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Genetics of oil content in cotton (*Gossypium hirsutum* L.) using generation mean analysis of 21 generations

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Abstract

Gene effects for oil content in cotton (*Gossypium hirsutum* L.) was studied 21 generations namely P₁, P₂, F₁, F₂, F₃, B₁, B₂, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S}, B_{2S}, B₁ x F₁, B₂ x F₁, F₂ x P₁, F₂ x P₂, F₂ x F₁, B₁ bip, B₂ bip and F₂ bip of four crosses viz., Deviraj x GBHV-170 (cross-1), G.Cot-10 x MR-786 (cross-2), G.Cot-12 x GTHV-95/145 (cross-3) and 76IH20 x GJHV-460 (cross-4). Scaling tests viz., A, B, D, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S}, B_{2S} and (F₂-L₃) in cross-1; B, D, B₂₁, B₂₂, B_{1S}, B_{2S}, X, Z, (B₁-L₁), (B₂-L₂) and (F₂-L₃) in cross-2; A, B, C, D, B₁₁, B₁₂, B₂₂, B₂₁, B_{1S}, Y and (B₁-L₁) in cross-3 and D, B_{1S}, Z and (B₁-L₁) in cross-4 were significant indicating presence of digenic and/or trigenic interactions. In six-parameter model, significant $\chi^2_{(2)}$ value at 15 degrees of freedom revealed the presence of higher order epistasis and/or linked digenic interactions. In ten-parameter model, 'm', [d], [h], [i], [j], [l], [w], [x], [y] and [z] in cross-1; for 'm', [h], [i], [j], [l], [x], [y] and [z] in cross-2; 'm', [d], [h], [i], [j], [l], [w], [x] and [z] (except [y]) in cross-3 and 'm', [d], [j], [l], [w], [x] and [z] in cross-4 were significant. The $\chi^2_{(3)}$ value was significant at 11 degrees of freedom indicating the presence of higher order epistasis. In twelve-parameter model, m+[h]+[l], m+[i], [p²i], [p¹l], [p²l], [p³l] and [p⁴l] in cross-1; m+[h]+[l], m+[i], [pi], [p²i], [p²l], [p³l] and [p⁴l] in cross-2; [d], m+[h]+[l], m+[i], [pi], [pj], [p²j], [p¹l], [p²l] and [p³l] in cross-3 and m+[h]+[l], m+[i], [p²l], [p³l] and [p⁴l] in cross-4 were significant. The $\chi^2_{(4)}$ value was significant at nine degrees of freedom indicating the presence of higher order linkage. Duplicate type of epistasis was responsible for the inheritance of oil content in all the four crosses of cotton.

Keywords: additive, dominance, epistatic and linked digenic gene effects, cotton

Introduction

Cotton (*Gossypium spp.*) is one of the important fibre as well as oilseed crops and plays a vital role as a cash crop in commerce, also known as "King of fibres" plays a remarkable role in Indian economy. Cotton seed oil is cooking oil extracted from the seeds of cotton plant of various species, mainly *Gossypium hirsutum* and *Gossypium herbaceum*. Cotton seed oil is the second largest source of vegetable oil in the world. The five largest producers (China, 27%; United states, 12%; India, 11%; former Soviet Union, 10%; Pakistan 9%) of cotton seed oil accounted for 70% of global output (Song and Zhang, 2007). The refined cotton seed oil is one of the best edible oils, which is used in most of the world including USA, Uzbekistan, and China etc. Refined cotton seed oil was also started to be used as an edible purposes in India and Pakistan. Cottonseed oil is typically composed of about 26% palmitic acid (C16:0), 15% oleic acid (C18:1), and 58% linoleic acid (C18:2), (Liu *et al.* 2002) [14]. The relatively high level of palmitic acid provides a degree of stability to the oil that makes it suitable for high-temperature applications, but is nutritionally undesirable because of the low-density lipoprotein cholesterol-raising properties.

