



Transgressive segregation in cotton (*Gossypium hirsutum* L.) affects the combining ability and heterotic patterns

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Abstract The inheritance of the studied traits in cotton breeding studies directs the selection method, and it is crucial to identify suitable parents and promising hybrids to be transferred to the next generations. Ten F_2 hybrid populations generated by line $\times$ tester mating design were compared with their parents and F_1 hybrids for seed cotton yield per plant, ginning out-turn, fiber length, fiber fineness, and fiber strength. The general/specific combining ability variance ratio in F_1 and results of a minimum norm quadratic unbiased estimation indicated that the dominant gene effect for seed cotton yield, additive gene effect for ginning out-turn and fiber fineness, both dominant and additive gene effects for fiber length and fiber strength were greater. Significant correlation coefficients between F_1 and F_2 hybrid performance and general combining ability effects for ginning out-turn and fiber length confirmed additive gene effects in the control of these traits. Although F_2 populations were higher than their parents and lower than F_1 populations regarding seed cotton yield and fiber strength, F_2 populations had the finest fibers. As a result of the combined evaluation of average performance,

general combining ability effects, and predicted additive effects for parents, Fiona and Gloria for ginning out-turn, İpek-607 for fiber length, Özbek-100 for fiber fineness, and Flash for fiber strength were the best combiners. Claudia $\times$ Özbek-100 was determined as the most promising F_1 hybrid combination for both hybrid variety breeding and transfer to the next generations in terms of all traits. Gloria $\times$ Flash, Claudia $\times$ Özbek-100, and Gloria $\times$ Özbek-100 hybrid combinations within the F_2 populations should be transferred to the next generations by applying the bulk method.

Keywords Combining ability · Fiber quality · Gene action · Heritability · Heterotic patterns

Introduction

Cotton, *Gossypium hirsutum* L., is the most important commercial cotton species, providing raw material for the textile industry. About 5–7 million years ago, diploid species differentiation occurred between the A genome of African origin and the D genome of Mexican origin (Wang et al. 2024). During domestication, cotton fibers also changed from the original short and sparse brown fibers to the current long and dense white fibers, resulting in higher yields and easier production (Bao et al. 2019). The main cultivated cotton varieties are the tetraploids *G. hirsutum* and *G. barbadense*, with the improved form

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of *G. hirsutum* (Upland cotton) accounting for more than 95% of global cotton fiber production due to its high yield and wide adaptability.

Cotton fiber quality traits are controlled by complex interactions of multiple genes. The assessment of cotton fiber quality is mainly based on fiber length, strength, micronaire, homogeneity, and elongation. Among these, fiber length and strength have been suggested to be the main properties determining fiber quality (Razzaq et al. 2022). Longer fibers with low short fiber content produce higher yarn count and strength, hence higher textile quality. Higher fiber strength increases fabric strength, making the end product robust and durable. Therefore, searching and identifying candidate genes for excellent fiber quality and breeding cotton varieties with elite fiber quality is extremely important.

Cotton breeding programs generally use elite germplasm and commercial varieties as parents in the hybridization stage. Genetic erosion and contraction due to decreasing genetic distance is the biggest problem (Bowman and Gutierrez 2003; Paterson et al. 2004). Cotton breeding is based on the selection of genotypes with superior traits from a genetically heterogeneous and heterozygous population. Pure lines are developed from segregating populations, and heterosis is used as an indicator of epistasis, dominance, and overdominance in autogamous plants such as cotton (Zeng et al. 2017). Due to fertility problems between tetraploid cotton species and their diploid relatives, new alleles need to be added through continuous crosses (Campbell et al. 2010; Saha et al. 2012). Growing the early generations of hybridization together with their parents gives direction to the selection method to be carried out, together with the selection of suitable parents and lines. The line $\times$ tester method is frequently used to genetically define many parents and lines, estimate their combining abilities, and determine which gene effects control the traits (Rathinavel et al. 2017).

In many studies conducted, line $\times$ tester was used as a mating design and genetic-statistical method, and parents and F_1 populations were evaluated for seed cotton yield, yield components, and fiber quality parameters (Ünay et al. 2019; Balcı et al. 2023; Farooq et al. 2023; Abdel-Aty et al. 2023). Considering the ratio of the variance of general combining ability to the variance of specific combining ability, these researchers emphasized that

gene effects are generally non-additive for seed cotton yield, whereas additive gene effects are significant for fiber traits. High narrow heritability due to the additive gene effect increases selection success and genetic progress (Baloch 2004; Khan et al. 2009a, b). The negative associations between yield, ginning out-turn, and fiber quality traits in promising lines to be transferred to the next generation require selection according to optimum values for the traits (Çakmak et al. 2023; Çakmak et al. 2023).

The term "segregation variance" refers to the increase in variation in F_2 as a result of alleles segregating from F_1 , resulting from distinct genetic lines or populations. When divergent populations are crossed, the variance of the F_1 generation is not enhanced since every F_1 offspring has heterozygous loci with one allele from each divergent parent. Nonetheless, the F_2 generation frequently exhibits an outbreak of variation brought about by recombination, known as the "segregation variance" (Lande 1981; Benowicz et al. 2020). In cotton, many studies evaluating parents, F_1 , and F_2 populations together have aimed to estimate genetic parameters (Balcı et al. 2021; Abd El Samad et al. 2023; Elhousary et al. 2023). In order to meet the demands of growers, ginning, and textile industrialists, cotton breeding studies aim to develop genotypes with fiber quality traits within commercial limits and high ginning out-turn and seed cotton yield. Therefore, we investigated the potential of newly improved cultivars in terms of their general combining ability, the specific combining ability of their hybrids, and heritability from F_1 and F_2 populations by line $\times$ tester analysis. In addition, variance components were compared with Line $\times$ Tester analysis results by applying the MINQUE model.

