



Exploiting combining ability and heterosis for yield and fiber quality improvement in cotton (*Gossypium barbadense* L.)

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Abstract

The present investigation in *Gossypium barbadense* L. using a full diallel mating design involving six diverse genotypes revealed substantial genetic variability in agronomic and fiber quality traits. Additive gene action predominated for ginning percentage, fiber length, and fiber strength, whereas seed cotton yield and days to first flowering were mainly governed by non-additive gene action with significant reciprocal effects. Parents RACT 3790 and RACT 5293 were superior general combiners for yield, whereas RACT 3844, RACT 5293, and RACT 5296 were valuable donors for fiber quality improvement. Hybrids RACT 3844 × RACT 5293, RACT 5293 × RACT 5296, and RACT 3790 × RACT 5296 were identified as promising combinations for yield improvement, whereas RACT 3959 × RACT 5294 was superior for fiber quality traits. These results provide valuable information for identification of parental lines and hybrid combinations for exploiting both the additive and non-additive gene actions for developing high-yielding cotton cultivars with improved fiber quality.

Keywords: Cotton, Diallel, reciprocal effects, gene action, GCA, SCA.

INTRODUCTION

Cotton, a cornerstone of the global textile industry, provides the world's most important natural fiber in terms of contribution to trade, textile industry, employment and foreign exchange (Rai and Sangwan, 2020, Senguttuvan *et al.*, 2024). Among the cultivated species, *Gossypium barbadense* (L.), commonly known as Sea Island, Pima, or Egyptian cotton, is renowned for producing extra-long staple (ELS) fibers of exceptional quality (Zhao, 2022). These fibers are distinguished by their superior length, remarkable strength, and exceptional fineness, making them the preferred raw material for luxury textiles and high-performance fabrics (Yuan, 2015). Despite its economic importance and desirable fiber characteristics, its commercial cultivation is limited due to relatively low productivity, long crop duration and narrow environmental adaptation. Breeding *G. barbadense* also poses certain challenges complicated by the difficulty of combining high yield, earliness, and superior fiber quality within a single genetic background (Lamlom *et al.*, 2024), as these traits often exhibit unfavourable associations (Clement *et al.*, 2012). Consequently, there is a need for a more thorough understanding of the genetics underlying the quantitative traits in question.

Combining ability analysis is a widely used biometric method that partitions genetic variance into GCA and SCA. In addition to the contribution of nuclear genes, there could be other sources of inheritance, such as the maternal effect and the cytoplasmic genome, which can be quantified using the reciprocal differences between the direct and reverse crosses. The sources of this reciprocal effect may originate from cytoplasmic

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genomes, maternal regulation during seed development, or nuclear–organellar interactions (Chu *et al.*, 2025). The estimation of reciprocal effects is highly recommended for genetically divergent materials because of the possible contribution of the cytoplasmic genome to heterosis (Fan *et al.*, 2014). Unfortunately, many cotton breeding programs fail to accurately estimate these reciprocal effects. Numerous genetic factors influence reciprocal differences, perhaps the most important of which is that two sets of chromosomes of the endosperm, which contain three sets of chromosomes, come from the maternal parent (Gonzalo *et al.*, 2007). Moreover, non-allelic reciprocal effects have been reported to invalidate the additive dominant model (Abedi *et al.*, 2015).

Heterosis is strongly influenced by the genetic divergence of the parents. Crossing adapted Indian and exotic germplasm can enhance recombination, promote favourable allele complementation, and improve the probability of identifying superior hybrids in the future. Therefore, the present study utilized six diverse *G. barbadense* genotypes in a full diallel mating design, including reciprocals, to (i) assess heterosis for yield, earliness, ginning percentage, and fiber quality traits; (ii) estimate GCA and SCA to understand the nature of gene action; and (iii) quantify reciprocal effects to determine the contribution of maternal inheritance and cross direction.

MATERIALS AND METHODS

The experimental material comprised six genetically diverse *G. barbadense* L. genotypes, comprising of three Indian and three exotic lines (**Table 1**), selected based on contrasting performance for yield, earliness and fiber quality traits and sourced from Rasi Seeds (P) Ltd., Attur, Tamil Nadu. The parental genotypes were crossed during winter 2024 in a full diallel mating design. The 30 F_1 hybrids (15 direct and 15 reciprocal crosses) along with six parental lines, were evaluated under during winter 2025 in a Randomized Complete Block Design (RCBD) with three replications at the Rasi Seeds research farm, Attur, Tamil Nadu, India. Each genotype plot was grown in a single 6 m row with 90 cm inter-row and 60 cm intra-row spacing. Recommended agronomic practices and need-based plant protection measures were followed throughout the crop period.

Observations on days to first flowering, plant height (cm), number of bolls plant⁻¹, boll weight (g), ginning percentage (%), and seed cotton yield (g), were recorded on three randomly selected and tagged plants per replication in each genotype. The mean of the above observations for each trait in each replication was calculated and used for statistical analysis. Fiber quality traits included fiber length (mm), fiber strength (g tex⁻¹), elongation (%) and micronaire were measured using a High-Volume Instrument (HVI) at Rasi Seeds (P) Ltd., Attur, Tamil Nadu, India.