The knowledge of gene effects for oil content in cotton is of prime importance before starting a rigorous breeding programme. Though generation mean analysis of six generations have been extensively used to understand the gene effects in cotton (El Lawendey *et al.*, 2010; Haleem *et al.*, 2010; Singh., 2010; Kannan *et al.*, 2013; Nassar., 2013; Siwach *et al.*, 2013; Deore *et al.*, 2014; Patel *et al.*, 2014; Srinivas and Bhadru., 2015a and 2015b) [5, 7, 22, 13, 18, 24, 4, 19, 26, 27], but very few reports are available on gene effects in cotton using more than six basic generations (Valu *et al.*, 2015a, and 2015b; Gawande *et al.*, 2016) [28, 29, 6]. Moreover, the information is available on gene systems especially linked digenic or higher order epistasis in other crops are meager (Shekhawat *et al.*, 2000; Sharma and Sain, 2002; Singh *et al.*, 2013) [20, 21, 23]. Hence, efforts have been made to estimate gene effects using 21 generation means (Jinks and Perkins, 1969) [12] for oil content in four crosses of cotton.

Materials and Methods

The basic set of twenty-one generations *viz.*, P₁, P₂, F₁, F₂, F₃, B₁ (F₁ x P₁), B₂ (F₁ x P₂), B₁₁ (B₁ x P₁), B₁₂ (B₁ x P₂), B₂₁ (B₂ x P₁), B₂₂ (B₂ x P₂), B_{1S}, B_{2S}, B₁ x F₁, B₂ x F₁, F₂ x P₁, F₂ x P₂, F₂ x F₁, B₁ bip, B₂ bip and F₂ bip, derived from four crosses namely Deviraj x GBHV-170 (cross 1), G.Cot-10 x MR-786 (cross 2), G.Cot-12 x GTHV-95/145 (cross 3) and 76IH20 x GJHV-460 (cross 4) were sown in Compact Family Block Design with two replications during *khariif* 2014. The plots of various generations contained different number of rows i.e., parents and F₁ in single row; B₁ and B₂ in two rows and F₂, F₃, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S}, B_{2S} B₁ x F₁, B₂ x F₁, F₂ x P₁, F₂ x P₂, F₂ x F₁, B₁ bip, B₂ bip and F₂ bip in four rows. Each row was of 4.5 m in length with 120 cm and 45 cm inter and intra row spacing, respectively. All the recommended agronomical practices and necessary plant protection measures were followed timely to raise good crop of cotton.

The observations were recorded on eight competitive and randomly selected plants from P₁, P₂ and F₁; fifteen plants from backcross (B₁ and B₂) and thirty plants from F₂, F₃, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S}, B_{2S}, B₁ x F₁, B₂ x F₁, F₂ x P₁, F₂ x P₂, F₂ x F₁; forty plants from B₁ bip, B₂ bip and eighty plants from F₂ bip generations in each replication for oil content. The oil content was estimated by Nuclear magnetic resonance (NMR) technique. The inheritance of oil content was computed through generation mean analysis methods (Hayman and Mather, 1955; Hayman, 1958 and Hill, 1966)^[9, 8, 10].

The data were initially subjected to simple scaling tests A, B, C and D. Besides simple scaling tests, special scaling tests *viz.*, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S} and B_{2S} given by Hill (1966)^[10]; and X, Y and Z given by Van Der Veen (1959) as well as ($E_1 - L_1$), ($E_2 - L_2$) and ($F_2 - L_2$) given by Jinks and Perkins (1969)^[12] were also computed. The results of simple scaling tests were further confirmed by joint scaling test (Cavalli, 1952), which effectively combines the whole set of simple scaling tests. Thus, it offers a more general, convenient, adoptable and informative approach for estimating gene effects and also for testing adequacy of various models.

