

Original Research

Insights into Non-Additive Type of Gene Action for Grain Yield and Yield-Related Traits in Wheat (*Triticum aestivum* L.) and its Breeding Implications

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Abstract

Line-by-tester combining ability analysis was carried out to investigate the heritable variations, GCA and SCA variances for lines (seven), testers (three), line \times tester F_2 populations (21), and inheritance of various morphological and yield traits in wheat. A randomized complete block design with three replications was utilized. Emasculation and pollen dusting was done manually. Analysis of variance revealed significant ($p \leq 0.01$) differences among all the studied parameters. Combining ability analysis discovered that lines had significant differences for the flag leaf area and 1000-grain weight. Testers were significant for 1000-grain weight and biological yield per plant. The ratio of variances due to GCA and SCA was smaller than unity, while the degree of dominance was greater than unity, which confirmed that all the traits were controlled by the non-additive gene effect. In proportional contribution, F_2 had the maximum share as compared to line and tester for five traits. For the flag leaf area, 1000-grain

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weight, the share of the parental line was leading as compared to testers and $L \times T$ interaction. Heritability ranged from 0.68 to 0.97. Genetic gain values ranged from 1.65 to 8.83 g. Non-additive gene actions indicated that the selection of promising populations in terms of morphological and yield traits should be delayed until later segregating generations. Based on present findings, promising populations could be used in future breeding programs to develop high-yielding wheat genotypes.

Keywords: *Triticum aestivum* L, gene action, general and specific combining ability, hybridization, F₂ populations

Introduction

Wheat (*Triticum aestivum* L.) is the main cereal crop of the world, followed by maize and rice, and is considered the 'King of the Cereal' because of its growing demand and evolution record [1, 2]. In Pakistan, it is ranked as the first cereal crop concerning its consumption, nutritional value, manufacturing, storage quality, variation, and world's food grain business [3]. During 2022-2023, in Pakistan, wheat was grown in an area of 9.040 million ha, which produced 28.18 million tons with an average grain yield of 2983 kg ha⁻¹. To cope with the food demand of the growing population of Pakistan, it is important to increase the per unit yield by developing new wheat genotypes with high-yielding ability and the best baking quality.

Combining ability analysis is a useful tool in the identification of the parental cultivars using general combining ability (GCA) and their potential recombinant (F₁ hybrids) by specific combining ability (SCA). In line by tester combining ability analysis, the parental lines and testers are crossed, and the promising and poor-performing general combiners and specific cross combinations can be sorted through SCA and GCA effects. General combining ability is defined as the average performance of genotypes in any cross combination; while specific combining ability indicates when the hybrids are better or poor performers based on their average performance in hybrid combinations. Thus, the SCA is essential for hybrid crop development, whereas the GCA is the identification of the best parent for hybridization [4]. Therefore, line \times tester combining ability analysis is an appropriate breeding approach for desirable parental genotypes and their F₁ hybrids.

Using hybridization for varietal development is considered laborious and time-consuming. Therefore, the use of combining ability analysis for cultivar development in wheat is regarded as an imperative technique. The significance of both SCA and GCA variances is indicative of additive and dominant gene actions. Positive GCA effects are more important for grain yield and yield-associated traits in wheat [5, 6].

Heritability serves as a measure of the transmissibility of genes from parents to their progenies and is therefore used as an important tool in plant breeding for the selection process [7]. There is a direct

relation between heritability and selection response; hence, the correlation between heritability and selection is regarded as genetic progress [8]. Similarly, the desired response to selection is also called genetic gain. High heritability and genetic gain are considered to be very effective for selection in breeding programs [9]. Phenotypic and genotypic coefficients of the variation, heritability, and genetic advance are used to know the level of variation in the wheat breeding material. Therefore, the wheat breeder needs to know the genetic variability and heritability of the imperative agronomic traits to increase yield effectively [10].

Grain yield is a complex polygenic trait; therefore, selection based on the genotypic performance of grain yield is not sufficient, as both physiological and morphological traits must be taken as the indirect selection criterion for yield improvement. The interrelationship of the traits and direct and indirect traits must be understood before launching a breeding program [11]. However, due to the polygenic control of the traits, these traits are influenced to a greater extent by the environment.

The correlation coefficient plays a significant role in the evaluation in terms of strength, direct and indirect effects on grain yield, and its contributing yield traits. Easily inheritable traits have high heritability and have a useful association with grain yield and therefore are regarded as useful tools in plant breeding. Therefore, grain yield was found to have a positive association with the plant height, spike length, and 1000-grain weight in diallel crosses [12]. Phenotypic and genotypic correlations of the plant height and 1000-grain weight were significantly positive with the grain yield in late and normal planting [13]. The present study was therefore carried out with the following objectives:

- Genetic potential of parental lines, testers, and their F₂ populations for various studied traits
- GCA and SCA effects for lines, testers, and $L \times T$ F₂ populations for various traits
- Best general and specific combiners, which could be used as a source material for further improvement in various traits of wheat
- Heritability and genetic gain for morphological and yield-related traits in wheat.

Experimental Methods

Experimental Site

The research work about the present study of the genetic potential and line \times tester combining ability in the parental and their F_2 populations in wheat was carried out at the National Agricultural Research Center, Islamabad, Pakistan.

Breeding Material and Procedure

The breeding material was procured from the Wheat Breeding Section, Cereal Crops Research Institute (CCRI), Pirsabak-Nowshera, Pakistan. The genetic material comprising of seven advanced wheat lines, i.e., 2768, 2769, 2785, 2805, 2806, 2835, and 2836 (obtained from IBWSN-International Bread Wheat Screening Nursery, CIMMYT-Mexico), was used as female parents, whereas three locally existing wheat cultivars (Pirsabak-2013, Shahkar-2013, and Punjab-2011) were considered as testers (Table 1). After advancing the generation, the seven lines and three testers' cultivars, along with 21 F_2 populations, were sown in a Randomized Complete Block Design (RCBD) with three replications at the University of Agriculture, Peshawar, Pakistan. Each entry was grown in four rows with four meters of length. Row-to-row and plant-to-plant distances were kept at 30 and 15 cm, respectively. All the agronomic practices and inputs, i.e., land preparation, hoeing, weeding, fertilizing, and irrigation, were adopted uniformly to reduce the experimental error. Weeds were controlled by spraying the post-broad and narrow-leaf herbicides manually. Data were recorded on 10 randomly chosen plants from each subplot for the following parameters.

The tillers were counted in selected plants in each genotype to get tillers per plant. The flag leaf area (cm^2) of the ten randomly chosen plants in every genotype/replication is determined using the following formula [14].

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

Ten spikes were taken from randomly selected plants in every subplot/replication and were hand-threshed to count grains per spike. 1000 grains (g) were taken randomly from each genotype in each replication and weighted by an electric balance to determine the 1000-grain weight in grams. The biological yield was recorded in grams by harvesting and drying the selected plants from every plot/replication. Grain yield per plant was recorded in grams after threshing plants from each genotype separately.

Statistical Analysis

Analysis of Variance

Earlier to line \times tester analysis, all recorded data was subject to the analysis of variances (ANOVA) to determine the differences between the genotypes for various traits (Steel et al., 1997). All the genotypic means for every parameter were separated and compared using the least significant differences (LSD) test at a 5% level of probability.

Line \times Tester Analysis

Line \times Tester analysis was conducted by following [15] to ascertain the variances suitable to the GCA and SCA for genotypes and gene action involved for various traits. In the current analysis, seven genotypes were used as female parents, of whom emasculation was done manually, whereas, three genotypes were kept as male parents, whose pollen grains were dusted onto the emasculated lines. On maturity, 21 cross combinations were harvested very carefully. The line \times tester combining ability analysis is considered the most reliable method in inheritance studies for understanding the genetic effect involved in the inheritance of any specific trait from parents to their offspring. The traits may either be controlled by additive or non-additive gene actions.

