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Investigating the role of genes in determining fibre quality and oil content in upland cotton (*Gossypium hirsutum* L.) through generation mean analysis

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Abstract
Cotton is one of the most important cash crops having global significance in relation to economics and social affairs. With this, knowledge of inheritance pattern of various gene(s) involved in fibre parameters and oil content is important for deployment of appropriate breeding strategy to improve them. In the present study, various genetic effects underlying such pattern of inheritance and their interactions were determined based on generation mean analysis of quantitative genetics. A total of four diverse experimental crosses and their six different generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2 were separately evaluated in the Compact Family Block Design (CFBD) with three replications during *kharif* 2022-23. An ANOVA indicated highly significant mean sum of square for all the characters in all of the four crosses. A best fit model of six parameters of generation mean analysis depicted the importance of additive and non-additive or additive and dominant gene actions for fibre length, fibre fineness and fibre strength whereas importance of additive and dominant gene actions for oil content. Duplicate type of epistasis was also observed in one or more crosses for all the four characters.

Keywords: Additive, dominant, non-additive, duplicate

Introduction
Cotton, widely known as 'king of fibre' or 'white gold', a significant cash crop, has held a proud place among major fibre crops since ancient times, exerting a considerable impact on global economics and social affairs. The technological and agricultural term in English, 'cotton', which defines cultivated species of *Gossypium*, comes from the Arabic word '*al qatan*' or '*qutum*' or '*kutum*' (Brown and Ware, 1958) [9]. Out of the 50 different cotton species identified all over the globe, only 4 species are in cultivation. Among them, 2 species *i.e.*, *Gossypium arboreum* and *Gossypium herbaceum* are diploids (2n = 2x = 26) and 2 species *i.e.*, *Gossypium hirsutum* and *Gossypium barbadense* are allotetraploids (2n = 4x = 52). The tetraploid cotton species occupies more than 80% area of cotton cultivation. However, diploid cotton species are being cultivated in the area of Asia and Middle East. The America, Africa, Egypt and India are among the tropical and subtropical places in the world where cotton is beloved to have native. Mexico has the most diverse range of wild cotton species, with Australia and Africa following closely behind. Both the Old and New Worlds independently domesticated cotton.

India is the only nation that grows cotton worldwide where all four commercially farmed species *viz.*, *G. arboreum*, *G. herbaceum*, *G. hirsutum* and *G. barbadense* are grown in the three distinct zones *i.e.*, North, Central and South (Khadi *et al.*, 2009) [26]. North zone represents states of Haryana, Punjab, Rajasthan and Western Uttar Pradesh; Central zone represents states of Madhya Pradesh, Maharashtra and Gujarat; South zone represents states of Andhra Pradesh, Karnataka and Telangana. All these states cover about 95% of cotton area and also contribute about 95% to the total cotton production in India. Besides these states, cotton is also grown on small areas in Bihar, Orissa, Assam, Tripura and Meghalaya. These states cover about 5% area and also contribute 5% to the national cotton production. During the year 2021-22, India has cultivation of cotton in an area of 120.69 lakh ha and production of 362.18 lakh bales of with average productivity of 510.16 kg/ha. While discussing about states wise scenario of cotton cultivation, Maharashtra, Gujarat and Telangana are the major cotton growing states covering around 68.00% (82.09 lakh hectare) area under cotton cultivation and producing 65.35% (236.69 lakh bales) of cotton in the country.

Maharashtra is the leading cotton producing state with total production of 89.86 lakh bale from 39.37 lakh ha area with average productivity of 388.02 kg/ha followed by Gujarat which has total production of 80.96 lakh bale from 22.57 lakh ha area with average productivity of 609.80 kg/ha and Telangana which has total production of 65.87 lakh bale from 20.15 lakh ha area with average productivity of 555.73 kg/ha (Anon., 2022) [4].

