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Genetic Analysis of Grain Yield and Stem Rust Resistance in Bread Wheat Using Six-Population Model

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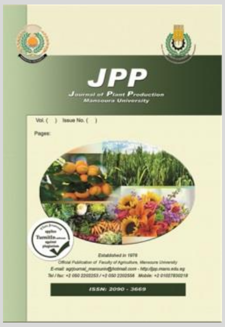

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ABSTRACT

This study was conducted at El-Gemmeiza Agricultural Research Station, Egypt, during 2022/23, 2023/24, and 2024/25 wheat growing seasons to investigate the genetic behavior of yield traits and stem rust resistance in bread wheat (*Triticum aestivum* L.). Six populations (P_1, P_2, F_1, F_2, BC_1, and BC_2) derived from three crosses (Line1 × Line2, Line1 × Misr2, and Line2 × Misr2) were evaluated using RCBD in three replications. Mean performance indicated that F_2 populations were generally intermediate and tended to be lower than F_1 means for several traits, particularly no. of spikes/plant and grain yield/plant. Significant positive heterobeltiosis was observed for no. of spikes/plant, no. of grains/spike, 100-grains weight, and grain yield/plant across the three crosses. Genetic analysis revealed that additive × additive and additive × dominance interactions were more important than dominance×dominance effects, while epistatic effects played a comparable role to additive and dominance gene actions. Concerning stem rust, Cross I(Line1 × Line2) showed complete resistance, while Misr2 was susceptible and the F_1 generations of Crosses II and III were moderate response to stem rust. Segregating generations (F_2, BC_1, and BC_2) displayed variable responses. Chi-square analyses confirmed that resistance in Crosses I and II followed a single dominant gene model (3R:1S), while Cross III fitted a complementary gene model (9R:7S). Overall, results highlight the significance of additive and epistatic effects in governing yield traits and demonstrate different modes of genetic controlling stem rust resistance. These findings provide useful implications for wheat breeding programs aimed at improving productivity and stem rust resistance.

Keywords: *Triticum aestivum* L., gene action, heritability, heterobiltiosis and stem rust.

INTRODUCTION

Among cereal crops, wheat dominates worldwide due to its vast cultivated area and high production levels, overall output, and international trade (Enghiad *et al*., 2017). In Egypt, wheat occupies about 3.213 million feddan (≈1.35 million ha), producing nearly 9.7 million tons annually (FAO, 2023). While wheat production has generally increased, the rapid and continuous population growth has created a widening gap between wheat demand and supply. Therefore, enhancing wheat productivity remains a critical priority to ensure food security. Genetic diversity for agronomically important traits, particularly disease resistance, represents a key resource for breeders to identify and utilize favorable alleles in developing improved cultivars (Sansaloni *et al*., 2020). Rust diseases, especially stem rust, continue to be among the most destructive biotic constraints, often causing severe damage within a short time span and posing a direct threat to global food security (Afzal *et al*., 2021).

Mean generation analysis offers an efficient biometrical approach to evaluate genetic effects based on the phenotypic performance of different breeding populations, including parents, F1, backcrosses, and segregating generations (Gamble, 1962). Estimating gene effects and partitioning the components of genetic variance are essential for determining the magnitude of heritable variation and predicting the efficiency of selection (Novoselovic *et al*., 2004).

On a global scale, about 20% of wheat production is lost annually due to the impact of biotic and abiotic stresses, with rust diseases alone destroying about 15 million tons of wheat annually and causing economic losses of approximately 2.9 billion USD (Pardey *et al*., 2013 and Lewis *et al*., 2024). Among these, stem rust, caused by *Puccinia graminis* f. sp. *tritici*, is especially destructive, capable of inflicting up to 100% yield losses, especially in warmer regions (Hodson, 2013 and Guo *et al*., 2022). Climate change has contributed to an increase in stem rust outbreaks in recent years, the emergence of highly virulent races such as Ug99 and its derivatives, the widespread use of susceptible cultivars, and over-reliance on fungicides (Wu *et al*., 2023).

Resistant cultivar development is still viewed as the most reliable, cost-efficient, and ecologically sound approach to managing the disease (Kumar *et al*., 2022). Achieving durable resistance requires combining both major genes that provide race-specific protection and minor genes that contribute to non-specific or slow-rusting resistance, which are essential for long-term disease control. (Huerta-Espino *et al*., 2020). Slow rusting, in particular, has long-lasting effects and is of special importance to breeders and pathologists (Ahmed *et al*., 2004). The use of diverse resistance resources, such as those available in the CIMMYT`s Stem Rust Resistance Screening Nursery (STEMRRSN), provides a valuable germplasm pool with high yield potential and broad rust resistance (Randhawa *et al*., 2018). Rigorous evaluation of these genotypes under high disease pressure in both greenhouse and field “hot spot” nurseries facilitates the identification of effective and durable resistance, while also helping to monitor pathogen evolution.