The combining ability effects of lines, testers, and hybrids were checked using the following formulas:

Estimations of GCA Effects:

a) Lines

$$G_l = \frac{(Xi...)}{tr} - \frac{(X...)}{ltr}$$

b) Testers

$$G_t = \frac{(Xj...)}{lr} - \frac{(X...)}{ltr}$$

Estimations of SCA Effects:

$$S_{ij} = \frac{(X_{ij})}{r} - \frac{(X_{i..})}{tr} - \frac{(X_{.j..})}{lr} + \frac{(X_{..})}{ltr}$$

The standard Error for Combining Ability Effects

a) Standard error (SE) for GCA effects of the line
 $= \sqrt{MSSE/rm}$

b) Standard error (SE) for GCA effects of the tester
 $= \sqrt{MSSE/rf}$

c) Standard error (SE) for the SCA effects
 $= \sqrt{MSSE/r}$

Gene action: Gene actions for various traits under evaluation were computed following Singh and Chaudhary (1985) [16].

The proportional contribution of line,
tester, and $L \times T$ interactions

$$\text{Lines} = \frac{ss(l) \times 100}{ss(\text{crosses})}$$

$$\text{Testers} = \frac{ss(t) \times 100}{ss(\text{crosses})}$$

$$L \times T \text{ Interaction} = \frac{ss(l \times t) \times 100}{ss(\text{crosses})}$$

Estimation of Genetic Parameter

Genotypic and phenotypic variance, genotypic (GCV) and phenotypic coefficient of variance (PCV), heritability, and genetic gain were computed using:

Genetic variance (V_g)

$$= \frac{\text{Genotypes mean squares (GMS)} - \text{Error mean squares (EMS)}}{\text{Number of replications (r)}}$$

Environmental variance (V_e) = Error mean squares (EMS)

Phenotypic variances (V_p) = $V_g + V_e$

Table 1. Pedigree of parental lines and testers used in line \times tester mating designs.

S. No.	Line / Tester code	Source / Institute	Parentage
Lines			
1	2768	IBWSN entry-11 (2013-14) (CIMMYT - Mexico)	ALTAR 84/AE.SUARROSA (221)/3*BORL95/3/ URES/JUN//KAUZ/4/WBLL1/5/MUTUS
2	2769	IBWSN entry- 13 (2013-14) (CIMMYT - Mexico)	CHIBIA//PRLII/CM65531/3/SKAUZ/BAV92/4/ MUNAL #1
3	2785	IBWSN entry- 223 (2013-14) (CIMMYT - Mexico)	BECARD#1/5/KIRITATI/4/2*SERI.1B*2/3/KAUZ*2/ BOW//KAUZ
4	2805	PR-105 (CCRI, Pirsabak -Nowshera)	MILAN/S87230//BABAX
5	2806	PR-108 (CCRI, Pirsabak -Nowshera)	WHEAR/KRONSTAD F 2004
6	2835	PR-114 (CCRI, Pirsabak -Nowshera)	WHEAR/ KRONSTAD F2004
7	2836	NR-390 (NARC - Islamabad)	KIRITATI/4/2*SERI.1B*2/3/KAUZ*2/BOW//KAUZ
Testers			
8	Pirsabak-2013	CCRI, Pirsabak – Nowshera	CS/TH.SC//3*PVN/3/MIRLO/BUC/4/MILAN /5/ TILHI
9	Shahkar-2013	CCRI, Pirsabak – Nowshera	CMH84.3379/CMH78.578//MILAN
10	Punjab-2011	AARI – Faisalabad	AMSEL/ATTILA \times INQ.91/ PEWS
Line \times Tester - F_2 Populations			
	L \times T F_2 Populations	S. No.	L \times T F_2 Populations
11	2768 \times Pirsabak-2013	22	2805 \times Punjab-11
12	2768 \times Shahkar-2013	23	2806 \times Pirsabak-2013
13	2768 \times Punjab-11	24	2806 \times Shahkar-2013
14	2769 \times Pirsabak-2013	25	2806 \times Punjab-11
15	2769 \times Shahkar-2013	26	2835 \times Pirsabak-2013
16	2769 \times Punjab-11	27	2835 \times Shahkar-2013
17	2785 \times Pirsabak-2013	28	2835 \times Punjab-11
18	2785 \times Shahkar-2013	29	2836 \times Pirsabak-2013
19	2785 \times Punjab-11	30	2836 \times Shahkar-2013
20	2805 \times Pirsabak-2013	31	2836 \times Punjab-11
21	2805 \times Shahkar-2013	-	-

IBWSN: International Bread Wheat Screening Nursery; CIMMYT: International Maize and Wheat Improvement Center; CCRI: Cereal Crops Research Institute; NARC: National Agriculture Research Center; AARI: Ayub Agricultural Research Institute.

Heritability (h^2) on entry means base calculated as:

$$h^2 = \frac{V_g}{V_p}$$

The expected response to the selection (Re) for every trait was calculated:

Where:

k = 20% selection intensity of the trait.

V_p = Phenotypic variances of traits.

h^2 = Broad sense heritability of traits.

Genotypic coefficient of the variations $GCV = \sqrt{V_g}/GM \times 100$

Phenotypic coefficient of the variations $PCV = \sqrt{V_p}/GM \times 100$

Where:

V_g = Genotypic variances

V_p = Phenotypic variances

GM = Grand mean of the traits

Mean Performance of Lines, Testers, and $L \times T$ F_2 Populations

Tillers per Plant

Tillers per plant among lines varied from 11.80 (line 2806) to 16.83 (line 2768); among testers, the tillers per plant ranged from 13.00 (Pirsabak-2013, Shahkar-13) to 15.4 (Punjab-2011), whereas in their F_2 populations, they varied from 11.6 (2835 \times Pirsabak-2013) to 16.1 (2768 \times Punjab-11) (Table 3). On the whole, the highest tillers per plant were recorded for line 2768 (16.8), followed by another line 2785 (16.2) and F_2 population 2765 \times Punjab-11. However, minimum tillers per plant were observed in F_2 population 2835 \times Pirsabak-13 followed by line 2806 (11.80), and F_2 population 2805 \times Shahkar-13 (12.4). The remaining genotypes including testers, lines, and F_2 populations showed average tillers per plant.

Flag Leaf Area

Flag leaf area ranged from 31.7 (line 2768) to 36.1 cm^2 (line 2769) among lines; testers ranged from 32.9 (Punjab-11) to 36.1 cm^2 (Shahkar-13) while their F_2 populations varied from 31.0 (2769 \times Punjab-11) to 36.3 cm^2 (2805 \times Pirsabak-13) (Table 3). On the whole, the increased flag leaf area was recorded for F_2 population 2805 \times Pirsabak-13 (36.3 cm^2), followed by one F_2 population, i.e., 2769 \times Shahkar-13, line 2768 (36.1 cm^2), and two testers, Punjab-11 (36.1 cm^2) and Pirsabak-13 (35.9 cm^2). Minimum flag leaf areas were found in the F_2 population 2769 \times Punjab-11 (31.0 cm^2), followed by the F_2 population 2768 \times Punjab-11 (31.5 cm^2) and line 2768 (31.7 cm^2). However, other lines, testers, and F_2 populations showed average flag leaf area.

Results

Analysis of Variance

Analysis of the variance showed significant ($p \leq 0.01$) differences among the wheat parental lines, testers, and F_1 populations for all the studied traits (Table 2). Hence the overall genetic variability was further partitioned into its components, i.e., combining ability (GCA and SCA) effects through line-by-tester analysis. Ahmad et al. (2017) conducted a study to estimate GCA, SCA, and heritability of wheat yield and yielding attributes parameters through $L \times T$ combining ability and observed significant differences among the genotypes of all the studied parameters [17].