The selection of a plant breeding technique to improve a given characteristic is primarily contingent upon the availability of dependable data regarding the type and extent of gene effects within the population. Various techniques in quantitative genetics can be employed to calculate distinct genetic components, such as additive, dominance, and epistatic interactions. The measurements of additive and dominant components may be inflated by the non-allelic gene interactions. In addition to additive and dominance, Hayman (1958) [19], Brim and Cockerham (1961) [7], Gamble (1962) [15], Matzinger (1968) [31], and Stuber and Moll (1974) [45] were among the first to recognize the importance of non-allelic interaction. Jinks (1955) [23] attributed the epistatic interaction as the primary cause of heterosis expression. Therefore, in addition to additive and dominant components, it is crucial to identify and quantify the epistasis components.

Experimental Material and Methodology Employed

Plant Genotypes

The genotypes of cotton used in the current experiment composed of six diverse parental lines (Table 1) were received from Main Cotton Research Station, Navsari Agricultural University, Surat. The selected parents differed with respect to fibre parameters.

Table 1: Details of parental genotypes used in hybridization program

Sr. No.	Parent	Source
1.	G. Cot 10 (BG II)	Main Cotton Research Station, NAU, Navsari
2.	G. Cot 16 (BG II)	Main Cotton Research Station, NAU, Navsari
3.	GSHV 95/216	Main Cotton Research Station, NAU, Navsari
4.	GSHV 303/15	Main Cotton Research Station, NAU, Navsari
5.	SCS 1062	University of Agricultural Sciences, Raichur, Karnataka
6.	HS 298	Chaudhary Charan Singh Haryana Agricultural University, Hisar, Haryana

Development of Experimental Materials

In the current study, four single crosses (F_1) was developed by using six diverse parental lines during the *kharif* 2021. In the next year *i.e.*, *kharif* 2022, second crossing programme was carried out to develop segregating generations *viz.*, BC_1, BC_2 and second filial (F_2). For this, BC_1 was developed by crossing of F_1 individuals (used as female) with P_1 (used as male); BC2 was developed by crossing of F_1 individuals (used as female) with P_2 (used as male); whereas F_2 was developed by selfing of F_1 individuals.

Crossing Technique

In the crossing or hybridization programme, Doak's (1934) method was used for the emasculation and pollination of flowers. Overnight, a red paper bags were used to cover the emasculated flower buds. The following morning (between 8:00 and 10:00 AM), the stigma of the emasculated flowers was covered with a white paper bag containing healthy pollens from the intended male flowers. Appropriate labelling was then applied, including the names of the parents engaged in that cross. Selfing was done by covering each flower bud of the parents and F_1 plants with a paper bag in order to produce selfed seeds of parental genotypes and F_2 generations. For the best possible crop growth and development, all relevant agronomic and plant protection measures were followed throughout the hybridization procedure.

Field Evaluation

All developed six different generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2 of the crosses G. Cot 10 (BG II) × GSHV 95/216 (cross I), G. Cot 10 (BG II) × SCS 1062 (cross II), G. Cot 16 (BG II) × GSHV 95/216 (cross III) and HS 298 × GSHV 303/15 (cross IV) were evaluated in a compact family block design (CFBD) in three replications at Main Cotton Research Station, Navsari Agricultural University, Surat during *kharif* 2022-23. The evaluation field representing the CFBD design, consisted of a block comprising one rows each of P_1, P_2 and F_1; two rows each of BC_1 and BC_2; and four rows of F_2, thereby ensuring a sufficient number of plant samples per generation. A sowing was carried out using a dibbling method at the inter and intra row spacing of 120 × 45 cm. All recommended agronomic practices were followed for good and healthy crop growth. All the observations were recorded plant basis for fibre characters and oil content. The fiber quality parameters were measured using High Volume Instrument (HVI) at Central Institute for Research on Cotton Technology (CIRCOT), Surat and oil content was measured by adopting solvent extraction method.

Statistical Analysis

The data attained were subjected to ANOVA using a compact family block design, as described by Panse and Sukhatme (1985) [36].

