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RESEARCH ARTICLE

Assessing gene action, combining ability and heterotic efficacy for grain yield and associated traits in maize (*Zea mays* L.) across heterogeneous environments

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Abstract

Breeding hybrid maize requires a thorough understanding of gene action, combining ability effects and heterosis across different germplasms of maize. Therefore, the present study aimed to assess the gene action, combining ability and heterotic efficacy for grain yield and its attributes in maize under heterogeneous environments. The study utilized 7 inbred lines, 21 hybrids produced through Griffing's diallel mating scheme-II and a check variety, arranged in a randomized block design. The results revealed highly significant general combining ability (GCA) effects among parents and specific combining ability (SCA) effects among hybrids for all evaluated traits. This indicates the presence of variability due to both additive and non-additive gene effects. With the exception of days to 50 % anthesis, ear length and 1000-grain weight, the mean square (MS) values for GCA × environment interactions were greater than those of the corresponding SCA × environment interactions for all traits under study. This suggests that GCA was more impacted by environment than SCA. Among the parental lines, P1 exhibited highly significant positive GCA effects for ear diameter, grain rows per ear, grains per row and grain yield per plant, along with highly significant negative GCA effects for days to 50 % anthesis and days to 50 % silking. This demonstrates its potential for enhancing grain yield per plant with promoting early flowering. The best-performing experimental hybrid combination, P1 × P7, displayed high standard heterosis, superior parent heterosis, high SCA and strong GCA effects for both parents. Additionally, it showed a heterotic response for grain yield per plant, making it a promising candidate for commercial exploitation following further critical testing. Furthermore, standard heterosis exhibited a highly significant positive correlation between the 2 flowering traits (days to 50 % anthesis and days to 50 % silking), while its correlation with other traits was found to be insignificant.

Keywords: combining ability effects; correlation; general combining ability × environments; heterotic efficacy; specific combining ability × environments

Introduction

Maize (*Zea mays* L., 2n = 20) is one of the most imperative crops for food, edible oil and animal feed, particularly for poultry and swine, due to its high availability, palatability and nutritional value (1). The term "corn" is widely recognized as meaning "that which sustains life". Additionally, maize plays a crucial role in the manufacturing of biofuel (ethanol) because of its clean ignition, biodegradability, potential to lower greenhouse gas emissions and contribute to increased energy security (2).

Zea is a member of the grass family Poaceae and specifically to the Maydeae tribe, which comprises 4 species. *Zea mays* L. is the most significantly economic species, while the other collectively known as teosinte, are primarily wild grasses native to Mexico and Central America. The maize plant is characterized by its male inflorescence (tassel) at the apex of the stem and female inflorescences (cobs or ears), which develop from condensed lateral branches called shanks that emerge from leaf axils. The kernels, which are tightly arranged on the cob, are botanically classified as caryopses - a type of dry fruit where the seed is fused to the inner tissues of the fruit case (3).

The United States Department of Agriculture (USDA) and the Foreign Agricultural Service (FAS), global maize production in 2023 reached 1.23 billion mt, marking a 6 % increase from the previous year. The total global maize cultivation area was approximately 205 million ha, with an average global productivity of ~5.9 metric tons per ha (MT/ha). The top maize- producing- countries like United States, China and Brazil, together account for more than 60 % of total global maize production (4). India ranked sixth position in maize production with 37.67 MMT, which represents 3.1 % of total global production (4). India produced 38085256.41 tonnes of corn from an area of 10743603 ha, with a productivity of 3544.90 kg/ha (5). Developing high-yielding hybrid maize is a realistic and useful alternative to fulfil the future food, feed and industrial needs of the world's geometrically rising population. The phenomenon of hybrid vigor, or heterosis phenomenon, was first observed by Darwin and is defined as the phenotypic superiority of hybrid F1 offspring over their parents (6).

Breeding practices show that the efficacy of parents alone is erratic with the performance of the hybrid. Outstanding hybrids are not always developed from the superior parents. Therefore, rather than focusing just on a parental line's performance solely based on its individual performance, breeders should consider how well-suited it is to create excellent hybrids. The concept of combining ability is being calculated and employed to choose desirable parental lines and promising hybrid combinations. GCA and SCA, which represents different genetic components, are predominantly influenced by additive and non-additive gene actions, respectively (7). The GCA of an inbred line is determined by the average performance of all hybrids derived using that line as a common parent, while the SCA for a specific cross is calculated as the difference between the observed hybrid performance and the expected performance based on parental GCA values (7).

Currently, maize is exposed to changing environmental circumstances that affect how well hybrid maize performs. GCA x E and SCA x E interactions play a crucial role in determining grain yield per plant and other agronomic traits, illustrating that the GCA of parental lines and the SCA rankings of hybrids change over different environments (8). An ideal parental line should be robust, exhibit steady and significantly positive GCA in hybrid combinations across diverse environments and contribute minimally to GCA x E interactions (9).

One of the main challenges in hybrid breeding programs is the complexity and time-intensive nature of GCA evaluation. Therefore, a deeper understanding of the genetic basis of heterosis and combining ability can enhance maize improvement programs and the accuracy of hybrid performance predictions (10).

Keeping above point into the consideration, the present investigation was carried out with an objective to disclose gene action, combining ability and heterotic efficacy across heterogeneous environments.

Materials and Methods

Experimental materials and field experiments

The 21 hybrids, excluding reciprocal crosses, were developed using the half-diallel mating design (Method II and Model I) (11) (Table 1 and Fig. 1), consisting of 7 inbred lines (Fig. 2). In total, 29 test entries, comprising 21 hybrids, 7 parental inbreds and a check variety (SHM-1), were assessed for their performance in a completely randomized block design (RCBD) with 3 replications across 6 diverse environments, including 3 locations and 2 successive growing seasons such as, Kharif 2019 and Rabi 2019 - 2020. The details of monthly weather report for each environment during crop growing season under study are represented in Fig. 3 and 4.

In each replication, every entry was planted in two 5-m rows, with a row to row spacing of 60 cm and a plant to plant spacing of 20 cm. After sowing 2 seeds per hill and after germination, thinning operation was carried out to maintain 1 healthy plant per hill. Standard agronomical practices were adopted in each trial for raising healthy crop.

Data collection and statistical analysis

Two key flowering-related characters, days to 50 % anthesis (DPA) and days to 50 % silk (DPS), were assessed for each plot and replication. At the time of harvest, additional agronomically important characters, such as plant height, ear length, ear diameter, grain rows per ear, grain number per ear and grain yield per plant, were measured from 10 randomly selected competitive plants located at the central portion of each row in every plot and replication. The bulked seeds of all 10 competing plants' ears in each plot and replication were used to calculate the 1000-grain

Table 1. A pedigree of 21 hybrid pairings produced using Method-II and Model-I of Griffing's (1956) diallel mating method