Table 2. Mean squares for various traits in lines, testers, and F_2 populations were studied through line \times tester combining ability in the wheat.

SOV	DF	Flag leaf area	Tillers plant ⁻¹	Grains spike ⁻¹	1000-grain weight	Biological yield plant ⁻¹	Grain yield plant ⁻¹
Replications	2	0.21	0.44	1.44	0.49	69.49	0.53
Genotypes	30	7.20**	4.79**	87.28	86.66**	162.42**	23.77**
Parents	9	6.89**	7.82**	78.33	65.08**	147.07**	18.45**
Crosses	20	8.69**	2.92**	65.08	65.12**	173.59**	27.15**
Lines	6	15.22*	2.73 ^{NS}	67.41	108.29**	223.15 ^{NS}	20.46 ^{NS}
Testers	2	9.21 ^{NS}	4.91 ^{NS}	60.11	115.67*	368.60*	22.42 ^{NS}
Line \times Tester	12	5.33**	2.68**	64.74	35.11**	116.32**	31.28**
Error	60	0.18	0.26	1.40	0.84	16.12	1.55
CV%	-	1.26	3.77	2.04	2.34	5.47	3.63

**, * = Significant at 1% and 5% levels of probability; N.S = Non Significant; CV = Coefficient of the variation.

Table 3. Mean performance of the lines, testers, and F_2 populations for various traits in wheat.

Lines, Testers & F_2 Populations	Tillers plant ⁻¹	Flag leaf area (cm ²)	Grains spike ⁻¹
Lines			
2768	16.8	31.7	52.0
2769	14.6	36.1	66.8
2785	16.2	34.8	67.0
2805	12.9	34.9	61.0
2806	11.8	33.1	62.0
2835	13.7	33.2	68.0
2836	14.9	34.3	56.6
Testers			
Pirsabak-2013	13.0	35.9	62.4
Shahkar-2013	13.0	36.1	57.5
Punjab-2011	15.4	32.9	63.3
F_2 populations			
2768 × Pirsabak-2013	14.2	34.1	56.0
2768 × Shahkar-2013	12.5	32.1	48.2
2768 × Punjab-11	16.1	31.5	55.6
2769 × Pirsabak-2013	13.2	32.4	55.3
2769 × Shahkar-2013	13.1	36.1	56.4
2769 × Punjab-11	13.9	31.0	63.1
2785 × Pirsabak-2013	14.9	32.2	53.6
2785 × Shahkar-2013	13.1	33.2	56.2
2785 × Punjab-11	12.8	34.4	59.5
2805 × Pirsabak-2013	13.5	36.3	56.4
2805 × Shahkar-2013	12.4	32.5	52.3
2805 × Punjab-11	13.8	34.3	54.5
2806 × Pirsabak-2013	12.5	31.8	54.6
2806 × Shahkar-2013	13.2	32.4	63.2
2806 × Punjab-11	12.9	31.8	53.4
2835 × Pirsabak-2013	11.6	33.1	68.3
2835 × Shahkar-2013	12.8	32.2	54.4
2835 × Punjab-11	13.3	33.0	58.8
2836 × Pirsabak-2013	12.6	33.1	52.2
2836 × Shahkar-2013	13.5	33.5	49.3
2836 × Punjab-11	14.5	31.7	58.0
LSD _{0.05}	0.84	0.69	1.93

Grains per Spike

Grains per spike varied from 52.0 (line 2768) to 68.0 (line 2835) among lines; testers ranged from 57.5 (Shahkar-13) to 63.3 (Punjab-11), while their F_2 populations varied from 48.2 (2768 × Shahkar-13) to 68.3 (2835 × Pirsabak-13) (Table 4). On the whole, the highest grains per spike were recorded for the F_2 population 2835 × Pirsabak-13 (68.3), followed by lines 2835 (68.0) and 2785 (67.0). Minimum grains per spike were observed in the F_2 population 2768 × Shahkar-13 (48.2), followed by the F_2 population 2836 × Shahkar-13 (49.3), and line 2768 (52.0). However, other lines, testers, and F_2 populations revealed average grains per spike.

1000-Grain Weight

The 1000-grain weight varied from 29.9 (line 2836) to 46.5 g (line 2835) among lines; testers ranged from 33.5 (Shahkar-13) to 37.5 g (Pirsabak-13), whereas their F_2 populations varied from 33.2 (2785 × Punjab-11) to 49.7 g (2835 × Pirsabak-13) (Table 4). Generally, the highest 1000-grain weights were recorded for F_2 population 2835 × Pirsabak-13 (49.7 g), followed by F_2 population 2769 × Punjab-11 (48.8 g), and line 2835 (46.5 g). Minimum 1000-grain weights were observed in line 2836 (29.9 g), followed by two other lines, i.e., 2785 (31.6 g) and 2805 (32.1 g). In the present study, the remaining lines, testers, and F_2 populations revealed average values for 1000-grain weight.

Biological Yield per Plant

Biological yield per plant ranged from 62.7 (line 2805) to 82.8 g (line 2785) among lines; testers ranged from 61.7 (Pirsabak-13) to 79.4 g (Punjab-11), while their F_2 populations ranged from 64.0 (2768 × Shahkar-13) to 90.6 g (2806 × Shahkar-13) (Table 4). Overall, the highest biological yield per plant was recorded for the F_2 population 2806 × Shahkar-13 (90.6 g), followed by the F_2 population 2805 × Shahkar-13 (88.9 g) and line 2785 (88.8 g). Minimum biological yield per plant was manifested by tester Pirsabak-13 (61.7 g), followed by lines 2805 (62.7 g), and F_2 population 2768 × Shahkar-13 (64.0 g). However, other genotypes including, lines, testers, and F_2 populations, showed an average mean value for biological yield per plant. Results further revealed that F_2 populations showed more biological yield than testers and lines.

Grain Yield per Plant

Grain yield per plant varied from 24.8 (line 2768) to 31.3 g (line 2835) among lines; testers ranged from 24.1 (Shahkar-13) to 29.0 g (Pirsabak-13), whereas their F_2 populations varied from 23.5 (2836 × Shahkar-13) to 36.3 g (2835 × Pirsabak-13) (Table 4). On the whole, the highest grain yield per plant was recorded for the F_2 population 2835 × Pirsabak-13 (36.3 g), followed by

the F_2 population 2785 \times Shahkar-13 (31.4 g), line 2835 (31.3 g). Minimum grain yield per plant was observed for F_2 population 2836 \times Shahkar-13 (23.5 g), followed

by other F_2 population 2835 \times Punjab-11 (23.7 g), and tester Shahkar-13 (24.1 g). Other genotypes, including lines, testers, and F_2 populations, showed average mean values for grain yield per plant.

Table 4. Mean performance of lines, testers, and F_2 populations for various traits in wheat.