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Previous studies have reported that resistance to rusts can be inherited either as a simple trait governed by one or a few genes, or as a quantitative trait controlled by multiple loci influenced by environmental conditions. In some cases, the additive genetic model is adequate, whereas dominance and epistatic interactions play a more prominent role in others, significantly influencing the expression of resistance (El-Seidy *et al*., 2017 and Sharshar and Esmail, 2019).

Grain yield in wheat is a complex quantitative trait that is largely determined by its primary components, namely the no. of spikes/unit area, grains/spike, and 1000-grains weight. These components not only influence final yield directly but also interact with each other, reflecting the plant's genetic potential and its response to environmental conditions. Breeding strategies that simultaneously improve yield components and resistance to major diseases are therefore essential for developing high-yielding, stable cultivars. Recent studies have emphasized the importance of these traits, reporting that selection for favorable combinations of yield components significantly enhances overall productivity and resilience under stress conditions (Ali *et al*., 2021; Sallam *et al*., 2022 and Elbasyoni *et al*., 2023). Thus, a comprehensive understanding of yield components, in parallel with resistance traits such as stem rust, is critical to achieving sustainable improvements in wheat production.

The objectives of this study were to examine the inheritance patterns of grain yield, its related traits and stem rust resistance, and to identify resistant genotypes suitable for the development of improved wheat cultivars.

MATERIALS AND METHODS

The field study was conducted at the Experimental Farm of El-Gemmeiza Agricultural Research Station, Gharbia, Egypt (N= 31o 07 ', E= 30o 48 '), over three consecutive wheat growing seasons (2022/2023, 2023/2024, and 2024/2025). The genetic material employed in the experiment consisted of three wheat crosses. Throughout the first season, hand emasculation and pollination were performed to develop the following hybrid combinations: Line 1 × Line 2 (cross I), Line 1 × Misr 2 (cross II), and Line 2 × Misr 2 (cross III). In the second season, The F_1 seeds were planted for the production of F_1 plants, some of which were self-pollinated to generate F_2 seeds, while others were backcrossed with their respective parents to obtain BC_1 and BC_2 generations. Additional F_1 seeds were also produced by repeating the crosses to ensure sufficient material. In the third season, all six populations of each cross (P_1, P_2, F_1, F_2, BC_1, and BC_2) were sown in a randomized complete block design (RCBD) with three replications. Each plot consisted of 12 rows (3 m long, 30 cm apart, with 20 cm between plants), arranged as follows: one row each for P_1, P_2, and F_1; two rows for BC_1 and BC_2; and five rows for F_2. Two border rows of the susceptible cultivar Morocco were planted around the experiment to assess stem rust reaction under natural infection conditions and to ensure uniform stem rust spread. Details of the parental genotypes, pedigree, rust reaction, and origin are provided in Table (1).

Table 1. Designation, pedigree, stem rust response, and origin of the evaluated parental bread wheat genotypes.

Parent	Name	Pedigree	Stem rust response	Origin
1	Line 1	MUTUS*2//TAM200/TURACO*2/3/KFA/2*KACHU CMSS14B01483T-099TOPY-099M-0SY-56M-0WGY	Resistant	CIMMYT, Mexico
2	Line 2	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1*2/4/NIINI #1/5/KFA/2*KACHU CMSS13B00653S-099M-099NJ-099NJ-1Y-0RGY	Resistant	CIMMYT, Mexico
3	Misr 2	SKAUZ/BAV92 CMSS96M03611S-1M-010SY-010M-010SY-8M-0Y-0S	Susceptible	EGYPT

For phenotypic evaluation, random samples were collected from each population as follows: 30 plants from P_1, P_2, and F_1; 200 plants from F_2; and 60 plants from each BC_1 and BC_2. The recorded traits included plant height (cm), no. of spikes/plant, no. of grains/spike, 100-grain weight (g), grain yield/plant (g), and stem rust response.

Genetic analysis:

Generation mean analysis was performed to detect the presence of non-allelic interactions using scaling tests A, B, and C Mather and Jinks (1982):

Gene effects were estimated using the six-parameter model Mather (1949); Hayman and Mather (1955) and Gamble (1962).

Genetic variances were partitioned as follows Mather and Jinks (1982):

$$\text{Environmental variance (E)} = \tfrac{1}{3}\,(VP_1 + VP_2 + VF_1)$$

$$\text{Additive variance (D)} = 4VF_2 - 2(VBC_1 + VBC_2)$$

$$\text{Dominance variance (H)} = 4(VF_2 - \tfrac{1}{2}VD - VE)$$

The significance of genetic components was tested by t-tests.

