RESEARCH ARTICLE

SABRAO Journal of Breeding and Genetics
57 (4) 1422-1432, 2025
http://doi.org/10.54910/sabrao2025.57.4.8
http://sabraojournal.org/
pISSN 1029-7073; eISSN 2224-8978

HETEROSIS AND INBREEDING DEPRESSION IN F_1 AND F_2 POPULATIONS OF BREAD WHEAT FOR QUANTITATIVE TRAITS

H. RAZA[*1], S.A. KHAN[*2], K. AFRIDI[3], N. ALI[2], I. HUSSAIN[2], S. ALI[2], J. KHAN[4], I. ULLAH[1], and A. ALI[2]

[1]Cereal Section, Agriculture Research Institute, Tarnab - Peshawar, Pakistan
[2]Department of Plant Breeding and Genetics, University of Haripur, Haripur, Pakistan
[3]Cereal Crops Research Institute, Pirsabak - Nowshera, Pakistan
[4]Department of Agriculture, University of Swabi, Swabi, Pakistan
*Corresponding author's emails: haneefagrian@gmail.com, sheraslamqau@gmail.com
Email addresses of co-authors: khilwatpbg@yahoo.com, naushadali@uoh.edu.pk izhar@uoh.edu.pk, sardarali@uoh.edu.pk, junaid_hort@yahoo.com, iltafullah@gmail.com, abbas2938@gmail.com

SUMMARY

This study aimed to evaluate the genetic potential, heterotic effects, and inbreeding depression in F_1 hybrids and F_2 wheat (*Triticum aestivum* L.) populations for yield and yield-related traits. Six wheat genotypes' crossing in a half-diallel fashion comprised Galaxy-13, Inqilab-91, Ghaznavi-98, Khaista-17, Benazir-13, and Parula to produce 15 F_1 hybrids. These hybrids and their six parental genotypes proceeded their planting in a randomized complete block design with three replications at the Cereal Crops Research Institute (CCRI), Pirsabak, Nowshera, during 2016–2017, with their F_2 populations evaluated in 2017–2018. Analysis of variance revealed significant differences among the genotypes, parents, parents vs. F_1 and F_2 populations in both generations for all traits. The recorded maximum grain yield per plant resulted in the F_1 hybrid Benazir-13 × Khaista-17 (38.12 g), followed by Khaista-17 × Galaxy-13 (37.58 g) and Khaista-17 × Parula (37.32 g). Mid-parent heterosis for grain yield per plant ranged from -2.77% (Benazir-13 × Inqilab-91) to 15.84% (Ghaznavi-98 × Parula). The best parent heterosis varied from -8.13% (Khaista-17 × Inqilab-91) to 13.11% (Ghaznavi-98 × Parula). Inbreeding depression ranged from 8.97% (Benazir-13 × Ghaznavi-98) to 36.00% (Benazir-13 × Galaxy-13). These promising F_1 and F_2 populations could be highly beneficial in future wheat breeding programs.

Keywords: Bread wheat (*T. aestivum* L.), F_1 and F_2 populations, heterosis, inbreeding depression, quantitative traits, grain yield

Communicating Editor: Prof. Naqib Ullah Khan

Manuscript received: March 23, 2025; Accepted: July 04, 2025.

Citation: Raza H, Khan SA, Afridi K, Ali N, Hussain I, Ali S, Khan J, Ullah I, Ali A (2025). Heterosis and inbreeding depression in f_1 and F_2 populations of bread wheat for quantitative traits. *SABRAO J. Breed. Genet.* 57(4): 1422-1432. http://doi.org/10.54910/sabrao2025.57.4.8.

Key findings: This study comprised evaluating the genetic potential, heterotic effects, and inbreeding depression in F_1 hybrids and F_2 wheat (*T. aestivum* L.) populations. The F_1 hybrid Benazir-13 × Khaista-17 showed the maximum grain yield per plant, while Ghaznavi-98 × Parula exhibited the highest mid- and better-parent heterosis. The F_2 population Benazir-13 × Galaxy-13 displayed the highest reduction in grain yield due to inbreeding depression.

INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is a self-pollinating crop and serves as one of the most essential food sources worldwide. Its domestication traces back to the Fertile Crescent in the Middle East (Bhanu *et al*., 2018). In Pakistan, wheat cultivation covers nearly 9.6 million hectares, with a record production of 31.4 million tons (PBS, 2023–2024). In sustaining the growing global population, projected to exceed 9.9 billion by 2050 (Hub, 2020), wheat production requires doubling to feed the expanding global population.

However, in major wheat-producing regions, yield improvement has plateaued over the past two decades, and climate change, particularly rising temperatures, poses an additional threat despite ongoing efforts by breeders and farmers (Gimenez *et al*., 2021). Challenges in wheat breeding include pest and disease resistance, water availability, and cultivar adaptation to specific environments (Herrera *et al*., 2022).

Heterosis, or hybrid vigor, enhances yield and other agronomic traits beyond the parental average. With optimal parental combinations, hybrid wheat can achieve up to 30% higher yields than conventional cultivars (Kalhoro *et al*., 2015). Understanding the extent of heterosis and inbreeding depression is critical for breeders when selecting appropriate breeding methods (Baloch *et al*., 2024).

