

GENERATION MEANS ANALYSIS FOR SOME QUANTITATIVE TRAITS IN SESAME (*SESAMUM INDICUM* L.) CROSSES FROM ETHIOPIA

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ABSTRACT: The nature of gene action governing the expression of various traits is very helpful in formulating an effective and sound breeding program. The objective of the present study was to determine the type and magnitude of gene action in sesame using generation means analysis to provide a basis for an evaluation of selection methods for the improvement of sesame. The six basic generations parent 1 (P_1), parent 2 (P_2), hybrid (F_1), F_2 , back cross 1 (BC_1) and back cross (BC_2) of five crosses such as cross-1 (EW002 x BG006), cross-2 (Dicho x EW006), cross-3 (EW002 x Dicho), cross-4 (Obsa x Dicho) and cross-5 (EW002 x Obsa) were planted in 2012 and 2013 at Uke trial site of Bako Agricultural Research Center in a randomized complete block design, with three replications. The combined analysis of variance indicated highly significant differences among generations for all the traits in all crosses. Simple additive-dominance model exhibited lack of good fit for all the characters studied in all the crosses, except days to maturity in cross 2. The result of the generation means analysis showed that days to flowering, plant height, branches per plant, and capsules per plant and yield per plant were found to be under the control of additive and non-additive gene effects, coupled with duplicate type of epistasis. Biparental mating followed by selection of desired recombinants from the segregating population is the most applicable breeding methodology for traits under the influence of duplicate type of epistasis. Complementary type of epistasis was only observed for plant height in cross 1 and capsules per plant in cross 3, which appeared to be desirable and would be helpful in further improvement of these traits.

Key words/phrases: Gene effects, Generation mean, Non-allelic interaction, scaling test, Sesame

INTRODUCTION

Sesame (*Sesamum indicum* L.) is a self-pollinated crop and it is one of the major oilseeds crop in Ethiopia. In terms of export earning, its contribution is second after coffee, accounting for over 90% of the value of oilseeds exports (Zerihun, 2012). At international market the demand for sesame from Ethiopia is high (Rutes *et al.*, 2015). This recalls that the increase in productivity of sesame can greatly contribute to the economic development of the country. In Ethiopia, the present sesame varieties under cultivation have less than 1 tone ha⁻¹ yield whereas its potential goes up to 2 tonnes ha⁻¹ (Wijnands *et al.*, 2007).

Knowledge of the way genes act and interact will determine which breeding system can optimize gene action more efficiently and will

help elucidate the role of breeding systems in the evolution of crop plants (Hallauer and Miranda, 1988). Gamble (1962) indicated that the estimates of genetic effects can help the plant breeders to decide the breeding procedures better suited for the improvement of the trait being analyzed.

Most of the earlier studies conducted on nature and magnitude of genetic variation in sesame were based on diallel, partial diallel, general combining ability and specific combining ability analysis with the assumption that the epistasis is negligible or absent (Ahmed and Adam, 2014). The results of different studies indicated that epistasis plays a significant role in the inheritance of yield and its component characters in sesame (Sandip *et al.*, 2013). Thus, the assumption of absence of epistasis may not hold true, suggesting that some breeding methods may not be appropriate for the genetic improvement of

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important quantitative traits, such as yield and its components.

Generation means analysis provides information on the relative importance of average effects of the genes (additive effects, dominance deviation and effects due to non-allelic genetic interaction) in determining genotypic values of the individual and consequently mean genotypic values of families and generations (Viana, 2000). Besides, it is breeder's interest to know how much of the variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment and interactions between genotypes and environments. It is possible to use basic generations to provide powerful tests of the adequacy of a simple genetic model and in particular, complex effects such as epistasis, maternal effects, etc (Kearsey and Pooni, 2004).

Several models have been developed for analysis of generation means as described by Hayman (1958) and Gamble (1962). Procedures used to estimate means and variance of quantitative traits were proposed by using six basic generations, which included parents (P_1 and P_2), F_1 , F_2 and first two backcrosses (BC_1 and BC_2). Additive (a) and dominance (d) are parameters of gene actions for additive-dominance model. The presence or absence of epistasis can be detected by analysis of generation mean using the scaling test, which measures epistasis accurately whether it is complementary (additive \times additive) or duplicate (additive \times dominance) and (dominance \times dominance) at digenic level.

Ethiopia is considered as the center of origin for sesame and the genetic diversity is high (Daniel and Parzies, 2011; Ahadu Menzir, 2012), which indicates that there is still scope to increase yield potential of varieties through genetic improvement in parental stock. With this context, the present investigation was designed to determine the type and magnitude of gene action in sesame using generation means analysis to provide a basis for an evaluation of selection methods for the improvement of sesame.

