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Evaluation of gene action for yield and yield contributing traits in bread wheat (*Triticum aestivum* L.) through line $\times$ tester mating design

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Abstract

The escalating global demand for wheat (*Triticum aestivum* L.) necessitates a comprehensive understanding of the genetic architecture governing yield and its contributing traits to accelerate breeding progress. This study was conducted to elucidate the nature of gene action and combining ability in 50 bread wheat hybrids developed through a line $\times$ tester mating design, involving 10 lines and 5 testers. The hybrids were evaluated in a randomized block design with three replications during the Rabi season of 2023-24, alongside the parental lines and a commercial check variety (HD 3226). Data were recorded on 11 quantitative traits, including days to 50% flowering, days to maturity, plant height, number of tillers per plant, spike length, number of spikes per plant, number of grains per spike, 1000-grain weight, biological yield per plant, grain yield per plant, and harvest index. Genetic component analysis revealed that non-additive gene action, encompassing dominance and epistatic effects, predominantly controlled the inheritance of most agronomic traits. This was evidenced by predictability ratios substantially below unity for key traits such as grain yield per plant (0.41), days to 50% flowering (0.16), and biological yield per plant (0.08). Specifically, grain yield per plant exhibited a higher dominance variance ($\sigma^2_D = 0.25$) compared to additive variance ($\sigma^2_A = 0.21$), highlighting the significant role of non-fixable genetic components. The average degree of dominance exceeded unity for several traits, further confirming the prevalence of over-dominance. Despite the predominance of non-additive effects, high narrow-sense heritability was recorded for number of seeds per spike (90.91%) and spike length (53.82%), accompanied by substantial genetic advance as a percentage of the mean, indicating the potential for reliable phenotypic selection for these specific yield components. These findings on gene action provide a robust genetic framework for formulating targeted breeding strategies. For traits governed by non-additive effects, recurrent selection or heterosis exploitation is recommended, whereas direct selection can be practiced for highly heritable component traits to enhance wheat productivity and contribute to nutritional self-sufficiency.

Keywords: Bread wheat, *Triticum aestivum*, gene action, combining ability, line $\times$ tester analysis, heritability, non-additive variance

1. Introduction

Wheat (*Triticum aestivum* L.; $2n=6x=42$, AABBDD) is a cornerstone of global food security, serving as a primary source of carbohydrates, protein (ranging from 6 to 21 percent), minerals (approximately 1.8 percent), and vitamins for a substantial portion of the world's population (Baloch *et al.*, 2016) ^[1]. The crop occupies a unique position in the agricultural economy of many nations, particularly India, where it is the second most important cereal grain after rice. In India, bread wheat dominates the cultivation landscape, covering approximately 86 percent of the total wheat area, followed by durum wheat (*Triticum durum*) at 12 percent and emmer wheat (*Triticum dicoccum*) at 2 percent. The country has achieved record production of 117.94 million tonnes during the 2024-25 cropping season from 32.8 million hectares, solidifying its position as the world's second-largest wheat producer behind China (Ministry of Agriculture and Farmers Welfare, 2025) ^[10]. This remarkable achievement builds upon the legacy of the Green Revolution, which transformed India from a food-deficient nation to a global agricultural powerhouse. The Food and Agriculture Organization of the United Nations forecasts global wheat production to reach 800.1 million tonnes in 2025, up from 797.7 million tonnes in 2024,

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reflecting a modest but steady increase (FAO, 2026) ^[5]. However, to meet the demands of a burgeoning global population projected to reach 9.7 billion by 2050, a consistent annual genetic gain of approximately 2 percent is required, which surpasses the current 1 percent annual progress achieved through conventional breeding programs (Emerick and Ronald, 2019) ^[3].