Heterosis and inbreeding depression:

Heterosis over the better parent was calculated as:

$$\text{Heterosis from the better-parent \% (BP)}=(F_1-BP)/BP) \times 100$$

Inbreeding depression was estimated as:

$$(I.D\ \%) = (F_1\text{-}F_2/F_1) \times 100$$

$$\text{Variances of I.D deviation} = VF_1+VF_2$$

$$T\text{: I. D}=F_1+F_2/\ (V.I.D)\ 0.5$$

Heritability and genetic advance:

Broad-sense heritability (h^2b) was calculated as VG/VP × 100, while narrow-sense heritability (h^2n) was estimated as ½D/VP × 100. Expected genetic advance under selection was computed following Allard (1999).

The expected gain from selection (G.S):was estimated following the method of Allard (1960), using the equation:

$$G.S\% = [(K \times \sigma\, ph \times h2\, n) / F_2] \times 100$$

Stem rust evaluation:

Disease severity for the P1, P2, P3, BC1, BC2, F1, and F2 plants for each cross was evaluated when the spreader cultivar Morocco reached maximum rust infection, using the modified Cobb scale (Peterson *et al*., 1948). Infection types were classified as Resistant (R, 0-5%), Resistant to Moderately Resistant (R-MR, 10-20%), Moderately Resistant (MR, 20-30%), Moderately Resistant to Moderately Susceptible (M, 30-40%), Moderately Susceptible (MS, 40-50%), Moderately Susceptible to Susceptible (S, 50-70%) and Susceptible (S, 70-100%) according to Roelfs (1992) and Singh *et al*. (2013). For quantitative analysis, infection severity was converted into an Average Coefficient of Infection (ACI) by multiplying the severity rating by constant coefficients of 0.2, 0.4, 0.6, 0.8, and 1 for R, MR, M, MS, and S, respectively (Saari and Wilcoxson, 1974).

Chi-square analysis:

Segregation ratios in the F2 populations were tested for goodness-of-fit to expected Mendelian ratios using chi-square (Snedecor and Cochran, 1989):

$$\chi c2 = \sum (Oi-Ei)^2 / Ei$$

Where:C =Degrees of freedom,Oi=Observed value(s),Ei=Expected value(s).

RESULTS AND DISCUSSION

Mean performance

Plant height

The analysis of plant height (Table 2) revealed that the F1 generations in the three crosses tended to be shorter than their respective parents, indicating dominance toward reduced plant stature. Interestingly, the F2 generation displayed taller plants, while the backcrosses exhibited intermediate values between their parents. Such a pattern suggests that the trait is influenced by additive as well as non-additive types of gene action., with partial dominance toward shorter plant height. Similar findings were reported by Patel *et al.* (2018), Shehab-Eldeen *et al.* (2020), and El-Nahas and El-Gabry (2021), who emphasized that reduced height is a desirable trait associated with lodging resistance and improved harvest index.

No. of spikes/plant

The mean performance of no. of spikes/plant (Table 2) demonstrated significant heterotic effects in the F1 of all crosses, with values exceeding the mid-parent and, in some cases, the better parent. However, F2 generations were lower than the F1 means, confirming the quantitative inheritance of this trait. BC1 and BC2 generations varied, each approaching the mean of its respective parent, suggesting the involvement of both additive and dominance effects. Comparable results were documented by Elmassry *et al.* (2020), Mohiy *et al.* (2021), and Rady (2022), who stated that spike number is a polygenic trait strongly affected by both genetic background and environmental conditions.

No. of grainss/spike

For grainss/spike (Table 2), the F1 means in all crosses recorded clear heterotic expression, surpassing both parents. In particular, BC1 populations of crosses II and III exhibited the highest grains numbers (72.53), pointing to the contribution of additive × dominance interactions. These results align with those of Patel *et al.* (2018) and Shehab-Eldeen *et al.* (2020), who also observed that grains number is a major yield component influenced by complex gene interactions.

100-grains weight

The average values for 100-grains weight (Table 2) showed that F1 generations outperformed the parental means in all three crosses, suggesting heterosis toward heavier grains. The maximum value was recorded in BC1 of cross II (5.27 g), which indicates the potential of utilizing such crosses in selection programs for grain weight improvement. Such findings are comparable to those reported by Elmassry *et al.* (2020) and Rady (2022), who highlighted the significance of grains weight as a stable yield component under both normal and stressed environments.

Table 2. Mean values ($\bar{X}$) and standard errors (SE) for six populations (P1, P2, F1, BC1, BC2, and F2) across the evaluated traits in three bread wheat crosses.