The $\chi^2_{(1)}$ of joint scaling test under three-parameter model (18 d.f.) gives idea about fitness of additive-dominance model. In addition to six generations and six-parameter model based on weighted least square technique of Cavalli (1952), the data were subjected to ten-parameter model given by Hill (1966)^[10]. He proposed estimation of first order and second order epistasis utilizing twelve generations including double backcross generations. The $\chi^2_{(2)}$ and $\chi^2_{(3)}$ values were estimated under six-parameter model at 15 degrees of freedom and for ten-parameter model at 11 degrees of freedom, respectively. To detect the presence of linked digenic epistasis, a model proposed by Jinks and Perkins (1969)^[12] was also used. This is an additional advantage of using 21 generations using twelve-parameter model (for linked digenic model) as it provides sufficient degree of freedom for testing validity and goodness of fit for different models.

Results and Discussion

The analysis of variance between families (crosses) revealed that the mean square due to crosses was significant for oil content. The analysis of variance among progenies within each family (21 generations) indicated significant differences among twenty-one generation means for oil content in all the four crosses.

The comparison of mean values for oil content in twenty-one

generations of four crosses is presented in Fig.1 and Table 1. In cross-1, there was very narrow numerical difference between two parental means for oil content. The mean performance of F₁ and F₂ mean were intermediate between both the parents and statistically at par with both the parental means showing partial dominance, whereas the mean of F₃ was significantly lowered than means of P₁, P₂, F₁ and F₂. The means of B₁, B₂, B₁₁, B₁₂, B₂₂, B₂₂, B_{1S} and B_{2S} were statistically at par with one another. The mean performance of F₂ bip was significantly differed from F₂ mean, while the mean values of B₁ bip and B₂ bip were statistically at par with each other as well as at par with means of B₁ and B₂. The mean of F₂ x P₁, F₂ x P₂, F₂ x F₁, B₁ x F₁ and B₂ x F₁ were also statistically at par with one another. In cross-2, mean value of male parent (MR-786) was numerically higher but statistically at par with the mean performance of female parent (G.Cot-10). The F₁ showed high mean outside the parental range indicating over dominance. The F₂ mean was lowered than F₁ and statistically at par with both parents. The mean value of F₃ was intermediate between means of F₁ and F₂ and statistically at par with the mean of F₁. B₁ and B₂₂ were statistically at par with each other, while the mean value of B₂ was also statistically at par with that of means of both the parents. The mean performance of B₁₁ showed the lowest oil content among all the twenty-one generations. The *per se* performance of B₁₂, B₂₁ and B_{1S} were also statistically at par with one another and outside the means of parental range. The mean performance of B_{2S} was statistically at par with mean of both the parents. All the three groups of bip (F₂ bip, B₁ bip and B₂ bip) were significantly higher than means of both the parents but significantly differed from one another. F₂ x P₁ and F₂ x F₁ were statistically at par with each other, while the mean values of B₁ x F₁ and B₂ x F₁ were also statistically at par with each other but significantly higher means than means of both the parents. The mean value of F₂ x P₂ was also significantly higher mean than means of both the parents.

In cross-3, the mean performance of female parent (G.Cot-12) was significantly higher than the male parent (GTHV-95/145). The F₁ recorded the highest mean performance among all the twenty-one generations showing over dominance towards oil content. The F₂ mean was intermediate between means of both the parents but less than F₁ mean showing inbreeding depression for this trait. The F₃ mean was less than the means of P₁, P₂, F₁ and F₂. Among the backcrosses, the mean performance of B₁ and B₂ were statistically at par with each other. Among the double backcrosses, means of B₁₁, B₁₂, B₂₂ and B₂₁ were also statistically at par with one another and numerically lowered than means of both the parents. Among the selfed backcrosses, the *per se* performance of B_{1S} and B_{2S} were also statistically at par with each other and mean of male parent (P₂). The mean performance of F₂ bip B₁ bip and B₂ bip were statistically at par with one another and also that with mean of male parent and F₂ mean. The mean performance of F₂ x P₁ and B₁ x F₁ were statistically at par with each other. Likewise, the mean values of F₂ x P₂ and F₂ x F₁ were also statistically at par with each other. The mean value of B₂ x F₁ was intermediate between both the parental means. In cross-4, the mean performance of F₁ was outside the parental range indicating over dominance for this trait but statistically at par with means of both the parents. The F₂ and F₃ means were statistically at par with each other and also with that means of both the parents. The mean of B₁, B_{1S} and B_{2S} were statistically at par with one another and outside the means of both the parents. The mean values of B₂, B₁₁, B₁₂ and B₂₂ were