MATERIALS AND METHODS

Three elite breeding lines (EW002, BG006 and EW006) and two improved sesame varieties (Obsa and Dicho) were used. Obsa and Dicho were released for high rainfall western Ethiopia

and similar agro ecologies for their high seed yield and bacterial blight resistance. Plant characters already recorded for the parents by oil crops improvement team of Bako Agricultural Research Center (BARC) was used as basic information for this study. Five crosses viz., EW002 \times BG006, Dicho \times EW006, EW002 \times Dicho, Obsa \times Dicho and EW002 \times Obsa were effected in 2010 by hand emasculation and pollination. Back crosses were made to produce the BC_1 (F_1 back crossed to P_1) and BC_2 (F_1 back crossed to P_2) generations and the F_1 hybrids were self-pollinated to obtain F_2 seeds.

The present investigation was carried out during main season of 2012 and 2013 at Uke testing sites of BARC (1383 m.a.s.l). The experimental material consisting of six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of the five crosses were planted in a randomized complete block design with three replications. The plot size comprised three rows each for P_1 , P_2 and F_1 , 12 rows each for BC_1 and BC_2 and 18 rows each for F_2 . Each row was 5 m long with row spacing of 50 cm and a distance of 25 cm between plants within row. The seed rate was 5 kg ha⁻¹ and 50 kg ha⁻¹ urea was applied at knee stage of the plant. Six characters viz., days to flowering, days to maturity, plant height (cm), branches per plant, capsule per plant and yield per plant (g) were recorded on sampled plants from each plot of P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 generations. The average value per plant was computed for further statistical analysis. For days to flowering, days taken to initiate flowering in 50 per cent of the sample plants was recorded. Days taken to mature in 90 per cent of individuals within the sample plants were taken as days to maturity. For plant height, the distance from ground level up to the terminal bud on main axis of a plant at maturity in centimeters was recorded. The total number of branches bearing capsules per plant were counted and recorded at maturity. Total number of seed bearing capsules on each plant including those on main stem and primary branches were counted and recorded. Yield of cleaned seeds averaged over sampled plants per treatment was recorded in grams. For each trait the parent with a higher mean value was considered as parent one (P_1) and the parent with the lower mean value was considered as parent two (P_2) according to the method suggested by Kearsey and Pooni (2004).

Combined analysis of variance (ANOVA) was carried out with SAS version 9.0 (SAS Institute),

using the GLM procedure. All the crosses showed significant differences among the entries for all characters and were subjected to generation mean analysis for the estimation of gene effects. The scaling tests as described by Hayman and Mather (1955) were used to check the adequacy of the additive-dominance model for different characters in each cross. The test of first condition provides information regarding the absence or presence of gene interaction.

The A, B and C scaling tests were made using the following equations for their values and variances (see Table 1). The A, B and C scaling tests failed to explain the variation in generation means. Therefore, the data was further subjected to the three-parameter model viz., (m), (a) and (d) of joint scaling test procedure as suggested by Cavalli (1952). The joint scaling test estimated the effects of the genetic parameters by procedure of weighted least squares using the inverse of the variance of each generation mean as weight following procedure developed by Kearsey and Pooni, 2004. All chi-square (χ^2) values were significant for these traits in all crosses, except days to maturity (cross 2), indicating the inadequacy of additive dominance model. Consequently, the joint scaling test described by Kearsey and Pooni (2004) was used to obtain estimates and standard errors for the six parameters model (see Table 2). The coefficients of the six parameters are given in Table 3. The test of significance of the gene effects was performed by comparing the calculated values of 't' with tabulated values of 't' at 5 per cent (1.96) and 1 per cent (2.58) levels of significance.

RESULTS AND DISCUSSION

The mean sum of squares indicated significant differences among the generations of all the five crosses for each of the traits except branches per plant in cross 5 (Table 4). This indicated sufficient diversity among the materials under study and comparison among themselves. The mean and standard error of the six generations of five crosses are presented in Table 5. The parents generally exhibited variable performance and none of them proved to considerably did well for all characters. However, parent Obsa was good for branches per plant, capsule per plant and yield per plant. This type of parent with multiple desirable traits may be of great value in sesame crossing program. The hybrid EW002 x Dicho exhibited the top performance for capsules per

plant and yield per plant. It is interesting to note that the best hybrids for yield, yield components parent Dicho was involved, and this may suggest the value of this parent for use in yield improvement program. The hybrid for capsules per plant and yield per plant were better than their respective parents in all crosses except cross EW002 x BG006 and this revealed the presence of heterosis.

The scaling tests revealed the presence of epistasis or non-allelic gene interactions for all the characters in the different crosses except days to maturity for cross 2 (Table 6). Moreover, chi-square (χ^2) values for the simple additive-dominance model showed significant differences for the traits in all crosses, confirming the presence of non-allelic gene interactions (Table 7). This led to fitting the data to the six parameters model of joint scaling to accommodate epistasis for these traits.

Estimates of genetic effects from generation mean analysis according to a six parameter model for all studied traits were presented in Table 8. The estimates of mean (m) were highly significant for all the traits studied in all crosses, showing that the six generations significantly differed from each other. Days to flowering (cross 2), days to maturity and plant height (cross 4), capsules per plant (cross 1 and 3) and yield per plant (crosses 1 and 3) exhibited significant differences for all tested six parameters, suggesting the presence of linkage or higher order epistatic interactions. Arun (2013) also reported similar result for these traits in sesame.