Traits	Cross	P1	P2	F1	F2	BC1	BC2
Plant height (cm)	I	111.33±0.26	109.17±0.19	108.03±0.15	112.73±0.53	110.40±0.54	106.83±0.63
	II	111.00±0.19	108.73±0.21	106.23±0.16	111.78±0.49	112.03±0.54	107.90±0.49
	III	109.07±0.17	108.03±0.19	106.47±0.19	111.37±0.51	110.42±0.62	107.87±0.53
No. of spikes/plant	I	11.43±0.22	9.03±0.21	12.03±0.24	11.03±0.29	12.88±0.34	8.930±0.32
	II	12.20±0.26	11.37±0.23	13.47±0.20	12.01±0.31	12.20±0.35	10.90±0.36
	III	8.73±0.15	10.57±0.21	11.40±0.22	10.42±0.26	11.63±0.26	10.85±0.25
No. of grains/spike	I	64.33±0.62	68.07±0.70	69.57±0.79	68.22±0.79	69.93±0.98	66.17±1.08
	II	67.60±0.32	66.13±0.31	69.20±0.17	68.94±0.43	72.53±0.53	69.88±0.43
	III	67.70±0.31	63.80±0.26	69.87±0.25	68.99±0.57	72.53±0.59	65.17±0.60
100-grains weight (g)	I	4.67±0.05	4.69±0.06	4.91±0.04	4.77±0.06	4.85±0.07	4.56±0.06
	II	4.47±0.04	4.51±0.05	4.69±0.05	4.60±0.05	5.27±0.04	4.74±0.04
	III	4.42±0.03	4.22±0.03	4.77±0.04	4.53±0.04	4.73±0.04	4.60±0.04
Grain yield/ plant (g)	I	34.14±0.25	31.28±0.22	36.94±0.24	34.07±0.52	34.33±0.60	32.26±0.61
	II	34.59±0.23	27.67±0.23	35.78±0.24	33.69±0.70	33.69±0.78	27.85±0.79
	III	32.78±0.25	30.45±0.19	34.80±0.19	31.42±0.48	34.54±0.31	31.94±0.51
Stem rust	I	0.11±0.01	0.36±0.07	0.21±0.04	0.46±0.03	0.27±0.04	0.26±0.04
	II	0.10±0.01	0.24±0.03	0.35±0.03	0.55±0.02	0.19±0.03	0.21±0.02
	III	0.11±0.01	0.52±0.03	0.49±0.02	0.56±0.03	0.26±0.02	0.37±0.03

Grain yield/plant

Grain yield/plant (Table 2) showed marked superiority of the F1 generation over both parents in all three crosses, confirming the presence of heterotic effects. However, F2 means were lower than those of the F1, again supporting the quantitative inheritance of yield traits. Backcross generations tended toward their respective parents, confirming the combined action of additive and non-additive gene effects. These findings are in accordance with Mohiy *et al.* (2021) and Rady (2022), who reported similar trends and emphasized that yield is a complex trait integrating multiple components.

Stem rust resistance

The assessment of stem rust resistance (Table 2) revealed clear genetic variability among the populations. In cross I, P1 was highly resistant while P2 and F1 were resistant. A similar trend was observed in cross III, where P2 was highly susceptible, shifting F1 resistance toward the mid-parent value. In cross II, both P1 and BC1 showed the best resistance. These results demonstrate partial dominance toward susceptibility and highlight the importance of selecting resistant parents in breeding programs. Comparable findings were reported by Patel *et al.* (2018), Shehab-Eldeen *et al.* (2020), and El-Nahas and El-Gabry (2021), who confirmed the complex inheritance of rust resistance and the necessity of incorporating resistant genotypes in hybridization schemes.

Genetic parameters

Genetic parameters including heterosis, inbreeding depression, heritability (broad- and narrow-sense), and genetic advance for the studied traits in three wheat crosses are presented in Table 3.

Heterosis (BP %)

The estimates of heterosis for plant height were negative across all crosses, indicating the absence of hybrid vigor for this trait. In contrast, traits such as no. of spikes/plant, no. of grains/spike, 100-grains weight, and grain yield/plant exhibited significant positive heterosis, most notably in crosses II and III, highlighting their potential for enhanced productivity. As far as stem rust resistance is concerned, the results varied: crosses I and III showed negative heterosis (indicating reduced resistance), whereas cross II displayed a strong positive heterotic effect, suggesting favorable gene complementation for resistance in that combination (Table 3).

Inbreeding Depression (ID %)

Traits like plant height exhibited moderate negative inbreeding depression, consistent with the loss of hybrid vigor in after F1 generation. Yield components (spikes/plant, No. of grains/spike, grain yield/plant) showed significant positive inbreeding depression, indicating the presence of dominant gene action in F_1 that was lost in F_2. For stem rust, strong negative values were observed in crosses I and II, indicating that resistance was not stably expressed under inbreeding, while cross III showed moderate loss in resistance (Table 3).