Scaling Tests

The adequacy of the additive-dominance model for all of four characters in each of the crosses was checked by applying scaling tests as suggested by Hayman and Mather (1955) [20]. The adequacy of this scale must fulfill two conditions (i) additive gene effect, which provides information about presence or absence of any gene action/interaction (ii) independence of heritable components from non-heritable component. If any of four scaling tests found to be significant, it indicates the epistasis and inadequacy of model. The A, B, C and D tests were made using the following equations for their values and variances.

$$A = 2\overline{BC_1} - \overline{P}_1 - \overline{F}_1$$

$$B = 2\overline{BC_2} - \overline{P}_2 - \overline{F}_1$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$$

$$D = 2\overline{F}_2 - \overline{BC_1} - \overline{BC_2}$$

Where P_1, P_2, F_1, F_2, BC_1 and BC_2 are means of different generations, respectively. The variances of the quantities A, B, C and D were calculated from respective variances of

different generations as given below:

Variance

The variances A, B, C and D were calculated as per the following formulae

$$V_A = 4V(\overline{BC_1}) + V(\overline{P_1}) + V(\overline{F_1})$$
$$V_B = 4V(\overline{BC_2}) + V(\overline{P_2}) + V(\overline{F_1})$$
$$V_C = 16V(\overline{F_2}) + 4V(\overline{F_1}) + V(\overline{P_1}) + V(\overline{P_2})$$
$$V_D = 4V(\overline{F_2}) + V(\overline{BC_1}) + V(\overline{BC_2})$$

Where, V_A, V_B, V_C and V_D are the variances of respective scales A, B, C and D; VP_1, VP_2, VF_1, VF_2, VBC_1 and VBC_2 are the variances of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations, respectively.

Standard Error

The standard error of each test was calculated as under

$$S.E.(A) = \sqrt{V_A}$$
$$S.E.(B) = \sqrt{V_B}$$
$$S.E.(C) = \sqrt{V_C}$$
$$S.E.(D) = \sqrt{V_D}$$

The significance of the scaling test was tested by calculating the 't' value as follows

$$t(A) = \frac{A}{S.E.(A)}$$
$$t(B) = \frac{B}{S.E.(B)}$$
$$t(C) = \frac{C}{S.E.(C)}$$
$$t(D) = \frac{D}{S.E.(D)}$$

The calculated values of 't' were compared with the table 't' value at 5% and 1% levels of significance, respectively at their respective degrees of freedom.

Joint scaling test

The Joint scaling test (additive-dominance model or non-epistatic model) outlined by Cavalli (1952) [10] was also applied to confirm the adequacy of the additive-dominance model to fit the three-parameter model, which consists of estimation of m, d and h parameters using weighted least square method, followed by a comparison of observed means with expected means. The comparison between observed and expected generation means was made by chi-square (χ^2) test assuming that the sum of squares minimized in the fitting process distributed as χ^2. The degree of freedom (df) equals the number of generations minus the number of estimated parameters.

Gene effects

After calculating scaling tests, if any one of them was found significant then the genetic effects were estimated by fitting the data into six-parameter models of the generation mean analysis as suggested by Hayman (1958) [19] to estimate the genetic parameters *viz.*, mean (m), additive (d), dominance (h), additive × additive (i), additive × dominance (j) and dominance × dominance (l).

Gene effect	Symbol	Method of estimation
Mean	$[\hat{m}]$	$\overline{F_2}$
Additive	$[\hat{d}]$	$\overline{BC_1} - \overline{BC_2}$
Dominance	$[\hat{h}]$	$\overline{F_1} - 4\overline{F_2} - {}^1/_2\,\overline{P_1} - {}^1/_2\,\overline{P_2} + 2\overline{BC_1} + 2\overline{BC_2}$
Additive × Additive	$[\hat{i}]$	$2\overline{BC_1} + 2\overline{BC_2} - 4\overline{F_2}$
Additive × Dominance	$[\hat{j}]$	$\overline{BC_1} - {}^1/_2\,\overline{P_1} - \overline{BC_2} + {}^1/_2\,\overline{P_2}$
Dominance × Dominance	$[\hat{l}]$	$\overline{P_1} + \overline{P_2} + 2\overline{F_1} + 4\overline{F_2} - 4\overline{BC_1} - 4\overline{BC_2}$

Where,

$\overline{P_1}$, $\overline{P_2}$, $\overline{F_1}$, $\overline{F_2}$, $\overline{BC_1}$ and $\overline{BC_2}$ are the mean values of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations, respectively.