SL NO.	Code	Pedigree
1	P1 × P2	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × BML-7
2	P1 × P3	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × VL-1055
3	P1 × P4	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × ZL-14501
4	P1 × P5	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × [CML-161/CML-165]-BBB-11- BBB/CML-193
5	P1 × P6	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × ZL-145312
6	P1 × P7	DTPYC9-F46-3-1-1-2-3-2-2-B*9 × CML-117-3-4-1-1-4-1
7	P2 × P3	BML-7 × VL-1055
8	P2 × P4	BML-7 × ZL-14501
9	P2 × P5	BML-7 × [CML-161/CML-165]-BBB-11-BBB/CML-193
10	P2 × P6	BML-7 × ZL-145312
11	P2 × P7	BML-7 × CML-117-3-4-1-1-4-1
12	P3 × P4	VL-1055 × ZL-14501
13	P3 × P5	VL-1055 × [CML-161/CML-165]-BBB-11-BBB/CML-193
14	P3 × P6	VL-1055 × ZL-145312
15	P3 × P7	VL-1055 × CML-117-3-4-1-1-4-1
16	P4 × P5	ZL-14501 × [CML-161/CML-165]-BBB-11-BBB/CML-193
17	P4 × P6	ZL-14501 × ZL-145312
18	P4 × P7	ZL-14501 × CML-117-3-4-1-1-4-1
19	P5 × P6	[CML-161/CML-165]-BBB-11-BBB/CML-193 × ZL-145312
20	P5 × P7	[CML-161/CML-165]-BBB-11-BBB/CML-193 × CML-117-3-4-1-1-4-1
21	P6 × P7	ZL-145312 × CML-117-3-4-1-1-4-1

Fig. 1. Field view of crossing block comprises 7 inbred lines under study.

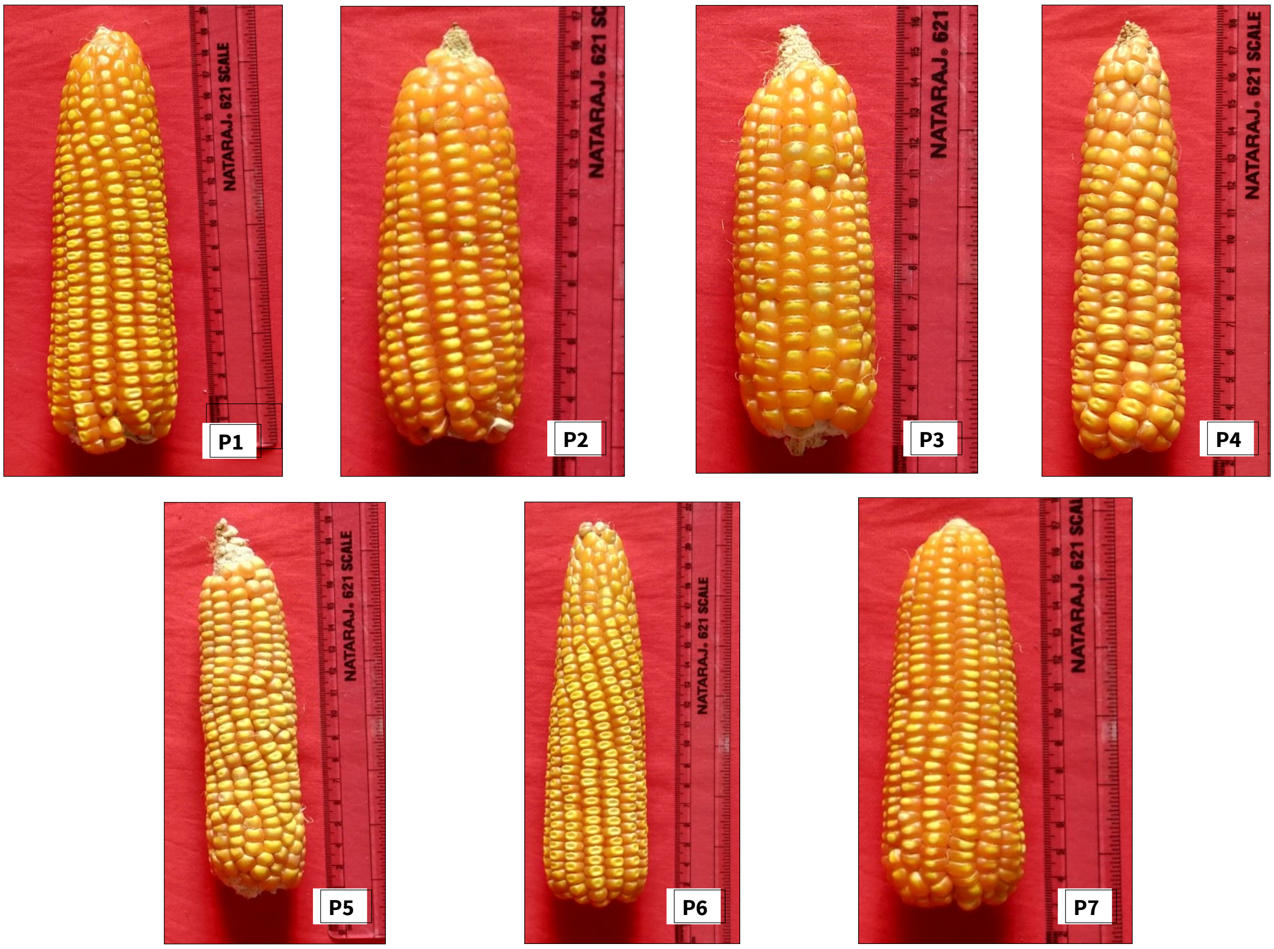
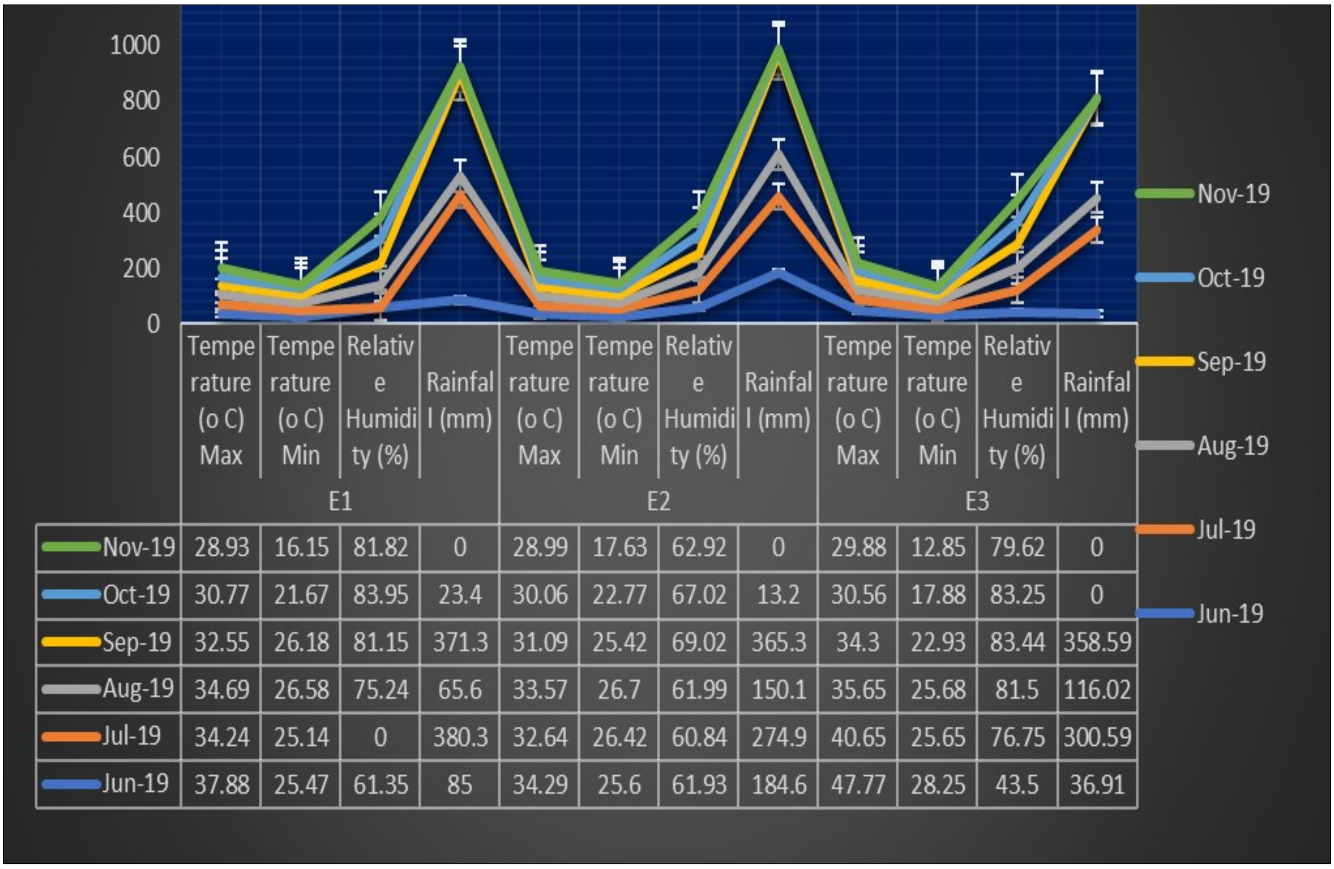
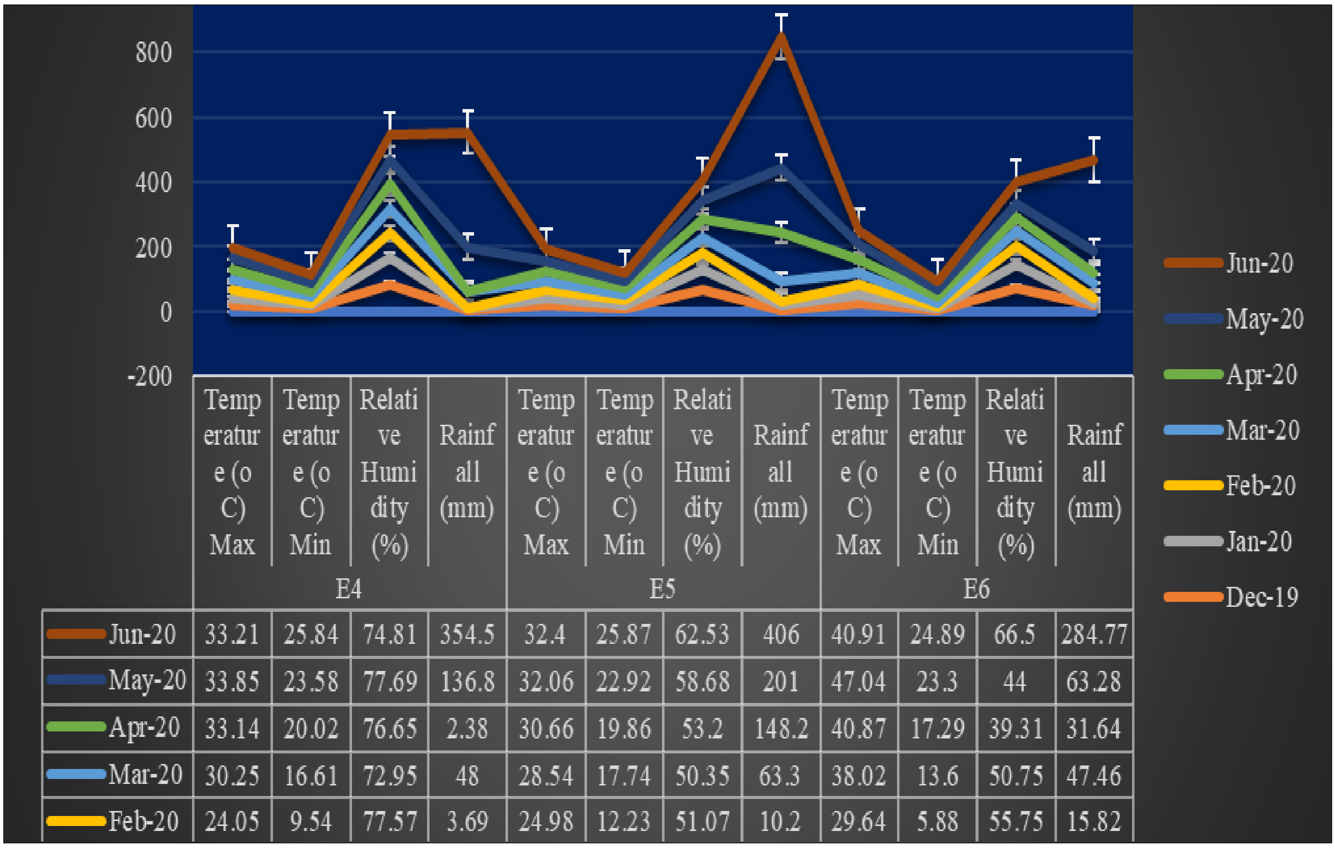


