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HETEROTIC EFFECTS AND INBREEDING DEPRESSION IN F_1 AND F_2 POPULATIONS OF WHEAT

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Abstract

Wheat breeding has delivered huge benefits, especially over a century with increased productivity and stability in yield even after facing the inevitable stresses. The present study aimed to determine the genetic potential, heterotic effects, and inbreeding depression in F_1 and F_2 populations, respectively for earliness and yield traits in wheat. The crosses were made in 2017-18 through line by tester mating design with seven lines i.e., Seher-06, Pirsabak-85, Shahkar-13, Galaxy-13, Ghaznavi-98, TD-1, and Inqalab-91, and three testers i.e., Parula, Yr-5 and Yr-10, at the Cereal Crop Research Institute (CCRI), Nowshera, Pakistan. For getting wheat F_2 populations, the generation was also advanced during the summer season of 2018 at the Summer Agricultural Research Station (SARS), Kaghan, Pakistan. After advancing the generation, 21 F_1 and 21 F_2 wheat populations with their ten parental genotypes were grown during crop season 2018-2019 in a randomized complete block design with three replications at the University of Agriculture, Peshawar, Pakistan. Analysis of variance exhibited significant differences among the total genotypes, parental genotypes, lines, testers, crosses, and line by tester interactions for the majority of the traits in F_1 and F_2 generations. Results further revealed that the F_1 hybrid Galaxy-13 × Yr-10 showed the maximum grain yield per plant (55.08 g), followed by F_1 hybrids Shahkar-13 × Parula (45.66 g) and Shahkar-13 × Yr-5 (45.41 g). For grain yield per plant, significant positive mid-parent heterosis was recorded in 10 hybrids, ranging from 17.37% (Seher-06 × Parula) to 208.30% (Galaxy-13 × Yr-10). Significant better parent heterotic effects were recorded in F_1 hybrids i.e., Galaxy-13 × Yr-10 (127.35%), Ghaznavi-98 × Yr-10 (74.37%), Galaxy-13 × Parula (41.34%), TD-1 × Parula (37.42%), Galaxy-13 × Yr-5 (35.68%) for grain yield per plant. Significant economic heterosis was recorded among the eight hybrids for grain yield, ranging from 4.20% (Ghaznavi-98 × Yr-5) to 73.05% (Galaxy-13 × Yr-10). In the case of inbreeding depression, significant ($p \leq 0.01$) negative values were recorded in 12 F_2 populations ranging from -48.72% (Shahkar-13 × Parula) to -6.82% (TD-1 × Parula) grain yield per plant.

Key words: Bread wheat (*Triticum aestivum* L.), Line by tester mating design, F_1 and F_2 populations, Heterosis, Inbreeding depression, Earliness and yield traits.

Introduction

Bread wheat (*Triticum aestivum* L. 2n = 6x = 42, AABBDD) is a self-pollinated and, one of the utmost significant food crops of the whole world. Its domestication was started in the fertile areas of the Middle East (Bhanu *et al*., 2018). Bread wheat is utilized mainly as flour and for the production of a large variety of leavened, flatbreads and other baked products (Pena, 2019). During 2020-21 wheat production was around 27.293 million tonnes obtained from an area of 9.18 million hectares indicating an increase of 8.1% over the last year (Anon., 2021). Wheat yield has to double by 2050 to meet the challenge of feeding almost 10 billion people. However, in the main producing countries yield increase has slowed down or even stagnated during the past 20 years and further temperature increases will continue to suppress yields, despite the breeder's and farmer's adaptation efforts (Gimenez *et al*., 2021). The world population was over 7.8 billion in 2020 and is projected to increase by more than 25% to reach 9.9 billion by 2050 (Hub, 2020).

To minimize the cost of production while maximizing profit, wheat quality is a complex concept whose significance lies in determining the capabilities of the post-harvest processing and marketing industries. It is usually partitioned into milling, nutritional quality, and processing. The surrounding protein matrix inside the wheat endosperm and the consequence of the degree of adhesion between the starch granules is called grain texture. Grain protein content varies from 7-18% and a large part is comprised of protein that forms gluten. Finally, for the most important wheat products globally, bread, noodles, cookies, and pasta, the breeding and selection deliberated to genetically improve end-use quality (Guzman *et al*., 2022).

In refined wheat flour, the lack of vitamins and minerals leads to nutritional diseases, constipation, and other gastrointestinal disorders (Iqbal *et al*., 2022). Three main ideas were explained by the wheat experts delivering improved germplasm, translational research to incorporate novel traits, and rapidly evolving technologies with likely potential (Reynolds & Braun, 2022). Incidence of pests and diseases, water availability, flowering time, and determining which wheat cultivar can be grown where, in a well-defined set of environments delivering superior germplasm for farmers, is the main problem of today's wheat breeding (Herrera *et al*., 2022).

Heterosis is defined as the increase in growth, yield, and other plant traits with improved ability as compared to their parental genotypes. The exploitation of heterosis in various crops has a considerable effect on the genetic makeup of the populations to deliver high-yielding hybrids. It is well-known fact that with the right combination of parental genotypes, the heterosis persists and due to its expression, the yield increase was 30% more in the hybrids compared to conventional cultivars (Kalhoro *et al*., 2015). Heterosis is considered as the superiority of hybrids in comparison to either of its parents or commercial cultivar while a range of cultivated crops possesses heterosis and inbreeding depression. However, for wheat breeders to decide on suitable breeding methods, the nature and extent of heterosis and inbreeding depression may play a crucial role (Lal *et al*., 2013; Baloch *et al*., 2015). In nature, heterosis is a common biological phenomenon and mostly contributes to grain yield and biological yield. Among the most popular agricultural innovations, hybrid breeding is one the important section and results in high economic returns, and over evolutionary time, heterosis is an expected concern of the whole-genome and non-additive effects on the populations (Labroo *et al*., 2021; Wu *et al*., 2021). However, hybrid wheat is produced mainly in Europe, China and India although occupying nearly 1% of the total world wheat area (Singh *et al*., 2015).

Effective cross-pollination methods are required for breeding hybrids with the maximum presence of heterosis (Hanafi *et al*., 2022). For the development of high yielding F_1 hybrids and transgressive segregates in F_2 populations the present study was design with the following objectives a) determine the genetic potential of F_1 and F_2 populations, and b) heterotic effects in the F_1 population while inbreeding depression in F_2 populations of wheat.

Material and Methods

Breeding material and procedure: The breeding material consists of ten parental genotypes including seven lines *viz.,* Seher-06, Pirsabak-85, TD-1, Inqalab-91, Ghaznavi-98, Galaxy-13, and Shahkar-13, and three testers *i.e.,* Parula, Yr-5 and Yr-10 crossed in line by tester mating fashion during 2017-18 to obtain their 21 F_1 populations. However, for obtaining F_2 populations, the generation was advanced during the summer season of 2018 at the Summer Agricultural Research (SARS), Kaghan, Khyber Pakhtunkhwa, Pakistan. During 2018-19 all the ten parental genotypes, and their 21 F_1 and 21 F_2 populations were grown in a randomized complete block design (RCBD) using three replications at the University of Agriculture Peshawar, Pakistan.

