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Genetic Analysis of Agronomic Traits in Bread Wheat (*Triticum aestivum* L.): Insights from Generation mean Analysis and Heritability Estimates

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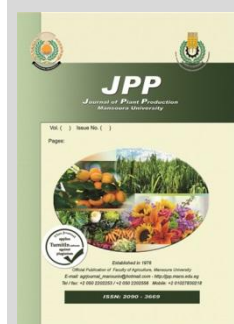
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ABSTRACT

This study investigated the genetic inheritance of key agronomic traits in wheat (*Triticum aestivum* L.) using generation mean analysis. Four wheat crosses (Line 1 × Misr 1, Line 1 × Sakha 95, Sakha 94 × Misr 1, and Sakha 94 × Sakha 95) were evaluated in season 2023/2024 at Sakha Agricultural Research Station, Egypt. A randomized complete block design (RCBD) with three replications was used to assess five populations (P₁, P₂, F₁, F₂, and F₃) of the four crosses. The evaluated traits included plant height, number of spikes per plant, average coefficient of infection (ACI), kernels per spike, 100-kernel weight, and grain yield. F₁ plants exhibited significant heterosis for most traits, with plant height increasing by 12–18% over the taller parent. F₂ and F₃ showed a decline in traits such as grain yield and plant height due to genetic segregation. Grain yield in F₁ was 15–20% higher than the best parent but dropped by 10–25% in F₃. Scaling tests revealed significant epistatic interactions, particularly for plant height, spikes per plant, and kernel weight, confirming the involvement of non-allelic interactions. Broad-sense heritability was high (>75%) for most traits, while narrow-sense heritability was moderate (30–50%), indicating contributions from both additive and non-additive gene effects. The highest genetic advance was observed for ACI (28.59%), suggesting effective selection for yellow rust resistance. These findings provide critical insights for wheat breeding, emphasizing the need for delayed selection to stabilize yield-related traits in later generations due to significant epistatic interactions.

Keywords: Wheat, Gene Effects, Heritability, Scaling Test, Grain Yield, Yellow Rust, Epistasis



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INTRODUCTION

Wheat (*Triticum aestivum* L.) is a fundamental staple crop worldwide, significantly contributing to human caloric intake and serving as a cornerstone of food security (Cao *et al.*, 2020). In Egypt, wheat's importance is underscored by its role in both agriculture and the national diet, necessitating ongoing efforts to enhance yield and quality to meet the demands of a growing population (El-Hosary & El-Sayed, 2023). The country's reliance on wheat imports further highlights the urgency of developing high-yielding, locally adapted cultivars (El-Hosary & El-Sayed, 2023). The genetic improvement of wheat has been a primary focus of plant breeding programs, aiming to develop cultivars with superior agronomic traits such as plant height (PH), seeds per plant (SPP), kernels per spike (KPS), 100-seed weight (HSW), and grain yield (GY) (Cao *et al.*, 2020). Understanding the genetic parameters underlying these traits is crucial for effective selection and breeding strategies (Liu *et al.*, 2015). Recent studies have highlighted the importance of assessing genetic variability and heritability to inform breeding decisions (Ali *et al.*, 2008). Generation means analysis (GMA) is a valuable tool in plant breeding, facilitating the estimation of various gene effects, including additive, dominance, and epistatic interactions (Sharma & Agrawal, 2020 c). This method involves evaluating multiple generations, such as parental (P₁ and P₂), first filial (F₁), and second filial (F₂) generations, although backcross generations (BC₁ and BC₂) were not included in this study (Mather & Jinks, 1982). By analyzing these generations, breeders can dissect the genetic architecture of key traits and evaluate the adequacy of

additive-dominance models (Sharma & Agrawal, 2020 a). Scaling tests, as described by Mather and Jinks (1982), are employed to assess the suitability of additive-dominance models for different characters in wheat crosses. The significance of these tests indicates the presence of epistasis, suggesting that non-allelic gene interactions play a role in trait inheritance (Sharma & Agrawal, 2020 b). When scaling tests reveal the inadequacy of simple additive-dominance models, more complex models, such as the five-parameter model, are utilized to estimate gene effects accurately (Ali *et al.*, 2008). The five-parameter model facilitates the estimation of additive, dominance, and epistatic effects, providing a comprehensive understanding of the genetic control of traits (Ali *et al.*, 2008). This model is particularly useful in advanced generations of wheat, where interactions between genes can significantly influence trait expression (Sharma & Agrawal, 2020 a). By applying this model, breeders can identify the most effective selection strategies to enhance desirable traits in wheat populations (Ali *et al.*, 2008). In wheat breeding programs, key agronomic traits such as plant height, seeds per plant, kernels per spike, 100-seed weight, and grain yield are of paramount importance (Cao *et al.*, 2020). These traits directly impact the productivity and economic value of wheat cultivars (Liu *et al.*, 2015). Understanding the genetic basis of these traits enables breeders to implement targeted selection strategies, thereby accelerating the development of improved wheat varieties (Cao *et al.*, 2020).

