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RESEARCH RARTICLE

Detection and estimation of trigenic and linked digenic interaction effects in castor (*Ricinus communis* L.) using 21 generations

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Abstract

The present investigation was undertaken with a view to generate genetic information on gene effects for seed yield and its component traits in castor (*Ricinus Communis* L.). The experimental materials consisted of twenty-one generations, namely P_1, P_2, F_1, F_2, F_3, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip of two crosses of castor *viz.,* JM-6 x 48-1 (cross-1) and JI-436 x PCS-124 (cross-2). Special scaling tests such as X, Y, Z, (B_1-L_1), (B_2-L_2) and (F_2-L_3) were significant either in cross-1 or cross-2 for most of the traits besides significance of other tests showing the presence of epistasis. The $\chi^2(2)$ value at fifteen degrees of freedom were significant in all the traits in both the crosses supported the presence of higher order epistasis. The $\chi^2(3)$ value at eleven degrees of freedom were significant for all the traits in both the crosses indicating the presence of higher order epistasis and/or linkage. The $\chi^2(4)$ value at nine degrees of freedom were significant in all the traits in both the crosses indicating the presence of higher order linkage. Duplicate type of epistasis was responsible for the inheritance of seed yield and its component traits in two crosses of castor. This is the first report of higher order interaction/linked digenic epistasis using 21 generations in castor.

Keywords: Castor, digenic, trigenic linked digenic gene effects, 21 generations

Introduction

Castor crop is of great importance globally because of its multiple uses in chemical industry including the pharmaceutical, insecticidal formulations and other industrial applications. It is generally grown the arid and semi-arid regions of the world. However, its oil is non-edible but it is the only source of hydroxylated fatty acid and therefore, it is having vast and varied industrial applications such as lubricants, surfactants, surface coating, cosmetics, resins, paints, pharmaceuticals, adhesives, waxes, polishes, varnishes, perfumes, flavors, textile dyes, textile furnishing agents, etc (Jombog and Enenebeaku 2008; Saribiyik et al. 2010; Severino et al. 2012). Castor also has tremendous future potential in enhancing farm income because of its industrial importance. India is the largest producer of castor with more than a tonne national average productivity where very few annual crops can match and it ranks first among the major castor producing countries *viz.,* India, China, Brazil and Thailand (Anonymous 2017). In India, castor is being grown for oil under wide range of environmental conditions. Gujarat is pioneer in the development and release of castor hybrid on commercial scale not only in the country but also worldwide (Anonymous 2017). The hybrid vigor in castor was commercially exploited in Gujarat by utilizing pistillate line TSP 10 R introduced from USA in early 1970's

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when the first castor hybrid GCH-3, giving 124 per cent higher yield than the checks, was release at country and state level by Gujarat. Then after several hybrids were developed and released for cultivation which results in quantum jump in production from 300 kg/ha in 1970 to about 1899 kg/ha during 2017-2018.

Comprehensive knowledge of epistatic (non-allelic interaction) gene action and genotype and environment interactions can contribute to determining the selection of breeding methods that efficiently exploits the genetic variance (Boubacar et al. 2020). The understanding of gene effects for seed yield and its component traits in castor is of prime importance before starting rigorous breeding programme. Though generation mean analysis using six generations have been extensively used to understand the gene effects in various crops (Kumar et al. 2008; Sumathi and Muralidharan 2010; Sandip et al. 2013 Jatoth et al. 2014; Pujar et al. 2022) but very few reports are available on gene effects using more than six basic generations in castor). Moreover, the information on gene systems especially linked digenic or higher order epistasis in other crops are also meager. There is yet no report on the linked digenic interactions in castor so far. Therefore, a study was conducted to determine the higher order interaction/linked digenic epistasis for seed yield and its component traits in two crosses of castor using 21 generations.

Materials and methods

The experimental material was comprised of four crosses viz., JM-6 × 48-1 (cross 1), JI-436 × PCS-124 (cross 2), SKI-346 × JI-35 (cross 3) and SKI-346 × SKI 215 (cross 4) each with twenty-one basic generations viz., P_1, P_2, F_1, F_2, F_3, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip. Results will be presented for only first two crosses 1 and 2 and their 21 generations.

Development of experimental material

Two crosses *viz.,* JM-6 × 48-1 and JI-436 × PCS-124 with their six generations P_1, P_2, F_1, F_2, BC_1 and BC_2 were procured from previous student during kharif 2017-18 and were utilized for making further generations. These four generations along with parents were grown at Main Oilseeds Research Station, Junagadh Agricultural University, Junagadh during kharif 2018-19 to develop the subsequent generations (B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, and B_{2S}) and also the fresh seeds of P_1, P_2, F_1, F_2, B_1 and B_2 generations. These four generations i.e., F_1, F_2, B_1 and B_2 along with parents were grown at Main Oilseeds Research Station, JAU, Junagadh during *kharif*-2019-20 to develop subsequent generations *viz.,* F_3, F_2 bip, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip, B_1 x F_1 and B_2 x F_1. The seeds of P_1, P_2, F_2, B_{1S} and B_{2S} were produced by selfing/sibbing, while seeds of F_1, B_1, B_2, B_{11} (B_1 x P_1), B_{12} (B_1 x P_2), B_{21} (B_2 x P_1) and B_{22} (B_2 x P_2) were produced by hand pollination. The seeds of F_3 were produced by selfing F_2, while F_2 bip, B_1 bip and B_2 bip were produced by intermating randomly selected plants of respective generations to produce biparental crosses. On the other hand, F_2 x P_1, F_2 x P_2 and F_2 x F_1 were produced by hand emasculation of F_2 plants with hand pollination of P_1, P_2 and F_1 plants, respectively. Likewise, B_1 x F_1 and B_2 x F_1 were produced by hand emasculation and pollination of B_1 and B_2 plants, respectively.