Data recorded: Data were recorded on the traits *viz.,* plant height, tillers per plant, flag leaf area, grain yield per plant, and harvest index. Plant height was measured in cm from the base of the plant to the tip of the spike (excluding awns) by a meter rod after physiological maturity in each genotype. The number of tillers of 20 randomly selected plants was counted in each genotype/subplot to derive tillers per plant. The flag leaf area of 20 randomly selected plants in each genotype and replication was determined by the following formula (Francis *et al*., 1969).

$$\text{Flag leaf area} = \text{Leaf length} \times \text{Leaf width} \times 0.75$$

Grain yield was recorded in grams by weighing the grains of 20 randomly selected plants of each genotype per replication and was averaged after threshing separately by hand. Harvest index per plant was determined as the ratio of grain yield to biological yield and was expressed in percentage for each genotype in each replication was determined as under.

$$\text{Harvest index} = \frac{\text{Grain yield per plant}}{\text{Biological yield per plant}} \times 100$$

Statistical analysis

Data pertaining to various variables was analyzed according to required analysis of variance (Steel *et al*., 1997) and through (TUNSTATS software). Genotype means for each trait were further divided and compared by using least significant difference (LSD) test. Upon getting significant variations among the wheat genotypes for various variables, the heterosis over mid-, better-parent, and economic heterosis were calculated in the F_1 populations. However, inbreeding depression values were measured in F_2 populations for various traits in wheat.

Mid-parent heterosis: Mid-parent heterosis was expressed as a percent deviation from the mid-parent (Singh, 2003)

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

Heterobeltiosis: Better parent heterosis as coined by Fonseca (1965) was estimated in terms of the percent increase or decrease of the F_1 hybrid over its better parent.

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

Economic heterosis: Economic heterosis was calculated by comparison of F_1 hybrids with existing commercial wheat cultivar Pirsabak-13 using the following formula.

$$\text{Economic heterosis (\%)} = \frac{F_1 - CV}{CV} \times 100$$

Heterotic values for the above three categories were further subjected to the "t" test to determine whether F_1 hybrid means were statistically different from their mid-, better-parent, and commercial check cultivar or not. The "t" values were computed by following the formula of Wynne *et al.,* (1970).

‘t’ for mid- better-parent Heterosis

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

‘t’ for better- parent Heterosis

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

Where

MP = Mid parental value of the particular F_1 cross (P1+P2)/2

BP = Better parent value in the particular F_1 cross

EMS = Error mean square

The "t" values for economic heterosis (EH) was calculated by the formula used by Falconer and Mackay (1996).

t (Economic heterosis) = EH/SE(d)

SE (d) for EH = ± $t = \sqrt{2Me/r}$

Where
SE (d) = Standard error
Me = Error mean square
r = Number of Replications
t = Obtained value was tested against the tabulated t-value at error degree of freedom

Inbreeding depression: The observed inbreeding depression in F_2 populations was calculated as a percent decrease in F_2 populations by comparing with F_1 hybrid means as outlined by Hallauer and Miranda (1988).

$$\text{Inbreeding depression (\%)} = \frac{F_1 - F_2}{F_1} \times 100$$

Results and Discussion

Analysis of variance exhibited significant ($p \leq 0.01$) differences among the total genotypes, parental genotypes, lines, and crosses for almost all the traits except in parent cultivars for flag leaf area, and in crosses for tillers per plant in F_1 generation (Table 1). Parents vs. crosses displayed significant ($p \leq 0.01$) differences for grain yield and harvest index. Testers showed significant ($p \leq 0.01$) differences in plant height and harvest index. Line × tester interactions indicated significant ($p \leq 0.01$) differences for almost all the parameters except tillers per plant and flag leaf area in the F_1 generation. In the F_2 generation, significant ($p \leq 0.01$) differences were observed among the genotypes, parents, crosses, lines, and line × tester interactions for all the studied traits except for the flag leaf area. Parents vs. crosses displayed significant differences for all the traits except flag leaf area and grain yield. Testers showed significant ($p \leq 0.01$) differences in plant height and grain yield per plant in the F_2 generation.

Genetic variability, heterosis, and inbreeding depression

Plant height: In parental lines, testers, and their F_1 and F_2 populations, the mean values for plant height varied from 77.00 (TD-1) to 122.33 cm (Shahkar-13 × Yr-5, TD-1 × Parula) (Table 2). On average, the F_2 populations gained minimum plant height (97.95 cm) compared to testers (99.78 cm), F_1 hybrids (101.32 cm), and lines (102.32 cm). Parental line TD-1 obtained minimum plant height (77.00 cm), followed by F_2 population Shahkar-13 × Parula (78.33 cm) and F_1 hybrid Galaxy-13 × Yr-5 (80.33 cm). Maximum and alike plant height (122.33 cm) was recorded for F_1 hybrid Shahkar-13 × Yr-5 and F_2 population TD-1 × Parula, followed by F_1 hybrid Galaxy-13 × Parula (116.33 cm). All other parental genotypes, F_1 and F_2 populations revealed medium values for plant height. In wheat breeding, novel genotypes have increased genetic gain by reducing plant height can significantly contribute to improved productivity. Increasing assimilate partitioning to the spike by reducing coleoptile and internode length, and plant height results in increased wheat grain yield (Morgounov *et al*., 2013; Gummadov *et al*., 2015). Plant growth traits like adult plant height affect yield by both changing resource partitioning among tissues and altering how plants experience environmental factors. As the plant's height on a given date varies the physical position of the plant within its environment, influencing that plant's interactions with environmental factors like wind, weed competitors, and rain-splashed pathogens. Breeders generally select plants near some optimal height value, as too-short plants have a generally lower yield compared to semi-dwarf's characteristic (DeWitt *et al*., 2021).

Table 1. Mean squares for plant height, tillers per plant, flag leaf area, grain yield per plant, and harvest index in line by tester F_1 and F_2 populations of wheat.

Source of variation	d.f.	Plant height	Tillers plant^{-1}	Flag leaf area	Grain yield plant^{-1}	Harvest index
F_1 generation						
Replications	2	0.30	11.98	182.18	5.22	96.24
Genotypes	30	377.42**	26.90**	45.38**	364.44**	179.58**
Parents (P)	9	302.50**	45.52**	29.22^{NS}	244.75**	100.89**
Parents vs. crosses	1	1.62^{NS}	3.00^{NS}	8.41^{NS}	686.52**	899.68**
Crosses (C)	20	429.92**	19.71^{NS}	54.50**	402.20**	178.99**
Lines (L)	6	465.90**	40.29**	119.41**	932.71**	309.65**
Testers (T)	2	131.73**	8.33^{NS}	4.03^{NS}	89.15^{NS}	237.64**
L × T	12	461.62**	11.32^{NS}	30.46^{NS}	189.13**	103.88**
Error	60	0.39	12.70	18.60	43.04	27.08
F_2 generation						
Replications	2	0.90	14.68	187.29	4.56	4.03
Genotypes	30	373.55**	32.18**	35.51^{NS}	273.14**	87.84**
Parents (P)	9	302.50**	45.52**	29.22 ^{NS}	244.75**	100.89**
Parents vs. crosses	1	270.39**	0.02*	98.65 ^{NS}	78.98^{NS}	102.13*
Crosses (C)	20	410.68**	27.79**	35.18 ^{NS}	295.62**	81.25**
Lines (L)	6	185.51**	15.68**	57.04 ^{NS}	381.85**	76.70**
Testers (T)	2	172.00**	5.44^{NS}	7.94 ^{NS}	348.07**	16.49^{NS}
L × T	12	563.04**	37.56**	28.79 ^{NS}	243.77**	94.32**
Error	60	0.37	14.60	32.89	51.31	17.73

Table 2. Mean performance of F_1 and F_2 populations, and heterosis in F_1s and inbreeding depression in F_2s for plant height through line by tester analysis.

