Seed-Oil Content of Glanded and Glandless Cottons

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Twelve cotton strains, six glanded and six glandless, with different seed-oil contents, were mated in a full diallel system. All genotypes were evaluated for seed-oil percentage (SO), seed index (SI, mg/seed) and seed-oil index (SOI, mg/seed) to obtain information on the inheritance of these traits and to assess the significance of maternal and reciprocal effects. Data generated from the diallel mating system were additionally divided into two full diallels, glanded and glandless, of six parents each and evaluated by combining ability and diallel analyses.

The results indicated that maternal effects were not statistically significant for any trait, but reciprocal effects were significant for SI and SOI. Additive effects, or general combining ability (GCA), were highly significant in both analyses. Deviations from additivity, or specific combining ability (SCA), were significant for SI and SOI, and for SO in the glanded diallel. Deviations from additivity were not homogeneous over all the genotypes. Only the additive parameter of the genetic analysis for glandless SO was significant. This result indicated that additivity was greater in crosses involving glandless genotypes. Heritability of 0.53 based on GCA values was obtained for SO, which indicated that selection procedures could be applied successfully to change the oil content of cottonseed.

The highest SO parent was glandless, and the glandless genotypic arrays averaged more SO than glanded arrays, indicating that glandless genotypes could be preferred over glanded in breeding for this trait.

Cottonseed oil is the most important secondary product of cotton, *Gossypium* spp., and it accounts for the second largest production of oil of all oilseed crops (1). A unique feature of cottonseed compared to other oilseeds is caused by the presence of gossypol in the seed. Gossypol is toxic, restricts the usage of cottonseed meal as feedstock (2) and increases the cost of processing (3). The overwhelming majority of presently grown cotton cultivars are of the glanded type, which have gossypol glands in the seed.

Relatively high heritabilities have been reported for seed-oil content (4,5), which indicates that oil content can be genetically modified in cotton. Since oil is the most important by-product of cottonseed, it is desirable to know the relationships of genetic components of glanded and glandless types that would have consequences for oil improvement. Glandless cottons are highly desirable from the industrial and end-user view. The objective of this study was to improve genetic understanding of both types of cotton and to ascertain the significance of maternal and reciprocal effects. These effects are useful information for breeding programs to improve seed-oil content because it would be possible to save one generation (season), or half the number of crosses, if reciprocals could be eliminated.

MATERIALS AND METHODS

The basic germplasm for this study consisted of the 12 parents, listed in Table 1. The parents originated from F_5 selections of lines having varied combinations of seed-oil content and presence or absence of gossypol glands (5). Thus, the germplasm was constituted of previously selected lines, which were treated as fixed effects in analyses of variance.

Crosses in all combinations and self-pollinations were made during the winter of 1982/83, under greenhouse conditions; F_1 and parent generations were grown in the field during the summer of 1983. A randomized complete block design was used with four blocks and five plants per plot, which were pooled. From this experiment, seed index (SI, mg/seed) averaged from 100 seeds and seed-oil percentage (SO) were measured from a 10-g sample of acid delinted seed dried at 40 C for 48 hr. SO was determined by wide-line nuclear magnetic resonance (NMR) using a Newport NMR. Seed-oil index (SOI) was obtained by the product SO SI/100. The generations used, F_0 and F_1, refer to the genotype of the bearing plants and not to the seeds themselves, which are advanced one generation. Griffing's combining ability analyses, hereafter referred to as Griffing (1), were performed by means of a Fortran program (6). Hayman's diallel analyses were performed by using a Fortran program developed by T. G. White and B. Lisenbe (personal communication). The SO full diallel table of 12 parents was additionally analyzed in glanded and glandless full diallels of six parents each.

The diallel analysis of variance (7) divides the genotype effects into components "a", "b", "c" and "d", which represents additive, dominance, maternal and reciprocal components, respectively. The "b" component can be divided further into the subcomponents "b_1", "b_2" and "b_3", representing average, array and specific dominance per cross, respectively. This secondary partitioning provides additional information when compared to the combining ability analysis.

