Short communication. Inheritance of yield, yield components and resistance to major diseases in *Sesamum indicum* L.

M. A. S. El-Bramawy[1]* and W. I. Shaban[2]

[1] *Agronomy Department.*
[2] *Agricultural Botany Department. Faculty of Agriculture. Suez Canal University. 41522 Ismailia, Egypt.*

Abstract

Field experiments were conducted over 2005 and 2006 to study the gene action associated with yield and ten yield components, as well as resistance Fusarium wilt, charcoal rot and Alternaria leaf spot, in 6x6 half-diallel sesame progenies (F_1). Highly significant differences among the 15 F_1s and their six parents were detected with respect to all the investigated traits. A preponderance of non-additive genetic variance was seen for all the studied traits, except for days to maturity and resistance to Alternaria leaf spot. Ten traits showed overdominance. Recessive alleles were predominantly involved in fruiting branches plant^{-1}, capsules plant^{-1} and single plant yield. The distribution of genes with positive and negative effects were symmetrical or nearly symmetrical with respect to 1000-seed weight, charcoal rot disease resistance, fruiting branches plant^{-1}, capsules plant^{-1}, single plant yield, and oil content. The parents possessed mostly negative genes in dominant form with respect to capsules plant^{-1}, 1000-seed weight, oil content, and resistance to charcoal rot and Alternaria leaf spot; positive genes in recessive form were observed for the rest of the studied traits. Given the gene action observed, biparental mating or diallel selective mating and heterosis breeding is suggested for the improvement of sesame.

Additional key words: Alternaria leaf spot, charcoal rot, Fusarium wilt, gene action, sesame.

Resumen

Comunicación corta. Heredabilidad de la producción, componentes de la producción y resistencia a las principales enfermedades en *Sesamum indicum* L.

Se llevaron a cabo experimentos de campo en 2005 y 2006, en progenies de sésamo (F_1) en medio dialelo 6 x 6, para estudiar la acción génica asociada con la producción y con 10 caracteres asociados a la producción, así como con resistencia a Fusarium wilt, pudrición carbonosa y Alternaria leaf spot. Se detectaron diferencias altamente significativas entre las 15 F_1s y sus parentales respecto a todos los caracteres estudiados. Para todos los caracteres estudiados, se observó una preponderancia de la variancia genética no-aditiva, excepto para días hasta la madurez y resistencia a Alternaria leaf spot. Diez caracteres mostraron sobredominancia. En los caracteres ramas frutales por planta, cápsulas por planta y producción individual de la planta estaban implicados, predominantemente, alelos recesivos. La distribución de genes con efectos positivos y negativos fue simétrica o casi simétrica respecto a peso de 1000 semillas, resistencia a pudrición carbonosa, ramas frutales por planta, cápsulas por planta, producción individual de la planta y contenido en aceite. Los parentales poseen principalmente genes dominantes negativos respecto a cápsulas por planta, peso de 1000 semillas, contenido en aceite y resistencia a charcoal rot y Alternaria leaf spot; para el resto de los caracteres estudiados se observaron genes recesivos positivos. Dada la acción génica observada, se sugieren para la mejora del sésamo cruces biparentales o cruces dialélicos selectivos y heterosis.

Palabras clave adicionales: acción génica, ajonjolí, Alternaria leaf spot, Fusarium wilt, pudrición carbonosa, sésamo.

In Egypt, 32,188 ha - some 0.49% of the total cultivated area – is dedicated to sesame (*Sesamum indicum* L.); it is therefore an important conventional oilseed crop. Indeed, in the Ismailia Governorate it is the second most important crop in terms of area of cultivation after groundnut, *Arachis villosulicarpa* Hoehne (El-Bramawy, 1997). It was probably the first oilseed crop known and used by Man; records of its use date back to 2130 BC (Weiss, 1983). Its recorded history in Egypt goes back to 1300 BC (Burkill, 1953).

