Gene action for quantitative traits through Generation means analysis in sesame (*Sesamum indicum*)

JAWAHAR LAL JATOTH[1], KULDEEP SINGH DANGI[2], and S SUDHEER KUMAR[3]

College of Agriculture, ANGRAU, Rajendranagar, Hyderabad, Andhra Pradesh 500 030

ABSTRACT

Understanding the nature of gene action in the breeding material is helpful for breeders in formulating breeder strategy. In order to understand the type of gene action operating in the breeding materials six generation means (P_1, P_2, F_1, F_2, BC_1 and BC_2) from five crosses were used to estimate the genetic effects of yield and some quantitative traits in sesame (*Sesamum indicum* L.) The analysis showed the presence of additive, dominance and epistatic gene interactions. The additive dominance model was adequate for capsule length in the KMR 108 × JCS 507 and KKS 98049 × IS 562 B crosses. An epistatic digenic model was assumed for the remaining crosses. Duplicate- type epistasis played a greater role than complementary epistasis. The study deciphered that simple additive dominance model exhibited lack of good fit for all the traits in five crosses studied, indicating the role of non-allelic interactions. Dominance and epistatic interactions played a major role in the inheritance of yield and yield contributing characters in sesame. It can be categorically stated that reciprocal recurrent selection or diallel selective mating system are the need of the hour to modify the genetic architecture of sesame for attaining higher yields with desirable oil content.

Key words: Gene effects, Generation mean analysis, Quantitative trait, Scaling tests, Sesame

Sesame (*Sesamum indicum* L.) is one of the oldest oil seed crops known and used by man. Regarded as the "Queen of oil seeds", oil extracted from sesame is among the highly prized few edible oils by virtue of its quality. The antioxidants sesamin and sesmolin increase the oil quality by making it resistant to rancidity. Sesame seed is rich in oil (50-53%) and protein (20-26%) on an average. Sesame oil is semidrying and most stable against oxidative rancidity and used in various industries besides in cooking. The oil is also rich in vitamin-E and contains an essential amino acid methionine (3.4%) (Mosjidis 1982).

Production of sesame hybrids can be accomplished either genetically using the cytoplasmic male sterility system, which have not been yet reported in sesame, or non-genetically by manual emasculation and crossing for the production of hybrids, which is the preferred route due to the fact that sesame has epipetalous stamens. Emasculation is the simplest crossing technique for producing sesame F1 hybrids it might be feasible to use this technique to produce hybrids and obtain a quantum jump in yield with minimal cost. In practice, however, this technique has not contributed much to the current oil seed scenario, with the average sesame productivity in India being practically stagnant

during last few years and not impressive as compared to other sesame growing countries of the world. So the challenge of the Indian sesame breeder is to step up yield through genetic improvement by adopting different breeding methodologies. For genetic improvement of the crop, the breeding method to be adopted depends mainly on the nature of gene action involved in the expression of quantitative trait. Line × Tester (L × T) analysis is used to select the parents based on their combining ability but fails to detect the epistasis, which remains the most complex problem and on which it is extremely difficult to obtain reliable results. The inherent drawback of L × T design is that, it estimates additive and dominance components of gene action only and information on epistasis cannot be estimated which is an integral component of genetic architecture of population. So, information on the presence of type of epistatic genetic efects in the inheritance of various quantitative traits is important for adopting suitable breeding procedures to improve the traits. Generation mean analysis (Hayman 1958) gives a comprehensive picture of gene action controlling the trait. It is relatively a simple first degree statistically analyzed technique to know the predominant genetic effects that are responsible in effecting the variation of character. In this area of generation mean analysis in sesame very little work has been done in India and abroad. Therefore, the present investigation was made with objective to estimate gene action through generation mean analysis.

[1]Scientist (e mail: jawaharlaljatoth@gmail.com), Directorate of Oilseeds Research, Rajendranagar, Hyderabad, Andhra Pradesh 500 030; [2]Professor (e mail: Dangiks404@rediffmail.com), [3]Professor (e mail: sagisudheer@yahoo.com), Department of Genetics and Plant Breeding

MATERIALS AND METHODS

We used sixteen *Sesamum indicum* L. cultivars (IS 1547 A, KKS 98049, PKDS 62, SI 7818, JCS 720, JCS 724, KMR 108, KMR 24, S 0018, CST 2001-5, KMS 5-396, JCS 507, IS 562 B, SI 3171, KMR 78 and TKG 22) collected from different agro morphological regions, India. These selected parents were crossed in L × T fashion to generate 60 hybrids in *kharif* 2007. These 60 crosses along with their parents and checks were evaluated in *rabi* 2007-08. From the above 60 crosses five promising crosses were selected and back crosses were made. F_1s are selfed to produce F_2 during *kharif*, 2008. All the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) were raised in randomized block design (RBD) with three replications in college farm, College of Agriculture, Rajendranagar, Hyderabad during *kharif* 2009-10.