Material and methods

Parental genotype and crossing

Claudia, Fiona, Gloria, İpek-607, and Lodos cultivars, which stand out regarding fiber quality traits in Aegean Region cotton cultivation, were used as lines. These parents were crossed with Flash and Özbek-100 in a line $\times$ tester mating design under field conditions in the 2020 summer growing season. Ten hybrid combinations were grown under greenhouse

conditions through the winter season to obtain the F₂ seed in 2021.

Experimental site and cultural management

In 2021, 27 genotypes, including seven parents, 10 F₁ and 10 F₂ hybrid combinations, were planted in a Randomized Complete Block Design with four replications. Genotypes were sown in a single row, each 6.0 m long, with row-to-row and plant-to-plant distances of 70 and 20 cm, respectively, after thinning. The standard cultural management, such as plant protection, hoeing, and irrigation for the Aegean Region, was followed. 180 kg ha⁻¹ N, 80 kg ha⁻¹ P₂O₅, and 80 kg ha⁻¹ K₂O were applied as basal fertilizer.

Data collection

Twenty plants per genotype were tagged randomly, excluding border plants, to record the data. Seed cotton yield per plant (g) was determined during the harvest period, and then the seed cotton was ginned to determine the ginning out-turn (%). Fiber fineness (mic.), fiber length (mm), and fiber strength (g tex⁻¹) were determined by the HVI 1000 instrument.

Statistical analysis

Firstly, in order to determine the genotypic difference, data were subjected to analysis of variance (ANOVA) according to Randomized Complete Block Design by the JMP® 14 statistical software (SAS Institute Inc. 2018). Orthogonal contrasts were defined between parents vs F₁, parents vs F₂, and F₁ vs F₂. The LSD means contrast function, as implemented in JMP® 14, has been used to test orthogonal contrasts between treatments using F statistics for different means. The mean of genotypes was compared by the LSD test at a 0.05 probability level proposed by Steel et al (1997). We used the line × tester method (Kempthorne 1957) to estimate the combining abilities of parents and hybrids using TARPOGEN software (Ozcan 1999). Gene action and degree of dominance of the studied traits were calculated (Singh and Chaudhary 1985). Heterosis, heterobeltiosis, and inbreeding depression were calculated using the following formulas in Microsoft Excel®.

$$\text{Heterosis (\%)} = \frac{F_1/F_2 - \text{mid parent}}{\text{mid parent}} \times 100 \text{ (Hallauer and Miranda 1981).}$$

$$\text{Heterobeltiosis (\%)} = \frac{F_1/F_2 - \text{better parent}}{\text{better parent}} \times 100 \text{ (Hallauer and Miranda 1981).}$$

$$\text{Inbreeding depression (\%)} = \frac{F_1 - F_2}{F_1} \times 100 \text{ (Singh 2003).}$$

The standard error for the significance of heterosis was $\sqrt{\frac{3 \times \text{mean sum of square due to error}}{2 \times \text{number of replications}}}$.

The standard error for the significance of heterobeltiosis and inbreeding depression was $\sqrt{\frac{2 \times \text{mean sum of square due to error}}{\text{number of replications}}}$.

The results were then analyzed using a linear mixed model approach, i.e., minimum quadratic unbiased estimation (MINQUE) (Rao 1971; Zhu 1989), in order to estimate all variance components. Additive and dominant effects were estimated using the adjusted prediction method developed by Zhu (1993). The ten-fold jackknife resampling method was performed to predict standard error for statistical tests for all predicted parameters (Wu et al. 2013). Data was analyzed using the 'qgtools' package (Wu et al. 2014) under R Studio.

Results

The significant genotypic variance found for all traits examined indicates a diversity in the material and enough genetic variability adequate for further biometrical assessment (Table 1). The significant and larger mean squares of parents vs. crosses for F₁ than those of F₂ in seed cotton yield result from inbreeding depression and loss of heterosis in F₂. F₁ populations have weaker fibers than their parents, but coarser fibres than F₂ populations (Tables 2 and 3). The combining ability analysis exhibited that the line effect for SCY and FL in F₂; for GOT in F₁ was significant, while the tester effect had a significant difference for FF in F₁ and for FL and FS in F₂. (Table 2). In the F₁ generation, a significant line × tester interaction, which is an indicator of non-additive gene effect, was found significant for all traits except FF, but only for

Table 1 ANOVA on the investigated genotypes comprising parents, F₁, and F₂ hybrids for the studied traits

Source of variation	df	SCY	GOT	FL	FF	FS
Replication	3	1202.25	1.74*	0.24	0.08	1.28
Genotypes	26	1436.84**	21.69**	3.51**	0.23**	12.20**
Error	78	460.23	0.44	0.26	0.06	0.64
<i>Contrasts</i>						
Parents vs F ₁	1	15,451.93**	2.00	0.66	0.12	19.83*
Parents vs F ₂	1	6265.53**	1.49	0.69	0.24	8.02
F ₁ vs F ₂	1	2475.42*	0.04	3.26	0.86**	3.19

