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Combining ability studies in *desi* cotton (*Gossypium arboreum* L.) genotypes

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Abstract

Background Studies on genetic variation and combining ability are essential tools to employ the suitable breeding programme, particularly for hybrid production, to exploit the heterosis in cross-pollinated crops like cotton. Thus, combining ability studies in *desi* cotton (*Gossypium arboreum* L.) was carried out using 13 diverse parents through diallel mating design, evaluating 78 F_1 hybrids along with their parents, without reciprocals using Griffing's and Hayman's approaches.

Results Genotypes H 509, AC 3265, AKH 496, and PBN 565 exhibited superior per se performance, indicating their potential use as parents in future breeding programs to develop superior hybrids. The general combining ability (GCA) effect of the genotypes revealed that AC 3097 and AKA 13-SP1 were good general combiners for most traits in this study. Genotypes PBS 1127-SP1, AKH 496, H 509, N11-54–31-32, and AKA 13-SP1 exhibited strong combining ability, contributing to a significant specific combining ability (SCA) effect in seven selected crosses (AC 3265 × PBS 1127-SP1, AKH 496 × H 509, AKH 496 × AC 3097, PBS 1127-SP1 × N11-54–31-32, AC 3216 × AKA 13-SP1, H 503 × N11-54–31-32, and H 509 × AKA 13-SP1) for yield improvement. These crosses showed positive heterosis in a positive direction.

Conclusion From the present study, five genotypes (AC 3097, AKA 13-SP1, N11-54–31-32, AC 3265, and H 509) were identified as good general combiners for producing hybrids, and seven combinations showed a promising hybrid for future breeding programs.

Keywords Combining ability, *Desi* cotton, Diallel analysis, Gene action

Background

Desi cotton, also referred to as diploid cotton or Asiatic cotton (*Gossypium arboreum* L.), possesses inherent tolerance to both biotic and abiotic stresses, making it well-suited for challenging environmental conditions (Sankaranarayanan et al. 2021). However, its yield potential is limited compared with tetraploid varieties. Globally, cotton was the first crop where heterosis was commercially exploited and hybrids were produced (Khan et al. 2023). India has been at the forefront of harnessing heterosis in cotton, leading to the release of numerous high-yielding hybrids (Subhan et al. 2003). In 1972, an intraspecific cross resulted in the creation of Hybrid-4 (H4), the first commercial cotton hybrid in the world, which was developed in India and released available for commercial cultivation (Basu et al. 1995). It increased cotton lint production from a modest 122 $kg{\cdot}ha^{-1}$ in 1992 to 290 $kg{\cdot}ha^{-1}$ in 1993. In the 1980s, the introduction of hybrids also triggered a brief employment boom, with approximately 25 million people, joining the labor-intensive hybrid industry. The performance of these hybrids has been remarkable, demonstrating not only higher yield potential but also improved fibre quality, which meets the demands of both domestic and

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international textile industries. These hybrids exhibit better resistance to biotic stresses like pests and diseases, reducing the need for chemical pesticides, and have also displayed enhanced tolerance to abiotic stresses, such as drought and heat, which are becoming more prevalent due to climate change (Salman et al. 2019). This combination of high yield, quality, and resilience makes cotton hybrids useful and essential for sustainable cotton production. The continued development and use of such hybrids are crucial for ensuring food security, stabilizing farmer incomes, and meeting the growing global demand for cotton.

Combining ability studies are crucial in plant breeding as they help identify parent genotypes capable of producing high-yielding and resilient hybrids, thereby optimizing the use of genetic resources for developing improved crop varieties. Diallel mating design is used to predict the combining ability of parents and the gene action of traits, which is essential for understanding the genetic mechanisms governing yield, a multifaceted trait, and for selecting suitable parental combinations to develop high-performing hybrids (Majeed et al. 2021). Griffing's approach to diallel analysis facilitates the estimation of both general combining ability (GCA) and specific combining ability (SCA), which provide insights into additive and non-additive gene actions, respectively (Griffing 1957). GCA indicates additive gene effects, showing the potential of genotypes to perform well across various crosses, while SCA reveals non-additive, such as dominant and epistatic effects, highlighting specific combinations with superior performance (Vasconcelos et al. 2018; Haffez et al. 2022). By using these approaches, breeders can effectively determine suitable parental combinations, making combining ability a fundamental tool for enhancing yield and developing superior hybrids through hybridization. Similarly, Hayman's graphical approach offers a robust framework to analyze diallel crosses by distinguishing between additive, dominant, and epistatic gene effects, making it a valuable method for studying genetic architecture in cotton (Hayman 1954).

In recent years, cotton breeders have faced increasing challenges due to climate change, including increased temperatures, altered precipitation patterns, and drought, all of which threaten cotton productivity. Developing cotton varieties with enhanced drought tolerance, water-use efficiency, and resilience to heat stress has become a pressing need (Patel et al. 2022). Studies have identified specific SNPs linked to quantitative trait loci (QTLs) that govern critical agronomic traits in cotton, aiding the selection of varieties capable of withstanding environmental stresses (Majeed et al. 2019; Manivannan et al., 2023). Additionally, the emergence of new pests and the adaptation of existing ones, such as the cotton bollworm, highlights the urgent necessity for breeding pest-resistant cotton varieties (Gupta et al. 2023).

Hybrid cotton continues to advance, with significant contributions from molecular breeding and biotechnological tools. Leading cotton-producing countries like India, China, and the United States have focused on developing hybrids that are not only high-yielding and pest-resistant but also more sustainable, requiring fewer chemical inputs and having a lower environmental impact (Khan et al. 2021; Liu et al. 2022). Furthermore, research is increasingly dedicated to understanding how to mitigate the adverse effects of heat stress on cotton growth and yield, highlighting the need for breeding strategies that enhance heat tolerance (Majeed et al. 2021).

Understanding combining ability and heterosis in cotton is essential for developing hybrids that address these evolving challenges. Studies on heterosis provide insights into exploiting hybrid vigour for commercial hybrid development in breeding programs. By assessing GCA, SCA, and heterosis, breeders can screen genotypes based on their genetic potential, ultimately selecting the best parental lines for producing viable and commercially successful hybrids. This study aims to evaluate the combining abilities, particularly GCA and SCA, of *Desi* cotton genotypes to identify the most promising combinations for harnessing heterosis based on SCA.