Combining ability was calculated using the Griffing's (1956) Method I by employing the diallel analysis module of TNAU STAT (Manivannan, 2014), which partitioned the

variance into GCA, SCA, reciprocal and error effects. Mid-parent heterosis (MPH) and better-parent heterosis (BPH) were estimated as the percentage deviation of the F_1 hybrid performance from the mid-parent and better-parent values, respectively, following Fonseca and Patterson (1968) and Wynne *et al.* (1970).

RESULTS AND DISCUSSION

Analysis of variance showed significant differences among genotypes for most of the traits studied. This indicates that there is considerable genetic variability among the parental lines and their hybrids (**Table 2**).

Significant GCA mean squares for number of bolls, boll weight, ginning percentage, seed cotton yield, fiber length, fiber strength, elongation and micronaire indicated the involvement of additive gene effects, whereas significant SCA mean squares for days to first flowering, number of bolls, boll weight, seed cotton yield, fiber length, fiber strength, elongation and micronaire suggested the contribution of non-additive gene effects. The GCA and SCA component estimates, together with the GCA/SCA ratio, further indicated a greater contribution of non-additive gene effects for all traits in this experimental material. Similar findings were reported by Abd El Razek *et al.* (2026) and El-Seidy *et al.* (2026) in cotton. Significant reciprocal effects were observed for days to first flowering, plant height, number of bolls, boll weight, seed cotton yield, fiber length, fiber strength, and micronaire, whereas ginning percentage and elongation showed non-significant reciprocal effects. Similar results for reciprocal effects of days to first flowering, plant height, number of bolls, boll weight, seed cotton yield and fibre elongation were in line with the findings of Lekshmi *et al.* (2023).

Mean performance

The mean performance of parents, direct crosses and their reciprocals for agronomic and fibre quality traits in F_1 s of studied *G. barbadense* crosses is shown in **Table 3**. Substantial variation among the six parents and their direct and reciprocal progenies, with mean values ranging from 61.24 to 67.89 days for days to first flowering, 138.67 to 179.67 cm for plant height, 50.00 to 136.00 bolls plant⁻¹, 2.90 to 4.43 g for boll weight, and 148.33 to 279.67 g for seed cotton yield. Fibre traits also showed appreciable variation, with fibre length ranging from 30.10 to 38.50 mm, strength from 38.60 to 55.20 g tex⁻¹, elongation from 5.40 to 7.30%, and micronaire from 3.50 to 5.60. Among the parents, RACT 5296 recorded the highest fibre strength (55.20 g tex⁻¹), while RACT 5293 and RACT 5294 showed high ginning percentage (38.50 and 38.90%, respectively), and RACT 3790 and RACT 3959 recorded relatively high seed cotton yield (206.67 and 208.33 g plant⁻¹, respectively).

The direct and reciprocal crosses exhibited considerable variation in mean performance, with several combinations

Table 1. List of *G. barbadense* genotypes used in this study

S.No.	Parent genotype	Geographical origin
1	RACT 3844	India
2	RACT 3790	India
3	RACT 3959	India
4	RACT 5293	Egypt
5	RACT 5294	Egypt
6	RACT 5296	Egypt

Table 2. Analysis of variance (mean squares) for ten morphological traits

Traits	Source of variation				Variance components		GCA/ SCA ratio	RECI	
	GCA MS	SCA MS	RECI MS	Error	GCA component	SCA component		RECI SS	RECI contribution
df	5	15	15	70					(%)
Days to first flowering	1.33	2.36 **	2.98 **	0.58	0.06	1.78	0.03	44.66	51.49
Plant height	55.00	48.63	146.62 *	73.04	1.5	24.41	0.06	2199.28	68.65
Number of bolls per plant	670.15 **	360.57 **	155.32 **	31.57	53.22	329	0.16	2329.83	21.01
Boll weight	0.14 **	0.12 **	0.1**	0.02	0.01	0.1	0.10	1.50	37.59
Ginning percentage	4.60 **	2.001	1.19	1.27	0.28	0.73	0.38	17.87	25.21
Seed cotton yield	711.47**	783.02 **	1390.16 **	158.48	46.08	624.54	0.07	20852.50	57.68
Fibre length	11.10 **	3.45 **	1.53 **	0.26	0.9	3.19	0.28	22.91	17.61
Fibre strength	55.09 **	12.32 **	5.22 **	0.99	4.51	11.32	0.40	78.25	14.53
Elongation	0.32 **	0.32 **	0.066	0.08	0.02	0.24	0.08	0.99	13.29
Micronaire	0.39 **	0.16 **	0.05 **	0.01	0.03	0.15	0.20	0.79	15.33

** Significance at 1% level

*Significance at 5% level

exceeding their parents for individual economic traits. Among the direct crosses, RACT 5293 × RACT 5294 recorded the highest seed cotton yield (279.67 g plant⁻¹), while RACT 3790 × RACT 5296 showed high yield (261.00 g plant⁻¹) together with high fibre length (38.27 mm) and strength (48.97 g tex⁻¹). Reciprocal combinations also displayed distinct performance; notably, RACT 5293 × RACT 3959 recorded the highest boll weight (4.43 g), whereas RACT 5296 × RACT 5294 showed relatively high seed cotton yield (241.33 g plant⁻¹). The differences between several direct and reciprocal combinations, particularly for seed cotton yield, boll weight and fibre traits, indicate that cross direction contributed to the expression of performance and therefore warranted further evaluation through reciprocal-effect analysis.