Fig. 2. Seven maize inbred lines used in crossing programme. P1: DTPYC9-F46-3-1-1-2-3-2-2-B*9, P2: BML-7, P3: VL-1055, P4: ZL-14501, P5: [CML-161/CML-165]-BBB-11- BBB/CML-193, P6: ZL-145312 and P7: CML-117-3-4-1-1-4-1.



	E1 Temperature (o C) Max	E1 Temperature (o C) Min	E1 Relative Humidity (%)	E1 Rainfall (mm)	E2 Temperature (o C) Max	E2 Temperature (o C) Min	E2 Relative Humidity (%)	E2 Rainfall (mm)	E3 Temperature (o C) Max	E3 Temperature (o C) Min	E3 Relative Humidity (%)	E3 Rainfall (mm)
Nov-19	28.93	16.15	81.82	0	28.99	17.63	62.92	0	29.88	12.85	79.62	0
Oct-19	30.77	21.67	83.95	23.4	30.06	22.77	67.02	13.2	30.56	17.88	83.25	0
Sep-19	32.55	26.18	81.15	371.3	31.09	25.42	69.02	365.3	34.3	22.93	83.44	358.59
Aug-19	34.69	26.58	75.24	65.6	33.57	26.7	61.99	150.1	35.65	25.68	81.5	116.02
Jul-19	34.24	25.14	0	380.3	32.64	26.42	60.84	274.9	40.65	25.65	76.75	300.59
Jun-19	37.88	25.47	61.35	85	34.29	25.6	61.93	184.6	47.77	28.25	43.5	36.91

Fig. 3. Avergae monthly weather report during crop growing in Kharif, 2019. The environments, E1: Bihar Agricultural college, BAU, Sabour, Bhagalpur, Bihar (Zone-IIIA), E2: Bhola Paswan Shastri Agricultural College, Purnea, Bihar (Zone-II) and E3: Pulse Research Centre, Mokama, Patna (Zone-IIIB) of Bihar where experiments were conducted. Max: Maximum, Min: Minimum and mm: millimetres.