Wheat is a special gift from nature to humanity due to its nutritional composition, which includes carbohydrates (60-67 percent), protein (6-21 percent), fat (1.5-2.0 percent), minerals (1.8 percent), vitamins, and cellulose (2.0-2.5 percent) (Baloch *et al.*, 2016) ^[1]. The crop's adaptability to diverse agro-climatic conditions, coupled with its high nutritional value, makes it an indispensable component of the global food system. To bridge the existing yield gap and ensure future food security, plant breeders must possess a precise understanding of the genetic system controlling character inheritance. Specifically, knowledge of the relative magnitude of additive versus non-additive gene action is paramount for selecting the most effective breeding strategy, whether it be pure-line selection, pedigree breeding, backcrossing, or hybrid development (Yadachi *et al.*, 2021) ^[16]. Additive gene action, which is fixable and heritable, responds favorably to simple selection methods because the effects of alleles are cumulative and transmitted unchanged from parents to offspring. In contrast, non-additive gene action, encompassing dominance and epistasis, contributes to heterosis or hybrid vigor and requires different population improvement methods such as recurrent selection or biparental mating for effective utilization.

Initiating a breeding program to enhance any crop variety requires breeders to understand the sort of gene action and genetic system that controls character inheritance, as well as the most effective breeding technique to use to create new high-yielding varieties (Yadachi *et al.*, 2021) ^[16]. There has been a 1 percent annual genetic advance in the yield of new varieties, thanks to very successful conventional breeding methods in enhancing wheat productivity. Nevertheless, a multitude of breeding strategies and statistical approaches for genetic analysis, which are being employed in self-pollinated crops, can still be used to greatly enhance the intrinsic production potential of already cultivated varieties. This might contribute to reaching the projected 2 percent annual gain needed to meet the nation's food needs.

The line $\times$ tester mating design, originally proposed by Kempthorne (1957) ^[9], remains a powerful and widely used biometrical tool for simultaneously estimating combining ability variances of parents and hybrids. This design partitions total genetic variance into general combining ability (GCA), which is attributed to additive genetic effects, and specific combining ability (SCA), which is attributed to non-additive effects including dominance and epistatic interactions (Dhadhal *et al.*, 2008) ^[2]. General combining ability reflects the average performance of a parent in a series of hybrid combinations and is primarily associated with additive gene action, while specific combining ability refers to the deviation of a particular hybrid from the performance expected based on the GCA of its parents and is associated with non-additive gene action. By understanding the nature of gene action, breeders can formulate targeted breeding strategies. For example, knowledge of heterosis, the phenomenon where hybrid offspring outperform their parents, allows breeders to exploit this genetic phenomenon by strategically selecting lines likely to exhibit this effect. In essence, line $\times$ tester analysis equips plant breeders with a powerful tool to accelerate wheat improvement programs (Ullah

et al., 2010) ^[15]. By enabling the selection of superior parental combinations and providing insights into gene action, this technique paves the way for the development of high-yielding, disease-resistant, and adaptable wheat varieties, which translates to a more robust and sustainable food system for generations to come.

Furthermore, the line $\times$ tester design facilitates the estimation of critical genetic parameters, including additive and dominance variance components, the average degree of dominance, narrow-sense heritability, and expected genetic advance. These parameters collectively provide a comprehensive picture of the genetic architecture of quantitative traits. Heritability in the narrow sense, which represents the proportion of total phenotypic variance attributable to additive genetic variance, is particularly important because it indicates the extent to which traits can be improved through phenotypic selection. Genetic advance, when considered together with heritability, gives a more reliable prediction of the expected gain from selection. Therefore, the present investigation was undertaken with the following specific objectives: (i) to assess the nature and magnitude of gene action for yield and its component traits in bread wheat using line $\times$ tester analysis, (ii) to estimate combining ability variances, heritability, and genetic advance, and (iii) to identify the predominant genetic effects to guide future breeding programs aimed at enhancing wheat productivity.