Heritability

Broad-sense heritability (h^2b) was found to be greater than 75% for the majority of traits, demonstrating that genetic variance largely explained the overall phenotypic variation. Narrow-sense heritability (h^2n), however, varied widely: Moderate values for plant height (30–47%) suggest both additive and non-additive effects. Relatively higher values for No. of grains/spike and grain yield/plant (up to 53%) indicate more reliable transmission of these traits to the next generation. Stem rust resistance showed low-to-moderate narrow-sense heritability in crosses I and II, but high (62%) in cross III, suggesting additive gene action is important for durable resistance (Table 3). With respect to stem rust resistance, narrow-sense heritability values varied considerably (from low to high) in the three crosses, indicating the predominance of additive genetic effects. The same inference has been drawn by many previous investigators, including Shehab Eldeen *et al.* (2020); Mohiy *et al.* (2021) and Haridy *et al.* (2021).

Table 3. Genetic parameters including better parent heterosis (BP), inbreeding depression (ID%), broad (h^2b) and narrow (h^2n) sense heritability, genetic advance (ΔG) and phenotypic (PCV) and genotypic (GCV) coefficient of variations for the studied traits in three wheat crosses.

Trait	Cross	Heterosis% (BP)	ID %	h^2b (%)	h^2n (%)	ΔG	ΔG%	PCV	GCV
Plant height	I	-1.04	-4.35**	98.03	34.82	7.66	6.8	5.12	5.03
	II	-2.3	-5.22**	97.25	47.36	8.49	7.6	4.84	4.76
	III	-1.45	-4.6**	97.65	34.97	6.16	5.53	5.04	4.97
No. of spikes/plant	I	5.25**	8.31**	82.69	35.63	3.85	34.92	28.88	26.57
	II	10.38**	10.83**	89.64	35.34	4.33	36.1	28.61	26.73
	III	7.89**	8.63**	82.12	53.69	5.38	51.63	27.71	25.56
No. of grains/spike	I	2.2**	1.94**	76.67	18.81	6.36	9.32	13.11	11.74
	II	2.37**	0.37**	96.13	41.39	5.9	8.56	6.82	6.52
	III	3.2**	1.25**	95.16	46.38	10.24	14.85	9.11	8.85
100-grains weight	I	4.6**	2.85**	90.2	37.58	0.72	15.09	12.91	11.76
	II	4.15**	1.86**	78.11	67.68	1.41	30.68	12.74	11.31
	III	8.09**	5.11**	76.57	53.32	0.91	20.18	10.56	9.54
Grain yield/plant	I	8.19**	7.76**	94.45	30.75	6.16	18.07	16.6	16.14
	II	3.46**	5.84**	97.09	36.55	9.89	29.36	22.73	22.41
	III	6.16**	9.72**	96.34	52.8	11.55	36.76	16.89	16.51
Stem rust	I	-41.74	-115	55.66	30.5	0.34	74.58	74.14	51.11
	II	44.44**	-57.69**	52.54	46.45	0.28	51.4	41.68	33.44
	III	-6.41**	-15.4**	91.79	62.54	0.81	143.89	62.63	59.4

Genetic Advance (ΔG) and Genetic Advance as % of Mean (ΔG. A %)

Plant height showed small expected genetic advance, reflecting the limited scope of selection for this trait. Yield components (no. of spikes/plant, no. of grains/spike, 100-grains weight, grain yield/plant) recorded high genetic advance percentages, especially in crosses II and III, indicating that selection can be very effective in improving these traits. Stem rust resistance exhibited high ΔG. A % values (especially cross III), highlighting the possibility of achieving large genetic gains under selection pressure, especially when additive variance is present.

Phenotypic and Genotypic Coefficients of Variation (PCV & GCV)

The results showed that, in most cases, phenotypic variability (PCV) was slightly higher than genotypic variability (GCV), suggesting that environmental influence was minor and that genetic factors predominantly controlled the traits. Stem rust resistance showed the largest gap between PCV and GCV, implying higher environmental interaction, which must be considered when selecting for this trait.

Generally, Additive variance plays a stronger role in traits like grains/spike, grain yield, and rust resistance (especially in cross III), making them suitable for direct selection. Non-additive variance (heterosis and inbreeding depression) dominates in spikes/plant and 100-grains weight, suggesting that hybrid breeding could be more effective. Stem rust resistance is promising in cross III due to its high heritability estimates, high genetic advance, and reduced environmental effects.