Materials and methods

A set of 816 accessions of *G. arboreum* were evaluated for two years (2015 and 2016) based on the single plant yield, from which 13 genotypes were selected as

Table 1 List of the genotypes used in this study and its origin

Parents	Genotype	Pedigree (Indigenous collection number)	Origin	Zone
1	AC 3265	439 895	Punjab	North India
2	AKH 496	439 820	Akola	Central India
3	PBS 1127-SP1	412 625	Punjab	North India
4	AC 3522 B	439 905	Punjab	North India
5	AC 3216	439 963	Punjab	North India
6	H 503	412 457	Parbhani	Central India
7	H 509	412 460	Parbhani	Central India
8	AC 3097	439 898	Punjab	North India
9	AKA 13-SP1	439 793	Akola	Central India
10	N11-54–31-32	412 573	Nanded	Central India
11	H 173	412 355	Parbhani	Central India
12	PBN 565	412 610	Parbhani	Central India
13	3930 A	439 649	Adoni	South India

Table 2 Diallel mating pattern with parents and without reciprocal crosses

Parents	AC 3265	AKH 496	PBS 1127-SP1	AC 3522 B	AC 3216	H 503	H 509	AC 3097	AKA 13-SP1	N11-54–31-32	H 173	PBN 565	3930 A
AC 3265		×	×	×	×	×	×	×	×	×	×	×	×
AKH 496			×	×	×	×	×	×	×	×	×	×	×
PBS 1127-SP1				×	×	×	×	×	×	×	×	×	×
AC 3522 B					×	×	×	×	×	×	×	×	×
AC 3216						×	×	×	×	×	×	×	×
H 503							×	×	×	×	×	×	×
H 509								×	×	×	×	×	×
AC 3097									×	×	×	×	×
AKA 13-SP1										×	×	×	×
N11-54–31-32											×	×	×
H 173												×	×
PBN 565													×
3930 A													

parents (Table 1) for exploiting their combining ability using a diallel mating design. The diallel design with parents and without reciprocal was followed (Table 2). The cotton was planted in the experimental field of ICAR-Central Institute for Cotton Research (CICR), Regional Station, Coimbatore, Tamil Nadu, India (11.0168° N, 76.9558° E) during two *kharif* crop seasons (2018–2019 and 2019–2020). The experiment plots were located under the southern hill and plateau region of India, the soil is typic *haplustalfs* (*Periyanaickanpalayam* series), medium deep, well-drained soils. These hybrids along with their parents were sown in three-rows' plots with spacing of 45 × 90 cm and length of 4.5 m amounting to the plot area of 7.5 m^2 in a randomized block design with two replications. All agronomical practices were followed as the Indian Council of Agricultural Research's recommendations for cotton cultivation. Essential data on traits including days to first flowering (DFF), boll number (BN), boll weight (BW), and single plant yield (SPY) were recorded by randomly selecting five plants from each replication of each cross.

The evaluation of general and specific combining ability effects for both parental lines and hybrids was conducted using the diallel mating design method established by Griffing (1957). Griffing's Method II (involving parental genotypes and one-way hybrids) with Model I (fixed effect) was employed for this study. Griffing's diallel analysis is a widely accepted tool for identifying superior hybrids. To complement the Griffing's approach, Hayman's graphical approach was also utilized. This method provides a visual representation of the genetic components of variance, enabling the identification of the relative contributions of additive, dominance, and epistatic effects to trait expression. The genetic components and combining abilities were analyzed using AGD-R v 4.0 software developed by CIMMYT (Rodríguez et al. 2015), which offers robust statistical tools for diallel analysis. Graphical representations were carried out using R software using the "ggbiplot" package (https://cran.r-project.org/package=ggbiplot).

Results

Combining ability analysis

Griffing's approach was carried out to evaluate the combining ability effects of 78 F_1 hybrids (without reciprocals) and 13 parents for the four traits: BW, BN, SPY, and DFF. The results showed that the GCA of parents and SCA of the hybrids were significant for all the four traits studied (Table 3).

Table 3 Analysis of variance for yield and yield attributing traits in *G. arboreum*

Source of variation	df	BW	BN	SPY	DFF
GCA	12	0.063*	209.38**	643.42*	24.74*
SCA	78	0.098*	106.21**	509.61*	15.41*
Error	78	0.013	11.99	21.62	1.70

* significant at 5%, **significant at 1%, *df*-degree of freedom, *GCA* general combining ability, *SCA* specific combing ability, *BW* boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering

The performance of the parents was presented in Table 4. Among the 13 genotypes, the boll weight of H 509, AC 3265, N11-54–31-32, AKH 496, and PBN 565 was significantly higher than that of other genotypes. For the boll number, the genotypes AKH 496, PBN 565, H 509, AKA 13-SP1, N11-54–31-32, PBS 1127-SP1, and AC 3522 B showed better mean performance. Genotypes namely H 509, AC 3265, AKH 496, PBN 565, AC 3522 B, AC 3097, AKA 13-SP1, and PBS 1127-SP1 outperformed other genotypes in terms of single plant yield. Furthermore, five genotypes, H 173, AC 3265, AKH 496, AC 3522 B, and H 509 were early in flowering than others.

General combining ability effects

General combining ability effects of parents were studied (Table 4, Fig. 1). Genotypes, AC 3216, H 503, AC 3097, AKA 13-SP1, and N11-54–31-32 were identified as good general combiners for single plant yield. Genotypes AC 3265, AKH 496, AC 3522 B, H 503, and 3930 A were found to be desirable in terms of earliness with good general combining ability. Four genotypes H 503, H 509, AC 3097, and AKA 13-SP1 possess significant positive GCA effects on boll number. In addition, N11-54–31-32, H 173, AC 3097, and AKA 13-SP1 exhibited significant positive GCA effects on boll weight.