statistically at par with one another and significantly lowered mean than means of both the parents. The mean performance of B₂₁ showed the highest mean among all the twenty-one generations. The *per se* performance of F₂ bip, B₁ bip and B₂ bip were statistically at par with each other and also with means of both the parents. The mean performance of F₂ x P₁, F₂ x P₂, F₂ x F₁, B₁ x F₁ and B₂ x F₁ were statistically at par with one another and all were outside the parental range in term of *per se* performance for oil content.

Out of all the scaling tests shown in Table 2 revealed that scaling tests viz., A, B, D, B₁₁, B₁₂, B₂₁, B₂₂, B_{1S}, B_{2S} and (F₂-L₃) were significant in cross-1; B, D, B₂₁, B₂₂, B_{1S}, B_{2S}, X, Z, (B₁-L₁), (B₂-L₂) and (F₂-L₃) in cross-2; A, B, C, D, B₁₁, B₁₂, B₂₂, B₂₁, B_{1S}, Y and (B₁-L₁) in cross-3 and D, B_{1S}, Z and (B₁-L₁) in cross-4 indicating the presence of digenic and/or

trigenic interactions for oil content. As per three-parameter model; 'm', and dominance [h] were significant in cross-1; all the three parameters i.e. 'm', additive, [d] and dominance [h] were significant in cross-2 and only one 'm' gene effects was significant in cross-3 and cross-4 for oil content. The $\chi^2_{(1)}$ value at 18 degrees of freedom of joint scaling test was significant in all the four crosses indicating failure of additive-dominance model which indirectly pointed out the presence of epistasis. Cockerham (1959)^[3] postulated that the epistatic gene action is common in the inheritance of quantitative traits and there is no sound biological reason why this type of gene action should be less common for polygenic various traits.

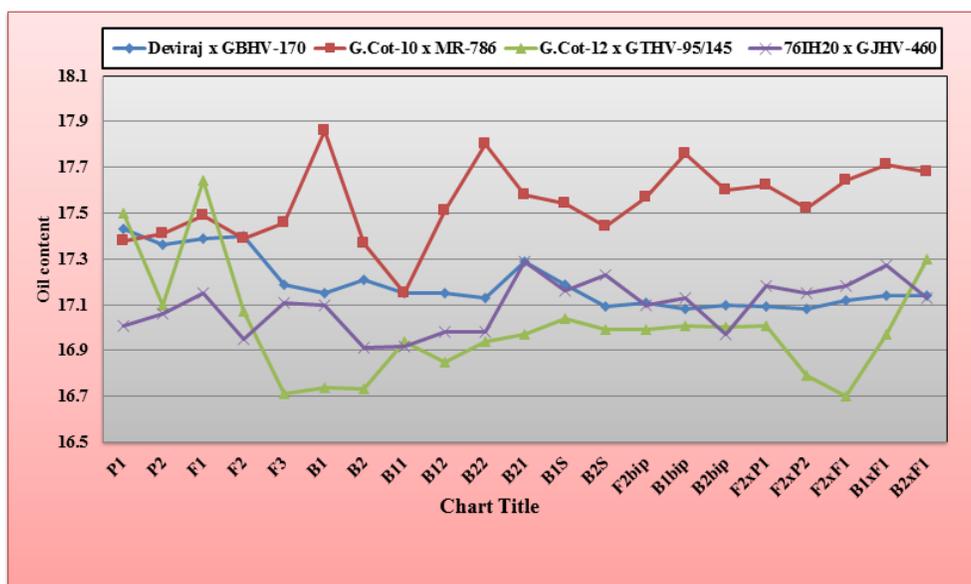


Fig 1: Trend of 21 generation means for oil content in cotton

Table 1: Mean performance of twenty-one generations of four crosses for oil content (%) in cotton

