

Maternal effects and generation mean analysis of seed-oil content in cotton (*Gossypium hirsutum* L.)

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Summary. The nature of gene action and of maternal influence governing cottonseed oil attributes were determined with four lines, two each with high and low seed-oil percentage. For this purpose, P1, P2, F0, F1, F2 and alternative sets of BC1 and BC2 generations were analysed in six cross-combinations and their reciprocals. Marginal extents of heterosis for seed-oil percentage were noticeable in F1, with inbreeding depression in F2. Data from reciprocal backcrosses provided evidence in favour of maternal rather than cytoplasmic effects of seed-oil development. Relatively higher extents of heterosis, sizeable inbreeding depression and reciprocally unequal F2 averages were characteristic of the seed index trait, which often showed a reversal of effects from F1 to F2. Reverse reciprocal backcrosses exhibited some differences, including greater resemblance between the types, (A/B)A and (B/A)A, in addition to variable dose effects in seed index. Thus, the differences between F1 seed index values were not due to cytoplasmic influence. Positive heterotic effects for seed-oil index, especially among the backcrosses, ranged between 16.08% and 47.29% over midparent averages. Genetic component estimates from analysis of similar sets of crosses differing only in reciprocal backcrosses, and also from sets of reciprocal crosses between any two parental combinations, were inconsistent. Scaling tests detected presence of epistasis within and between a majority of cross-combinations. Despite reciprocal differences, additive gene effects for seed-oil percentage were significant in 7 out of 24 crosses, representing high \times low, low \times high and low \times low seed-oil parents. Those were, however, accompanied by significant dominance effects of higher order. In crosses in-

volving low seed-oil percentage parents SA1060 and SA229, all six components were detected significant, with opposite effects of dominance and dominance \times dominance epistatic components. Significant additive components were also detected for seed index and seed-oil index in 7 and 5 out of 24 crosses, respectively. In the inheritance of seed index and seed-oil index, dominance effects were more important. Epistatic components of additive \times additive, and to a lesser extent, those of dominant \times dominant were found significant.

Key words: *Gossypium hirsutum* – Oil content – Seed generation – Reciprocal backcrosses – Scaling tests

Introduction

In his study of stability and transfer of high oil traits, Kohel (1980) had inferred that seed-oil in cotton is governed by additive genes and can be altered through breeding and selection, despite sizeable influence of the environmental factors. Effects of intraseasonal environmental variation can be significant enough to warrant sampling considerations of seed quality (Kohel and Cherry 1983; Dani 1984 a, b, 1985; Dani and Kohel 1987; Kashalkar et al. 1988). Barring isolated reports, there has been little genetic information in *G. hirsutum* pertinent to choosing appropriate procedures for increasing oil content in seed (Dani 1989).

It has been a common observation that in most genetic studies involving statistical models, not all assumptions are met (Meredith 1984). Knowledge of genetic trends is nevertheless, necessary for developing efficient methods and genetic populations. Generation means for

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Table 1. Average values (\pm S.E.) of seed-oil percentage, seed index and seed oil index in 4 parents and 12 reciprocal generations within 6 cross-combinations