Scaling tests:

The outcomes of scaling tests A, B, and C (Table 4) showed significant values for most traits across the three crosses, pointing to the involvement of non-allelic interactions. This implies that a simple genetic model may not adequately describe the differences among population means. Conversely, when the scaling test values are non-significant, it suggests the absence of such interactions and that the basic model can sufficiently account for the genetic variation in these traits.

Nature of gene action

Selection is considered one of the most effective breeding approaches, and its success relies on a clear understanding of the genetic architecture of the traits under study, as this knowledge guides the choice of suitable improvement strategies. In this context, the type of gene action was evaluated according to Gamble (1962), and the estimated effects contributing to genetic variability are summarized in (Table 4). Results of the scaling tests (A, B, and C) across the studied traits and crosses revealed marked deviations from the additive–dominance model, demonstrating the involvement of epistatic interactions in several cases. Furthermore, the genetic components (m, a, d, aa, ad, dd) provided deeper insight into the relative roles of additive, dominance, and epistatic effects in the inheritance of these traits.

Plant height

In cross I, scaling tests A and C were highly significant, while B was non-significant, indicating the presence of non-allelic interactions, particularly additive × additive and dominance × dominance epistasis. The genetic components showed a highly significant mean effect (m = 112.73**), with significant additive effect (a = 3.57**) and significant additive × additive (aa) and dominance × dominance (dd) interactions, suggesting that both fixable and non-fixable genetic variances contribute to inheritance. In cross II, scaling tests A and C were significant, with moderate additive effects and negative dominance values, implying partial dominance accompanied by some epistatic effects. cross III exhibited significant scaling tests A, B, and C, with a moderate positive additive effect and highly significant additive × additive interactions, indicating complementary gene action.

Table 4. Scaling test results and gene effect estimates related to the studied traits across three bread wheat crosses.

Trait	Cross	Scaling test			Genetic components					
		A	B	C	m	A	d	aa	ad	dd
Plant height	I	1.44	-3.53	14.37**	112.73**	3.57**	-18.69	-16.47	2.48**	18.56**
	II	6.83**	0.83	14.93**	111.78**	4.13**	-10.91	-7.27	3.00**	-0.39
	III	5.30**	1.23	15.43**	111.37**	2.55**	-10.98	-8.90	2.03*	2.37
No. of spikes/plant	I	2.30**	-3.20	-0.40	11.03**	3.95**	1.30	-0.50	2.75**	1.40
	II	-1.27	-3.03	-2.47	12.01**	1.30**	-0.15	-1.83	0.88	6.13*
	III	3.13**	-0.27	-0.43	10.42**	0.78*	5.05**	3.30**	1.70**	-6.17
No. of grains/spike	I	5.97**	-5.30	1.33	68.22**	3.77**	2.70	-0.67	5.63**	0.00
	II	8.27**	4.43**	3.63*	68.94**	2.65**	11.40**	9.07**	1.92**	-21.77
	III	3.70**	-3.33	4.73*	68.99**	5.47**	-0.25	-4.37	3.52**	4.00
100-grains weight	I	0.12	-0.48	-0.10	4.77**	0.29**	-0.03	-0.26	0.30**	0.62
	II	1.38**	0.28*	0.06	4.60**	0.53**	1.81**	1.60**	0.55**	-3.27
	III	0.27**	0.21*	-0.07	4.53**	0.12*	1.00**	0.55**	0.03	-1.03
Grain yield/plant	I	-2.42	-3.69	-3.01	34.07**	2.07*	1.13	-3.10	0.64	9.21*
	II	-3.00	-7.76	0.95	33.69**	5.84**	-7.05	-11.7	2.38*	22.46**
	III	1.49*	-1.38	-7.17	31.42**	2.6**	10.46**	7.28**	1.44*	-7.39
Stem rust	I	0.21*	-0.06	0.92**	0.46**	0.01	-0.79	-0.77	0.13*	0.62*
	II	-0.07	-0.16	1.15**	0.55**	-0.02	-1.20	-1.38	0.05	1.61**
	III	-0.08	-0.27	0.65**	0.56**	-0.11	-0.81	-0.99	0.10*	1.34**

No. of spikes/plant

For cross I, significant A and B scaling tests were observed, suggesting epistasis. Both additive and ad (additive × dominance) effects were significant, with moderate dominance deviations, indicating that selection in segregating generations could be effective. cross II showed non-significance in most scaling tests but high dominance deviations (dd = 6.13*), implying the role of duplicate epistasis in reducing the efficiency of early generation selection. cross III had highly significant scaling tests A and C, with strong dominance and epistatic effects, suggesting a predominance of non-additive variance.