Heterosis is a widespread biological phenomenon contributing to grain and biomass yield. Hybrid breeding is among the most impactful agricultural innovations, providing significant economic benefits. Over evolutionary time, heterosis involves non-additive effects (Labroo *et al*., 2021). Currently, the cultivation of hybrid wheat mainly happens in Europe, China, and India, covering only about 1% of the global wheat area (Singh *et al*., 2015).

Efficient cross-pollination techniques are necessary to maximize heterosis in hybrid wheat breeding (Hanafi *et al*., 2022). This study's design sought to a) assess the genetic potential of F_1 and F_2 wheat populations and b) evaluate heterotic effects in F_1 hybrids and inbreeding depression in F_2 populations.

MATERIALS AND METHODS

Breeding material and procedure

Crossing six wheat (*T. aestivum* L.) genotypes in a half-diallel fashion included Galaxy-13, Inqilab-91, Ghaznavi-98, Khaista-17, Benazir-13, and Parula to produce 15 F_1 hybrids (Table 1). The 15 F_1 hybrids and their six parental genotypes succeeded in planting using a randomized complete block design with three

Table 1. Pedigree and Yr resistance of wheat parental cultivars used in diallel crosses.

Genotypes	Pedigree	Color / general look	Yr Resistance
Benazir-13	Chen/Aegilops Squarrosa (TAUS)//BCN/3/VEE#7/…	Dark green	Resistant
Khaista-17	KAUZ//ALTAR84/AOS/3/MILAN/KAUZ/4/HUITE	Waxy green	Resistant
Inqilab-91	WL711/CROW	Yellowish green	Susceptible
Ghaznavi-98	JUP/BJY//URES	Waxy green	Susceptible
Galaxy-13	Punjab96/V87094//MH-97	Waxy green	Susceptible
Parula	FKN/3/2*FR//KAD/GB/4/BB/CHA	Waxy green	Resistant

Zhang *et al*. (2023)

replications at the Cereal Crops Research Institute (CCRI), Pirsabak, Nowshera, Pakistan, during 2016–2017, with their F_2 populations studied the year after.

Data recorded

Data recording ensued on various morphological parameters from 20 randomly selected plants per genotype. Flag leaf area calculation by measuring the leaf length and width used a ruler and multiplying their product by a correction factor (0.75), as described by Francis *et al*. (1969).

Flag leaf area = Leaf length × Leaf width × 0.75

Grains per spike processing had each spike counted manually in 20 randomly chosen plants and then underwent averaging to get grains per spike. Similarly, for the 1000-grain weight, a thousand grains from each genotype yielded weights through an electronic balance. However, grain yield per plant (g) measurements continued by manually threshing the grains from 20 plants per genotype in each replication, with the average yield being calculated.

Statistical analysis

All the recorded data's subjection to analysis followed the method given by Steel *et al.* (1997), using Statistix 8.1 software. The least significant test application compared the mean for each trait. Though all the data revealed significant differences, hence average heterosis, heterobeltiosis (better parent heterosis) in F_1 hybrids, and inbreeding depression succeeded calculation in the F_2 generation for various traits in bread wheat.

Heterotic effects

Heterosis over high-parent, as calculated, employed the percent increase (+) or decrease (-) of the F_1 hybrids over its better-parent value for all the traits (Fonseca, 1965).

$$\text{Heterobeltiosis (\%)} = \frac{F_1 - HP}{HP} \times 100$$

Heterosis over mid-parent calculation depended on the percent increase (+) or decrease (-) of the F_1 hybrids over its mid-parent value (Singh, 2003).

$$\text{Heterosis (\%)} = \frac{\overline{F_1} - \overline{MP}}{\overline{MP}} \times 100$$

Heterotic values for the three categories of heterosis further sustained analysis using a *t*-test to assess whether the F_1 hybrid means significantly differ from their better parent. The *t* values' computation used the formulas of Wynne *et al*. (1970).

't' for mid-parent heterosis:

$$t = \frac{F_1 - MP}{\sqrt{\frac{3}{2r}(EMS)}}$$

't' for better-parent heterosis:

$$t = \frac{F_1 - BP}{\sqrt{\frac{2}{r}(EMS)}}$$

Where:
MP = the mid-parent value of the specific F_1 cross,
BP = the better-parent value of the specific F_1 cross, and
EMS = Error mean square.

The "t" values for economic heterosis, as calculated, engaged the following formulas.

t (Economic heterosis) = SH/SE(d);

SE (d) for EH = ± $t = \sqrt{2Me/r}$

Where SE, r, and t are the standard error, replications, and t as the calculated value, respectively.

Table 2. Mean squares for various traits in 6 × 6 half-diallel F_1 and F_2 populations of wheat.