2. Materials and Methods

2.1. Experimental Site and Climatic Conditions

The experiment was conducted at the Agriculture Research Farm, Department of Genetics and Plant Breeding, Lovely Professional University, Phagwara, Punjab, India, during two consecutive Rabi (winter) seasons of 2022-23 for crossing and 2023-24 for evaluation. The geographical coordinates of the experimental site are 31°19'32" North latitude and 75°34'45" East longitude, with an elevation of 243 meters above mean sea level. The region experiences a humid subtropical climate characterized by hot summers and cool winters. The soil of the experimental field was sandy loam in texture, with low available nitrogen, medium available phosphorus, high available potassium, and a slightly alkaline pH ranging from 7.8 to 8.5. The site received an average annual rainfall of approximately 650 mm, predominantly concentrated during the monsoon months of July to September.

2.2. Plant Material and Crossing Program

The experimental material comprised 15 parental genotypes, including 10 lines (female parents) and 5 testers (male parents), along with one commercial check variety, HD 3226. The list of parental genotypes used in the crossing program is presented in Table 1. The lines were selected based on their diverse geographical origins and contrasting agronomic characteristics, while the testers were chosen for their known combining ability and adaptation to the local growing conditions. The crossing program was executed during the Rabi season of 2022-23 using a line $\times$ tester mating design as described by Kempthorne (1957) ^[9]. The 10 lines were crossed with 5 testers in all possible combinations, resulting in 50 F₁ hybrids (10 lines $\times$ 5 testers). Crosses were performed using standard emasculation and pollination techniques following the method described by Giriraj and Swamy (1973) ^[6]. For emasculation, florets of the female parents were carefully opened using forceps, and the three anthers were removed before they reached dehiscence. The emasculated florets were immediately covered with butter paper

bags to prevent unwanted cross-pollination. Pollination was carried out two to three days after emasculation by collecting fresh pollen from the designated male parents and gently dusting it onto the receptive stigmas of the emasculated florets. The pollinated florets were again covered with paper bags until seed set was confirmed. Crossing was carried out on plants spaced at 45 cm between rows and 30 cm between plants on raised ridges to facilitate easy access and management.

Table 1: List of parental genotypes used in the crossing programme

S. No.	Genotypes	
	Lines	Testers
1.	MEX 48	PBW 824
2.	HW 2045	JAUW 672
3.	VB 2565	HD-3059
4.	HD3043	DBW-222
5.	WH 147	WB-2
6.	WL711	
7.	JW17	Check
8.	SAWYT/2020- 21/303	HD 3226
9.	RSP 561	
10.	Faisalabad 2008	

A total of 15 parents were used, comprising 10 female lines and 5 male testers, with a commercial check variety HD 3226 included for comparison in the evaluation phase.

2.3. Field Evaluation and Experimental Design

The 50 F₁ hybrids, along with their 15 parental lines and the check variety HD 3226, were evaluated in a Randomized Complete Block Design (RBD) with three replications during the Rabi season of 2023-24. Each plot consisted of a 3 square meter area with row length of 3 meters. A spacing of 10 centimeters between plants within a row and 22.5 centimeters between rows was maintained to provide adequate growing space for each plant. Sowing was carried out on November 15, 2023, which falls within the optimal sowing window for the Punjab region. Standard agronomic practices were followed throughout the crop growing period to ensure healthy crop growth and development. A fertilizer dose of 150:60:40 kg NPK per hectare was applied, with full doses of phosphorus and potassium and half dose of nitrogen applied as basal at the time of sowing. The remaining half dose of nitrogen was applied as a top dressing at the time of first irrigation, approximately 25 days after sowing. Three irrigations were provided at critical growth stages: crown root initiation, tillering, and grain filling. Weed control was achieved through a combination of manual weeding and pre-emergence application of pendimethalin at 1.0 kg active ingredient per hectare. Plant protection measures were taken as needed to manage foliar diseases and insect pests.

2.4. Observations Recorded

Data were recorded on five randomly selected competitive plants per plot per replication for the following 11 quantitative traits, following standard descriptor guidelines for wheat:

- **Days to 50 percent flowering (D50%):** The number of days from sowing to the day when 50 percent of the plants in a plot had at least one emerged spike.
- **Days to maturity (DM):** The number of days from sowing to the day when 90 percent of the spikes in a plot turned yellow and the grains became hard.
- **Plant height (PH, cm):** Measured from the ground level to the tip of the spike (excluding awns) at maturity, recorded in centimeters.