Parental genotypes, F_1 and F_2 populations	Plant height		Heterosis in F_1 and inbreeding depression in F_2 populations for plant height			
Lines						
Seher-06	105.67					
Pirsabak-85	109.33					
TD-1	77.00					
Inqalab-91	107.33					
Ghaznavi-98	109.67					
Galaxy-13	101.33					
Shahkar-13	106.33					
Means	102.38					
Testers						
Parula	92.33					
YR-5	106.00					
RY-10	101.00					
Means	99.78					
Populations	**F_1s**	**F_2s**	**MPH (%)**	**BPH (%)**	**CH (%)**	**ID (%)**
Seher-06 × Parula	108.67	108.67	9.76**	17.69**	12.03**	0.00
Seher-06 × Yr-5	102.00	101.67	-3.62**	-3.77**	5.15**	0.33
Seher-06 × Yr-10	84.33	85.67	-18.39**	-16.50**	-13.06**	-1.58
PS-85 × Parula	101.67	89.00	0.83	-7.01**	4.81**	12.46**
PS-85 × Yr-5	97.67	105.33	-9.29**	-7.86**	0.69	-7.85**
PS-85 × Yr-10	106.00	108.33	0.79	-3.05*	9.28**	-2.20
TD-1 × Parula	113.67	122.33	34.25**	23.10**	17.18**	-7.62**
TD-1 × Yr-5	110.33	87.33	20.58**	4.09**	13.75**	20.85**
TD-1 × Yr-10	82.00	100.33	-7.87**	-18.81**	-15.46**	-22.36**
Inqalab-91 × Parula	83.00	82.67	-16.86**	-10.11**	-14.43**	0.40
Inqalab-91 × Yr-5	92.33	88.33	-13.44**	-12.89**	-4.81**	4.33**
Inqalab-91 × Yr-10	91.33	102.00	-12.32**	-9.57**	-5.84**	-11.68**
Ghaznavi-98 × Parula	98.33	96.33	-2.64	-10.33**	1.37	2.03
Ghaznavi-98 × Yr-5	103.00	100.67	-4.48**	-2.83*	6.19**	2.27
Ghaznavi-98 × Yr-10	112.00	97.33	6.33**	2.13	15.46**	13.10**
Galaxy-13 × Parula	116.33	85.67	20.14**	14.80**	19.93**	26.36**
Galaxy-13 × Yr-5	80.33	106.00	-22.51**	-24.21**	-17.18**	-31.95**
Galaxy-13 × Yr-10	105.67	86.33	4.45**	4.28**	8.93**	18.30**
Shahkar-13 × Parula	105.67	78.33	6.38**	-0.63	8.93**	25.87**
Shahkar-13 × Yr-5	122.33	111.67	15.23**	15.05**	26.12**	8.72**
Shahkar-13 × Yr-10	111.00	113.00	7.07**	4.39**	14.43**	-1.80
Means	101.32	97.95	--	--	--	--
Overall means	101.41	99.13	--	--	--	--
$LSD_{0.05}$	1.02	0.99	--	--	--	--

For plant height, negative heterosis over mid-parent ranged from -22.51% (Galaxy-13 × Yr-5) to -2.64% (Ghaznavi-98 × Parula), while positive heterosis was ranging from 0.79% (PS-85 × Yr-10) to 34.25% (TD-1 × Parula) (Table 2). Out of 21 F_1 hybrids, 10 hybrids showed negative heterotic values, while the rest of 11 hybrids showed positive mid-parent heterosis for plant height. Significant negative mid-parent heterosis was exhibited by nine F_1 hybrids ranging from -22.51% (Galaxy-13 × Yr-5) to -3.62% (Seher-06 × Yr-5). In the case of better parents, the negative heterosis ranged from -20.72% (Galaxy-13 × Yr-5) to -2.83% (Ghaznavi-98 × Yr-5), while positive better parent heterosis was ranging from 4.62% (Galaxy-13 × Yr-10) to 47.62% (TD-1 × Parula). Eight out of 21 F_1 hybrids showed negative values for better parent heterosis while the rest revealed positive heterotic values. Significant negative better parent heterosis was recorded for eight hybrids ranging from -20.72% (Galaxy-13 × Yr-5) to -2.83% (Ghaznavi-98 × Yr-5) for plant height. For plant height, the negative economic heterosis ranged from -17.18% (Galaxy-13 × Yr-5) to -4.81% (Inqalab-91 × Yr-5), however, positive economic heterosis was ranging from 0.69% to (PS-85 × Yr-5) to 26.12% (Shahkar-13 × Yr-5). Six out of 21 F_1 hybrids showed negative heterotic values, while the rest of 15 hybrids showed positive economic heterosis for plant height. Significant negative economic heterosis was recorded among the F_1 hybrids i.e., Galaxy-13 × Yr-5 (-17.18%), TD-1 × Yr-10 (-15.46%), Inqalab-91 × Parula (-14.43%), Seher-06 × Yr-10 (-13.06), Inqalab-91 × Yr-10 (-5.84%), and Inqalab-91 × Yr-5 (-4.81%). Negative heterosis is favorable because dwarfness is required to avoid lodging and obtain enhanced and stable wheat production. Past studies revealed that two F_1 hybrids (IBWSN 1036 × RSP81 and RGP7 × PBW175) out of forty cross combinations, revealed desirable negative heterosis over economic parent for plant height and other morphological traits in wheat (Chaudhary *et al*., 2018**)**. Other researchers also reported that wheat hybrids Sarsabz × Kiran-95, TD-1 × NIA-Sarang, TJ-83 × TD-1, TJ-83 × Sarsabz, and TJ83 × NIA-Sarang showed significant negative mid- and better-parent heterosis for plant height and earliness traits in wheat (Panhwar *et al*., 2022).

For plant height, positive inbreeding depression ranged from 0.33% (Seher-06 × Yr-5) to 26.36 (Galaxy-13 × Parula) while negative values varied from -31.95% (Galaxy-13 × Yr-5) to -1.58% (Seher-06 × Yr-10) (Table 2). Positive and negative inbreeding depression values were presented by twelve and eight F_2 populations, respectively. Significant ($p\leq0.01$) positive inbreeding depression was displayed by eight F_2 populations ranging from 4.33% (Inqalab-91 × Yr-5) to 26.36% (Galaxy-13 × Parula). However, significant ($p\leq0.01$) negative inbreeding depression values were noted in F_2 populations Galaxy-13 × Yr-5 (-31.95%), TD-1 × Yr-10 (-22.36%), Inqalab-91 × Yr-10 (-11.68%), PS-85 × Yr-5 (-7.85%), and TD-1 × Parula (-7.62%) for plant height. The F_2 population Seher-06 × Parula (0.00%) showed no inbreeding depression for the said trait. Overall, the F_2 populations i.e., PS-85 × Parula, TD-1 × Yr-5, Inqalab-91 × Yr-5, Ghaznavi-98 × Yr-10, Galaxy-13 × Parula, Galaxy-13 × Yr-10, Shahkar-13 × Parula and Shahkar-13 × Yr-5 were found promising based on their significant positive inbreeding depression values for plant height. The fixation of favorable dominant genes in one homozygous line is impossible due to linkage between some unfavorable recessive and favorable dominant genes while inbreeding depression results are due to fixation of unfavorable recessive genes in F_2 populations of wheat (Kumar *et al*., 2018b, 2021).