The variances of these estimates were obtained using the following formulae:

$$V(\hat{m}) = V(\overline{F_2})$$
$$V(\hat{d}) = V(\overline{BC_1}) + V(\overline{BC_2})$$
$$V(\hat{h}) = V(\overline{F_1}) + 16V(\overline{F_2}) + {}^1/_4\,V(\overline{P_1}) + {}^1/_4\,V(\overline{P_2}) + 4V(\overline{BC_1}) + 4V(\overline{BC_2})$$
$$V(\hat{i}) = 4V(\overline{BC_1}) + 4V(\overline{BC_2}) + 16V(\overline{F_2})$$
$$V(\hat{j}) = V(\overline{BC_1}) + {}^1/_4\,V(\overline{P_1}) + V(\overline{BC_2}) + {}^1/_4\,V(\overline{P_2})$$
$$V(\hat{l}) = V(\overline{P_1}) + V(\overline{P_2}) + 4V(\overline{F_1}) + 16V(\overline{F_2}) + 16V(\overline{BC_1}) + 16V(\overline{BC_2})$$

Where,

$V(\overline{P_1})$, $V(\overline{P_2})$, $V(\overline{F_1})$, $V(\overline{F_2})$, $V(\overline{BC_1})$ and $V(\overline{BC_2})$ are the variances of means of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations, respectively.

The standard error of each of the gene effects was computed as follows:

$$S.E.(\hat{m}) = \sqrt{V(m)}$$
$$S.E.(\hat{d}) = \sqrt{V(d)}$$
$$S.E.(\hat{h}) = \sqrt{V(h)}$$
$$S.E.(\hat{i}) = \sqrt{V(i)}$$
$$S.E.(\hat{j}) = \sqrt{V(j)}$$

$$S.E.\left(\hat{l}\right) = \sqrt{V(l)}$$

Then, the 't' values were obtained as follows:

$$t\left(\hat{m}\right) = \frac{m}{S.E.(m)}$$
$$t\left(\hat{d}\right) = \frac{d}{S.E.(d)}$$
$$t\left(\hat{h}\right) = \frac{h}{S.E.(h)}$$
$$t\left(\hat{i}\right) = \frac{i}{S.E.(i)}$$
$$t\left(\hat{j}\right) = \frac{j}{S.E.(j)}$$
$$t\left(\hat{l}\right) = \frac{l}{S.E.(l)}$$

The calculated values of 't' were compared with table values of 't' at 5% and 1% levels of significance, respectively. Because the six components from six observed mean have been estimated, there is no degree of freedom left for testing the adequacy of the digenic model. Fitting a five-parameter model by omitting non-significant parameters would allow testing of the goodness of fit utilizing chi-square with an appropriate degree of freedom and at the same time, improve the precision with which the remaining parameters are estimated. This approach is generally known as the best fit or reduced model. This best fit or reduced model approach is used in present investigation.

Results and Discussion

Analysis of variance (ANOVA)

The analysis of variance (ANOVA) between generation within crosses (Table 2) for different four characters revealed significant difference for mean sum of square, thereby indicating presence of ample amount of genetic variation in experimental material used.

Table 2: Analysis of variance (ANOVA) between generation within cross

Cross	Replication df = 2	Generation df = 5	Error df = 10	Cross	Replication df = 2	Generation df = 5	Error df = 10
Fibre length (mm)				**Fibre strength (g/tex)**			
Cross I	0.285	7.260**	0.377	Cross I	0.068	0.868*	0.213
Cross II	0.203	1.758**	0.144	Cross II	0.176	4.112**	0.163
Cross III	0.268	22.158**	0.286	Cross III	0.098	1.274**	0.074
Cross IV	0.116	3.431**	0.107	Cross IV	0.850	6.956**	0.636
Fibre fineness (mv)				**Oil content (%)**			
Cross I	0.185	0.657*	0.145	Cross I	1.934	3.406*	0.776
Cross II	0.003	0.433**	0.009	Cross II	0.168	4.130**	0.604
Cross III	0.061	0.453**	0.065	Cross III	0.718	1.784**	0.200
Cross IV	0.083	0.129*	0.036	Cross IV	0.063	1.022**	0.062

