Research Article

Genetic architecture of oil content in cotton (*Gossypium hirsutum* L.)

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Abstract
The present investigation was undertaken with a view to generate genetic information on gene effects for oil content in cotton (*Gossypium hirsutum* L.). The experimental materials consisted of twelve generations, namely P_1, P_2, F_1, F_2, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_1s and B_2s in four crosses of cotton *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, C, B_{11}, B_{12}, B_{21}, B_1s, B_2s, X and Y in cross-1; B_{11}, B_1s and B_2s in cross-2; A, B, C, B_1s and B_2s in cross-3 and A, B, C, B_{11}, B_{12} and X in cross-4 were significant showing presence of digenic and trigenic gene interaction. In six parameter model based on weighted least square technique, 'm', [d], [j] and [l] in cross-1; all the parameters except [j] in cross-2; 'm', [d] and [j] in cross-3 and 'm', [d], [h], [i], [j] and [l] in cross-4 were significant. The $\chi^2_{(2)}$ value at six degrees of freedom was found non-significant in cross-4 proving the six parameter model as the best fit model in cross-4 and significant in cross-1, cross-2 and cross-3 supporting the presence of higher order epistasis. In ten parameter model, 'm', [h], [i], [l], [x], [y] and [z] in cross-1; 'm', [l] and [z] in cross-2 and only 'm' in cross-3 were significant. The $\chi^2_{(3)}$ value at two degrees of freedom was non-significant in cross-2 proving the ten parameter model as the best fit model and significant in cross-1 and cross-3 indicating the presence of higher order epistasis and/or linkage. Duplicate type of epistatic gene action was responsible for the inheritance of oil content in all the four crosses of cotton.

Introduction

Cotton is an important fibre crop of global significance and is grown in tropical and subtropical regions of more than eighty countries. Cotton is primarily cultivated for its lint or fibre, in other words, lint is the main product of cotton crop. Now-a-days, cotton seed oil is also widely used for human consumption. Thus, cotton has become a fibre cum oil yielding crop. Its seeds contain 18 to 26 per cent oil. Cottonseed oil, also termed as "Heart Oil" is among the most unsaturated edible oils. Cottonseed oil is used for salad oil, mayonnaise, salad dressing, and similar products because of its flavor stability. An additional benefit that accrues from cottonseed oil is its high level of antioxidants - tocopherols that contribute to its long life on the shelf. The information on the nature of gene action could be helpful in predicting the effectiveness of selection in a population. A distinct knowledge of the type of gene action, its magnitude and composition of genetic variance are of fundamental importance to a plant breeder which helps in formulating an effective and sound breeding programme. The assessment of the magnitude of gene action for oil content in cotton is helpful in deciding the appropriate breeding procedures. Hence, the experiment was planned to study the genetic architecture of oil content in cotton.

Materials and methods

The basic set of twelve generations *viz.*, P_1, P_2, F_1, F_2, B_1 (F_1 x P_1), B_2 (F_1 x P_2), B_{11} (B_1 x P_1), B_{12} (B_1 x P_2), B_{21} (B_2 x P_1), B_{22} (B_2 x P_2), B_1s (B_1 selfed) and B_2s (B_2 selfed), 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 three replications during *Kharif* 2013. The plots of various generations contained different number of rows i.e., parents and F_1 in single row; B_1 and B_2 in two rows and F_2, B_1s, B_{11}, B_{12}, B_2s, B_{21} and B_{22} in three rows. Each row was of 6.3 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 individual plant basis in each replication on randomly selected five plants in each replication for P_1, P_2 and F_1; ten plants for B_1 and B_2 and twenty plants for each of F_2, B_{11}, B_{12}, B_{21}, B_{22}, B_1s and B_2s generations 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). The $\chi^2_{(1)}$ of joint scaling test under three-parameter model gives idea about fitness of additive-dominance model. Using six basic generations, six parameter model given by Hayman (1958) was also fitted. Finally, the data were subjected to ten-parameter model given by

Hill (1966). 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 six degrees of freedom and under ten-parameter model at two degrees of freedom, respectively. This is an additional advantage of using twelve generations and ten-parameter model as it provides sufficient degree of freedom for testing validity and goodness of fit for different models. The results of models given by Hayman (1958) and Hill (1966) were compared whenever six-parameter model was satisfactory for inheritance of the trait.