Lines, Testers & F_2 Populations	1000-grain weight (g)	Biological yield plant ⁻¹	Grain yield plant ⁻¹
Lines			
2768	32.9	74.8	24.8
2769	35.4	76.2	30.8
2785	31.6	82.8	27.7
2805	32.1	62.7	25.3
2806	32.6	67.2	29.6
2835	46.5	68.7	31.3
2836	29.9	71.0	28.3
Testers			
Pirsabak-2013	37.5	61.7	29.0
Shahkar-2013	33.5	76.0	24.1
Punjab-2011	34.4	79.4	27.2
F_2 populations			
2768 \times Pirsabak-2013	38.2	66.7	28.1
2768 \times Shahkar-2013	41.1	64.0	25.0
2768 \times Punjab-11	44.2	65.6	27.8
2769 \times Pirsabak-2013	44.6	68.5	27.0
2769 \times Shahkar-2013	38.7	71.0	26.1
2769 \times Punjab-11	48.8	66.2	30.0
2785 \times Pirsabak-2013	40.6	72.2	28.1
2785 \times Shahkar-2013	34.1	79.8	31.4
2785 \times Punjab-11	33.2	82.6	24.1
2805 \times Pirsabak-2013	40.4	74.8	27.2
2805 \times Shahkar-2013	41.8	88.9	29.0
2805 \times Punjab-11	43.2	70.5	25.8
2806 \times Pirsabak-2013	45.0	71.6	24.9
2806 \times Shahkar-2013	35.5	90.6	29.5
2806 \times Punjab-11	38.2	65.2	26.8
2835 \times Pirsabak-2013	49.7	69.5	36.3
2835 \times Shahkar-2013	39.5	81.8	28.3
2835 \times Punjab-11	45.7	78.5	23.7
2836 \times Pirsabak-2013	39.1	72.0	25.3
2836 \times Shahkar-2013	35.1	75.0	23.5
2836 \times Punjab-11	35.1	79.0	24.5
LSD _{0.05}	1.49	6.56	2.03

Combining Ability Analysis

Analysis of variance for combining ability showed significant ($p \leq 0.01$) differences among lines for 1000-grain weight while the significant ($p \leq 0.05$) for flag leaf area (Table 2). In the cases of testers, significant ($p \leq 0.05$) differences were obtained for 1000-grain weight and biological yield per plant. In the case of line \times tester interactions, significant ($p \leq 0.01$) differences were observed for all the parameters studied, i.e., flag leaf area, tillers per plant, grains per spike, 1000-grain weight, biological yield, and grain yield per plant.

General and Specific Combining Ability Effects

In the case of the testers, the GCA effects ranged from -4.09 to 2.44. The highest negative GCA values were revealed by the tester Pirsabak-13 (-4.09), while the highest positive GCA effects were manifested by the tester Punjab-11 (2.44). These promising parental genotypes with maximum negative GCA effects were identified as the best general combiners that can be used in future wheat breeding programs to reduce vegetative growth.

Ten F_2 populations showed desirable negative SCA effects while the remaining 11 F_2 populations showed positive SCA effects. Minimum and desirable SCA effects were found in F_2 population 2805 \times Shahkar-13 (-7.82), followed by 2806 \times Pirsabak-13 (-7.33) and 2785 \times Shahkar-13 (-4.26). However, maximum positive SCA effects were possessed by the F_2 population, i.e., 2805 \times Pirsabak-13 (7.99), followed by 2806 \times Punjab-11 (6.67) and 2768 \times Shahkar-13 (3.83).

For the tillers per plant, the GCA effects among lines ranged from -0.78 to 0.91 (Table 5). The greatest positive GCA effect was observed in line 2768 (0.91) followed by 2785 (0.25). However, the smallest and most negative GCA value was exposed by line 2835 (-0.78) followed by 2806 (-0.51). In the case of the testers, the GCA effects ranged from -0.40 to 0.54 for tillers per plant. Maximum positive GCA effect was observed in tester Punjab-11 (0.54), while minimum and negative GCA effect was recorded in tester Shahkar-13 (-0.40) for tillers per plant. Generally, maximum positives and desirable GCA effects were observed in parental line 2768 (0.91) followed by tester Punjab-11 (0.54) and were considered as a better general combiner for tillers per plant in the current study.

In F_2 populations, the specific combining ability effects for tillers per plant ranged from -1.34 to 1.45 (Table 6). Twenty-one F_2 populations, of which eleven F_2 populations revealed positive SCA effects, and the remaining 10 F_2 populations showed negative SCA effects. Maximum positive SCA effects were possessed

Table 5. General combining ability effects among lines and testers for various traits in the wheat.

Parental genotypes	Flag leaf area	Tillers plant ⁻¹	Grains spike ⁻¹	1000-grain weight	Biological yield plant ⁻¹	Grain yield plant ⁻¹
Lines						
2768	-0.65**	0.91**	-2.77**	0.60*	-8.55**	-0.27
2769	-0.04	0.05	2.20**	3.46**	-5.46**	0.45
2785	0.05	0.25	0.37	-4.58**	4.21**	0.60
2805	2.80**	-0.12	-1.62**	1.23**	4.05**	0.05
2806	-1.20**	-0.51**	1.04*	-0.99**	1.81	-0.19
2835	-0.46**	-0.78**	3.71**	4.41**	2.60	2.20**
2836	-0.49**	0.20	-2.94**	-4.12**	1.32	-2.85**
S.E.	0.14	0.17	0.39	0.30	1.34	0.42
Testers						
Pirsabak-2013	0.07	-0.14	0.25	1.96**	-3.24**	0.88*
Shahkar-13	0.63*	-0.40**	-1.77**	-2.60**	4.73**	0.26
Punjab-2011	-0.69**	0.54**	1.52**	0.64	-1.49	-1.14**
S.E.	0.10	0.12	0.28	0.22	0.95	0.29

**, * = Significant at the 1% and 5% levels of the probability; S.E. = Standard errors

by the F_2 population 2785 \times Pirsabak-13 (1.45), followed by two other populations, i.e., 2768 \times Punjab-11 (1.32) and 2806 \times Shahkar-13 (0.71). However, minimum and negative SCA effects were owned by the F_2 population 2768 \times Shahkar-13 (-1.34), followed by 2785 \times Punjab-11 (-1.33) and 2835 \times Pirsabak-13.

For the flag leaf area, the GCA effects among lines ranged from -1.20 to 2.80 (Table 5). Most positive GCA effects were exhibited by line 2805 (2.80), followed by 2785 (0.50). However, minimum negative GCA effects were exhibited by line 2806 (-1.20), followed by two other parental lines, i.e., 2768 (-0.65) and 2836 (-0.49). In the case of testers, the flag leaf area, the GCA effects ranged from -0.69 to 0.63. The highest positive GCA effects were observed in tester Shahkar-13 (0.63). However, minimum and negative GCA effects were owned by the tester Punjab-11 (-0.69). Generally, the highest positive and desirable GCA values were observed in parental line 2805 (2.80), followed by tester Shahkar-13 (0.63), and considered as good general combiners for the flag leaf area.

In the F_2 populations, the specific combining ability effect for the flag leaf area ranged from -1.50 to 2.32 (Table 6). Ten out of 21 F_2 populations revealed positive SCA effects for said trait. However, 11 F_2 populations showed negative SCA effects. Maximum positive and desirable SCA effects were possessed by F_2 populations 2769 \times Shahkar-13 (2.32) followed by two other populations, i.e., 2785 \times Punjab-11 (1.82) and 2768 \times Pirsabak-13 (1.42). These potential populations can be used in future breeding programs to develop wheat genotypes by increasing the flag leaf area. Further, the

minimum and negative SCA effects were noted in the F_2 population of 2769 \times Punjab-11 (-1.50), followed by two other populations, i.e., 2835 \times Shahkar-13 (-1.19) and 2785 \times Pirsabak-13 -1.15.

For grains per spike, among lines, the GCA effects ranged from -2.94 to 3.71 (Table 5). Maximum positive desirable GCA values were exhibited by line 2835 (3.71) followed by two other parental lines, i.e., 2769 (2.20) and 2806 (1.04) for the said trait. However, negative GCA effects were observed in line 2836 (-2.94) followed by 2768 (-2.77). In testers, the GCA effects ranged from -1.77 to 1.52 for the grains per spike. The most positive and desirable GCA effects were observed in the tester Punjab-11 (1.52). However, minimum and negative GCA values were possessed by the tester Shahkar-13 (-1.77) for grains per spike. Overall, the positive and desirable GCA effects were observed in parental line 2835 (3.71), followed by line 2769 (2.20), and tester Punjab-11(1.52) and considered the most excellent general combiner for grains per spike.