The additive (a) gene effects were found to be significant and positive for days to maturity (crosses 2, 3, and 4), plant height (crosses 4 and 5), branches per plant (cross 3), capsules per plant (crosses 3 and 4), yield per plant (crosses 3, 4 and 5), suggesting the potential for obtaining further improvement of these traits by using pedigree breeding. Sumathi and Muralidharan (2014) reported additive action for days to flowering, days to maturity, plant height and branches per plant in different crosses of sesame. On the other hand, highly significant negative additive effects were observed for plant height (crosses 2 and 3), capsules per plant and yield per plant (cross 1), indicating the additive effects were less important in the inheritance of these traits in these crosses.

Table 1. Scaling test

Scales	Variances	Standard error	t-test
Scale A= $2\bar{B}_1 - \bar{P}_1 - \bar{F}_1$	$V_A = 4V_{B1} + V_{P1} + V_{F1}$	$S.E.(A) = (V_A)^{1/2}$	$t(A) = A / S.E.(A)$
Scale B= $2\bar{B}_2 + \bar{F}_2 - \bar{F}_1$	$V_B = 4V_{B2} + V_{P2} + V_{F1}$	$S.E.(B) = (V_B)^{1/2}$	$t(B) = B / S.E.(B)$
Scale C= $4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{F}_2$	$V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$	$S.E.(C) = (V_C)^{1/2}$	$t(C) = C / S.E.(C)$

The significance of A and B scales indicates the presence of all the three types of non-allelic gene interaction, viz., additive × additive (i); additive × dominance (j) and dominance × dominance (l). The significance of C scale suggests dominance × dominance (l) type of non-allelic gene interaction.

Table 2. Six parametric models

Parameters	Variances	Standard error	t-test
m= mid-parents =mean= \bar{F}_2	$V(\bar{F}_2)$	$S.E.(m) = (V_m)^{1/2}$	$t(m) = m / S.E.(m)$
a=additive effect= $\bar{B}C_1 - \bar{B}C_2 =$	$V(\bar{B}C_1) + V(\bar{B}C_2)$	$S.E.(a) = (V_a)^{1/2}$	$t(a) = a / S.E.(a)$
d=dominance effect= $\bar{F}_1 - 4\bar{F}_2 - (1/2)\bar{P}_1 - (1/2)\bar{P}_2 + 2\bar{B}C_1 + 2\bar{B}C_2$	$V(\bar{F}_1) + 16V(\bar{F}_2) + 1/4V(\bar{P}_1) + 1/4V(\bar{P}_2) + 4V(\bar{B}C_1)$	$S.E.(d) = (V_d)^{1/2}$	$t(d) = d / S.E.(d)$
i=additive × additive= $2\bar{B}C_1 - 2\bar{B}C_2 - 4\bar{F}_2$	$4V(\bar{B}C_1) + 4V(\bar{B}C_2) + 16V(\bar{F}_2)$	$S.E.(i) = (V_i)^{1/2}$	$t(i) = i / S.E.(i)$
j =additive × dominance= $\bar{B}C_1 - 1/2\bar{P}_1 - \bar{B}C_2 + 1/2\bar{P}_2$	$V(\bar{B}C_1) + 1/4V(\bar{P}_1) + V(\bar{B}C_2) + 1/4V(\bar{P}_2)$	$S.E.(j) = (V_j)^{1/2}$	$t(j) = j / S.E.(j)$
l=dominance × dominance= $\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}C_1 - 4\bar{B}C_2$	$V(\bar{P}_1) + V(\bar{P}_2) + 4V(\bar{F}_1) + 16V(\bar{F}_2) + 16V(\bar{B}C_1) + 16V(\bar{B}C_2)$	$S.E.(l) = (V_l)^{1/2}$	$t(l) = l / S.E.(l)$

Table 3. Coefficients utilized for the construction of different models in generation means analysis

Generations	genetic effects						
	M	A	d	aa (i)	ad(j)	dd(l)	
P ₁	1	1	0	1	0	0	
P ₂	1	-1	0	1	0	0	
F ₁	1	0	1	0	0	1	
F ₂	1	0	0.5	0	0	0.25	
BC ₁	1	0.5	0.5	0.25	0.25	0.25	
BC ₂	1	-0.5	0.5	0.25	-0.25	0.25	

Table 4. ANOVA for generation means of five crosses of sesame tested for different characters at Uke location during 2012 and 2013