Generation	Seed-oil (%)	Seed-index (mg/seed)	Seed-oil index (mg/seed)
F0 SA 1169	22.78 \pm 1.57	103.90 \pm 14.67	23.93 \pm 4.74
F0 SA 1060	20.04 \pm 1.19	91.23 \pm 5.33	19.63 \pm 1.52
F0 SA 229	19.81 \pm 1.09	105.43 \pm 19.41	20.93 \pm 4.40
F0 SA 59	23.61 \pm 0.87	98.83 \pm 5.30	23.40 \pm 1.81
F1 1169/1060	23.52 \pm 0.97	110.67 \pm 7.85	26.27 \pm 2.51
F1 1060/1169	23.16 \pm 0.53	109.40 \pm 10.87	25.13 \pm 2.70
BC1 (1169/1060) 1169	21.59 \pm 3.38	104.53 \pm 19.78	23.27 \pm 7.41
BC2 (1169/1060) 1060	23.34 \pm 1.02	114.43 \pm 5.02	26.93 \pm 1.59
BC2 (1060/1169) 1169	23.55 \pm 0.29	108.30 \pm 2.94	25.57 \pm 0.80
BC1 (1060/1169) 1060	23.22 \pm 1.25	112.30 \pm 4.06	26.17 \pm 2.13
RBC1 1169 (1169/1060)	23.24 \pm 0.43	113.43 \pm 7.87	26.33 \pm 2.47
RBC2 1060 (1169/1060)	23.21 \pm 0.37	112.93 \pm 10.51	26.57 \pm 1.79
RBC2 1169 (1060/1169)	24.27 \pm 0.38	124.83 \pm 5.08	30.30 \pm 1.64
RBC1 1060 (1060/1169)	23.65 \pm 1.33	99.23 \pm 12.56	23.30 \pm 3.80
F2 1169/1060	22.16 \pm 2.26	111.13 \pm 1.77	25.60 \pm 0.86
F2 1060/1169	22.62 \pm 0.37	103.33 \pm 10.39	23.40 \pm 2.27
F1 1169/229	23.67 \pm 1.02	125.33 \pm 5.01	29.23 \pm 0.98
F1 229/1169	18.64 \pm 0.87	104.67 \pm 2.75	21.47 \pm 1.2
BC1 (1169/229) 1169	21.48 \pm 1.03	101.17 \pm 4.51	21.87 \pm 1.67
BC2 (1169/229) 229	22.77 \pm 0.95	121.07 \pm 11.18	27.73 \pm 3.67
BC2 (229/1169) 1169	21.95 \pm 0.09	104.07 \pm 10.28	22.93 \pm 2.29
BC1 (229/1169) 229	22.23 \pm 0.79	132.81 \pm 23.57	29.60 \pm 5.94
RBC1 1169 (1169/229)	23.46 \pm 0.87	135.00 \pm 9.79	32.90 \pm 3.13
RBC2 229 (1169/229)	21.10 \pm 1.57	100.77 \pm 6.43	21.57 \pm 2.86
RBC2 1169 (229/1169)	22.17 \pm 1.66	124.50 \pm 8.05	27.73 \pm 3.84
RBC1 229 (229/1169)	20.72 \pm 2.19	106.20 \pm 6.48	22.63 \pm 3.79
F2 1169/229	21.42 \pm 0.71	110.30 \pm 4.32	23.63 \pm 0.84
F2 229/1169	21.57 \pm 0.43	110.17 \pm 6.42	23.80 \pm 2.48
F1 1169/59	25.02 \pm 0.39	121.07 \pm 7.30	30.27 \pm 1.33
F1 59/1169	23.71 \pm 0.71	105.80 \pm 3.18	25.17 \pm 0.19
BC1 (1169/59) 1169	24.56 \pm 0.73	102.43 \pm 4.74	25.40 \pm 1.31
BC2 (1169/59) 59	23.87 \pm 0.63	117.30 \pm 8.09	28.03 \pm 2.25
BC2 (59/1169) 1169	23.96 \pm 1.26	102.23 \pm 2.75	24.53 \pm 1.84
BC1 (59/1169) 59	24.67 \pm 0.55	105.80 \pm 7.45	26.33 \pm 1.66
RBC1 1169 (1169/59)	23.68 \pm 1.02	112.97 \pm 9.84	26.93 \pm 3.59
RBC2 59 (1169/59)	23.62 \pm 1.17	105.50 \pm 2.62	25.03 \pm 1.92
RBC2 1169 (59/1169)	24.43 \pm 0.85	119.23 \pm 8.97	29.27 \pm 2.79
RBC1 59 (59/1169)	23.10 \pm 1.36	107.37 \pm 10.88	25.13 \pm 3.55
F2 1169/59	22.81 \pm 0.87	101.57 \pm 2.81	23.17 \pm 0.24
F2 59/1169	23.70 \pm 0.62	106.47 \pm 6.86	25.23 \pm 2.07
F1 1060/229	23.11 \pm 1.45	124.93 \pm 6.57	29.87 \pm 1.07
F1 229/1060	20.22 \pm 1.27	106.83 \pm 5.28	21.73 \pm 2.24
BC1 (1060/229) 1060	21.09 \pm 0.17	111.90 \pm 9.30	23.73 \pm 1.36
BC2 (1060/229) 229	18.74 \pm 1.27	103.00 \pm 9.85	19.87 \pm 3.11
BC2 (229/1060) 1060	21.56 \pm 1.84	113.70 \pm 5.40	24.57 \pm 3.01
BC1 (229/1060) 229	20.48 \pm 0.15	114.97 \pm 11.67	23.03 \pm 2.07
RBC1 1060 (1060/229)	23.81 \pm 0.86	123.37 \pm 8.10	29.27 \pm 1.53
RBC2 229 (1060/229)	20.50 \pm 1.34	108.33 \pm 10.14	22.67 \pm 3.00
RBC2 1060 (229/1060)	22.61 \pm 0.26	110.13 \pm 11.00	24.97 \pm 2.56
RBC1 229 (229/1060)	20.34 \pm 2.10	104.00 \pm 11.70	21.73 \pm 4.21
F2 1060/229	18.95 \pm 0.67	95.95 \pm 8.08	18.27 \pm 2.12
F2 229/1060	18.96 \pm 0.37	100.40 \pm 2.14	19.10 \pm 0.43
F1 1060/59	23.25 \pm 1.15	120.17 \pm 6.28	27.83 \pm 2.25
F1 59/1060	23.81 \pm 0.90	96.30 \pm 5.05	23.00 \pm 1.88
BC1 (1060/59) 1060	23.58 \pm 0.42	105.73 \pm 3.00	24.97 \pm 0.85
BC2 (1060/59) 59	24.29 \pm 0.54	108.80 \pm 5.27	26.27 \pm 0.78
BC2 (59/1060) 1060	22.24 \pm 0.49	100.57 \pm 13.36	23.37 \pm 2.78
BC1 (59/1060) 59	23.05 \pm 1.13	106.30 \pm 6.90	24.67 \pm 2.71