Specific combining ability effects

Specific crosses were taken separately to study the SCA (Table 5). For days to first flowering, the following crosses AC 3265 × PBS 1127-SP1, AC 3265 × AKA 13-SP1, AC 3216 × AKA 13-SP1, AC 3216 × 3930A, H 509 × AKA 13-SP1, H 173 × PBN 563, and H 173 × 3930 A showed significant SCA effects. Hybrids AC 3265 × AKA 13-SP1, AC 3265 × H 173, AKH 496 × H 509, AKH 496 × AC 3097, PBS 1127-SP1 × N 11–54-31–32, AC 3216 × 3930A, H 503 × N11-54–31-32, and H 509 × AKA 13-SP1 exhibited significant SCA effects for boll weight. Notably, the cross H 509 × AC 3097 showed the highest SCA effect for boll number. Seven crosses viz., AC 3265 × PBS 1127-SP1, AKH 496 × H 509, AKH 496 × AC 3097, PBS 1127-SP1 × N11-54–31-32, AC 3216 × AKA

Table 4 Pooled mean values and general combining ability (GCA) effects of *desi* cotton parental lines for yield and related traits

Parents code	Genotype	Pooled mean				GCA effects			
		BW/g	BN	SPY/ (g·plant^{-1})	DFF/d	BW	BN	SPY	DFF
1	AC 3265	2.90	25.50	69.50	59.50	0.12	−1.01	−3.87 **	−1.31 **
2	AKH 496	2.70	40.00	69.00	60.00	0.96	0.02	0.62	−1.21 **
3	PBS 1127-SP1	2.55	29.00	65.00	62.50	−0.18	0.42	−0.23	−0.31
4	AC 3522 B	2.60	29.00	66.50	60.00	−0.01	−2.11 *	0.20	−1.08 **
5	AC 3216	2.35	18.00	40.50	62.50	−0.05	0.55	2.60 *	0.49
6	H 503	2.55	24.00	55.50	61.50	−0.06	2.09 *	2.43 *	−1.48 **
7	H 509	3.00	34.00	69.50	60.50	0.36	5.29 **	0.98	0.35
8	AC 3097	2.55	26.00	66.50	65.00	0.89*	5.49 **	4.05 **	−0.35
9	AKA 13-SP1	2.25	31.00	65.00	68.00	0.75*	3.22 **	7.15 **	0.55
10	N11-54–31-32	2.90	29.50	60.50	61.50	0.96*	1.25	13.09 **	1.62 **
11	H 173	2.60	14.50	57.50	56.50	0.81*	−6.51 **	−10.37 **	3.02 **
12	PBN 565	2.70	40.00	69.00	62.00	−0.07	−2.48 **	−8.39 **	0.39
13	3930 A	1.90	20.50	27.50	64.50	0.13	−6.21 **	−8.30 **	−0.68 *
	Overall Mean	2.58	27.77	60.12	61.85				
	CD	0.11	1.72	1.30	4.53				

* significant at 5%, **significant at 1%, *BW* boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering, *CD* critical difference

13-SP1, H 503 × N11-54–31-32, and H 509 × AKA 13-SP1 showed significant SCA effect for single plant yield.

Gene action estimation

The magnitude of SCA variance was higher than GCA variance for all the four traits (Table 6) which indicates the preponderance of non-additive gene action.

Correlation study

In the present study, a strong ($0.75 \leq r < 1.00$) and highly significant correlation ($r = 0.76$, $P < 0.01$) was observed between boll weight and single plant yield (Fig. 2). Additionaly, a positively significant and intermediate correlation ($0.25 \leq r < 0.75$) was found between boll number and single plant yield ($r = 0.65$, $P < 0.05$). A negative significant

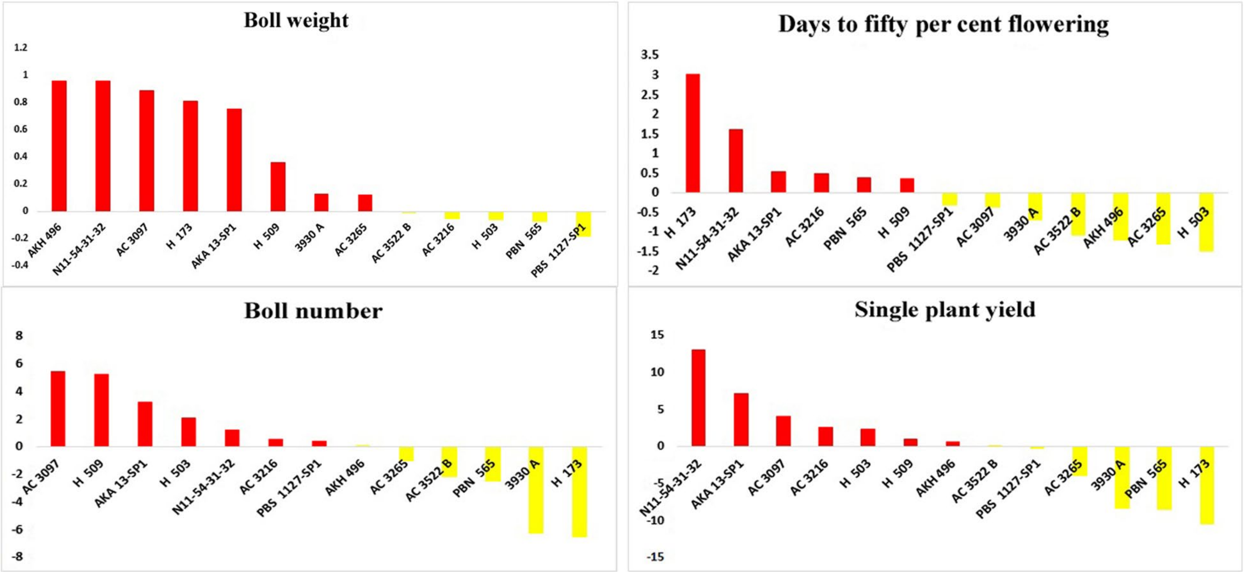

Fig. 1 General combining ability effects of yield and yield attributing traits in *G. arboreum* genotypes