In this study, we evaluated five populations including two parents (P₁ and P₂), F₁, F₂, and F₃ derived from four wheat crosses. We measured key agronomic traits, including plant

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height, seeds per plant, kernels per spike, 100-seed weight, and grain yield. Through the application of scaling tests and the five-parameter model, we analyzed genetic parameters and estimated gene effects, including additive (a), dominance (d), additive $\times$ additive (aa), and dominance $\times$ dominance (dd) interactions. Our aim was to elucidate the genetic architecture of these traits to inform breeding strategies for the development of high-yielding and resilient wheat cultivars.

MATERIALS AND METHODS

The field experiment was conducted at the Experimental Farm of Sakha Agricultural Research Station, Agricultural Research Center, Egypt, over four growing seasons of 2020/21, 2021/22, 2022/23, and 2023/24. Details regarding the parental genotypes, including their selection history are provided in Table 1. During the 2020/21 season, parental genotypes were crossed to develop four F_1 hybrids: Cross 1 (Line 1 $\times$ Misr 1), Cross 2 (Line 1 $\times$ Sakha 95), Cross 3 (Sakha 94 $\times$ Misr 1), and Cross 4 (Sakha 94 $\times$ Sakha 95). A portion of the grains from the F_1 and F_2 generations of these crosses were sown in the 2021/22 and 2022/23 seasons to generate the F_2 and F_3 populations, respectively.

In the 2023/24 season, the parental lines, F_1 , F_2 , and F_3 populations of all four crosses were evaluated. The experiment followed a randomized complete block design (RCBD) with three replications. Each plot consisted of 13 rows: one row each for P_1 , P_2 , and F_1 ; five rows each for F_2 and F_3 ; and two border rows to minimize edge effects. The rows were 3 m long, spaced 20 cm apart, with 10 cm between plants within each row. Standard agronomic practices were followed throughout the growing season. Data were collected

from 30 randomly selected plants per parent and F_1 generation and from 200 plants per F_2 and F_3 population to evaluate key agronomic traits, including plant height (cm), number of spikes per plant, average coefficient of infection (ACI) for yellow rust, number of kernels per spike, 100-kernel weight (g), and grain yield per plant (g).

Biometrical and Genetic Methods

The five-parameter model described by Gamble (1962) was used to estimate additive, dominance, and epistatic gene effects. The scaling test was applied to predict and assess epistatic interactions. The variance, standard error, and t-test of the scaling test were calculated to determine genetic interactions or to assess the fit of a simple additive-dominance model. Population mean analysis was conducted using the biometrical approach developed by Mather and Jinks (1982) to estimate genetic parameters. The means of the six population in each cross were used to estimate the six parameters (mean effect (m), additive gene effect(d), dominant gene effect(h), additive $\times$ additive as type of epistasis(i), additive $\times$ dominance as type of epistasis (j) and dominance $\times$ dominance as type of epistasis (l)) and tested using the t-test for all studied traits, based on Hayman's model (1958), as described by Singh and Chaudhary (1985). Broad-sense (h^2_b) and narrow-sense (h^2_n) heritability were estimated, along with the mean degree of dominance, inbreeding depression (%), and heterosis relative to the mid-parent and better-parent values, according to Mather and Jinks (1982). Additionally, the expected genetic advance (GA%) as a percentage of the F_2 mean was calculated following the method reported by Allard (1999).

Table 1. Names and pedigree of the studied parental Egyptian bread wheat genotypes.

Name	Pedigree
Sakha 94	OPATA/RAYON/KAUZ. CMBW90Y31800-TOPM-3Y-010M-010M-010Y-10M-015Y0Y-0AB-0S
Sakha 95	PASTOR/SITE/MO/3/CHEN/AEGILOPSSQUARROSA (TAUS)/BCN/4/WBLL1. CMSA01Y00158S-040P0Y-040M-030ZTM-040SY-26M-0Y0SY-0S.
Misr 1	OASIS/KAUZ//4*BCN/3/2*PASTOR. CMSS00Y01881T -050M-030M-030M-030WGY-33M- 0Y-0S - 0EGY.
Line 1	SAKHA8/YECORA ROJO

RESULTS AND DISCUSSION

Mean Performance

Means and variances of the five populations of the four crosses are shown in Table 2 (a, b, c and d). Data showed highly significant differences among the investigated populations and their respective parents for most studied traits.