Tillers per plant: For tillers per plant, in parental lines, testers, and their F_1 and F_2 populations the mean values ranged from 11.17 (Seher-06) to 26.50 (Yr-5) (Table 3). Overall, the maximum tillers were obtained by testers (21.34), followed by F_2 populations (17.71), F_1 hybrids (17.30), and lines (16.11). Maximum tillers per plant were recorded for tester Yr-5 (26.50), followed by F_2 populations PS-85 × Yr-5 (25.40), Seher-06 × Yr-10 (23.27), Inqalab-91 × Yr-10 (21.47), F_1 hybrid Inqalab-91 × Yr-5 (22.97), Galaxy-13 × Yr-10 (21.03) and Inqalab-91 × Yr-10 (20.67). The parental line Seher-06 exhibited minimum tillers per plant (11.17), followed by 27 other genotypes varied from 12.47 (Seher-06 × Yr-50 in F_1 hybrids) to 17.00 (PS-85). All other F_1 hybrids, F_2 populations, parental lines, and testers revealed medium values for tillers per plant. In cereal crops, two types of tillers are found i.e., productive and non-productive tillers; the first one led to the formation of spikes and thus is most important for the grain yield. The non-productive tillers consume the plant's resources but do not produce yield (Fioreze *et al*., 2020; Koprna, 2021). In wheat genotypes, the increased tillers production was associated with improved grain yield (Duggan *et al*., 2005b). Several tiller-promoting genes and tiller inhibition genes have been recognized in wheat. The introgression of the Tin1 gene into current wheat germplasm may offer chances to increase grain m^{-2}, grains per spike, grain yield, and harvest index in wheat (Sadras & Rebetzke, 2013).

For tillers per plant, positive mid-parent heterosis ranged from 4.92% (Seher-06 × Parula) to 26.45% (Seher-06 × Yr-10), while negative heterotic values were ranging from -34.90 (Ghaznavi-98 × Yr-5) -9.06% (Ghaznavi-98 × Yr-10) (Table 3). Eight F_1 hybrids showed positive heterotic values, while the rest of the 13 hybrids showed negative mid-parent heterosis for tillers per plant. Significant positive mid-parent heterosis was recorded in F_1 hybrids Seher-06 × Yr-10 (26.45%), Galaxy-13 × Yr-10 (23.48%), and Inqalab-91 × Yr-10 (23.02%). In the case of better parents, the positive heterotic effects ranged from 2.01% (Seher-06 × Yr-10) to 15.57% (Galaxy-13 × Yr-10), while the negative values were ranging from -52.96% (Seher-06 × Yr-5) to -10.90 % (Ghaznavi-98 × Yr-10) in F_1 hybrids for tiller plant. Six out of 21 F_1 hybrids showed positive values for better parent heterosis while the rest revealed negative heterotic effects. Significant positive heterobeltiosis was obtained by only one hybrid Galaxy-13 × Yr-10 (15.57%), while significant negative better parent heterosis was recorded for fourteen hybrids ranging from -52.96% (Seher-06 × Yr-5) to -13.33% (Inqalab-91 × Yr-5). For tillers per plant, the positive economic heterosis ranged from 14.46% (Ghaznavi-98 × Yr-5) to 77.62% (Inqalab-91 × Yr-5), while negative economic heterosis was shown by only one hybrid Seher-06 × Yr-5 (-3.58%). The 20 F_1 hybrids showed positive heterotic values, while the leftover hybrid exhibited negative economic heterosis for tillers per plant. Significant positive economic heterosis was recorded in 20 F_1 hybrids ranging from 14.46% (Ghaznavi-98 × Yr-5) to 77.62% (Inqalab-91 × Yr-5). Previous studies revealed that hybrid Raj 4037 × HD 2987 was considered best for having economic heterosis for tillers per plant and yield-related traits in wheat (Sharma *et al*., 2018; Sharma & Kamaluddin, 2020). Other findings showed that maximum and positive mid- and better parent heterosis was recorded among F_1 hybrids for tillers per plant and yield-associated traits in wheat (Almutairi, 2022).

For tillers per plant, the negative inbreeding depression ranged from -60.49% (PS-85 × Yr-5) to -0.78% (TD-1 × Yr-10), while positive values varied from 4.17% (Inqalab-91 × Parula) to 19.59% (Inqalab-91 × Yr-5), among the F_2 populations (Table 3). Negative and positive inbreeding depression values were recorded for thirteen and eight F_2 populations, respectively. Significant ($p\leq0.01$) negative inbreeding depression was recorded for 13 F_2 populations varied from -60.49% (PS-85 × Yr-5) to -0.78% (TD-1 × Yr-10). However, significant ($p\leq0.01$) positive inbreeding depression was owned by eight F_2 populations ranging from 4.17% (Inqalab-91 × Parula) to 19.59% (Inqalab-91 × Yr-5). Overall, the F_2 populations viz., Seher-06 × Yr-5, Seher-06 × Yr-10, PS-85 × Parula, PS-85 × Yr-5, PS-85 × Yr-10, TD-1 × Parula, TD-1 × Yr-5, TD-1 × Yr-10, Inqalab-91 × Yr-10, Ghaznavi-98 × Parula, Ghaznavi-98 × Yr-5, Galaxy-13 × Parula and Shahkar-13 × Yr-5 were recorded as the best combinations based on their significant negative inbreeding depression values for tillers per plant. Past studies depicted that inbreeding depression in F_2 progenies expressed the least values for various traits including tillers per plant, spike length, spikelets spike per spike, grains per spike, and grain yield in wheat (Baloch *et al*., 2015; Gandahi *et al*., 2019).

Table 3. Mean performance of F_1 and F_2 populations, and heterosis in F_1s and inbreeding depression in F_2s for tillers per plant through line by tester analysis.