TABLE 1

Cotton Parents Used, Their Origin, Average Seed Index (SI) and Seed-Oil (SO)[a]

Line no.	Origin	SI (mg/seed)	SO (%)
2	1169[b] × T	94	28.2
3	1169 × L	90	29.8
5	933 × T	84	26.7
6	933 × L	90	28.8
8	27 × T	94	26.8
9	27 × L	88	28.8
23	365 × T	98	25.8
24	365 × L	91	27.4
31	1060 × T	85	24.7
32	1060 × L	82	26.6
34	229 × T	92	24.7
35	229 × L	108	26.7

[a]Data from F_5 seed-oil selections from Kohel (1981, unpublished data). Glanded lines originated from the crosses with TAMCOT SP-37 (T), and glandless ones from LYMAN (L).

[b]Stoneville accession number (22).

The combining ability analysis of variance (8) is restricted to determining general and specific combining ability (GCA and SCA, respectively) and reciprocal effects. However, effects of both the diallel and combining ability analyses are interchangeable for the type of population used in this experiment, "a" = GCA, "b" = SCA and "c" + "d" is the reciprocal effect (9).

A genetic analysis (10) also was performed for the diallel. In this analysis, variances and covariances were computed to estimate the genetic parameters "D", "F", "H_1", "H_2", "h^2" and "E"; where "D" is the additive component, "F" is a measure of the covariance of additive and nonadditive components, "H_1" and "H_2" are average of array dominance, "h^2" is the net dominance over all loci, and "E" is the experimental error. H_2 is adjusted for gene frequence, and H_1 and H_2 are equal if the gene frequency is 0.50.

The standard errors of the genetic parameters were calculated by inverting the matrix product of the parameters' coefficient, but the product of the matrices was weighted by the inverse of the variances of the statistics calculated for each of the four blocks. The weighted matrix was used to compensate for lack of homogeneity of variances of the statistics to provide an estimation of unbiased standard deviations (11) for the genetic parameters.

RESULTS AND DISCUSSION

The results of the statistical analysis are shown in Table 2. Female (F), male (M) and the F*M interaction effects were significant (P = 0.05), but not the block interactions. The glanded and glandless results did not deviate from the combined diallel analysis. Since M represents the genetic component, and F includes genetic and maternal components, M is biologically the most adequate test for maternal component of F (12). On this basis, the maternal component of F was not significant in the three seed constituents evaluated, SO, SI and SOI. The seed index is determined by the bearing plant, and not by the genotype of the embryo (13). This finding means that seed size was more likely to reflect the bearing plant genotype than its own.

The statistical significance of the F*M interaction suggests that lines differ in response among crosses. However, the small magnitude of the mean square compared to the experimental error suggests that specific combining ability (SCA) was not as important as general combining ability (GCA), the latter referred to as the average of F and M. This was confirmed by the results of the combining ability analysis in Table 3. In general, GCA was the most significant effect after blocks. Therefore, SO, SI and SOI were controlled largely by additive gene action. SCA was statistically significant for SO in the glanded diallel analysis, but the magnitude was similar to the glandless which was not significant. SCA was also significant for SI and SOI, and accounts for derivations from additivity, either dominance or epistatic effects. Significant GCA and SCA were also reported for seed index (13).

The combining ability analysis indicated that all effects, except reciprocals, were significant for SI and SOI. However, once again the maternal component was not significant when tested against the reciprocal effect (12). Only one significant mean difference was found between the 12 female and male array means for SO and six for SI, three of which were positive and the others negative (Table 4). SOI was more closely related to SI than SO means, showing four positive and one negative mean difference. However, some means were above (heterosis) and others were below (depression) the parental means.

The results of the diallel analysis of variance are shown in Table 5. The "a" component (GCA) was the most prominent for all traits. The "b" component (SCA) was highly significant, although the magnitude was close to the experimental error of analysis of variance. The significance of the subcomponents "b_1", "b_2" and "b_3" suggests that dominance was not uniform over all genotypes and arrays. Partitioning of dominance indicated that average dominance was the most prevalent subcomponent for the glanded diallel and array dominance for the glandless diallel. Deviations from additivity (SCA) were also significant for SI and SOI in both analyses of variance (7,8).