1. Plant height, cm (PH)

Plant height varied across the generations, with F_1 plants generally exhibiting greater height than their parents in all four crosses. In Line 1 $\times$ Misr 1 and Line 1 $\times$ Sakha 95 crosses, F_1 plants showed significant hybrid vigor (heterosis), with heights surpassing both parental lines. However, in F_2 , a noticeable decline was observed, followed by an even greater reduction in F_3 , indicating the effects of genetic segregation. A similar trend was seen in Sakha 94 $\times$ Misr 1 and Sakha 94 $\times$ Sakha 95 crosses, where F_1 plants outperformed both parents, but later generations exhibited reduced height due to the breakdown of heterozygosity. This pattern aligns with previous findings in wheat and other cereal crops, where F_1 plants typically display increased plant height due to heterosis, followed by a gradual decline in later generations due to genetic recombination (Singh *et al.*, 2020). The reduction in F_3 height suggests the presence of recessive

alleles affecting plant height and emphasizes the need for selection to stabilize desirable plant architecture.

2. Spikes number per plant (S.p)

The number of spikes per plant varied among crosses, but a common trend of reduction in later generations was evident. In Line 1 $\times$ Misr 1, F_1 plants exhibited the highest number of spikes per plant, with a steady decline in F_2 and F_3 . Similarly, in Line 1 $\times$ Sakha 95, an increase from P_1 to F_1 was observed, followed by a slight drop in F_2 and a more pronounced reduction in F_3 . In contrast, in Sakha 94 $\times$ Misr 1, P_2 had the highest spikes count per plant, with F_1 and F_2 maintaining similar values before a decrease in F_3 . The Sakha 94 $\times$ Sakha 95 cross showed a relatively stable trait across all generations, with minor exceptions. These results align with previous studies in wheat, where F_1 plants exhibit an increase in spikes number due to heterotic effects, followed by segregation in later generations (Kumar *et al.*, 2018). The reduction in F_3 could be attributed to genetic recombination, leading to increased variability among segregating populations. Breeding strategies focusing on spikes retention in later generations can help maintain high-yielding genotypes.

3. Average Coefficient of Infection (ACI) for Yellow Rust

The ACI values indicated varying levels of yellow rust infection across generations. In Line 1 $\times$ Misr 1, F_1

exhibited the lowest ACI, suggesting a higher resistance level compared to the parents. However, F₂ showed an increase in ACI, and F₃ exhibited even higher susceptibility, reflecting segregation for resistance genes. A similar trend was observed in Line 1 × Sakha 95, where F₁ had the lowest ACI, followed by an increase in F₂ and a peak in F₃. In Sakha 94 × Misr 1, resistance appeared more stable across generations, with only a slight increase in F₃. Meanwhile, in Sakha 94 × Sakha 95,

susceptibility remained relatively high across all generations, indicating a lack of strong resistance genes. Previous studies have shown that yellow rust resistance in wheat is often conferred by major genes that segregate in later generations, leading to increased infection rates in F₂ and F₃ (Ali *et al.*, 2021). The increase in ACI in later generations highlights the importance of marker-assisted selection (MAS) for retaining resistant genotypes in breeding programs.

Table 2-a. Means ($\bar{X}$) and variances (S^2) for all the studied traits using five populations for Line 1 x Misr 1 cross

Cross	Statistical parameter	Trait	P ₁	P ₂	F ₁	F ₂	F ₃
Line 1 x Misr 1	Mean	PH	94.71 ***	109.65 ***	109.76 ***	106.99 ***	99.1
	Variance		1.39	27.85	1.19	39.37	59.65
	Mean	S.P	27.34 ***	22.7 ***	26 ***	23.44 ***	15.91
	Variance		76.41	23.41	38.2	60.31	39.68
	Mean	ACI	26.29 ***	37.44 ***	44.29 *	20.24 ***	47.49
	Variance		24.03	209.97	25.71	824.9	1389.3
	Mean	GY	22 **	36.91 ***	32.46 ***	29.68 ***	21.03
	Variance		3.29	1.28	94.96	120.82	84.47
	Mean	KSP	46.2 ***	62.77 ***	57.67 ***	56.97 ***	41.08
	Variance		0.81	0.66	1.03	141.24	157.67
	Mean	100KW	2.74 ***	3.55 ***	3.93 ***	3.25 ***	1.52
	Variance		0.01	0	0.01	0.37	0.42

Table 2. b. Means ($\bar{X}$) and variances (S^2) for all the studied traits using five populations for Line 1 x Sakha 95 cross

Cross	Statistical parameter	Trait	P ₁	P ₂	F ₁	F ₂	F ₃
Line 1 x Sakha 95	Mean	PH	89.15 ***	111.06 ***	110 ***	107.91 ***	100.07
	Variance		24.88	24.62	8.11	104.77	105.52
	Mean	S.p	15.9 ***	19.52	26.29 ***	25.68 ***	20.17
	Variance		9.89	26.26	43.08	48.21	42.28
	Mean	ACI	78.05 ***	18.91 ***	77.89 ***	16.49 ***	52.78
	Variance		31.1	15.27	17.07	737.51	1674.6
	Mean	GY	12.58 ***	48.83 ***	43.48 ***	39.43 ***	27.24
	Variance		27.3	184.79	146.19	226.67	169.44
	Mean	KSP	35.22 **	43.45	47.76 *	55 ***	41.46
	Variance		147.83	267.82	318.46	142.84	197.6
	Mean	100KW	1.36 **	2.5 ***	2.68 ***	3.48 ***	1.63
	Variance		0.37	0.4	0.61	0.52	0.65