- **Number of productive tillers per plant (NTP):** The total number of tillers bearing a fully emerged spike was counted on each selected plant.
- **Spike length (SL, cm):** Measured from the base of the spike (the first fertile floret) to the tip of the uppermost spikelet, excluding awns, recorded in centimeters.
- **Number of spikes per plant (NSPS):** The total number of spikes produced by each selected plant was counted.
- **Number of grains per spike (NGPS):** After threshing, the total number of grains from each spike was counted.
- **1000-grain weight (1000GW, g):** A random sample of 1000 grains from each plot was weighed using an electronic balance, and the weight was recorded in grams.
- **Biological yield per plant (BY, g):** The total above-ground dry matter weight of each selected plant, including both grain and straw, was recorded after sun-drying to constant moisture content.
- **Grain yield per plant (GY, g):** The weight of threshed and cleaned grains from each selected plant was recorded.
- **Harvest index (HI, percent):** Calculated as the ratio of grain yield to biological yield, expressed as a percentage.

2.5. Statistical Analysis

The analysis of variance (ANOVA) for the randomized block design was first performed to test the significance of differences among the genotypes for all 11 traits. Following the establishment of significant genotypic differences, combining ability analysis was performed using the line $\times$ tester method as described by Kempthorne (1957) [9]. The total sum of squares for hybrids was partitioned into sums of squares due to lines, testers, and line $\times$ tester interaction. The following linear model was used for the analysis:

$$Y_{ijk} = \mu + l_i + t_j + (l \times t)_{ij} + \epsilon_{ijk}$$

Where:

Y_{ijk} is the observed value of the cross between the i -th line and j -th tester in the k -th replication,

μ is the general mean,

l_i is the effect of the i -th line,

t_j is the effect of the j -th tester,

$(l \times t)_{ij}$ is the interaction effect between the i -th line and j -th tester,

ϵ_{ijk} is the error term.

The variance components for GCA (σ^2_{GCA}) and SCA (σ^2_{SCA}) were computed as follows:

$$\sigma^2_{GCA} = (MS \text{ lines} + MS \text{ testers}) / (l + t)$$

$$\sigma^2_{SCA} = MS \text{ lines} \times \text{testers} - MS \text{ error}$$

The additive genetic variance (σ^2_A) was estimated as $2 \times \sigma^2_{GCA}$, and the dominance genetic variance (σ^2_D) was estimated as σ^2_{SCA} . The total phenotypic variance (σ^2_P) was computed as the sum of σ^2_A , σ^2_D , and the environmental variance (σ^2_E), where σ^2_E was taken as the error mean square from the ANOVA.

The following genetic parameters were subsequently calculated: Average degree of dominance was computed as the square root of $(2 \times \sigma^2_{SCA} / \sigma^2_{GCA})$ or alternatively as the square root of $(\sigma^2_D / \sigma^2_A)$. An average degree of dominance value of zero

indicates no dominance, a value between zero and one indicates partial dominance, a value equal to one indicates complete dominance, and a value greater than one indicates over-dominance.

Predictability ratio was calculated as $\sigma^2\text{GCA}$ divided by $\sigma^2\text{SCA}$. A predictability ratio greater than unity indicates predominance of additive gene action, while a ratio less than unity indicates predominance of non-additive gene action.

Narrow-sense heritability $h^2(\text{ns})$ was calculated as the ratio of additive genetic variance to total phenotypic variance, multiplied by 100:

$$h^2(\text{ns}) = (\sigma^2\text{A} / \sigma^2\text{P}) \times 100$$

Genetic advance (GA) was calculated using the formula:

$$\text{GA} = k \times h^2(\text{ns}) \times \sigma\text{P}$$

where k is the selection differential at 5 percent selection intensity ($k = 2.06$), $h^2(\text{ns})$ is the narrow-sense heritability expressed as a decimal, and σP is the phenotypic standard

deviation. Genetic advance as a percentage of the mean was then calculated as $(\text{GA} / \text{grand mean}) \times 100$.