Table 1. (Continued)

Generation	Seed-oil (%)	Seed-index (mg/seed)	Seed-oil index (mg/seed)
RBC1 1060 (1060/59)	23.16 ± 0.74	118.40 ± 10.69	27.43 ± 3.19
RBC2 59 (1060/59)	22.38 ± 1.52	101.50 ± 5.70	22.77 ± 2.35
RBC2 1060 (59/1060)	23.27 ± 0.19	118.27 ± 6.27	27.57 ± 1.46
RBC1 59 (59/1060)	22.89 ± 0.08	100.87 ± 5.04	23.17 ± 0.94
F2 1060/59	23.04 ± 0.54	92.52 ± 5.39	21.37 ± 1.46
F2 59/1060	23.41 ± 0.87	98.13 ± 10.39	23.07 ± 3.08
F1 229/59	20.57 ± 1.83	118.10 ± 6.58	25.73 ± 3.62
F1 59/229	23.21 ± 0.82	109.60 ± 4.02	25.53 ± 2.15
BC1 (229/59) 229	21.95 ± 0.35	116.97 ± 10.65	25.67 ± 2.56
BC2 (229/59) 59	20.57 ± 0.79	99.63 ± 10.70	21.87 ± 1.26
BC2 (59/229) 229	21.66 ± 1.36	107.90 ± 4.67	23.13 ± 1.97
BC1 (59/229) 59	21.53 ± 0.62	102.83 ± 9.78	22.40 ± 1.59
RBC1 229 (229/59)	21.19 ± 0.98	116.63 ± 2.22	24.80 ± 1.43
RBC2 59 (229/59)	23.96 ± 0.70	105.70 ± 4.55	25.27 ± 2.79
RBC2 229 (59/229)	20.28 ± 1.44	106.87 ± 16.16	22.07 ± 3.92
RBC1 59 (59/229)	23.69 ± 1.05	108.87 ± 6.56	23.87 ± 1.79
F2 229/59	21.28 ± 0.76	96.40 ± 1.80	21.23 ± 0.51
F2 59/229	20.50 ± 0.91	90.33 ± 4.35	18.60 ± 2.85

gene action estimates have been used in cotton for studying the inheritance of lint index (Ramey 1963), components of yield and fibre quality (Meredith et al. 1970; Meredith and Bridge 1972; Bains et al. 1982) and allelochemicals relating to host-plant resistance (White et al. 1982). Ramos (1985) has concluded that analysis of gene effects by generation means would be adequate to investigate gene action for cottonseed oil characteristics.