The experiments involved the six basic generations (the P_1 and P_2 parent cultivars, the F_1 and F_2 first and second filial generations, and the BC_1 and BC_2 first and second back crosses) of five combinations of the parental cultivars, these combinations being KMR 108 × JCS 507, KKS 98049 × IS 562 B, S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396. The segregating and non-segregating parental populations were cultivated in a Randomized block design with three replications at the Agricultural College farm, Rajendranagar, Hyderabad, India. We used the parents of the respective crosses as the male parent and the F_1 generation as the female parent and effected back crosses to produce the B_1 (F_1 back crossed to P_1) and B_2 (F_1 back crossed to P_2) generations and the F_1 hybrids were selfed to obtain F_2 seeds. All these generations were produced during two cropping seasons and, as such, all the six generations had to be grown together during the same cropping season. The row-length was always five meters but the number of rows varied as follows: three rows, for the non-segregating P_1, P_2 and F_1; 40 rows for the F_2; and 20 rows for the BC_1 and BC_2 generations. Since the non-segregating generations represent the homogeneous population while the segregating generations represent the heterogeneous population the sample size (*i.e.* number of plants analyzed) varied as follows: 30 plants for the P_1, P_2 and F_1 generations, 400 plants for the F_2 generations and 200 plants in the BC_1 and BC_2 generations. The traits assessed were days to 50% flowering, number of days to maturity, plant height (cm), number of primaries/plant, number of capsules/plant, capsule length (cm), number of seeds/capsule, weight of 1 000 seeds (g), seed yield/plant (g) and oil content (%).

The mean values, standard errors and variances of the different generations were subjected to weighed least-squares analysis using the scaling test (Mather 1949) and the joint scaling test to estimate gene effects. The genetic effects were estimated using the models suggested by Mather and Jinks (1971) and Jinks and Jones (1958). The significance of the scales and gene effects were tested by using the t-test (Singh and Chaudhary 1985).

The A, B and C scaling tests were carried out for eleven traits indicated the presence of non-allelic interactions in almost all cases. The A and B scaling tests provided the evidence for the presence of additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) type gene interactions. The C scaling test provided a test for type l epistasis. The type of epistasis was determined only when dominance (*h*) and dominance × dominance (*l*) effects were significant, when these effects had the same sign the effects were complementary while different signs indicated duplicate epistasis (Kearsey and Pooni 1996).

RESULTS AND DISCUSSION

The mean and standard error of the six generations with four crosses for seven traits are presented in Table 1, with the means values for the scaling joint scaling tests and their interaction effects being presented in Table 2. In general, however, the trait mean values for the F_1 and F_2 generations were higher than the corresponding values for the BC_1 and BC_2 generations, while the values for the F_2 generation were lower than the corresponding values for the F_1 generation. The mean performance of the BC_2 segregating generation was lower than that of the BC_1 generation for all crosses and traits except for days to 50% flowering for the KMR 108 × JCS 507 and KKS 98049 × TKG 22 cross, capsules/plant for the S 0018 × SI 3171 and KKS 98049 × TKG 22, capsule length for the KKS 98049 × IS 562 B and KKS 98049 × TKG 22, 1000 seed weight for the KKS 98049 × IS 562 B and S 0018 × SI 3171, oil content for the S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 and for the seed yield/plant KKS 98049 × IS 562 B, S 0018 × SI 3171 and KKS 98049 × TKG 22 crosses. The expected mean (*m*) of the four possible homozygote's was positive and significant in all the crosses for all the traits.

A simple additive/dominance model was adequate as inferred from the non-significance of all the scales for capsule length in the KMR 108 × JCS 507 and KKS 98049 × IS 562 B crosses. For the remaining crosses, an epistatic digenic interaction was found to be a suitable fit, since the scaling and/or joint scaling tests were significant.

The additive, dominance and epistatic types of gene interaction in each cross for different trait were found to be different from each other. The dominance × dominance (*l*) interaction was larger than the additive × additive (*i*) and additive × dominance (*j*) effects put together, while for the main effects the dominance component (*h*) was greater than the additive (*d*) component. The dominance (*h*) and dominance × dominance (*l*) effects were in the opposite direction, suggesting that duplicate-type epistasis occurred in most cases and indicating predominantly dispersed alleles at the interacting loci (Jinks and Jones 1958). Dominance gene effects were found to be relatively more important, as indicated by the fact that in all cases the dominance (*h*) values were higher than the additive (*d*) values.

The 'days to 50 percent flowering' trait two crosses exhibited highly significant and negative dominance [*h*] genetic effects as well as additive × additive [*i*] interaction effects with higher magnitude except S 0018 × SI 3171,

Table 1   Mean and their standard error of six generations with five crosses for ten   traits