S. No.	Generations	Crosses			
		Deviraj x GBHV-170 (cross 1)	G.Cot-10 x MR-786 (cross 2)	G.Cot-12 x GTHV-95/145 (cross 3)	76IH20 x GJHV-460 (cross 4)
1	P ₁	17.43 ± 0.08	17.38 ± 0.08	17.50 ± 0.06	17.01 ± 0.08
2	P ₂	17.36 ± 0.07	17.41 ± 0.06	17.10 ± 0.07	17.06 ± 0.11
3	F ₁	17.39 ± 0.09	17.49 ± 0.06	17.64 ± 0.07	17.15 ± 0.09
4	F ₂	17.40 ± 0.04	17.39 ± 0.05	17.07 ± 0.06	16.95 ± 0.06
5	F ₃	17.19 ± 0.07	17.46 ± 0.05	16.71 ± 0.08	17.11 ± 0.07
6	B ₁	17.15 ± 0.04	17.86 ± 0.05	16.74 ± 0.06	17.10 ± 0.05
7	B ₂	17.21 ± 0.04	17.37 ± 0.04	16.73 ± 0.03	16.91 ± 0.05
8	B ₁₁	17.15 ± 0.03	17.15 ± 0.03	16.94 ± 0.04	16.92 ± 0.04
9	B ₁₂	17.15 ± 0.05	17.51 ± 0.03	16.85 ± 0.05	16.98 ± 0.05
10	B ₂₂	17.13 ± 0.03	17.80 ± 0.03	16.94 ± 0.04	16.98 ± 0.04
11	B ₂₁	17.29 ± 0.02	17.58 ± 0.02	16.97 ± 0.03	17.29 ± 0.02
12	B _{1S}	17.19 ± 0.05	17.54 ± 0.03	17.04 ± 0.05	17.16 ± 0.05
13	B _{2S}	17.09 ± 0.03	17.44 ± 0.04	16.99 ± 0.05	17.23 ± 0.04
14	F ₂ bip	17.11 ± 0.03	17.57 ± 0.05	16.99 ± 0.05	17.10 ± 0.05
15	B ₁ bip	17.08 ± 0.02	17.76 ± 0.04	17.01 ± 0.07	17.13 ± 0.04
16	B ₂ bip	17.10 ± 0.04	17.60 ± 0.03	17.00 ± 0.07	16.97 ± 0.04
17	F ₂ x P ₁	17.09 ± 0.03	17.62 ± 0.04	17.01 ± 0.05	17.18 ± 0.04
18	F ₂ x P ₂	17.08 ± 0.02	17.52 ± 0.03	16.79 ± 0.05	17.15 ± 0.04
19	F ₂ x F ₁	17.12 ± 0.03	17.64 ± 0.04	16.70 ± 0.04	17.18 ± 0.04
20	B ₁ x F ₁	17.14 ± 0.03	17.71 ± 0.04	16.97 ± 0.06	17.27 ± 0.04
21	B ₂ x F ₁	17.14 ± 0.04	17.68 ± 0.04	17.30 ± 0.09	17.13 ± 0.04
S. E. ±		0.05	0.02	0.03	0.06
C. D. at 5%		0.16	0.06	0.10	0.17

Table 2: Scaling tests and estimation of gene effects for oil content (%) in four crosses of cotton