Table 2. c. Means ($\bar{X}$) and variances (S^2) for all the studied traits using five populations for Sakha 94 x Misr 1 cross

Cross	Statistical parameter	Trait	P ₁	P ₂	F ₁	F ₂	F ₃
Sakha 94 x Misr 1	Mean	PH	117.64 ***	114.88 ***	114.88 ***	116.88 ***	108.49
	Variance		6.41	24.99	21.14	41.27	58.4
	Mean	S.p	23.44 **	26.93 ***	25.52 ***	23.33 ***	18.76
	Variance		74.83	40.12	56	59.1	31.87
	Mean	ACI	0.4 ***	0.1 ***	0.4 ***	1.42	1.87
	Variance		0	0	0	10.31	12.59
	Mean	GY	28.5 ***	35.55 *	39.01 *	36.91 *	34.39
	Variance		2.31	4.55	124.23	244.28	204.01
	Mean	KSP	66.5 ***	68.93 ***	59.65 ***	56.76 ***	49.48
	Variance		0.54	0.9	1.46	183.66	178.03
	Mean	100KW	3.74 ***	3.55 ***	4.07 ***	3.73 ***	2.27
	Variance		0	0	0.01	0.23	0.57

Table 2. d. Means ($\bar{X}$) and variances (S^2) for all the studied traits using five populations for Sakha 94 x Sakha 95 cross

Cross	Statistical parameter	Trait	P ₁	P ₂	F ₁	F ₂	F ₃
Sakha 94xSakha 95	Mean	PH	120.31 ***	121.84 ***	122.42 ***	119.56 ***	112.3
	Variance		1.51	8.92	14.78	101.22	114.72
	Mean	S.p	21.16 *	21.89 *	20.9 *	22.01 ***	18.37
	Variance		42.72	37.88	37.16	45.91	17.51
	Mean	ACI	1.15 *	0.1 ***	1.64 ***	0.48	0.6
	Variance		1.59	0	2.38	1.04	1.13
	Mean	GY	27.41 ***	54.79 ***	35.5	39.12 ***	32.31
	Variance		1.99	1.29	200.53	305.71	234.99
	Mean	KSP	70.62 ***	72.26 ***	65.45 ***	57.12 ***	48.33
	Variance		0.95	32.54	0.46	232.06	230.47
	Mean	100KW	3.79 ***	3.99 ***	4.17 ***	3.43 ***	1.98
	Variance		0	0	0.01	0.37	0.62

4. Grain Yield plant⁻¹, g (GY)

Grain yield followed a typical trend of heterosis in early generations, with a subsequent decline. In Line 1 × Misr 1, F₁ and F₂ showed higher grain yield per plant than P₁, but F₃ exhibited a notable decrease. The same pattern was seen in Line 1 × Sakha 95, where F₁ and F₂ outperformed P₁, but F₃

experienced a drop. In Sakha 94 × Misr 1, F₁ yield was higher than the parents, but later generations saw a gradual reduction. In Sakha 94 × Sakha 95, P₂ had the highest grain yield per plant, but values declined in F₃, reflecting segregation and environmental variation. Studies by Sharma *et al.* (2019) has reported similar findings in wheat, where grain yield is the

highest in early generations due to the combined effects of heterosis and better adaptability, but declines in F_3 due to segregation and environmental interactions. The observed decrease in later generations highlights the importance of selecting high-yielding lines with stable genetic backgrounds.

5. Kernels number per Spike (K/SP)

Kernels no. per spike showed a similar trend of higher values in early generations, followed by a decline in later generations. In Line 1 $\times$ Misr 1, both parents and F_1 had the highest kernels count, while noticeable reductions were seen in F_2 and F_3 . In Line 1 $\times$ Sakha 95, a peak in F_2 was observed before a decline in F_3 . In Sakha 94 $\times$ Misr 1, P_2 had the highest K/SP, with subsequent generations showing a steady decline. A similar pattern was seen in Sakha 94 $\times$ Sakha 95, where P_2 outperformed other generations, followed by a downward trend in F_2 and F_3 . Previous research has confirmed that kernels number is a key yield component in wheat and is highly influenced by genetic background and environmental factors (Iqbal *et al.*, 2020). The decline in F_3 suggests the need for further selection to stabilize this trait in segregating populations.

