HETEROgenic 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, Pirsa bāk-85, Shahkar-13, Galaxy-13, Ghaznavi-98, TD-1, and Inqlab-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 $F_2$ 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 ($p<0.01$) 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 (Bhana 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 were 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 (Kalhor 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 F1 hybrids and transgressive segregates in F2 populations the present study was design with the following objectives a) determine the genetic potential of F1 and F2 populations, and b) heterotic effects in the F1 population while inbreeding depression in F2 populations of wheat.

Material and Methods

Breeding material and procedure: The breeding material consists of ten parental genotypes including seven lines viz., Seher-06, Pirshabak-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 F1 populations. However, for obtaining F2 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 F1 and 21 F2 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 F1 populations. However, inbreeding depression values were measured in F2 populations for various traits in wheat.

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

\[ \text{Midparentheterosis} \% = \frac{\text{F}_1 - \text{MP}}{\text{MP}} \times 100 \]

Heterobeltiosis: Better parent heterosis as coined by Fonseca (1965) was estimated in terms of the percent increase or decrease of the F1 hybrid over its better parent.

\[ \text{Heterobeltiosis} \% = \frac{\text{F}_1 - \text{BP}}{\text{BP}} \times 100 \]

Economic heterosis: Economic heterosis was calculated by comparison of F1 hybrids with existing commercial wheat cultivar Pirshabak-13 using the following formula.

\[ \text{Economic heterosis} \% = \frac{\text{F}_1 - \text{CV}}{\text{CV}} \times 100 \]

Heterotic values for the above three categories were further subjected to the "t" test to determine whether F1 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).

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

\[ t = \frac{F_1 - BP}{\frac{2}{r}(\text{EMS})} \]

Where

MP = Mid parental value of the particular F1 cross (P1+P2)/2
BP = Better parent value in the particular F1 cross
EMS = Error mean square

The "t" values for economic heterosis (EH) was calculated by the formula used by Falconer and Mackay (1996).
Inbreeding depression: The observed inbreeding depression in F₂ populations was calculated as a percent decrease in F₂ populations by comparing with F₁ 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≤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 F₁ generation (Table 1). Parents vs. crosses displayed significant (p≤0.01) differences for grain yield and harvest index. Testers showed significant (p≤0.01) differences in plant height and harvest index. Line × tester interactions indicated significant (p≤0.01) differences for almost all the parameters except tillers per plant and flag leaf area in the F₁ generation. In the F₂ generation, significant (p≤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≤0.01) differences in plant height and grain yield per plant in the F₂ generation.

Genetic variability, heterosis, and inbreeding depression

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>Plant height</th>
<th>Tillers plant⁻¹</th>
<th>Flag leaf area</th>
<th>Grain yield plant⁻¹</th>
<th>Harvest index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>F₁ generation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Replications</td>
<td>2</td>
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<td>11.98</td>
<td>182.18</td>
<td>5.22</td>
<td>96.24</td>
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<tr>
<td>Genotypes</td>
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<td>377.42**</td>
<td>26.90**</td>
<td>45.38**</td>
<td>364.44**</td>
<td>179.58**</td>
</tr>
<tr>
<td>Parents (P)</td>
<td>9</td>
<td>302.50**</td>
<td>45.52**</td>
<td>29.22NS</td>
<td>244.75**</td>
<td>100.89**</td>
</tr>
<tr>
<td>Parents vs. crosses</td>
<td>1</td>
<td>1.62NS</td>
<td>3.00NS</td>
<td>8.41NS</td>
<td>686.52**</td>
<td>899.68**</td>
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<tr>
<td>Crosses (C)</td>
<td>20</td>
<td>429.92**</td>
<td>19.71NS</td>
<td>54.50NS</td>
<td>402.20**</td>
<td>178.99**</td>
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<tr>
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<td>40.29**</td>
<td>119.41**</td>
<td>932.71**</td>
<td>309.65**</td>
</tr>
<tr>
<td>Testers (T)</td>
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<td>131.73**</td>
<td>8.33NS</td>
<td>4.03NS</td>
<td>89.15NS</td>
<td>237.64**</td>
</tr>
<tr>
<td>L × T</td>
<td>12</td>
<td>461.62**</td>
<td>11.32NS</td>
<td>30.46NS</td>
<td>189.13**</td>
<td>103.88**</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>0.39</td>
<td>12.70</td>
<td>18.60</td>
<td>43.04</td>
<td>27.08</td>
</tr>
<tr>
<td><strong>F₂ generation</strong></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
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<tr>
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<td>302.50**</td>
<td>45.52**</td>
<td>29.22NS</td>
<td>244.75**</td>
<td>100.89**</td>
</tr>
<tr>
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<td>0.02</td>
<td>98.65NS</td>
<td>78.98NS</td>
<td>102.13**</td>
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<tr>
<td>Crosses (C)</td>
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<td>27.79**</td>
<td>35.18NS</td>
<td>295.62**</td>
<td>81.25**</td>
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<tr>
<td>Lines (L)</td>
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<td>185.51**</td>
<td>15.68**</td>
<td>57.04NS</td>
<td>381.85**</td>
<td>76.70**</td>
</tr>
<tr>
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<td>7.94NS</td>
<td>348.07**</td>
<td>16.49NS</td>
</tr>
<tr>
<td>L × T</td>
<td>12</td>
<td>563.04**</td>
<td>37.56**</td>
<td>28.79NS</td>
<td>243.77**</td>
<td>94.32**</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>0.37</td>
<td>14.60</td>
<td>32.89</td>
<td>51.31</td>
<td>17.73</td>
</tr>
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</table>
Table 2. Mean performance of $F_1$ and $F_2$ populations, and heterosis in $F_3$ and inbreeding depression in $F_2$ populations for plant height through line by tester analysis.