Scaling tests / gene effects	Deviraj x GBHV-170 (cross 1)	G.Cot-10 x MR-786 (cross 2)	G.Cot-12 x GTHV-95/145 (cross 3)	76IH20 x GJHV-460 (cross 4)
A	-0.43* ± 0.18	0.05 ± 0.15	-1.72** ± 0.19	0.06 ± 0.19
B	-0.45** ± 0.13	0.82** ± 0.14	-1.26** ± 0.16	-0.01 ± 0.18
C	0.02 ± 0.26	-0.21 ± 0.24	-1.60** ± 0.29	-0.56 ± 0.32
D	0.45** ± 0.11	-0.55** ± 0.12	0.69** ± 0.15	-0.31* ± 0.14
B ₁₁	0.93** ± 0.32	-0.54 ± 0.28	1.98** ± 0.27	-0.43 ± 0.33
B ₁₂	1.18** ± 0.29	0.11 ± 0.24	2.06** ± 0.30	-0.39 ± 0.32
B ₂₁	1.06** ± 0.25	0.55** ± 0.26	0.99** ± 0.29	-0.06 ± 0.40
B ₂₂	1.26** ± 0.29	-1.19** ± 0.24	2.40** ± 0.35	-0.05 ± 0.32
B _{1S}	2.13** ± 0.50	-2.36** ± 0.54	4.14** ± 0.57	-1.76** ± 0.57
B _{2S}	1.91** ± 0.49	-2.01** ± 0.45	-0.12 ± 0.79	-0.40 ± 0.66
X	-0.05 ± 0.08	0.33** ± 0.09	0.16 ± 0.11	-0.18 ± 0.11
Y	0.11 ± 0.12	0.01 ± 0.10	0.37** ± 0.14	0.01 ± 0.14
Z	0.02 ± 0.13	-0.37** ± 0.13	0.01 ± 0.19	0.44** ± 0.14
B ₁ -L ₁	0.04 ± 0.07	0.32** ± 0.06	-0.23* ± 0.10	0.19* ± 0.08
B ₂ -L ₂	-0.01 ± 0.06	0.36** ± 0.06	-0.11 ± 0.08	0.12 ± 0.07
F ₂ -L ₃	0.27** ± 0.05	-0.41** ± 0.05	0.13 ± 0.07	-0.03 ± 0.07
Three parameter model				
m	17.20** ± 0.02	17.52** ± 0.02	16.85** ± 0.02	17.10** ± 0.02
(d)	-0.002 ± 0.02	-0.07** ± 0.02	0.10** ± 0.02	-0.008 ± 0.02
(h)	-0.09* ± 0.04	0.08* ± 0.04	0.19** ± 0.05	0.06 ± 0.06
$\chi^2_{(1)}$ (18df)	126.93**	333.11**	336.42**	160.31**
Six parameter model (Digenic interactions)				
m	17.41** ± 0.06	17.59** ± 0.06	17.00** ± 0.06	17.21** ± 0.08
(d)	0.002 ± 0.04	-0.006 ± 0.03	0.10** ± 0.03	0.11* ± 0.05
(h)	-0.82** ± 0.21	0.02 ± 0.21	-1.13** ± 0.21	-0.28 ± 0.26
(i)	-0.18** ± 0.06	-0.14* ± 0.06	0.26** ± 0.06	-0.13 ± 0.07
(j)	-0.02 ± 0.09	-0.22* ± 0.10	-0.03 ± 0.11	-0.34** ± 0.12
(l)	0.62** ± 0.19	-0.06 ± 0.18	1.72** ± 0.19	0.28 ± 0.23
$\chi^2_{(2)}$ (15df)	113.88**	317.64**	152.91**	150.34**
Ten-parameter model (Trigenic interactions)				
m	16.80** ± 0.15	17.10** ± 0.16	15.89** ± 0.16	16.80** ± 0.19
(d)	-0.28* ± 0.11	0.20 ± 0.14	-0.93** ± 0.18	0.38** ± 0.14
(h)	2.36** ± 0.81	2.72** ± 0.85	5.60** ± 0.97	1.99 ± 1.04
(i)	0.56** ± 0.15	0.38* ± 0.16	1.43** ± 0.16	0.31 ± 0.20
(j)	0.77** ± 0.26	-1.02** ± 0.31	1.43** ± 0.36	-0.78* ± 0.31
(l)	-4.05** ± 1.44	-4.60** ± 1.46	-9.80** ± 1.77	-3.67* ± 1.80
(w)	0.31* ± 0.13	-0.18 ± 0.14	1.12** ± 0.19	-0.35* ± 0.15
(x)	-2.27** ± 0.41	-1.49** ± 0.44	-3.86** ± 0.50	-1.24* ± 0.51
(y)	-0.76** ± 0.24	0.98** ± 0.29	-0.009 ± 0.38	0.08 ± 0.30
(z)	2.13* ± 0.84	2.40** ± 0.80	5.98** ± 1.00	2.19* ± 1.02
$\chi^2_{(3)}$ (11df)	68.93**	291.42**	46.98**	137.79**
Types of epistasis	Duplicate	Duplicate	Duplicate	Duplicate
Twelve-parameter model (Linked digenic interactions)				
(d)	0.05 ± 0.04	-0.01 ± 0.04	0.14** ± 0.04	0.08 ± 0.05
m+h+l	17.23** ± 0.05	17.59** ± 0.05	17.55** ± 0.06	17.21** ± 0.06
m+i	17.36** ± 0.04	17.46** ± 0.04	17.35** ± 0.04	17.14** ± 0.06
pi	-0.08 ± 0.05	-0.22** ± 0.06	-0.27** ± 0.08	-0.05 ± 0.06
p ² i	-0.25** ± 0.07	-0.30** ± 0.07	-0.04 ± 0.09	-0.04 ± 0.09
pj	-0.08 ± 0.07	-0.07 ± 0.07	-0.29** ± 0.09	-0.11 ± 0.09
p ² j	-0.09 ± 0.10	0.03 ± 0.10	-0.40** ± 0.14	-0.01 ± 0.12
Pl	0.50** ± 0.11	-0.18 ± 0.11	1.70** ± 0.14	0.02 ± 0.13
p ² l	0.48** ± 0.09	-0.55** ± 0.09	1.09** ± 0.12	-0.31** ± 0.11
p ³ l	0.54** ± 0.10	-0.99** ± 0.10	0.88** ± 0.13	-0.53** ± 0.12
p ⁴ l	0.57** ± 0.10	-1.32** ± 0.11	0.11 ± 0.15	-0.66** ± 0.13
$\chi^2_{(4)}$ (9df)	27.51**	1578.17**	217.35**	79.32**