	E4 Temperature (o C) Max	E4 Temperature (o C) Min	E4 Relative Humidity (%)	E4 Rainfall (mm)	E5 Temperature (o C) Max	E5 Temperature (o C) Min	E5 Relative Humidity (%)	E5 Rainfall (mm)	E6 Temperature (o C) Max	E6 Temperature (o C) Min	E6 Relative Humidity (%)	E6 Rainfall (mm)
Jun-20	33.21	25.84	74.81	354.5	32.4	25.87	62.53	406	40.91	24.89	66.5	284.77
May-20	33.85	23.58	77.69	136.8	32.06	22.92	58.68	201	47.04	23.3	44	63.28
Apr-20	33.14	20.02	76.65	2.38	30.66	19.86	53.2	148.2	40.87	17.29	39.31	31.64
Mar-20	30.25	16.61	72.95	48	28.54	17.74	50.35	63.3	38.02	13.6	50.75	47.46
Feb-20	24.05	9.54	77.57	3.69	24.98	12.23	51.07	10.2	29.64	5.88	55.75	15.82

Fig. 4. Avergae monthly weather report during crop growing in Rabi, 2019-20. The environments, E4: Bihar Agricultural college, BAU, Sabour, Bhagalpur, Bihar (Zone-IIIA), E5: Bhola Paswan Shastri Agricultural College, Purnea, Bihar (Zone-II) and E6: Pulse Research Centre, Mokama, Patna (Zone IIIB) was the location of Bihar where experiments were conducted. Max: Maximum, Min: Minimum and mm: millimeters.

weight. The grain yield per plant (g) at 15 % moisture was calculated following modified formula (12).

$$\text{Grain yield per plant (g)} = \text{Fresh ear weight (g)} \times \frac{100 - \text{Grain moisture at harvest}}{100 - 15} \times \frac{0.80 \times 1.176}{10}$$

Here,

The shelling coefficient is 0.80

A constant factor of 1.176 is used to modify grain yield at 15 % moisture content.

10 is the sample plants were chosen at random.

15 is the required moisture percentage in maize grain for storage.

Griffing's Method-II and Model-I (1956a) was used to quantify the impacts of parental lines' general combining ability (GCA) and hybrids' specific combining ability (SCA). Heterosis was calculated grounded on 2 principles, better parent heterosis (BPH) and standard heterosis (SH), by means of the following formulas:

$$\text{Better parent heterosis} = \frac{\overline{F}_1 - \overline{BP}}{\overline{BP}} \times 100$$

$$\text{Standard heterosis} = \frac{\overline{F}_1 - \overline{SH}}{SH} \times 100$$

Where, $\overline{F}_1, \overline{BP}, \overline{SH}$ are the average performance over replication of F_1 hybrid, better parent and standard hybrid as check, respectively.

The correlation coefficients for heterosis were assessed by using the R-studio software version 4.4.1.

Results and Discussion

Combining ability for quantitative characters using analysis of variance

Highly significant GCA effects for parental lines and SCA effects for hybrids were observed for all the quantitative traits under study (Table 2) indicating the presence of variability due to both additive and non-additive gene effects. In addition to finding high yielding unchanging single cross, it is imperative to determine parent lines that have the average grain yield but also have stable GCA effects, in order to tailor the environmental deviations.

In the present study, highly significant GCA x environments and SCA x environments interactions were observed for all characters (Table 2). These results suggested that both GCA and SCA were strongly influenced by environmental factors. With the exception of days to 50 % anthesis, ear length and 1000 grain weight, the mean squares resulting from GCA x environments were larger than those from SCA x environment interactions for all other traits. This indicates that GCA was more influenced by environment than SCA.

For all traits examined, the pooled variance component estimates revealed a lower ratio of σ^2 gca/σ^2 sca, indicating a preponderance of non-additive gene effects in character expression, thereby highlighting the potential benefits of heterosis breeding. Additionally, all studied traits exhibited high broad-sense heritability estimates (0.92 - 0.96), demonstrating that phenotypic variation in yield-related parameters and flowering time was highly heritable. These results are in close conformity with the previous findings for these test characters (13-20).

Variable combining ability effects made by genotypes

Several parental lines in this study, displayed favorable GCA effects in the desirable direction. On the basis of the estimated GCA effects of the 7 parental lines, P1 and P5 exhibited highly significant negative GCA effects for days to 50 % anthesis (DPA) and Days to 50 % silking (DPS), suggesting their genetic potential for reducing flowering time. Similarly, P3 showed highly significant negative GCA effects for plant height (PH) and ear height (EH), suggesting its potential for reducing plant height (Table 3).

Parental line P1 exhibited highly significant positive GCA effects for ear diameter (ED), grain rows per ear (GRPE), grain number per row (GNPR) and grain yield per plant (GYPP), along with highly significant negative GCA effects for DPA and DPS, highlighting its potential for improving GYPP while promoting early flowering. Additionally, P6 and P7

Table 2. Combining ability and heritability for quantitative characteristics under investigation using pooled analysis of variance

Source of variation	d.f.	Mean squares									
		DPA	DPS	PH	EH	EL	ED	GRPE	GNPR	TGW	GYPP
GCA	6	73.34**	126.30**	2349.38**	2037.24**	8.95**	0.51**	7.70**	118.53**	12423.64**	1681.51**
SCA	21	70.36**	73.67**	2388.89**	662.18**	19.42**	1.09**	12.35**	222.25**	6552.92**	9451.71**
Environments	5	14352.40 **	14890.89**	3185.79**	3002.90**	36.84**	1.47**	4.51**	267.29**	37098.83**	24895.80**
GCA x Environments	30	6.63 **	8.25**	171.16**	111.44**	0.99**	0.08**	2.06**	11.44**	728.62**	499.77**
SCA x Environments	105	7.24 **	6.86**	104.00**	54.32**	1.087**	0.04**	1.44**	6.23**	733.22**	356.43**
Error	324	1.23	1.21	46.04	22.66	0.44	0.01	0.17	1.77	214.75	90.43
Heritability (bs)		0.95	0.96	0.93	0.92	0.92	0.96	0.95	0.97	0.92	0.96
σ^2 gca/ σ^2 sca		0.12	0.19	0.11	0.35	0.05	0.05	0.07	0.06	0.21	0.02

* & **: level of significance at 5 % and 1 %, respectively. DPA: Days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, TGW: 1000-grain weight and GYPP: grain yield per plant.

Table 3. General combining ability (GCA) effects estimates for 7 parental lines for the quantitative variables under investigation

Sources	DPA	DPS	PH	EH	EL	ED	GRPE	GNPR	TGW	GYPP
P1	-2.25**	-2.94**	2.44**	4.87**	0.01	0.04**	0.59**	0.34*	-7.51**	5.67**
P2	-0.06	0.07	3.14**	0.41	-0.75**	0.19**	0.36**	-0.73**	-1.39	0.31
P3	1.21**	1.68**	-14.60**	-12.46**	-0.23**	-0.08**	-0.43**	-1.58**	1.05	-4.98**
P4	0.48**	0.61**	1.26	-0.34	0.17*	-0.10**	-0.38**	-0.46**	12.28**	-6.38**
P5	-0.51**	-0.68**	1.55	-0.71	0.55**	-0.04**	0.12*	-0.17	-3.76*	-2.31
P6	0.06	-0.06	5.21**	1.59**	0.05	-0.04**	-0.19**	-0.49**	23.70**	6.37**
P7	1.07**	1.32**	1.02	6.63**	0.21*	0.02	-0.07	3.09**	-24.38**	9.05**
SE(gi)	0.14	0.14	0.86	0.60	0.08	0.01	0.05	0.17	1.85	1.20
C.D. at 5 %	0.28	0.27	1.68	1.18	0.17	0.03	0.10	0.33	3.63	2.36
SE (gi-gj)	0.21	0.21	1.31	0.92	0.13	0.02	0.08	0.26	2.82	1.83
C.D. at 5 %	0.42	0.67	2.57	1.80	0.25	0.04	0.16	0.50	5.55	3.60

* & **: level of significance at 5 % and 1 %, respectively. DPA: Days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, TGW: 1000-grain weight and GYPP: grain yield per plant.

showed highly significant positive GCA effects for GYPP and one or more of its contributing traits. Therefore, P1, P6 and P7 could be effectively utilized for enhancing hybrid yield potential, while P3 could be employed to reduce plant height in breeding programs. These findings are consistent with earlier studies on seed yield and its attributes (21-26).