<table>
<thead>
<tr>
<th>Testers</th>
<th>$F_1$</th>
<th>$F_2$</th>
<th>MPH (%)</th>
<th>BPH (%)</th>
<th>CH (%)</th>
<th>ID (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parula</td>
<td>92.33</td>
<td>101.00</td>
<td>99.78</td>
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<td></td>
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<tr>
<td>YR-5</td>
<td>106.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>FY-5</td>
<td>101.00</td>
<td></td>
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<tr>
<td>Means</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>102.38</td>
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<tr>
<td>Galaxies</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pirbak -85</td>
<td>109.33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TD-1</td>
<td>77.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inqalab -91</td>
<td>107.33</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Ghaznavi -98</td>
<td>109.67</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Galaxy -13</td>
<td>101.33</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Shahkar -13</td>
<td>106.33</td>
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<tr>
<td>Means</td>
<td>102.38</td>
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</table>

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) for plant height. For plant height, negative economic heterosis was ranging from -17.18% (Galaxy-13 × Yr-5) to -4.81% (Inqalab-91 × Yr-5), however, positive economic heterosis was ranging from 0.69% to 8.78% (Galaxy-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 × R8P81 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-Saran, TJ-83 × TD-1, TJ-83 × Sarsabz, and TJ83 × NIA-Saran showed significant negative mid- and better-parent heterosis for plant height and earliness traits in wheat (Panhwara 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 F₂ populations, respectively. Significant (p≤0.01) positive inbreeding depression was displayed by eight F₂ populations ranging from 4.33% (Inqalab-91 × Yr-5) to 26.36% (Galaxy-13 × Parula). However, significant (p≤0.01) negative inbreeding depression values were noted in F₂ 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 F₂ population Seher-06 × Parula (0.00%) showed no inbreeding depression for the said trait. Overall, the F₂ 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 F₂ populations of wheat (Kumar et al., 2018b, 2021).

**Tillers per plant**: For tillers per plant, in parental lines, testers, and their F₁ and F₂ 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 F₂ populations (17.71), F₁ hybrids (17.30), and lines (16.11). Maximum tillers per plant were recorded for tester Yr-5 (26.50), followed by F₂ populations PS-85 × Yr-5 (25.40), Seher-06 × Yr-10 (23.27), Inqalab-91 × Yr-10 (21.47), F₁ 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 F₂ hybrids) to 17.00 (PS-85). All other F₁ hybrids, F₂ 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 Tml gene into current wheat germplasm may offer chances to increase grain m²⁻¹, 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 F₁ 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 F₁ 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 F₁ hybrids for tiller plant. Six out of 21 F₁ 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 F₁ 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 F₁ 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 F₁ 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 F₂ populations (Table 3). Negative and positive inbreeding depression values were recorded for thirteen and eight F₂ populations, respectively. Significant (p≤0.01) negative inbreeding depression was recorded for 13 F₂ populations varied from -60.49% (PS-85 × Yr-5) to -0.78% (TD-1 × Yr-10). However, significant (p≤0.01) positive inbreeding depression was owned by eight F₂ populations ranging from 4.17% (Inqalab-91 × Parula) to 19.59% (Inqalab-91 × Yr-5). Overall, the F₂ 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 F₂ 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 F₁ and F₂ populations, and heterosis in F₁s and inbreeding depression in F₂s for tillers per plant through line by tester analysis.