Generation and trait	KMR-108 × JCS-507	KKS-98049 × IS 562 B	S-0018 × SI-3171	KKS-98049 × TKG-22	CST 2001-5 × KMS 5-396
Days to 50 % flowering					
P_1	37.00 ± 0.21	40.00 ± 0.21	40.33 ± 0.12	40.00 ± 0.21	40.66 ± 0.12
P_2	41.00 ± 0.21	41.00 ± 0.21	38.00 ± 0.21	40.66 ± 0.12	38.33 ± 0.33
F_1	39.66 ± 0.12	37.66 ± 0.33	36.00 ± 0.21	37.66 ± 0.33	40.00 ± 0.21
F_2	41.33 ± 0.03	39.00 ± 0.06	37.00 ± 0.06	34.33 ± 0.10	38.00 ± 0.06
B_1	37.33 ± 0.05	39.33 ± 0.05	39.00 ± 0.09	39.33 ± 0.05	40.33 ± 0.05
B_2	40.00 ± 0.09	37.33 ± 0.14	36.66 ± 0.05	40.66 ± 0.05	38.33 ± 0.05
Days to maturity					
P_1	99.33 ± 0.25	93.33 ± 0.12	99.00 ± 0.21	93.33 ± 0.12	94.00 ± 0.21
P_2	93.66 ± 0.33	100.33 ± 0.12	92.66 ± 0.12	95.66 ± 0.12	93.00 ± 0.21
F_1	95.00 ± 0.22	94.00 ± 0.21	95.66 ± 0.25	95.00 ± 0.21	93.00 ± 0.21
F_2	94.66 ± 0.04	94.00 ± 0.06	94.00 ± 0.06	94.00 ± 0.06	94.00 ± 0.06
B_1	95.66 ± 0.05	94.00 ± 0.09	96.00 ± 0.09	96.33 ± 0.05	95.33 ± 0.05
B_2	94.00 ± 0.09	96.66 ± 0.05	96.33 ± 0.05	96.33 ± 0.05	94.66 ± 0.05
Plant height					
P_1	133.37± 1.28	145.95 ± 1.17	145.02 ± 1.03	145.95 ± 1.17	126.19 ± 1.20
P_2	136.07 ± 1.18	140.10 ± 0.74	129.94 ± 0.74	120.20 ± 0.68	134.41 ± 0.81
F_1	135.07 ± 0.84	135.86 ± 1.19	124.10 ± 0.69	124.81 ± 0.91	135.44 ± 1.16
F_2	135.65 ± 0.09	143.01 ± 0.42	118.90 ± 0.23	131.10 ± 0.20	124.07 ± 0.27
B_1	140.24 ± 0.70	141.68 ± 0.57	136.12 ± 0.54	149.94 ± 0.66	142.23 ± 0.33
B_2	139.65 ± 0.47	137.98 ± 0.43	134.56 ± 0.44	126.87 ± 0.48	131.77± 0.39
Primaries per plant					
P_1	6.70 ± 0.26	7.00 ± 0.09	6.46 ± 0.12	7.00 ± 0.09	7.50 ± 0.09
P_2	6.70 ± 0.16	7.00 ± 0.13	6.90 ± 0.06	6.43 ± 0.15	8.03 ± 0.03
F_1	8.96 ± 0.14	8.50 ± 0.10	9.40 ± 0.07	7.43 ± 0.07	6.23 ± 0.05
F_2	9.16 ± 0.04	8.63 ± 0.02	8.16 ± 0.02	7.70 ± 0.02	7.20 ± 0.02
B_1	7.10 ± 0.06	8.20 ± 0.08	8.70 ± 0.02	7.60 ± 0.00	7.70 ± 0.01
B_2	8.50 ± 0.04	8.40 ± 0.02	7.86 ± 0.03	6.73 ± 0.03	7.23 ± 0.04
Capsules per plant					
P_1	135.63 ± 11.36	80.03 ± 1.32	91.36 ± 2.11	80.03 ± 1.32	90.60 ± 1.72
P_2	88.13 ± 1.22	103.83 ± 1.03	121.43 ± 0.94	106.43 ± 2.00	96.33 ± 0.31
F_1	111.93 ± 1.99	121.20 ± 2.23	126.86 ± 1.34	105.16 ± 0.97	98.70 ± 1.37
F_2	114.03 ± 0.35	128.30 ± 0.47	123.73 ± 0.30	116.26 ± 0.26	101.23 ± 0.33
B_1	109.03 ± 0.43	104.16 ± 0.35	116.33 ± 0.40	125.06 ± 0.66	123.30 ± 0.65
B_2	106.53 ± 0.58	96.73 ± 0.35	139.36 ± 0.53	126.96 ± 0.32	104.46 ± 0.51
Capsule length (cm)					
P_1	2.25 ± 0.03	2.60 ± 0.01	2.59 ± 0.07	2.59 ± 0.01	2.73 ± 0.01
P_2	2.38 ± 0.01	2.84 ± 0.07	2.64 ± 0.01	2.67 ± 0.06	2.68 ± 0.06
F_1	2.57 ± 0.03	2.52 ± 0.02	2.65 ± 0.08	2.52 ± 0.00	2.55 ± 0.07
F_2	2.47 ± 0.01	2.48 ± 0.00	2.72 ± 0.01	2.52 ± 0.00	2.61 ± 0.00
B_1	2.45 ± 0.01	2.58 ± 0.01	2.62 ± 0.00	2.57 ± 0.02	2.55 ± 0.01
B_2	2.46 ± 0.00	2.67 ± 0.00	2.57 ± 0.01	2.64 ± 0.00	2.56 ± 0.01
No.of seeds per capsule					
P_1	59.38 ± 0.78	58.07 ± 0.49	73.34 ± 0.88	58.07 ± 0.49	67.29 ± 0.37
P_2	66.73 ± 0.35	62.61 ± 0.48	59.95 ± 0.56	73.52 ± 0.63	70.19 ± 0.73
F_1	55.82 ± 0.33	48.11 ± 0.44	60.54 ± 0.67	60.30 ± 0.72	62.33 ± 0.50
F_2	60.11 ± 0.08	49.59 ± 0.13	58.53 ± 0.19	54.05 ± 0.23	60.88 ± 0.15
B_1	57.40 ± 0.14	52.31 ± 0.43	70.92 ± 0.19	61.16 ± 0.25	65.02 ± 0.13
B_2	64.16 ± 0.18	57.18 ± 0.56	56.43 ± 0.18	67.93 ± 0.23	60.14 ± 0.24
1000 seed weight					
P_1	2.47 ± 0.01	2.67 ± 0.01	2.46 ± 0.02	2.67 ± 0.01	2.94 ± 0.01
P_2	2.46 ± 0.01	2.85 ± 0.06	2.70 ± 0.05	2.91 ± 0.03	2.76 ± 0.04
F_1	2.56 ± 0.02	2.45 ± 0.01	2.61 ± 0.02	2.50 ± 0.01	3.49 ± 0.05
F_2	2.62 ± 0.00	2.51 ± 0.00	2.59 ± 0.01	2.53 ± 0.00	3.57 ± 0.02