Cross	Source of Variation	df	Mean square					
			DF	DM	PH	BP	CP	YP
C1	Years	1	56.25**	94.54**	382.36 ^{ns}	16.75**	740.11 ^{ns}	4.00
	Reps(years)	4	4.55 ^{ns}	7.55 ^{ns}	214.50 ^{ns}	1.08*	306.21 ^{ns}	10.55 ^{ns}
	Generation	5	30.02**	25.69**	668.53**	5.20**	4015.69**	55.04**
	Gen x years	5	7.31 ^{ns}	40.107**	801.84**	6.00**	3395.77**	55.40**
	Pooled error	20	3.15	6.65	101.04	0.35	611.74	4.75
	CV%		2.99	1.99	10.36	8.87	18.41	14.43
C2	Years	1	9.00 ^{ns}	367.09**	6647.41**	112.39**	97790.04**	1100.02**
	Reps(years)	4	10.47 ^{ns}	9.34 ^{ns}	94.54 ^{ns}	0.77 ^{ns}	1037.80 ^{ns}	11.72 ^{ns}
	Generation	5	30.91**	79.94**	1594.78**	12.13**	12261.21**	137.05**
	Gen x years	5	11.8 ^{ns}	27.80**	81.54 ^{ns}	1.71 ^{ns}	7218.97**	82.02**
	Pooled error	20	5.75	2.98	167.41	1.17	1789.02	19.42
	CV%		3.87	1.68	11.59	13.25	28.26	28.28
C3	Years	1	4.69 ^{ns}	195.58**	2366.17**	16.85**	24908.7**	266.75**
	Reps(years)	4	7.02 ^{ns}	2.32 ^{ns}	97.98 ^{ns}	0.86 ^{ns}	1373.7 ^{ns}	15.02 ^{ns}
	Generation	5	57.82**	147.35**	434.46**	17.34**	11990.97**	147.77**
	Gen x years	5	8.09 ^{ns}	23.96**	358.20**	9.41**	592.51 ^{ns}	7.57 ^{ns}
	Pooled error	20	4.42	5.23	84.04	0.6	902.18	10.76
	CV%		3.5	1.77	8.09	9.97	16.90	17.70
C4	Years	1	21.27 ^{ns}	40.83*	2322.59**	95.94**	99172.08**	890.02**
	Reps(years)	4	1.47 ^{ns}	6.20 ^{ns}	149.88 ^{ns}	0.57 ^{ns}	745.73 ^{ns}	7.62 ^{ns}
	Generation	5	58.53**	31.26**	840.68**	22.65**	6325.26**	69.69**
	Gen x years	5	8.17 ^{ns}	92.82**	424.86*	49.32**	5346.87**	53.29**
	Pooled error	20	8.63	5.18	130.79	0.93	1295.09	14.04
	CV%		4.92	1.83	9.99	9.10	19.81	20.98
C5	Years	1	4.00 ^{ns}	0.96 ^{ns}	215.35 ^{ns}	70.95**	27144.75**	78.02**
	Reps(years)	4	0.66 ^{ns}	9.64 ^{ns}	80.30 ^{ns}	6.66 ^{ns}	1346.90 ^{ns}	4.72 ^{ns}
	Generation	5	57.86**	158.65**	867.59**	7.09 ^{ns}	8431.27**	97.05**
	Gen x years	5	18.8 ^{ns}	7.20 ^{ns}	1196.45**	21.35**	7731.04**	53.22**
	Pooled error	20	4.55	5.77	126.39	2.53	1091.66	9.52
	CV%			1.93	9.06	17.76	17.92	17.22

Note. ** = Significant at 1 % probability level; * = Significant at 5 % probability level; ns = Non-significant. DF=days to flowering; DM= days to maturity; PH=plant height (cm); BP=branches per plants; CP=capsules per plant; YP= yield per plant (g). C1=EW002 x BG006; C2=Dicho x EW006; C3=EW002 x Dicho; C4=Obsa x Dicho; C5=EW002 x Obsa.

Table 5. Mean performance of six generations for six characters in five crosses of sesame tested at Uke location during 2012 and 2013

Trait/generation	EW002/BG006	Dicho/ EW006	EW002/ Dicho	Obsa/ Dicho	EW002/Obsa
Days to flowering					
P1	63±0.43	63±0.24	64±0.65	64±0.45	63±0.67
P2	61±0.43	64±0.25	62±0.74	63±0.49	65±0.59
F1	57±0.35	57±0.23	56±0.61	57±0.48	56±0.79
F2	58±0.12	59±0.09	58±0.33	58±0.10	57±0.23
Bc1	58±0.26	62±0.16	59±0.46	59±0.26	60±0.49
Bc2	59±0.18	60±0.21	58±0.44	56±0.03	58±0.48
Days to maturity					
P1	132±0.99	132±0.75	135±0.56	125±0.60	127±0.67
P2	130±0.84	129±0.47	132±0.92	122±0.73	128±0.48
F1	126±1.03	121±0.40	120±0.77	127±0.92	119±0.66
F2	130±0.42	126±0.10	127±0.37	121±0.28	118±0.37
Bc1	129±0.53	125±0.37	130±0.52	124±0.60	122±0.31
Bc2	130±0.55	126±0.29	128±0.34	125±0.51	121±0.35
Plant height (cm)					
P1	89±5.14	92±3.65	104±1.99	126±2.59	141±3.6
P2	92±4.42	108±3.56	118±3.39	100±3.80	112±2.86
F1	110±3.58	142±3.08	125±3.44	124±4.03	109±3.67
F2	111±2.33	109±1.30	119±0.83	125±1.16	131±0.98
Trait/generation	EW002/BG006	Dicho/ EW006	EW002/ Dicho	Obsa/ Dicho	EW002/Obsa