<table>
<thead>
<tr>
<th>Parental genotypes, F₁ and F₂ populations</th>
<th>Tillers plant¹</th>
<th>Heterosis in F₁ and inbreeding depression in F₂ populations for tillers plant¹</th>
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<tbody>
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<td>Parsabak-85</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Inqalab-91</td>
<td>15.40</td>
<td></td>
</tr>
<tr>
<td>Ghaznavi-98</td>
<td>18.97</td>
<td></td>
</tr>
<tr>
<td>Galaxy-13</td>
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<td></td>
</tr>
<tr>
<td>Shahkar</td>
<td>16.13</td>
<td></td>
</tr>
<tr>
<td>Means</td>
<td>16.11</td>
<td></td>
</tr>
<tr>
<td><strong>Testers</strong></td>
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<td></td>
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<td>19.33</td>
<td></td>
</tr>
<tr>
<td>YR-5</td>
<td>26.50</td>
<td></td>
</tr>
<tr>
<td>RY-10</td>
<td>18.20</td>
<td></td>
</tr>
<tr>
<td>Means</td>
<td>21.34</td>
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<table>
<thead>
<tr>
<th>Populations</th>
<th>F₁S</th>
<th>F₂S</th>
<th>MPH (%)</th>
<th>BPH (%)</th>
<th>CH (%)</th>
<th>ID (%)</th>
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<td>13.03</td>
<td>4.92</td>
<td>-17.24 *</td>
<td>23.74 **</td>
<td>18.54 **</td>
</tr>
<tr>
<td>Seher-06 × Yr-5</td>
<td>12.47</td>
<td>13.20</td>
<td>-33.81 **</td>
<td>-52.96 **</td>
<td>-3.58</td>
<td>-5.88 **</td>
</tr>
<tr>
<td>Seher-06 × Yr-10</td>
<td>18.57</td>
<td>23.27</td>
<td>26.45 **</td>
<td>2.01</td>
<td>43.59 **</td>
<td>-25.31 **</td>
</tr>
<tr>
<td>PS-85 × Yr-5</td>
<td>15.83</td>
<td>25.40</td>
<td>-27.23 **</td>
<td>-40.28 **</td>
<td>22.40 **</td>
<td>-60.49 **</td>
</tr>
<tr>
<td>PS-85 × Yr-10</td>
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<td>16.42</td>
<td>-12.08</td>
<td>-8.98</td>
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<td>-6.10 **</td>
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<tr>
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<td>-18.79</td>
<td>21.42 **</td>
<td>-10.83 **</td>
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<tr>
<td>TD-1 × Yr-5</td>
<td>16.97</td>
<td>17.40</td>
<td>-24.20 **</td>
<td>-35.97 **</td>
<td>31.22 **</td>
<td>-2.55 **</td>
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<tr>
<td>TD-1 × Yr-10</td>
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<td>15.45</td>
<td>-15.90</td>
<td>-15.75 **</td>
<td>18.59 **</td>
<td>-0.78 **</td>
</tr>
<tr>
<td>Inqalab-91 × Parula</td>
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<td>19.17</td>
<td>15.16</td>
<td>3.45</td>
<td>54.68 **</td>
<td>4.17 **</td>
</tr>
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<td>Inqalab-91 × Yr-5</td>
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<td>18.47</td>
<td>9.63</td>
<td>-13.33 **</td>
<td>77.62 **</td>
<td>19.59 **</td>
</tr>
<tr>
<td>Inqalab-91 × Yr-10</td>
<td>20.67</td>
<td>21.47</td>
<td>23.02 **</td>
<td>13.55</td>
<td>59.84 **</td>
<td>-3.87 **</td>
</tr>
<tr>
<td>Ghaznavi-98 × Parula</td>
<td>15.60</td>
<td>19.33</td>
<td>-18.54</td>
<td>-17.75 **</td>
<td>20.65 **</td>
<td>-23.93 **</td>
</tr>
<tr>
<td>Ghaznavi-98 × Yr-5</td>
<td>14.80</td>
<td>16.23</td>
<td>-34.90 **</td>
<td>-44.15 **</td>
<td>14.46 **</td>
<td>-9.68 **</td>
</tr>
<tr>
<td>Ghaznavi-98 × Yr-10</td>
<td>16.90</td>
<td>14.40</td>
<td>-9.06</td>
<td>-10.90</td>
<td>30.70 **</td>
<td>14.79 **</td>
</tr>
<tr>
<td>Galaxy-13 × Parula</td>
<td>15.03</td>
<td>16.30</td>
<td>-14.58</td>
<td>-5.25</td>
<td>16.27 **</td>
<td>-8.43 **</td>
</tr>
<tr>
<td>Galaxy-13 × Yr-10</td>
<td>21.03</td>
<td>19.73</td>
<td>23.48 **</td>
<td>32.56 **</td>
<td>62.67 **</td>
<td>6.18 **</td>
</tr>
<tr>
<td>Shahkar-13 × Parula</td>
<td>20.13</td>
<td>18.37</td>
<td>13.53</td>
<td>24.79 **</td>
<td>55.71 **</td>
<td>8.77 **</td>
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<tr>
<td>Shahkar-13 × Yr-5</td>
<td>17.00</td>
<td>18.23</td>
<td>-20.25 **</td>
<td>5.37</td>
<td>31.48 **</td>
<td>-7.25 **</td>
</tr>
<tr>
<td>Shahkar-13 × Yr-10</td>
<td>18.20</td>
<td>16.13</td>
<td>6.02</td>
<td>12.81</td>
<td>40.76 **</td>
<td>11.36 **</td>
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<tr>
<td>Means</td>
<td>17.30</td>
<td>17.71</td>
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</tr>
<tr>
<td>Overall means</td>
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<td>17.70</td>
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<td>--</td>
</tr>
<tr>
<td>LSD₀.₀５</td>
<td>5.82</td>
<td>6.24</td>
<td>--</td>
<td>--</td>
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<td>--</td>
</tr>
</tbody>
</table>