6. 100-Kernel Weight, g (100KW)

Kernel weight was generally highest in F_1 across all crosses before decreasing in later generations. In Line 1 $\times$ Misr 1, F_1 had the highest weight, followed by a reduction in F_2 and F_3 . A similar pattern was seen in Line 1 $\times$ Sakha 95, where values increased from P_1 to F_2 before declining in F_3 . In Sakha 94 $\times$ Misr 1, F_1 had the highest 100-kernel weight, which decreased in later generations. The Sakha 94 $\times$ Sakha 95 cross followed the same trend, with F_1 reaching the highest value and a subsequent reduction in F_3 . Similar findings were reported by Mohammadi *et al.* (2021), where 100-kernel weight was the highest in early generations due to heterotic effects but declined in later generations due to segregation. The reduction in kernel weight in F_3 highlights the need for selection programs aimed at improving grain filling and maintaining seed weight stability. Generally, the results indicate that F_1 plants typically outperform their parents in most traits due to heterosis. However, F_2 maintains high values but shows increased variability, while F_3 exhibits a decline in performance due to genetic segregation. This trend has been widely observed in wheat breeding programs (Singh *et al.*, 2020). The decline in later generations suggests the need for selective breeding to retain desirable traits. Interestingly, some traits, such as ACI in the Sakha 94 $\times$ Sakha 95 cross, remained stable, indicating a low level of genetic variation for yellow rust resistance in this background. This suggests that certain parental combinations may lack resistance alleles, making MAS essential for improving disease resistance in wheat breeding programs. Overall, this study highlights the importance of selecting superior F_3 families with stable agronomic and disease resistance traits for future breeding efforts. Further research should focus on genomic selection and MAS to enhance yield stability and disease resistance in wheat cultivars.

The evaluated traits included plant height (PH), spikes number per plant (S.p), Average coefficient of infection (ACI), grain yield/plant (GY), kernels number per spike (KSP), and 100-kernel weight (100KW). These traits represent key morphological, physiological, and yield-related characteristics in the study.

Scaling test and gene effects:

Scaling test estimates of the investigated traits in the four crosses are presented in Table 3. At least one of the estimated values of C and D scaling test recorded significance in all cases except for average coefficient of infection, grain

yield per plant and kernels number per spike in Sakha 94 $\times$ Misr 1 and Sakha 94 $\times$ Sakha 95 crosses. The significant scaling test values indicate the presence of non-allelic interactions and underscore the role of epistasis in the inheritance of these traits. These findings are consistent with recent studies that have highlighted the importance of epistatic interactions in shaping complex traits in wheat. For instance, a study by Jiang *et al.* (2021) utilized a co-genome-wide association approach to uncover the genetic architecture of plant-plant interactions affecting biomass and disease severity in wheat mixtures. Similarly, Lozada *et al.* (2017) demonstrated that incorporating additive-by-additive epistasis in genomic prediction models improved the predictive ability for grain yield in wheat. These studies reinforce the notion that epistasis plays a crucial role in the genetic architecture of quantitative traits in wheat.

The results of the five-parameter genetic model revealed the nature of gene action, as presented in Table. Non-significant F_2 mean effects (m) across evaluated traits suggest that these traits may not follow a simple additive inheritance pattern and could be influenced by complex genetic interactions or environmental factors (Sharma & Agrawal, 2020 c). This observation indicates the potential involvement of non-allelic interactions, such as epistasis, in the genetic control of these traits (Sharma & Agrawal, 2020 b). Similar conclusions were drawn by Moroni *et al.* (2013 a), who reported significant additive gene action in wheat seedlings, indicating quantitative inheritance for manganese tolerance at the seedling stage. Additionally, a study by Baric *et al.* (2004) highlighted the quantitative inheritance of certain wheat plant traits, further supporting these observations.

Significant additive gene effects have been reported for various traits. For example, in Gemmeiza 7 $\times$ Sids 1 cross, most traits exhibited significant additive effects, except for spikes number per plant (Ahmed *et al.*, 2021). Additionally, additive $\times$ dominance interactions have been shown to influence several wheat traits, including heading date, spike length, kernels number, and grain yield (Hassan *et al.*, 2015). These findings support the observed significant additive effects for ACI in the Line 1 $\times$ Sakha 95, Sakha 94 $\times$ Misr 1, and Sakha 94 $\times$ Sakha 95 crosses, as well as for hundred-kernel weight in Sakha 94 $\times$ Misr 1 cross.

Negative and highly significant additive effects were recorded for plant height, grain yield per plant, kernels number per spike, and 100-kernel weight in Line 1 $\times$ Misr 1 and Sakha 94 $\times$ Sakha 95. Similarly, negative and highly significant estimates were observed for grain yield per plant and kernels number per spike in Sakha 94 $\times$ Misr 1, as well as for plant height and grain yield per plant in Line 1 $\times$ Sakha 95. These results indicate the complexity of genetic interactions influencing these traits. Moreover, spikes per plant, average coefficient of infection, and plant height in various wheat crosses suggest that intricate genetic relationships play a crucial role in determining these characteristics. A study by Cui *et al.* (2012) similarly found that spike length, spikelets number per spike, kernels number per spike, and thousand-kernel weight have strong genetic associations with kernel weight per spike, highlighting the complex interactions among these yield components.