Evalution of experimental material

Compact Family Block Design with three replications was followed for planting the material derived from JM-6 × 48-1 and JI-436 × PCS-124 crosses during *kharif* 2020-21. 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, F_3, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip in four rows. Each row was of 6 m in length with 120 cm and 60 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 castor. The observations on number of effective branches per plant, number of capsules on primary raceme, oil content shelling out turn, 100-seed weight and seed yield per plant were recorded on five competitive and randomly selected plants from P_1, P_2 and F_1; ten plants from backcross (B_1 and B_2) and twenty plants from F_2, F_3, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip generations in each replication for seed yield and its component traits. The oil content was estimated by Nuclear magnetic resonance (NMR) technique (Tiwari et al. 1974). The gene effects for seed yield and its component traits were computed through generation mean analysis (Hayman and Mather 1955; Hayman 1958; Hill 1966 and Jinks and Perkins 1969). The data were initially subjected to simple scaling tests A, B, C and D. Besides simple scaling tests, special scaling tests *viz.*, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S} and B_{2S} given by Hill (1966); X, Y and Z given by Van Der Veen (1959) as well as (B_1-L_1), (B_2-L_2) and (F_2-L_3) given by Jinks and Perkins (1969) 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, six-parameter model based on weighted least square technique of Cavalli (1952) was performed; the data were further subjected to ten-parameter model as per notations 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 15 degrees of freedom and for ten-parameter model at 11 degrees of

freedom, respectively. To detect the presence of linked digenic epistasis and to estimate gene effects for seed yield and its component traits, a model proposed by Jinks and Perkins (1969) was also used. The $\chi^2(4)$ value were estimated under twelve-parameter model at 9 degrees of freedom. This is an additional advantage of using 21 generations under 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

Out of all the scaling tests, it revealed that scaling tests *viz.*, A, D, B_{11}, B_{12}, B_{21}, B_{1S}, B_{2S}, X, Y, Z and (F_2-L_3) were significant in cross-1 and B_{11}, B_{12}, B_{21}, B_{1S} and Y in cross-2 indicating the presence of digenic and/or trigenic interactions for seed yield per plant. The trend in mean yield (g) per plant in 21 generations of 21 generations derived from both the crosses is depicted in Fig. 1. The scales B, C, B_{11}, B_{12}, B_{22}, B_{21}, B_{1S}, B_{2S}, X, Z, (B_1-L_1), (B_2-L_2) and (F_2-L_3) in cross-1 and B, D, B_{11}, B_{12}, B_{22}, B_{1S}, B_{2S}, Y, (B_2-L_2) and (F_2-L_3) in cross-2 were significant showing the presence of epistasis for oil content. The trend of 21 generations means for oil content (%) is shown in Fig. 2. For shelling out turn, the scales namely A, B, C, D, B_{11}, B_{22}, B_{1S}, B_{2S}, X, Y, (B_1-L_1) and (B_2-L_2) in cross-1 and scaling tests B, C, B_{11}, B_{12}, B_{22}, B_{21}, B_{1S}, B_{2S}, X, Y, as well as special scales (B_1-L_1), (B_2-L_2) and (F_2-L_3) in cross-2 were significant showing the presence of epistasis. For 100-seed weight, A, D, B_{11}, B_{12}, B_{22}, B_{21}, B_{2S}, X, Y, (B_1-L_1) and (B_2-L_2) in cross-1 and all scaling tests except B and Y in cross-2 were significant indicating the presence of digenic and trigenic epistasis. On the other hand, the scaling tests D, B_{11}, B_{22}, X, (B_1-L_1) and (F_2-L_3) in cross-1 and all the scales except B_{11} and (F_2-L_3) in cross-2 were significant showing the presence of digenic and trigenic gene interaction for number of effective branches per plant, while scales A, B, C, D, B_{11}, B_{12}, B_{22}, B_{21}, B_{1S}, X as well as special scales (B_1-L_1) and (F_2-L_3) in cross-1 and A, B, C, B_1, B_{12}, B_{22}, B_{21}, B_{1S}, B_{2S}, X, Z, (B_1-L_1), (B_2-L_2) and (F_2-L_3) in cross-2 were significant showing the presence of epistasis for number of capsules on primary raceme. For total length of primary raceme, B, C, D, B_{11}, B_{12}, B_{22}, B_{21}, B_{1S}, X, Y as well as special scale (F_2-L_3) in cross-1 and scaling tests B_{22}, B_{1S}, B_{2S}, X, Y, (B_1-L_1) and (B_2-L_2) in cross-2 were significant indicating the presence of digenic and trigenic epistasis, while scales A, B, C, D, B_{11}, B_{12}, B_{22}, B_{21}, B_{1S}, X, Y, Z and (F_2-L_3) were significant in cross-1 and B_{22}, B_{1S}, B_{2S}, X, Y, (B_1-L_1) and (B_2-L_2) in cross-2 were significant showing the presence of epistasis for effective length of primary raceme. All the three parameters *i.e.* 'm', additive [d] and dominance [h] of three parameter model were significant either in cross-1 or cross-2 for all the characters under study. The $\chi^2(1)$ values with 18 degrees of freedom of joint scaling test was significant in all the characters indicating 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]) based on weighted least square technique proposed by Hill (1966) was tested, which had provision of testing the adequacy of model with 15 degrees of freedom besides being utilizing means of all the twenty-one generations. According to the six parameter model, the $\chi^2(2)$ value at 15 degrees of freedom were significant in all the traits in both the crosses indicating the presence of higher order epistasis. In ten parameter model, significant estimates of 'm', dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [1], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] gene effects in cross-1 and 'm', dominance [h], additive x additive [i], dominance x dominance [1], additive x additive x dominance [x] and dominance x dominance x dominance [z] in cross-2 were significant for seed yield per plant. For oil content, 'm', additive [d], dominance [h] and additive x additive x additive [w] gene effects in cross-1 and 'm', dominance x dominance [1] and dominance x dominance x dominance [z] gene effects in cross-2 were significant (Table 1). All the gene effects except [j] were found significant in cross-1 and 'm', additive [d], additive x additive [i], additive x dominance [j], additive x additive x additive [w], additive x additive x dominance [x] and additive x dominance x dominance [y] in cross-2 were significant for shelling out turn. For 100-seed weight, the estimates of 'm', additive [d], dominance [h], additive x dominance [j], dominance x dominance [1], additive x additive x additive [w], additive x additive x dominance [x] and dominance x dominance x dominance [z] gene effects in cross-1 and all the gene effects except additive [d] and [w] in cross-2 were found significant (Table 2). All the gene effects were found significant in cross-1 and cross-2 for number of effective branches per plant. For number of capsules on primary raceme, all the gene effects except additive [d] in cross-1 and 'm', additive x dominance [j], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] in cross-2 were significant (Table 3). The gene effects viz., 'm', dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [1], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-1 and only the estimate 'm' and additive x dominance x dominance [y] were significant in cross-2 for total length of primary raceme. For effective length of primary raceme, significant estimates were observed for 'm', dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [1], additive x additive x dominance [x], additive x dominance