(Conitnued)

Table 1 *(Conitnued)*

Generation and trait	KMR-108 × JCS-507	KKS-98049 × IS 562 B	S-0018 × SI-3171	KKS-98049 × TKG-22	CST 2001-5 × KMS 5-396
B_1	2.42 ± 0.00	2.49 ± 0.01	2.38 ± 0.00	2.78 ± 0.01	3.06 ± 0.00
B_2	2.41 ± 0.01	2.52 ± 0.00	2.64 ± 0.00	2.74 ±0.01	2.87 ± 0.00
Oil content (%)					
P_1	44.46 ± 0.05	44.10 ± 0.08	38.40 ± 0.05	44.10 ± 0.08	44.40 ± 0.05
P_2	42.33 ± 0.04	33.46 ± 0.08	48.26 ± 0.08	35.46 ± 0.08	46.26 ± 0.04
F_1	40.63 ± 0.08	39.56 ± 0.07	41.96 ± 0.09	40.50 ± 0.05	40.73 ± 0.13
F_2	41.80 ± 0.02	40.60 ± 0.01	43.26 ± 0.01	38.63 ± 0.00	42.76 ± 0.01
B_1	44.20 ± 0.03	43.36 ± 0.05	40.43 ± 0.02	42.63 ± 0.01	43.36 ± 0.02
B_2	41.86 ± 0.02	37.80 ± 0.02	45.86 ± 0.02	39.23 ± 0.02	44.60 ± 0.03
Seed yield per plant (g)					
P_1	19.14 ± 0.32	11.78 ± 0.31	11.86 ± 0.35	11.78 ± 0.31	14.76± 0.13
P_2	9.08 ± 0.34	9.88 ± 0.12	11.69 ± 0.16	13.00 ± 0.33	9.73 ± 0.17
F_1	12.66 ± 0.16	10.68 ± 0.10	11.76 ± 0.20	10.37 ± 0.17	16.84 ± 0.25
F_2	12.05 ± 0.02	12.12 ± 0.03	9.65 ± 0.07	12.45 ± 0.04	17.48 ± 0.09
B_1	15.52 ± 0.10	9.21 ± 0.12	10.64 ± 0.07	14.68 ± 0.09	12.36 ± 0.09
B_2	9.78± 0.09	10.71 ± 0.17	12.44 ± 0.10	13.51 ± 0.12	13.53 ± 0.09

Table 2   Means ± standard error and scaling test and genetic effects for different sesame traits