General combining ability effects

The *gca* effects revealed differential parental contributions toward yield and fiber quality improvement (Table 4). With respect to seed cotton yield, RACT 3790 (10.18) had higher *gca* effects followed by RACT 5293 (7.98), making these two parents good initial donors for enhancing the yield. For the trait number of bolls per plant, RACT 3959 (8.57), RACT 3790 (7.77), and RACT 5293 (3.55) demonstrated superior general combining ability. In case of fiber quality traits, (1.18) was found to be better for fiber length because of its high *gca* effects, whereas RACT 5296 (4.13) was found to be a better general combiner for fiber strength. Among the parents, RACT 5293 emerged as the most versatile genotype owing to the presence of favourable genes in relation to earliness (-0.52), boll weight (0.18), seed cotton yield (7.98), and fiber length (1.18) traits. This could be attributed to the fact that it harbours various favourable genes and hence suited as an effective donor parent in hybridization programs as well as for varietal improvement. Despite exhibiting

negative *gca* effects for most traits, RACT 5294 showed significant positive *gca* effects for ginning percent (0.73) and elongation (0.19), indicating that it could serve as a useful donor parent for improving ginning percent and elongation trait specifically in breeding programmes.

Specific combining ability effects and Heterosis

Significant *sca* effects (Table 5) were observed in several crosses, indicating the importance of non-additive gene interactions. In case of seed cotton yield, the cross RACT 3844 × RACT 5293 (35.16) showed the maximum positive and significant *sca* effect, followed by RACT 5293 × RACT 5296 (21.94), suggesting their use in hybrid development. For the number of bolls, RACT 3844 × RACT 5293 (12.56), RACT 3959 × RACT 5294 (12.04), and RACT 3844 × RACT 5294 (11.70) showed high *sca* effects. Negative and significant *sca* effects were observed in the crosses RACT 3844 × RACT 5296 (-1.25) RACT 3844 × RACT 3959 (-1.12) and RACT 3790 × RACT 3959 (-1.06) for days to first flowering.

High *sca* effects for all the fiber traits (fiber length, fiber strength, and micronaire) were observed in the cross RACT 3959 × RACT 5294. Similar high *sca* effects for fiber quality and yield-related traits has been reported by Shahzad *et al.* (2019) in upland cotton. The crosses RACT 3959 × RACT 5294 and RACT 3790 × RACT 5296 showed highly significant *sca* effects for both fiber length and fiber strength. This superior performance is reflective of the dominance effect which is not fixable, hence it can be exploited through hybrid breeding. In case of the trait fibre elongation, significant *sca* effect was observed in the cross RACT 3790 × RACT 5294 cross. High values of *sca* for fiber quality traits, in combination with improved fiber quality performance, have also been reported by Mohokar *et al.* (2025). Hybrids with high *sca* effects on

Table 3. Mean performance of parents, direct crosses and their reciprocals for agronomic and fibre quality traits in *G. barbadense*