According to six-parameter model, the estimates 'm', dominance [d], and digenic [i] and [l] in cross-1; 'm' and digenic [l] and [j] in cross-2; 'm', additive [d], dominance [h] and digenic [i] and [j] in cross-3 and 'm', additive [d] and digenic [j] in cross-4 were significant. Significant $\chi^2_{(2)}$ value at 15 degrees of freedom revealed the presence of higher order epistasis and/or linked digenic interactions.

Under ten-parameter model, significant estimates were observed for all the ten-parameters viz., 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] in cross-1; 'm', dominance [h], additive x

additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] in cross-2; 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x] and dominance x dominance x dominance [z] (except [y]) in cross-3 and 'm', additive [d], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x] and dominance x dominance x dominance [z] in cross-4 were significant. The $\chi^2_{(3)}$ value was significant at 11 degrees of freedom indicating the presence of higher order epistasis.

According to twelve-parameter model, the gene effects viz., m+[h]+[l], m+[i], [p²i], [pl], [p²l], [p³l] and [p⁴l] in cross-1; m+[h]+[l], m+[i], [pi], [p²i], [p²l], [p³l] and [p⁴l] in cross-2; [d], m+[h]+[l], m+[i], [pi], [pj], [p²j], [pl], [p²l] and [p³l] in cross-3 and m+[h]+[l], m+[i], [p²l], [p³l] and [p⁴l] in cross-4 were significant. The $\chi^2_{(4)}$ value was significant at nine degrees of freedom indicating the presence of higher order linkage.