Abdel-Bary et al. (1975) concluded that heterosis, inbreeding depression and epistasis occurred for oil, protein and seed index in Egyptian cotton, depending on parentage of particular crosses. Dani (1984c) observed reciprocal differences in heterosis and general and specific combining ability (GCA/SCA) effects for cottonseed oil traits. Knowledge of maternal effects is necessary for genetic studies with reciprocal crosses. Maternal influence on oil content in seed of F1 have been detected more recently by Kohel (1980) and Ramos (1985), following earlier reports by van Heerden (1969) and Christiansen and Lewis (1973). The extents of maternal effects other than those on the seeds of F1 and F2 have not yet been examined in this crop. Since maternal effects can also be caused by cytoplasmic effects, it is necessary to isolate the sources. For this purpose, ancillary data from backcross and reciprocal backcross generations can be used (Mosjidis and Yermanos 1984).

The purpose of this paper is to report results from an investigation of gene action and maternal influence on seed-oil characteristics in cotton. The study was based on generation means from four lines differing in oil content and in seed index, and their F1, F2 and reciprocal sets of backcross generations within six cross-combinations of parents.

Materials and methods

Parental lines for the present investigation were obtained from the cottonseed improvement programme initiated by Kohel (1978), which represented selections from the Upland Germplasm Collection maintained at Stoneville, Mississippi. On the basis of consistency of performance over 4 years, a group of ten high and ten low seed-oil percentage lines were initially isolated (Kohel 1980). From these, two lines with high seed-oil percentage, viz. SA 1169 (Verden) and SA 59 (Petal Spot), and two lines with low seed-oil percentage, viz. SA 1060 (Fox 4,205) and SA 229 (Lancinate Leaf) were selected for the present study. They were grown in the Cotton Genetics Nursery at College Station in 1979 in an RCB design consisting of one-row plots of five plants (2.5 × 1.0 m), and replicated three times. The four lines were crossed in a diallel fashion to obtain six crosses and their reciprocals. In the season of 1980, parents and F1s were similarly grown in three replications. A total of 60 cross-combinations, including 12 new F1s, 12 BC1s, and 12 BC2s (using F1s as female parents), and 12 reciprocal RBC1s and 12 RBC2s (using F1s as male parents) were effected within each replication (Table 1). Bolls were self-pollinated on F1 plants and in parental lines. From each cross-combination, five crossed (maternal) bolls per replication were acid-delinted and dried by forced air at 40°C for 24 h. Seed-oil percentage was determined nondestructively on individual boll samples with a wide-line nuclear magnetic resonance instrument. Similarly, five selfed parental bolls and ten selfed bolls from F1 plants were analysed for seed-oil percentage. Seed index (mg per seed) was calculated on 100 seed basis. Seed-oil index, expressed in milligrams of oil per seed, was obtained by the product of seed oil percentage and seed index. Analysis of generation means was based on Hayman (1958), using scaling tests of Mather (1949).

Results and discussion

Means of parents and of various generations for seed oil percentage, seed index and seed-oil index have been given

Table 2. Tests of significance for three (non-interacting) and six (interacting) genetic components of generation means for: 1 seed-oil percentage, 2 seed index and 3 seed-oil index in six cotton crosses and reciprocals