Positive and significant dominance effects were observed for the average coefficient of infection and hundred-kernel weight in all four studied crosses. Additionally, plant height exhibited positive and significant dominance in the Line 1 $\times$ Misr 1 and Line 1 $\times$ Sakha 95 crosses, while kernels per spike showed significant dominance in Line 1 $\times$ Misr 1, and spikes number per plant in Line 1 $\times$ Sakha 95. Similar

findings have been reported in other studies, where significant dominance effects were observed for plant height and the number of grains per spike in wheat crosses (Ojaghi & Akhundova, 2010).

However, negative and significant dominance effects were recorded for kernels number per spike in Sakha 94 × Misr 1 and Sakha 94 × Sakha 95 crosses, suggesting the influence of non-additive genetic factors, including dominance and epistasis, in the inheritance of these traits. This indicates that interactions between alleles at the same locus (dominance) and across different loci (epistasis) play a crucial role in determining these phenotypic expressions. Similar findings have been reported in studies analyzing the genetic architecture of wheat, where complex interactions contribute significantly to trait variability (Liu *et al.*, 2022).

Negative and highly significant additive × additive gene interactions were observed for plant height and average coefficient of infection in the Line 1 × Misr 1 and Line 1 × Sakha 95 crosses, as well as for hundred-kernel weight in Sakha 94 × Misr 1 and Sakha 94 × Sakha 95. These findings suggest that selection for these traits may not be effective in early generations. Recent studies indicate that additive × additive interactions can complicate selection, reducing its efficiency in early generations. Research on common bean and bread wheat has shown that such interactions may hinder

genetic progress, making delayed selection in later generations a more effective breeding strategy (Sharma & Agrawal, 2020b and c; Kumar *et al.*, 2021c).

Dominance × dominance (dd) gene effects were significant and positive for the average coefficient of infection in the Line 1 × Misr 1 and Line 1 × Sakha 95 crosses. Similar findings have been reported in other studies. For instance, significant dominance effects were observed for plant height and number of grains per spike in wheat crosses (Ojaghi & Akhundova, 2010). Dominance × dominance (dd) gene effects were significant or highly significant and negative in Line 1 × Misr 1 and Line 1 × Sakha 95 for spikes number per plant grain yield per plant, kernels number per spike and hundred-kernel weight, in addition spikes number per plant in Sakha 94 × Misr 1 and Sakha 94 × Sakha 95 and plant height in Line 1 × Sakha 95. A study by Kumar *et al.* (2021 a) reported that dominance × dominance interactions were negatively significant for most traits studied across three wheat crosses, suggesting that non-additive gene effects play a crucial role in the inheritance of these traits. Similarly, research by Khan *et al.* (2003 b) found that both dominance and dominance × dominance effects were highly significant for plant height and grain yield in wheat, indicating the importance of non-fixable gene interactions in the expression of these traits.

Table 3. Estimates of scaling test and gene effects of all the studied traits for the four crosses.

Crosses	Traits	Scaling test			Genetic component			
		C	D	m	a	d	aa	dd
Line 1 x Misr 1	PH	-12.4697 *	-6.5827	106.099	-7.197 ***	7.803 ***	-10.1364 *	-6.5827
	S.P	-7.911	-7.3417 *	27.4882	3.6637	2.4974	-5.2042	-7.3417*
	ACI	-63.804 **	48.3519 *	36.5734	-2.7224	17.38 ***	-40.5915 *	48.3519*
	GY	-12.6762	-14.192 *	34.508	-7.018 ***	9.1734	-10.9248	-14.192*
	KSP	11.4236	-29.88**	55.9513	-8.2498***	2.8869***	4.2683	-29.88**
	100KW	-1.1689	-2.007 **	3.5383	-0.416 ***	0.818 ***	-0.9936	-2.007 **
Line 1 x Sakha 95	PH	-12.4326 *	-6.5903	105.484	-11.725**	9.0326***	-10.7326 *	-6.5903
	S.P	-0.9449	-13.3977 *	22.4103	-2.1235	8.4522 *	-4.6986	-13.3977 *
	ACI	-159.99***	102.066**	64.6923	30.616***	30.615***	-95.308***	102.066**
	GY	5.7765	-23.1191 *	35.5195	-21.130***	6.5608	-0.3922	-23.1191 *
	KSP	38.1559 *	-42.856 **	41.4371	-2.965	4.035	17.0605	-42.856 **
	100KW	1.8242	-3.1657 **	2.28555	-0.5862	0.5744 *	0.6249	-3.1657 **
Sakha 94 x Misr 1	PH	4.4111	-10.1975 *	115.556	1.4444	-1.111***	2.7611	-10.1975 *
	S.P	-4.3386	-6.3429 *	28.0116	-0.1889	1.0677	-2.7031	-6.3429 *
	ACI	2.6171	5.4735	0.325	0.15 ***	0.15 ***	1.2336	5.4735
	GY	-1.1642	-9.6231	35.2020	-3.5889 **	6.5596	-3.8619	-9.6231
	KSP	2.8414	-3.846	63.6616	-1.2 *	-8.232***	5.5369	-3.846
	100KW	-1.1492 **	-1.0186	3.85742	0.0978 *	0.4215***	-0.7854 *	-1.0186
Sakha 94 x Sakha 95	PH	4.4111	-10.1975 *	121.44	-1.0119***	0.8631	-3.6214	-4.9083
	S.P	-4.3386	-6.3429*	27.953	-1.9573	-3.6558	7.9141	-16.16***
	ACI	2.6171	5.4735	1.0625	0.15 ***	1.625 *	-1.0517	2.7443
	GY	-1.1642	-9.6231	39.696	-13.559***	-2.4912	7.4495	-14.8993
	KSP	2.8414	-3.846	68.3466	-0.9468 *	-6.318***	-2.2327	1.2832
	100KW	-1.1492 **	-1.0186	4.00563	-0.1066 **	0.2569***	-0.9036 *	-0.6655