All statistical analyses were performed using appropriate statistical software packages, and significance was tested at the 5 percent and 1 percent probability levels.

3. Results

3.1. Analysis of Variance for Combining Ability

The analysis of variance for combining ability revealed significant differences among the 50 F_1 hybrids for all 11 traits under study, indicating the presence of substantial genetic variability among the hybrid populations. The partitioning of hybrid sum of squares into components attributable to lines, testers, and line $\times$ tester interaction showed that both GCA and SCA variances contributed significantly to the total genetic variation for most traits, although their relative magnitudes varied considerably across traits. The results of the combining ability analysis, including the variance components, average degree of dominance, predictability ratio, additive and dominance variances, narrow-sense heritability, and genetic advance as a percentage of the mean, are presented in Table 2.

Table 2: Components of variance, degree of dominance, additive and dominance components, narrow-sense heritability, and genetic advance for 11 characters in bread wheat (F_1 hybrids)

Characters	Gca variance ($\sigma^2\text{g}$)	Sca variance ($\sigma^2\text{s}$)	Average degree of dominance	Predictability ratio	$\sigma^2\text{A}$	$\sigma^2\text{D}$	Heritability ($h^2(\text{ns})\%$)	Genetic advance in per cent of mean
D50%	2.3144*	14.0926**	4.04	24.72	4.63	14.10	20.84	2.02
DM	0.09	2.5238**	0.33	6.44	0.17	2.52	3.65	0.16
PH	0.10	5.7083**	0.54	3.40	0.20	5.71	2.27	0.14
NTP	0.03	0.23	0.06	23.25	0.07	0.23	225.68	0.82
SL	0.05	0.08	0.04	53.82	0.09	0.08	21.60	0.30
NSPS	0.24	0.05	0.08	90.91	0.48	0.05	21.53	0.67
NGPS	0.09	0.46	0.14	27.65	0.17	0.46	53.47	0.63
1000GW	0.07	0.34	0.11	30.32	0.15	0.34	25.73	0.40
BY	0.31	4.0250**	0.79	13.44	0.62	4.03	9.33	0.50
GYP	0.1026**	0.25	0.11	45.55	0.21	0.25	13.06	0.34
HI	0.02	0.20	0.04	13.32	0.03	0.20	2.74	0.06

$\sigma^2\text{GCA}$: General combining ability variance; $\sigma^2\text{SCA}$: Specific combining ability variance; $\sigma^2\text{A}$: Additive genetic variance; $\sigma^2\text{D}$: Dominance genetic variance; $h^2(\text{ns})$: Narrow-sense heritability; GA: Genetic advance

3.2. Components of Genetic Variance

The GCA variance ($\sigma^2\text{GCA}$) ranged from 0.02 for harvest index to 2.31 for days to 50 percent flowering. The SCA variance ($\sigma^2\text{SCA}$) was generally higher than the corresponding GCA variance for most traits, including days to 50 percent flowering (14.09), plant height (5.71), biological yield (4.03), days to maturity (2.52), and number of grains per spike (0.46). For days to 50 percent flowering, the SCA variance was more than six times larger than the GCA variance, indicating the predominance of non-additive gene action for this trait. Similarly, for plant height and biological yield, the SCA variances were substantially larger than the GCA variances. However, for number of spikes per plant, the GCA variance (0.24) was considerably larger than the SCA variance (0.05), suggesting the importance of additive gene action for this trait. For grain yield per plant, the GCA variance was 0.10, while the SCA variance was 0.25, again indicating a larger contribution of non-additive effects.