Source of variation	d.f.	FLA	GPS	1000-gwt	GYP
F_1 generation					
Replications	2	0.58	8.35	7.61	0.54
Genotypes	20	40.27**	75.91**	32.86**	17.09**
Parents	5	23.07**	80.76**	33.26**	26.04**
F_1 hybrids	14	47.16**	73.05**	32.92**	9.24**
Parents vs. F_1	1	29.77*	91.78**	30.12**	82.30**
Error	40	5.49	5.55	2.91	3.50
F_2 generation					
Replications	2	3.47**	208.69**	11.16	22.75**
Genotypes	20	31.66**	28.20**	102.45**	16.21**
Parents	5	64.85**	35.16**	21.93**	13.75**
F_2 populations	14	19.51**	21.56*	138.52**	17.01**
Parents vs. F_2	1	35.76**	86.40**	0.00	17.47
Error	40	0.23	9.66	5.04	3.63

****:** Significant at 1% level and ***:** Significant at 5% level. FLA = Flag leaf area (cm^2), GPS= Grains per spike, 1000-gwt = 1000-grain weight (g), and GYP = Grain yield $plant^{-1}$ (g).

Inbreeding depression

The observed inbreeding depression in F_2 populations underwent calculation as a percent decrease in F_2 populations by comparing with F_1 hybrid means, as outlined by Hallauer and Miranda-Filho (1988).

$$\text{Inbreeding Depression (\%)} = \frac{F_1 - F_2}{F_1} \, x \, 100$$

RESULTS

Analysis of variance revealed significant differences for genotypes, parents, F_1 hybrids, and parents vs. F_1 hybrids for all the traits in the F_1 generation. However, in F_2 generations, total genotypes, parents, and parents vs. F_2 populations revealed significant differences for all the traits (Table 2).

Flag leaf area

The maximum flag leaf area was visible for the F_1 hybrid, Khaista × Parula (39.61 cm^2), and at par with Benazir-13 × Khaista-17 (39.25 cm^2) and Benazir-13 × Galaxy-13 (39.15 cm^2). The latter F_1 hybrid again appeared similar with seven F_1 hybrids ranging from 35.74 to 37.71 cm^2 (Table 3). However, the minimum flag leaf area resulted in the F_1 hybrid, Ghaznavi-98 × Parula (28.06 cm^2), which showed at par with other three genotypes (two F_1 hybrids and one parental cultivar), ranging from 28.73 to 29.70 cm^2. In the case of the F_2 generation, the maximum flag leaf area was notable in the F_2 generations, Benazir-13 × Khaista-17 (31.03 cm^2) and Galaxy-13 × Parula (30.53 cm^2). However, the minimum flag leaf area was evident in the parental cultivars, Ghaznavi-98 and Inqilab-91, with the mean values of 18.63 and 21.23 cm^2, respectively.

For flag leaf area, mid-parent heterosis among 13 F_1 hybrids ranged from -14.86% (Ghaznavi-98 × Parula) to 16.32% (Inqilab-91 × Galaxy-13), with the maximum in Inqilab-91 × Galaxy-13 (16.32%), followed by Benazir-13 × Galaxy-13 (13.54%) (Table 3). Significant negative heterosis occurred in Ghaznavi-98 × Parula (-14.86%) and Benazir-13 × Ghaznavi-98 (-14.59%). Better-parent heterosis varied from -19.61% (Benazir-13 × Ghaznavi-98) to 10.16% (Inqilab-91 × Galaxy-13), with six hybrids showing remarkable positive heterosis, while four hybrids exhibited negative heterosis, ranging from -19.61% to -9.93%.

The inbreeding depression for flag leaf area among the F_1 hybrids ranged from -4.52% (Benazir-13 × Ghaznavi-98) to 38.23% (Inqilab-91 × Galaxy-13) (Table 3). The maximum inbreeding depression resulted in Inqilab-91 × Galaxy-13 (38.23%), followed by Inqilab-91 × Ghaznavi-98 (29.46%), Khaista-

Table 3. Mean performance, heterosis, and inbreeding depression in 6 × 6 half-diallel F_1 and F_2 populations for flag leaf area in wheat.

Genotypes	Flag leaf area (cm^2)	Heterosis			Inbreeding depression
Benazir-13	35.74				
Khaista-17	37.30				
Inqilab-91	29.70				
Ghaznavi-98	31.54				
Galaxy-13	33.21				
Parula	34.36				
Populations	F_1's	F_2's	MPH (%)	BPH (%)	ID (%)
Benazir-13 × Khaista-17	39.25	31.03	7.48	5.24*	20.94**
Benazir-13 × Inqilab-91	36.98	27.53	13.01**	3.45	25.55**
Benazir-13 × Ghaznavi-98	28.73	30.03	-14.59**	-19.61**	-4.52
Benazir-13 × Galaxy-13	39.15	29.00	13.54**	9.53*	25.93
Benazir-13 × Parula	36.91	26.90	5.29	3.26	27.12**
Khaista-17 × Inqilab-91	35.85	26.20	7.02	-3.89	26.92
Khaista-17 × Ghaznavi-98	33.59	24.47	-2.41	-9.93**	27.15**
Khaista-17 × Galaxy-13	39.1	27.70	10.90**	4.83**	29.16
Khaista-17 × Parula	39.61	29.93	10.54**	6.20**	24.44
Inqilab-91 × Ghaznavi-98	33.13	23.37	8.19	5.02	29.46**
Inqilab-91 × Galaxy-13	36.59	22.60	16.32**	10.16**	38.23**
Inqilab-91 × Parula	29.13	26.00	-9.04	-15.22**	10.74**
Ghaznavi-98 × Galaxy-13	33.69	27.23	4.04	1.42	19.17*
Ghaznavi-98 × Parula	28.06	28.07	-14.86**	-18.35**	-0.04
Galaxy-13 × Parula	37.71	30.53	11.59**	9.73*	19.04**
Means	35.17	27.37			
$LSD_{0.05}$	3.87	0.80			

17 × Galaxy-13 (29.16%), Benazir-13 × Parula (27.12%), Khaista-17 × Ghaznavi-98 (27.15%), and Benazir-13 × Inqilab-91 (25.55%).