SCY: seed cotton yield per plant (g), GOT ginning out-turn (%), FL fiber length (mm), Fiber fineness (micronaire), FS fiber strength (g tex⁻¹)

* $p \leq 0.05$; ** $p \leq 0.01$

Table 2 Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) in the investigated genotypes

Source of variation	Generation	SCY	GOT	FL	FF	FS
Replication	F ₁	15.94	0.24	0.01	0.05	0.41
	F ₂	676.84	3.73**	0.32	0.04	0.92
Genotype	F ₁	137.36**	24.54**	3.98**	0.30**	16.09**
	F ₂	1528.73**	27.79**	3.87**	0.23**	11.69**
Parent	F ₁	248.49**	45.34**	6.04**	0.47**	19.87**
	F ₂	248.49	45.34**	6.04**	0.47**	19.87**
Parent vs Hybrid	F ₁	15,451.93**	2.00**	0.66	0.12	19.83**
	F ₂	6265.53**	1.49	0.69	0.24	8.02**
Hybrid	F ₁	406.25**	13.17**	2.97**	0.20**	13.16**
	F ₂	1855.91**	19.01**	2.78**	0.07	6.64**
Line	F ₁	340.44	28.44**	5.62	0.07	20.04
	F ₂	3565.80*	32.10	3.19*	0.07	5.56
Tester	F ₁	686.74	1.15	0.64	1.46**	24.15
	F ₂	1368.32	1.23	11.46**	0.06	31.83*
Line × Tester	F ₁	401.92**	0.91*	0.91**	0.03	3.53**
	F ₂	267.92	10.37**	0.21	0.07	1.42
Error	F ₁	9.37	0.26	0.18	0.04	0.50
	F ₂	499.30	0.42	0.36	0.07	0.63
GCA / SCA variance ratio	F ₁	0.003	5.21	0.78	-3.00	0.88
	F ₂	-1.90	0.24	-4.81	0.00	1.83

SCY seed cotton yield per plant (g plant⁻¹), GOT ginning out-turn (%), FL fiber length (mm), fiber fineness (micronaire), FS fiber strength (g tex⁻¹)

* $p \leq 0.05$; ** $p \leq 0.01$

FF in the F₂ generation. The GCA/SCA ratios in F₁ and F₂ were completely different. Non-additive gene effects were higher in the control of SCY, FL, and FS in the F₁ generation and GOT and FF in the F₂ generation.

In the F₂ generation, the highest seed cotton yield (117.08 g) in the Gloria × Flash combination and the lowest seed cotton yield (50.28 g) in the İpek-607 × Flash combination are indicative of transgressive segregations. The seed cotton yields of

Gloria × Özbek-100 in both the F₁ and F₂ generations followed the Gloria × Flash combination. Also, the F₂ population of the Flash × Fiona combination exhibited positive transgressive segregation for GOT. A 40% and above ginning out-turn was encountered except for the combinations with İpek-607. The hybrid combinations, İpek-607 × Flash and İpek-607 × Özbek-100 in F₁ generation, İpek-607 × Flash in F₂, and Gloria × Flash in F₁, had the longest fibers over 32 mm. The fiber fineness of the F × population ranging

Table 3 Mean performance of investigated genotypes for the studied traits

Genotype	Generation	SCY	GOT	FL	FF	FS
Claudia	Parent	69.57	41.45	30.54	4.67	33.62
Fiona	Parent	65.30	43.01	31.63	4.47	31.69
Gloria	Parent	58.67	40.94	30.86	4.67	35.14
İpek-607	Parent	53.90	32.78	32.86	4.10	32.09
Lodos	Parent	76.23	41.03	30.83	4.21	29.63
Flash	Parent	72.87	39.64	30.68	5.11	32.36
Özbek-100	Parent	69.07	38.00	28.78	4.38	28.60
Claudia × Flash	F ₁	77.13	40.07	30.47	4.90	32.95
Claudia × Özbek-100	F ₁	103.73	40.30	30.76	4.40	32.72
Fiona × Flash	F ₁	96.10	41.98	31.10	4.76	33.08
Fiona × Özbek-100	F ₁	91.83	41.95	31.15	4.28	29.81
Gloria × Flash	F ₁	99.47	40.77	32.09	4.83	31.30
Gloria × Özbek-100	F ₁	114.70	40.47	30.67	4.60	28.64
İpek-607 × Flash	F ₁	103.77	36.89	32.29	4.65	29.03
İpek-607 × Özbek-100	F ₁	96.17	36.80	32.23	4.34	28.23
Lodos × Flash	F ₁	88.53	40.63	30.09	4.81	31.42
Lodos × Özbek-100	F ₁	100.00	39.13	29.97	4.44	30.62
Claudia × Flash	F ₂	81.51	38.89	31.18	4.60	31.80
Claudia × Özbek-100	F ₂	109.01	40.80	30.02	4.38	30.31
Fiona × Flash	F ₂	77.90	44.21	31.23	4.32	31.66
Fiona × Özbek-100	F ₂	89.34	40.37	30.34	4.44	30.55
Gloria × Flash	F ₂	117.08	40.98	31.07	4.44	33.92
Gloria × Özbek-100	F ₂	113.88	40.25	30.19	4.34	30.69
İpek-607 × Flash	F ₂	50.28	36.04	32.38	4.37	32.31
İpek-607 × Özbek-100	F ₂	67.30	37.50	30.77	4.48	30.56
Lodos × Flash	F ₂	74.09	40.00	30.21	4.39	30.65
Lodos × Özbek-100	F ₂	79.81	39.45	29.39	4.15	29.32
LSD _(0.05)		30.20	0.94	0.72	0.34	1.14
<i>Ave. of Parents</i>		66.51	39.55	30.88	4.52	31.88
<i>Ave. of F₁</i>		97.14	39.90	31.08	4.60	30.78
<i>Ave. of F₂</i>		86.02	39.85	30.68	4.39	31.18
<i>Grand Ave</i>		85.08	39.79	30.88	4.50	31.21
CV (%)		21.02	1.66	1.66	5.26	2.56
Correlation	F₁ with F₂	0.34	0.86**	0.70*	0.27	0.17