Results and discussion
The analysis of variance between families revealed that mean square due to crosses was non-significant for oil content. Bartlett's test for homogeneity of error variances indicated that error variance was homogeneous for oil content. Among the progenies within each family, the analysis of variance indicated significant differences among the generation means for the trait under study in all the four crosses.

The comparison of mean values for oil content in twelve generations of four crosses is presented in Figure-1. The mean performance of female parent in cross-1 was significantly higher than the male parent. The F_1 recorded the highest mean (18.89) performance among all the twelve generations showing over dominance. The F_2 mean was higher than mean of male parent and less than means of P_1 and F_1 showing inbreeding depression. B_1 and B_2 showed intermediate mean performance when compared with the parental means and were closer to the means of P_1 and F_2. Whereas the mean values of all the double backcrosses were statistically at par with one another and with mean of P_2 (except B_{21}). In cross-2, male parent (MR-786) showed significantly higher mean performance than female parent (G.Cot-10). The F_1 recorded the highest mean performance among all the twelve generations showing over dominance. The F_2 mean was higher than means of both the parents but less than F_1 mean showing inbreeding depression. B_1 and B_2 were closer and statistically at par with each other and with mean of P_2 and F_2. The mean values of all the double backcrosses were numerically higher than means of both the parents and statistically at par with one another and with means of P_2 and F_2. In cross-3, the mean value of male parent (GTHV-95/145) was numerically higher than female parent (G.Cot-12). The F_1 mean was outside the parental range indicating over dominance. The mean performance of F_2 was higher than F_1 mean showing transgressive segregation. The mean

performance of B_1 and B_2 were closer and higher than means of both the parents, but statistically at par with means of F_1 and F_2. Whereas the mean values of all the double backcrosses were statistically at par with one another and with mean of P_2. There was significant variation in mean performance of both the parents for oil content in cross-4. The F_1 recorded the highest mean (18.96) performance among all the twelve generations showing over dominance. The F_2 mean (18.57) was intermediate between both the parents but less than the F_1 showing inbreeding depression. The backcrosses, B_1 and B_2 means were statistically at par with mean of P_1 and P_2, respectively. The mean performance of all the double backcrosses B_{12}, B_{22}, B_{21}, B_{1s} and B_{2s} (except B_{11}) were statistically at par with one another and with mean of P_2 and F_2, while the mean performances of B_{11} was statistically at par with the female parent P_1.

The data were initially subjected to simple scaling tests A, B, C and D. Significant estimates of any one or more of these tests indicate the presence of digenic interactions. Further, simple scaling tests B_{11}, B_{12}, B_{21}, B_{22}, B_{1s} and B_{2s} given by Hill (1966) and X and Y given by Van Der Veen (1959) were also computed. The significant estimate of the test(s) given by Hill (1966) shows the contribution of particular generation to higher order epistasis which is indirectly indicating the presence of epistasis. If any of the Van Der Veen's tests deviate significantly from zero, it also indicates presence of trigenic or higher order epistasis. 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 additive-dominance model. The $\chi^2_{(1)}$ test with nine degrees of freedom; $\chi^2_{(2)}$ at six degrees of freedom and $\chi^2_{(3)}$ at two degrees of freedom was applied to test the fitness of three-parameter model, six-parameter model and ten-parameter model, respectively. Non-fitting of ten-parameter model was used to know the presence of higher order epistasis (Hill, 1966). To draw inference on adequacy of ten-parameter model, chi-square test $\chi^2_{(3)}$ at two degrees of freedom was applied. The degree of freedom for χ^2 was computed by subtracting number of parameters considered under the respective model from the number of generations.