S.No.	CROSS	Type	Days to first flowering	Plant height (cm)	Number of bolls per plant	Boll weight (g)	Ginning percentage	Seed cotton yield (g)	Fibre length (mm)	Fibre strength (g tex ⁻¹)	Elongation (%)	Micro naire
1	RACT 3844 x RACT 3844	Parent	67.89	149.00	70.00	2.90	35.13	178.00	36.10	38.60	7.10	3.50
2	RACT 3790 x RACT 3790	Parent	66.78	166.00	136.00	3.50	34.70	206.67	36.30	40.90	6.20	3.80
3	RACT 3959 x RACT 3959	Parent	65.11	160.00	121.00	3.70	32.40	208.33	31.70	42.00	6.70	4.00
4	RACT 5293 x RACT 5293	Parent	63.33	150.00	90.00	3.50	38.50	162.67	38.20	50.30	6.60	4.80
5	RACT 5294 x RACT 5294	Parent	64.25	149.00	50.00	3.40	38.90	193.00	30.10	43.80	7.30	5.60
6	RACT 5296 x RACT 5296	Parent	63.11	170.00	94.00	3.90	39.10	177.33	34.20	55.20	6.60	5.20
7	RACT 3844 x RACT 3790	Direct	64.23	155.67	117.00	3.70	37.77	196.33	34.63	44.27	6.70	4.13
8	RACT 3844 x RACT 3959	Direct	65.99	153.67	111.33	3.30	37.70	224.33	36.90	44.23	6.33	4.50
9	RACT 3844 x RACT 5293	Direct	65.07	166.33	126.00	3.93	37.47	260.00	37.70	44.57	6.30	4.33
10	RACT 3844 x RACT 5294	Direct	64.43	141.67	81.67	3.20	37.30	190.00	32.97	41.50	6.47	4.30
11	RACT 3844 x RACT 5296	Direct	64.53	158.00	92.67	3.27	37.00	188.67	36.67	48.60	5.83	4.27
12	RACT 3790 x RACT 3959	Direct	64.31	172.00	114.33	3.20	37.00	237.33	37.97	46.03	6.37	4.30
13	RACT 3790 x RACT 5293	Direct	65.10	158.00	110.33	3.53	37.70	260.33	38.50	46.40	5.93	4.13
14	RACT 3790 x RACT 5294	Direct	63.13	147.33	123.33	3.03	38.00	223.67	34.33	38.83	7.03	4.23
15	RACT 3790 x RACT 5296	Direct	65.20	141.67	88.33	3.70	37.30	261.00	38.27	48.97	5.57	4.53
16	RACT 3959 x RACT 5293	Direct	62.03	143.00	128.67	3.07	34.73	233.67	37.70	41.37	5.97	4.10
17	RACT 3959 x RACT 5294	Direct	63.60	162.33	123.67	3.13	36.90	148.33	36.70	52.47	5.73	4.10
18	RACT 3959 x RACT 5296	Direct	67.23	179.67	111.67	3.30	35.50	180.33	35.77	50.27	6.50	4.20
19	RACT 5293 x RACT 5294	Direct	63.81	159.00	110.00	3.37	37.10	279.67	36.60	42.83	6.23	4.13
20	RACT 5293 x RACT 5296	Direct	62.75	164.67	117.00	3.90	35.90	243.33	37.37	48.87	6.00	4.37
21	RACT 5294 x RACT 5296	Direct	62.90	149.67	104.00	3.03	36.40	182.33	35.10	46.57	6.13	4.57
22	RACT 3790 x RACT 3844	Reciprocal	63.35	157.67	102.00	3.83	36.33	237.67	37.70	44.37	6.27	3.97
23	RACT 3959 x RACT 3844	Reciprocal	61.24	153.33	113.67	3.37	34.93	185.67	37.93	46.90	6.00	3.87
24	RACT 5293 x RACT 3844	Reciprocal	61.50	150.00	109.00	3.47	37.10	238.33	37.03	44.83	6.07	3.83
25	RACT 5294 x RACT 3844	Reciprocal	64.53	165.00	132.00	3.80	36.77	227.00	37.03	44.57	6.33	4.17
26	RACT 5296 x RACT 3844	Reciprocal	61.43	138.67	91.33	3.27	34.27	168.33	37.77	49.73	5.73	3.70
27	RACT 3959 x RACT 3790	Reciprocal	63.33	147.67	114.33	3.30	36.67	189.67	36.27	46.33	6.53	4.17
28	RACT 5293 x RACT 3790	Reciprocal	63.77	141.67	118.67	3.23	38.17	192.33	36.27	41.20	6.13	4.17
29	RACT 5294 x RACT 3790	Reciprocal	64.00	149.00	115.00	3.00	38.83	228.00	32.90	41.67	6.83	4.23
30	RACT 5296 x RACT 3790	Reciprocal	63.83	162.33	123.67	3.13	36.90	189.00	36.70	52.47	5.73	4.10
31	RACT 5293 x RACT 3959	Reciprocal	65.90	163.67	126.67	4.43	37.50	170.67	37.83	47.03	5.93	4.63
32	RACT 5294 x RACT 3959	Reciprocal	66.40	154.33	122.67	3.30	36.60	224.00	36.03	46.77	5.40	4.20
33	RACT 5296 x RACT 3959	Reciprocal	65.20	148.33	99.67	3.17	38.07	193.67	35.07	46.50	5.43	4.27
34	RACT 5294 x RACT 5293	Reciprocal	62.59	154.00	112.67	3.43	37.73	178.33	34.90	40.83	6.10	4.10
35	RACT 5296 x RACT 5293	Reciprocal	65.23	145.33	109.33	3.97	36.83	220.33	37.40	46.90	5.63	4.47
36	RACT 5296 x RACT 5294	Reciprocal	64.81	156.67	105.67	3.27	37.57	241.33	36.07	48.70	5.90	4.33
Mean												
Min.												
Max.												
SE(d)												
CD (5%)												

Table 4. Estimates of general combining ability effects (*gca*) for various characters in *G. barbadense*

S. No.	Parents	Days to first flowering	Plant height	Number of bolls per plant	Boll weight	Ginning percentage	Seed cotton yield	Fibre length	Fibre strength	Elongation	Micronaire
1	RACT 3844	0.12	-1.95	-7.43 **	-0.02	-0.45	-2.85	0.41 **	-1.47 **	0.14	-0.02
2	RACT 3790	0.26	0.3	7.77 **	-0.04	0.15	10.18 **	0.21	-1.34 **	0.08	-0.04
3	RACT 3959	0.4 *	3.05	8.57 **	-0.02	-0.99 **	-8.52 *	-0.17	0.29	-0.08	-0.02
4	RACT 5293	-0.52 *	-1.31	3.55 *	0.18 **	0.41	7.98 *	1.18 **	-0.25	-0.09	0.18 **
5	RACT 5294	-0.16	-2.04	-6.26 **	-0.15 **	0.73 *	0.18	-1.73 **	-1.34 **	0.19 *	-0.15 **
6	RACT 5296	-0.11	1.96	-6.2 **	0.05	0.14	-6.96 *	0.08	4.13 **	-0.24 **	0.05
	SE	0.20	2.25	1.48	0.04	0.3	3.32	0.13	0.26	0.08	0.03

** Significance at 1% level

*Significance at 5% level

fiber traits usually tend to display improved heterosis vigour and better spinning quality (Sawarkar *et al.*, 2015).