SCY: Seed cotton yield per plant (g plant⁻¹); GOT: Ginning out-turn (%); FL: Fiber length (mm); Fiber fineness (micronaire); FS: Fiber strength (g tex⁻¹)

from 4.15 mic. (Lodos × Uzbek-100) to 4.60 mic. (Claudia × Flash) was within desirable limits. Gloria × Flash (F₂), Fiona × Flash (F₁), Claudia × Flash (F₁), Claudia × Özbek-100 (F₁), and İpek-607 × Flash (F₂) were the populations with the strongest fibers. Notably, the Flash genotype was the parent in 4 out of 5 combinations. This was supported by Flash parents' positive and significant GCA effects for FS (Table 4). Gloria was the best combiner for SCY and GOT in F₁ and F₂, and FS in F₂. Özbek-100 was found to be the parent with an effect that increased the seed

cotton yield and thinned the fiber fineness in the F₁ generation. İpek-607 for FL and Fiona for GOT were good combiners. The significant and positive correlation among the combining abilities of parents in the F₁ and F₂ generations indicated that their combining ability moved in parallel in both generations.

In principal component biplot analyses, it is possible to visually display the relationships between genotypes and the traits examined together (Fig. 1). The traits that contributed most to the total variation were GOT and FS. Vector lengths also showed

Table 4 GCA effects of parents and SCA effects of hybrids in F₁ and F₂ generations

Genotype	Generation	SCY	GOT	FL	FF	FS
Claudia	F ₁	−6.71**	0.29	−0.47**	0.05	2.06**
	F ₂	9.24	−0.01	−0.08	0.12	−0.12
Fiona	F ₁	−3.18**	2.07**	0.04	−0.08	0.66*
	F ₂	−2.40	2.44**	0.10	−0.02	−0.07
Gloria	F ₁	9.94**	0.72**	0.30*	0.11	−0.81**
	F ₂	29.46**	0.77**	−0.05	−0.01	1.13**
İpek-607	F ₁	2.82*	−3.06**	1.18**	−0.11	−2.15**
	F ₂	−27.23**	−3.08**	0.90**	0.03	0.26
Lodos	F ₁	−2.88*	−0.02	−1.06**	0.03	0.24
	F ₂	−9.07	−0.13	−0.88**	−0.13	−1.19**
Flash	F ₁	−4.14**	0.17	0.13	0.19**	0.78**
	F ₂	−5.85	0.18	0.54**	0.04	0.89**
Özbek-100	F ₁	4.14**	−0.17	−0.13	−0.19**	−0.78**
	F ₂	5.85	−0.18	−0.54**	−0.04	−0.89**
<i>Correlation</i>	<i>F₁ with F₂</i>	<i>0.40</i>	<i>0.99**</i>	<i>0.86*</i>	<i>0.24</i>	<i>−0.10</i>
Claudia×Flash	F ₁	−9.16**	−0.28*	−0.27	0.06	−0.66
	F ₂	−7.91	−1.13**	0.04	0.10	−0.15
Claudia×Özbek-100	F ₁	9.16**	0.28*	0.27	−0.06	0.66
	F ₂	7.91	1.13**	−0.04	−0.10	0.15
Fiona×Flash	F ₁	6.28**	−0.15	−0.15	0.05	0.86*
	F ₂	0.13	1.75**	−0.09	−0.10	−0.33
Fiona×Özbek-100	F ₁	−6.28**	0.15	0.15	−0.05	−0.86*
	F ₂	−0.13	−1.75**	0.09	0.10	0.33
Gloria×Flash	F ₁	−3.47*	−0.02	0.59**	−0.07	0.55
	F ₂	7.45	0.19	−0.10	0.01	0.72
Gloria×Özbek-100	F ₁	3.47*	0.02	−0.59**	0.07	−0.55
	F ₂	−7.45	−0.19	0.10	−0.01	−0.72
İpek-607×Flash	F ₁	7.94**	−0.12	−0.09	−0.04	−0.38
	F ₂	−2.66	−0.91**	0.27	−0.10	−0.02
İpek-607×Özbek-100	F ₁	−7.94**	0.13	0.09	0.04	0.38
	F ₂	2.66	0.91**	−0.27	0.10	0.02
Lodos×Flash	F ₁	−1.59	0.58*	−0.07	−0.01	−0.38
	F ₂	2.99	0.10	−0.12	0.10	−0.23
Lodos×Özbek-100	F ₁	1.59	−0.58*	0.07	−0.01	0.38
	F ₂	−2.99	−0.10	0.12	−0.10	0.23
<i>Correlation</i>	<i>F₁ with F₂</i>	<i>0.13</i>	<i>0.14</i>	<i>−0.33</i>	<i>0.19</i>	<i>0.28</i>