In F_2 populations, the specific combining ability effects of the grains per spike ranged from -5.17 to 7.92 (Table 6). Nine out of 21 F_2 populations revealed positive SCA effects for said trait. However, 12 F_2 populations showed a negative SCA effect. Maximum positive and desirable SCA effects were possessed by the F_2 population 2806 \times Shahkar-13 (7.92), and it was followed by the other populations, i.e., 2835 \times Pirsabak-13 (6.01) and 2836 \times Punjab-11 (3.38), which was found to be the best specific combiner of the grains per spike. However, minimum negative SCA effects were exhibited by the F_2 population 2806 \times Punjab-11 (-5.17), followed by two

Table 6. Specific combining ability effects among F_2 populations for the various traits in wheat.

F_2 populations	Flag leaf area	Tillers plant ⁻¹	Grains spike ⁻¹	1000-grain weight	Biological yield plant ⁻¹	Grain yield plant ⁻¹
2768 × Pirsabak-2013	1.42**	0.02	2.49	-4.90**	4.48	0.28
2768 × Shahkar-2013	-1.07**	-1.34**	-3.33	2.50**	-6.15*	-2.28**
2768 × Punjab-11	-0.35	1.32**	0.85	2.40**	1.67	2.00**
2769 × Pirsabak-2013	-0.82**	-0.09	-3.21	-1.40*	3.20	-1.61*
2769 × Shahkar-2013	2.32**	0.11	-0.10	-2.77**	-2.31	-1.83*
2769 × Punjab-11	-1.50**	-0.03	3.31	4.16**	-0.89	3.43**
2785 × Pirsabak-2013	-1.15**	1.45**	-3.09	2.68**	-2.74	-0.65
2785 × Shahkar-2013	-0.67**	-0.12	1.57	0.71	-3.11	3.28**
2785 × Punjab-11	1.82**	-1.33**	1.52	-3.39**	5.85*	-2.63**
2805 × Pirsabak-2013	0.24	0.42	1.74	-3.33**	-0.05	-1.00
2805 × Shahkar-2013	0.79**	-0.44	-0.31	2.60**	6.11*	1.39
2805 × Punjab-11	-1.03**	0.02	-1.43	0.73	-6.06*	-0.39
2806 × Pirsabak-2013	-0.26	-0.19	-2.76	3.43**	-0.94	-3.04**
2806 × Shahkar-2013	-0.25	0.71*	7.92	-1.44**	10.02**	2.15**
2806 × Punjab-11	0.50*	-0.52	-5.17	-1.98**	-9.09**	0.89
2835 × Pirsabak-2013	0.27	-0.82**	6.01	2.79**	-3.86	6.00**
2835 × Shahkar-2013	-1.19**	0.65*	-3.55	-2.88**	0.50	-1.42**
2835 × Punjab-11	0.93**	0.17	-2.47	0.08	3.36	-4.58**
2836 × Pirsabak-2013	0.30	-0.80*	-1.18	0.72	-0.09	0.02
2836 × Shahkar-2013	0.07	0.43	-2.20	1.28*	-5.06**	-1.29
2836 × Punjab-11	-0.37	0.36	3.38	-1.99**	5.16**	1.27
S.E.	0.24	0.30	0.68	0.53	2.32	0.72

**, * = Significantly at the 1% and 5% levels of the probability; S.E. = Standard errors

other populations, i.e., 2835 × Shahkar-13 (-3.55) and 2768 × Shahkar-13 (-3.33).

For thousand grain weight, the lines GCA effects range from -4.58 to 4.41 (Table 5). Maximum positive desirable GCA effects were observed in line 2835 (4.41), followed by two other lines, i.e., 2769 (3.46) and 2805 (1.23). However, negative GCA effects were observed in line 2785 (-4.58), followed by 2836 (-4.12) and 2806 (-0.99). In testers for thousand-grain weight, the GCA effects ranged from -2.60 to 1.96. Maximum positive desirable GCA effects were recorded in testers Pirsabak-13 (1.96). However, minimum and negative GCA effects were exhibited by the tester Shakar-13 (-2.60). Generally, the highest positive and desirable GCA effects were observed in parental line 2835 (4.41), followed by line 2769 (3.46), and tester Pirsabak-13 (1.96). These promising genotypes were identified as the best general combiner for the 1000-grain weight.

In F_2 populations, for thousand-grain weight, the specific combining ability effects ranged from -4.90 to 4.16 (Table 6). Twelve out of the 21 F_2 populations

revealed positive SCA effects, however, nine F_2 populations showed negative SCA effects for the said trait. The maximum positive desirable SCA effects were possessed by the F_2 population 2769 × Punjab-11 (4.16), followed by other populations i.e., 2806 × Pirsabak-13 (3.43) and 2785 × Pirsabak-13 (2.68), and were considered the most excellent specific combiner for 1000-grain weight. However, minimum and negative SCA effects were noted in the F_2 population 2768 × Pirsabak-2013 (-4.90), followed by two other populations, i.e., 2785 × Punjab-11 (-3.39) and 2805 × Pirsabak-13 (-3.33).

For the biological yield among lines, GCA effects ranged from -8.55 to 4.21 (Table 5). Maximum positive desirable GCA effects were shown by line 2785 (4.21), followed by two other lines, i.e., 2805 (4.05) and 2835 (2.60) for the said trait. However, negative GCA effects were exhibited by the line 2768 (-8.55), followed by 2769 (-5.46). In testers, the GCA effects ranged from -3.24 to 4.73 for biological yield. The highest positive and desirable GCA effects were observed in the tester Shakar-13 (4.73). However, minimum and negative

GCA effects were recorded in tester Pirsabak-13 (-3.24). Generally, the highest positive desirable GCA effect was exhibited by the parental tester Shakar-13 (4.73) followed by lines 2785 (4.21) and 2805 (4.05), which were suggested to be the better general combiners for biological yield and can be used in future breeding programs to develop wheat genotypes with the maximum biological yield.

In F_2 populations, the specific combining ability effects of the biological yield ranged from -9.09 to 10.02 (Table 6). Nine out of 21 F_2 populations exposed positive SCA effects, while twelve F_2 populations showed negative SCA effects. Maximum positive and desirable SCA effects were possessed by the F_2 population 2806 \times Shahkar-13 (10.02), followed by two other populations, i.e., 2805 \times Shahkar-13 (6.11) and 2785 \times Punjab-11 (5.85), and suggested as the best specific combiner for the biological yield. However, minimum and negative SCA effects were possessed by the F_2 population 2806 \times Punjab-11 (-9.09), followed by 2768 \times Punjab-11 (-6.15) and 2805 \times Punjab-11 (-6.06). For the grain yield per plant, lines GCA effects ranged from -2.85 to 2.20 (Table 5). Maximum positive and desirable GCA effects were observed in line 2835 (2.20), followed by 2785 (0.60) for grain yield. However, negative GCA effects were possessed by line 2836 (-2.85), followed by two other lines, i.e., 2768 (-0.27) and 2806 (-0.19). In the case of testers, the GCA effects ranged from -1.14 to 0.88 for the grain yield per plant. Maximum positive desirable GCA effects were recorded for tester Pirsabak-13 (0.88). However, minimum and negative GCA effects were observed in tester Punjab-11 (-1.14). Generally, the highest positive and desirable GCA effects were noted in the parental line 2835 (2.20), followed by tester Pirsabak-13 (0.88), and were considered the best general combiner for the grain yield per plant.

For grain yield per plant, the F_2 population-specific combining ability effects ranged from -4.58 to 6.00 (Table 6). Eleven out of 21 F_2 populations exposed positive and desirable SCA effects, while the remaining 10 F_2 populations showed negative SCA effects for the

said trait. Maximum positive and desirable SCA effects were possessed by the F_2 population 2835 \times Pirsabak-13 (6.0), followed by the two other populations, i.e., 2769 \times Punjab-11 (3.43) and 2785 \times Shahkar-13 (3.28), and were found as specific cross combinations for the grain yield per plant. However, minimum negative SCA effects were exhibited by the F_2 population 2835 \times Punjab-11 (-4.58), followed by other populations, i.e., 2806 \times Pirsabak-13 (-3.04) and 2785 \times Punjab-11 (-2.63).