By 2020, the national edible oil requirement is expected to be around 20.8 million Mg, equivalent to 60 million Mg of oilseeds. Unfortunately, the average sesame seed production in Egypt is only about 1.15 Mg ha^{-1} (Anonymous, 2005), and the yield potential of this crop is very low. Production could be increased, however, using new, efficient agronomic practices in a sustainable manner.

One of the main problems with sesame in Egypt and other countries is the high level of fungal disease this crop suffers; in all growing regions, sesame is prone at least eight economically important fungal diseases (Kolte, 1985). It has been reported that *Fusarium oxysporum* (Schelt) f. sp. *sesami* Jacz, *Macrophomina phaseolina* (Tassi) Goid, and *Alternaria sesami* (Kawamura) Mohanty & Behera, the causal organisms of Fusarium wilt, charcoal rot and Alternaria leaf spot cause yield losses of 25-40% (Ragab *et al*., 2002; El-Bramawy, 2003, 2006).

Plants inoculated with *A. sesami* at 8 and 12 weeks of age are most susceptible to Alternaria leaf spot, while those inoculated at 4 weeks show the least susceptibility (Ojiambo *et al.,* 1999). However, great differences in resistance to Fusarium wilt, charcoal rot and Alternaria leaf spot have been observed in sesame breeding genotypes (Ragab *et al*., 2002; El-Bramawy and Abdul Wahid, 2006; El-Shakhess and Kalifa, 2007).

The breeding methodology chosen in sesame improvement (i.e., the selection, pedigree method and crossing technique) depends considerably upon the nature and magnitude of the gene action controlling the genetic behaviour of the traits of interest. Knowledge regarding the nature and magnitude of the gene action governing the inheritance of yield and yield components, as well as resistance to Fusarium wilt, charcoal rot and Alternaria leaf spot, is essential for designing efficient breeding strategies. Additive gene effects are easily fixed, and the improvement of traits with predominantly additive effects, such as plant height, capsule size, number of capsules on the main stem, capsules plant^{-1}, 1000-seed weight and resistance to charcoal rot, can be achieved by single plant selection or the selection of superior segregates in early generations (Zhao, 1999). The aim of the present study was to determine the nature of the gene action associated with different quantitative and qualitative traits in sesame, including resistance to major diseases, through the analysis of the corresponding genetic components in the F_1 of a 6x6 half-diallel cross.

In May 2005, all possible single crosses, excluding reciprocals, were made between six different sesame genotypes. The sources of sesame germplasm were: the new genotypes Taka 1, Taka 2 and Taka 3 from the Nuclear Research Center, Atomic Energy Authority, Egypt; Mutant 48 and Mutant 3 from the Faculty of Agriculture, Cairo University, Giza, Egypt; and Giza 32, a commercial variety donated by the Agriculture Research Center, Giza, Egypt. All these were selected for their good qualities in terms of production in Egypt. In addition, they show genetic variation in terms of their economic characteristics *i.e.,* in terms of plant height, branches plant^{-1}, number of capsules plant^{-1}, 1000-seed weight, single plant yield and oil content, as well as different degrees of resistance to Fusarium wilt, charcoal rot and Alternaria leaf spot.

The six parental lines and their 15 F_1s were grown in May 2006 in a randomized complete block design with four replicates (4 m long four-row field plots; spacing between rows=45 cm**;** spacing between plants in the same row=10 cm). All experiments were conducted over two summer seasons at the Suez Canal University Experimental Farm, Faculty of Agriculture, Ismailia, Egypt. "Days to 50% flowering" was recorded as the number of days from sowing until 50% of the plants had flowered. "Days to maturity" was recorded for whole plots as the number of days from sowing until harvest. Plant height, fruiting branches plant^{-1}, number of capsules plant^{-1}, 1000-seed weight and single plant yield were recorded for 10 randomly chosen plants in each plot. Oil content was determined according to the methods described by the AOAC (1985) using a Soxhlet apparatus.