SCY: Seed cotton yield per plant (g plant^{−1}); GOT: Ginning out-turn (%); FL: Fiber length (mm); Fiber fineness (micronaire); FS: Fiber strength (g tex^{−1})

* $p \leq 0.05$; ** $p \leq 0.01$

a genotype-dependent variation of the above-mentioned traits. When genotype×trait is considered, F₁ populations Gloria×Flash, Claudia×Özbek-100, Fiona×Flash, and Gloria×Flash were positioned on the axis between FS and SCY vectors. Similarly, F₂ populations such as Gloria×Flash and Fiona×Flash were also placed in the zone of high performance for all traits.

We found significant and positive specific combining ability only in F₁ generation in Claudia×Özbek-100, Fiona×Flash, Gloria×Özbek-100, and İpek-607×Flash hybrids in terms of seed cotton yield. Moreover, Gloria×Özbek-100, İpek-607×Özbek-100, and Lodos×Flash hybrid combinations were distinguished by their significant and positive SCA effects for GOT. In the F₁ generation, Gloria×Flash for FL and Fiona×Flash for

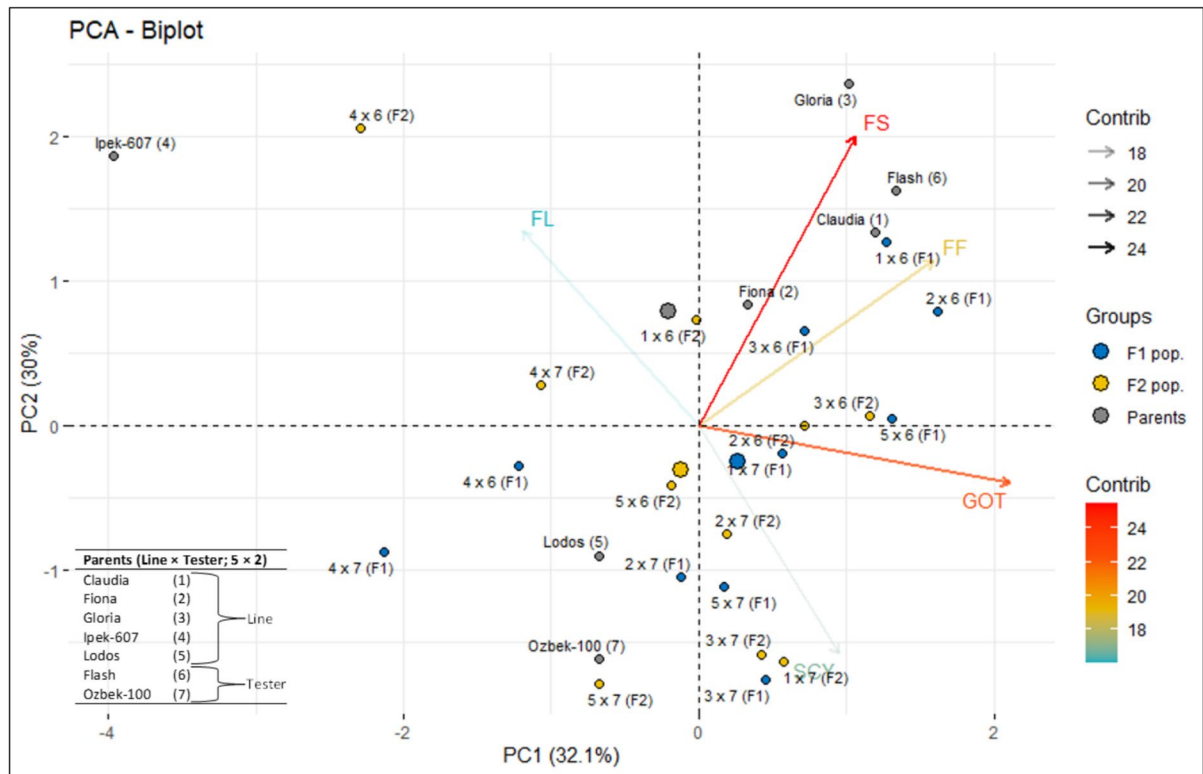


Fig. 1 Bi-plot graph for genotype × traits

FS combinations exhibited significant and desirable SCA effects (Table 4).

In terms of SCY, Claudia × Özbek-100, Gloria × Flash, and Gloria × Özbek-100 cross combinations exhibited significant and positive heterotic effects, whereas İpek-607 × Flash exhibited significant and negative inbreeding depression (Table 5). As for the GOT, Fiona × Flash had significant and positive heterotic effects and inbreeding depression in the F₂ generation. Fiona × Flash and Gloria × Flash had significant and positive heterotic effects and inbreeding depression for FL.

Table 6 presents the genetic basis of combining abilities according to MINQUE. Significant additive variance for FF and GOT was detected, whereas dominant variance was significant for SCY. In terms of FL and FS, both dominant and additive genes were found to be effective. Selection breeding, starting with single plant selection in early generations, can be effective for FF and GOT. Delaying single plant selection

to later generations or using heterosis is inevitable for seed cotton yields.