Table 1. Estimation of gene effects for seed yield per plant and oil content in two crosses of castor

Scaling tests/gene effects	Seed yield per plant						Oil content					
	JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)			JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)		
Ten-parameter model (Trigenic interactions model)												
m	110.83**	±	28.58	95.67**	±	22.31	49.71**	±	0.38	48.30**	±	0.31
(d)	13.89	±	29.21	-2.31	±	23.23	1.23**	±	0.46	-0.24	±	0.37
(h)	460.54**	±	138.38	436.99**	±	110.35	-5.04*	±	2.07	2.95	±	1.72
(i)	82.60**	±	28.71	65.93**	±	22.34	-0.66	±	0.38	-0.15	±	0.32
(j)	-171.16*	±	75.78	2.72	±	60.42	-1.31	±	1.29	-0.42	±	1.05
(l)	-980.87**	±	215.93	-788.48**	±	170.37	6.72	±	3.50	-7.27*	±	2.98
(w)	23.17	±	28.88	-15.28	±	23.21	-1.33**	±	0.45	0.14	±	0.36
(x)	-194.65**	±	72.57	-174.18**	±	58.39	1.07	±	1.13	0.36	±	0.93
(y)	155.71*	±	66.89	-35.03	±	56.69	-0.82	±	1.28	-0.36	±	1.00
(z)	654.15**	±	111.01	424.51**	±	83.51	-2.03	±	1.87	5.20**	±	1.70
$\chi^2_{(3)}$ (11df)	113.72**			25.36**			126.15**			91.01**		
Types of epistasis	Duplicate			Duplicate			Duplicate			Duplicate		
Twelve-parameter model (Linked digenic interactions model)												
d	35.33**	±	3.80	-16.82**	±	1.58	-0.02	±	0.06	-0.22**	±	0.07
m+h+l	212.65**	±	5.68	166.51**	±	1.82	49.34**	±	0.09	48.72**	±	0.10
m+i	201.48**	±	3.91	163.29**	±	1.58	49.05**	±	0.06	48.33**	±	0.07
pi	-9.16	±	10.19	12.97	±	7.95	-0.29*	±	0.14	-0.13	±	0.12
p_2i	-47.17**	±	11.47	5.22	±	7.94	-0.82**	±	0.18	-0.14	±	0.15
pj	-73.00**	±	7.43	-4.54	±	4.69	0.60**	±	0.14	-0.44**	±	0.13
p_2j	-48.28**	±	12.54	-20.52*	±	8.18	1.08**	±	0.24	-0.49*	±	0.20
pl	63.56**	±	14.47	-7.65	±	9.24	0.89**	±	0.23	-0.49*	±	0.22
p_2l	67.72**	±	13.11	-2.40	±	8.68	0.29	±	0.20	-0.87**	±	0.19
p_3l	91.20**	±	18.12	-22.79	±	13.11	0.42	±	0.24	-1.22**	±	0.21
p_4l	159.05**	±	22.77	-31.20	±	17.26	1.41**	±	0.26	-1.11**	±	0.22
$\chi^2_{(4)}$ (9df)	129.53**			44.44**			51.41**			81.07**		