Flag leaf area: In parental lines, testers, and their F₁ and F₂ populations for flag leaf area, the mean values ranged from 38.92 (Seher-06 × Yr-5) to 56.57 cm² (Shahkar-13 × Parula) (Table 4). In overall mean performance, the F₁ hybrids obtained the highest flag leaf area (59.96 cm²) compared to lines (50.02 cm²), testers (47.68 cm²), and F₂ populations (47.11 cm²). Maximum flag leaf area was recorded in F₁ hybrid Shahkar-13 × Parula (56.57 cm²), followed by 27 other genotypes ranging from 48.78 cm² (Shahkar-13) to 55.81 cm² (Ghaznavi-98 × Parula in F₁ hybrids). F₁ hybrid Seher-06 × Yr-5 showed the minimum flag leaf area (38.92 cm²), followed by 16 other genotypes varied from 41.06 (PS-85 × Yr-5 in F₂ populations) to 47.13 cm² (TD-1 × Parula in F₂ populations). All other parental genotypes, F₁ and F₂ 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 F₁ and F₂ populations with maximum flag leaf area also showed increased grain yield in wheat (Ullah et al., 2021).
Table 4. Mean performance of F<sub>1</sub> and F<sub>2</sub> populations, and heterosis in F<sub>1</sub> and inbreeding depression in F<sub>2</sub> for flag leaf area through line by tester analysis.