No. of grains/spike

For all crosses, the mean effect (m) was highly significant, reflecting the high inherent productivity of the parental combinations. Cross, I showed significant additive effects and strong additive × dominance epistasis, while cross II exhibited large dominance effects (d = 11.40**) along with negative dominance × dominance deviations (dd = −21.77), indicating duplicate epistasis. Cross III demonstrated significant additive effects and positive additive × dominance interactions, suggesting complementary epistasis and the potential for improvement through hybridization.

100-Grains weight

The scaling test values were mostly non-significant in cross I, indicating an adequate fit to the additive–dominance model. Additive effects were generally small, while dominance and dominance × dominance effects varied among crosses. Cross II revealed significant dominance effects and positive additive × dominance interactions, whereas cross III displayed low additive effects with moderate dominance deviations, highlighting the influence of non-additive variance on grains weight.

Grain yield/plant

This trait exhibited high mean values in all crosses, but scaling tests revealed inconsistent patterns. Cross, I showed a significant additive effect with small non-additive contributions, indicating that additive variance is more important for this combination. Cross II had strong negative dominance and large positive dominance × dominance deviations (dd = 22.46**), indicative of duplicate epistasis, which could complicate selection. Cross III displayed strong dominance effects and significant additive × dominance interactions, pointing to complementary gene action in yield determination.

Stem rust resistance

The scaling tests for stem rust resistance were significant for test C in all crosses, suggesting the presence of non-allelic gene interactions. Additive effects were generally small and non-significant, while dominance effects were negative in most cases, reflecting that resistance is primarily controlled by non-additive variance. Significant additive × dominance (ad) and dominance × dominance (dd) effects in some crosses indicate that both complementary and duplicate epistasis are engaged in the genetic control of this trait.

Findings from the present study demonstrated that epistatic effects played a role as important as additive and dominance effects in the inheritance of most traits. These observations are consistent with the results reported by Shehab-Eldeen *et al.* (2020), Mohiy *et al.* (2021), Rady (2022) and Mohamed & Eissa (2022).

Stem rust assessment at the adult plant stage:

At the adult plant stage, the parental lines displayed P1 and P2 exhibited complete resistance to stem rust, while P3 was susceptible with a mean severity score of 20S (Table 5). In the Cross I, all F1 plants was completely resistant while the backcross populations (BC1 and BC2) showed varied response from resistance to susceptibility. BC1 expressing severities values of 0, 5S and 10S and BC2 with values 0, Trace S, 5S and 10S. The F2 population segregated with variable phenotypes from trace R to 5S. For Cross II, F1 plants exhibited intermediate response with mean rust severity from 10MR to 30MRMS while BC1 and BC2 showed varied response from resistance to susceptibility. BC1with values 0, 5S, 10S and 20S and BC2 with values 0, 20S and 30S. The F2 population showed variation from full resistance (0) to highly susceptible (60S). For Cross III, all F1plants were intermediate (10MR to 20MRMS), while BC1 and BC2 showed varied response from resistance to susceptibility. BC1with values 0, TS and 20S and BC2 with values 0, TS and 20S. The F2 population segregated from R to S (20S).

Table 5. Stem rust response at adult plant stage six populations of three wheat crosses.

Cross name	No. of tested plants	Stem rust responses classes						
		R	R-MR	MR	MR-MS	MS	MS-S	S
Cross I	$P1_{30}$	10	20	0	0	0	0	0
	$P2_{30}$	12	18	0	0	0	0	0
	$F1_{30}$	30	0	0	0	0	0	0
	$F2_{200}$	73	26	53	0	19	0	29
	$BC1_{60}$	44	0	0	0	0	0	16
	$BC2_{60}$	45	0	0	0	0	0	15
Cross II	$P1_{30}$	30	0	0	0	0	0	0
	$P2_{30}$	0	0	0	0	0	0	30
	$F1_{30}$	0	0	14	16	0	-	-
	$F2_{200}$	43	30	78	0	0	23	26
	$BC1_{60}$	48	0	0	0	0	0	12
	$BC2_{60}$	40	0	0	0	0	0	20
Cross III	$P1_{30}$	30	0	0	0	0	0	0
	$P2_{30}$	0	0	0	0	0	0	30
	$F1_{30}$	0	0	13	17	0	-	-
	$F2_{200}$	72	27	24	0	0	33	44
	$BC1_{60}$	36	0	0	0	0	0	24
	$BC2_{60}$	21	0	0	0	0	0	37

R= resistant, MR= moderately resistance, S= Susceptible, and MS= moderately susceptible.