Scaling Tests:

Based on the individual scaling test 'A', 'B', 'C' and 'D', the additive-dominance model was found inadequate for description of variation in generation mean for all the four characters of all the four crosses, either the entire four or any three, two or one individual scaling test (out of 'A', 'B', 'C' and 'D') were found significant (Table 3) which indicated the presence of digenic interaction which implies that the additive-dominance model is inadequate. These results were supported by the significant value of χ^2 joint scaling test (Cavali, 1952) [10] for all the four characters of all the four crosses. Therefore, six parameter model (Hayman, 1958) [19] was used for estimation of genetic components.

Genetic Effects

As described, in the preset study for six parameter model, no degree of freedom was available for χ^2 (chi-square) test to check goodness of fit (Singh and Narayanan, 2017) [41]. This six parameter model for all the four characters were analyzed to detect if any non-significant parameter(s) had occurred. Whenever such case was found, the omission of non-significant parameters of perfect fit solution and reanalysis based on the remaining four or five parameter(s) was practiced in all such cases. This exercise resulted into increased precision of the estimated parameters to provide the test for goodness of fit of the model. This could be seen by a considerable change in the magnitude of different parameters.

Table 3: Estimation of scaling tests for various characters in four crosses of cotton

Cross	Scaling tests A	B	C	D	χ^2	Cross	Scaling tests A	B	C	D	χ^2
Fibre length (mm)						**Fibre strength (g/tex)**					
Cross I	-5.03**	-3.05**	-11.57**	-1.75**	**	Cross I	-0.70*	1.09**	-2.98**	-1.68**	**
Cross II	-3.18**	0.85**	0.04	1.18**	**	Cross II	-5.10**	-3.36**	-1.11	3.68**	**
Cross III	-11.52**	-3.87**	-20.98**	-2.79**	**	Cross III	-1.64**	-0.88**	-4.99**	-1.23**	**
Cross IV	-1.36**	-1.47**	-10.09**	-3.63**	**	Cross IV	-2.83**	-3.35**	-12.81**	-3.31**	**
Fibre fineness (mv)						**Oil content (%)**					
Cross I	1.07**	1.94**	2.71**	-0.15	**	Cross I	-2.06**	-1.49*	-9.51**	-2.98**	**
Cross II	0.43**	0.11	2.38**	0.92**	**	Cross II	-3.03**	-3.41**	1.04	3.74**	**
Cross III	0.03	1.51**	2.94**	0.70**	**	Cross III	-0.28	1.66**	-6.32**	-3.85**	**
Cross IV	1.04**	-0.13	0.44**	-0.24**	**	Cross IV	-0.55	-2.58**	0.28	1.71**	**

Fibre length (mm): With respect to this trait, mean (m) was found to be highly significant in all of the crosses studied. The value of mean (m) was also higher than other genetic effect of best fit model. The results (Table 4) also showed that additive (d), additive × additive (i), additive × dominance (j) and dominance × dominance (l) gene effects were highly significant cross I; dominance (h), additive × additive (i), additive × dominance (j) and dominance × dominance (l) gene effects were highly significant in cross II; additive × additive (i), additive × dominance (j) and dominance × dominance (l) gene effects were highly significant in cross III; additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) gene effects were highly significant in cross VI. This indicates the predominance of both additive and non-additive gene actions in cross I, cross II and cross III while, predominance of both additive and dominance gene actions in cross IV. The results of present study are in agreement to the findings of Srinivas and Bhadru (2015a) [44] and Kamaran *et al*. (2018) [24] for both additive and non-additive gene actions; whereas Smith *et al*. (2009) [42], El-Rafaey and El-Razek (2013) [13], Gawande *et al*. (2015) [16], Muhammad *et al*. (2019) [34] for additive and dominant gene actions. Besides these, Karademir and Gencer (2010) [25], Shaukat *et al*. (2013) [40] reported additive gene action; Abo Sen *et al*. (2022) [1] reported dominant gene action and Ashokkumar *et al*. (2010) [5], Basal *et al*. (2011) [6], Suryakumar *et al*. (2014) [46], Patel *et al*. (2014) [37], Khokhar *et al*. (2018) [27], Kirthika *et al*. (2020) [28] and Mudhalvan *et al*. (2021) [33] reported non-additive gene action for the inheritance of fibre length in cotton.