3.3. Additive and Dominance Variance Components

The additive genetic variance ($\sigma^2\text{A}$) ranged from 0.03 for harvest index to 4.63 for days to 50 percent flowering. The dominance genetic variance ($\sigma^2\text{D}$) ranged from 0.05 for number of spikes per plant to 14.10 for days to 50 percent flowering. For the majority of traits, the dominance variance was larger than the

additive variance. Specifically, for days to 50 percent flowering, the dominance variance (14.10) was approximately three times larger than the additive variance (4.63). For grain yield per plant, the dominance variance (0.25) was slightly larger than the additive variance (0.21). For number of tillers per plant, the dominance variance (0.23) was more than three times larger than the additive variance (0.07). For biological yield, the dominance variance (4.03) was more than six times larger than the additive variance (0.62). These results consistently indicate that non-additive genetic effects played a predominant role in the inheritance of these agronomically important traits. In contrast, for number of spikes per plant, the additive variance (0.48) was substantially larger than the dominance variance (0.05), indicating the predominance of additive gene action for this trait. For spike length, the additive variance (0.09) and dominance variance (0.08) were nearly equal, suggesting that both types of gene action contributed to the inheritance of this trait.

3.4. Average Degree of Dominance

The average degree of dominance ranged from 0.04 for spike length to 4.04 for days to 50 percent flowering. For days to 50 percent flowering, the average degree of dominance was 4.04, which is substantially greater than unity, indicating over-dominance for this trait. For plant height, the average degree of dominance was 0.54, which falls between zero and one,

indicating partial dominance. For days to maturity, the value was 0.33, also indicating partial dominance. For grain yield per plant, the average degree of dominance was 0.11, indicating partial dominance. For number of grains per spike, the value was 0.14, indicating partial dominance. For number of spikes per plant, the average degree of dominance was 0.08, which is close to zero, indicating a near absence of dominance for this trait. The wide range of average degree of dominance values across traits reflects the diversity in genetic control mechanisms operating for different agronomic characters.

3.5. Predictability Ratio

The predictability ratio, calculated as the ratio of GCA variance to SCA variance, was substantially below unity for most traits. For days to 50 percent flowering, the predictability ratio was 0.16, indicating that non-additive gene action was about six times more important than additive gene action. For plant height, the ratio was 0.02, indicating an overwhelming predominance of non-additive effects. For biological yield, the ratio was 0.08. For grain yield per plant, the ratio was 0.41, still well below unity. For harvest index, the ratio was 0.10. For days to maturity, the ratio was 0.04. These values consistently point to the predominance of non-additive gene action for the majority of the traits studied. However, for number of spikes per plant, the predictability ratio was 4.80, which is substantially greater than unity, indicating the predominance of additive gene action for this trait. For spike length, the predictability ratio was 0.63, which is still below unity but closer to parity, suggesting a more balanced contribution of additive and non-additive effects.

3.6. Narrow-Sense Heritability

Narrow-sense heritability estimates varied widely across the 11 traits, ranging from as low as 2.27 percent for plant height to as high as 225.68 percent for number of tillers per plant. The heritability estimate for number of tillers per plant exceeded 100 percent, which is theoretically impossible and indicates that the estimate was inflated due to sampling error or violations of underlying assumptions. Therefore, this estimate should be interpreted with caution. For number of spikes per plant, narrow-sense heritability was 90.91 percent, which is high and indicates that a large proportion of the phenotypic variation for this trait is attributable to additive genetic effects. For number of grains per spike, heritability was 53.47 percent, which is moderate. For 1000-grain weight, heritability was 25.73 percent, which is low to moderate. For grain yield per plant, heritability was 13.06 percent, which is low. For days to 50 percent flowering, heritability was 20.84 percent. For biological yield, heritability was 9.33 percent. The low heritability estimates for grain yield and its related traits indicate that environmental factors played a substantial role in the expression of these traits, and that selection based solely on phenotypic values may not be highly effective.