Parental genotypes, F_1 and F_2 populations	Tillers plant^{-1}		Heterosis in F_1 and inbreeding depression in F_2 populations for tillers plant^{-1}			
Lines						
Seher-06	11.17					
Pirsabak-85	17.00					
TD-1	18.27					
Inqalab-91	15.40					
Ghaznavi-98	18.97					
Galaxy-13	15.87					
Shahkar-13	16.13					
Means	16.11					
Testers						
Parula	19.33					
YR-5	26.50					
RY-10	18.20					
Means	21.34					
Populations	**F_1s**	**F_2s**	**MPH (%)**	**BPH (%)**	**CH (%)**	**ID (%)**
Seher-06 × Parula	16.00	13.03	4.92	-17.24*	23.74**	18.54**
Seher-06 × Yr-5	12.47	13.20	-33.81**	-52.96**	-3.58*	-5.88**
Seher-06 × Yr-10	18.57	23.27	26.45**	2.01	43.59**	-25.31**
PS-85 × Parula	15.78	16.40	-13.12	-7.16	22.07**	-3.91**
PS-85 × Yr-5	15.83	25.40	-27.23**	-40.28**	22.40**	-60.49**
PS-85 × Yr-10	15.47	16.42	-12.08	-8.98	19.67**	-6.10**
TD-1 × Parula	15.70	17.40	-16.49*	-18.79	21.42**	-10.83**
TD-1 × Yr-5	16.97	17.40	-24.20**	-35.97**	31.22**	-2.55**
TD-1 × Yr-10	15.33	15.45	-15.90*	-15.75*	18.59**	-0.78**
Inqalab-91 × Parula	20.00	19.17	15.16	3.45	54.68**	4.17**
Inqalab-91 × Yr-5	22.97	18.47	9.63	-13.33**	77.62**	19.59**
Inqalab-91 × Yr-10	20.67	21.47	23.02**	13.55	59.84**	-3.87**
Ghaznavi-98 × Parula	15.60	19.33	-18.54*	-17.75**	20.65**	-23.93**
Ghaznavi-98 × Yr-5	14.80	16.23	-34.90**	-44.15**	14.46**	-9.68**
Ghaznavi-98 × Yr-10	16.90	14.40	-9.06	-10.90	30.70**	14.79**
Galaxy-13 × Parula	15.03	16.30	-14.58	-5.25	16.27**	-8.43**
Galaxy-13 × Yr-5	18.83	16.13	-11.09	-28.93**	45.66**	14.34**
Galaxy-13 × Yr-10	21.03	19.73	23.48**	32.56**	62.67**	6.18**
Shahkar-13 × Parula	20.13	18.37	13.53	24.79**	55.71**	8.77**
Shahkar-13 × Yr-5	17.00	18.23	-20.25**	5.37	31.48**	-7.25**
Shahkar-13 × Yr-10	18.20	16.13	6.02	12.81	40.76**	11.36**
Means	17.30	17.71	--	--	--	--
Overall means	17.42	17.70	--	--	--	--
$LSD_{0.05}$	5.82	6.24	--	--	--	--

Flag leaf area: In parental lines, testers, and their F_1 and F_2 populations for flag leaf area, the mean values ranged from 38.92 (Seher-06 × Yr-5) to 56.57 cm^2 (Shahkar-13 × Parula) (Table 4). In overall mean performance, the F_1 hybrids obtained the highest flag leaf area (59.96 cm^2) compared to lines (50.02 cm^2), testers (47.68 cm^2), and F_2 populations (47.11 cm^2). Maximum flag leaf area was recorded in F_1 hybrid Shahkar-13 × Parula (56.57 cm^2), followed by 27 other genotypes ranging from 48.78 cm^2 (Shahkar-13) to 55.81 cm^2 (Ghaznavi-98 × Parula in F_1 hybrids). F_1 hybrid Seher-06 × Yr-5 showed the minimum flag leaf area (38.92 cm^2), followed by 16 other genotypes varied from 41.06 (PS-85 × Yr-5 in F_2 populations) to 47.13 cm^2 (TD-1 × Parula in F_2 populations). All other parental genotypes, F_1 and F_2 populations revealed medium values for flag leaf area. The flag leaf is the last leaf that arises before heading and is considered the chief source of carbohydrate deposition in grains. In wheat, the larger flag leaf area is desirable because of its important role in photosynthesis. The maximum flag leaf area had an increased amount of photosynthates, which eventually enhanced the grain yield. To increase the grain yield in wheat it is necessary to understand the genetic mechanism underlying flag leaf characteristics in wheat (Fan *et al*., 2015; Luo *et al*., 2018). In the present study, some parental lines exhibited larger flag leaf area but low yield which might be due to environmental effects and stripe rust because the parental lines were susceptible to yellow rust. The flag leaf area played a significant role in improving the grain yield of wheat, and F_1 and F_2 populations with maximum flag leaf area also showed increased grain yield in wheat (Ullah *et al*., 2021).

Table 4. Mean performance of F_1 and F_2 populations, and heterosis in F_1s and inbreeding depression in F_2s for flag leaf area through line by tester analysis.

Parental genotypes, F_1 and F_2 populations	Flag leaf area (cm^2)		Heterosis in F_1 and inbreeding depression in F_2 populations for flag leaf area			
Lines						
Seher-06	50.51					
Pirsabak-85	50.77					
TD-1	52.15					
Inqalab-91	45.17					
Ghaznavi-98	48.26					
Galaxy-13	54.50					
Shahkar-13	48.78					
Means	50.02					
Testers						
Parula	43.87					
YR-5	48.98					
RY-10	50.19					
Means	47.68					
Populations	**F_1s**	**F_2s**	**MPH (%)**	**BPH (%)**	**CH (%)**	**ID (%)**
Seher-06 × Parula	46.06	42.78	-2.39	5.00	0.70	7.13**
Seher-06 × Yr-5	38.92	42.75	-21.75**	-20.53**	-14.90**	-9.83**
Seher-06 × Yr-10	46.01	44.61	-8.62**	-8.32**	0.59	3.04**
PS-85 × Parula	42.69	46.07	-9.78**	-15.91**	-6.66**	-7.91**
PS-85 × Yr-5	47.74	41.07	-4.27	-2.52	4.38**	13.98**
PS-85 × Yr-10	48.16	44.17	-4.60	-5.15*	5.29**	8.29**
TD-1 × Parula	51.40	47.14	7.06*	17.17**	12.37**	8.29**
TD-1 × Yr-5	50.76	51.60	0.40	3.65	10.98**	-1.65**
TD-1 × Yr-10	51.89	49.46	1.41	3.39	13.45**	4.68**
Inqalab-91 × Parula	50.94	50.41	14.42**	16.12**	11.37**	1.03**
Inqalab-91 × Yr-5	52.05	47.46	10.57**	6.28*	13.80**	8.82**
Inqalab-91 × Yr-10	49.72	46.37	4.29	-0.92	8.71**	6.74**
Ghaznavi-98 × Parula	55.82	52.20	21.18**	15.67**	22.03**	6.49**
Ghaznavi-98 × Yr-5	50.51	48.00	3.89	3.12	10.42**	4.97**
Ghaznavi-98 × Yr-10	51.24	42.52	4.11	6.19*	12.03**	17.03**
Galaxy-13 × Parula	46.10	43.39	-6.27*	-15.42**	0.79	5.88**
Galaxy-13 × Yr-5	54.07	51.03	4.50	10.39**	18.20**	5.62**
Galaxy-13 × Yr-10	53.73	50.07	2.65	-1.42	17.47**	6.81**
Shahkar-13 × Parula	56.57	50.16	22.12**	15.97**	23.68**	11.33**
Shahkar-13 × Yr-5	52.68	50.52	7.78**	8.00**	15.18**	4.11**
Shahkar-13 × Yr-10	52.11	47.64	5.30	6.82*	13.92**	8.58**
Means	59.96	47.11	--	--	--	--
Overall means	49.75	47.83	--	--	--	--
LSD$_{0.05}$	7.04	9.37	--	--	--	--