<table>
<thead>
<tr>
<th>Parental genotypes, F&lt;sub&gt;1&lt;/sub&gt; and F&lt;sub&gt;2&lt;/sub&gt; populations</th>
<th>Flag leaf area (cm&lt;sup&gt;2&lt;/sup&gt;)</th>
<th>Heterosis in F&lt;sub&gt;1&lt;/sub&gt; and inbreeding depression in F&lt;sub&gt;2&lt;/sub&gt; populations for flag leaf area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lines</strong></td>
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</tr>
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<td>Seher-06</td>
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</tr>
<tr>
<td>Parsak-85</td>
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<td>TD-1</td>
<td>52.15</td>
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<td>Inqalab-91</td>
<td>45.17</td>
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<td>Ghaznavi-98</td>
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<td>Galaxy-13</td>
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<td>Shahkar-13</td>
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<td></td>
</tr>
<tr>
<td>Means</td>
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<tr>
<td><strong>Testers</strong></td>
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<tr>
<td>Parula</td>
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</tr>
<tr>
<td>YR-5</td>
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<td>RY-10</td>
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</tr>
<tr>
<td>Means</td>
<td>47.68</td>
<td></td>
</tr>
<tr>
<td><strong>Populations</strong></td>
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<td>F&lt;sub&gt;2&lt;/sub&gt;</td>
</tr>
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<td>42.78</td>
</tr>
<tr>
<td>Seher-06 × Yr-5</td>
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<td>42.75</td>
</tr>
<tr>
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<td>44.61</td>
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<tr>
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<td>41.07</td>
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<td>PS-85 × Yr-10</td>
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</tr>
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<td>47.14</td>
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<td>TD-1 × Yr-5</td>
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<td>LSD&lt;sub&gt;0.05&lt;/sub&gt;</td>
<td>7.04</td>
<td>9.37</td>
</tr>
</tbody>
</table>

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<sub>1</sub> 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<sub>1</sub> 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<sub>1</sub> 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<sub>1</sub> hybrids showed positive values while the rest of the populations revealed negative heterotic effects. Significant positive better parent heterotic values were observed in F<sub>1</sub> 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<sub>1</sub> 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 F₁ 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 F₁ 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 F₂ populations, respectively for the flag leaf area. Significant (p≤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≤0.01) positive inbreeding depression was recorded for 18 F₂ populations ranging from 1.03% (Inqalab-91 × Parula) to 17.03% (Ghaznavi-98 × Yr-10). Overall, the F₂ 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 F₂ 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 F₂ 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 F₁ and F₂ populations (Table 5). Overall, the maximum grain yield per plant was exhibited by F₁ hybrids (30.23 g) as compared to testers (28.14 g), F₀00 populations (26.39 g), and lines (22.83 g). The F₁ hybrid Galaxy-13 × Yr-10 showed maximum grain yield per plant (55.08), followed by F₁ 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 F₂) to 22.25 g (PS-85 × Yr-10 in F₁). In the leftover parental lines and testers, their F₁, and F₂ 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 F₁ 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 F₁ 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 F₁ 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 F₁ hybrids showed positive values for better parent heterosis while the rest revealed negative heterotic values. Significant positive better parent heterosis was recorded in F₁ 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 F₁ 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 F₁ populations (Kumar et al., 2021). Other studies also showed that the average mid-parent heterosis was positive among the majority of the F₁ hybrids for grain yield, while in the case of better parent heterosis, positive values were determined by half of the F₁ 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 F2 populations, respectively for grain yield per plant. Significant ($p \leq 0.01$) negative inbreeding depression was recorded for five F2 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 F2 populations ranging from 6.82% (TD-1 × Parula) to 48.72% (Shahkar-13 × Parula). Overall, the eight F2 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 F2 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 F1 and F2 populations, and heterosis in F1s and inbreeding depression in F2s for grain yield plant$^{-1}$ through line by tester analysis.

<table>
<thead>
<tr>
<th>Lines</th>
<th>Parental genotypes, F1 and F2 populations</th>
<th>Heterosis in F1 and inbreeding depression in F2 populations for grain yield plant$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parental genotypes, F1 and F2 populations</td>
<td>Grain yield plant$^{-1}$ (g)</td>
<td>MPH (%)</td>
</tr>
<tr>
<td>----------------------------</td>
<td>--------------------------------------------</td>
<td>---------------------------------</td>
</tr>
<tr>
<td>Lines</td>
<td>Parental genotypes, F1 and F2 populations</td>
<td>Heterosis in F1 and inbreeding depression in F2 populations for grain yield plant$^{-1}$</td>
</tr>
<tr>
<td>Seher-06 × Parula</td>
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<td>PS-85 × Yr-10</td>
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<td>37.58</td>
</tr>
<tr>
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</tr>
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</tr>
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<td>Inqalab-91 × Yr-5</td>
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<td>22.17</td>
</tr>
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<td>Inqalab-91 × Yr-10</td>
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Table 6. Mean performance of F₁ and F₂ populations, and heterosis in Fₛ and inbreeding depression in F₂ for harvest index through line by tester analysis.