x dominance [y] and dominance x dominance x dominance [z] gene effects in cross-1 and 'm', additive x dominance [j] and additive x dominance x dominance [y] in cross-2 (Table 4). The $\chi^2(3)$ value at 11 degrees of freedom was significant in all the (Table 4). The $\chi^2(3)$ value at 11 degrees of freedom was significant in all the traits under study for both the crosses indicating the presence of higher order epistasis and/or linkage.

The twelve-parameter model showed significant estimates for all the gene effects except [pi] in cross-1 and the gene effects *viz.,* d, m+[h]+[l], m+[i] and [p^2j] in cross-2 for seed yield per plant. For oil content, the gene effects *viz.,* m+[h]+[l], m+[i], [pi], [p^2i], [pj], [p^2j], [pl] and [p^4l] in cross-1 and d, m+[h]+[l], m+[i], [pj], [p^2j], [pl], [p^2l], [p^3l] and [p4l] gene effects in cross-2 were significant (Table 1). All the gene effects were found significant in cross-1 and the gene effects *viz*., d, m+[h]+[l], m+[i], [pi], [p^2i], [pj], [p^2j] and [pl] in cross-2 for shelling out turn. For 100-seed weight, the estimates of d, m+[h]+[l], m+[i], [p^2i], [pj], [p^2j], [pl], [p^2l] and [p^3l] gene effects in cross-1 and the gene effects *viz*., d, m+[h]+[l], m+[i], [pi], [p^2i], [pj], [p^2j] and [p^2l] in cross-2 were found significant (Table 2). The gene effects d, m+[h]+[l], m+[i], [pi], [pj], [p^2j], [p^3l] and [p^4l] in cross-1 and the gene effects *viz*., d, m+[h]+[l], m+[i], [p^2i], [p^2j], [p^3l] and [p^4l] in cross-2 were found significant for number of effective branches per plant. For number of capsules on primary raceme, the gene effects *viz*., d, m+[h]+[l], m+[i], [p^2i], [pj], [pl] and [p^2l] in cross-1 and the gene effects *viz*., m+[h]+[i], m+[i], [p^2i], [pl], [p^2l] and [p^4l] in cross-2 were significant (Table 3). The gene effects *viz*., d, m+[h]+[l], m+[i], [p^3l] and [p^4l] were found significant in cross-1 and only four gene effects *viz*., d, m+[h]+[l], m+[i] and [p^2i] were significant in cross-2 for total length of primary raceme and effective length of primary raceme (Table 4). The $\chi^2(4)$ value at 9 degrees of freedom was significant in all the traits under study for both the crosses indicating the presence of higher order linkage.

Table 2. Estimation of gene effects for shelling out turn and 100-seed weight in two crosses of castor

Scaling tests/gene effects	Shelling out turn						100-seed weight					
	JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)			JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)		
Ten-parameter model (Trigenic interactions model)												
m	53.47**	±	1.80	67.98**	±	1.81	30.22**	±	1.25	38.77**	±	0.97
(d)	11.58**	±	2.01	-9.25**	±	2.21	-6.17**	±	1.51	0.85	±	1.28
(h)	67.50**	±	9.35	-6.27	±	9.19	19.65**	±	6.40	-56.94**	±	4.99
(i)	7.26**	±	1.81	-9.23**	±	1.83	0.39	±	1.25	-13.43**	±	0.97
(j)	-0.78	±	5.58	25.29**	±	5.98	13.36**	±	3.82	-7.71*	±	3.30
(l)	-110.36**	±	15.18	8.39	±	14.72	-53.17**	±	10.33	85.08**	±	8.07
(w)	-9.21**	±	1.99	7.19**	±	2.18	8.38**	±	1.49	0.75	±	1.27
(x)	-49.20**	±	5.03	22.95**	±	4.89	8.43*	±	3.41	41.14**	±	2.71
(y)	-14.17**	±	5.42	-23.26**	±	5.61	1.15	±	3.57	14.79**	±	2.97
(z)	53.75**	±	7.85	-6.83	±	7.50	37.07**	±	5.30	-40.07**	±	4.16
$\chi^2_{(3)}$ (11df)	227.03**			297.71**			223.63**			586.47**		
Types of epistasis	Duplicate			Duplicate			Duplicate			Duplicate		
Twelve-parameter model (Linked digenic interactions model)												
d	3.54**	±	0.32	-1.41**	±	0.36	1.65**	±	0.20	1.12**	±	0.16
m+h+l	63.51**	±	0.32	63.06**	±	0.24	32.50**	±	0.22	26.73**	±	0.17
m+i	60.30**	±	0.32	59.49**	±	0.37	32.35**	±	0.21	25.44**	±	0.16
pi	2.33**	±	0.67	2.97**	±	0.68	-0.82	±	0.52	-2.72**	±	0.39
p_2i	3.34**	±	0.82	8.85**	±	0.67	-1.91**	±	0.46	3.14**	±	0.41
pj	4.74**	±	0.63	-2.66**	±	0.66	1.91**	±	0.35	1.09**	±	0.33
p_2j	6.37**	±	1.01	-6.72**	±	0.96	3.08**	±	0.55	3.15**	±	0.54
pl	3.46**	±	0.94	-7.04**	±	0.92	-2.03**	±	0.64	-1.00	±	0.53
p_2l	10.54**	±	0.82	-1.17	±	0.78	-3.69**	±	0.46	-3.28**	±	0.43
p_3l	11.94**	±	1.09	-0.07	±	0.91	-3.30**	±	0.63	-0.91	±	0.55
p_4l	12.39**	±	1.29	-1.12	±	1.16	0.17	±	0.84	-1.27	±	0.67
$\chi^2_{(4)}$(9df)	113.28**			65.06**			357.04**			582.78**		