3.7. Genetic Advance as Percentage of Mean

Genetic advance as a percentage of the mean ranged from 0.06 percent for harvest index to 0.82 percent for number of tillers per plant. For number of spikes per plant, genetic advance was 0.67 percent of the mean. For number of grains per spike, it was 0.63 percent. For biological yield, it was 0.50 percent. For grain yield per plant, it was 0.34 percent. The generally low values of genetic advance as a percentage of the mean, particularly for yield-related traits, suggest that the expected gain from selection in these hybrid populations would be modest, especially when considered together with the low heritability estimates for these

traits.

4. Discussion

The primary objective of this study was to elucidate the nature of gene action governing the inheritance of yield and its component traits in bread wheat using a line $\times$ tester mating design. The results obtained provide valuable insights into the genetic architecture of these traits and have important implications for the design of effective breeding strategies for wheat improvement.

4.1. Predominance of Non-Additive Gene Action

The most striking finding of this investigation is the predominance of non-additive gene action for the majority of the 11 traits examined. This conclusion is supported by multiple lines of evidence from the genetic analysis. First, the SCA variance (σ^2_{SCA}) was consistently larger than the GCA variance (σ^2_{GCA}) for most traits, including days to 50 percent flowering, plant height, biological yield, grain yield per plant, days to maturity, and number of grains per spike. Second, the predictability ratio ($\sigma^2_{GCA}/\sigma^2_{SCA}$) was substantially below unity for these same traits, indicating that non-additive effects contributed more to the total genetic variation than additive effects. Third, the dominance variance (σ^2_D) exceeded the additive variance (σ^2_A) for the majority of traits. Fourth, the average degree of dominance exceeded unity for days to 50 percent flowering, indicating over-dominance, while for other traits it indicated partial dominance.

The predominance of non-additive gene action for grain yield per plant is particularly noteworthy. Grain yield is a complex quantitative trait that is influenced by many component traits and is known to be highly sensitive to environmental fluctuations. The finding that dominance variance (0.25) was greater than additive variance (0.21) for grain yield indicates that heterosis or hybrid vigor could potentially be exploited to enhance wheat productivity. This result is consistent with the findings of several earlier studies in wheat. Sharma and Chaudhary (2009) ^[14] reported that non-additive gene action played a predominant role in the inheritance of grain yield in bread wheat. Similarly, Hakeem, Chand, and Maurya (2020) ^[7] observed that specific combining ability effects were more important than general combining ability effects for grain yield and several yield-related traits, indicating the importance of non-additive effects. Ullah *et al.* (2010) ^[15] also reported that non-additive gene action governed the inheritance of grain yield in spring wheat.

The predominance of non-additive effects for days to 50 percent flowering and days to maturity is also consistent with previous reports. These phenological traits are critical for adaptation to specific growing environments and for escaping terminal heat or drought stress. The high SCA variance and low predictability ratio for these traits suggest that hybrid combinations can be identified that flower and mature at optimal times, potentially contributing to yield stability under stress conditions. Saleem *et al.* (2024) ^[12] recently reported that non-additive effects predominate for yield and phenological traits in wheat under drought stress conditions, highlighting the importance of heterosis breeding for developing climate-resilient varieties.

The predominance of non-additive gene action for plant height is an interesting finding. Plant height is often considered a highly heritable trait with predominantly additive gene action, particularly in the context of semi-dwarfing genes that have been widely deployed in modern wheat varieties. However, the present results indicate that for the specific set of parents used in

this study, non-additive effects were more important for plant height. This discrepancy may be due to the specific genetic backgrounds of the parental lines used, which may have included both dwarf and tall genotypes, leading to dominance effects in the hybrid combinations.

4.2. Implications for Breeding Strategies

The predominance of non-additive gene action for grain yield and other important agronomic traits has important implications for the choice of breeding strategies. In self-pollinated crops like wheat, conventional breeding methods such as pedigree selection, bulk population breeding, and single seed descent rely primarily on additive genetic variance for progress from selection. When non-additive variance predominates, these methods may be less effective because the superior performance of hybrid combinations in the F_1 generation is not fully transmitted to subsequent generations due to the breakdown of dominance and epistatic effects.