During the same seasons, root rot severity and percentage wilt disease were determined (individually) under greenhouse conditions in separate trials. Fusarium wilt and charcoal rot pathogens for inocula were prepared by growing the causal fungi in a sand:barley:water medium (1:3:3 w:w:w) for 2 weeks at 28±2°C. Soil was infested with each fungus at the rate of 3% (w:w; *i.e.,* 3 g barley media/100 g soil) according to Pastor-Corrales and Abawi (1988) and Nawar (2007).

Control pots were filled with the same amount of sterilized barley medium. Sesame seeds were surface-sterilized with 3% sodium hypochlorite solution for 3 min and 15 seeds were sown in each pot. Four replicates (one replicate = 21 pots [6 parent + 15 hybrids pots]) were prepared for each treatment. Charcoal rot was recorded 60 d after planting (DAP) according to the method of Ahmed (2002). Plants affected by fusarium wilt plants were counted and disease severity assessed daily, starting 15 DAP, on the scale described by Marlatt *et al.* (1996).

For Alternaria leaf spor experiments, PDA plates on which *A. sesami* had been grown for 15 d were used to prepare the corresponding spore suspension (2×1000 spore mL^{-1}). Sesame plants (45 d-old), grown in a greenhouse, were sprayed with this suspension, then covered with plastic bags to ensure humidity around the plant leaves for the next 72 h. They were then removed. Plants sprayed with water were used as controls. The development of disease was assessed one week after inoculation according to Karunanithi (1996).

Genetic analyses were performed using the model of Hayman (1954). The sesame improvement program leans heavily on the magnitude of genetic variability and the proportion of it that is heritable. Unless the amount of genetic gain measured as a percentage of the mean is substantial, heritability alone cannot predict the possible improvement of a trait achievable by selection.

Further estimates of total genetic variance in the F_1 were performed to separate the phenotypic, genotypic and environmental components (including additive and dominance effects) as well as various ratios between the genetic components. This required the approach proposed by Hayman (1954). Such estimates can be very useful for improving different traits. To a certain extent they also assist the breeder in making inferences regarding the nature of the gene action involved in a trait that can be improved through selection.

Table 1 shows the mean performance of the six parents and their respective crosses (15 F_1s) with respect to the investigated traits. A wide range of variation among the parentals was observed. Mutant 48 (P_4) and Mutant 8 (P_5) showed the best properties for most of the traits studied. Mutant 8 (P_5) showed the greatest resistance to disease. Taka 3 (P_3) was the poorest in terms of single plant yield and sensitivity to disease. The crosses

Table 1. Mean performance of the parental sesame genotypes and their F_1s (6x6 diallel cross) with respect to all traits studied