The evaluated traits included plant height (PH), spikes per plant (S.p), Average coefficient of infection (ACI), grain yield (GY), kernel per spike (KSP), and 100-kernel weight (100KW). These traits represent key morphological, physiological, and yield-related characteristics in the study.

Overall, the scaling test estimates and genetic components analyses indicate the complex inheritance patterns governing the investigated traits across the four wheat crosses. The significant C and D scaling test values in most cases highlight the involvement of non-allelic interactions, particularly epistasis, in shaping these traits (Jiang *et al.*, 2021; Lozada *et al.*, 2017). The presence of both positive and negative significant gene effects suggests that different traits exhibit varying modes of inheritance, with some traits primarily controlled by additive effects (Ahmed *et al.*, 2021; Moroni *et al.*, 2013b) while others are influenced

by dominance and epistatic interactions (Ojaghi & Akhundova, 2010; Liu *et al.*, 2022). The positive dominance effects observed for traits such as plant height, kernels number per spike, and hundred-kernel weight suggest the potential for hybrid vigor, whereas the negative dominance and epistatic interactions in certain traits indicate challenges in early-generation selection (Sharma & Agrawal, 2020a; Kumar *et al.*, 2021b). These findings emphasize the importance of considering gene interactions in wheat breeding programs and suggest that selection strategies should be tailored accordingly favoring early-generation selection for additive traits while delaying selection for traits influenced by non-additive gene action (Khan *et al.*, 2003 a; Baric *et al.*, 2004). Understanding these genetic complexities will aid in the development of more effective breeding strategies for improving wheat yield and resilience.

Heritability and genetic advance:

Tables 4 present the estimates of both broad-sense (h^2_b) and narrow-sense (h^2_n) heritability, along with genetic advance values. Broad-sense heritability (h^2_b) accounts for all genetic variance components, while plant breeders primarily focus on narrow-sense heritability (h^2_n), which represents the additive genetic variance. The lower h^2_n values compared to h^2_b indicate the presence of dominance effects in the genetic makeup of these traits.

Broad-sense heritability estimates were generally high for most traits across the four crosses, except for spikes number per plant in the Line 1 × Misr 1, Line 1 × Sakha 95, and Sakha 94 × Sakha 95 crosses. In Line 1 × Misr 1 cross, h^2_b ranged from 15.08% for spikes number per plant to 99.91% for hundred-kernel weight. In Line 1 × Sakha 95 cross, it varied from 60.11% for grain yield per plant to 99.26% for the average coefficient of infection. Similarly, in the Sakha 94 × Misr 1 cross, broad-sense heritability ranged from 38.7% for spikes number per plant to 99.74% for kernels number per spike. In Sakha 94 × Sakha 95 cross, values ranged from 75.7% for grain yield to 99.33% for hundred-kernel weight.

Narrow-sense heritability (h^2_n) values were moderate for most traits, except for spikes number per plant in the Line 1 × Misr 1, Line 1 × Sakha 95, and Sakha 94 × Sakha 95 crosses. In the first cross (Line 1 × Misr 1), h^2_n ranged from 7.54% for spikes per plant to 49.96% for kernels number per spike and hundred-kernel weight. In Line 1 × Sakha 95 cross, values varied between 30.05% for grain yield and 48.22% for hundred-kernel weight. For the third cross, narrow-sense heritability ranged from 38.7% for spikes number per plant to

99.74% for kernels number per spike. In Sakha 94 × Sakha 95 cross, estimates ranged from 14.86% for spikes per plant to 49.66% for hundred-kernel weight.

These findings suggest that the studied traits are influenced by both additive and non-additive genetic effects and exhibit substantial heritable variation. Consequently, selection for these traits is expected to be effective, with minimal environmental influence. These results align with previous studies that have reported the importance of both additive and non-additive genetic components in the inheritance of wheat traits (Al-Naggar, *et al.*, 2015) and (Salih and Al-Doss, 2021).