The present findings are in accordance with previous reports based on investigations done by several researchers in different crops, who also found gene effects in mostly up to the digenic and trigenic interactions. Jatoth et al. (2014) reported significant epistatic gene action for seed yield and its related traits *viz.,* days to 50% flowering, days to maturity, plant height, number of branches per plant, number of capsules per plant in sesame. Sandip et al. (2013) also reported epistasis of additive x additive (aa) and dominance x dominance (dd) in different crosses of sesame in which duplicate type epistasis played a greater role than complementary epistasis. However**,** there is no report on linked digenic interactions in castor so far. Bhapkar and D'cruz (1967) reported that epistasis played a major role in castor beans with high oil content. There are only a few reports on trigenic interactions in castor, however, the results on digenic interactions in other crops have been reported by several researchers (Solanki et al. 2017). Most of the agronomic and economic traits such seed yield, No. of branches, No. of capsules, 1000 seed weight and oil contents are inherited in a quantitative manner. Additive gene effects are important that are determining the number of recemes per plant and seed oil contents (Swarnlata and Rana 1984) and the No. of capsules per primary branch and the seed weight, earliness and plant height have also been shown to be additively inherited in castor (Solanki and Joshi 2000).

Very limited studies on gene effects of oil content in castor (*Ricinus communis* L.) using more number of generations are meagure. Similarly reports on trigenic interactions are also limited but linked digenic interactions have been reported by Solanki et al. (2017) for oil content in cotton. For seed yield and its components trait in castor generally, there is evidence of both [i] and [l] types of interactions but not of the [j] types (few case). Further, the [i] and [l] type 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]

Table 3. Estimation of gene effects for number of effective branches per plant and number of capsules on primary raceme in two crosses of castor.

Scaling tests/gene effects	Number of effective branches per plant						Number of capsules on primary raceme					
	JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)			JM-6 x 48-1 (cross 1)			JI-436 x PCS-124 (cross 2)		
Ten-parameter model (Trigenic interactions model)												
m	8.16**	±	0.83	1.46	±	0.77	74.53**	±	10.72	61.05**	±	4.87
(d)	-5.09**	±	0.89	-3.68**w	±	0.90	13.34	±	12.12	-9.13	±	5.63
(h)	-28.20**	±	4.01	16.61**	±	3.98	156.68**	±	51.91	6.80	±	24.56
(i)	-4.52**	±	0.83	4.17**	±	0.77	40.81**	±	10.73	8.74	±	4.89
(j)	15.00**	±	2.36	11.59**	±	2.33	-74.69*	±	30.29	41.96**	±	14.80
(l)	42.91**	±	6.34	-29.97**	±	6.50	-285.28**	±	80.20	-50.50	±	38.39
(w)	2.82**	±	0.88	2.72**	±	0.89	30.88*	±	12.09	7.42	±	5.60
(x)	15.28**	±	2.00	-10.11**	±	2.12	-144.56**	±	27.55	-33.02*	±	13.50
(y)	-18.28**	±	2.18	-12.45**	±	2.10	146.39**	±	25.27	-55.16**	±	13.34
(z)	-20.05**	±	3.31	16.90**	±	3.49	167.25**	±	40.73	57.03**	±	19.04
$\chi^2_{(3)}$ (11df)	84.61**			74.90**			54.02**			142.38**		
Types of epistasis	Duplicate			Duplicate			Duplicate			Duplicate		
Twelve-parameter model (Linked digenic interactions model)												
d	-1.62**	±	0.13	-0.71**	±	0.12	41.86**	±	0.82	-0.42	±	0.63
m+h+l	2.51**	±	0.17	4.46**	±	0.19	109.47**	±	1.92	73.96**	±	0.56
m+i	3.23**	±	0.13	5.69**	±	0.12	114.98**	±	0.83	70.98**	±	0.64
pi	-1.10**	±	0.28	0.15	±	0.30	3.43	±	3.92	-2.73	±	1.79
p_2i	-0.53	±	0.30	-1.25**	±	0.29	-11.02*	±	4.32	-15.97**	±	1.98
pj	-0.58*	±	0.24	-0.16	±	0.23	-18.33**	±	2.97	1.01	±	1.55
p_2j	-1.59**	±	0.37	-0.99**	±	0.35	-2.17	±	5.48	3.55	±	2.62
pl	0.60	±	0.42	0.62	±	0.44	22.00**	±	5.46	24.01**	±	2.37
p_2l	0.25	±	0.37	-0.13	±	0.35	10.01*	±	4.85	10.44**	±	2.21
p_3l	1.76**	±	0.47	-1.17*	±	0.46	-7.93	±	6.30	2.29	±	2.84
p_4l	2.93**	±	0.59	-1.45*	±	0.58	-10.89	±	7.64	9.81**	±	3.37
$\chi^2_{(4)}$ (9df)	87.16**			77.51**			184.66**			97.24**		