Cross	Mean (m)			Additive (d)			Dominance (h)			Add × Add (i)			Add × Dom (j)			Dom × Dom (l)		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
@ 1169/1060 a)	**	**	**	-NS	-NS	-NS	NS	NS	NS	.	-NS	-NS	.	-NS	-NS	.	-NS	-NS
1169/1060 b)	**	**	**	NS	NS	-NS	NS	NS	NS	.	NS	-NS	.	NS	-NS	.	-NS	-NS
1060/1169 a)	**	**	**	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	-NS	-NS	-**	-NS	-NS
1060/1169 b)	**	**	**	-NS	-**	-*	**	NS	NS	*	NS	NS	-NS	-NS	-NS	-**	-NS	-NS
1169/229 a)	**	**	**	-NS	-*	-*	NS	NS	NS	.	-NS	.	.	-NS	.	.	-NS	.
1169/229 b)	**	**	**	**	**	**	*	*	**	.	NS	*	.	*	.	-**	-NS	-NS
229/1169 a)	**	**	**	NS	NS	NS	NS	NS	NS	NS	.	.	NS
229/1169 b)	**	**	**	-NS	-*	-NS	-NS	NS	NS	-NS	NS	.	NS	NS	-NS	-NS	-NS	.
1169/59 a)	**	**	**	NS	-*	-NS	**	**	**	*	*	*	NS	-**	-NS	-NS	-NS	-NS
1169/59 b)	**	**	**	NS	NS	NS	NS	**	**	NS	NS	NS	NS	-NS	-NS	-NS	-NS	-NS
59/1169 a)	**	**	**	NS	NS	NS	NS	-NS	NS	NS	.	.	NS
59/1169 b)	**	**	**	-NS	-NS	-NS	NS	NS	NS
1060/229 a)	**	**	**	**	NS	NS	*	**	**	NS	NS	NS	*	NS	NS	NS	-NS	-NS
1060/229 b)	**	**	**	**	-NS	**	**	*	**	NS	NS	*	*	NS	-NS	-**	-NS	*
229/1060 a)	**	**	**	-NS	NS	-NS	**	*	**	.	.	.	-NS
229/1060 b)	**	**	**	-NS	-NS	-NS	**	NS	*	NS	NS	-NS	-NS	-NS	-NS	*	-NS	-NS
1060/59 a)	**	**	**	-NS	-NS	-NS	**	**	**	*	**	*	NS	NS	NS	-**	-*	NS
1060/59 b)	**	**	**	NS	*	NS	NS	**	**	.	*	*	.	*	.	.	*	NS
59/1060 a)	**	**	**	-NS	NS	NS	NS	-NS	NS	-NS	-NS	.	.
59/1060 b)	**	**	**	-*	-NS	-**	NS	NS	NS	-NS	NS	-**	-NS	-NS	-NS	NS	-NS	*
229/59 a)	**	**	**	*	NS	NS	-NS	**	**	-NS	*	*	**	NS	NS	-NS	-NS	.
229/59 b)	**	**	**	-**	**	-NS	NS	**	**	NS	NS	NS	NS	NS	NS	-NS	-**	.
59/229 a)	**	**	**	-NS	-NS	-NS	NS	**	**	NS	-NS	-NS	-NS	-NS	-NS	-NS	-NS	-NS
59/229 b)	**	**	**	**	NS	NS	**	**	**	NS	*	*	NS	NS	NS	NS	-NS	-NS

*, ** Significant at the 0.05 and 0.01 levels of probability

NS, not significant, sign indicates direction of effect

@ Reciprocal BC with a) F₁ as female parent and b) F₁ as male parent

in Table 1. Results from the tests of significance for three (non-interacting) and six (interacting) genetic components of generation means for the three characters have been summarized in Table 2.

Analysis of maternal and cytoplasmic effects

Cotton is an embryonic seed type with a possibility of maternal effects, since the development of the seed totally depends upon the nutrients provided by the mother plant. Methods and assumptions used to determine maternal and cytoplasmic effects in seeds with negligible endosperm were reviewed by Mosjidis and Yermanos (1984). Differences between reciprocal F2 populations would be expected mainly due to cytoplasmic effects. Environmental factors such as flower manipulation at the time of crossing, temperature during seed development or differences in flowering time may influence the results. To overcome these problems, use of backcrosses that have the F1 plants as maternal parents can be made, since they have equal developmental timing normally controlled by nuclear genotype. If seeds borne on F1 A/B crossed to parent A have the same value for the trait being studied as those backcrossed to parent B, it indicates that maternal genotype controls the trait. Similarly, if the backcross (A/B)A is not equal to (B/A)A, it indicates that cytoplasmic inheritance is present, because between these, only the maternal cytoplasm is different.