Under conditions of predominant non-additive gene action, several alternative breeding strategies may be more effective. Recurrent selection methods, including simple recurrent selection, reciprocal recurrent selection, and recurrent selection for specific combining ability, can be used to accumulate favorable alleles while maintaining heterozygosity and exploiting non-additive effects. Biparental mating or diallel selective mating can also be used to break undesirable linkages and create new recombinants with enhanced yield potential. Another approach is to exploit heterosis directly through the development of hybrid wheat. Although hybrid wheat has not been widely adopted due to the high cost of hybrid seed production and the modest levels of heterosis typically observed in wheat compared to cross-pollinated crops like maize, advances in male sterility systems and seed production technology may make hybrid wheat more feasible in the future.

Despite the predominance of non-additive effects for most traits, the presence of high narrow-sense heritability for number of spikes per plant (90.91 percent) and spike length (53.82 percent) indicates that additive variance is substantial for these traits. Therefore, direct phenotypic selection for these component traits could be effective in improving yield potential, even if grain yield itself is primarily under non-additive control. This observation is consistent with the findings of Johnson, Robinson, and Comstock (1955) [8], who emphasized that heritability estimates should be considered together with genetic advance to predict the expected response to selection. In the present study, the high heritability for number of spikes per plant, combined with moderate genetic advance, suggests that selection for this trait would be rewarding.

4.3. Comparison with Previous Studies

The findings of this study are broadly consistent with the results of previous line $\times$ tester analyses in wheat. Dhadhal *et al.* (2008) [2] reported that non-additive gene action was predominant for grain yield and most yield-related traits in bread wheat. They recommended reciprocal recurrent selection or biparental mating for improving these traits. Yadachi *et al.* (2021) [16] also observed that SCA variance was larger than GCA variance for grain yield, indicating the importance of non-additive effects. However, some studies have reported the opposite pattern, with additive effects predominating for certain traits. For example, Ullah *et al.* (2010) [15] found that additive gene action was more important for plant height and tiller number in some wheat crosses, while non-additive effects were more important for grain yield. These discrepancies highlight the fact that the

relative importance of additive versus non-additive effects depends on the specific genetic material under investigation, the environmental conditions, and the trait being studied.

The high narrow-sense heritability for number of spikes per plant observed in this study is consistent with the findings of Raffo *et al.* (2023) [11], who reported that additive epistasis is important for genomic prediction in advanced wheat lines. The moderate heritability for number of grains per spike and 1000-grain weight is also in general agreement with previous reports. The low heritability for grain yield per plant is a common finding in wheat breeding studies, reflecting the complex genetic control of yield and its high sensitivity to environmental variation.

5. Conclusion

This line $\times$ tester analysis of 50 bread wheat hybrids, derived from 10 lines and 5 testers, has provided comprehensive insights into the genetic architecture governing yield and its component traits. The study conclusively demonstrates that non-additive gene action, encompassing dominance and epistatic effects, predominantly controls the inheritance of most agronomically important traits, including grain yield per plant, days to 50 percent flowering, plant height, and biological yield. This conclusion is supported by multiple genetic parameters: the predictability ratios were substantially below unity for these traits, the SCA variances exceeded the GCA variances, and the dominance variance components were larger than the additive variance components. The average degree of dominance exceeded unity for days to 50 percent flowering, indicating over-dominance, while partial dominance was observed for other traits. The findings of this study have important implications for wheat breeding programs. For traits governed by non-additive effects, breeding strategies such as recurrent selection, biparental mating, or delayed selection in segregating generations are recommended. For highly heritable component traits, direct phenotypic selection can be practiced. The identification of specific hybrid combinations with superior combining ability can guide the development of high-yielding varieties. Overall, this research provides a robust genetic framework for formulating targeted breeding strategies to enhance wheat productivity and contribute to global food security and nutritional self-sufficiency.

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