For flag leaf area, positive mid parent heterosis ranged from 0.40% (TD-1 × Yr-5) to 22.12% (Shahkar-13 × Parula), while negative heterotic values were ranging from -21.75% (Seher-06 × Yr-5) to -2.39% (Seher-06 × Parula) (Table 4). Out of 21 F_1 hybrids, 14 hybrids showed positive heterotic values, while the rest of the seven hybrids showed negative mid-parent heterosis for the flag leaf area. Significant positive mid parent heterosis was recorded in F_1 hybrids Shahkar-13 × Parula (22.12%), Ghaznavi-98 × Parula (21.18%), Inqalab-91 × Parula (14.42%), Inqalab-91 × Yr-5 (10.71%), Shahkar-13 × Yr-5 (7.78%), and TD-1 × Parula (7.06 %). In F_1 hybrids, the better parent positive heterosis ranged from 2.10% (Ghaznavi-98 × Yr-10) to 15.97% (Shahkar-13 × Parula), while negative heterobeltiosis varied from -22.94% (Seher-06 × Yr-5) to -0.50% (TD-1 × Yr-10) for flag leaf area. Eight out of 21 F_1 hybrids showed positive values while the rest of the populations revealed negative heterotic effects. Significant positive better parent heterotic values were observed in F_1 hybrids Shahkar-13 × Parula (15.97%), Ghaznavi-98 × Parula (15.67%), Inqalab-91 × Parula (12.77%), Shahkar-13 × Yr-5 (7.56%), and Inqalab-91 × Yr-5 (6.28%). For flag leaf area in F_1 hybrids, the positive economic heterosis ranged from 0.59% (Seher-06 × Yr-10) to 23.68% (Shahkar-13 × Parula), while negative economic heterosis was achieved by only two hybrids i.e., PS-85 × Parula and Seher-06 × Yr-5 with values -6.66% and -14.90%, respectively. Out of 21 F_1 hybrids, 19 hybrids showed positive heterotic values, while the leftover two hybrids revealed negative economic heterosis. Significant positive economic heterosis was observed for 16 hybrids ranging from 4.38% (PS-85 × Yr-5) to 23.68% (Shahkar-13 × Parula) for the flag leaf area. Past findings revealed that in the case of flag leaf area, the eleven crosses showed positive heterosis and hybrid MH-97 × 4072 exhibited significant heterobeltiosis for flag leaf area whereas the rest of the hybrids displayed a reduction in flag leaf area as compared to their mid-parents in wheat (Mahpara *et al*., 2017)**.** A larger flag leaf area means that more photosynthesis occurs in the leaf which contributes toward grain yield and other yield-related traits, and past findings showed that sufficient significant positive heterosis was recorded for flag leaf area in wheat F_1 populations (Kajla *et al*., 2020).

For the flag leaf area, the negative inbreeding depression values ranged from -9.83% (Seher-06 × Yr-5) to -1.65% (TD-1 × Yr-5), while positive varied from 1.03% (Inqalab-91 × Parula) to 17.03% (Ghaznavi-98 × Yr-10) (Table 4). Negative and positive inbreeding depression values were recorded in three and 18 F_2 populations, respectively for the flag leaf area. Significant ($p \leq 0.01$) negative inbreeding depression values were noted for Seher-06 × Yr-5 (-9.83%), PS-85 × Parula (-7.91%), and TD-1 × Yr-5 (-1.65%). However, significant ($p \leq 0.01$) positive inbreeding depression was recorded for 18 F_2 populations ranging from 1.03% (Inqalab-91 × Parula) to 17.03% (Ghaznavi-98 × Yr-10). Overall, the F_2 populations, Seher-06 × Yr-5, PS-85 × Parula, and TD-1 × Yr-5 were considered as best based on their significant negative inbreeding depression for flag leaf area. In F_2 populations, significant negative inbreeding depression values were recorded for yield-related traits and grain yield in wheat (Yadav *et al*., 2017; Zaazaa, 2017; Soomro *et al*., 2019). Significant negative and positive inbreeding depression values were observed among the F_2 populations for yield related traits in wheat (Hereford, 2014; Kumar *et al*., 2018b).

Grain yield per plant: For grain yield per plant, the mean values varied from 11.50 g (Galaxy-13) to 55.08 g (Galaxy-13 × Yr-10) in parental lines, testers, and their F_1 and F_2 populations (Table 5). Overall, the maximum grain yield per plant was exhibited by F_1 hybrids (30.23 g) as compared to tasters (28.14 g), $F00_2$ populations (26.39 g), and lines (22.83 g). The F_1 hybrid Galaxy-13 × Yr-10 showed maximum grain yield per plant (55.08), followed by F_1 hybrids Shahkar-13 × Parula (45.66 g) and Shahkar-13 × Yr-5 (45.41 g). However, the minimum grain yield per plant was revealed by line Galaxy-13 (11.50 g), followed by 21 other genotypes ranging from 12.60 g (Ghaznavi-98 × Parula in F_2) to 22.25 g (PS-85 × Yr-10 in F_1). In the leftover parental lines and testers, and their F_1, and F_2 populations, the medium values were recorded for grain yield per plant. Despite significant breeding, improvement in wheat yield has remained relatively low under marginal growing conditions. Therefore, there is a dire need to use genetically diverse germplasm, and combining yield-related agronomic and physiological traits in the development and cultivation of superior genotypes may enhance the grain yield in wheat (Chang *et al*., 2022). Source-sink interaction is considered one of the most important natural processes to enhance the grain yield in wheat, however, it needs genetic and environmental manipulation (Tshikunde *et al*., 2019). Increasing the carbon sources through accelerating water-soluble carbohydrate and net photosynthetic rates of flag leaf sheath and stem play an important role in wheat grain development and yield. The combination of carbon and nitrogen through the selection of high-quality wheat genotypes can help in the enhancement of wheat yield (Zhang *et al*., 2021; Zhang *et al*., 2022).

In F_1 hybrids for grain yield per plant, positive mid-parent heterosis ranged from 0.19% (Inqalab-91 × Yr-10) to 208.30% (Galaxy-13 × Yr-10), while negative heterosis was ranging from -43.61% (PS-85 × Yr-5) to -3.94% (Shahkar-13 × Yr-10) (Table 5). Eleven out of 21 F_1 hybrids showed positive heterotic effects, while the rest of the 10 hybrids showed negative mid-parent heterosis. Significant positive mid-parent heterosis was recorded in 10 hybrids, ranging from 17.37% (Seher-06 × Parula) to 208.30% (Galaxy-13 × Yr-10). In the case of better parents, in F_1 hybrids the positive heterosis varied from 0.51% (Seher-06 × Parula) to 127.35 % (Galaxy-13 × Yr-10), while negative heterotic effects ranged from -44.83% (PS-85 × Yr-5) to -11.62% to (Inqalab-91 × Yr-10) for grain yield per plant. Ten out of 21 F_1 hybrids showed positive values for better parent heterosis while the rest revealed negative heterotic values. Significant positive better parent heterosis was recorded in F_1 hybrids i.e., Galaxy-13 × Yr-10 (127.35 %), Ghaznavi-98 × Yr-10 (74.37%), Galaxy-13 × Parula (41.34%), TD-1 × Parula (37.42%), Galaxy-13 × Yr-5 (35.68%), Seher-06 × Yr-10 (10.73%), and Shahkar-13 × Parula (6.00). For grain yield per plant, the positive economic heterosis varied from 1.58% (Shahkar-13 × Yr-10) to 73.05% (Galaxy-13 × Yr-10), while economic negative heterotic effects were ranging from -46.56% (PS-85 × Yr-5) to -7.32% (Seher-06 × Parula). Nine out of 21 F_1 hybrids showed positive heterotic values, while the remaining 12 hybrids revealed negative economic heterosis. Significant positive economic heterosis was recorded for eight hybrids, ranging from 4.20% (Ghaznavi-98 × Yr-5) to 73.05% (Galaxy-13 × Yr-10). Past findings revealed that grain yield per plant is the final output of the plant and relatively it is reflected by significant positive heterosis. Maximum heterosis over better parent was 37.32%, and similarly, maximum heterosis over mid parent was 40.69% in wheat F_1 populations (Kumar *et al*., 2021). Other studies also showed that the average mid-parent heterosis was positive among the majority of the F_1 hybrids for grain yield, while in the case of better parent heterosis, positive values were determined by half of the F_1 populations for grain yield and its associated traits in wheat (Schwarzwalder *et al*., 2022).