Table 5 Specific combining ability (SCA) effects of the crosses

Crosses	Traits	SCA	SH
AC 3265 × PBS 1127-SP1	SPY	45.68 **	307.27 **
AC 3265 × PBS 1127-SP1	DFF	−2.45 **	−15.50 **
AC 3265 × AKA 13-SP1	BW	0.35 **	60.53 **
AC 3265 × AKA 13-SP1	DFF	−1.15 *	−11.63 **
AC 3265 × H 173	BW	0.69 **	81.58 **
AKA 496 × H 509	BW	0.34 **	68.42 **
AKA 496 × H 509	SPY	13.08 *	192.73 *
AKA 496 × AC 3097	BW	0.25 *	60.53 **
AKA 496 × AC 3097	SPY	20.85 **	225.82 *
PBS 1127-SP1 × N11-54–31-32	BW	0.49 **	68.42 **
PBS 1127-SP1 × N11-54–31-32	SPY	17.40 **	233.64 *
AC 3216 × AKA 13-SP1	SPY	50.96 **	328.36 **
AC 3216 × AKA 13-SP1	DFF	−3.61 **	−13.18 **
AC 3216 × 3930A	BW	0.86 **	89.47 **
AC 3216 × 3930A	DFF	−0.11	−10.08 **
H 503 × N11-54–31-32	BW	0.37 **	63.16 **
H 503 × N11-54–31-32	SPY	30.29 **	279.27 **
H 509 × AC 3097	BN	17.92 **	148.78 **
H 509 × AKA 13-SP1	BW	0.27 *	55.26 *
H 509 × AKA 13-SP1	SPY	25.45 **	250.55 **
H 509 × AKA 13-SP1	DFF	−1.55 **	−11.63 **
H 173 × PBN 563	DFF	−4.51 **	−11.63 **
H 173 × 3930 A	DFF	−2.31 **	−10.08 **

[*] significant at 5%, **significant at 1%, *BW* boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering, *SH* standard heterosis

Table 6 Estimation of gene action for four yield and yield attributing traits in *G. arboreum*

	GCA variance	SCA variance	GCA/SCA	Gene action
BW	-0.001 9	0.005 2	−0.365 4	Non-additive
BN	13.159 1	94.214 9	0.139 7	Non-additive
SPY	41.453 6	487.997 3	0.084 9	Non-additive
DFF	1.536 2	13.710 3	0.112 0	Non-additive

BW boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering

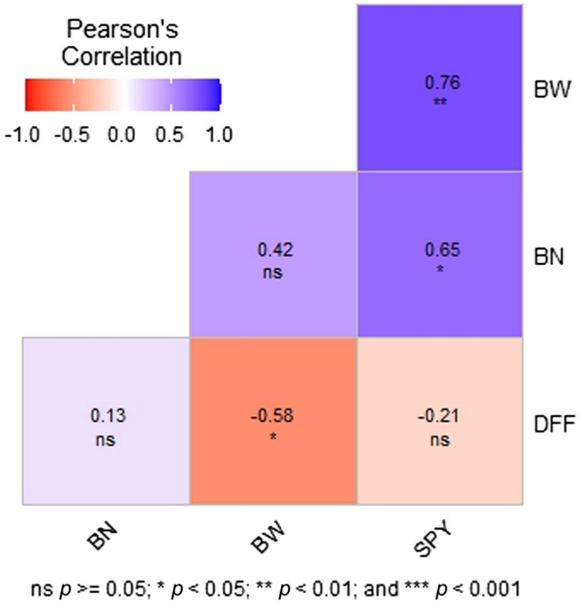

Fig. 2 Pearson analysis of yield and its component traits; BW is boll weight, BN is boll number, SPY is single plant yield, and DFF is days to first flowering

correlation was found between boll weight and days to first flowering ($r = -0.58$, $P < 0.05$).

Hayman's graphical approach: insights into gene action

Results based on the Hayman approach showed that the estimates of the uniformity test and t^2 values were non-significant. This indicates that no epistatic interactions were present for the studied traits. These findings suggest that the assumptions underlying diallel analysis, as proposed by Hayman (1954), hold true for all the traits under investigation. The absence of significant epistasis means that the genetic variance observed can largely be attributed to additive and dominance effects, allowing for a more straightforward interpretation of genetic parameters and making the breeding predictions more reliable. Thus, Wr (covariance between parents and their offspring) and Vr (parental variance) uniformity values were estimated. These Vr and Wr values were depicted in Table 7 which was used to plot the Wr-Vr graph for the studied traits.

Amid the components of variance, additive (D) and average degree of dominance $(H_1/D)^{1/2}$ were found to be lower for all four traits than the dominance components of variance (H_1 and H_2), which indicates that the studied traits were governed by over-dominance gene action (Table 8). Except for boll weight, all other studied traits exhibited an average degree of dominance $(H_1/D)^{1/2}$ greater than 1, further indicating the predominance of over-dominance gene action.

Differences between H_1 and H_2 values were identified for the traits, BW values were small, while SPY values were large. This revealed the asymmetrical distribution pattern of both positive and negative genes for these traits which was also substantiated by the $H_2/4H_1$ values which were not equal to 0.25. This implied that these traits were mainly governed by more dominant genes. Positive F value and proportion of dominant and recessive genes in parents > 1 depicting the multiple dominant genes governed by boll number, single plant yield, and days to first flowering. Boll weight was

Table 7 Variances and co-variances for four yield and yield attributing traits in *G. arboreum*

Genotypes	BW		BN		SPY		DFF	
	Vr	Wr	Vr	Wr	Vr	Wr	Vr	Wr
AC 3265	0.10	−0.01	38.52	−34.41	469.02	−42.59	21.67	−8.13
AKH 496	0.07	0.02	83.03	8.53	596.51	41.61	7.52	−0.79
PBS 1127-SP1	0.16	−0.02	131.52	−63.03	584.85	−5.50	12.77	−3.71
AC 3522 B	0.08	0.01	60.96	−27.2	792.62	−70.48	15.14	−3.25
AC 3216	0.15	−0.01	117.31	30.12	626.41	26.83	18.06	−1.15
H 503	0.06	0.02	107.19	20.11	354.15	58.65	15.53	−5.75
H 509	0.10	0.01	271.73	−13.87	420.64	−5.84	18.19	1.19
AC 3097	0.07	−0.01	252.13	89.2	579.61	31.36	20.69	−0.63
AKA 13-SP1	0.10	0.02	66.67	−52.57	687.45	4.46	15.55	1.02
N11-54–31-32	0.09	0.02	82.89	−3.16	511.94	−36.09	12.06	−1.75
H 173	0.09	0.02	33.10	17.09	540.26	−46.47	16.93	2.00
PBN 565	0.03	0.02	121.44	34.56	489.72	−8.40	13.09	−3.77
3930 A	0.17	−0.03	56.56	18.48	415.82	−32.24	9.23	2.75

BW boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering, *Wr* covariance between parents and their offspring, *Vr* parental variance

Table 8 Genetic components of variance for four yield and yield attributing traits in *G. arboreum*