The relationship between combining ability and heterosis was further examined to determine whether the superior *sca* effects were reflected in hybrid vigour. Yield is a polygenic trait controlled by boll retention, assimilation, reproductive efficiency, and adaptability to environmental fluctuations. Dominance and epistatic interactions play significant roles in hybrid vigour (Liu *et al.*, 2020). The extent of mid-parent and better-parent heterosis for different traits in the 30 F_1 hybrids is presented in **Fig. 1a and 1b**, respectively. The heterosis results were generally consistent with the combining ability effects. Similarly, the crosses RACT 3959 $\times$ RACT 5294 and RACT 5294 $\times$ RACT 3959 displayed high mid-parent and better parent heterosis for fiber quality traits, *viz.*, fiber length, fiber strength, and micronaire in the desired direction, which correlated well with the high *sca* values. However, some combinations exhibited heterosis but did not have significant effects on their combining abilities. The crosses RACT 3844 $\times$ RACT 5293 and RACT 5293 $\times$ RACT 3844 exhibited high mid-parent and better parent heterosis for earliness, boll weight, and seed cotton yield, but these results were not consistent with the *sca* effects. Crosses RACT 3844 $\times$ RACT 5296 and RACT 5296 $\times$ RACT 3844 exhibited significant better parent heterosis for ginning percentage even though *gca* and *sca* effects were non-significant. Reports specifically documenting high heterosis in the absence of significant SCA effects are limited in cotton; however, Azad *et al.* (2022) reported a similar phenomenon in rice, where IR62629A $\times$ IR46R exhibited high heterosis despite a non-significant SCA effect.

General combining ability (*gca*) provides an estimate of the average breeding value of a parent. However, superior general combiners do not always lead to the best-performing hybrids, and parents with poor or average *gca* may still produce promising cross combinations (Wagaw *et al.*, 2020). Similarly, heterosis is not always closely correlated with *gca* or *sca* estimates, since heterosis

measures the superiority of a hybrid over its parents, whereas combining ability reflects the underlying genetic effects governing hybrid performance. Consequently, the two approaches should be regarded as complementary rather than mutually predictive in the selection of superior hybrids. Interestingly, the crosses RACT 3790 $\times$ RACT 3959 and RACT 3959 $\times$ RACT 3790 exhibited significant mid-parent heterosis for ginning percentage, even though *gca* and *sca* effects were non-significant. However, the lack of substantial better parent heterosis suggests that the hybrid advantage was sufficient to exceed the parental mean but not the superior parent. This indicates that superior hybrid vigour could be possible because of the positive allelic effect distribution of the parents, which makes the gene action complementary in some hybrids (Springer and Stupar, 2007). In addition, the dominance complementation of parental genomes (Lippman and Zamir, 2007) and epistatic interactions among loci (Yu *et al.*, 1997) may also play other roles in the cause of hybrid vigour. Therefore, exclusive reliance on parental performance or *gca* effects may overlook potentially valuable hybrids with a strong specific combining ability and heterotic advantage.

Several cross combinations showed significant and desirable heterosis over the mid-parent and better parent, suggesting their potential for simultaneous improvement of agronomic and fiber quality traits. The crosses RACT 3844 $\times$ RACT 5293 and RACT 5293 $\times$ RACT 3844 showed significant heterosis for earliness and seed cotton yield under both mid parent and better parent heterosis, while heterosis for boll weight under mid parent and number of bolls under better parent heterosis were significant respectively, indicating consistent hybrid superiority for yield and earliness with partial expression of their yield component traits. Likewise, RACT 3844 $\times$ RACT 3790, RACT 3790 $\times$ RACT 3844, RACT 3844 $\times$ RACT 3959, RACT 3959 $\times$ RACT 3844, RACT 3790 $\times$ RACT 3959 and RACT 3959 $\times$ RACT 3790 expressed significant mid parent and better parent heterosis for earliness and fiber strength, whereas ginning percentage and fiber length was restricted to the mid parent heterosis estimates in

Table 5. Estimates of specific combining ability effects (sca) for various plant characters in B x B hybrids