Grains per spike

The maximum grains per spike were prominent in the F_1 hybrid Benazir-13 × Khaista-17 (71.15), which was at par with Benazir-13 × Galaxy-13 (70.04) and Benazir-13 × Parula (69.46) (Table 4). The latter F_1 hybrid was also alike with Khaista-17 × Galaxy-13 (68.92) and Khaista-17 × Parula (68.77). However, the minimum grains per spike manifested in the F_1 hybrid Ghaznavi-98 × Parula (55.94) and appeared on par with Inqilab-91 × Galaxy-13 (56.34) and Inqilab-91 × Ghaznavi-98 (57.33). Furthermore, in the F_2 generation, maximum grains per spike was noteworthy for the F_2 population Khaista-17 × Parula (62.44), showing at par with Benazir-13 × Khaista-17 (59.10), Benazir-13 × Inqilab-91 (58.89), and Benazir-13 × Parula (58.83). Meanwhile, the minimum grains per spike resulted in the F_2 population Khaista-17 × Ghaznavi-98 (51.01).

For grains per spike, the mid-parent heterosis ranged from -5.96% (Inqilab-91 × Galaxy-13) to 16.29% (Inqilab-91 × Parula) among the 15 F_1 hybrids (Table 4). Significant and maximum mid-parent heterosis emerged in Inqilab-91 × Parula (16.29%), followed by Benazir-13 × Parula (14.92%) and Benazir-13 × Galaxy-13 (10.02%). Conversely, substantial negative mid-parent heterosis surfaced for Ghaznavi-98 × Parula (-5.79%). For grains per spike, the better-parent heterosis ranged from -11.41% (Ghaznavi-98 × Parula) to 14.71% (Benazir-13 × Inqilab-91). Maximum better-parent heterosis was distinct in Benazir-13 × Inqilab-91 (14.71%), while considerable negative values were noticeable for Ghaznavi-98 × Parula (-11.41%).

The inbreeding depression for grains per spike among the F_2 population ranged from -2.08% (Inqilab-91 × Ghaznavi-98) to 22.83% (Khaista-17 × Ghaznavi-98) (Table 4). The maximum inbreeding depression resulted in

Table 4. Mean performance, heterosis, and inbreeding depression in 6 × 6 half-diallel F_1 and F_2 populations for grains per spike in wheat.

Genotypes	Grains per spike		Heterosis		Inbreeding depression
Benazir-13	65.27				
Khaista-17	70.03				
Inqilab-91	57.78				
Ghaznavi-98	63.15				
Galaxy-13	62.05				
Parula	55.61				
Populations	F_1's	F_2's	MPH (%)	BPH (%)	ID (%)
Benazir-13 × Khaista-17	71.15	59.10	5.17*	1.59**	16.94
Benazir-13 × Inqilab-91	66.28	58.89	7.73**	14.71	11.15
Benazir-13 × Ghaznavi-98	63.47	58.58	-1.16	-2.77	7.70**
Benazir-13 × Galaxy-13	70.04	54.17	10.02**	7.30*	22.66
Benazir-13 × Parula	69.46	58.83	14.92**	6.41*	15.30**
Khaista-17 × Inqilab-91	65.00	58.46	1.71	-7.19*	10.06
Khaista-17 × Ghaznavi-98	66.10	51.01	-0.74	-5.62	22.83**
Khaista-17 × Galaxy-13	68.92	55.41	4.35	-1.60**	19.60**
Khaista-17 × Parula	68.77	62.44	9.47**	-1.80**	9.20**
Inqilab-91 × Ghaznavi-98	57.33	58.52	-5.18	-9.21**	-2.08
Inqilab-91 × Galaxy-13	56.34	55.97	-5.96	-9.20**	0.66**
Inqilab-91 × Parula	65.93	55.39	16.29**	14.10**	15.99
Ghaznavi-98 × Galaxy-13	66.83	56.28	6.76**	5.83**	15.79**
Ghaznavi-98 × Parula	55.94	55.58	-5.79*	-11.41	0.64
Galaxy-13 × Parula	63.26	56.73	7.52**	1.94**	10.32**
Means	64.99	57.0			
$LSD_{0.05}$	3.89	5.13			

Khaista-17 × Ghaznavi-98 (22.83%), followed by Benazir-13 × Galaxy-13 (22.66%) and Khaista-17 × Galaxy-13 (19.60%). Other hybrids with positive inbreeding depression included Benazir-13 × Parula (15.30%), Galaxy-13 × Parula (10.32%), and Khaista-17 × Parula (9.20%).