Gene Action and Proportional Contribution of Populations to the Total Variance

The variances of the general combining ability (σ^2_{GCA}) were lower than the specific combining ability variances (σ^2_{SCA}) for all the traits, suggesting the preponderance of non-additive gene actions (Table 7). The value of dominance genetic variance was greater than additive genetic variance for all the traits. The present findings were also authenticated by the ratio of the variance of the general to specific combining ability ($\sigma^2_{GCA}/\sigma^2_{SCA}$) which was smaller than unity, and by the degree of dominance (σ^2_D/σ^2_A)^{1/2} which revealed the values superior to unity. For that reason, it appeared that the inheritance of all the studied characters was controlled by the non-additive gene effects. Genes action indicated that the selection of the populations in terms of the morphological and yield-related traits must be delayed to late segregating generations. However, optimized trait selection can be performed using advanced techniques like marker-assisted selection in the genotypes identified as having the non-additive type of gene action that will speed up the breeding process.

In proportional contributions to the total variances, the line by-tester interactions have the maximum role (as compared to the parental lines and testers) for the five traits, i.e., tillers per plant (55.06%), grains per spike (59.69%), biological yield per plant (40.20%), grain yield per plant (58.13%), followed by lines (Table 8). For trait i.e., flag leaf area (52.56%), and 1000-grain weight (49.89%), the contribution of the parental lines was

Table 7. Genetic components for the various traits in the wheat.

Genetic Components	Flag leaf area	Tillers plant ⁻¹	Grains spike ⁻¹	1000-grain weight	Biological yield plant ⁻¹	Grain yield plant ⁻¹
σ^2_{GCA}	0.09	0.006	0.01	0.78	1.49	0.03
σ^2_{SCA}	1.72	0.80	18.56	11.42	33.40	9.76
σ^2_A	0.17	0.013	0.02	1.56	2.98	0.05
σ^2_D	1.72	0.80	18.56	11.42	33.40	9.76
$\sigma^2_{SCA}/\sigma^2_{SCA}$	0.05	0.01	0.001	0.07	0.04	0.003
σ^2_A/σ^2_D	0.10	0.02	0.001	0.14	0.09	0.01
$[\sigma^2_D/\sigma^2_A]^{1/2}$	3.1	8.0	30.9	2.7	3.3	13.7

σ^2_A : additive genetics variances; σ^2_D : dominant genetics variances; σ^2_{GCA} : GCA variances; σ^2_{SCA} : SCA variances; $\sigma^2_{GCA}/\sigma^2_{SCA}$: average degrees of dominance.

Table 8. The proportional contribution of lines, testers, and line \times tester interaction to total variance.

Variables	Lines (%)	Testers (%)	Line \times Tester F ₂ populations (%)
Flag leaf area	52.56	10.60	36.84
Tillers plant ⁻¹	28.11	16.83	55.06
Grains spike ⁻¹	31.07	9.24	59.69
1000-grain weight	49.89	17.76	32.35
Biological yield plant ⁻¹	38.56	21.23	40.20
Grain yield plant ⁻¹	30.47	11.40	58.13

Table 9. Heritability estimates for various traits in wheat.

Parameters	Vg	Vp	GCV (%)	PCV (%)	<i>h</i> ² (bs)	Genetic gain
Flag leaf area (cm ²)	2.34	2.52	4.57	4.74	0.93	2.15
Tiller plant ⁻¹	1.51	1.77	9.00	9.76	0.85	1.65
Grain spike ⁻¹	26.95	28.35	9.23	9.45	0.95	7.62
1000-grain weight (g)	28.61	29.45	13.83	14.03	0.97	7.69
Biological yield plant ⁻¹ (g)	48.77	64.88	9.51	10.98	0.75	8.83
Grain yield plant ⁻¹ (g)	7.41	8.96	10.67	11.59	0.83	3.91

Vg: genetic variance; Vp: phenotypic variance; GCV: genotypic coefficient of variance; PCV: phenotypic coefficient of variance; *h*² (bs); heritability (broad sense).

leading as compared to the parental testers and L \times T F₂ populations. Results further revealed that line \times tester interaction and parental lines managed the majority of the variation in the expression of these traits.

Genetic Parameters, Heritability (Broad Sense), and Genetic Gain

For the flag leaf area, the value of genotypic variance (2.51) was greater than phenotypic variance (2.34) while the GCV and PCV values were 4.57% and 4.74%, respectively. Broad sense heritability and genetic gain values for flag leaf area were 0.93 and 2.15 cm², respectively. For tiller per plant, the value of phenotypic variance (1.50) was smaller than genotypic variance (1.70), while the values of GCV and PCV were 9.00% and 9.76%, respectively. Broad sense heritability and genetic gain values were 0.86 and 1.65, respectively, for the tillers plant. For grains per spike, the genotypic variance (28.35) value was greater in magnitude than the phenotypic variance (26.95), while the GCV and PCV values were 9.23% and 9.45%, respectively. However, the heritability (broad sense) and genetic gain values were 0.95 and 7.62, respectively, for grains per spike.

For 1000-grain weight, the value of genotypic variance (28.60) was smaller than phenotypic variance (29.44), which revealed a greater role in the environment in the management of the said trait (Table 7). The GCV and PCV values were 13.83% and 14.03%, respectively. The values of heritability (broad sense) and genetic

gain were recorded as 0.97 and 7.69 g, respectively, for thousand-grain weight (Table 9). For biological yield, the value of phenotypic variance (48.76) was smaller than genotypic variance (64.88) while the GCV and PCV values were 9.51% and 10.98%, respectively, for said trait. High broad sense heritability and genetic gain values were recorded as 0.75 and 8.83 g, respectively, for biological yield. For grain yield per plant, the genotypic variance (7.40) was smaller than the phenotypic variance (8.95), which shows a greater role of the environment. The GCV and PCV values were 10.67% and 11.59%, respectively. Broad sense heritability and genetic gain values were 0.83 and 3.91 g, respectively, for grain yield.

Discussion

The wheat testers, lines, F₁, and F₂ populations all showed similar variations in the number of tillers per plant, and previous research findings showed that genotypes with the most tillers have higher biological and grain yields [18, 19]. Previous research found a link between wheat flag leaf areas and ultimate grain yield by observing substantial variations and higher genetic variation in several wheat lines, testers, F₁, and F₂ populations [20, 21]. Significant differences were observed in the different wheat populations for the flag leaf area and its considerable positive correlation with the grain yield [22]. It is reported that the significant

differences among various populations of wheat for the grains per spike and grain yield traits [12, 23]. Past and present findings confirmed that grains per spike is a very essential trait, and the grain yield is fully dependent on it, and increased grains per spike effects directly affect grain yield.

Findings revealed considerable changes in 1000-grain weight between different wheat populations, including lines, test subjects, and F_1 and F_2 populations [24]. Due to its correlation with grain yield in wheat, previous research revealed that larger grains would produce an overall increase in grain yield for the various wheat genotypes [25]. Previous studies found that amongst lines, testers, F_1 and F_2 populations, the theoretical yield of wheat per plant varied significantly [26]. Other earlier research similarly revealed significant variations in biological yield per plant for wheat among tests, lines, and F_1 and F_2 populations [18, 27].