Several commonly used parental lines exhibited highly desirable GCA effects and SCA analysis indicated that hybrids with elite parental lines were identified as combinations with significantly positive SCA effects (Table 4 and Fig. 5). Based on SCA effect estimates, the hybrids P3 × P6, P4 × P5, P2 × P5, P2 × P3, P2 × P4, P3 × P4, P2 × P6, P3 × P5, P1 × P5, P1 × P6, P3 × P7, P4 × P7, P1 × P7, P1 × P2, P6 × P7, P1 × P3, P5 × P6 and P1 × P4 demonstrated highly significant positive SCA effects for grain yield per plant (GYPP) and yield-related traits, making them promising combinations for these traits.

Additionally, the hybrid P4 × P6 exhibited highly significant negative SCA effects for PH and EH, making it a suitable specific combination for reducing plant and ear height. Almost all hybrid combinations in this study showed significant to highly significant negative SCA effects for DPA and DPS, except for P1 × P7, P2 × P7, P3 × P5 and P5 × P7, indicating their genetic potential for early flowering.

Among the hybrids, P1 × P2, P1 × P3, P1 × P4, P1 × P5, P1 × P6, P1 × P7 and P6 × P7 were the most promising experimental hybrids, exhibiting high SCA and high GCA for at least 1 female parent, making them valuable for hybrid maize breeding programs or the development of synthetic maize varieties. These results align with previous findings in maize for the traits under investigation (16, 22, 23, 25-28).

Widespread heterosis seen for different traits

Significant to highly significant better parent heterosis (BPH) and standard heterosis (SH) were observed for almost all the characters under test (Table 5 and Fig. 6). The flowering traits, like DPA and DPS exhibited highly significant negative BPH for

Table 4. The specific combining ability (SCA) effects for the quantitative variables under investigation

Hybrids	DPA	DPS	PH	EH	EL	ED	GRPE	GNPR	TGW	GYPP
P1 × P2	-3.61**	-3.69**	2.66	-0.73	0.43	0.22**	0.10	1.69**	23.94**	17.38**
P1 × P3	-2.33**	-1.80**	8.35**	4.97**	0.58*	0.37**	1.20**	3.50**	15.73**	14.71**
P1 × P4	-2.82**	-3.06**	9.75**	6.40**	0.72**	0.13**	0.19	2.33**	19.58**	13.16**
P1 × P5	-1.95**	-2.06**	9.45**	5.48**	1.04**	0.10**	0.82**	2.36**	21.77**	22.64**
P1 × P6	-1.74**	-2.12**	10.35**	4.65**	0.77**	0.20**	0.34*	1.40**	28.60**	20.16**
P1 × P7	-0.47	-0.67	8.39**	1.66	0.28	0.06	-0.36*	2.74**	9.76	18.75**
P2 × P3	-0.90*	-1.09**	14.78**	11.49**	1.58**	0.44**	1.70**	4.02**	26.27**	30.68**
P2 × P4	-1.343 **	-1.07**	16.67**	6.80**	0.87**	0.29**	1.04**	3.54**	16.03**	28.49**
P2 x P5	-1.36**	-1.45**	13.79**	8.41**	1.46**	0.22**	0.59**	5.27**	11.79*	30.81**
P2 x P6	-1.48**	-1.29**	12.05**	3.098	0.70**	0.23**	0.31*	2.87**	18.86**	23.33**
P2 x P7	-0.26	-0.45	1.85	2.56	0.07	0.15**	0.14	2.37**	-3.60	5.91
P3 x P4	-3.00**	-3.35**	15.81**	7.59**	1.78**	0.32**	1.17**	4.39**	33.80**	27.15**
P3 x P5	-0.57	-0.62	16.27**	7.42**	1.17**	0.28**	1.35**	5.58**	5.792	22.82**
P3 x P6	-2.97**	-3.51**	14.67**	8.49**	1.79**	0.36**	0.96**	3.70**	41.30**	34.09**
P3 x P7	-1.09**	-1.34**	9.62**	3.92*	0.81**	0.24**	1.45**	4.03**	8.89	19.46**
P4 x P5	-3.34**	-2.77**	12.24**	6.39**	1.29**	0.28**	0.85**	3.41**	15.71**	31.13**
P4 x P6	1.98**	1.67**	-12.45**	-5.70**	-1.66**	-0.31**	-0.87**	-2.98**	-32.62**	-32.12**
P4 x P7	-1.25**	-1.10**	7.24**	3.24	0.65**	0.07	0.14	2.11**	17.25**	19.29**
P5 x P6	-2.31**	-1.88**	6.32*	0.96	0.77**	0.19**	0.48**	2.23**	11.80*	13.16**
P5 x P7	-0.54	-0.37	4.36	6.42**	0.73**	0.03	0.17	2.61**	5.42	6.74
P6 x P7	-1.39**	-1.77**	12.83**	7.01**	0.83**	0.06	0.50**	2.30**	0.72	15.40**
SE (Sij)	0.35	0.34	2.12	1.48	0.21	0.03	0.13	0.42	4.57	2.97
C.D. at 5 %	0.68	0.67	4.16	2.92	0.41	0.06	0.25	0.82	8.99	5.83
SE (Sij-Sik)	0.60	0.60	3.70	2.59	0.36	0.06	0.22	0.73	8.00	5.18
C.D. at 5 %	1.19	1.18	7.27	5.10	0.71	0.11	0.44	1.43	15.69	10.18
SE (Sij-Skm)	0.57	0.56	3.46	2.42	0.34	0.05	0.21	0.68	7.46	4.84
C.D. at 5 %	1.11	1.10	6.80	4.77	0.67	0.10	0.41	1.33	14.68	9.53

* & **: level of significance at 5 % and 1 %, respectively. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, GPP: grains per plant, TGW: 1000-grain weight and GYPP: grain yield per plant.