Out of all the scaling tests (Table-1), A, C, B_{11}, B_{12}, B_{21}, B_{1s}, B_{2s}, X and Y in cross-1; B_{11}, B_{1s} and B_{2s} in cross-2; A, B, C, B_{1s} and B_{2s} in cross-3 and A, B, C, B_{11}, B_{12} and X in cross-4 were significant showing presence of digenic and/or

trigenic gene action for oil content. All the three parameters i.e. 'm', additive [d] and dominance [h] of three parameter model were significant in all the four crosses for oil content. The $\chi^2_{(1)}$ values at nine degrees of freedom of joint scaling test was significant in all the four crosses resulting to the failure of additive-dominance model which indirectly pointed out the presence of epistasis. Cockerham (1959) 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 these traits.

When the simple additive-dominance model failed to explain the variation among generation means, a six parameter model involving three digenic interactions ([i], [j] and [l]) proposed by Hayman (1958) was applied. This model utilized only six basic generation *viz.*, P_1, P_2, F_1, F_2, B_1 and B_2. The goodness of fit for six-parameter model of Hayman (1958) could not be tested because no degrees of freedom left for testing chi-square estimates for oil content. According to six parameter model of Hayman (1958), the parameters 'm', dominance [h] and additive x dominance [j] in cross-1; 'm' and dominance x dominance [l] in cross-2; 'm', additive [d] and additive x dominance [j] in cross-3 and 'm' and dominance x dominance [l] in cross-4 were significant. On the other hand, based on weighted least square technique, digenic interaction model of Hill (1966) was tested which had provision of testing the adequacy of model with six degrees of freedom besides being utilizing means of all the twelve generations. According to the six parameter model of Hill (1966), the parameters 'm', additive [d] and digenic ([j] and [l]) in cross-1; all the parameters except digenic [j] in cross-2; 'm', additive [d], digenic [j] in cross-3 and all the individual and digenic gene effects in cross-4 were significant for oil content. The $\chi^2_{(2)}$ value at six degrees of freedom were significant in cross-1, cross-2 and cross-3 supporting the presence of higher order epistasis while, the non-significant $\chi^2_{(2)}$ in cross-4 indicating six parameter model as the best fit model.

In ten parameter model, 'm', dominance [h], additive x additive [i], 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-1; 'm', dominance x dominance [l] and dominance x dominance x dominance [z] in cross-2 and only 'm' in cross-3 were significant for oil content. The $\chi^2_{(3)}$ value at two degrees of freedom was non-significant in cross-2 for oil content proving the ten parameter model as the best fit model. While, the $\chi^2_{(3)}$ value was significant in cross-1

and cross-3 indicating the presence of higher order epistasis and/or linkage.

These findings were further confirmed from the investigations done by several researchers who worked on different kind of gene effects in mostly up to digenic interactions and there is no report on trigenic interactions in cotton so far. Bhapkar and D'cruz (1967) reported that epistasis played a major role in castor beans with high oil content. The results are also in agreement with findings of Singh *et al.* (2013) who reported digenic and trigenic epistasis for oil content in castor. The opposite signs of either two or all the three gene effects *viz.*, dominance [h], dominance x dominance [l] and dominance x dominance x dominance [z] suggested the presence of duplicate type of epistasis. In present study, duplicate epistasis was observed in all the four crosses for oil content. Duplicate type of epistasis also reported by Singh *et al.* (2013) for oil content in castor; by Mehetre *et al.* (2003) for number of sympodia per plant and boll weight; by Haleem *et al.* (2010) for number of open bolls, seed cotton yield and boll weight and by Kannan *et al.* (2013) for number of sympodia per plant, number of bolls, boll weight and single plant yield in cotton.