The expected genetic advance, expressed as a percentage of F_2 (GA%), is presented in Table 4. The results indicated that GA% values ranged from 0.593% for spikes per plant in Line 1 × Misr 1 cross to 28.59% for the average coefficient of infection in the same cross. The highest estimates of GA%, along with the highest narrow-sense heritability (h^2_n), were observed for the average coefficient of infection and hundred-kernel weight in the first cross, as well as for kernels per spike in Line 1 × Sakha 95 cross.

These results indicated the existence amount of variability for the improvement of those traits and the selection could be effective in the optimum populations. Then, selection for average coefficient of infection, hundred-kernel weight, and kernels number per spike in these studied populations help breeders in selecting high yielding genotypes. Generally, most of the obtained parameters detected the cross (Line 1 × Misr 1) and cross (Line 1 × Sakha 95).

Table 4. Genetic parameters of all the studied traits for the three bread wheat crosses

Crosses	Genetic parameters	PH	S.P	ACI	GY	KSP	100KW
Line 1 x Misr 1	h^2_b	84.03	15.08	95.49	55.23	99.91	99.91
	h^2_n	42.01	7.54	47.74	27.61	49.96	49.96
	GA%	6.2046	0.5913	28.5934	5.7089	24.9408	2.6696
Line 1 x Sakha 95	h^2_b	89.91	79.13	99.26	60.11	87.48	96.45
	h^2_n	44.96	39.56	49.63	30.05	43.74	48.22
	GA%	9.4728	7.4589	26.4731	10.1622	21.4567	2.5536
Sakha 94 x Misr 1	h^2_b	92.48	38.7	100	86.15	99.74	97.95
	h^2_n	46.24	19.35	50	43.08	49.87	48.97
	GA%	10.6905	2.7600	4.8699	15.5333	16.3891	0.5200
Sakha 94 x Sakha 95	h^2_b	92.93	29.72	97.86	75.7	95.88	99.33
	h^2_n	46.47	14.86	48.93	37.85	47.94	49.66
	GA%	9.8046	2.1082	6.2416	12.3180	16.1267	0.6653

The evaluated traits included plant height (PH), spikes per plant (S.p), Average coefficient of infection (ACI), grain yield (GY), kernel per spike (KSP), and 100-kernel weight (100KW). These traits represent key morphological, physiological, and yield-related characteristics in the study.

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التحليل الوراثي لصفات المحصول ومكوناته في قمح الخبز (*Triticum aestivum* L.) بطريقة تحليل متوسط الأجيال وتقديرات درجة التوريث

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المخلص

يهدف هذه البحث لدراسة طبيعة التوارث للصفات المحصولية الرئيسية في قمح الخبز باستخدام تحليل متوسط الأجيال. حيث تم تقييم أربعة هجن من قمح الخبز (سلالة 1 × مصر 1، سلالة 1 × سكا 95، سكا 94 × مصر 1، وسكا 94 × سكا 95) في موسم 2024/2023 بمحطة البحوث الزراعية بسكا، مصر. تم استخدام تصميم قطاعات العشوائية بثلاث مكررات لتقييم خمسة عشر وهي (F₃، F₂، F₁، P₂، P₁) للأربع هجن وكانت الصفات المدروسة وهي: ارتفاع النبات، عدد السنابل لكل نبات، معامل الإصالة ACI، عدد الحبوب لكل سنبل، وزن 100 حبة، ومحصول الحبوب للنبات. أظهرت نباتات الجيل الأول F₁ قوة هجين معنوية لمعظم الصفات، مع زيادة ارتفاع النبات بنسبة 12-18% عن أطول الأبوين. ومع ذلك، أظهر F₂ و F₃ انخفاضاً بسبب التفاعل الجيني. كان محصول الحبوب في الجيل الأول أعلى بنسبة 15-20% من أفضل الأبوين، ولكنه انخفض بنسبة 10-25% في الجيل الثالث. أظهرت النتائج أن هناك تفاعلات وراثية مهمة ومعنوية، لا سيما في ارتفاع النبات، وعدد السنابل لكل نبات، ووزن الحبة، مما يؤكد وجود تفاعلات غير أليلية. كانت نسبة التوريث بالمعنى الواسع عالية (أكثر من 75%) لمعظم الصفات، بينما كانت نسبة التوريث بالمعنى الضيق معتدلة (30-50%)، مما يشير إلى مساهمات من التأثيرات الجينية الإضافية وغير الإضافية. لوحظ أعلى تحسين وراثي في (ACI 28.59%)، مما يشير إلى أن الانتخاب فعال لمقاومة الصدأ الأصفر. توفر هذه النتائج رؤى مهمة لتربية القمح، مؤكدة على ضرورة الانتخاب المتأخر لتثبيت الصفات المرتبطة بالمحصول في الأجيال المتعزلة التالية.