Analysis of reciprocal backcrosses suggested the existence of maternal effects rather than cytoplasmic effects of seed-oil (Table 1). Reciprocal F2 average seed-oil percentages from the cross SA 1060 \times SA 59 were similar to each other, with a marginally higher value when SA 59 was used as female parent. Seeds borne on F1 1060 \times 59 backcrossed to 1060 did not show significantly different mean seed-oil percentage and standard error (S.E.) components from those borne on F1 1060 \times 59 backcrossed to 59. Similarly, the mean seed-oil percentages of (59/1060)1060 and (59/1060)59 were not significantly different. Backcross (1060/59)1060 resembled (59/1060)1060, as also the mean seed-oil percentage of (1060/59)59 and (59/1060)59 were comparable to each other.

Results from the four reverse combinations of reciprocal backcrosses did not appear to be contradictory. In the case of SA 1169 \times SA 229, the F1 average seed-oil percentage resembled that in the high maternal parent. The F2 reciprocal means were more or less similar to each other, despite the small inbreeding depression. Tests of backcrosses indicated small or negligible cytoplasmic influence; reverse reciprocal backcrosses exhibited some differences. Seed-oil percentages in 1169 (1169/229) and 1169 (229/1169) were not similar. Such results were also observed in the case of SA 229 \times SA 59, except that the

reverse backcrosses had close resemblance of 229 (229/59) versus 229 (59/229), as also for 59 (229/59) and 59 (59/229). On an average, the performance of selfed seed appeared to be generally lower than the crossed seed. Differences were observed between selfed versus crossed seed among the crosses involving low-oil parents SA 229 and SA 1169. In his earlier study, Dani (1984c) had noticed marginal negative heterosis for seed-oil percentage in some crosses. In cotton, genetic variation for seed-quality tends to be confounded with non-genetic variation due to hand-emasculation and damage to floral parts (Kohel 1968). The correlation between F1 and F2 seed-oil percentages obtained from the present study was of the order 0.074, indicating high extents of environmental variation, which is consistent with Kohel (1980).

In SA 1060 \times SA 59, the F1 seed index was significantly higher than F1 59 \times 1060, with relatively higher heterotic effects. However, at F2 there was an apparent reversal of seed index with overall inbreeding depression, such that the F2 59 \times 1060 seeds were heavier than their reciprocals. Seed index in one set of backcrosses, viz. BC1 (1060/59)1060, was different from that of BC2 (59/1060)1060 with a large S.E. component. In the other set of backcrosses, viz. (1060/59)59 and (59/1060)59, seed indexes and S.E. components were comparable. The reverse reciprocal backcross data of seed index presented some striking resemblances within BC1s and BC2s. These were different also than straight reciprocal BC1s and BC2s, since the seed index indicated a reverse effect due to SA 1060.

Contrary to these results, the higher effect for seed index in reverse reciprocal BC2s in SA 1169 \times SA 59 and in SA 1169 \times SA 229 could be associated with the heavy-seeded maternal parent. F2 seed index averages in 1169 \times 229 showed no reciprocal differences, while those from 1169 \times 59 were different. Positive heterotic effects for F1 seed index and inbreeding depression at F2 with a reversal in favour of the heavy-seeded maternal parent were also observed in SA 1060 \times SA 229 progenies. In SA 229 \times SA 59, the F1 seed index indicated reciprocal differences due to maternal effects, which continued at F2 despite an overall reduction in the seed index values. In his studies on cottonseed, van Heerden (1969) did not find an extension of maternal effects beyond the seeds of F1 generation. Garwood et al. (1970) also noticed the reversal of effects between F1 and F2 seed indexes in maize. They concluded that cytoplasmic inheritance was present but that it changed direction from generation to generation.

In the present study, some contradictory evidence for inheritance of seed index was noticed. For instance, in SA 1169 \times SA 1060 progenies, reciprocal differences were continued and intensified in F2, suggestive of cytoplasmic inheritance. On the other hand, seed indexes of BC2 (1169/1060)1060 and BC2 (1060/1169)1060 were

comparable to each other, thus ruling out cytoplasmic effects. In cotton, very little variability may be present among cytoplasms (Merdith 1984). Maternal effects may not be attributed to chloroplast DNA or mitochondrial genetic variability (Altman and Thomas 1985). Results from the analysis of seed-oil index data in the present study were generally comparable to those of seed index. In 1169×1960 , 1169×229 , and 59×1169 , reciprocal heterotic effects for seed-oil index in F2 were greater than those due to seed-oil percentage.