None of the parents had significant additive gene effects for SCY (Table 7). The significant additive gene effects found for Fiona and Gloria in terms of GOT support these parents' significant and positive GCA effects. The additive gene effect of İpek-607, which had positive and significant GCA in terms of FL, was also high and significant. Although not in agreement with GCA effects, we found additive effects for FF in the desired direction in İpek-607 and Lodos parents. We found that additive gene effects were high in Gloria, Flash, Fiona, and Claudia, with positive and significant GCA effects for FS.

Table 8 summarises the two types of dominance effects: homozygous dominant and heterozygous dominant. Negative and significant homozygous dominant effect for SCY in all parents indicated that inbreeding depression was high in F₂ combinations with these parents. Inconsistent with the dominant effects of parents, Gloria × Flash, Gloria × Özbek-100, and Claudia × Özbek-100 F₂ combinations

Table 5 Heterosis (Ht), heterobeltiosis (Hb) and inbreeding depression (ID) of the studied traits in F₁ and F₂ generations

Genotype	SCY			GOT			FL			FF			FS		
	Ht	Hb	ID	Ht	Hb	ID	Ht	Hb	ID	Ht	Hb	ID	Ht	Hb	ID
Claudia × Flash	F ₁	8.31	5.85	-1.18	-3.33**	-0.47	-0.70	0.21	-4.10	-0.12	-1.99		-0.12	-1.99	
	F ₂	14.45	11.85	-5.67	-6.17**	2.94*	1.63	-2.34	-9.01**	5.12	-5.40**	3.48	-3.60*	-5.40**	3.48
Claudia × Özbek-100	F ₁	49.65*	49.11*	1.43	-2.78*	3.72**	0.73	-2.94	-5.85	5.17**	-2.68		5.17**	-2.68	
	F ₂	57.27**	56.69*	-5.09	-1.57	-1.25	-1.69	2.40*	-6.24	0.41	-9.84**	7.36**	-2.57	-9.84**	7.36**
Fiona × Flash	F ₁	39.11*	31.88	1.60	-2.39*	-0.16	-1.68	-0.55	-6.78*	3.30*	2.21		3.30*	2.21	
	F ₂	12.76	6.90	18.94	7.00**	-5.32**	-1.27	-0.41	-15.47**	9.32*	-2.16	4.28*	-1.12	-2.16	4.28*
Fiona × Özbek-100	F ₁	36.69	32.96		-2.47*	3.12**	-1.51	-3.13	-4.22	-1.11	-5.95**		-1.11	-5.95**	
	F ₂	32.98	29.34	2.72	-6.13**	3.75**	-4.09**	2.62*	-0.72	1.35	-3.61*	-2.48	1.35	-3.61*	-2.48
Gloria × Flash	F ₁	51.24*	36.50	1.19	-0.42	4.30**	3.99**	-1.20	-5.45	-7.26**	-10.93**		-7.26**	-10.93**	
	F ₂	78.02**	60.66**	-17.70	1.71	0.09	-0.52	3.19**	-13.05**	8.04*	-3.47*	-8.37**	0.50	-3.47*	-8.37**
Gloria × Özbek-100	F ₁	79.59**	66.06**	2.53*	-1.15	2.85**	-0.62	1.66	-1.60	-10.14**	-18.51**		-10.14**	-18.51**	
	F ₂	78.31**	64.88**	0.71	-1.68	0.53	-2.17	1.56	-7.01	5.50	-12.67**	-7.16**	-3.71*	-12.67**	-7.16**
İpek-607 × Flash	F ₁	63.71**	42.40*	1.86	-6.95**	1.65	-1.73	1.18	-8.98**	-9.91**	-10.30**		-9.91**	-10.30**	
	F ₂	-20.68	-31.00	51.55**	-0.47	-9.08**	-1.46	-0.27	-14.61**	6.18	-0.15	-11.32**	0.28	-0.15	-11.32**
İpek-607 × Özbek-100	F ₁	56.41*	39.23	3.97**	-3.17*	4.57**	-1.92	2.38	-0.90	-6.96**	-12.30**		-6.96**	-12.30**	
	F ₂	9.45	-2.57	30.02	5.97**	-1.31	-1.92	4.52**	2.20	-3.13	-4.76**	-8.26**	0.73	-4.76**	-8.26**
Lodos × Flash	F ₁	18.76	16.14	0.74	-0.98	-2.15*	-2.41*	3.28	-5.88	1.39	-2.90		1.39	-2.90	
	F ₂	-0.62	-2.81	16.32	-2.50*	-1.75	-2.00	-0.42	-14.20**	8.84*	-5.29**	2.46	-1.10	-5.29**	2.46
Lodos × Özbek-100	F ₁	37.65*	31.18	-0.95	-4.62**	0.56	-2.80*	3.48	1.35	5.18**	3.33		5.18**	3.33	
	F ₂	9.85	4.69	20.20	-0.16	-3.86**	-0.80	1.92	-5.30	6.56	-1.04	4.23*	0.73	-1.04	4.23*
Ave. of F ₁		44.11	35.13	1.48	-2.83	1.80	-0.86	0.44	-4.24	-2.05	-5.97		-2.05	-5.97	
Ave. of F ₂		27.18	19.86	11.20	-2.94	0.46	-2.14	1.28	-8.34	4.32	-4.84	-1.58	-0.85	-4.84	-1.58
Correlation F ₁ with F ₂		0.39	0.47	0.57	0.67*	0.38	0.57	0.12	0.69*	-0.07	0.45		-0.07	0.45	