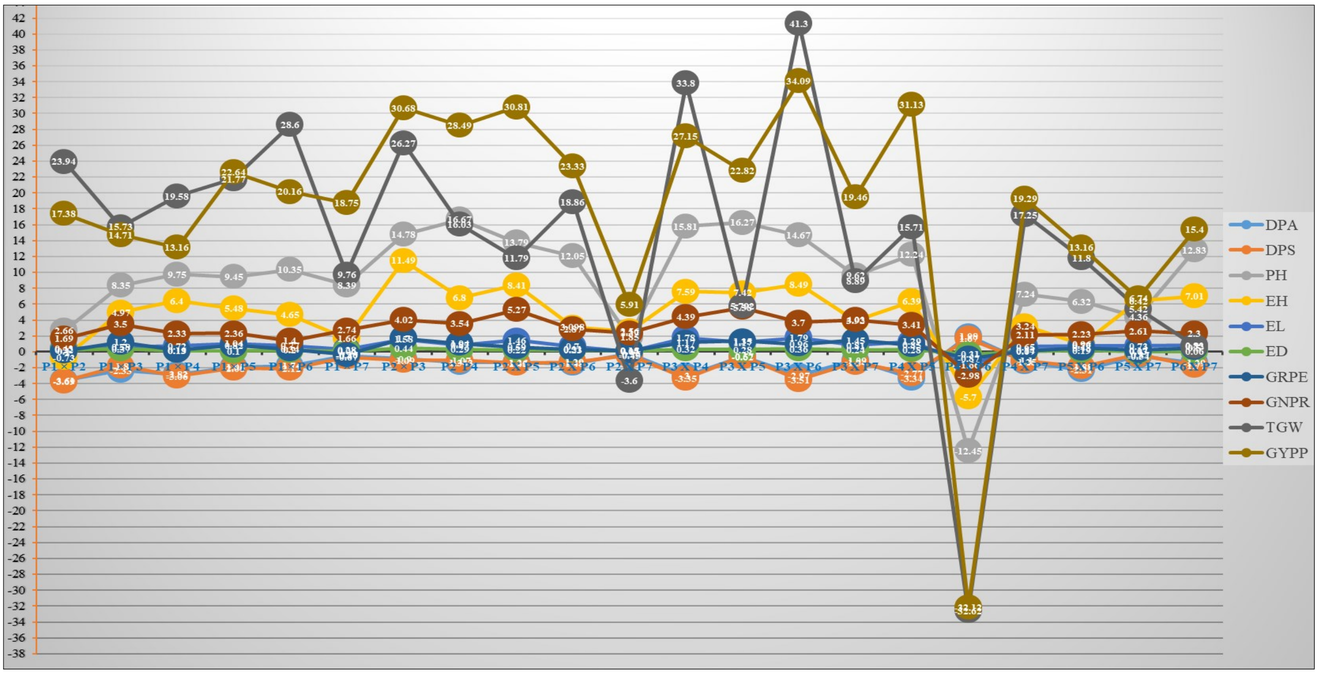


Fig. 5. The specific combining ability (SCA) effects for the quantitative traits. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, TGW: 1000-grain weight and GYPP: grain yield per plant.

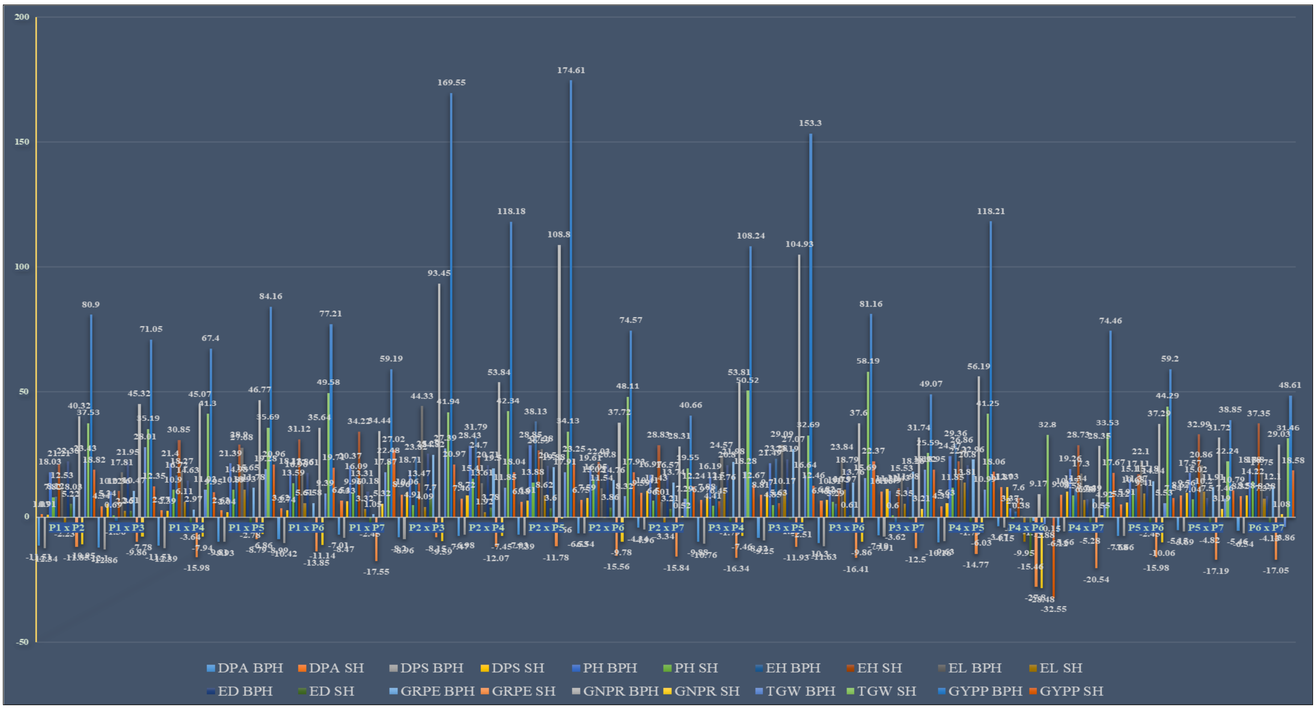


Fig. 6. Heterotic performance of hybrids for different quantitative traits. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, TGW: 1000-grain weight, GYPP: grain yield per plant, BPH: better parent heterosis and SH: standard heterosis.

all the hybrids under investigation, indicating that these hybrids had genetic potential for early flowering.

The top 5 hybrids with the highest significant BPH effects for GYP identified in the current study were P2 × P5, P2 × P3, P3 × P5, P4 × P5 and P2 × P4 (Table 5).

These hybrids also demonstrated highly significant positive BPH responses for yield-related traits such as 1000-grain weight (TGW), grain number per row (GNPR), grain rows per ear (GRPE), ear diameter (ED) and ear length (EL). However, P2 × P4 for EL and TGW and P4 × P5 for TGW, showed non-significant positive BPH responses. Almost all hybrid combinations under study exhibited highly significant SH for GYPP and at least 1 of its contributing traits. Among them, the most promising experimental hybrid, P1 × P7, exhibited high SH, high BPH, high SCA and high GCA for both parental lines, along with a strong heterotic response for grain yield per plant. Therefore, after rigorous multi-environmental testing to confirm its superiority and stability, this hybrid holds potential for commercial utilization.