Components	BW	BN	SPY	DFF
t^2 values	24.288	5.178	2.683	0.910
D	−0.046	128.991	18.631	7.697
H_1	0.163	537.531	2 179.044	71.717
H_2	0.189	344.172	1 899.495	47.396
$(H_1/D)^{1/2}$	−1.891	2.041	10.815	3.053
F	−0.077	254.311	70.112	22.679
h_2	0.023	29.970	191.662	50.267
E	0.092	11.909	22.061	1.720
$H_2/4H_1$	0.290	0.160	0.218	0.165
$V4dh_1+F/V4DH_1\text{-}F$	0.384	2.868	1.421	2.866
h_2/H_2	0.121	0.087	0.101	1.061
h^2(ns)	0.018	0.258	0.187	0.256

BW boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering; *D* component of variation due to additive effect of gene, H_1 component of variation due to dominant effect of gene, H_2 proportion of dominance variance due to positive and negative effect of gene, h_2 dominance effect expressed as the algebraic sum over all loci in heterozygous phase in all crosses, *F* mean of covariance of additive and non-additive effect over arrays, $(H_1/D)^{1/2}$ average degree of dominance, $H_2/4H_1$ proportion of genes with positive and negative efect in the parents, $V4dh_1+F/V4DH_1\text{-}F$ proportion of dominance and recessive genes in the parents, h^2*(ns)* heritability in narrow-sense

mainly controlled by more number of recessive genes as it was evidenced by the negative *F* value and proportion of dominant and recessive genes in parents which was less than unity. For all the traits studied, positive h^2 estimates were observed.

Thirteen parents were utilized in this study, as shown by the numbers along the regression line in the Vr-Wr graph (Fig. 3). More dominant genes were present in parents at the origin, and duplicate gene action was present above the regression line while complementary gene action was predominant below it. In the Vr-Wr graph, the regression line passes above the origin indicating the presence of partial dominant genes for all the studied traits. Parents such as PBN 565, H 173, and 3930 A were found to have a high frequency of dominant genes for single plant yield, while H 173 and 3930 A were prominent for boll number. Similarly, PBN 565 and H 503 showed a higher presence of dominant genes for boll weight, and AKH 496, PBS 1127-SP1, and 3930 A were notable for days to first flowering.

The Fr value, often referred to in genetic studies, is an indicator of the balance between dominant and recessive alleles within the parents for a specific trait. More recessive genes were present for a given trait in parents with negative Fr values, whereas more dominant genes were present in parents with positive Fr values. Fr values of each parent for BN, BW, SPY, and DFF were calculated (Table 9). Except PBN 565, all other parents had negative Fr values for boll weight indicating the more recessive genes. Parents H 509 and AC 3097 had negative Fr values for the boll number while all other parents had positive values. For single plant yield, AKH 496, PBS 1127-SP1, AC 3522 B, AC 3216, AC 3097, and AKA 13-SP1 had negative Fr values while all parents had positive Fr values for days to first flowering.

Discussion

Desi cotton, known for its resilience to biotic and abiotic stresses, is well-suited for cultivation in rainfed and marginal soils, making it an ideal crop in the face of climate change. However, its small boll size and lower locule