Chi-square analysis:

Segregation analysis of F_2 populations from three wheat crosses was performed to clarify the genetic basis of stem rust resistance using the Chi-square (χ^2) test (Table 6). In Cross I and Cross II, the observed segregation ratios were 152R:48S and 151R:49S, respectively, which did not deviate significantly from the expected 3:1 ratio for a single dominant resistance gene. The χ^2 values were very low (0.107 and 0.027), with corresponding p-values of 0.7440 and 0.8703. In Cross III, the segregation ratio of 123R:77S fit a 9:7 ratio, with a χ^2 value of 2.24 and p-value of 0.13, indicating that resistance is governed by two dominant genes with duplicate recessive epistasis. Similar results were reported by Agrios (2005) and Olivera *et al.* (2018). Additionally, Mohamed and Ibrahim (2022) found that the cross Sr2 × Misr2 exhibited complementary gene action, also following a 9:7 ratio.

Table 6. Segregation of stem rust resistance in F_2 populations derived from three wheat crosses.

Cross name	No. of tested F_2 plants	Observed ratio		Expected ratio		χ^2	p-value
		R	S	R	S		
Cross I	200	152	48	3	1	0.10	0.74
Cross II	200	151	49	3	1	0.02	0.87
Cross III	200	123	77	9	7	2.24	0.13

R= Resistant and S= Susceptible

CONCLUSION

The present investigation demonstrated substantial genetic variability among the studied wheat crosses for grain yield traits and stem rust resistance. Heritability estimates and genetic advance confirmed that additive gene effects played a major role in the inheritance of several yield components, while non-additive and epistatic interactions were also significant. Cross II and Cross III proved to be promising for grain yield improvement, whereas Cross I and Cross II showed stable resistance to stem rust, controlled mainly by dominant genes. he presents results demonstrate that effective improvement of yield traits can be achieved through selection in early segregating generations, while resistance breeding may benefit from combining dominant and epistatic effects to ensure durable resistance. Overall, the evaluated crosses represent valuable genetic resources for wheat improvement programs under Egyptian conditions.

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التحليل الوراثي لمحصول الحبوب ومقاومة صدأ الساق في قمح الخبز باستخدام نموذج العشائر الست

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الملخص

أجريت هذه الدراسة في محطة البحوث الزراعية بالجميزة - مصر خلال مواسم ٢٠٢٣/٢٠٢٢، ٢٠٢٤/٢٠٢٣ و٢٠٢٥/٢٠٢٤ بهدف دراسة السلوك الوراثي لصفات المحصول، ومكوناته وطبيعة توريث مقاومة صدأ الساق في قمح الخبز (*Triticum aestivum* L.). شملت الدراسة ستة عشائر (P_1، P_2، F_1، F_2، BC_1، وBC_2) ناتجة من ثلاثة هجن: سلالة١ × سلالة٢، سلالة١ × مصر٢، وسلالة٢ × مصر٢، وتم تقييمها باستخدام تصميم القطاعات الكاملة العشوائية في ثلاث مكررات. أظهرت النتائج أن متوسطات الجيل الثاني (F_2) كانت غالبًا متوسطة بين الأبوين وأقل من الجيل الأول (F_1) في بعض الصفات مثل عدد السنابل/نبات ومحصول الحبوب/نبات. ظهر قوة هجين معنوية موجبة في جميع الهجن الثلاثة خاصة لعدد السنابل/نبات، عدد الحبوب/سنبلة، وزن المائة حبة، ومحصول الحبوب/نبات. أوضحت التحليلات أن التفاعلات الجينية من نوع (مضيف × مضيف) و(مضيف × سيادي) كان لها الدور الأكبر مقارنة بتفاعلات (سيادي × سيادي)، كما كان للتأثيرات المتفوقة (Epistasis) دور مهم يماثل تأثير الجينات المضيفة والسيادية. بالنسبة لصدأ الساق، أظهرت نتائج الهجين الأول أن السلالة١ والسلالة٢ والجيل الأول كانت مقاومة تماما للصدأ، بينما كان صنف مصر ٢ مصاب بينما اظهر الجيل الأول من الهجينين الثاني والثالث مقاومة متوسطة. وأظهرت الأجيال الانعزالية (F_2، BC_1، BC_2) استجابات متباينة في جميع الهجن. وأكدت اختبارات مربع كاي أن المقاومة في الهجينين الأول والثاني تتحكم فيها جين سائد واحد (٣ مقاوم: ١ مصاب)، بينما اتبع الهجين الثالث نموذج التفاعل التكميلي بين جينين (٩ مقاوم: ٧ مصاب). بوجه عام، أوضحت النتائج أهمية التأثيرات المضيفة والمتفوقة في التحكم في صفة المحصول ومكوناته، كما أظهرت النتائج أن المقاومة لصدأ الساق تخضع لأنماط مختلفة من التحكم الوراثي مما يوفر معلومات مهمة لبرامج تربية القمح لتحسين الإنتاجية والمقاومة لمرض صدأ الساق.