1000-grain weight

The maximum 1000-grain weight in F_1 hybrids was notable for Benazir-13 × Khaista-17 (48.11 g), followed by Khaista-17 × Parula (47.83 g) and Khaista-17 × Ghaznavi-98 (47.30 g) (Table 5). These were comparable to Khaista-17 × Galaxy-13 (46.08 g) and Benazir-13 × Parula (45.63 g). The minimum value appeared for Benazir-13 × Ghaznavi-98 (36.92 g). In the F_2 population, Khaista-17 × Parula had the maximum 1000-grain weight (52.53 g), followed by Benazir-13 × Ghaznavi-98 (46.29 g), while the minimum was in Benazir-13 × Galaxy-13 (24.25 g).

For 1000-grain weight, mid-parent heterosis among 15 F_1 hybrids ranged from -11.41% (Ghaznavi-98 × Parula) to 14.71% (Benazir-13 × Inqilab-91), with the maximum in Benazir-13 × Inqilab-91 (14.71%), followed by Inqilab-91 × Parula (14.10%) (Table 5). Significant negative heterosis was apparent in Ghaznavi-98 × Parula (-11.41%) and Inqilab-91 × Ghaznavi-98 (-9.21%). Better-parent heterosis ranged from -17.79% (Benazir-13 × Ghaznavi-98) to 8.65% (Galaxy-13 × Parula), with the maximum in Galaxy-13 × Parula (8.65%). Significant negative heterosis was discernible in Benazir-13 × Ghaznavi-98 (-17.79%) and Khaista-17 × Inqilab-91 (-10.74%), while some hybrids exhibited moderate positive heterosis.

The inbreeding depression for 1000-grain weight among the F_2 population ranged from -25.38% (Benazir-13 × Ghaznavi-98) to 43.45% (Benazir-13 × Galaxy-13) (Table 5). The maximum inbreeding depression appeared in Benazir-13 × Galaxy-13 (43.45%), followed

Table 5. Mean performance, heterosis, and inbreeding depression in 6 × 6 half-diallel F_1 and F_2 populations for 1000-grain weight in wheat.

Genotypes	1000-grain weight (g)		Heterosis		Inbreeding depression
Benazir-13	44.91				
Khaista-17	47.52				
Inqilab-91	43.43				
Ghaznavi-98	39.71				
Galaxy-13	41.76				
Parula	38.57				
Populations	F_1's	F_2's	MPH (%)	BPH (%)	ID (%)
Benazir-13 × Khaista-17	48.11	38.81	4.12	1.26**	19.33**
Benazir-13 × Inqilab-91	45.22	35.92	2.39	0.71	20.57*
Benazir-13 × Ghaznavi-98	36.92	46.29	-12.74**	-17.79**	-25.38
Benazir-13 × Galaxy-13	42.88	24.25	-1.03	-4.51	43.45*
Benazir-13 × Parula	45.63	36.33	9.33**	1.62	20.38
Khaista-17 × Inqilab-91	42.41	41.45	-6.73**	-10.74**	-0.10
Khaista-17 × Ghaznavi-98	47.30	38.00	8.44**	-0.46	19.66**
Khaista-17 × Galaxy-13	46.08	27.60	3.23	-3.03**	40.10
Khaista-17 × Parula	47.83	52.53	11.11**	0.65**	-9.83**
Inqilab-91 × Ghaznavi-98	45.16	31.63	8.62**	3.98**	29.96**
Inqilab-91 × Galaxy-13	44.21	37.08	3.80	1.80	16.13
Inqilab-91 × Parula	42.92	33.62	4.68	-1.17**	21.67**
Ghaznavi-98 × Galaxy-13	45.23	35.93	11.04**	8.33*	20.56
Ghaznavi-98 × Parula	37.42	37.12	-4.41	-5.79	0.83
Galaxy-13 × Parula	45.37	38.07	12.96**	8.65**	16.09**
Means	44.2	37.0			
$LSD_{0.05}$	2.81	3.71			

by Khaista-17 × Galaxy-13 (40.10%) and Inqilab-91 × Ghaznavi-98 (29.96%). Other F_2 populations with positive inbreeding depression included Benazir-13 × Khaista-17 (19.33%), Khaista-17 × Ghaznavi-98 (19.66%), and Galaxy-13 × Parula (16.09%). Conversely, negative inbreeding depression was evident in Benazir-13 × Ghaznavi-98 (-25.38%) and Khaista-17 × Parula (-9.83%), indicating a reduction in 1000-grain weight for these populations.

Grain yield per plant

The maximum grain yield per plant in F_1 hybrids was prominent for Benazir-13 × Khaista-17 (38.12 g), followed by Khaista-17 × Galaxy-13 (37.58 g) and Khaista-17 × Parula (37.32 g) (Table 6). The minimum resulted in Ghaznavi-98 × Parula (29.82 g), while the remaining hybrids ranged from 32.32 to 34.88 g. In F_2 populations, Khaista-17 × Parula had the maximum grain yield (30.71 g), followed by Benazir-13 × Ghaznavi-98 (29.93 g). The minimum yield emerged in Benazir-13 × Galaxy-13 (22.63 g), with the remaining populations ranging between 25.46 and 26.61 g.