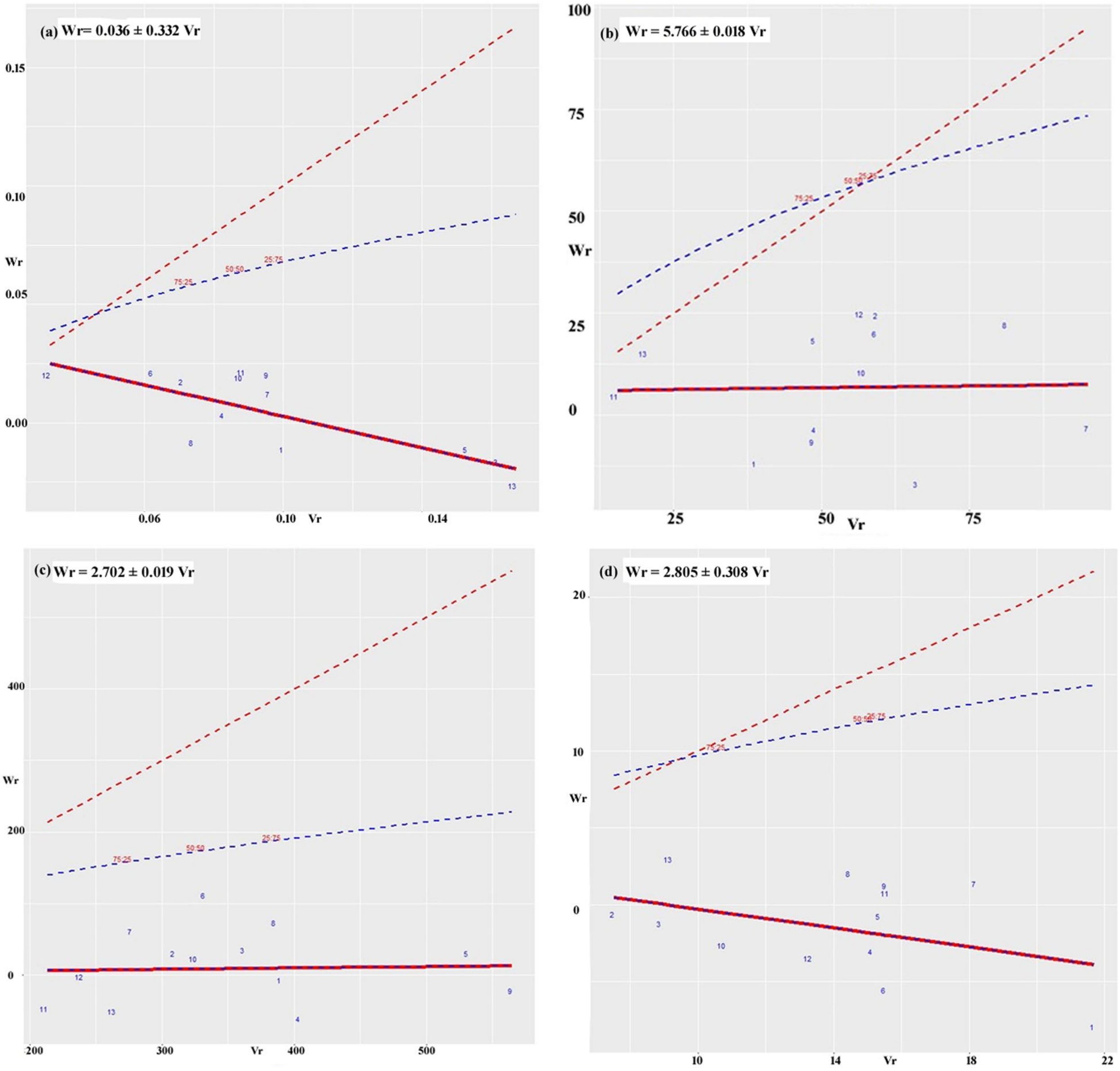

Fig. 3 Vr-Wr graph. **a** Boll weight (**b**) Boll number (**c**) Single plant yield (**d**) Days to first flowering. Blue colored numerical 1–13 indicates parental genotypes; 1 is AC 3265, 2 is AKH 496, 3 is PBS 1127-SP1, 4 is AC 3522 B, 5 is AC 3216, 6 is H 503, 7 is H 509, 8 is AC 3097, 9 is AKA 13-SP1, 10 is N11-54–31-32, 11 is H 173, 12 is PBN 565, 13 is 3930 A

retention limit its production potential (Sankaranarayanan et al., 2021). Hybridization offers a viable solution to enhance its productivity (Sukrutha et al. 2023). Understanding combining ability is crucial for exploiting heterosis and designing effective mating strategies (Çetin et al., 2022). GCA, linked to additive gene effects, is essential for selecting optimal genotypes, while SCA, associated with non-additive gene effects like dominance or epistasis, is valuable for developing hybrids with superior performance and stability (Jenkins et al. 2009). GCA benefits selection and hybridization programs, whereas SCA aids in hybrid production and maximizing heterotic effects. Diallel mating is a preferred statistically proven breeding design model that simplifies the identification of parents with good GCA effects and hybrids with favorable SCA effects. Additionally, it offers crucial details on gene function and the inheritance of traits. Hence, a diallel mating design was employed to assess both the general combining ability of parents and the specific combining ability of crosses, aiming to elucidate the genetic actions

Table 9 Fr values for four yield and yield attributing traits in *G. arboreum*

Genotypes	BW	BN	SPY	DFF
AC 3265	−0.049	468.705	291.756	22.424
AKH 496	−0.048	293.807	−131.619	36.059
PBS 1127-SP1	−0.163	339.932	−14.084	31.399
AC 3522 B	−0.044	409.371	−299.659	25.739
AC 3216	−0.155	182.057	−161.852	15.690
H 503	−0.038	222.311	319.030	29.969
H 509	−0.088	−38.818	315.018	10.774
AC 3097	−0.003	−205.754	−77.309	9.392
AKA 13-SP1	−0.103	448.705	−239.215	16.383
N11-54–31-32	−0.086	317.436	192.923	28.905
H 173	−0.092	376.538	157.032	11.655
PBN 565	0.023	164.920	181.978	30.883
3930 A	−0.153	326.830	377.458	25.559

BW boll weight, *BN* boll number, *SPY* single plant yield, *DFF* days to first flowering

underlying high-yielding hybrids. The ANOVA results of this study showed significant general and specific combining abilities indicating that the importance of both additive and non-additive gene action for BW, BN, SPY, and DFF, which are in concurrence with Gnanasekaran et al. (2021), Bourgou et al. (2023), and Sukrutha et al. (2023). Selecting parents with good mean performance serves as a basis for hybrid production (Mudhalvan et al., 2021). Based on the per se performance of the 13 parents, H 509 was found to be the superior line with high yield coupled with high boll number and boll weight. Genotypes namely, AC 3265, AKH 496, and PBN 565 were also reported to be high-yielding lines with superior boll traits. Utilizing these parents in hybrid programs would facilitate the development of superior varieties. GCA effects of parental genotypes revealed that AC 3097 and AKA 13-SP1 are good general combiners for most of the traits under study except for days to first flowering. However, none of the parents exhibited good combining ability for all the traits. H 503 was found to be a good general combiner for yield, boll number, and days to first flowering. H 509 was identified as a good general combiner for the boll number while N11-54–31-32 for the boll weight and single plant yield. This implied that these lines could carry additive genes that contribute to favorable traits related to cotton yield (Sukrutha et al. 2023). These potential lines could be used to make crosses in all possible combinations to identify the desirable cross with good yield and attributing traits. As a result, these genotypes were thought to hold promise for improving cotton yield throughout breeding operations (Deshmukh et al., 2021).

The current study revealed that SCA effects were more predominant than GCA effects for yield traits, which aligns with the findings of Kumar et al. (2014), Kannan et al. (2015), and Pushpam et al. (2015), who highlighted the importance of non-additive gene actions in trait determination. These non-additive effects can be harnessed in heterosis breeding to improve hybrid performance. Notably, genotypes such as PBS 1127-SP1, AKH 496, H 509, N11-54–31-32, and AKA 13-SP1 exhibited strong combining abilities, resulting in significant SCA effects in seven combinations, including AC 3265 × PBS 1127-SP1, AKH 496 × H 509, and PBS 1127-SP1 × N11-54–31-32 and so on. These findings align with previous studies by Hinze et al. (2011) and Thiyagu et al. (2019), which also reported significant SCA effects for yield-related traits in cotton hybrids.

Furthermore, the positive heterosis observed in these combinations supports the findings of Ashwathama et al. (2003) and Rauf et al. (2005), emphasizing the potential of hybrid breeding to enhance yield in *desi* cotton. The superior performance of specific combinations like AC 3265 × PBS 1127-SP1 and AKH 496 × H 509 underscores the role of non-additive gene actions, such as dominance and over-dominance, in boosting yield. Thus, exploiting heterosis through hybrid breeding is a promising strategy for increasing productivity in *desi* cotton, consistent with earlier reports of positive heterotic effects.

Boll weight is directly associated with yield, larger boll weight generally lead to better yield (Manivannan et al., 2020). Boll weight and boll number were significantly correlated with the productivity of the plant in this study, which was in accordance with Manivannan et al. (2018). Iyanar et al. (2005) and Leela Pratap et al. (2006) also reported similar findings regarding non-additive components for boll weight. A combination of H 509 × AC 3097 alone was found to be a significant SCA effect for boll numbers in the present study.