S.No.	Crosses	Days to first flowering	Plant height	Number of bolls per plant	Boll weight	Ginning percentage	Seed cotton yield	Fibre length	Fibre strength	Elongation	Micronaire
1	RACT 3844 x RACT 3790	-0.81	3.20	0.34	0.40 **	0.49	0.80	-0.59	1.43 *	0.05	0.17 *
2	RACT 3844 x RACT 3959	-1.13 *	-2.71	2.54	-0.06	0.90	7.49	1.04 **	1.05	-0.11	0.24 **
3	RACT 3844 x RACT 5293	-0.54	6.31	12.56 **	0.11	0.46	35.16 **	-0.36	0.72	-0.08	0.01
4	RACT 3844 x RACT 5294	0.30	2.20	11.7 **	0.24 **	-0.1	2.3	0.18	0.15	-0.14	0.02
5	RACT 3844 x RACT 5296	-1.25 **	-6.80	-3.19	-0.20 *	-0.91	-20.56 **	0.59	0.81	-0.33	-0.20 *
6	RACT 3790 x RACT 3959	-1.07 *	1.37	-10.82 **	-0.12	0.82	2.96	0.94 **	1.54 *	0.24	0.17 *
7	RACT 3790 x RACT 5293	0.47	-4.27	-5.63	-0.19 *	0.51	-0.7	-0.14	-0.31	-0.17	-0.04
8	RACT 3790 x RACT 5294	-0.76	-5.21	8.84 *	-0.22 **	0.68	6.6	-1 **	-2.77 **	0.46 *	-0.10
9	RACT 3790 x RACT 5296	0.14	-5.38	-4.38	-0.02	-0.05	12.91	1.05 **	2.23 **	-0.40 *	0.01
10	RACT 3959 x RACT 5293	-0.14	-3.52	6.73 *	0.16	-0.16	-6.18	0.62 *	-1.54 *	-0.10	0.11
11	RACT 3959 x RACT 5294	0.54	2.20	12.04 **	-0.05	0.15	-14.37	2.13 **	4.97 **	-0.75 **	-0.25 **
12	RACT 3959 x RACT 5296	1.7 **	3.87	-5.52	-0.23 **	0.78	-6.4	-0.63 *	-1.73 **	0.07	-0.14
13	RACT 5293 x RACT 5294	-0.34	4.73	5.23	-0.06	-0.58	11.96	0.17	-2.28 **	-0.14	-0.41 **
14	RACT 5293 x RACT 5296	0.40	-0.77	7.01 *	0.27 **	-1.04	21.94 **	-0.01	-1.7 **	-0.07	-0.08
15	RACT 5294 x RACT 5296	-0.09	-1.88	8.48 *	-0.18 *	-0.74	9.74	1.10 **	-0.85	-0.14	-0.19 *
	SE	0.46	5.14	3.38	0.08	0.68	7.57	0.31	0.6	0.18	0.08

**Significance at 1% level

*Significance at 5% level

Table 6. Estimates of reciprocal effects for various plant characters in B x B hybrids

S.No.	Crosses	Days to first flowering	Plant height	Number of bolls per plant	Boll weight	Ginning percentage	Seed cotton yield	Fibre length	Fibre strength	Elongation	Micronaire
1	RACT 3844 x RACT 3790	0.44	-1.00	7.50	-0.07	0.72	-20.67 *	-1.53 **	-0.05	0.22	0.08
2	RACT 3844 x RACT 3959	2.38 **	0.17	-1.17	-0.03	1.38	19.33 *	-0.52	-1.33	0.17	0.32 **
3	RACT 3844 x RACT 5293	1.78 **	8.17	8.50 *	0.23 *	0.18	10.83	0.33	-0.13	0.12	0.25 **
4	RACT 3844 x RACT 5294	-0.05	-11.67	-25.17 **	-0.3 **	0.27	-18.5 *	-2.03 **	-1.53 *	0.07	0.07
5	RACT 3844 x RACT 5296	1.55 **	9.67	0.67	0	1.37	10.17	-0.55	-0.57	0.05	0.28 **
6	RACT 3790 x RACT 3959	0.49	12.17 *	0	-0.05	0.17	23.83 **	0.85 *	-0.15	-0.08	0.07
7	RACT 3790 x RACT 5293	0.67	8.17	-4.17	0.15	-0.23	34 **	1.12 **	2.6 **	-0.10	-0.02
8	RACT 3790 x RACT 5294	-0.43	-0.83	4.17	0.02	-0.42	-2.17	0.72	-1.42 *	0.10	0
9	RACT 3790 x RACT 5296	0.68	-10.33	-17.67 **	0.28 **	0.20	36 **	0.78 *	-1.75 *	-0.08	0.22 *
10	RACT 3959 x RACT 5293	-1.93 **	-10.33	1.00	-0.68 **	-1.38	31.5 **	-0.07	-2.83 **	0.02	-0.27 **
11	RACT 3959 x RACT 5294	-1.40 *	4.00	0.50	-0.08	0.15	-37.83 **	0.33	2.85 **	0.17	-0.05
12	RACT 3959 x RACT 5296	1.02	15.67 *	6.00	0.07	-1.28	-6.67	0.35	1.88 **	0.53 *	-0.03
13	RACT 5293 x RACT 5294	0.61	2.50	-1.33	-0.03	-0.32	50.67 **	0.85 *	1.00	0.07	0.02
14	RACT 5293 x RACT 5296	-1.24 *	9.67	3.83	-0.03	-0.47	11.5	-0.02	0.98	0.18	-0.05
15	RACT 5294 x RACT 5296	-0.96	-3.50	-0.83	-0.12	-0.58	-29.50 **	-0.48	-1.07	0.12	0.12
	SE	0.54	6.04	3.97	0.1	0.8	8.9	0.36	0.71	0.21	0.09