Parentals and their crosses	Alternaria leaf spot (%)	Charcoal rot (%)	Fusarium wilt (%)	Oil content (%)	Single plant yield (g)	1000-seed weight (g)	Capsules plant^{-1}	Branches plant^{-1}	Plant height (cm)	Days to maturity	Days to 50% flowering
P_1	2.35	8.98	11.68	55.11	8.65	3.81	76.21	4.65	132.87	120.32	54.21
P_2	5.2	7.97	10.12	55.38	7.78	3.75	65.64	3.87	127.48	124.68	55.21
P_3	4.23	15.25	21.32	56.17	7.41	3.46	51.02	3.11	124.23	129.87	58.21
P_4	3.65	7.98	12.26	58.95	10.01	3.98	86.24	5.42	126.57	115.69	50.69
P_5	1.98	5.12	6.12	56.69	11.12	3.90	78.69	5.71	145.21	119.21	54.65
P_6	12.69	24.11	30.10	52.98	5.94	3.78	64.13	4.13	129.54	124.32	51.41
P_1 x P_2	6.68	7.32	8.10	54.10	7.98	3.81	66.54	4.45	134.82	124.32	53.34
P_1 x P_3	8.65	8.10	13.16	55.07	6.54	3.65	51.54	3.68	130.12	120.35	51.32
P_1 x P_4	1.58	3.21	5.14	57.77	7.10	3.69	67.36	3.73	129.21	121.31	53.10
P_1 x P_5	3.25	10.21	12.36	58.68	6.94	3.57	61.34	3.59	122.32	124.87	53.17
P_1 x P_6	7.65	13.54	19.87	56.12	7.32	3.72	70.12	4.01	137.89	127.65	56.21
P_2 x P_3	6.38	8.12	14.97	57.41	9.18	3.89	80.32	4.58	140.32	121.21	54.32
P_2 x P_4	4.32	4.21	7.10	57.59	5.94	3.64	46.21	3.64	121.87	126.34	55.12
P_2 x P_5	6.54	5.12	9.14	55.59	5.64	3.62	42.32	3.72	119.81	128.10	57.21
P_2 x P_6	6.21	10.32	16.38	55.45	9.21	3.76	81.69	3.89	130.51	119.32	52.69
P_3 x P_4	5.69	11.36	15.12	58.41	7.48	3.67	71.22	3.24	121.38	125.13	54.69
P_3 x P_5	9.65	7.11	12.32	57.01	9.98	3.90	78.28	4.60	139.14	112.68	49.87
P_3 x P_6	18.54	23.21	28.14	56.17	5.91	3.64	49.87	3.68	131.65	126.21	54.10
P_4 x P_5	1.98	5.54	9.12	58.19	11.79	4.11	89.68	5.68	149.67	109.21	49.14
P_4 x P_6	3.64	4.65	10.36	54.10	8.38	3.81	77.36	3.68	123.98	122.31	53.69
P_5 x P_6	1.32	4.35	8.12	57.16	12.28	4.21	98.12	6.12	155.28	111.98	50.12
LSD$_{0.05}$	1.98	2.95	3.58	0.89	0.23	0.62	2.91	0.18	3.94	3.52	2.12

P_4 x P_5 and P_5 x P_6 were the best hybrids for all the studied traits, showing them to be important for sesame improvement programs.

Table 2 shows the results of the analysis of variance, providing information on the inheritance of the traits. Based on the analysis of variance, only days to maturity, fruiting branches per plant and alternaria leaf spot presented significant differences between parents. However, all studied traits presented significant differences between the crosses. This indicates that there was transgressive segregation due to interaction between parents.

ANOVA (Table 2) showed there to be highly significant variations among the 21 genotypes (15 F_1s + six parents) for all the investigated traits, indicating considerable genetic diversity among the parents and their respective crosses. These findings suggest there to be sufficient genetic variability to allow further biometric assessment of these traits in future work. These results confirm the findings of El-Shakhess (1998), Ragab *et al.* (2002), El-Bramawy (2003, 2006) and El-Bramawy and Abdul Wahid (2006), who reported significant genetic variation among sesame genotypes with respect to yield and its attributes, as well as in terms of resistance to common diseases.

ANOVA was then performed to test the consistency of *Wr* (the covariance between the parents and their offspring) and *Vr* (the variance of one array, taking into account the cultivar/parent and all crosses in which it was involved) for the all studied traits. Table 2 confirms the validity of the assumptions reported by Hayman (1954).

Estimates of the components of genetic variance (Table 3) showed that the additive component (*D*) was significant with respect to days to maturity, plant height, capsules plant-1, 1000-seed weight, resistance to Fusarium wilt, charcoal rot Alternaria leaf spot, and oil content. The genetic variances of dominance components (H_1 and H_2) were significant for all the studied traits, except days to maturity and resistance to Alternaria leaf spot. This indicates the importance of both additive and non-additive genetic variances in the expression of these traits. The non-additive component was predominant in all traits except for days to maturity and oil content. These results agree with those reported by El-Shakhess (1998), Bayoumi (2003) and El-Bramawy (2003).