Cross	A	B	C	m	[d]	[h]	[i]	[j]	[l]	Epistasis
Days to 50 % flowering										
C_1	*	*	*	49.67 **± 0.31	-2.00**± 0.15	-23.33**± 0.87	-10.67**± 0.27	-0.67**± 0.19	13.33**± 0.61	D
C_2	*	*	NS	43.17**± 0.44	-0.50** ± 0.15	-11.17** ± 1.21	-2.67** ± 0.41	2.50** ± 0.22	5.67** ± 1.00	D
C_3	*	*	*	35.83** ± 0.37	1.17** ± 0.13	4.50** ±0.95	3.33** ± 0.35	1.17 ± 0.17	-4.33** ± 0.72	D
C_4	*	*	*	17.67 ** ± 0.45	-0.33 * ± 0.13	46.67 ** ± 1.07	22.67** ± 0.44	-1.00** ± 0.15	-26.67** ± 0.88	D
C_5	NS	*	*	34.17** ± 0.36	1.17** ± 1.18	9.50** ± 0.91	5.33** ± 0.31	0.83** ± 0.19	-3.67** ± 0.70	D
Days to maturity										
C_1	*	NS	*	95.83**± 0.34	2.83 **± 0.20	-3.83 **± 0.99	0.67*± 0.27	-1.17**± 0.24	3.00 **± 0.76	D
C_2	*	*	*	91.50**± 0.35	-3.50 **± 0.09	7.50** ± 0.91	5.33** ± 0.35	0.83**± 0.14	-5.00**± 0.70	D
C_3	*	*	*	87.17**± 0.37	3.17** ± 0.13	18.83**± 0.96	8.67** ± 0.35	-3.50** ± 0.17	-10.33**± 0.76	D
C_4	*	*	*	85.17**± 0.32	-1.17**± 0.09	25.50**± 0.79	9.33** ± 0.31	1.17**± 0.12	-15.17**± 0.62	D
C_5	*	*	*	89.50**± 0.35	0.50**± 0.15	14.50** ± 0.87	4.00** ±0.31	0.17 ± 0.17NS	-11.00** ± 0.67	D
Plant height										
C_1	*	*	*	154.21 **± 1.94	-1.34 ± 0.87NS	-37.34**± 5.81	-19.49 *± 1.73	9.13**± 1.21	18.78 **± 4.17	D
C_2	NS	NS	*	155.76**± 2.34	2.92**± 0.69	-31.08**± 6.12	-12.73 **± 2.24	0.77 ± 1.00 NS	11.18 *± 4.34	D
C_3	NS	*	*	71.72**± 1.80	7.54**± 0.64	136.36**± 5.04	65.77**± 1.69	-5.98± 0.95	-83.97**± 3.52	D
C_4	*	*	*	103.84** ± 1.97	12.87** ± 0.68	88.06**± 5.68	29.23**± 1.85	10.20**± 1.07	-67.09**± 4.09	D
C_5	*	*	*	78.59**± 1.67	-4.11**± 0.73	125.10**± 4.52	51.72**± 1.50	14.57 **± 0.89	-68.25 **± 3.60	D
Primaries per plant										
C_1	*	*	*	12.17 **± 0.28	6.55**± 0.13	-8.80**± 0.76	-5.47**± 0.23	-1.40**± 0.17	5.60**± 0.55	D
C_2	*	*	*	8.20 **± 0.21	-	1.43* ± 0.61	-1.20 **± 0.19	-0.13± 0.12 NS	-1.13*± 0.44	D
C_3	*	*	*	6.21**± 0.15	-0.22** ± 0.07	4.62* ± 0.40	0.47**± 0.13	1.05**± 0.08	-1.43 **± 0.29	D
C_4	*	*	*	8.85**± 0.15	0.28**± 0.09	-3.18**± 0.40	-2.13**± 0.12	0.58**± 0.10	1.77**± 0.29	D
C_5	*	NS	*	6.70**± 0.14	-0.27**± 0.05	2.47**± 0.38	1.07**± 0.13	0.73**± 0.07	-2.93**± 0.26	D
Capsules per plant										
C_1	*	*	NS	136.88 **± 6.07	23.75 **± 5.71	-66.45 **± 18.03	-25.00**± 2.04	-21.25**± 5.76	-41.50**± 12.53	C
C_2	*	*	*	203.33**± 2.31	-11.90**± 0.84	-218.00** ± 5.92	-111.40**± 2.16	19.33**± 0.98	135.87 **± 5.52	D
C_3	*	*	*	89.93**± 2.16	-15.03**± 1.16	98.27** ± 6.02	16.47**± 1.83	-8.00** ± 1.33	-61.33**± 4.62	D
C_4	*	*	*	54.23**± 2.19	-13.20**± 1.20	197.20**± 6.18	39.00**± 1.83	11.30**± 1.41	-146.27**± 4.41	D
C_5	*	*	*	42.87**± 2.32	-2.87**± 0.88	177.63**± 6.43	50.60**± 2.15	21.70**± 1.21	-121.80**± 4.87	D
Capsule length										
C_1	NS	NS	NS	2.37**± 0.03	-0.07**± 0.02	0.19*± 0.09	-0.05*± 0.02	0.05**± 0.02	0.01± 0.086NS	C
C_2	NS	NS	*	2.12 **± 0.05	-0.12 **± 0.04	1.04 **± 0.14	0.60**± 0.03	0.04 ± 0.04 NS	-0.64 **± 0.11	D

(Conitnued)