Bc1	90±2.80	110±2.40	106±1.90	108±1.76	129±1.91
Bc2	89±2.75	109±1.84	108±1.56	104±2.09	129±1.31
Branches per plant					
P1	7±0.52	8±0.38	8±0.36	9±0.44	10±0.51
P2	7±0.45	7±0.37	7±0.28	8±0.20	9±0.43
F1	6±0.39	11±0.40	11±0.39	13±0.44	12±0.42
F2	8±0.27	8±0.17	8±0.10	12±0.26	11±0.22
Bc1	6±0.21	8±0.24	7±0.18	11±0.31	10±0.30
Bc2	6±0.27	14±0.23	9±0.20	10±0.27	12±0.63
Capsules per plant					
P1	108±9.31	125±4.17	147±8.84	160±4.09	145±3.20
P2	173±10.55	121±9.30	116±10.29	117±10.08	138±2.12
F1	124±8.60	235±6.55	239±9.11	203±11.30	222±4.77
F2	168±5.12	137±1.98	177±3.74	198±3.43	180±4.33
Bc1	129±6.24	164±10.12	216±6.17	193±3.57	190±5.07
Bc2	113±4.13	115±5.65	220±5.75	175±6.42	229±6.81
Yield per plant (g)					
P1	12±0.87	13±0.43	15±0.92	16±0.42	14±0.28
P2	18±1.1	12±0.93	12±1.08	12±1.02	13±0.20
F1	13±0.87	24±0.66	25±0.95	21±1.15	23±0.35
F2	17±0.51	14±0.20	19±0.39	21±0.36	17±0.40
Bc1	14±0.65	17±1.10	23±0.64	20±0.37	18±0.48
Bc2	12±0.43	12±0.60	23±0.59	18±0.66	22±0.62

Table 6. The results of scaling tests for six characters in five crosses of sesame evaluated at Uke location during 2012 and 2013

Cross	Trait	A	B	C
EW002/BG006	days to flowering	-4±0.62**	0±0.56 ^{ns}	55±0.96**
	days to maturity	0±1.78 ^{ns}	4±1.72*	6±2.99*
	plant height (cm)	-19±8.40*	-24±7.92*	43±13.5*
	branches per plant	-1±0.77 ^{ns}	-1±0.82 ^{ns}	6±1.50**
	capsules per plant;	26±17.29 ^{ns}	-71±14.82**	143±30.23**
	yield per plant (g)	3±1.79**	-3±1.64 ^{ns}	12±3.10**
Dicho/ EW006	days to flowering	4±0.46**	0.0±0.54 ^{ns}	55±0.70**
	days to maturity	-3±1.62 ^{ns}	2±1.43 ^{ns}	1±2.13 ^{ns}
	plant height (cm)	-4±6.04 ^{ns}	-32±5.99**	-46±9.55**
	branches per plant	-3±0.74**	-4±0.74**	-5±1.19**
	capsules per plant;	-32±21.68 ^{ns}	-126±16.03**	-168±18.40**
	yield per plant (g)	-3±2.35 ^{ns}	-12±1.66**	-23±1.87**
EW002/Dicho	days to flowering	-2±1.29 ^{ns}	-2±1.3 ^{ns}	56±2.02**
	days to maturity	5±1.4**	4±1.39**	1±2.42 ^{ns}
	plant height (cm)	-17±5.50**	-27±5.76**	4±8.61 ^{ns}
	branches per plant	-5±0.59**	0±0.67 ^{ns}	-21±1.00**
	capsules per plant;	46±17.71*	-15±16.70 ^{ns}	-61±27.22**
	yield per plant (g)	6±1.85**	10.6±1.66**	-1±2.85 ^{ns}
Obsa/Dicho	days to flowering	-3±0.84**	-8±0.70**	54±1.26**
	days to maturity	-4±1.62**	1±1.56 ^{ns}	-17±2.37**
	plant height (cm)	-43±5.96**	-16±6.95**	26±10.38**
	branches per plant	0±0.90 ^{ns}	-1±0.94 ^{ns}	6±1.58**
	capsules per plant;	23±13.98 ^{ns}	30±19.86 ^{ns}	109±28.60**
	yield per plant (g)	6±1.43**	3±2.03 ^{ns}	14±2.94**
EW002/Obsa	days to flowering	1±1.44 ^{ns}	-5±1.42**	53±2.055**
	days to maturity	-2±1.14 ^{ns}	-5±1.08**	-21±2.18**
	plant height (cm)	8±6.42 ^{ns}	37±5.34**	53±9.52**
	branches per plant	-2±0.81*	3±1.41*	1±1.40 ^{ns}
	capsules per plant;	13±11.65 ^{ns}	98±14.78**	-7±20.15 ^{ns}
	yield per plant (g)	-1±1.06 ^{ns}	8±1.31**	-5±1.81*

* Significant at the 0.05 probability level, ** Significant at the 0.01 probability level and ns=not significant.