The mid-parent heterosis for grain yield per plant among 15 F_1 hybrids ranged from -2.77% (Benazir-13 × Inqilab-91) to 15.84% (Ghaznavi-98 × Parula), with the maximum in Ghaznavi-98 × Parula (15.84%), followed by Inqilab-91 × Ghaznavi-98 (15.77%) (Table 6). Negative heterosis was definite in Benazir-13 × Inqilab-91 (-2.77%) and Khaista-17 × Inqilab-91 (-1.58%). The best-parent heterosis varied from -8.13% (Khaista-17 × Inqilab-91) to 13.11% (Ghaznavi-98 × Parula), with positive values in Inqilab-91 × Ghaznavi-98 (9.94%) and Galaxy-13 × Parula (8.96%), while negative heterosis arose in Khaista-17 × Inqilab-91 (-8.13%).

The inbreeding depression for grain yield per plant among the F_2 population ranged from 8.97% (Benazir-13 × Ghaznavi-98) to 36.00% (Benazir-13 × Galaxy-13) (Table 6).

Table 6. Mean performance, heterosis, and inbreeding depression in 6 × 6 half-diallel F_1 and F_2 populations for grain yield per plant in wheat.

Genotypes	Grain yield per plant (g)		Heterosis		Inbreeding depression
Benazir-13	34.50				
Khaista-17	36.90				
Inqilab-91	31.99				
Ghaznavi-98	28.78				
Galaxy-13	31.68				
Parula	30.19				
Populations	F_1's	F_2's	MPH (%)	BPH (%)	ID (%)
Benazir-13 × Khaista-17	38.12	28.60	6.77	3.29*	24.97**
Benazir-13 × Inqilab-91	32.32	26.61	-2.77	-6.31	17.67*
Benazir-13 × Ghaznavi-98	32.88	29.93	3.93	-4.71	8.97*
Benazir-13 × Galaxy-13	35.36	22.63	6.87	2.51	36.00**
Benazir-13 × Parula	35.30	27.54	9.13*	2.32*	21.98
Khaista-17 × Inqilab-91	33.90	29.74	-1.58	-8.13	12.27
Khaista-17 × Ghaznavi-98	35.23	27.72	7.31	-4.52	21.32**
Khaista-17 × Galaxy-13	37.58	24.74	9.60*	1.85**	34.17
Khaista-17 × Parula	37.32	30.71	11.26**	1.15**	17.71
Inqilab-91 × Ghaznavi-98	35.17	23.21	15.77**	9.94**	34.01**
Inqilab-91 × Galaxy-13	34.88	25.77	9.36*	8.84	26.12
Inqilab-91 × Parula	32.56	27.10	4.73	1.79	16.77
Ghaznavi-98 × Galaxy-13	33.79	26.58	11.80**	6.65	21.34*
Ghaznavi-98 × Parula	29.82	25.46	15.84	13.11	14.62
Galaxy-13 × Parula	34.52	28.83	11.58**	8.96**	16.48**
Means	34.60	27.00			
$LSD_{0.05}$	3.20	3.15			

The topmost inbreeding depression resulted in Benazir-13 × Galaxy-13 (36.00%), followed by Khaista-17 × Galaxy-13 (34.17%), Inqilab-91 × Ghaznavi-98 (34.01%), Inqilab-91 × Galaxy-13 (26.12%), Benazir-13 × Khaista-17 (24.97%), and Benazir-13 × Parula (21.98%). Other populations with positive inbreeding depression included Khaista-17 × Ghaznavi-98 (21.32%), Ghaznavi-98 × Galaxy-13 (21.34%), and Benazir-13 × Inqilab-91 (17.67%).

DISCUSSION

A larger flag leaf, the main source of grain carbohydrates in wheat, enhances photosynthesis and yield, making its genetic improvement vital for productivity (Luo *et al*., 2018). Most F_1 hybrids revealed positive and significant mid-parent heterotic effects for flag leaf area (Ayyub *et al*., 2024). Similar results have also appeared for flag leaf area in wheat F_1 hybrids with significant positive mid-parent heterosis (Kájla *et al*., 2020). Conversely, the findings of other research scientists have revealed a decrease in flag leaf area compared with their respective mid-parent heterosis values in wheat (Mahpara *et al*., 2017). Positive inbreeding depression emerged for Galaxy-13 × Parula and Ghaznavi-98 × Galaxy-13. Contrastingly, a negative inbreeding depression resulted in Benazir-13 × Ghaznavi-98, indicating a reduction in flag leaf area for this cross. Significant negative inbreeding depression values were evident for yield and its components in the F_2 population of bread wheat (Soomro *et al*., 2019). These findings received further authentication from other wheat scientists who observed negative values for inbreeding depression for flag leaf area, tillers per square meter, grains per spike, 1000-grain weight, and grain yield in F_1 hybrids of bread wheat (Kumar *et al*., 2018).

The trait grains per spike is an important trait directly linked with grain yield of wheat (Al-Bakry, 2021). These results coincided with findings of other research scientists who reported grains per spike increased grain yield per plant in wheat (Sakuma and Schnurbusch, 2020). The inbreeding depression in the F_2 population is a reliable indicator for heterosis in F_1 hybrids (Kumar *et al*., 2018). Eight crosses exhibited significant positive mid-parent heterosis for grains per spike, highlighting the importance of the trait's selection based on mid-parent heterotic effects that could increase grain yield (Kalhoro *et al*., 2015). Negative inbreeding depression manifested in Inqilab-91 × Ghaznavi-98, indicating a reduction in grains per spike. This negative inbreeding depression is ascribable to the population buffering effect, which may arise in later generations due to gene segregation or occasionally through the formation of superior gene combinations (Al-Bakry, 2021). However, in the F_2 generation, a reduction in heterozygosity occurs due to the diminished dominance effect. This makes negative inbreeding depression beneficial for 1000-grain weight and other yield-related traits (Burdak *et al*., 2023).