Several previous studies have also emphasized the significance of heterosis and its application in plant

Table 5. Heterotic performance of hybrids for different quantitative traits under study

Hybrid	DPA		DPS		PH		EH		EL		ED		GRPE		GNPR		TGW		GYPP	
	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH	BPH	SH
P1 x P2	-11.51**	1.07	-12.34**	0.91	18.03**	7.82	18.03**	7.82	8.12	21.21*	12.53	-2.23	22.38**	5.22	8.03	-11.85**	40.32**	-10.95	23.43**	37.53**
P1 x P3	-12.10**	4.34*	-12.86**	5.34**	10.22	0.69	10.22	0.69	-1.56	10.36	17.81*	2.36	21.95**	2.51	10.47*	-9.86**	45.32**	-7.78	28.01**	35.19**
P1 x P4	-11.51**	2.77	-12.39**	2.39	21.40**	10.9	21.40**	10.9	16.72	30.85**	18.27*	6.11	14.63**	-3.64	2.97	-15.98**	45.07**	-7.94	11.03	41.30**
P1 x P5	-9.81**	2.63	-9.93**	2.04	21.39**	10.89	21.39**	10.89	14.98	28.90**	27.68**	10.93	15.65**	-2.78	11.78*	-8.79*	46.77**	-6.86	19.28**	35.69**
P1 x P6	-8.99**	3.62	-10.42**	2.74	18.13**	13.59*	18.13**	13.59*	16.96	31.12**	17.86*	5.61	17.61**	-0.39	5.58	-13.85**	35.64**	-11.14	9.39	49.58**
P1 x P7	-7.01**	6.54**	-8.47**	6.33**	20.37**	9.96	20.37**	9.96	16.09	34.22**	13.31	3.32	10.18**	-2.45	1.05	-17.55**	34.44**	5.32	17.87*	22.48**
P2 x P3	-8.20**	8.96**	-8.96**	10.06**	18.71**	4.91	18.71**	4.91	23.82*	13.47	44.33**	4.09	25.27**	7.70*	24.82**	-8.15*	93.45**	-9.59	27.39**	41.94**
P2 x P4	-7.47**	7.46**	-6.98**	8.72**	28.43**	15.41**	28.43**	15.41**	31.79**	24.70*	13.61	1.92	20.71**	3.78	19.50**	-12.07**	53.84**	-7.45	11.85	42.34**
P2 x P5	-7.03**	6.18**	-7.39**	6.61**	28.85**	13.88*	28.85**	13.88*	38.13**	26.59**	27.28**	8.62	20.50**	3.6	19.88**	-11.78**	108.80**	-0.66	17.91*	34.13**
P2 x P6	-6.53**	6.75**	-6.54**	7.59**	19.61**	15.02**	19.61**	15.02**	16.05	22.03*	11.54	-0.05	20.80**	3.86	14.76**	-15.56**	37.72**	-9.78	8.32	48.11**
P2 x P7	-4.34*	9.59**	-4.96**	10.41**	16.97**	6.5	16.97**	6.5	11.43	28.83**	6.01	-3.34	16.57**	3.21	13.74**	-15.84**	28.31**	0.52	7.29	19.55*
P3 x P4	-9.88**	6.97**	-10.76**	7.88**	16.19*	4.41	16.19*	4.41	12.5	6.45	24.57**	11.76	20.80**	-1.79	21.98**	-16.34**	53.81**	-7.46	18.28**	50.52**
P3 x P5	-8.32**	8.81**	-9.25**	9.70**	21.49**	4.85	21.49**	4.85	23.28	5.63	29.09**	10.17	23.19**	-1.24	27.07**	-11.93**	104.93**	-2.51	16.64*	32.69**
P3 x P6	-10.30**	6.47**	-11.63**	6.82**	10.31	6.07	10.31	6.07	5.29	10.73	23.84**	10.97	18.79**	0.61	13.76**	-16.41**	37.60**	-9.86	15.69*	58.19**
P3 x P7	-7.19**	10.16**	-7.91**	11.32**	10.49	0.6	10.49	0.6	-3.62	11.43	15.53*	5.35	11.98**	-0.85	18.26**	-12.50**	31.74**	3.21	18.92*	25.59**
P4 x P5	-10.16**	4.34*	-9.63**	5.63**	24.47**	11.85*	24.47**	11.85*	29.36**	22.40*	26.86**	13.81*	20.80**	-1.79	22.96**	-14.77**	56.19**	-6.03	10.99	41.25**
P4 x P6	-3.67*	11.87**	-4.15*	12.03**	3.37	-0.6	3.37	-0.6	2.32	7.6	0.38	-9.95	-0.18	-15.46**	-1.74	-27.80**	9.17	-28.48**	-2.88	32.80**
P4 x P7	-6.12**	9.03**	-5.66**	10.27**	19.26**	8.58	19.26**	8.58	11.34	28.73**	17.30*	6.95	6.98	-5.28	7.39	-20.54**	28.35**	0.55	4.92	33.53**
P5 x P6	-7.68**	5.12*	-7.66**	5.91**	15.10*	10.68	15.10*	10.68	11.37	17.11	22.10**	9.41	15.18**	-2.45	14.34**	-15.98**	37.29**	-10.06	5.53	44.29**
P5 x P7	-5.15**	8.67**	-5.69**	9.56**	17.57**	7.04	17.57**	7.04	15.02	32.99**	20.86**	10.2	7.5	-4.82	11.91*	-17.19**	31.72**	3.19	7.46	22.24**
P6 x P7	-5.46**	8.32**	-6.54**	8.58**	18.78**	14.22*	18.78**	14.22*	18.80*	37.35**	17.75*	7.37	8.28*	-4.13	12.10*	-17.05**	29.03**	1.08	-3.86	31.46**
S.E. (d)	1.57	1.57	1.55	1.55	9.60	9.60	6.73	6.73	0.94	0.94	0.15	0.15	0.58	0.58	1.88	1.88	20.72	20.72	13.45	13.45
C.D.at 5 %	3.09	3.09	3.05	3.05	18.88	18.88	13.24	13.24	1.85	1.85	0.29	0.29	1.14	1.14	3.70	3.70	40.77	40.77	26.46	26.46

* & **: level of significance at 5 % and 1 %, respectively. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, GPP: grains per plant, TGW: 1000-grain weight and GYPP: grain yield per plant.

breeding (23, 26, 29-31).

Heterosis for related traits with high correlation

Significant variations were observed in the correlations of heterosis among different attributes (Fig. 7 and 8). SH had exceedingly noteworthy positive relationship (0.98***) between 2 flowering traits, DPA and DPS, while the correlation of these traits with other were insignificant (Fig. 7).

GYPP showed a highly significant positive SH association with ED followed by GNPR and GRPE. Additionally, ED showed highly significant and positive correlation with GRPE.

A similar pattern was noted for the BHP which had highly significant positive correlation (0.97***) between 2 flowering traits, DPA and DPS. However, these flowering traits exhibited a significant negative correlation with ED and TGW (Fig. 8).

Among yield-related traits, GYPP had the highest significant positive BPH correlation with GNPR, followed by ear length (EL), ED, GRPE, ear height (EH), plant height (PH) and TGW. Additionally, PH displayed a highly significant positive association with EH, whereas ED was strongly correlated with TGW, GRPE, EL, GNPR and GYPP.

These findings suggest that heterotic performance is strongly influenced by associated traits and is primarily genotype-dependent. The results are in close agreement with previous studies (20, 32).

Conclusion

The investigation highlighted that the effects of GCA and SCA were highly noteworthy for all the test characters, which disclose the existence of both additive and non-additive gene effects. Highly significant GCA x environments and SCA x environments interactions were found for all the test traits suggested that both GCA and SCA were greatly affected by environments.

Several parental lines displayed desirable GCA effects; however, P1 was the only parental line that demonstrated highly significant positive GCA effects for ED, GRPE, GNPR and GYPP, along with highly significant negative GCA effects for DPA and DPS. This highlights its potential in increasing GYPP while promoting early flowering.