**Significance at 1% level

*Significance at 5% level

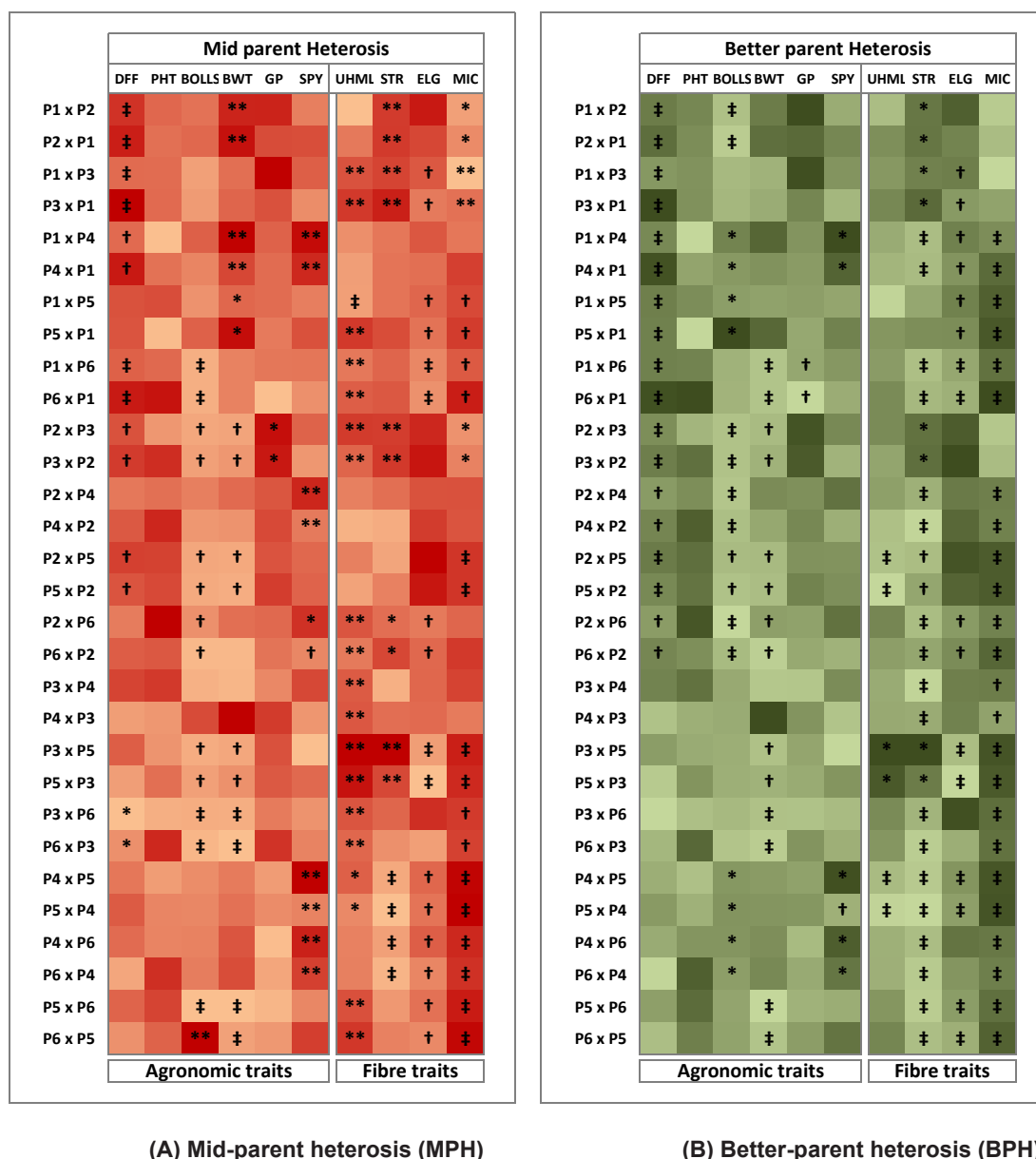


Fig. 1. Trait-wise heatmaps illustrating the magnitude and significance of heterosis for agronomic and fibre quality traits in 30 F_1 hybrids of *Gossypium barbadense*

Fig. 1. Comparative heatmaps depicting the magnitude and significance of (A) mid-parent heterosis (MPH) and (B) better-parent heterosis (BPH) for ten agronomic and fibre quality traits across 30 F_1 hybrids of *Gossypium barbadense* L. Colour intensity represents the relative magnitude of heterosis within each trait based on trait-wise normalization, with darker shades indicating more desirable heterotic performance. For days to first flowering (DFF), plant height (PHT) and micronaire (MIC), the colour scale was reversed so that darker shades represent lower (more desirable) values. Asterisks (*, **) denote significant positive heterosis at $P \leq 0.05$ and $P \leq 0.01$, respectively, whereas daggers (†, ‡) denote significant negative heterosis at $P \leq 0.05$ and $P \leq 0.01$, respectively.

DFF: Days to first flowering, PHT: Plant height, BOLLS: Number of bolls per plant, BWT: Boll weight, GP: Ginning percentage, SPY: Seed cotton yield, UHML: Fibre length, STR: Fibre Strength, ELG: Elongation, MIC: Micronaire

Refer Table 1 for name of genotypes

RACT 3790 × RACT 3959 and RACT 3959 × RACT 3790, suggesting favourable allelic interactions that enhanced hybrid performance without consistently surpassing the superior parent. Further, the cross RACT 3959 × RACT 5294 exhibited highly significant *sca* effects along with significant better-parent heterosis for fiber length and fiber strength, demonstrating a strong correspondence between combining ability and hybrid performance. Collectively, the crosses RACT 3844 × RACT 5293, RACT 5293 × RACT 3844, RACT 3844 × RACT 3790, RACT 3790 × RACT 3844, RACT 3844 × RACT 3959, RACT 3959 × RACT 3844, RACT 3790 × RACT 3959, RACT 3959 × RACT 3790, RACT 3959 × RACT 5294 and RACT 5294 × RACT 3959 represent promising genetic combinations for the simultaneous improvement of earliness, yield components, ginning percentage and fiber quality in *G. barbadense*.