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<td>Shahkar</td>
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<tr>
<td>KY-10</td>
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<th>F₂</th>
<th>MPH (%)</th>
<th>BPH (%)</th>
<th>CH (%)</th>
<th>ID (%)</th>
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<td>40.67</td>
<td>11.41**</td>
<td>14.42**</td>
<td>-5.94**</td>
<td>0.81</td>
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<tr>
<td>Seher-06 × Yr-5</td>
<td>34.33</td>
<td>33.40</td>
<td>-11.63**</td>
<td>-14.02**</td>
<td>-21.24**</td>
<td>2.72**</td>
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<tr>
<td>Seher-06 × Yr-10</td>
<td>54.64</td>
<td>37.03</td>
<td>49.22**</td>
<td>54.06***</td>
<td>25.35**</td>
<td>32.22**</td>
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<td>PS-85 × Parula</td>
<td>36.93</td>
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<td>-14.57**</td>
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<td>PS-85 × Yr-5</td>
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<td>-43.96**</td>
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<td>TD-1 × Parula</td>
<td>42.70</td>
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<td>3.27**</td>
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<td>TD-1 × Yr-5</td>
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<td>-20.79**</td>
<td>12.34**</td>
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<td>Inqalab-91 × Yr-5</td>
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<td>-11.94**</td>
<td>-19.32**</td>
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<td>46.81**</td>
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<tr>
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<td>48.40</td>
<td>41.80</td>
<td>46.15**</td>
<td>57.31**</td>
<td>11.03**</td>
<td>13.64**</td>
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<tr>
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<td>46.87</td>
<td>41.10</td>
<td>61.45**</td>
<td>110.89**</td>
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<td>52.03</td>
<td>41.57</td>
<td>80.39**</td>
<td>134.14**</td>
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<td>20.12**</td>
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<td>Shahkar × Parula</td>
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<td>-3.11</td>
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<td>Shahkar × Yr-5</td>
<td>46.53</td>
<td>44.83</td>
<td>11.77**</td>
<td>7.38**</td>
<td>6.75**</td>
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<td>Shahkar × Yr-10</td>
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<td>43.83</td>
<td>18.02**</td>
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<tr>
<td>Means</td>
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<td>37.31</td>
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<tr>
<td>Overall means</td>
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<td>36.59</td>
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<tr>
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<td>10.03</td>
<td>6.88</td>
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</table>

**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 F₁ and F₂ populations (Table 6). On average, the maximum harvest index was obtained by F₁ hybrids (41.72%), followed by F₂ populations (37.31%), testers (37.08%), and lines (34.21%). The highest harvest index was shown by F₁ hybrid Seher-06 × Yr-10 (54.63%), followed by six other F₁ 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 F₂ populations Ghaznavi-98 × Parula (25.56%), PS-85 × Yr-10 (28.00%), and TD-1 × Yr-5 (30.30%) and two F₁ 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 F₁ and F₂ 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 F₁ 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 F₁ 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 F₁ 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 F₁ 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 F₁ hybrids for harvest index per plant. Nine out of 21 F₁ 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 F₁ 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% (Ghaznavi-98 × Parula) (Table 22). Negative and positive inbreeding depression values were noted for three and 18 F₂ populations, respectively for the harvest index. Significant (p<0.01) negative inbreeding depression values were recorded for F₂ three populations varied from -43.96% (PS-85 × Yr-5) to -2.94% (Inqalab-91 × Yr-10). However, significant (p<0.01, p<0.05) positive inbreeding depression values were recorded for 17 F₂ populations ranging from 1.62% (PS-85 × Parula) to 47.70% (Ghaznavi-98 × Parula). Overall, the three F₂ populations, which exhibited significant negative inbreeding depression, were considered as best for harvest index. Previous studies indicated significant positive and negative heterosis in F₁ and inbreeding depression among F₂ 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 F₁ and F₂ generations. The F₁ 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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HETEROTIC EFFECTS AND INBREEDING DEPRESSION IN WHEAT


(Received for publication 07 October 2022)