The above findings were further confirmed from the investigations done by several researchers who worked on different kind of gene effects in mostly up to digenic and trigenic interactions and there is no report on linked digenic interactions in cotton so far. Bhapkar and D'cruz (1967) [1] reported that epistasis played a major role in castor beans with high oil content. There is only a few reports on trigenic interactions in cotton (Valu *et al.*, 2015c and Gawande *et al.*, 2016) [30, 6]. Valu *et al.* (2015c) [30] using 12 generations studied genetic architecture of oil content in cotton (*Gossypium hirsutum* L.) and Gawande *et al.*, (2016) [6] estimated the nature and magnitude of gene effects using 12 generations for fibre quality traits in three crosses of cotton. Similar findings of trigenic interactions were also reported by Modha (2010) [17] for fruit yield and its component traits in okra as well as Singh *et al.*, (2013) [23] for seed yield and its component traits in castor.

For oil content in general, there is evidence of both [i] and [l] types of interactions but not of the [j] types (few case). Further, the [i] and [l] types effects had opposite sign in most cases. Where many pairs of genes of unknown distribution between the parents were involved in the interactions, the interpretation of the estimates rests on the relative sign of the [h] and [l] effects (Jinks and Jones, 1958) [11]. While the sign of the [l] type of interaction is negative, one cannot direct estimate of the sign or magnitude of [h] because it is compounded with those of 'm' and [l]. The three unsatisfactory models in all the traits in four crosses, however, provide estimates of [h] and all were mostly positive in most of the cases. Since there were no significant differences among those three estimates of [h]. It was safe to assume that it would take similar value in the linked digenic interaction model. Therefore, the [h] and [l] effects had opposite signs and that the gene interactions were duplicate epistasis in nature (Jinks and Jones, 1958) [11].

The distribution of the genes between the parental lines affects the magnitude of [d] and [j] effects and the magnitude and sign of [i] effects. Since diverse parents extracted by selfing in four cotton crosses, it was quite cleared that the genes of increasing and decreasing effect were dispersed between two parental lines. In the presence of dispersion, [j] type of interactions between different pair of loci cancel out when summed over all pairs of interacting genes and [i] may

have the opposite sign to that of the individual i's (Jinks and Jones, 1958) [11].

Both of the above consequences of dispersion can be recognized in the estimates of [i] and [j] parameters in linked digenic interaction model. Thus, the estimates of [j] were small and non-significant in most of the cases with few expectations, while [i] had opposite sign to those of [j] and [l] and the opposite sign to that expected for duplicate interactions (Jinks and Perkins, 1969) [12].

Linked digenic model showed that the magnitude of combination of three gene effects i.e. m+[h]+[l] as well as combination of two gene effects viz., m+[i] were equally important to explain variation in generation means for all the traits in four crosses and both were superior over additive [d] gene effects for oil content in four crosses. While comparing linkage v/s non-linkage parameters, it was inferred that absolute totals of non-linkage parameters exceeded 7 to 17 times higher than that of absolute totals of linkage parameters which revealed that there will be very less possibility of presence of linkage than the absence of linkage at digenic level. However, significant $\chi^2_{(4)}$ value at 9 degree of freedom revealed possibility of linkage at higher order epistasis which was beyond the scope of the present investigation. Therefore, conclusions drawn on the basis of trigenic interactions model was more valid and realistic than that of linked digenic model. It could be concluded from the present study that oil content recorded in four cotton crosses were governed by additive, dominance, digenic and trigenic epistasis and/or linked digenic epistasis gene effects along with duplicate type of gene action. When additive as well as non-additive gene effects are involved, a breeding scheme efficient in exploiting both types of gene effects should be employed. Biparental mating could be followed which would facilitate exploitation of both additive and non-additive gene effects simultaneously for genetic improvement of seed cotton yield and its component traits in cotton.

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