Reciprocal effects and cross-direction

The reciprocal effects of the fifteen crosses are given in **Table 6**. Maternal effects were found to be of major significance for plant height, seed cotton yield and days to first flowering. Plant height showed a high proportion of reciprocal contributions (68.65 %), followed by *sca* (22.77 %) and *gca* (8.58 %) followed by trait single plant yield and days to first flowering with the of reciprocal contributions of 57.68 and 51.49 percent respectively (as in **Table 2**). This shows that considering the direction of crossing is extremely important. The significant impact of the reciprocal effect on seed cotton yield, measured at 1390.16, indicates that the direction of the cross should be taken into account when developing hybrids. In certain crosses, such as RACT 3790 × RACT 5293 (34.00), RACT 3790 × RACT 5296 (36.00), and RACT 5293 × RACT 5294 (50.67) for seed cotton yield trait, one parent performed significantly better than the other as a female plant, suggesting the possible involvement of cytoplasmic genes or maternal effects on seed vigour, embryo development, or organelle-nuclear interactions. Crosses RACT 5293 × RACT 5294 (*gca* of RACT 5293 = 7.98) and RACT 3790 × RACT 5293 (*gca* of RACT 3790 = 10.18), which showed significant reciprocal effects, also showed marked heterosis despite having non-significant *sca* values for seed cotton yield. This suggests a greater contribution of additive effects and maternal influence than specific non-additive interactions. Accordingly, the superior performance of these hybrids is likely to reflect the accumulation of favourable additive genetic effects contributed by their parental lines, with specific parental interactions providing an additional, but comparatively smaller, contribution (John *et al.*, 2024). In the case of the hybrid of the cross RACT 3790 × RACT 5293, the cross performed better when Parent RACT 3790 (*gca* = 10.18) was used as the female, despite the non-significant *sca* for seed cotton yield, demonstrating that maternal effects contributed more strongly than specific combining ability. This suggests that maternal effects may substantially contribute to hybrid performance in certain combinations of species. Reciprocal significance for seed cotton yield

was also observed in most hybrid combinations by Balci *et al.* (2025).

For earliness, significant negative *sca* and reciprocal effects in some crosses indicated the roles of dominance and maternal effects in reducing the number of days to first flowering. In the RACT 3959 × RACT 5293 cross, negative reciprocal effects (-1.93) implied early flowering when RACT 3959 served as the maternal plant. It is also worth noting that the *gca* of RACT 3959 (+0.40) and *sca* of RACT 3959 × RACT 5293 (-0.14) in the trait days to first flowering. Khan *et al.* (2011) also reported significant reciprocal effects on days to flowering in early generations. Reciprocal differences could be involved in trait expression, in addition to nuclear gene action, maternal effects, and cytoplasmic effects (Mahgoub, 2011). The early nature of flowering can be associated with physiological coordination between the growth stages of vegetative and reproductive organs, which explains the involvement of both maternal and nuclear effects (Shakeel *et al.*, 2011) in the development of this trait.

Among all the cross-combinations, RACT 3790 × RACT 3959 and its reciprocal, RACT 3959 × RACT 3790, appear particularly valuable because they combine favourable heterosis (**Fig. 1a** and **1b**) for earliness, ginning percentage, and fiber quality traits. Although not always the highest for any single trait, such balanced multi-trait performance is often more desirable in practical breeding programs than superiority for only one economic character. Therefore, these combinations merit further evaluation as stable, multipurpose hybrids. Earlier studies have reported reciprocal effects as a basis for selection in early generations; however, their expression and breeding relevance may become clearer in later generations as homozygosity and population homogeneity increase. Supporting this, Balci *et al.* (2025) observed significant differences in ginning out-turn between ST-468 × Claudia, Flash × Claudia, and their reciprocals in the F4 and F5 generations. This suggests that reciprocal differences identified in early generations may warrant validation in later generations to determine their consistency and breeding value, particularly for traits such as ginning percentage that may be influenced by cross direction.

The present study demonstrated that the development of superior *G. barbadense* combinations requires the simultaneous consideration of per se performance, heterosis, general combining ability (GCA), specific combining ability (SCA), and reciprocal effects rather than reliance on GCA alone. Significant additive and non-additive gene actions contributed to the inheritance of yield and fibre quality traits, while reciprocal effects further highlighted the importance of cross direction in exploiting desirable hybrid performance. RACT 3790 and RACT 5293 emerged as superior general combiners for yield, whereas RACT 3844, RACT 5293, and RACT 5296 were valuable donors for fibre quality improvement. Among the

hybrids, RACT 3844 × RACT 5293, RACT 5293 × RACT 5296, and RACT 3790 × RACT 5296 were identified as promising combinations for yield improvement, while RACT 3959 × RACT 5294 showed particular potential for fibre quality enhancement. The results emphasize that integrating parental combining ability with hybrid per se performance, heterotic expression, and reciprocal effects can provide a more effective strategy for identifying superior combinations and selecting appropriate parents for the genetic improvement of yield and fibre quality in *G. barbadense*.

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