Table 7. Estimates of genetic parameters model (m, [a], [d]), and χ^2 using six generations of five crosses of sesame tested at Uke in 2012 and 2013

Cross	Parameter	Characters					
		DF	DM	PH	BP	CP	YP
C1	M	61.06±0.20**	131.45±0.56**	79.27±2.73**	7.03 ±0.28**	138.42±5.78**	14.37±0.57**
	[a]	0.01±0.19 ^{ns}	0.22±0.49 ^{ns}	-0.40 ±2.56 ^{ns}	-0.14±0.24 ^{ns}	78.39±5.00**	-0.22 ±.50 ^{ns}
	[d]	-5.21±0.39**	-3.95±1.11**	19.14 ±4.92**	-0.96±0.52 ^{ns}	3.35±10.94 ^{ns}	-0.97±1.09 ^{ns}
	χ^2	54.15**	41.2**	112.61**	39.20**	358.30**	82.65**
C2	M	63.19±0.14**		92.16±2.09**	7.63±0.23**	92.94±4.03**	21.13±0.41**
	[a]	0.40±0.14*		-3.83±1.93*	-2.05±0.21**	25.97±4.22**	2.69±0.43**
	[d]	-6.59±0.27**		38.20±3.94**	3.70±0.45**	100.30±7.90**	10.19±0.80**
	χ^2	248.52**		126.52**	566.92**	220.141**	4401.2**
C3	M	62.06±0.41**	134.25±0.44**	108.54±1.66**	6.73±0.20**	138.19±5.70**	14.46±0.59**
	[a]	1.09±0.36*	1.15±0.38**	-3.46±1.66**	-0.61±0.17*	5.95±5.27 ^{ns}	0.65±0.55 ^{ns}
	[d]	-6.88±0.78**	-12.71±0.88**	13.49±3.38**	2.75±0.40**	110.50±10.95**	12.07±1.14**
	χ^2	7.31 ^{ns}	23.91**	72.68**	8.87*	254.66**	53.79**
C4	M	61.67±0.27**	113.87±0.66**	113.84±2.00**	8.62±0.30**	146.02±4.61**	14.47±0.45**
	[a]	3.25±0.15**	1.95±0.62**	7.87±1.74**	0.752±0.27**	15.36±4.20**	1.92±0.41**
	[d]	-7.99±0.55**	16.11±1.31**	6.55±3.99 ^{ns}	4.68±0.57**	84.73±9.03**	10.15±1.00**
	χ^2	148.50**	995.20**	125.42**	21.88**	17.33**	30.42**
C5	M	63.11±0.40**	126.52± 0.36**	131.64±1.98**	9.43±0.28**	142.22±1.85**	13.45±0.16**
	[a]	-0.20±0.37 ^{ns}	-0.03± 0.30 ^{ns}	7.67±1.6**	-0.08±0.28 ^{ns}	2.44±1.85 ^{ns}	0.32±0.17 ^{ns}
	[d]	-10.26±0.80**	-10.73± 0.71**	-4.68±3.90 ^{ns}	2.61±0.53**	87.96±4.54**	9.59±0.37 **
	χ^2	59.72**	115.74**	134.64**	13.27**	47.78**	50.27**

m=mean; a=additive; d=dominance; χ^2 = Chi-square; C1= EW002 x BG006; C2=Dicho x EW006; C3=EW002 x Dicho; C4=Obsa x Dicho; C5 =EW002 x Obsa. DM= days to maturity; PH=plant height (cm); BP=branches per plant=capsules per plant; YP= yield per plant (g)

Table 8. Estimates of gene effects and type of epitasis (TE) of five crosses of sesame tested for six characters at Uke location during 2012 and 2013