SCA variance was higher than GCA variance, indicating that the non-additive gene effect was more predominant in the traits under this study, which could be exploited by heterosis studies and population improvement methods. The presence of non-additive gene action for the traits under investigation suggested that these genotypes would be desirable for the production of hybrids (Griffing 1957). Studies by Anil et al. (2017), Choudhary et al. (2017), Vekariya et al. (2017) and Gunjiganvi et al. (2018) also identified significant SCA effects, highlighting the role of non-additive gene action in enhancing yield and other agronomic traits. More recent studies by Madhu et al. (2023) and Sukrutha et al. (2023) have further reinforced this concept, showing that non-additive effects are crucial for improving complex traits in cotton. These studies, in conjunction with our results, emphasize the importance of selecting parent lines that demonstrate strong SCA to achieve desirable hybrid performance.

Nonadditive gene action, where genes from distinct parental lines combine to produce offspring with superior traits, plays a pivotal role in hybrid vigour or heterosis. Breeders can exploit this variation to develop superior cotton hybrids through strategic hybrid breeding. The dominance of SCA variance over GCA variance for all traits highlights the significance of specific parental combinations in determining hybrid performance. Evaluating hybrids for their SCA is crucial to identifying crosses that exhibit high heterosis and improved performance, enabling the development of high-yielding, resilient cotton varieties for diverse environmental conditions.

Hayman's graphical approach revealed that dominance components (H_1, H_2) were larger than the additive component (D) which suggested that overdominance plays a major role in these traits. In this connection, heterozygotes those with two different alleles perform better than either homozygotes (Sukrutha et al. 2023). In terms of performance, this indicates that those with two different alleles at these loci do better performance than those with two identical alleles. Except for boll weight, the average degree of dominance $(H_1/D)^{1/2}$ for the other three traits is shown > 1, indicating the presence of overdominance. This suggested that heterosis breeding might be advantageous to get higher gain in cotton. Previous studies such as Zapadiya et al. (2021), Madhu et al. (2023), and Sukrutha et al. (2023) have also reported the prevalence of over-dominance in cotton, emphasizing its role in enhancing yield and other agronomic traits. In contrast, boll weight exhibited a dominance ratio (H_1/D) less than 1, indicating that boll weight was influenced more by dominance genes rather than over-dominance. This observation aligns with the findings of Vasconcelos et al. (2018) and Hussain et al. (2019), who also identified dominance genes influencing boll weight. Overall, non-additive gene action was found to be the main determinant of cotton yield-attributing traits (Madhu et al. 2023; Sukrutha et al. 2023).

The Vr-Wr graph further elucidates the genetic basis of the traits. The results indicate that the presence of partial dominance for all the studied traits, suggesting a mix of dominant and recessive genes influencing these traits. Additionally, the parents PBN 565, H 173, and 3930 A had a high frequency of dominant genes for single plant yield, while H 173 and 3930 A were prominent for boll number. PBN 565 and H 503 showed a higher presence of dominant genes for boll weight, and AKH 496, PBS 1127-SP1, and 3930 A were notable for days to first flowering. These parents possess significant amounts of dominant genes, making them valuable for future breeding programs.

Overall, the findings of the current study shed information on the genetic makeup and gene action of the four yield-related traits, emphasizing the significance of dominance and over-dominance gene effects in influencing *G. arboreum* cotton hybrid performance. These findings may have an impact on cotton breeding initiatives that seek to enhance varieties with desired features by leveraging parents with beneficial gene combinations.

Conclusion

Identifying superior parents and combinations with high mean performance and positive SCA effects, while demonstrating stability across different environments is essential for breeding programs. Both Griffing's and Hayman's analyses revealed that non-additive gene action is predominant, with greater SCA variance than GCA variance. Future research should explore traits like fiber quality, disease resistance, and drought tolerance with these lines and combinations, and conduct multi-environment trials to assess stability and genotype × environment interactions. This would pave the way to identify and develop superior hybrids with wider adaptability coupled with yield and fibre quality.

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Authors' contributions

Alagarsamy M conceived the idea, executed the research, collected data, did statistical analysis and prepared the manuscript single-handedly.

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Data availability

The datasets used during this study can be provided on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The author has no conflict of interest.

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References

Anil K, Narendra J, Neelima S. Heterosis and combining ability analysis in upland cotton (*Gossypium hirsutum* L.). J Cotton Res Dev. 2017;31:236–42.

Ashwathama VH, Patil BC, Kareeakatti SR, et al. Studies on heterosis for biophysical traits and yield attributes in cotton hybrids. In: World Cotton Research Conference 3. Bangalore: International Cotton Advisory Committee; 2003. p. 240–7.

Basu AK, Paroda RS. Hybrid cotton in India: a success story. Bangkok: Asia-Pacific Association of Agricultural Research Institutions, FAO Regional Office for Asia & the Pacific; 1995. p. 38.

Bourgou L, Dever JK, Sheehan M, et al. Diallel crosses of cotton (*Gossypium hirsutum* L.) - enhancement of fiber properties in future cultivars for Burkina Faso. Agronomy. 2023;13(12):2864. https://doi.org/10.3390/agronomy13122864.

Çetin B, Çopur O. Combining ability and heterosis for fiber color and quality in cotton (*Gossypium hirsutum* L). Not Bot Horti Agrobo. 2022;50(2):12782. https://doi.org/10.15835/nbha50212782.

Deshmukh KH, Chinchane VN, Kalpande HV, et al. Combining ability studies for yield and yield contributing traits in *desi* cotton (*Gossypium arboreum* L.). Electron J Plant Breed. 2021;10(8):39–41.

Gnanasekaran M, Thiyagu K. Gene action, combining ability and standard heterosis for seed cotton yield and fibre quality components in upland cotton. Electron J Plant Breed. 2021;12(2):325–34.

Griffing BI. Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci. 1957;9:463–93.

Gunjiganvi A, Patil BR. Combining ability analysis for seed cotton yield and its contributing traits in upland cotton (*Gossypium hirsutum* L.). J Farm Sci. 2018;31:20–4.

Gupta M, Kumar A, Singh S. Pest resistance in cotton: an integrated approach for sustainable production. Plant Prot Sci. 2023;59(2):101–10.

Haffez SH, Hamed HH, Darwesh AE. Evaluation of combining ability and heterosis for some yield and fiber quality properties in cotton (*Gossypium barbadense* L.) obtained by half diallel mating design. J Plant Prod. 2022;13(8):581–8.

Hayman BI. The theory and analysis of diallel crosses. Genetics. 1954;39(6):789–809. https://doi.org/10.1093/genetics/39.6.789.