The end product generated through interactions of numerous yield-contributing features in wheat is grain yield per plant. For the grain yield per plant, the genetic diversity of several wheat genotypes, including lines, testers, F_1 , and F_2 populations, was found to be more pronounced and significant in earlier investigations. In past studies, more significant genetic variation was observed among different wheat genotypes, including lines, testers, F_1 and F_2 populations [28]. Significant variations in grain production per plant have been found among lines, testers, F_1 and F_2 populations [18, 26]. Previous research on line-by-tester analysis also demonstrated very significant differences for tillers per plant, thousand-grain weight, and yield-related characteristics, as well as line-by-tester interactions and population genetic variability for morphological and yield parameters [29]. In a previous study, the 10 wheat populations showed the highest levels of both undesirable and favorable general and specific combining ability impacts [6].

In a variety of wheat lines, testers, and their cross combinations for yield and yield-attributing traits in line by tester analyses in wheat, Nour et al. (2011) also discovered similar ranges of specific and general combining ability effects [27]. Wheat breeding programs promote genotypes with the most tillers per plant because they produce the most grain and provide the most animal feed [30-32]. Genotype 9469 exposed maximum positive GCA effects, whereas genotypes Aas-11 and Iqbal-200 exhibit negative GCA effects for the flag leaf area [15, 33, 34]. According to previous research, 55% of F_1 populations had favorable specific combining ability impacts for traits related to yield and grains per spike, and they were recommended as the best specific combiner in wheat [27, 30]. An earlier study demonstrated favorable SCA effects in the F_1 population Inqlab-91 Chakwal-86 and indicated these specific combiners as the most suitable ones for wheat's thousand-grain weight [27, 32]. According to research by Khan et al. (2010), the wheat genotypes Uqab-200 and V-0055, as well as the F_1 population SH-02 \times

Uqab-2000, were discovered to be the best general and specific combiners for attributes linked to 1000-grain weight and yield in wheat [35]. Previous research found that lines, testers, and the $L \times T$ F_1 population UP-238 \times Pavon-76 showed desirable SCA and GCA effects and were recommended as the best specific combiners for biological yield in wheat [36, 37]. The improvement in grain yield and features that are connected to yield have been explored in previous studies. Significant GCA and SCA effects from $L \times T$ combinations led researchers to conclude that they would make good general and specific combiners to use in hybridization programs [30]. In some other studies, the general combiner was identified as the promising lines and testers, whereas the best specific combiner was determined to be F_1 populations with desirable SCA and mean performance to be used in future breeding programs to improve yield-related traits and grain yield in wheat [38].

Previous studies showed that the variance of the general and specific combining ability and ratios showed that the non-additive gene action was key for the majority of yield-related traits in wheat [38, 39]. Line \times tester combining ability indicated the additive gene effects were less important than non-additive gene effects, and non-additive gene actions have a prime role in the inheritance of morphological and yield-related traits in wheat [27].

For line-by-tester combining ability analysis, previous research studies revealed that line-tester interactions contribution to total variance was found to be greater than lines and testers individually for yield and yield components in bread wheat [40]. Earlier studies about line-by-tester combining ability analysis revealed that the contribution of line \times tester interactions to total variance was greater than lines and testers by managing the variances in populations for morphological and yield-associated traits in wheat [34, 41]. In earlier studies, the values of genotypic and phenotypic variances, GCV and PCV, heritability (broad sense), and genetic gain were reported for morphological traits, i.e., flag leaf area and tillers per plant, among F_1 and F_2 populations studied through line by tester combining ability analysis in wheat [27, 33, 34].

Conclusions

A promising F_2 population with a desired SCA was produced using high \times low and high general combiner. It was confirmed that all traits were controlled by non-additive gene effects when the ratio of variations attributable to GC and SC effects ($2GCA/2SCA$) was smaller than unity and the degree of dominance ($2D/2A$)^{1/2} was greater than unity. Selection of the promising populations in terms of morphological and yield attributes should be delayed to later segregating generations, according to non-additive gene actions. Based on current findings, it has been determined that the aforementioned populations in progress could be

utilized in a future breeding program to create high-yielding wheat genotypes. However, there is no indirect impact of combining ability analysis because of the involvement of genes in the inheritance of any specific trait under consideration.

Authors Contribution

Humaira Iqbal and Muhammad Jalal Hassan designed the study and conducted the research. Maqsood Qamar, Sundas Waqar, and Muhammad Shahbaz Farooq helped Humaira Iqbal to perform the experiments and analysis. Muhammad Usman, Samman Gul Vaseer, Muhammad Uzair, and Muhammad Arshad helped with data analysis, software standardization, and the writing of the original draft. Kotb A. Attia, Arif Ahmed Mohammed, and Muhammad Uzair provided technical expertise to improve the article and helped in funding acquisition. All authors reviewed and edited the manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

References

- GIRALDO P., BENAVENTE E., MANZANO-AGUGLIARO F., GIMENEZ E. Worldwide research trends on wheat and barley: A bibliometric comparative analysis. *Agronomy*. **9** (7), 352, **2019**.
- KHALID A., HAMEED A., TAHIR M.F. Wheat quality: A review on chemical composition, nutritional attributes, grain anatomy, types, classification, and function of seed storage proteins in bread making quality. *Frontiers in Nutrition*. **10**, 1053196, **2023**.
- ALI S., LIU Y., ISHAQ M., SHAH T., ABDULLAH, ILYAS A., DIN I.U. Climate change and its impact on the yield of major food crops: Evidence from Pakistan. *Foods*. **6** (6), 39, **2017**.
- ELMYHUN M., LIYEW C., SHITA A., ANDUALEM M. Combining ability performance and heterotic grouping of maize (*Zea mays*) inbred lines in testcross formation in Western Amhara, North West Ethiopia. *Cogent Food & Agriculture*. **6** (1), 1727625, **2020**.
- FAROOQ M.U., ISHAAQ I., MAQBOOL R., ASLAM I., NAQVI S., MUSTAFA S. Heritability, genetic gain and detection of gene action in hexaploid wheat for yield and its related attributes. *AIMS Agriculture and Food*. **4** (1), 56, **2019**.
- KAMARA M.M., IBRAHIM K.M., MANSOUR E., KHEIR A.M., GERMOUSH M.O., ABD EL-MONEIM D., MOTAWEI M.I., ALHUSAYS A.Y., FARID M.A., REHAN M. Combining ability and gene action controlling grain yield and its related traits in bread wheat under heat stress and normal conditions. *Agronomy*. **11** (8), 1450, **2021**.
- SCHMIDT P., HARTUNG J., BENNEWITZ J., PIEPHO H.-P. Heritability in plant breeding on a genotype-difference basis. *Genetics*. **212** (4), 991, **2019**.
- AL-ASHKAR I., IBRAHIM A., GHAZY A., ATTIA K., AL-GHAMDI A.A., AL-DOSARY M.A. Assessing the correlations and selection criteria between different traits in wheat salt-tolerant genotypes. *Saudi Journal of Biological Sciences*. **28** (9), 5414, **2021**.
- XU Y., LI P., ZOU C., LU Y., XIE C., ZHANG X., PRASANNA B.M., OLSEN M.S. Enhancing genetic gain in the era of molecular breeding. *Journal of Experimental Botany*. **68** (11), 2641, **2017**.
- PARVEEN N., KANWAL A., AMIN E., SHAHZADI F., ALEEM S., TAHIR M., YOUNAS A., ASLAM R., ASLAM N., GHAFOR I. Assessment of heritable variation and best combining genotypes for grain yield and its attributes in bread wheat. *American Journal of Plant Sciences*. **9** (08), 1688, **2018**.
- TULIOZI B., MANTOVANI R., SCHOEPI I., TSURUTA S., MANCIN E., SARTORI C. Genetic correlations of direct and indirect genetic components of social dominance with fitness and morphology traits in cattle. *Genetics Selection Evolution*. **55** (1), 84, **2023**.
- ULLAH M.I., MAHPARA S., BIBI R., SHAH R.U., ULLAH R., ABBAS S., ULLAH M.I., HASSAN A.M., EL-SHEHAWI A.M., BRESTIC M. Grain yield and correlated traits of bread wheat lines: Implications for yield improvement. *Saudi Journal of Biological Sciences*. **28** (10), 5714, **2021**.
- MAHDY R.E., ASHEHRI D., ALATAWI H.A., AL-AMRAH H., MAHDY E.E. Direct and indirect selection for grain yield and grain weight in late generations of bread wheat under drought stress and normal irrigation environments. *Plants*. **11** (12), 1604, **2022**.
- YANG D., LIU Y., CHENG H., CHANG L., CHEN J., CHAI S., LI M. Genetic dissection of flag leaf morphology in wheat (*Triticum aestivum* L.) under diverse water regimes. *BMC genetics*. **17**, 1, **2016**.
- AKRAM A., KHAN T.N., MINHAS N.M., NAWAB N.N., JAVED A., RASHID S., ATIF M.J., SHAH S.U.S. Line \times tester analysis for studying various agronomic and yield related traits in field tomato (*Solanum lycopersicum* L.). *Pakistan Journal of Botany*. **51** (5), 1661, **2019**.
- DEVI A., KUMARI P., DWIVEDI R., DWIVEDI S., VERMA O., SINGH P., DWIVEDI D. Gene action and combining ability analysis for yield and yield contributing traits in rice (*Oryza sativa* L.) over environment. *Journal of Pharmacognosy and Phytochemistry*. **6** (3), 662, **2017**.
- AHMAD E., AKHTAR M., BADONI S., JAISWAL J. Combining ability studies for seed yield related attributes and quality parameters in bread wheat (*Triticum aestivum* L.). *Journal of Genetics, Genomics and Plant Breeding*. **1**, 21, **2017**.
- DIN K., KHAN N., GUL S., KHAN S., TAHIR I., BIBI Z., ALI S., KHAN S., ALI N., KHALIL I. Combining ability effects and inheritance of maturity and yield associated traits in F₂ populations of wheat. *The Journal of Animal & Plant Sciences*. **30** (4), 988, **2020**.
- RAUF A., KHAN M., JAN F., GUL S., AFRIDI K., KHAN I., BIBI H., KHAN R., KHAN W., KUMAR T. Genetic analysis for production traits in wheat using line