Cross	Trait	m	A	d	aa (i)	ad(j)	dd(l)	TE
C1	Df	60±1.18**	1±0.24**	-5±2.66 ^{ns}	2±1.16 ^{ns}	-4±0.66**	2±1.64 ^{ns}	-
	Dm	133±2.41**	1± 0.65 ^{ns}	-5 ± 6.18 ^{ns}	-2 ±0 .32 ^{ns}	-4 ± 2.01*	-2 ± 2.0 ^{ns}	-
	Ph	176.37± 8.43**	-2.32±3.38 ^{ns}	195.12±31.92**	-86 ± 12.18**	6.65 ± 10.39 ^{ns}	128.75 ± 20.76**	C
	Bn	15 ± 1.3**	0 ± 0.34 ^{ns}	-19±3.20**	-8±1.82**	0±0.98 ^{ns}	10± 2.05**	D
	CP	328.5± 26.33**	-32.35±7.04**	-437.5±64.93**	-188±25.37**	97±±20.55**	233±42.55**	D
	Yp	31±2.75**	-3±0.70**	-38±6.77**	-16±2.66**	10±2.2.10**	20±4.41**	D
C2	Df	55.5±0.69**	-0.50±0.17*	12.5±1.88**	8±0.66**	5±0.64**	-11±1.27**	D
	Dm	132±2.26**	1.5±0.54*	-30±5.82**	A	A	A	-
	Ph	98±8.39**	-8±2.55**	0±40.90 ^{ns}	2± 7.99 ^{ns}	18±7.92**	-392±15.44**	-
	Bn	6.5± 1**	-3±0.26**	-7.5± 2.61**	-2±0.96*	1±0.86 ^{ns}	5±1.81**	D
	CP	113. ±25.03**	2±5.09 ^{ns}	-26±73.27 ^{ns}	10±24.5 ^{ns}	94±25.33**	148±49.89**	-
	Yp	10.5±2.7**	0.5±0.51 ^{ns}	0.5±7.9 ^{ns}	2±2.65 ^{ns}	9±2.72**	13±5.38*	-
C3	Df	61±1.9**	1±0.24*	-7±4.94 ^{ns}	2±1.84 ^{ns}	0±1.60 ^{ns}	2±0.71 ^{ns}	-
	Dm	125.5±2.04**	1.5±0.54*	11.5±5.15*	8 ±1.96**	1 ±1.65 ^{ns}	-17 ± 3.48**	D
	Ph	159±6.27**	-7±1.96*	-126±17.62**	-48±5.96**	10±6.30 ^{ns}	92±13.08**	D
	Bn	7.5± 13.25 ^{ns}	0.5±5.73 ^{ns}	-1.5±6.61 ^{ns}	0±0.68 ^{ns}	-5±1.8*	5±3.96 ^{ns}	-
	CP	67±22.64**	15.5±6.78**	-1904.5±59.83**	304±21.61**	61±20.66**	-95±41.36**	C
	Yp	7.9±2.15**	1.5±0.71**	27.3±6.8**	16±2.26**	7.4±2.26**	-10±4.34**	D
C4	Df	65.5±0.76**	0.5±0.33 ^{ns}	-21.5±2.13**	-2±0.68*	5±0.85**	13±1.65**	D
	Dm	109± 2.01**	1.5±0.47**	28± 5.53**	14± 1.95**	-5± 1.84*	-11± 3.95*	D
	Ph	189±7.53**	13±0.70**	-189±20.44**	-76±7.19**	-18±6.13*	126±15.05**	D
	Bn	14.5±1.4**	0.5±0.37 ^{ns}	-8.5±3.50*	-6±1.36**	1±1.12 ^{ns}	7±2.31**	D
	CP	194.5±20.84**	21.5±5.44**	5.5±55.63 ^{ns}	-56±20.12*	-7±15.79 ^{ns}	3±41.02 ^{ns}	-
	Yp	22±2.23**	2±0.70*	-3±5.71 ^{ns}	-8±2.09*	0±1.69 ^{ns}	2±4.2 ^{ns}	-
C5	Df	56±1.72**	-1±0.45**	4±4.80 ^{ns}	8±1.66**	6±1.64**	-4±3.44 ^{ns}	-
	Dm	113.5± 1.83**	-0.5±0.41 ^{ns}	12.5±4.39*	14 ±1.79**	3±1.26*	-7± 2.89*	D
	Ph	134.5± 6.51**	14.5± 2.30**	11.5± 17.83 ^{ns}	-8± 17.83 ^{ns}	-29± 6.91**	-37**± 13.30*	-
	Bn	9.5±1.70**	0.5±0.33 ^{ns}	3.5±4.73 ^{ns}	0±1.67 ^{ns}	-5±1.5**	-1±3.15 ^{ns}	-
	CP	23.5± 24.34 ^{ns}	3.5± 1.92 ^{ns}	427.5± 62.32**	118±24.26**	-85± 17.41**	-229± 39.92**	D
	Yp	1.5±2.27 ^{ns}	0.5±0.17*	40.5± 5.78**	12±2.26**	-9±1.61**	-19± 3.49**	D

* = Significant at 5% probability level, ** = Significant at 1% probability level; ns = Non significant; a= additive –dominant model, C1= EW002 x BG006; C2=Dicho x EW006; C3=EW002 x Dicho; C4=Obsa x Dicho; C5 =EW002 x Obsa. DM= days to maturity; PH=plant height (cm); BP=branches per plant=capsules per plant; YP= yield per plant (g)

The estimates of dominance (d) effects were significant and positive for days to maturity (crosses 3, 4 and 5), branches per plant (cross 2), plant height (cross 1), capsules per plant (crosses 3 and 5), and yield per plant (crosses 3 and 5), indicating the importance of dominance gene effects in the inheritance of these traits. Gaikwad *et al.* (2009) reported that additive and dominance gene effects were equally important for number of capsules per plant and yield per plant.

The dominance gene effect (d) was significant and greater in magnitude than the additive effect in most of the crosses for different characters such as days to flowering (cross 2), days to maturity (crosses 3, 4 and 5), branches per plant (cross 2), capsules per plant (crosses 3 and 5) and yield per plant (crosses 3 and 5), demonstrating a predominant role of dominance gene action in controlling these traits in sesame. Ali (2015) also reported dominant gene effect for seed yield per plant. Additive, dominance and epistatic genetic components are important for the expression of traits studied. Positive dominance gene effects suggest its enhancing effects on the performance of different traits. However, for days to flowering (crosses 4) and for days to maturity (cross 2) dominance gene effects possessed negative sign, indicating that dominance is in direction of early maturity, which is desirable in sesame is breeding.