SCY: Seed cotton yield per plant (g plant⁻¹); GOT: Ginning out-turn (%); FL: Fiber length (mm); FF: Fiber fineness (micronaire); FS: Fiber strength (g tex⁻¹)**p* ≤ 0.05; ***p* ≤ 0.01

Table 6 ANOVA based on MINQUE (minimum norm quadratic unbiased estimation) on the investigated genotypes

	SCY	GOT	FL	FF	FS
V (A)	1.24	5.02**	0.59**	0.03**	1.29**
V (D)	294.92**	0.40	0.31**	0.00	1.77**
V (B)	2.58	0.04	0.002	0.001	0.01
V (E)	414.33**	0.84**	0.29**	0.07**	0.99**
V (A) / VP	0.002	0.80**	0.50**	0.30**	0.32**
V (D) / VP	0.41**	0.06	0.26**	0.00	0.44**
V (B) / VP	0.004	0.01	0.001	0.004	0.003
V (E) / VP	0.58**	0.13**	0.24**	0.70**	0.24**

V (A): Additive variance; V (D): Dominance variance; V (B): Variance due to blocking (replication); V (E): Environmental variance; VP: Phenotypic variance, SCY: Seed cotton yield per plant (g plant^{-1}); GOT: Ginning out-turn (%); FL: Fiber length (mm); Fiber fineness (micronaire); FS: Fiber strength (g tex^{-1})

* $p \leq 0.05$; ** $p \leq 0.01$

Table 7 Predicted additive effects for parents

Parents	SCY	GOT	FL	FF	FS
Claudia	-0.01	0.57**	-0.14	0.07**	0.85**
Fiona	-0.16	1.96**	0.27**	-0.04	0.19**
Gloria	0.19	0.71**	0.10	0.05	0.92**
İpek-607	-0.39	-3.17**	0.97**	-0.13**	-0.16*
Lodos	-0.07	0.36**	-0.37**	-0.11**	-0.55**
Flash	0.04	0.04	-0.06	0.22**	0.11**
Özbek-100	0.39	-0.46**	-0.77**	-0.05	-1.37**

SCY: Seed cotton yield per plant (g plant^{-1}); GOT: Ginning out-turn (%); FL: Fiber length (mm); Fiber fineness (micronaire); FS: Fiber strength (g tex^{-1})

* $p \leq 0.05$; ** $p \leq 0.01$

with significant and positive heterozygous dominant effects indicated these combinations can be used as commercial F_2 hybrids. Claudia and Lodos for GOT; Lodos for FL; Gloria, İpek-607, and Flash for FS were suitable parents. In terms of FL and FS, Claudia $\times$ Özbek-100 was the most promising F_2 hybrid.

Discussion

Despite the negative correlation between yield and fiber quality (Clement et al. 2012; Campbell and Myers 2015; Koebernick et al. 2019), the main objective of cotton breeders is to create variation and new

lines that can effectively increase fiber yield and quality (Dawson and Goldringer 2012; Bradshaw 2017; Liu et al. 2023). In the current study, the significant differences among the hybrids for all the traits in both generations indicated that there was sufficient variation in the population for selection. We found that F_1 and F_2 populations were superior to parents regarding seed cotton yield, but F_1 populations exhibited the highest performance. The position of the overall mean of the F_1 populations in the bi-plot graph confirmed this. The F_2 population produced finer and stronger fibres overall. It was observed in the bi-plot graph that İpek-607 and F_1 hybrids with this parent were the worst genotypes in terms of other traits except fiber length. F_1 performance has been mentioned in many studies (Liangliang et al. 2023; Abd El Samad et al. 2023). In addition, Zhang et al (2017) revealed that dominance and dominant $\times$ dominant epistatic effects decreased by 50% in the F_2 generation due to homozygosity compared to the F_1 generation. The differences in the ratio of GCA/SCA variances between F_1 and F_2 for the traits examined may also be due to homozygosity. In contrast to F_1 populations, we found that FF and GOT were dominant, FS was additive, and SCY and FL were under the control of epistatic genes in F_2 , according to the evaluation by Matzinger (1963). Except for FS, our results contradict Joshi and Patil (2018), who estimated high heritability for GOT, SCY, FF, and FL due to their evaluation of the F_2 generation. Kumar and Katageri (2017) found low heritability for SCY but high heritability for GOT in F_2 . Their studies in Nazmeyer et al (2010) F_1 and F_2 generations pointed out non-additive gene effects for SCY, FL, and FS according to the GCA/SCA ratio. When MINQUE results and GCA/SCA were evaluated together, it was observed that epistatic genes were effective in the control of SCY and FL, but additive genes were effective in the control of FS. The fact that none of the parents had an additive effect regarding single plant yield and the heterozygosity in the hybrids was significant confirms the additive $\times$ dominant and dominant $\times$ dominant epistatic effect. The significant and positive correlation coefficients between F_1 and F_2 in terms of hybrid performances and GCA effects of parents for GOT and FL indicated that additive effects were predominantly for both traits. In other words, the consistency of parent performance for GOT and FL is very important (Zhang et al. 2016).