Hinze LL, Kohel RJ, Campbell BT, et al. Variability in four diverse cotton (*Gossypium hirsutum* L.) germplasm populations. Genet Resour Crop Evol. 2011;58:561–70.

Hussain A, Zafar ZU, Rahman MH, et al. Assessing gene action for hypoxia tolerance in cotton (*Gossypium hirsutum* L.). Agron Mesoam. 2019;30(1):51–62.

Iyanar K, Ravikesavan R, Subramanian A. Studies on combining ability status in relation to heterosis in cotton (*Gossypium hirsutum* L.). Adv Plant Sci. 2005;18(1):317–22.

Jenkins JN, McCarty JC, Wu J, et al. Genetic variance components and genetic effects among eleven diverse upland cotton lines and their F_2 hybrids. Euphytica. 2009;167:397–408. https://doi.org/10.1007/s10681-009-9902-y.

Kannan N, Saravanan K. Heterosis and combining ability analysis in tetraploid cotton (*Gossypium hirsutum* L. and *Gossypium barbadense* L.). Int J Curr Res. 2015;7:16590–5.

Khan MA, Iqbal Z, Ahmad S. Advances in hybrid cotton breeding: Global perspectives and future strategies. Plant Breed Rev. 2021;45:113–45.

Khan Z, Khan SH, Ahmed A, et al. Genome editing in cotton: challenges and opportunities. J Cotton Res. 2023;6:3. https://doi.org/10.1186/s42397-023-00140-3.

Kumar K, Ashokkumar K, Ravikesavan R. Genetic effects of combining ability studies for yield and fiber quality traits in diallel crosses of upland cotton (*Gossypium hirsutum* L.). Afr J Biotechnol. 2014;13:119–26.

Leela Pratap K, Chenga Reddy V, Reddy KVS, et al. Combining ability for yield and yield component traits in cotton (*Gossypium hirsutum* L.). Andhra Agric J. 2006;53:152–6.

Liu Y, Zhang L, Huang J. Sustainable cotton production: The role of hybrid cotton in reducing environmental impact. Agric Sustain. 2022;5(3):180–92.

Madhu B, Sivakumar S, Manickam S, et al. Improvising cotton (*Gossypium hirsutum* L.) genotypes for compact plant architecture traits suitable for mechanical harvesting. Indian J Genet Plant Breed. 2023;83(3):398–406.

Majeed S, Rana IA, Atif RM, et al. Role of SNPs in determining QTLs for major traits in cotton. J Cotton Res. 2019;2:5. https://doi.org/10.1186/s42397-019-0022-5.

Majeed M, Rana IA, Mubarik MS, et al. Heat stress in cotton: a review on predicted and unpredicted growth-yield anomalies and mitigating breeding strategies. Agronomy. 2021;11(9):1825.

Manivannan A, Amal TC. Deciphering the complex cotton genome for improving fiber traits and abiotic stress resilience in sustainable agriculture. Mol Biol Rep. 2023;50:6937–53. https://doi.org/10.1007/s11033-023-08565-4.

Manivannan A, Waghmare VN. Assessment of genetic divergence in diploid cotton (*Gossypium arboreum* L.) germplasm using fibre quality traits. Plant Genet Resour. 2020;18(5):351–8.

Manivannan A, Mohan P, Saravanan M, et al. Morphological characterization of Asiatic cotton (*Gossypium arboreum*) germplasm of India. Electron J Plant Breed. 2018;9(2):673–81.

Mudhalvan S, Rajeswari S, Mahalingam L, et al. Combining ability estimates and heterosis analysis on major yield attributing traits and lint quality in American cotton (*Gossypium hirsutum* L.). Electron J Plant Breed. 2021;12(4):1111–9.

Patel R, Sharma V, Singh P. Breeding strategies for developing drought-tolerant cotton varieties: challenges and opportunities. J Cotton Res Dev. 2022;36(4):195–202.

Pusphpam R, Thanaraj K, Raveendran TS. Heterosis and combining ability studies in upland cotton for yield characters. Electron J Plant Breed. 2015;6:459–63.

Rauf S, Khan TM, Nazir S. Combining ability and heterosis in *Gossypium hirsutum* L. Int J Agric Biol. 2005;7(1):109–13.

Rodríguez F, Alvarado G, Pacheco Á, et al. Analysis of genetic designs with R for Windows (AGD-r) version 4.0. In: Biometrics and statistical unit. El Batań: Centro Internacional de Mejoramientode Maizy Trigo; 2015.

Salman M, Zia ZU, Rana IA, et al. Genetic effects conferring heat tolerance in upland cotton (*Gossypium hirsutum* L.). J Cotton Res. 2019;2:9. https://doi.org/10.1186/s42397-019-0025-2.

Sankaranarayanan K, Venugopalan MV, Kanjana D. Assessment of production potential of long-linted *Gossypium arboreum* L. genotypes under different sowing times. Bull Natl Res Cent. 2021;45:106. https://doi.org/10.1186/s42269-021-00553-7.

Subhan M, Qasim M, Ahmad R, et al. Diallel analysis for estimating combining ability of quantitatively inherited traits in cotton. Asian J Plant Sci. 2003;2(11):853–7.

Sukrutha B, Rajeswari S, Premalathi N, et al. Combining ability and gene action studies for yield and fibre traits in *Gossypiumarboreum* using Griffings numerical and Haymans graphical approach. J Cotton Res. 2023;6:12. https://doi.org/10.1186/s42397-023-00149-8.

Thiyagu K, Gnanasekaran M, Gunasekaran M. Components and fibre quality traits in upland cotton (*Gossypium hirsutum* L.). Electro J Plant Breed. 2019;10(4):1501–11.

Vasconcelos UAA, Cavalcanti JJV, Farias FJC, et al. Diallel analysis in cotton (*Gossypium hirsutum* L.) for water stress tolerance. Crop Breed Appl Biotechnol. 2018;18:24–30.

Vekariya N, Chovatia V, Pansuriya A, et al. Combining ability analysis for yield and its attributes in American cotton (*Gossypium hirsutum* L.). Electro J Plant Breed. 2017;8:292–6.

Zapadiya VJ, Valu MG. Gene action studies in the inheritance of yield and quality attributing traits in diallel cross of cotton (*Gossypium hirsutum* L.). Int J Pure App Biosci. 2021;9(3):105–9.