Genetic components from analysis of generation means

Within each one of the six possible cross-combinations, the analysis of generation means with P1, P2, F1, F2, and BC1 and BC2 was performed in four combinations (Table 2). Two sets of reciprocal backcrosses, each with F1 as male and alternatively as female parent, were analysed individually with common P1, P2, F1 and F2 generation data, to determine the extents and pattern of differences in genetic component estimates. Scaling tests (Mather 1949) were not significant in some cases. In many among those, the values of one or more criteria were rather close to the values that would have suggested the presence of epistasis. A general feature of the generation mean analysis was that there was no consistent pattern in terms of genetic component estimates, either within the sets of crosses differing only in reciprocal backcrosses, or between the two sets of reciprocal crosses involving any two parents.

Significant epistatic effects for seed-oil percentage were detected from one or more sets of generations within each one of the six cross combinations and their progenies. Significant and highly significant positive additive effects were obtained in at least one out of four combinations involving high \times low, low \times high and low \times low seed-oil parents. The positively significant effects in 1169×229 b) (using F1s as male parent), 1060×229 a) (using F1s as female parent), and in 59×229 b) were accompanied by significant and positive dominance components, all of relatively greater magnitude (Table 2). In 1060×229 , the additive \times dominance component was positively significant and was greater than the additive component. In 1060×229 b), all three components of epistasis were significant, greater than the additive component, and duplicate type of epistasis was suggested by the opposite signs of 'h' and 'l'. Significant dominance, additive \times additive and dominance \times dominance effects were obtained in 1060×229 b) and in 1060×59 b), with duplicate type of epistasis and the 'l' component larger than 'h' and 'i'.

The extent of heterotic effects for seed-oil percentage in most crosses having significant dominance effects, however, was low to marginal. Bains et al. (1982) interpreted such a situation with reference to yield traits in cotton in terms of a possible cancellation of component

effects, amounting to a disadvantageous role in limiting heterosis. Such a situation could be overcome by changes in gene combinations of parental lines or varieties. The genetic analysis based on parents, F1s and F2s, by Ramos (1985) has detected similar additive effects and also the epistasis of additive type, and to a large extent, the epistasis of dominance type for seed-oil percentage, seed index and seed-oil index. All additive and most epistatic parameters were positive. In cotton, selection for seed-oil content is possible (Ramos and Kohel 1987). Diallel analysis by Singh et al. (1985) detected non-additive genetic effects for control of protein and oil content in the seed from F1 plants of cotton.

Significant additive effects were detected for seed index among five out of six combinations; those in 1169×229 b) and 1060×59 b) were positively significant. The corresponding dominance component in these three cases was significant, positive and of a relatively higher order. Among those, in 1169×229 b), additive \times dominance component of epistasis was significant, in 1060×59 b) additive \times additive and additive \times dominance, and in 229×59 b) additive \times additive and dominance \times dominance effects were significant. Duplicate type of epistasis was noticeable in 1060×59 b), and in 229×59 b). The overall heterotic effects for the seed index trait were of a higher order, especially among progenies of backcrosses and reciprocals. Van Heerden (1969), Al-Rawi and Kohel (1969) and others earlier obtained significant GCA and SCA effects for seed index in cotton. Results from generation mean analysis of seed-oil index were closely comparable to those of seed index, as was to be expected.

Problems in estimation of genetic parameters are often associated with the presence of large extents of non-fixable epistatic variation. Other assumptions for the genetic analysis are that parental lines are highly inbred, that there are no reciprocal effects and that the genes effecting the traits measured are not linked. In the present study, all parents were highly inbred. The parents were not tested for linkage. Genetic estimates were generally consistent with earlier studies. Within-plant variation imposes a common limitation to genetic studies and to reciprocal backcrosses. The indeterminate flowering pattern of cotton results in a period of several weeks between the set of first and last bolls, which in turn are affected by environmental and internal factors. Lines by weeks of boll set interactions for seed-oil percentage in a study involving the low and high seed-oil parental lines used in the present investigation have been reported by Dani and Kohel (1987). Sampling of bolls set during the initial 4 weeks was considered adequate for determining uniform estimates of the performance potential. Contradictory results from reciprocal crosses would be due to minor differences in vegetative growth periods of the parental lines.

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