Table 4: Estimation of gene effects for fibre length (mm) in four crosses of cotton

Gene effects	Cross I		Cross II		Cross III		Cross IV	
	Value	SE	Value	SE	Value	SE	Value	SE
(m)	23.56**	±0.12	27.80**	±0.52	21.68**	±0.11	19.79**	±0.47
(d)	-0.84**	±0.07	--	--	--	--	-0.66**	±0.06
(h)	--	--	-6.16**	±1.20	--	--	12.03**	±1.20
(i)	3.14**	±0.14	-2.37**	±0.52	5.99**	±0.13	7.28**	±0.47
(j)	-2.01**	±0.38	-4.07**	±0.26	-7.81**	±0.32	--	--
(l)	5.13**	±0.14	4.70**	±0.70	9.15**	±0.17	-4.47**	±0.76
χ^2	0.42		0.18		1.34		0.10	
Epistasis	--		Duplicate		--		Duplicate	

Fibre fineness (mv): For this trait, mean (m) was found highly significant and higher than other estimated parameters of best fit model of generation mean analysis (Table 5). Apart from the mean (m), other gene effects were also found highly significant in different crosses *viz.*, additive (d), dominance (h), additive × dominance (j) and dominance × dominance (l) gene effects in cross I; additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) gene effects in cross II; additive (d), dominance (h), additive × additive (i) and additive × dominance (j) gene effects in cross III; additive (d), dominance (h), additive × dominance (j) and dominance × dominance (l) gene effects in cross VI. These results revealed the importance of both additive and non-additive gene action in the cross I, cross III and cross IV; while importance of additive and dominant gene actions for the cross II. The results of present study are akin with findings of El-Rafaey and El-Razek (2013) [13] and Muhammad *et al*. (2019) [34] for additive and non-additive gene actions; Gawande *et al*. (2015) [16] and Kamaran *et al*. (2018) [24] for additive and dominant gene actions; Karademir and Gencer (2010) [25], Eswari *et al*. (2016) [14], Hamed and Said (2021) [18] for additive gene action; Srinivas and Bhadru (2015a) [44] and Al-Hibbiny *et al*. (2020a) [2] for dominant gene action and Basal *et al*. (2011) [6], Suryakumar *et al*. (2014) [46], Thiyagu *et al*. (2019) [47], Al-Hibbiny *et al*. (2020b) [3], Kirthika *et al*. (2020) [28] and Hafez *et al*. (2022) [17] for non-additive gene action for the inheritance of fibre fineness in cotton.

Table 5: Estimation of gene effects for fibre fineness (mv) in four crosses of cotton

Gene effects	Cross I		Cross II		Cross III		Cross IV	
	Value	SE	Value	SE	Value	SE	Value	SE
(m)	3.91**	±0.02	6.42**	±0.27	5.27**	±0.06	4.32**	±0.01
(d)	0.39**	±0.02	-0.41**	±0.03	0.31**	±0.01	-0.19**	±0.01
(h)	2.27**	±0.12	-2.87**	±0.62	-1.87**	±0.07	0.54**	±0.09
(i)	--	--	-1.63**	±0.27	-1.49**	±0.07	--	--
(j)	-1.06**	±0.15	--	--	-1.49**	±0.14	1.16**	±0.11
(l)	-2.77**	±0.12	0.86*	±0.36	--	--	-0.69**	±0.09
χ^2	1.48		2.58		0.22		9.26**	
Epistasis	Duplicate		Duplicate		--		Duplicate	