effects (Jinks and Jones 1958). While the sign of [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 two 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). 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 were used in two crosses of castor, it was quite clear 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). 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). 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 two crosses and both were superior over additive [d] gene effects for seed yield and its component traits in two crosses. While comparing linkage v/s non-linkage parameters, it was inferred that absolute totals of non-linkage parameters exceeded 2 to 8 times higher than that of absolute totals of

Table 4. Estimation of gene effects for total length of primary raceme and effective length of primary raceme in two crosses of castor

Scalingtests/gene effects	Total length of primary raceme						Effective length of primary raceme					
	JM-6 x 48-1(cross1)			JI-436 x PCS-124(cross2)			JM-6 x 48-1(cross1)			JI-436xPCS-124(cross2)		
Ten-parameter model (Trigenic interactions model)												
m	38.46**	±	7.26	57.15**	±	4.62	37.37**	±	7.16	54.10**	±	4.37
(d)	12.34	±	8.48	-7.84	±	5.04	7.88	±	8.45	-8.82	±	4.82
(h)	253.18**	±	35.55	-29.30	±	23.10	244.57**	±	35.55	-29.40	±	21.81
(i)	38.55**	±	7.28	0.09	±	4.65	38.26**	±	7.18	0.72	±	4.40
(j)	-60.20**	±	20.65	23.19	±	13.43	-46.50*	±	20.87	27.70*	±	12.82
(l)	-450.23**	±	55.13	56.59	±	36.05	-441.18**	±	55.90	56.66	±	34.17
(w)	2.38	±	8.42	5.21	±	4.99	7.65	±	8.38	6.55	±	4.78
(x)	-117.44**	±	19.30	-2.11	±	12.52	-115.01**	±	19.33	-1.06	±	11.80
(y)	126.31**	±	17.25	-27.80*	±	12.24	111.81**	±	17.82	-33.26**	±	11.54
(z)	255.13**	±	27.77	-33.33	±	18.09	255.10**	±	28.54	-32.54	±	17.33
$\chi^2_{(3)}$(11df)	49.48**			51.32**			51.85**			57.87**		
Types of epistasis	Duplicate			Duplicate			Duplicate			Duplicate		
Twelve-parameter model (Linked digenic interactions model)												
d	10.14**	±	0.84	-2.16**	±	0.72	11.56**	±	0.91	-1.38*	±	0.69
m+h+l	88.28**	±	1.23	52.82**	±	0.74	87.15**	±	1.34	50.74**	±	0.78
m+i	80.56**	±	0.86	56.52**	±	0.74	78.49**	±	0.93	54.04**	±	0.71
pi	1.41	±	2.81	1.42	±	1.59	2.00	±	2.78	0.87	±	1.54
p_2i	-2.22	±	3.04	-5.81**	±	1.74	-2.46	±	3.09	-6.53**	±	1.66
pj	4.09	±	2.28	-1.29	±	1.40	1.34	±	2.35	-2.23	±	1.33
p_2j	3.80	±	3.96	-3.11	±	2.21	-0.05	±	4.03	-4.05	±	2.12
pl	2.99	±	3.87	-0.72	±	2.18	4.63	±	3.94	0.11	±	2.16
p_2l	-1.60	±	3.52	-1.49	±	1.90	-1.49	±	3.59	-1.38	±	1.85
p_3l	-11.39*	±	4.51	-4.61	±	2.46	-12.84**	±	4.55	-3.98	±	2.37
p_4l	-16.79**	±	5.32	-0.83	±	3.12	-17.27**	±	5.27	0.22	±	2.99
$\chi^2_{(4)}$ (9df)	266.65**			44.11**			229.46**			47.77**		

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. Seed yield per plant and its component traits recorded in two crosses of castor were governed by additive, dominance, digenic and trigenic epistasis and/or linked digenic epistasis gene effects along with duplicate type of gene action. Sharmila et al. (2007) reported duplicate epistasis between additive- and dominance-increasing alleles and further elabnorated that the epistatic gene effects may be considered either complementary or duplicate depending on whether the additive x additive and dominance x dominance interactions are all significant and positive/negative or all significant with one negative and the other positive.In the present study non-additive type of gene action was predominant in the inheritance of seed yield and its components traits. Therefore heterosis breeding can be fully exploited in castor for genetic improvement in term of seed yield and its components. 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 for genetic improvement of seed yield and its component traits in castor.