Grain yield per plant had a highly substantial positive correlation with the 1000-grain weight (Choudhary *et al*., 2025). These assessments agree with the findings concluded by several earlier studies (Ibrahim, 2019). All these studies reported significant variation among all parameters of wheat. Similar findings came from Bilgrami *et al*. (2018). Most F_1 hybrids revealed notable negative mid- and better-parent heterosis for 1000-grain weight (Baloch *et al*., 2024). Better-parent heterosis for 1000-grain weight in wheat plays a vital role in yield improvement (Khan *et al*., 2024). Similarly, Kumar *et al*. (2018) found remarkable heterotic effects in F_1 hybrids, highlighting the potential of selective breeding to enhance 1000-grain weight. These studies underscore the value of identifying superior parent combinations to increase grain yield in wheat. Recent studies highlighted the impact of inbreeding depression on 1000-grain weight and grain yield in wheat. Burdak *et al*. (2023) found no inbreeding depression for grain yield in late-sown wheat, while Rajane *et al*. (2023) observed both positive and negative effects in F_2 and F_3 generations. Nageshwar *et al*. (2024) reported significant inbreeding depression in all 45 F_2 crosses, and Baloch *et al*. (2024) noted varying levels across traits, emphasizing the need for careful parental selection. These findings underscore the genetic complexity of inbreeding depression in wheat breeding.

Previous studies have shown pivotal positive better-parent heterosis for grain yield per plant, an increase of 37.32% over the better parent and 40.69% over the mid parent in F_1 hybrids in wheat (Saeed *et al*., 2024). Research has documented both meaningful positive and negative effects of inbreeding depression on yield and its associated traits in wheat (Kumar *et al*., 2018; Choudhary *et al*., 2018). Selecting promising segregating wheat preserves genetic variation, boosts yield, aids transgressive segregants, and reduces inbreeding depression (Hill and Li, 2022).

CONCLUSIONS

The analysis of variance disclosed significant differences among genotypes, parents, parents vs. F_1 hybrids, and the F_2 population in both generations for all traits. The maximum grain yield per plant was noteworthy in the F_1 hybrid Benazir-13 × Khaista-17. The F_1 hybrid Ghaznavi-98 × Parula exhibited significant positive mid-parent heterosis, while the same cross also showed positive and remarkable best-parent heterosis for grain yield per plant. Inbreeding depression for grain yield per plant was prominent in the F_2 population Benazir-13 × Galaxy-13. Based on these findings, Benazir-13 × Khaista-17 and Ghaznavi-98 × Parula are the best options for further evaluation and potential use in wheat breeding programs.

REFERENCES

Al-Bakry MRI (2021). Novel transgressive segregation in bread wheat. *Egypt. J. Genet. Cytol.* 50(2): 119-138.

Ayyub M, Khan M, Malik SA, Ali S, Shamsullah S, Azam M (2024). Estimation of genetic variability in relation to heterosis and combining ability of wheat from subtropical and temperate zones. *Sarhad J. Agric*. 40(2): 431-439.

Baloch TA, Jatoi WA, Mari SN, Baloch SN, Lal K (2024). Superior wheat hybrids development for physiological and yield-related traits under adverse environmental conditions. *SABRAO J. Breed. Genet.* 56(3): 1022-1036.

Bhanu AN, Arun B, Mishra VK (2018). Genetic variability, heritability and correlation study of physiological and yield traits in relation to heat tolerance in wheat (*Triticum aestivum* L.). *Biomed. J. Sci. Technol. Res.* 2(1): 1-5.

Bilgrami SS, Fakheri BA, Shariati JV (2018). Evaluation of agro-morphological traits related to grain yield of Iranian wheat genotypes in drought-stress. *Australian J. Crop Sci. 12*(5): 738-748.

Burdak A, Yadav RS, Kumar A (2023). Evaluation of heterosis and inbreeding depression for grain yield and its contributing traits in bread wheat under late sown conditions. *PharmaInnov. J. 12(3)*: 3037-3042.

Choudhary R, Singh H, Lal C, Bhat D (2018). Inbreeding depression analysis for yield and associated traits in late sown condition in bread wheat (*Triticum aestivum* L. em. Thell). *Int. J. Curr. Microbiol. Appl. Sci.* 7(7): 1986-1993.

Choudhary S, Gaur SC, Kumar S (2025). Studies on correlation and path coefficient analysis for yield and yield-associated traits in wheat (*Triticum aestivum* L.) genotypes. *J. Adv. Biol. Biotechnol.* 28(1): 56-68.

Fonseca S (1965). Heterosis, heterobeltiosis, diallel analysis and gene action in crosses of *T. aestivum* L. Ph.D. Dissertation, Purdue University, USA.