Table 8 Predicted (homozygous for parents and heterozygous for hybrid genotypes) dominance effects

Genotypes	SCY	GOT	FL	FF	FS
Claudia	−7.60**	0.38*	−0.22	0.00	−0.09
Fiona	−11.03**	0.11	0.01	0.00	−0.27*
Gloria	−22.85**	−0.03	−0.50**	0.00	2.36**
İpek-607	−18.99**	−1.35**	−0.05	0.00	1.63**
Lodos	−5.59**	0.35**	0.29**	0.00	−1.03**
Flash	−19.71**	−0.20	−0.22*	0.00	0.84**
Özbek-100	−28.92**	0.72**	−1.28**	0.00	−0.09
Claudia × Flash	−7.21**	−0.78*	−0.22	0.00	0.06
Claudia × Özbek-100	21.25**	0.53**	0.48**	0.00	1.38**
Fiona × Flash	11.50**	1.22**	−0.14	0.00	1.10**
Fiona × Özbek-100	5.77*	0.31	0.45**	0.00	−0.28
Gloria × Flash	23.29**	0.34**	0.91**	0.00	−0.77*
Gloria × Özbek-100	27.71**	0.35**	0.21**	0.00	−2.59**
İpek-607 × Flash	15.43**	−0.53**	0.57**	0.00	−2.08**
İpek-607 × Özbek-100	9.01**	0.40*	0.74**	0.00	−1.41**
Lodos × Flash	1.11	0.18	−0.75**	0.00	0.19
Lodos × Özbek-100	6.83**	−0.56**	−0.28**	0.00	1.04**

SCY: Seed cotton yield per plant (g plant^{−1}); GOT: Ginning out-turn (%); FL: Fiber length (mm); Fiber fineness (micronaire); FS: Fiber strength (g tex^{−1})

* $p \leq 0.05$; ** $p \leq 0.01$

In general, transgressive segregation, defined in F_2 and later generations, is the superiority of plants identified in the segregating generation over the better parental line (Revanasiddayya et al. 2023). On the other hand, transgressions are only observed when one or both parents do not have a genotype that causes an extreme degree of a distinct phenotypic trait (Amanturdiviev 2024). In our study, high values in 7 out of 10 F_2 populations for single plant yield and high GOT in 1 population were indicative of both heterobeltiosis and transgressive segregation. It was concluded that the F_1 line selection was unsuccessful in terms of yield, fibre fineness, and fibre strength. Similarly, Khan et al. (2009a, b) stated that F_1 hybrids cannot predict seed cotton yield in further generations, whereas the combined performance of hybrids in F_1 and F_2 is a good indicator for identifying a promising population.

The GCA effect of parents was more important than the SCA effect of the cross for all fibre quality parameters, whereas both combining ability effects were determinants for GOT and SCY (Koebernick et al. 2019). Two female parents, Gloria and Claudia, were involved in the highest-yielding combinations. Gloria was particularly notable for its low yield but positive and significant GCA effect. Moreover, Gloria had positive and significant GCA effects regarding GOT and FS. Also, the combinations with Gloria

as the best combiner had high average performances. It has been emphasized in many studies that parents with positive and significant GCA effects will produce high-yielding hybrid combinations (Coyle and Smith 1997; Hassan et al. 2000; Lukonge et al. 2008).

To evaluate the reduction in performance, the extent of inbreeding depression was estimated for examined traits and in the case of heterotic effects and inbreeding depression of SCY, three combinations, Claudia × Özbek-100, Gloria × Flash, and Gloria × Özbek-100, exhibited significant and positive heterotic effects and unfavorable inbreeding depression. The superiority of some F_2 hybrid combinations over both F_1 populations and parents due to transgressive segregation was reported in many studies (Campbell et al. 2008; Khan et al. 2010; Panni et al. 2012). GOT and FL, under the control of additive genes, showed low values of heterotic effects and inbreeding depression. Soomro and Kalhor (2000) and Khan et al (2005) also reported low values of heterotic effects. All combinations except Fiona × Flash for GOT and Claudia × Flash for FL had significant and unfavorable heterotic effects and inbreeding depression. Significant heterotic effects and inbreeding depression were detected, leading to finer fibres, whereas generally negative and significant heterotic effects showed that fibre strength decreased. On the other hand, high yield

and strength were combined in the F_2 generation of hybrid combinations such as Gloria $\times$ Flash. The complementarity between parents in terms of FS and SCY indicated that the combination of traits could provide further improvement in the combination of traits. This result supports previous studies (Jenkins et al. 2009; Zeng et al. 2011; Campbell et al. 2013).

Conclusion

The present study showed that the high heterosis values observed in F_1 for yield did not reflect the yield potential of F_2 . It was determined that high-yielding, high-ginning out-turn, and superior fiber quality traits were not found in a single parent or hybrid. However, when the minimum desirable lower limits were determined for each trait, it was concluded that Gloria $\times$ Flash, Claudia $\times$ Özbek-100, and Gloria $\times$ Özbek-100 hybrid combinations were the most promising genotypes for further breeding studies. Due to non-additive gene effects, SCA effects, and hybrid performance in the F_2 population, it was shown that the Gloria $\times$ Flash hybrid combination was a genotype in which all traits were optimized. It was concluded that it would be beneficial to maintain this hybrid combination until the F_6 generation according to the bulk method. The significant environmental variance for all traits investigated in the study indicated that there may be non-genetic effects in the emergence of phenotypic performance. Therefore, future studies should be planned in different locations, and the number of genotypes evaluated should be increased.

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Declarations

Competing interest The authors declare no competing interests.

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