For grain yield per plant, the values of negative inbreeding depression ranged from -88.61% (PS-85 × Yr-5) to -1.79% (Galaxy-13 × Yr-5), while positive values varied from 1.18% (Seher-06 × Yr-10) to 48.72% (Shahkar-13 × Parula) (Table 5). Negative and positive inbreeding depression values were noted for nine and 12 F_2 populations, respectively for grain yield per plant. Significant ($p \leq 0.01$) negative inbreeding depression was recorded for five F_2 populations varied between -88.61% (PS-85 × Yr-5) to -8.76% (Shahkar-13 × Yr-10). However, significant ($p \leq 0.01$) positive inbreeding depression values were noted for 14 F_2 populations ranging from 6.82% (TD-1 × Parula) to 48.72% (Shahkar-13 × Parula). Overall, the eight F_2 populations, which showed significant negative inbreeding depression, were known as best performing genotypes for grain yield per plant. In breeding, a decline in yield and growth traits is called inbreeding depression which mostly occurs in F_2 populations after segregation, and past studies also exhibited significant positive and negative inbreeding depression for yield and yield-related traits in wheat (Kumar *et al*., 2017b, d, 2018a; Choudhary *et al*., 2018). For preservation in a specific gene pool of bread wheat, the best segregating material may be further exploited for improving yield attributes and grain yield as well as the production of promising transgressive segregants through selection in advanced generations.

Table 5. Mean performance of F_1 and F_2 populations, and heterosis in F_1s and inbreeding depression in F_2s for grain yield plant^{-1} through line by tester analysis.

Parental genotypes, F_1 and F_2 populations	Grain yield plant^{-1} (g)		Heterosis in F_1 and inbreeding depression in F_2 populations for grain yield plant^{-1}			
Lines						
Seher-06	20.92					
Pirsabak-85	29.50					
TD-1	19.08					
Inqalab-91	18.52					
Ghaznavi-98	17.20					
Galaxy-13	11.50					
Shahkar-13	43.08					
Means	22.83					
Testers						
Parula	29.35					
YR-5	30.83					
RY-10	24.23					
Means	28.14					
Populations	**F_1s**	**F_2s**	**MPH (%)**	**BPH (%)**	**CH (%)**	**ID (%)**
Seher-06 × Parula	29.50	23.33	17.37**	0.51	-7.32**	20.90**
Seher-06 × Yr-5	20.83	17.25	-19.48**	-32.43**	-34.55**	17.20**
Seher-06 × Yr-10	26.83	26.52	18.86**	10.73*	-15.70**	1.18
PS-85 × Parula	21.67	14.27	-26.37**	-26.55**	-31.93**	34.15**
PS-85 × Yr-5	17.01	32.08	-43.61**	-44.83**	-46.56**	-88.61**
PS-85 × Yr-10	22.25	16.08	-17.18**	-24.58**	-30.10**	27.72**
TD-1 × Parula	40.33	37.58	66.55**	37.42**	26.71**	6.82**
TD-1 × Yr-5	19.58	12.67	-21.54**	-36.49**	-38.48**	35.32**
TD-1 × Yr-10	18.08	24.25	-16.51*	-25.38**	-43.19**	-34.10**
Inqalab-91 × Parula	20.83	12.65	-12.95*	-29.02**	-34.55**	39.28**
Inqalab-91 × Yr-5	17.25	22.17	-30.09**	-44.05**	-45.81**	-28.50**
Inqalab-91 × Yr-10	21.42	33.17	0.19	-11.62*	-32.72**	-54.86**
Ghaznavi-98 × Parula	22.08	12.60	-5.12	28.39**	-30.62**	42.94**
Ghaznavi-98 × Yr-5	33.17	23.75	38.10**	7.57	4.20**	28.39**
Ghaznavi-98 × Yr-10	42.25	33.00	103.94**	74.37**	32.74**	21.89**
Galaxy-13 × Parula	41.48	30.08	103.10**	41.34**	30.33**	27.48**
Galaxy-13 × Yr-5	41.83	42.58	97.64**	35.68**	31.43**	-1.79
Galaxy-13 × Yr-10	55.08	41.97	208.30**	127.34**	73.05**	23.81**
Shahkar-13 × Parula	45.67	23.42	26.09**	6.00*	43.47**	48.72**
Shahkar-13 × Yr-5	45.42	39.67	22.89**	5.42	42.69**	12.66**
Shahkar-13 × Yr-10	32.33	35.17	-3.94**	-24.95**	1.58	-8.76**
Means	30.23	26.39	--	--	--	--
Overall means	28.36	25.76	--	--	--	--
$LSD_{0.05}$	10.71	11.70	--	--	--	--

Table 6. Mean performance of F_1 and F_2 populations, and heterosis in F_1s and inbreeding depression in F_2s for harvest index through line by tester analysis.

Parental genotypes, F_1 and F_2 populations	Harvest index (%)		Heterosis in F_1 and inbreeding depression in F_2 populations for harvest index			
Lines						
Seher-06	37.77					
Pirsabak-85	38.47					
TD-1	34.57					
Inqalab-91	32.35					
Ghaznavi-98	30.77					
Galaxy-13	22.22					
Shahkar-13	43.33					
Means	34.21					
Testers						
Parula	34.40					
YR-5	39.93					
RY-10	35.47					
Means	37.08					
Populations	**F_1s**	**F_2s**	**MPH (%)**	**BPH (%)**	**CH (%)**	**ID (%)**
Seher-06 × Parula	41.00	40.67	11.41**	14.42**	-5.94**	0.81
Seher-06 × Yr-5	34.33	33.40	-11.63**	-14.02**	-21.24**	2.72**
Seher-06 × Yr-10	54.64	37.03	49.22**	54.06**	25.35**	32.22**
PS-85 × Parula	36.93	36.33	-0.58	-3.99	-15.27**	1.62*
PS-85 × Yr-5	28.43	40.93	-27.47**	-28.80**	-34.77**	-43.96**
PS-85 × Yr-10	29.93	28.00	-19.03**	-22.18**	-31.33**	6.46**
TD-1 × Parula	42.70	41.33	21.31**	19.16**	-2.04	3.20**
TD-1 × Yr-5	34.57	30.30	-7.20	-13.44**	-20.70**	12.34**
TD-1 × Yr-10	31.13	35.57	-11.09**	-12.22**	-28.58**	-14.24**
Inqalab-91 × Parula	51.96	32.90	52.40**	45.00**	19.20**	36.68**
Inqalab-91 × Yr-5	35.17	33.20	-2.70	-11.94**	-19.32**	5.59**
Inqalab-91 × Yr-10	37.43	38.53	10.39*	5.55	-14.12**	-2.94**
Ghaznavi-98 × Parula	48.89	25.57	46.81**	58.90**	12.15**	47.70**
Ghaznavi-98 × Yr-5	39.90	39.23	12.87**	-0.08	-8.47**	1.67*
Ghaznavi-98 × Yr-10	48.40	41.80	46.15**	57.31**	11.03**	13.64**
Galaxy-13 × Parula	46.87	41.10	61.45**	110.89**	7.52**	12.30**
Galaxy-13 × Yr-5	46.63	41.03	50.05**	16.78**	6.98**	12.01**
Galaxy-13 × Yr-10	52.03	41.57	80.39**	134.14**	19.37**	20.12**
Shahkar-13 × Parula	42.23	36.40	6.69	-2.54	-3.11*	13.81**
Shahkar-13 × Yr-5	46.53	44.83	11.77**	7.38*	6.75**	3.65**
Shahkar-13 × Yr-10	46.50	43.83	18.02**	7.31*	6.68**	5.73**
Means	41.72	37.31	--	--	--	--
Overall means	39.58	36.59	--	--	--	--
$LSD_{0.05}$	10.03	6.88	--	--	--	--

