.16	0.06	6.03	0.05
h_2 narrow sense (%)	41.12	36.16	29.18	17.06	65.28	38.06	72.13	26.03	71.83	39.11	76.32	36.27	68.41	38.49
R	0.70	0.05	0.62	-0.06	0.69	0.86	-0.04	0.05	-0.60	-0.49	-0.56	-0.03	-0.62	-0.03

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