Table 2 *(Conitnued)*

Cross	A	B	C	m	[d]	[h]	[i]	[j]	[l]	Epistasis
C_3	NS	NS	NS	3.11**± 0.06	-0.02± 0.03 NS	-1.09**± 0.18	-0.49**± 0.53	0.07± 0.04NS	0.64**± 0.19	D
C_4	NS	NS	*	2.29**± 0.06	-0.04± 0.03 NS	0.69**± 0.17	0.35**± 0.05	-0.02 ± 0.04NS	-0.46**± 0.11	D
C_5	*	NS	NS	2.92 **± 0.06	0.03 ± 0.03 NS	-0.87**± 0.17	-0.21**± 0.04	-0.03± 0.04 NS	0.51**± 0.18	D
Number of seeds per capsule										
C_1	NS	*	*	59.50**± 0.72	-3.67**± 0.43	6.14 **± 2.05	3.56 **± 0.58	-3.54*± 0.49	-9.82 **± 1.48	D
C_2	NS	*	*	39.70 **± 1.56	-2.27 **± 0.35	31.15 ** ± 4.55	20.64**± 1.53	-2.60 **± 0.79	-22.73 **± 3.10	D
C_3	*	*	*	46.05**± 1.08	6.70**± 0.53	35.43**± 2.82	20.60**± 0.94	7.79**± 0.59	-20.93**± 2.16	D
C_4	*	NS	*	23.80**± 1.24	-7.73** ± 0.40	84.50**± 3.13	41.99**± 1.17	0.96± 0.53NS	-48.00**± 2.35	D
C_5	NS	*	*	62.42**± 0.92	-1.95**± 0.41	-6.09 *± 2.45	6.82**± 0.82	6.83**± 0.50	5.10**± 1.82	D
1000 seed weight										
C_1	*	*	*	3.29**± 0.03	0.00± 0.01NS	-1.94**± 0.07	-0.81**± 0.02	0.01± 0.01NS	1.22**± 0.07	D
C_2	*	*	*	2.79**± 0.05	-0.09**± 0.03	-0.75**± 0.15	-0.02 ± 0.04 NS	0.06 ± 0.04 NS	0.41 **± 0.11	D
C_3	*	NS	*	3.07**±0.06	0.03± 0.03NS	-1.44**± 0.14	-0.34**± 0.05	-0.29**± 0.03	0.68**± 0.10	D
C_4	*	NS	*	1.88**± 0.05	-0.12**± 0.02	1.10**± 0.14	0.92**± 0.04	0.16**± 0.03	-1.36**± 0.09	D
C_5	*	*	*	5.25**± 0.10	0.09**± 0.02	-4.95**± 0.21	-2.39**± 0.09	0.10**± 0.02	-3.19**± 0.16	C
Oil content (%)										
C_1	*	*	*	38.72 **± 0.13	1.32**± 0.04	10.42**± 0.34	4.93**± 0.12	1.02**± 0.06	-8.50**± 0..27	D
C_2	*	*	*	38.85**± 0.16	5.32 **± 0.06	6.28 **± 0.46	-0.07 ± 0.015 NS	0.25 **± 0.09	-5.57 **± 0.33	D
C_3	*	*	*	43.80 **± 0.11	-4.93 **± 0.05	-0.30 ± 0.31NS	-0.47 **± 0.09	-0.50**± 0.06	-1.53 **± 0.27	C
C_4	*	*	*	30.58**± 0.09	4.32**± 0.06	22.28**± 0.28	9.20**± 0.07	-0.92**± 0.07	-12.37**± 0.21	D
C_5	*	*	*	40.47**± 0.11	-0.93**± 0.04	8.93**± 0.33	4.87**± 0.11	-0.30**± 0.06	-8.67**± 0.33	D
Seed yield per plant (g)										
C_1	NS	*	*	11.71**± 0.38	5.03**± 0.24	0.41 ± 1.12NS	2.40**± 0.30	0.71**± 0.27	0.53 ± 0.81NS	C
C_2	*	*	*	19.49 **± 0.49	0.95**± 0.17	-20.62**± 1.43	-8.65 **± 0.46	-2.45 **± 0.27	11.82 **± 0.97	D
C_3	*	*	*	4.24**± 0.43	0.08± 0.19NS	14.14**± 1.12	7.54**± 0.38	-1.88 **± 0.23	-6.61 **± 0.81	C
C_4	*	*	*	5.91**± 0.42	-0.60*± 0.23	21.72**± 1.22	6.48** ± 0.35	1.75**± 0.28	-17.25**± 0.87	C
C_5	*	NS	*	30.39**± 0.47	2.51**± 0.11	-38.07**± 1.17	-18.14**± 0.46	-3.69**± 0.17	24.53**± 0.85	D

Key: C_1 = KMR-108 × JCS-507; C_2 = KKS-98049 × IS 562 B; C_3 = S-0018 × SI-3171; C_4 = KKS-98049 × TKG-22; C_5 = CST 2001-5 × KMS 5-396; *m* = mid point; [d] = additive; [h] = dominance; [i] = additive × additive; [j] = additive × dominance; [l] = dominance × dominance; (*) indicates the value was significant by the t-test at the 5% probability level, D & C = Duplicate and Complementary type epistasis.

KKS 98049 × TKG 22, CST 2001-5 × KMS 5-396 which had positively significant effects. Additive × dominance [*j*] effects were significant and negative in all the crosses except in KKS 980489 × IS 5462 and CST 2001-5 × KMS 5-396, dominance × dominance [*l*] interaction effects were positive and significant in two crosses studied except in S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 which had negative and significant effect. For this trait additive (*d*), dominance (*h*) and dominance × dominance (*l*) gene interaction were found to play a major role. Duplicate type of epistasis for this traithas also been reported by Pathak and Dixit (1998).

For the number of days to maturity trait the dominance [*h*] effects were predominantly significant and positive in case of KKS 98049 × IS 562 B, S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396, while the other cross (KMR 108 × JCS 507) had negative significant [*h*] effect. Among the interaction effects positive and significant effects were noticed for additive × additive[*i*] type for all the crosses under study. For additive × dominance [*j*], negative significant values were seen in case of KMR 108 × JCS 507 and S 0018 × SI 3171 but positive and

significant values were found in combinations of KKS 90849 × IS 562 B and KKS 98049 × TKG 22. The dominance × dominance [*l*] effects were negative and significant in four crosses, viz. KKS 98049 × IS 562 B, S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 positive significant values of [*l*] effect was observed with the other cross. In four crosses the dominance [*h*] and dominance × dominance [*l*] effects were operating in opposite direction. Duplicate epistasis for this trait had been reported by Pathak and Dixit (1988).