The *F* component was significant and positive for plant height, Fusarium wilt resistance and oil content, while they it effects on other traits was insignificant. This indicate that the presence of an excess of dominant alleles (Table 3). Recessive alleles were in the majority with respect to capsules plant-1. For the remaining traits, a symmetrical distribution of dominant and recessive alleles seems to be the case. The environmental component of variance (*E*) was small on most studied traits, except for days to maturity, plant height, 1000-seed weight and resistance to Alternaria leaf spot (Table 3). These characters are qualitative, so they should have little effect by environment due to the low number of genes which control these above mentioned characters. Similar results were reported by El-Bramawy (2003).

It should be noted that h^2 – an overall measure of the dominance effects of heterozygous loci – was significant and positive for days to flowering, plant height, branches plant-1, capsules plant-1, single plant yield and oil content. These results indicate that the mean direction of dominance was positive for these traits. The non-

Table 2. Analysis of variance and uniformity of *Wr* and *Vr* in the F_1s to test the validity of the diallel model assumptions for the studied traits

Alternaria leaf spot (%)	Charcoal rot (%)	Fusarium wilt (%)	Oil content (%)	Single plant yield (g)	1000-seed weight (g)	Capsules plant-1	Fruiting branches plant-1	Plant height	Days to maturity	Days to 50% flowering	DF	Source of variance
1.25	3.11	4.14	1.28	1.99	0.49	2.31	1.01	3.12	1.29	1.56	3	Replicates
21.09**	35.10**	49.14**	12.56 **	8.10**	1.01**	365.17**	6.18**	410.25**	26.89**	19.14**	20	Genotypes
2.08	2.78	3.99	0.95	1.19	0.28	3.29	1.98	10.28	1.87	1.68	60	Error
Validity testing												
1.28	3.28	3.95	1.15	0.69	0.04	10.29	0.98	51.18	3.29	4.08	3	Replicates
10.91*	11.25	15.29	2.98	4.98	0.44	17.82	5.28**	29.10	19.58**	8.10	5	Parents
3.59	4.58	6.41	1.95	4.25	0.24	11.28	1.29	69.48	4.25	5.98	15	Error

Wr: covariance between the parents and their off-sprig. *Vr*: variance of one array. *DF*: degrees of freedom for each item. *, ** : significant at P<0.05 and P<0.01, respectively (T- test).

Table 3. Estimates of genetic variance components and related statistics in F_1s for studied traits, after Hayman´s analysis of a diallel between six sesame lines

Component	Alternaria leaf spot (%)	Charcoal rot (%)	Fusarium wilt (%)	Oil content (%)	Single plant yield (g)	1000-seed weight (g)	Capsules plant⁻¹	Branches plant⁻¹	Plant height (cm)	Days to maturity	Days to 50% flowering
D	5.08**	2.88*	21.29**	8.69**	0.39	0.16**	71.45**	0.19	266.94**	12.11**	0.81
H_1	3.70	8.91**	42.69**	16.28**	120.13*	0.21**	14,643.03**	9.88**	319.95**	8.99	8.53**
H_2	2.48	5.88**	19.61**	12.17**	106.12	0.19**	13,959.39**	8.86**	290.41**	7.92	6.59**
F	2.46	2.67	17.18**	5.29**	0.47	0.05	-345.12	-0.68	67.04**	2.04	0.57
h^2	0.67	0.70	-0.28	38.19**	89.59**	0.02	11,680.70**	5.33**	150.12**	5.18	4.92**
E	1.30*	0.23	1.43	2.49	0.26	0.06*	47.17	0.11	12.97**	1.96*	0.49
$\sqrt{H_1/D}$	1.69	2.01	1.41	1.32	18.99	1.31	13.13	9.48	1.96	0.86	2.91
UV	0.17	0.25	0.11	0.24	0.23	0.25	0.23	0.24	0.22	0.22	0.21
KD/KR	195	2.15	2.13	1.59	0.89	1.26	0.82	0.72	1.26	1.42	1.35
K	0.31	0.16	-0.05	0.89	0.97	-0.04	0.90	0.57	0.54	0.66	0.69
$r(Y_r, W_r+V_r)$	0.23	0.41	-0.20	0.80	-0.32	0.50	0.31	-0.47	-0.43	-0.59	-0.21