It can be concluded from the present study that oil content recorded in four cotton crosses was governed by additive, dominance and digenic and/or trigenic 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 could be employed. Biparental mating could be followed which would facilitate exploitation of both additive and non-additive gene effects simultaneously.

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Table1. 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	-0.38**	±	0.11	-0.08	±	0.13	0.57**	±	0.15	-0.41*	±	0.16
B	0.10	±	0.13	-0.30	±	0.16	0.56**	±	0.16	-0.59**	±	0.16
C	-0.56*	±	0.27	0.06	±	0.27	0.82**	±	0.29	-0.62*	±	0.27
D	-0.14	±	0.14	0.22	±	0.14	-0.15	±	0.16	0.19	±	0.16
B_{11}	1.64**	±	0.28	-0.68*	±	0.34	-0.37	±	0.25	0.58*	±	0.28
B_{12}	1.51**	±	0.23	0.59	±	0.31	0.52	±	0.26	1.61**	±	0.32
B_{21}	1.85**	±	0.25	0.30	±	0.28	0.02	±	0.31	0.41	±	0.32
B_{22}	-0.06	±	0.28	-0.16	±	0.28	-0.05	±	0.32	0.49	±	0.27
B_{1S}	2.80**	±	0.65	-1.72**	±	0.58	-1.30*	±	0.52	-0.69	±	0.59
B_{2S}	1.28*	±	0.58	-1.03	±	0.54	-1.45*	±	0.60	-0.27	±	0.55
X	0.34**	±	0.12	-0.06	±	0.13	0.04	±	0.12	0.32*	±	0.13
Y	0.45**	±	0.12	0.43**	±	0.14	0.24	±	0.13	0.24	±	0.14
Three parameter model												
m	18.33**	±	0.03	18.43**	±	0.03	18.31**	±	0.03	18.47**	±	0.02
(d)	0.16**	±	0.03	-0.09**	±	0.03	-0.11**	±	0.03	-0.25**	±	0.02
(h)	0.38**	±	0.05	0.31**	±	0.06	0.33**	±	0.05	0.30**	±	0.05
$\chi^2_{(1)}$ (9 df)	114.66**			26.86**			56.99**			46.30**		
Six parameter model (Hayman)												
m	18.53**	±	0.06	18.60**	±	0.06	18.62**	±	0.06	18.57**	±	0.06
(d)	0.04	±	0.07	-0.02	±	0.09	-0.11	±	0.09	-0.18	±	0.10
(h)	0.71*	±	0.29	0.03	±	0.30	0.70*	±	0.33	0.08	±	0.33
(i)	0.27	±	0.29	-0.44	±	0.29	0.31	±	0.32	-0.38	±	0.32
(j)	-0.24**	±	0.08	0.11	±	0.09	0.01	±	0.10	0.09	±	0.11
(l)	0.01	±	0.39	0.82*	±	0.38	-1.44**	±	0.48	1.39**	±	0.50
Six parameter model (Hill)												
m	18.34**	±	0.15	18.92**	±	0.15	18.50**	±	0.15	19.18**	±	0.16
(d)	0.23**	±	0.03	-0.11**	±	0.04	-0.12**	±	0.04	-0.28**	±	0.03
(h)	-0.19	±	0.37	-0.89*	±	0.39	0.36	±	0.40	-1.91**	±	0.42
(i)	0.11	±	0.15	-0.53**	±	0.15	-0.27	±	0.15	-0.67**	±	0.16
(j)	-0.35**	±	0.13	0.16	±	0.14	0.28*	±	0.14	0.29*	±	0.14
(l)	0.66**	±	0.25	0.72*	±	0.29	-0.34	±	0.29	1.65**	±	0.29
$\chi^2_{(2)}$ (6 df)	77.61**			13.14*			30.69**			11.19		
Ten parameter model												
m	16.80**	±	0.43	18.76**	±	0.41	17.99**	±	0.42	-		
(d)	0.42	±	0.34	-0.06	±	0.31	-0.17	±	0.31	-		
(h)	8.11**	±	2.17	0.24	±	2.07	3.22	±	2.15	-		
(i)	1.61**	±	0.43	-0.41	±	0.41	0.21	±	0.42	-		
(j)	-1.69	±	0.87	0.14	±	0.87	-0.09	±	0.84	-		
(l)	-12.58**	±	3.24	-2.29*	±	1.08	-5.18	±	3.28	-		
(w)	-0.16	±	0.34	-0.07	±	0.31	0.07	±	0.31	-		
(x)	-3.95**	±	1.23	0.29	±	1.15	-1.18	±	1.23	-		
(y)	1.99*	±	0.79	-0.08	±	0.84	0.69	±	0.79	-		
(z)	6.52**	±	1.52	1.93**	±	0.54	2.54	±	1.57	-		
$\chi^2_{(3)}$ (2 df)	46.04**			2.45			24.48**			-		
Type of epistasis	Duplicate			Duplicate			Duplicate			Duplicate		