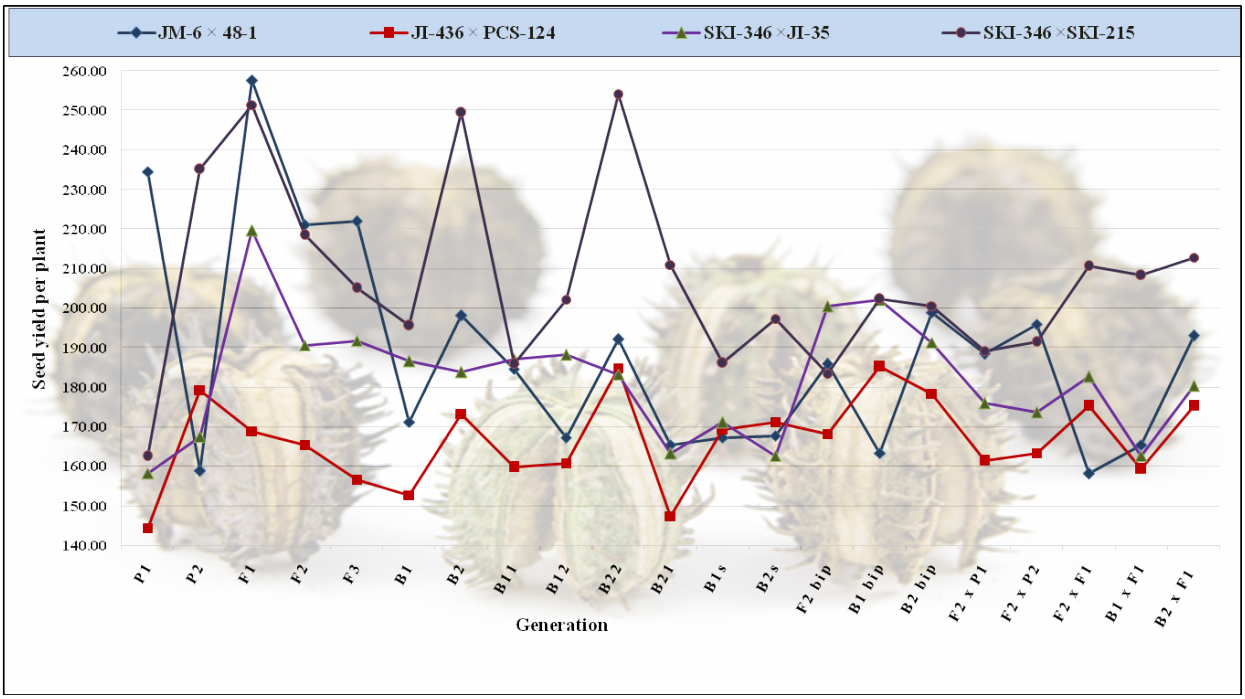

Fig. 1. Trends of 21 generation means for seed yield per plant (g) in castor.

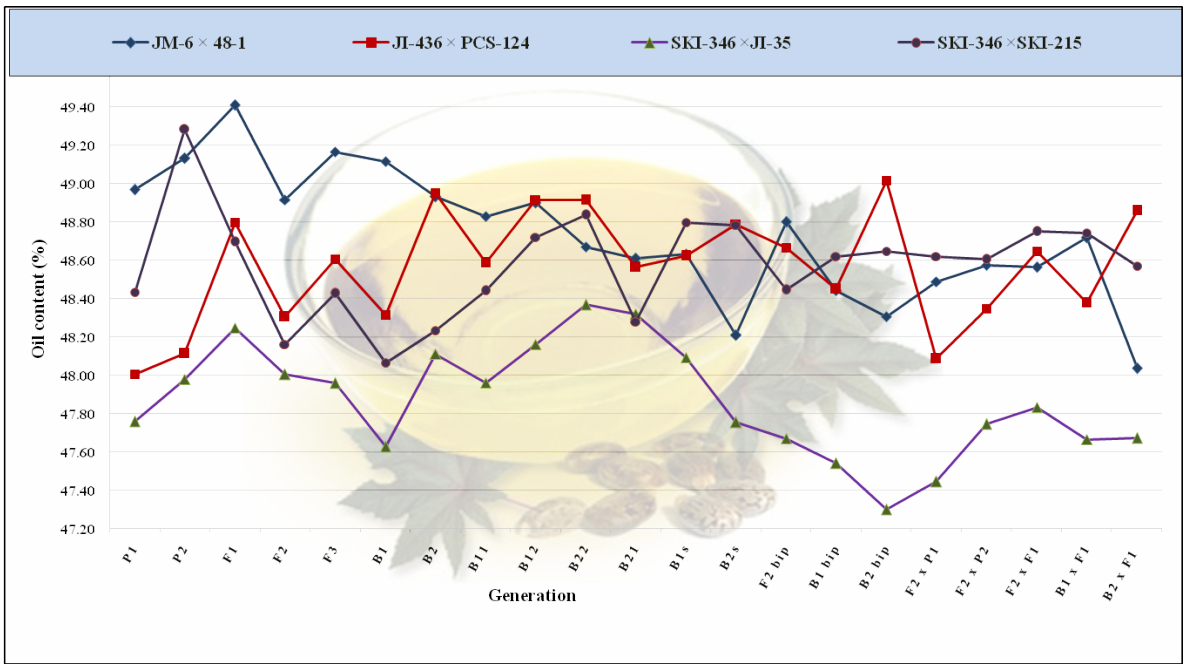

Fig. 2. Trends of 21 generation means for oil content (%) in castor.