D: Component of variance due to additive effects; H_1: Component of variance due to dominance effects; H_2: dominance effects indicating the symmetry of positive and negative effects of (U) proportion of homozygous parents; F: Covariance of additive and dominance effects; h^2: dominance effect, estimated as the algebraic sum over all loci in heterozygous phase in all crosses; E: environmental or non-heritable components of variance; $\sqrt{H_1/D}$: average degree of dominance over all loci; UV: product of proportion of negative genes and positive genes in the parents; KD/KR: ratio of total number of dominant to recessive genes in all parents; K: Number of gene groups which control the trait and exhibit dominance; $r(Y_r, W_r+V_r)$: correlation coefficient between parental means averaged over blocks (Y_r) and the parental order of dominance (W_r+V_r) of each array averaged over blocks, gives an idea of the direction of the dominance, *i.e,* if the increasing or decreasing genes for the trait are the dominant ones.

significant values of h^2 for the remaining traits indicate no direction of dominance. This finding is in agreement with results reported by Bayoumi (2003).

The mean degree of dominance for all loci ($\sqrt{H_1/D}$) indicated overdominance for ten traits (days to 50% flowering, branches plant⁻¹, capsules plant⁻¹, 1000-seed weight, Fusarium wilt, charcoal rot and Alternaria leaf spot resistance, single plant yield, plant height and oil content), partial to nearly complete dominance for days to maturity, and slight overdominance to complete dominance for plant height. The over-dominance observed in most of the traits may not be an index of true over-dominance since the degree of dominance could be biased due to linkage, epistasis or both (Comstock and Robinson, 1952).

The gene frequency among the sesame parentals, estimated by means of U and V ($H_2/4H_1$), indicated a symmetrical distribution of genes with positive and negative effects for 1000-seed weight and charcoal rot disease resistance. The distribution seemed to be nearly symmetrical for days to maturity, fruiting branches plant⁻¹, capsules plant⁻¹, single plant yield and oil content.

KD/KR (the ratio of the total number of dominant to recessive genes in all parents) was greater than one for all traits, except for fruiting branches plant⁻¹ (0.72) and capsules plant⁻¹ (0.82). This indicates a preponderance of dominant genes in the parents. For fruiting branches plant⁻¹ and capsules plant⁻¹, an excess of recessive genes was evident. These results agree with those reported by El-Bramawy (2003).

The value of K (h^2/H_2, which stands for the number of groups of genes that exhibit dominance for each trait) was <1 for all the studied traits, suggesting that just one group of genes showing dominance governed them all, although this parameter can be underestimated when the dominance effects of all the genes concerned are not equal in size and distribution, when the distribution of genes is correlated (Jinks, 1954), or when complementary gene interactions occur (Mather and Jinks, 1971).

The correlation between parental performance (Y_r) and parental order of dominance (W_r+V_r) was positive for capsules plant⁻¹, 1000-seed weight, resistance to charcoal rot and Alternaria leaf spot, and oil content, indicating that the parents possessed mostly negative genes in dominant form for these traits. For the remaining traits, positive genes were mostly dominant.

The results indicate that both additive and non-additive components of genetic variance were involved in

the inheritance behaviour of the traits studied, with a predominance of dominance variance components for all the studied traits, except for days to maturity and resistance to Alternaria leaf spot, which presented mostly additive variance. Pedigree selection would be an appropriate method for improving days to maturity and oil content since additive variance is predominant for both these traits. As selection based on progeny performance exploits only the additive component of genetic variances, bi-parental mating or diallel selective mating (which allows inter-mating among selected segregates in different cycles) would be useful for recovering the better homozygotes in later generations. In addition, the contribution of dominance and overdominance seen indicates the scope for heterosis breeding in sesame, which exploits non-additive gene action.

Acknowledgements

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