Francis CA, Rutger JN, Palmer AFE (1969). A rapid method for plant leaf area estimation in maize. *Crop Sci*. 9(5): 537-539.

Gimenez K, Blanc P, Argillier O, Pierre JB, Gouis JL, Paux E (2021). Dissecting bread wheat heterosis through the integration of agronomic and physiological traits. *Biology*. 10(907): 1-20.

Hallauer AR, Miranda-Filho JB (1988). Quantitative Genetics in Maize Breeding. 2nd Ed., Iowa State Univ. Press, USA.

Hanafi SE, Cherkaoui S, Kehel Z, Garcia MS, Baenziger S, Tadesse W (2022). Hybrid seed set in relation with male floral traits, estimation of heterosis and combining abilities for yield and its components in wheat (*Triticum aestivum* L.). *Plants.* 11(4): 508.

Herrera LAC, Crossa J, Vargas M, Bram HJ (2022). Defining targets in wheat breeding environments. Wheat Improvement. Chapter 3, pp: 31.

Hill CB, Li C (2022). Genetic improvement of heat stress tolerance in cereal crops. *Agronomy,* 12(5): 1205.

Hub SK (2020). World population to reach 9.9 billion by 2050. SDG Knowledge Hub: IISD.

Ibrahim AU (2019). Genetic variability, correlation and path analysis for yield and yield components in F6 generation of wheat (*Triticum aestivum* Em. Thell.). *IOSR J. Agric. Vet. Sci*. *12*: 17-23.

Kájla SL, Sharma AK, Singh H (2020). Heterosis analysis in F_1 hybrids of bread wheat (*Triticum aestivum* L. em. Thell.) over environments. *Int. J. Curr. Microbiol. Appl. Sci*. 9(5): 2052-2057.

Kalhoro FA, Rajpar AA, Kalhoro SA, Maher A, Ali A (2015). Heterosis and combining ability in F_1 population of hexaploid wheat (*Triticum aestivum* L.). *Amer. J. Plant Sci*. 6: 1011-1026.

Khan R, Prasad B, Bhatt B (2024). Study of heterosis for grain yield and its components in wheat (*Triticum aestivum* L. em. Thell.). *Environ. Conserv.* J. 25(1): 56-61.

Kumar A, Razdan AK, Sharma V, Kumar N, Kumar D (2018). Study of heterosis and inbreeding depression for economic and biochemical traits in bread wheat (*Triticum aestivum* L.). *J. Pharm. Phytochem.* 7(4): 558-564.

Labroo MR, Studer AJ, Rutkoski JE (2021). Heterosis and hybrid crop breeding: A multidisciplinary review. *Front. Genet*. 12 (643761): 1-19.

Luo F, Deng X, Li Y, Yan Y (2018). Identification of phosphorylation proteins in response to water deficit during wheat flag leaf and grain development. *Bot. Stud.* 59(28): 1-17.

Mahpara S, Rehmani MIA, Hussain S, Iqbal J, Qureshi MK, Shazad MA, Dar JS (2017). Heterosis for some physio-morphological plant traits in spring wheat crosses. *Pure Appl. Biol*. 6: 1103-1110.

Nageshwar R, Patil SC, Ghorade RB (2024). Heterosis and inbreeding depression for yield and yield-contributing traits in wheat (*Triticum aestivum* L.). *Electron. J. Plant Breed*. *15(1),* 101-107.

PBS (2023–2024). Economic Adviser's Wing, Finance Division, Government of Pakistan, Islamabad.

Rajane AR, Babar SB, Kshirsagar DB (2023). Inbreeding depression study in F_2 and F_3 segregating generations of bread wheat (*Triticum aestivum* L.). *Biol. Forum Int. J. 15(3)*: 160-164.

Saeed S, Khan NU, Khalil IH, Ali S, Afridi K (2024). Heterotic effects and inbreeding depression in F_1 and F_2 populations of wheat. *Pak. J. Bot*. 56(3): 1001-1013.

Sakuma S, Schnurbusch T (2020). Of floral fortune: Tinkering with the grain yield potential of cereal crops. *New Phytologist*. *225*(5): 1873-1882.

Singh P (2003). Essential of Plant Breeding. 2nd Ed. Kalyani Publishers. New Delhi, India.

Singh SP, Srivastava R, Kumar J (2015). Male sterility systems in wheat and opportunities for hybrid wheat development. *Acta Physiol. Plant.* 37: 1713.

Soomro ZA, Khalid M, Shar PA, Hassni MD, Shah RA (2019). Response of intraspecific crosses in F_1 and their deterioration in F_2 generation of bread wheat (*Triticum aestivum* L.). *Int. J. Sustain. Agric. Res*. 6(4): 198-202.

Steel RGD, Torrie JH, Dickey DA (1997). Principles and Procedures of Statistics: A Biometrical Approach, 3rd Ed. McGraw Hill Book Co. Inc. New York, USA.

Wynne JC, Emery DA, Rice PH (1970). Combining ability estimation in *Arachis hypogea* L. field performance of F_1 hybrids. *Crop Sci*. 10: 713-715.

Zhang W, Boyle K, Francis T, Fobert PR (2023). Systematic characterization of multi-rust resistance genes from a 'Parula × Thatcher' population with a high-density genetic map. *Phytopathology* 113(5): 847-857.