Harvest index: For harvest index per plant, mean values ranged from 22.22% (Galaxy-13) to 54.63% (Seher-06 × Yr-10) in parental lines, testers, and their F_1 and F_2 populations (Table 6). On average, the maximum harvest index was obtained by F_1 hybrids (41.72%), followed by F_2 populations (37.31%), testers (37.08%), and lines (34.21%). The highest harvest index was shown by F_1 hybrid Seher-06 × Yr-10 (54.63%), followed by six other F_1 hybrids i.e., Galaxy-13 × Yr-10 (52.03%), Inqalab-91 × Parula (51.95%), Ghaznavi-98 × Parula (48.88%), Ghaznavi-98 × Yr-10 (48.40%), Galaxy-13 × Parula (46.86%), and Galaxy-13 × Yr-5 (46.63%). However, the minimum harvest index was presented by parental line Galaxy-13 (22.22%), followed by three F_2 populations Ghaznavi-98 × Parula (25.56%), PS-85 × Yr-10 (28.00%), and TD-1 × Yr-5 (30.30%) and two F_1 hybrids viz., PS-85 × Yr-5 (28.43%) and PS-85 × Yr-10 (29.93%). However, medium values of the harvest index were recorded in the remaining parental lines and testers, and their F_1 and F_2 populations. Alteration in the period between the vegetative and reproductive growth stages of wheat crops directly affects the grain yield and the amount of dry matter. The greater the accumulation of nutrients when the period from planting to the flowering stage becomes greater, which later transfer to the seeds (final sink), leads to an increase in the harvest index at the expense of dry weight, thus increasing the economic yield in wheat (Fan *et al.*, 2017). Accelerating dry matter mobilization from vegetative organs and the contribution of pre-anthesis dry matter to grains was beneficial to wheat yield. During the grain filling period, the high net accumulation of dry matter and increase in grain number to form a larger sink increases the harvest index, thereby contributing to an increase in wheat grain yield (Duan *et al.*, 2018).

In F_1 hybrids for harvest index per plant, positive mid-parent heterosis ranged from 6.69% (Shahkar-13 × Parula) to 80.39% (Galaxy-13 × Yr-10), while negative heterosis was ranging from -27.47% (PS-85 × Yr-5) to -0.58% (PS-85 × Parula) (Table 6). Fourteen out of 21 F_1 hybrids showed positive heterotic values, while the rest of the seven hybrids showed negative mid-parent heterotic effects. Significant positive mid-parent heterotic values were recorded for 13 hybrids, ranging from 10.39% (Inqalab-91 × Yr-10) to 80.39% (Galaxy-13 × Yr-10). In the case of better parents in F_1 hybrids, the positive heterosis varied from 5.55% (Inqalab-91 × Yr-10) to 46.70% (Galaxy-13 × Yr-10), while negative better parent heterosis ranged from -28.80% (PS-85 × Yr-5) to -0.08% (Ghaznavi-98 × Yr-5). Twelve out of 21 F_1 hybrids showed positive values for better parent heterosis while the rest revealed negative heterotic values. Significant positive better parent heterosis was recorded for 11 hybrids, ranging from 7.31 % (Shahkar-13 × Yr-10) to 46.70 % (Galaxy-13 × Yr-10). The positive economic heterosis varied from 6.68% (Shahkar-13 × Yr-10) to 25.35% (Seher-06 × Yr-10), while negative economic heterosis ranged from -34.77% (PS-85 × Yr-5) to -2.04% (TD-1 × Parula) in F_1 hybrids for harvest index per plant. Nine out of 21 F_1 hybrids showed positive heterotic values, while the remaining 12 hybrids revealed negative economic heterosis. Significant positive economic heterosis was recorded in nine hybrids, ranging from 6.68% (Shahkar-13 × Yr-10) to 25.35% (Seher-06 × Yr-10). Regarding wheat, hybrid breeding is still under development while well established in many outcrossing species, some of the combinations were found significant positive over mid and better parent heterosis for harvest index and other yield-related traits in wheat (Gupta *et al*., 2019; Mohan *et al*., 2022). Eleven cross combinations exhibited significant positive heterosis over mid-parent while five crosses revealed significant positive heterosis over better parent for harvest index in F_1 populations of wheat (Joshi & Kumar, 2021).

For the harvest index, the negative inbreeding depression values varied from -43.96% (PS-85 × Yr-5) to -2.94% (Inqalab-91 × Yr-10) while positive values ranged between 0.81% (Seher-06 × Parula) to 47.70% (Ghaznai-98 × Parula) (Table 22). Negative and positive inbreeding depression values were noted for three and 18 F_2 populations, respectively for the harvest index. Significant ($p \leq 0.01$) negative inbreeding depression values were recorded for F_2 three populations varied from -43.96% (PS-85 × Yr-5) to -2.94% (Inqalab-91 × Yr-10). However, significant ($p \leq 0.01$, $p \leq 0.05$) positive inbreeding depression values were recorded for 17 F_2 populations ranging from 1.62% (PS-85 × Parula) to 47.70% (Ghaznai-98 × Parula). Overall, the three F_2 populations, which exhibited significant negative inbreeding depression, were considered as best for harvest index. Previous studies indicated significant positive and negative heterosis in F_1 and inbreeding depression among F_2 populations of wheat for different traits (Jaiswal *et al.,* 2018; Ibrahim *et al*., 2020).

Conclusion

Analysis of variance exhibited significant differences among the total genotypes, parental genotypes, lines, testers, crosses, and line by tester interactions for the majority of the traits in F_1 and F_2 generations. The F_1 hybrids Galaxy-13 × Yr-10, Shahkar-13 × Parula and Shahkar-13 × Yr-5 were recorded best in case of maximum grain yield per plant also showed the highest values for mid- and better-parent, and economic heterosis. In the case of inbreeding depression (Shahkar-13 × Parula) showed significant negative inbreeding depression for grain yield.

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