Both additive and dominance gene actions were found to be present for days to maturity (crosses 3 and 4), capsules per plant (cross 1) and yield per plant (crosses 3 and 5). Additive and non-additive gene actions were important in the inheritance of seed yield in sesame as reported by Gaikwad *et al.* (2010), Sumathi and Muralidharan (2010a) and Jatoth *et al.* (2014). The simultaneous occurrence of the additive and dominance gene action makes it necessary for resorting to special techniques like inter-mating the segregation generations or recurrent selection to exploit the different kinds of gene effects.

The additive x additive gene action was the only fixable component of genetic interaction observed for days to flowering (crosses 2 and 5), days to maturity (crosses 4 and 5) branches per plant (cross 2), capsules per plant (crosses 3 and 5) and yield per plant (crosses 3 and 5). In such cases, the pedigree method will be rewarding to improve the traits in a particular cross. The prevalence of additive x additive epistasis for days to flowering, days to maturity, branches per plant, and capsules per plant and yield per plant

was reported by Sumathi and Muralidharan (2014).

The positive and significant additive x dominance for days to flowering (crosses 2, 4 and 5), days to maturity (cross 5), plant height (cross 2), and capsules per plant and yield per plant (crosses 1 and 2) revealed that selection through self-pollination is not effective for improvement of these traits. For days to maturity a parameter specifying dominance x dominance type of non-allelic interaction had a negative sign, which implies that this non-allelic interaction tends to induce early maturity (crosses 3, 4 and 5).

Dominance x dominance type of interaction also showed greater effects in the present study. It was found to be significant and positive for plant height (crosses 1, 3 and 4), branches per plant (crosses 1, 3 and 4), capsules per plant (crosses 1 and 2) and yield per plant (crosses 1 and 2). On the other hand, highly significant negative dominance x dominance observed for capsules per plant (cross 3). Gamble (1962) suggested that negative effect of dominance x dominance is undesirable.

The dominance x dominance interaction was larger than the additive x additive for plant height, branches per plant, capsules per plant and yield per plant (cross 1), capsule per plant and yield per plant (cross 2), days to flowering, plant height and branches per plant (cross 4). Dominance and epistatic gene action was also reported by Ahmed and Ahmed (2013) for days to flowering, days to maturity and plant height in sesame.

Complementary epistasis was observed for plant height (cross 1) and capsules per plant (cross 3), which appeared to be desirable and would be helpful in further improvement of these traits. In agreement with this result, complementary epistasis for plant height was reported by Sundari *et al.*, (2012). Jinks and Jones (1958) suggested that heterosis is likely to be expressed with greater magnitude in crosses where complementary type of interaction is observed, while it may not be observed at all in crosses showing duplicate type of gene action. Opposite and significant signs of 'd' and 'dd' components indicated the importance of duplicate epistasis in all the crosses for most of the studied characters. Hence, there is a hindrance in selection as well as the complex nature of inheritance for improvement of these traits. In duplicate type of epistasis, the internal cancellation of 'd' and 'dd' could reduce the

heterosis effect. In such situation, reciprocal recurrent selection is likely to be useful for effective utilization of both types of additive and non-additive gene effects simultaneously. Similarly, Sumathi and Murlidharan (2010b) and Jatothu *et al.* (2013) reported significant epistatic gene action for seed yield and its related traits viz., days to 50 per cent 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.

From the present study the inadequacy of scaling and joint scaling test for almost all traits indicated the presence of non-allelic interactions and involvement of all three kinds of gene effects viz., additive, dominance and epistasis and their interactions and suggested the application of higher order interaction model. The next possibility is to include the effect of epistasis which can be estimated as additive x additive, dominance x dominance and additive x dominance gene effects in the inheritance of the characters. Hence, further study will be envisaged to involve higher order interaction model to estimate the gene and their interaction effect in superior cross combinations. In such situations, simple pedigree method of selection alone is ineffective. Instead, biparental mating followed by selection of desired recombinants from the segregating population is more applicable to break the undesirable linkage and allow the accumulation of favorable alleles for the improvement of the traits.

CONCLUSION

The nature and magnitude of gene effects vary depending on the crosses and characters studied. Hence, specific breeding strategy has to be adopted for a particular cross to get improvement in different traits. Besides, the results showed that additive, dominance and epistatic genetic components were important for the expression of most of characters studied. In such situations, simple pedigree method of selection alone is ineffective. Instead, biparental mating followed by selection of desired recombinants from the segregating population is desirable. Since considerable amount of dominance effect was also present for most of the

traits, selection of superior segregants has to be delayed to later generations until homozygosity is achieved. Complementary epistasis was observed only for plant height (cross 1) and capsules per plant (cross 3), which appeared to be desirable and would be helpful in further improvement of these traits.

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