In case of the 'plant height' trait the additive [*d*] genetic effects were significant in cross combinations of KKS 98049 × IS 562 B, S 0018 × SI 3171 and KKS 98049 × TKG 22, whereas the remaining one cross had negative significant [*d*] effect and another one cross had significant effect. All the crosses except KMR 108 × JCS 507 and KKS 98049 × IS 562 B recorded highly significant and positive dominance [*h*] effects. The interaction additive × additive [*i*] effects were positively significant for three crosses, and negatively significant in respect of KMR 108 × JCS 507 and KKS 98049 × IS 562 B. Positively significant additive × dominance [*j*] effects were observed for the crosses *viz.,*

KMR 108 × JCS 507, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 the remaining two crosses found to be non-significant. The crosses S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 were recorded highly significant and negative dominance × dominance [*l*] effects, the positively significant [*l*] effects were observed in KMR 108 × JCS 507 and KKS 98049 × IS 562 B. The trait showed duplicate type of epistasis in all crosses. Ganesh and Sakila (1999) reported duplicate epistasis for this trait.

In regard to number of capsules per plant, additive[*d*] genetic effects were significant and negative in four crosses, viz. KKS 98049 × IS 562B, S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 and rest of the one cross had positive effect. Except KMR 108 × JCS 507 and KKS 98049 × IS 562 B, all the crosses were observed with highly significant and positive dominance [*h*] genetic effects. The magnitude of dominance [*h*] effects were found to be relatively more important because of the dominance values were higher than additive (*d*) in all the five crosses. Non-allelic additive × dominance (*j*) and dominance × dominance (*l*) interactions and duplicate type epistasis were observed for this trait. Deenamani and Dorauraj (1994) reported duplicate epistasis for this trait. Additive × dominance [*j*] epistatic effects were negatively significant in two crosses and positively significant in three crosses of KKS 98049 × IS 562 B, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396. The dominance × dominance effects was negatively significant in three crosses, i.e S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396. The rest two crosses were positively significant.

The number of effective primaries per plant KMR 108 × JCS 507 and KKS 98049 × TKG 22 recorded significant and positive and the other three crosses had negative additive [*d*] genetic effects. Significant and negative dominance [*h*] effects were recorded in KMR 108 × JCS-507 and KKS 98049 × TKG 22, While in case of KKS 98049 × IS 562 B, S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 significant and positive [*h*] effects were observed. Among the interaction effects significant and positive dominance × dominance [*l*] effects were expressed in KMR 108 × JCS 507 and KKS 98049 × TKG 22 and negatively significant effects were observed in KKS 98049 × IS 562 B, S 0018 × SI 3171 and CST 2001-5 KMS 5-396 with higher magnitude (Table 2). Additive × additive [*i*] effects were negative and significant in all the crosses except to S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 where the effects were positively significant. The additive × dominance [*j*] effects were positively significant for all the crosses studied and negatively significant in KMR 108 × JCS 507. The direction for dominance [*h*] and dominance × dominance [*l*] genetic effects were opposite for all the crosses studied. Duplicate type of epistasis was also reported for this trait by Kumar *et al.* (1998).

In case of capsule length the Predominant role of dominance [*h*] effects were observed for all the crosses, but S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 exhibited

negative and significant effects. The Additive × additive effects were negative and significant in case of KMR 108 × JCS 507, S 0018 × SI 3171 and CST 2001-5 × KMS 5-396, while the remaining crosses showed positively significant effects. Additive × dominance [*j*] was non-significant in case of KKS 98049 × IS 562 B, S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 and the remaining cross showed positively significant effect. The entire cross combinations expressed negative and significant dominance × dominance [*l*] effects and was positive in case of S-00187 × SI-3171 and CST 20001-5 × KMS 5-396. The direction of genetic effects, viz. dominance [*h*] and dominance × dominance [*l*] was opposite for all the crosses studied.

For number of seeds per capsule dominance [*h*] effects were positive and significant in case of KMR 108 × JCS 507, KKS 98049 × IS 562 B, S 0018 × SI 3171 and KKS 98049 × TKG 22 whereas, CST 2001-5 × KMS 5-396 exhibited significant but negative [*h*] effects. Among the epistatic interaction effects, additive × additive [*i*] genetic effects were positively significant in all the crosses studied. Additive × dominance [*j*] effects were positive and significant in cross combinations of S-0018 × SI-3171 and CST 2001-5 × KMS 5-396. Positive and significant dominance × dominance [*l*] effects were noticed with CST 2001-5 × KMS 5-396 and the remaining crosses exhibited significant negative [*l*] effects. The direction of genetic effects, viz. dominance [*h*] and dominance × dominance [*l*] was opposite for all the crosses indicating duplicate gene action.