- x tester combining ability analysis. SABRAO Journal of Breeding and Genetics. **55** (2), 358, **2023**.
20. KUTLU I., SIREL Z. Using line× tester method and heterotic grouping to select high yielding genotypes of bread wheat (*Triticum aestivum* L.). Turkish Journal of Field Crops. **24** (2), 185, **2019**.
 21. AHMED M., QAMAR M., WAQAR S., NAEEM A., JAVAID R., TANVEER S., HUSSAIN I. Estimation of genetic components, heterosis and combining ability of elite Pakistani wheat varieties for yield attributing traits and stripe rust response. Vavilov Journal of Genetics and Breeding. **27** (6), 609, **2023**.
 22. RACZ I., HIRIȘCĂU D., BERINDEAN I., KADAR R., MUNTEAN E., TRITEAN N., RUSSU F., ONA A., MUNTEAN L. The Influence of flag leaf removal and its characteristics on main yield components and yield quality indices on wheat. Agronomy. **12** (10), 2545, **2022**.
 23. PHILIPP N., WEICHERT H., BOHRA U., WESCHKE W., SCHULTHEISS A.W., WEBER H. Grain number and grain yield distribution along the spike remain stable despite breeding for high yield in winter wheat. PloS One. **13** (10), e0205452, **2018**.
 24. HALEEM A., HASSAN G., IQBAL A., KHAN F.U., SAJID M., AHMAD F., KHAN R.U., ILYAS M. Genetic variability and correlation analysis in F2 wheat populations. Sarhad Journal of Agriculture. **38** (2), 398, **2022**.
 25. MSUNDI E.A., OWUOCHE J.O., OYOO M.E., MACHARIA G., SINGH R.P., RANDHAWA M.S. Identification of bread wheat genotypes with superior grain yield and agronomic traits through evaluation under rust epiphytotic conditions in Kenya. Scientific Reports. **11** (1), 21415, **2021**.
 26. SAEED S., KHAN N., KHALIL I.H., ALI S., AFRIDI K. Wheat assessment through line by tester combining ability analysis for maturity and yield traits. International Journal of Agriculture & Biology. **26**, 597, **2021**.
 27. ABDEL NOUR N., EL-FATEH H.S., MOSTAFA A.K. Line x Tester analysis for yield and its traits in bread wheat. Egyptian Journal of Agricultural Research. **89** (3), 979, **2011**.
 28. AFRIDI K., KHAN N.U., MOHAMMAD F., KHAN S.U., SHAH S.H., SHAH S.J.A. Genetic expression of yellow rust resistance, yield and yield related traits in wheat using Griffing's combining ability analysis. Pakistan Journal of Botany. **49** (5), 2005, **2017**.
 29. AHTISHAM S., AHMAD S., KASHIF M., ALI Q. Role of combining ability to develop higher yielding wheat (*T. aestivum* L.) genotypes. Nature and Science. **12** (11), 155, **2014**.
 30. VERMA S., MAURYA R., MAURYA S. Prediction of gene action and combining ability for yield and quality traits in F1 and F2 generations of wheat (*Triticum aestivum* L.). Tropical Plant Research. **3** (2), 449, **2016**.
 31. DIVYA P., PANWAR I.S. Detection of genetic components through triple test cross and line× tester analysis in bread wheat. Indian Journal of Ecology. **43** (2), 537, **2007**.
 32. MAJEED S., SAJJAD M., KHAN S.H. Exploitation of non-additive gene actions of yield traits for hybrid breeding in spring wheat. Journal of Agriculture and Social Sciences. **7**(4), 131, **2011**.
 33. AHMED H., RIZWAN M., ANWAAR H.A., QADEER A., ZAFAR Z., JAMIL H. Combining ability analysis for morphological traits in wheat. International Journal of Biosciences. **11** (4), 41, **2017**.
 34. AKBAR M., ANWAR J., HUSSAIN M., QURESHI M.H., KHAN S. Line Tester Analysis in Bread Wheat (*Triticum aestivum* L.). Journal of Agricultural Research. **47** (1), **2009**.
 35. KHAN A., AZAM F., ALI A. Relationship of morphological traits and grain yield in recombinant inbred wheat lines grown under drought conditions. Pakistan Journal of Botany. **42** (1), 259, **2010**.
 36. ARAUS J., CAIRNS J. Analysis of general combining ability for yield and yield related associated traits. Universal Journal of Plant Science. **19** (1), 52, **2016**.
 37. MURUGAN A., KANNAN R. Heterosis and combining ability analysis for yield traits of Indian hexaploid wheat (*Triticum aestivum* L.). International Journal of Recent Scientific Research. **8**(7), 18242, **2017**.
 38. SAEED M., KHALIL I.H. Combining ability and narrow-sense heritability in wheat (*Triticum aestivum* L.) under rainfed environment. Sarhad Journal of Agriculture. **33** (1), 22, **2017**.
 39. INGLE N., WADIKAR P., SALUNKE P. Combining ability and gene action studies for grain yield and yield contributing traits in wheat (*T. aestivum* L.). International Journal of Current Microbiology and Applied Sciences. **7** (8), 2684, **2018**.
 40. ISTIPLILER D., ILKER E., TONK F.A., GIZEM C., TOSUN M. Line× tester analysis and estimating combining abilities for yield and some yield components in bread wheat. Turkish Journal of Field Crops. **20** (1), 72, **2015**.
 41. SATTAR S., NAWAZ B., TAHIR A., AHMED A., NAEEM M., GHOURI M., JAMSHAD M. Gene action and combining ability analysis of quantitative traits associated with grain yield in wheat under drought stress and normal irrigation conditions. Global Journal of Biochemistry and Biotechnology. **7** (4), 642, **2018**.