Fibre strength (g/tex): The highly significant and higher mean (m) as compared to other gene effects was observed for fibre strength (Table 6) in all of the four crosses included in present investigation. Among all the four crosses evaluated, in cross I, highly significance gene effects were additive (d), dominance (h), additive × additive (i) and additive × dominance (j); in cross II, highly significance gene effects were additive (d), dominance (h), additive × additive (i) and dominance × dominance (l); in cross III, highly significance gene effects were additive (d), dominance (h), additive × additive (i) and additive × dominance (j); in cross IV, highly significance gene effects were additive (d), dominance (h), additive × additive (i) and additive × dominance (j). The importance of additive and non-additive genes action was reported in the cross I, cross III and cross IV; whereas, the cross II reported additive and dominant gene actions for the trait, fibre strength. The results of present study are in accordance to finding of Al-Hibbiny *et al*. (2020a) [2] for both additive and non-additive gene actions; El-Rafaey and El-Razek (2013) [13], Gawande *et al*. (2015) [16], Kamaran *et al*. (2018) [24] for both additive and dominant gene actions; Shaukat *et al*. (2013) [40], Patel *et al*. (2014) [37], Muhammad *et al*. (2019) [34], Al-Hibbiny *et al*. (2020b) [3], Hamed and Said (2021) [18] for additive gene action; Ashokkumar *et al*. (2010) [5], Karademir and Gencer (2010) [25], Khokhar *et al*. (2018) [27], Kirthika *et al*. (2020) [28] and Hafez *et al*. (2022) [17] for non-additive gene action for the inheritance of fibre strength in cotton.

Table 6: Estimation of gene effects for fibre strength (g/tex) in four crosses of cotton

Gene Effects	Cross I		Cross II		Cross III		Cross IV	
	Value	SE	Value	SE	Value	SE	Value	SE
(m)	24.78**	±0.20	33.34**	±0.82	24.45**	±0.15	22.23**	±0.18
(d)	0.49**	±0.06	-0.48**	±0.03	0.65**	±0.06	1.10**	±0.06
(h)	1.77**	±0.22	-19.37**	±1.98	2.70**	±0.22	7.72**	±0.26
(i)	1.03**	±0.21	-6.36**	±0.82	2.49**	±0.16	6.40**	±0.19
(j)	-2.40**	±0.33	--	--	-0.76**	±0.22	0.66*	±0.31
(l)	--	--	13.84**	±1.20	--	--	--	--
χ^2	21.29**		8.19**		0.01		0.25	
Epistasis	--		Duplicate		--		--	

Oil content (%): With respect to the best fitting or best fit mode, the highly significant mean (m) was observed for all of the four crosses. Besides these, it was higher than other gene effects in respective cross (Table 7) except cross III. The results indicated that cross I exhibited highly significant estimates of dominance (h) and additive × additive (i); cross II exhibited highly significant estimates of additive (d), dominance (h), additive × additive (i) and dominance × dominance (l); cross III exhibited highly significant estimates of additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) and cross IV exhibited highly significant estimates of additive (d), dominance (h), additive × additive (i) and dominance × dominance (l). The estimates of gene effects for oil content revealed the importance of both additive and dominant gene actions in all the four crosses. The population improvement approaches *i.e.*, bi-parental mating and reciprocal recurrent selection would be effective in the crosses with both additive and dominant gene actions. The preponderance of additive and dominant gene actions for the oil content was observed by Mert *et al*. (2004) [32].

Table 7: Estimation of gene effects for oil content (%) in four crosses of cotton

Gene Effects	Cross I		Cross II		Cross III		Cross IV	
	Value	SE	Value	SE	Value	SE	Value	SE
(m)	11.60**	±0.47	22.32**	±0.84	8.06**	±0.93	19.30**	±0.49
(d)	--	--	0.96**	±0.15	0.15**	±0.04	-0.43**	±0.04
(h)	6.65**	±0.68	-19.80**	±2.07	18.83**	±2.24	-12.01**	±1.17
(i)	4.66**	±0.51	-7.47**	±0.82	8.35**	±0.93	-4.33**	±0.49
(j)	--	--	--	--	--	--	--	--
(l)	--	--	13.88**	±1.30	-10.42**	±1.35	8.40**	±0.70
χ^2	2.80		0.35		10.38**		37.58**	
Epistasis	--		Duplicate		Duplicate		Duplicate	

The non-significant estimate of χ^2 from best fit model indicates the presence of digenic interactions only and the absence of higher order interactions, thereby suggesting digenic model adequate; while the significant or highly significant estimates of χ^2 from best fit model revealed the presence of higher order interactions thereby, suggesting digenic model inadequate.