The 'weight per 1000 seeds' trait the crosses S-0018 × SI 3171 and KMR 108 × JCS 507 had non-significant additive [*d*] genetic effects, while two crosses had significant negative, one cross has positive significant effect. Dominance [*h*] effects were negative and significant in KMR 108 × JCS 507, KKS 98049 × IS 562 B, S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 the remaining cross had positively significant effect. The magnitude of dominance effects was more than additive effects. The additive × additive [*i*] interaction effects were negative and significant for KMR 108 × JCS 507, S 0018 × SI 3171 and CST 2001-5 × KMS 5-396 and the remaining crosses had positively significant [*i*] effects. Dominance × dominance [*l*] effects were positively significant in case of KMR 108 × JCS 507, KS 98049 × IS 562 B and S 0018 × SI 3171. Additive × dominance [*j*] effects were positively significant for KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 and two crosses had non-significant and one cross had significant positive effect. The dominance [*h*] genetic effects and dominance × dominance [*l*] interaction effects were operating in opposite direction for all the crosses, except for the cross CST 2001-5 × KMS 5-396. The *d*, *h* and additive × additive (*i*) type gene interactions indicate that this trait is under the control of both fixable and non-fixable gene effects. The additive × additive (*i*) type gene interaction and duplicate epistasis seen in this trait suggest the possibilities of obtaining transgressive segregants in later

generations.

With regards to 'oil content' trait the significant positive additive [d] genetic effects were observed in the crosses, viz. KMR 108 × JCS 507, KKS 98049 × IS 562 B and KKS 98049 × TKG 22. The remaining crosses had negative and significant [d] effects. Dominance [h] effects were significant and positive in KMR 108 × JCS 507, KKS 98049 × IS 562 B, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396. Additive × additive effects were positive and significant in KMR 108 × JCS 507, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396. Three crosses S 0018 × SI 3171, KKS 98049 × TKG 22 and CST 2001-5 × KMS 5-396 were recorded negatively and the remaining crosses were positively significant for additive × dominance [j] interaction effects. Among the five crosses studied all of them recorded negatively significant dominance × dominance[l] genetic effects. The dominance [h] and dominance × dominance [l] effects were found to be in opposite direction for oil content, except for S 0018 × SI 3171 which indicates the complementary type of epistasis in the expression of this trait.

For 'seed yield per plant' trait the additive [d] genetic effects were positive and significant in KMR 108 × JCS 507, KKS 98049 × IS 562 B and CST 2001-5 × KMS 5-396 where as in case of KKS 98049 × TKG 22 the [d] effect was negative and significant. The dominance [h] effects were significant and positive in case of S 0018 × SI 3171 and KKS 98049 × TKG 22 and the remaining crosses observed with negative values. Among the three epistatic effects additive × additive[i] were positive and significant in KMR 108 × JCS 507, S 0018 × SI 3171 and KKS 98049 × TKG 22 and negatively significant in KKS 98049 × IS 562 B and CST 2001-5 × KMS 5-396. Three crosses recorded significant and negative additive × dominance [j] effects except KMR 108 × JCS 507 and KKS 98049 × TKG 22 where the effects were positive and significant. The dominance × dominance [l] effects were positively significant in KKS 98049 × IS 562 B and CST 2001-5 × KMS 5-396 and negatively significant in S 0018 × SI 3171 and KKS 98049 × TKG 22, while the remaining cross had non-significant effect. These results indicates that seed yield per plant is predominantly controlled by dominance × dominance (l) type interaction effects. The dominance (h) and dominance × dominance (l) gene effects showed opposite signs, indicating the presence of duplicate dominant epistasis in the expression of this trait.

A additive × dominance (j) type interaction was observed for the 'number of capsules per plant' and 'seed yield per plant' traits and the h gene effect was found to be predominant in the expression of these traits. These findings are in good agreement with those of Deenamani and Dorairaj (1994) for the 'number of capsules per plant' trait and with Ganesh and Sakila (1999) for the 'seed yield per plant' trait, who also reported duplicate epistasis for this trait.

The additive effects and gene interaction dominance × dominance (l) or other type digenic complementary gene interaction can be exploited effectively by selection for the improvement the characters. Use of reciprocal recurrent selection or Bi-parental mating suggested improving the characters when both additive and non- additive gene effects are involved in the expression of these traits. Presence of non-additive gene for days to 50 percent flowering, effective primaries/plant, number of capsules/plant, 1000 seed weight, oil content and seed yield/plant indicating that conventional selection procedure may not be effective enough for improvement of yield. Therefore postponement of selection in later generations or intermating among the selected segregants followed by one or two generations of selfing could be suggested to break the undesirable linkage and allow the accumulation of favorable alleles for the improvement of this trait.

The different types of gene effects estimated provided a test for gene action and are useful for analyzing the genetic architecture of a crop so as to further improve desirable traits. The estimates obtained from each cross may be unique to that cross and may not be applicable to the parental population. Additive genetic variance formed the major part of the genetic variance for the important yield component 'weight per 1000 seeds' trait. Therefore genetic improvement in the 'seed yield per plant' trait would be easier through indirect selection for a component trait such as the 'weight per 1000 seeds' trait than through direct selection for seed yield itself.

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