Vast range of heterosis was seen in the present study for different traits however, with the hybrid P1 × P7 emerging as the most promising, as it exhibited high SH, BPH, high SCA and high GCA for both parents, along with a heterotic response to grain yield per plant. Hence, this hybrid holds commercial potential and can be utilized following rigorous testing to ensure its superiority and stability.

Furthermore, a highly significant correlation was observed for SH between 2 flowering traits, DPA and DPS, whereas their correlation with other traits was insignificant. These findings explained the objectives of present investigations.

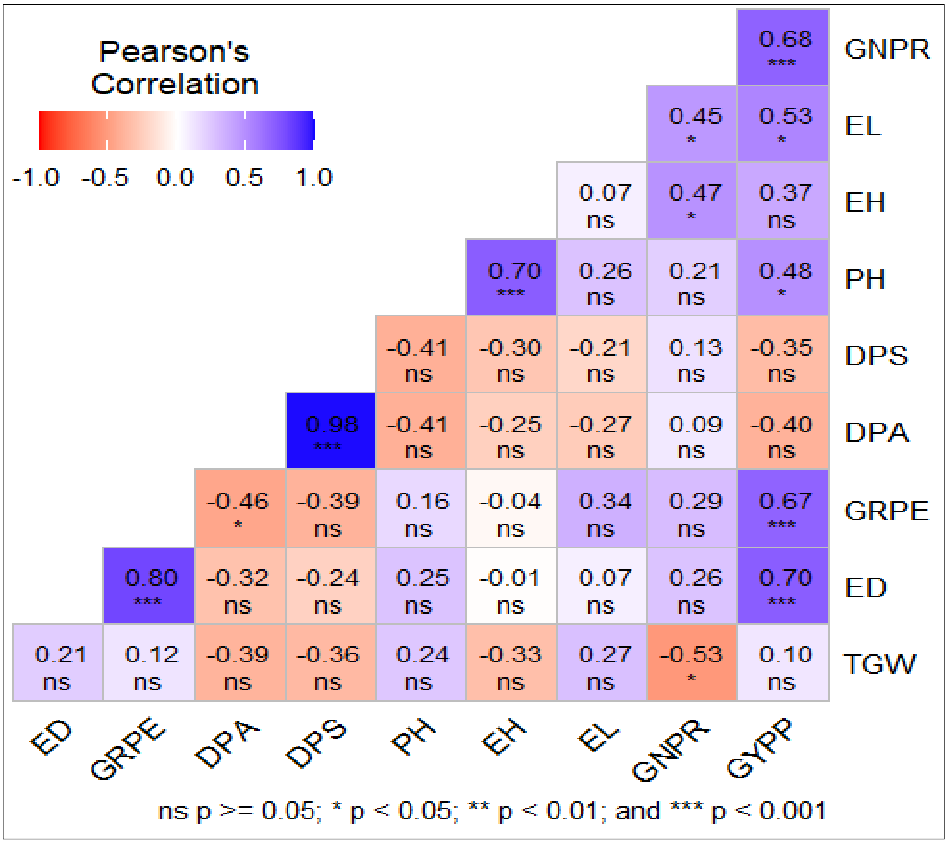


Fig. 7. The correlation coefficient for standard heterosis among the characters under investigation. The correlation level is color-coded rendering to the color keys. The blue and red boxes indicate positive and negative correlation coefficients, respectively. The symbols *, ** and *** indicate significance at 0.05, 0.01 and 0.001 probability levels, respectively. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, GPP: grains per plant, TGW: 1000-grain weight and GYPP: grain yield per plant.

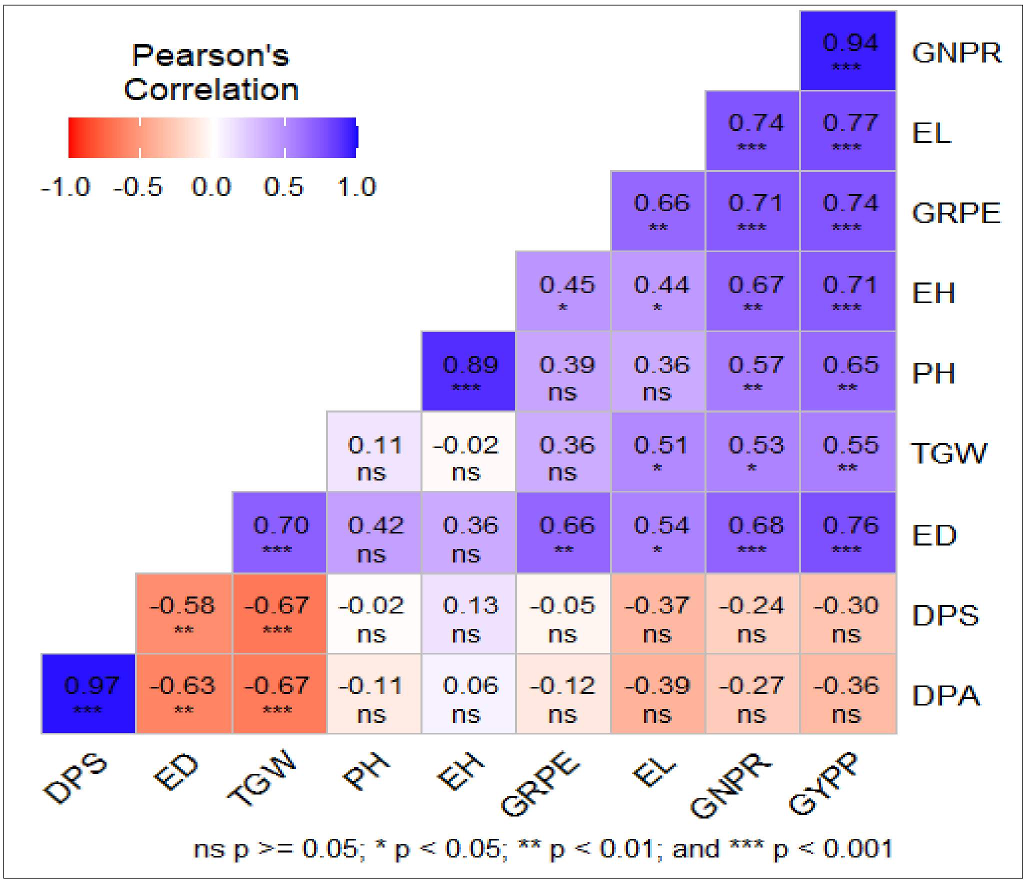


Fig. 8. The correlation coefficient for better parent heterosis among the characters under investigation. The correlation level is color-coded rendering to the color keys. The blue and red boxes indicate positive and negative correlation coefficients, respectively. The symbols *, ** and *** indicate significance at 0.05, 0.01 and 0.001 probability levels, respectively. DPA: days to 50 % anthesis, DPS: days to 50 % silk, PH: plant height, EH: ear height, EL: ear length, ED: ear diameter, GRPE: grain rows per ear, GNPR: grain number per row, GPP: grains per plant, TGW: 1000-grain weight and GYPP: grain yield per plant.

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Authors' contributions

NKC carried out research work, participated in data collection, analysis and drafting of manuscript. RBPN participated conceived of the study and participated in its design, participated in data collection, analysis and drafting of manuscript. HB and NR participated in writing and proofreading of manuscript. All the authors read and agreed for the final shape of manuscript.

Compliance with ethical standards

Conflict of interest: The authors declares that they have no competing interests.

Ethical issues: None

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