Authors' contribution

Conceptualization of research (IRD, RBM); Designing of the experiments (IRD, RBM, AVG); Contribution of experimental materials (IRD, RBM, AVG); Execution of field/lab experiments and data collection (IRD, RBM, AVG); Analysis of data and interpretation (IRD, RBM, AVG); Preparation of the manuscript (IRD, AVG).

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References

Anonymous 2017. Directors Report: Castor Annual Report 2016-2017, pp 19.

Bhapkar D.G. and D'Cruz R. 1967. Inheritance of oil content in Ricinus communis L. Indian J. Genet., **27**: 152-153.

Cavalli L.L. 1952. An analysis of linkage in quantitative inheritance. In "Quantitative Inheritance". Ed. E. C. R. Reeve and C. H. Waddington, HMSO, London. pp. 135-144.

Cockerham C.C. 1959. Partition of hereditary variance for various genetic models, Genetics, **44**: 1141-1148.

Hayman B.I. 1958. The separation of epistatic from additive and dominance variation in generation means. Heredity, **12**(3): 371-390.

Hayman B.I. and Mather K. 1955. The description of genetic interactions in continuous variation. Biometrics, **11**(1): 69-82.

Hill J. 1966. Recurrent back crossing in the study of quantitative inheritance. Heredity, **21**(1): 85-120.

Jatoth J.L., Dangi K.S. and Kumar S.S. 2014. Gene action for quantitative traits through generation means analysis in sesame (Sesamum indicum). Indian J. agric. Sci., **84**: 1369 -1375.

Jinks J.L. and Jones R.M. 1958. Estimation of the components of heterosis. Genetics, **43**: 223-234.

Jinks J.L. and Perkins J.M. 1969. The detection of linked epistatic genes for a metrical trait. Heridity, **24**: 465-475.

Jombog G.T.A. and Enenebeaku M.N.O. 2008. Antibacterial profile of fermented seed extracts of *Ricinus communis* L. Findings from a preliminary analysis. Nigerian J. Physiol. Sci., **23**(1-2): 55-59.

Pujar M., Govindraj M., Gangaprasad S., Kanatti A., Gowda T.H., Dushyantha kumar B.M. and Satish K.M. 2022. Generation mean analysis reveals the predominant gene effects for grain iron and zink content in pearl millet. Front. Plant Sci. doi: 10.3389/fpls2021.693680.

Saribiyik O.Y., Ozcanli M., Serin H., Serin S. and Aydin K. 2010. Biodiesel production from Ricinus communis oil and its blends with soybean biodiesel. Strojniski Vestnik - J. Mech. Engg., **56**(12): 811-816.

Sandip P.A. Desai R.T. and Atul P.B. 2013. Generation Mean Analysis in Sesame (*Sesamum indicum* L.). Indian J. agric. Sci., **6**: 272-276.

Severino Liv S., Auld Dick L., Baldanzi M., Cândido M. J. D., Chen G., Crosby W., Tan D., He Xiaohua, Lakshmamma P. and Lavanya C. et al. 2012. A Review on the challenges for increased production of castor. Agron J.. **104**(4): 853-880. https://doi.org/10.2134/agronj2011.0210

Sharmila V., S. K. Ganesh and M. Gunasekaran. 2007: Generation mean analysis for quantitative traits in sesame (*Sesamum indicum* L.) crosses. Gen. Mol. Biol., **30**: 80-84.

Solanki S.S. and P. Joshi. 2000. Combining ability analysis over environments of diverse pistillate and male parents for seed yield and other traits in castor (*Ricinus communis* L.). Indian J. Genet. Plant Breed., **60**: 201–212.

Solanki H. V., Mehta D. R., Madariya R. B., Rathod V. B. and Odedra R. K. 2017. Genetics of oil content in cotton (*Gossypium hirsutum* L.) using generation mean analysis of 21 generations. J. Pharmaco. Phytochem., **6**(5): 2605-2610.

Sumathi P. and Muralidharan V. 2010. Inheritance of branching and important biometrical traits in sesame (*Sesamum indicum* L.). Indian J. Genet. Plant Breed., **70**: 97-101.

Swarnlata M.V.R.P. and B.S. Rana. 1984. Inheritance of yield and its components in castor. Indian J. Genet. Plant Breed., **44**: 538-543.

Tiwari P.N., Gambhir P.M. and Rajan T.S. 1974. Rapid and non destructive determination of seed oil by pulsed NMR technique. J. American Oil Chem. Soc., **51**: 104-109

Van Der Veen J.H. 1959. Test of non-allelic interaction and linkage for quantitative characters in generations derived from two diploid pure lines. Genetica, **30**: 201-232.