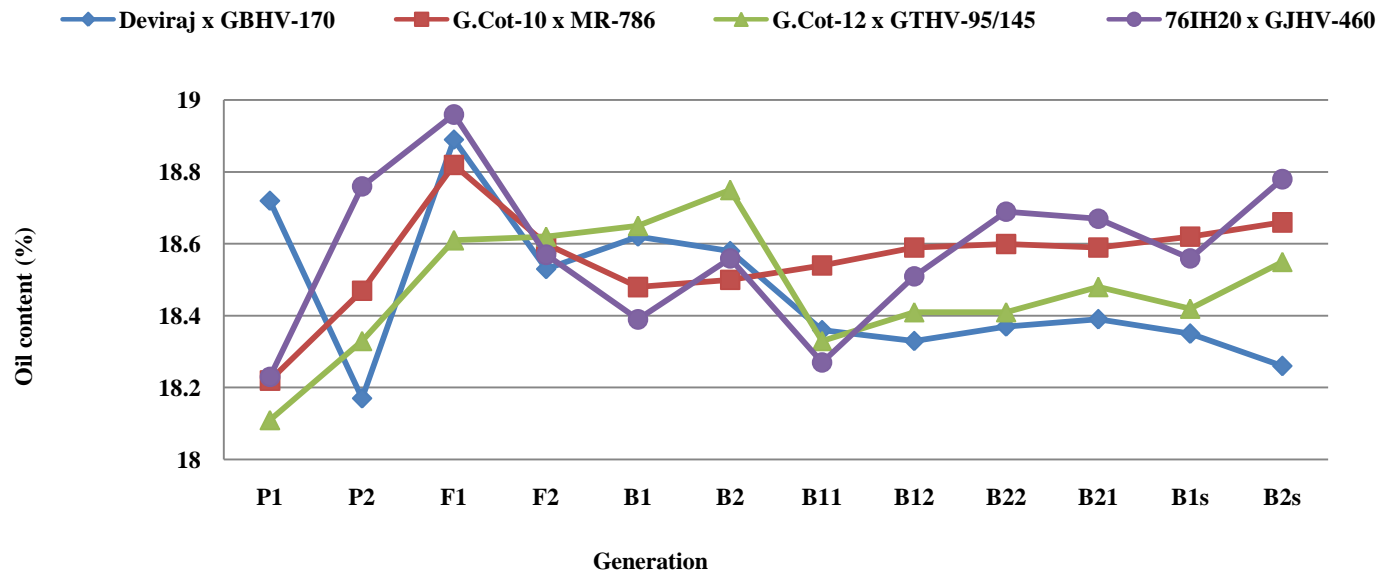*, ** Significant at 5 and 1 per cent levels, respectively

Figure 1.   Generation mean trends in four families of cotton for oil content