For all of four traits, both of the additive and non-additive or additive and dominant gene actions played a major role in all of the crosses included in present investigation. This suggested that homozygous recombinants along with desired phenotype of character could be developed by following reciprocal recurrent selection since it is developed to expand the frequency of desirable genes/alleles (for the trait undergoing selection) in inhabitant for quantitative traits, further breeding efforts are needed to release a cultivar from a recurrent selection population. But main challenge in reciprocal recurrent selection is difficulty in intermating and more number of crosses to be performed (Orf, 2008) [35], inter crossing of desired segregants keeping adequate population may be followed or population improvement using recurrent selection involving a genetic male sterility (GMS) system could be followed (Orf, 2008) [35]. The usage of genetic male sterility (GMS) to enable crossing especially in recurrent selection schemes has been used to some extent since the 1970s (Brim and Stuber, 1973; Lewers *et al.*, 1996) [8, 45]. Specht and Graaf (1990) [43] described a breeding method called male sterile facilitated cyclic breeding (MSFCB) for cultivar development. This method combines the best aspects of conventional breeding and diallel selective mating as described by Jensen (1970) [22].

The direction of dominance gene (h) and dominance × dominance (l) for all the four characters of four crosses of cotton are depicted in Table 8. The sign of dominance (h) and dominance × dominance (l) parameter being opposite indicates involvement of duplicate type of epistasis in the inheritance of a trait, while similar sign indicates the involvement of complementary epistasis in the expression of a trait (Singh and Narayanan, 2017) [41]. Such type of epistasis was also observed for fibre length in cross II and cross IV; for fibre fineness in cross I, cross II and cross IV; for fibre strength in cross II and for oil content in cross II, cross III and cross IV in the present investigation. These results are in agreement with Srinivas and Bhadru (2015a) [44] for fibre length, fibre fineness and fibre strength; Kamaran *et al.* (2018) [24] for fibre fineness and Muhammad *et al*. (2019) [34] for fibre length and fibre fineness. The presence of duplicate epistasis would be detrimental for rapid progress, making it difficult to fix genotypes with increased level of character manifestation because the opposite effect of one parameter would be cancelled out by the negative effect of another parameter (Sagar, 1990) [39] but one can expect some progress in selection programme due to presence of substantial amount of non-allelic interactions (Rani *et al.*, 2013) [38] and due to presence of greater genetic diversity (Kumar, 2021) [29].

Table 8: Direction of dominance (h) and dominance × dominance (l) gene effects for various characters in four crosses of cotton

Characters	Gene effects	Cross I	Cross II	Cross III	Cross IV
11. Fibre length (mm)	(h)	0	-	0	+
	(l)	+	+	+	-
12. Fibre fineness (mm)	(h)	+	-	-	+
	(l)	-	+	0	-
13. Fibre strength (g/tex)	(h)	+	-	+	+
	(l)	0	+	0	0
14. Oil content (%)	(h)	+	-	+	-
	(l)	0	+	-	+

+	Significant positive direction
-	Significant negative direction
0	Non-significant effect

In the characters *viz.*, fibre length, fibre fineness, fibre strength and oil content main gene effect and duplicate epistasis were involved. This suggests the need of specific breeding procedure such as intermating of most desirable segregants followed by selfing and selecting superior genotypes coupled with progeny testing to exploit the population under study. Also, these traits might be improved through recurrent selection in bi-parental progenies that would help in exploiting the duplicate type of non-allelic interaction and allow recombination and concentration of gene having cumulative effects in population as this method is helpful in breaking up undesirable linkage (Deokar *et al.*, 2022) [11].

A selection of desirable phenotypes in early stage or generation would be beneficial in case where additive gene effect are more than dominant or non-additive gene effect; whereas, improvement of any traits requires intense form of selection through later stage where non-additive gene effects ae more (Jagtap, 1986) [21].

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