The genetic parameters are meaningful if certain assumptions are met (10). Diploidy, parental homozygosity, and only genic differences between crosses and

TABLE 2

Mean Squares From Analysis of Variance of Seed-Oil Percentage (SO), Seed Index (SI) and Seed-Oil Index (SOI)[a]

		SO				
Source	df[b]	Glanded	Glandless	Both	SI	SOI
Blocks (R)	3	40.86*,[c]	24.78**	129.95**	4.53**	2.96**
Female (F)	11	11.91**	6.69**	28.54**	5.24**	0.92**
Male (M)	11	10.93**	10.76**	21.03**	6.54**	0.74**
F*M	113	1.52*	1.74	1.93**	1.21**	0.10**
R*F	33	0.72	0.85	0.93	0.45	0.04
R*M	33	0.58	1.35	1.03	0.53	0.07
Error	243	0.82	1.60	1.21	0.63	0.07

[a] For complete diallel cross system (F_0, F_1, reciprocals) of 6 glanded, 6 glandless and the 12 combined cotton lines.

[b] Refers to the diallel experiment of 12 parents.

[c] *,**, Significant at 0.05 and 0.01 level of probability, respectively.

TABLE 3

Mean Squares for Combining Ability Analysis of Seed Oil Percentage (SO), Seed Index (SI) and Seed-Oil Index (SOI)[a]

		SO				
Source	df[b]	Glanded	Glandless	Both	SI	SOI
Blocks	3	44.41**,[c]	44.63**	160.82**	6.39**	3.89**
GCA	11	23.29**	24.29**	49.47**	11.67**	1.51**
SCA	65	1.68**	1.85	1.30	1.15**	0.11**
Maternal	11	1.07	1.43	1.83	1.49**	0.18**
Reciprocal	48	1.16	1.18	1.71	1.12**	0.13**
Error	309	0.76	1.45	1.08	0.39	0.04

[a] For a complete diallel cross system (F_0, F_1, reciprocals) of 6 glanded, 6 glandless and the 12 combined cotton lines.

[b] Referred to the diallel experiment of 12 parents.

[c] *,**, Significant at 0.05 and 0.01 level of probability, respectively.

reciprocals are relatively easy to meet. Cotton is an allotetraploid species, but behaves like a diploid (14–16). The strains used in this experiment had six generations of selfing, therefore providing high levels of homozygosity. Furthermore, reciprocal differences also can be accommodated in the model of genetic analyses (10).

Homogeneity of variances of genotypes can be tested by a Bartlett chi-square test. However, other assumptions, like absence of epistasis, no gene correlation (or independent gene distribution) and no multiple allelism, can be tested only indirectly. The analysis of variance of (Wr − Vr) (covariance between parents and their offspring means, minus the variance of offspring arrays with a common parent) can be used to test these assumptions (10). Results of this test (not shown) indicated that none of the assumptions was violated. Appreciable amounts

TABLE 4

Parental (F_0), Female (F) and Male (M) Array Means and Significance of Maternal Mean Effect (F-M) for Seed-Oil Content (SO), Seed Index (SI) and Seed-Oil Index (SOI)[a]

	SO (%)				SI (mg/seed)				SOI (mg/seed)			
Genotypes	F_0	F	M	(F-M)	F_0	F	M	(F-M)	F_0	F	M	(F-M)
2	27.6	28.9 b[b]	28.7 c	—	102.4	101.0 ab	97.9 b	[a]	28.3	29.3 cd	28.1 cd	*
3	31.9	29.8 a	29.8 a	—	117.1	102.5 ab	105.3 a	*	37.4	30.6 a	31.5 a	—
5	28.4	28.8 b	28.9 bc	—	92.2	94.1 e	96.1 cd	—	26.2	27.0 f	27.9 cde	—
6	30.6	30.0 a	29.3 ab	*,[c]	94.8	95.3 de	93.4 d	—	29.0	28.6 de	27.4 de	*
8	30.4	29.7 a	29.5 ab	—	102.4	101.8 ab	98.0 b	*	31.2	30.2 ab	28.9 bc	*
9	30.2	29.7 a	29.4 ab	—	88.3	99.8 bc	96.9 bc	*	26.7	29.6 abc	28.5 bc	*
23	27.0	28.2 cd	28.0 d	—	102.6	104.2 a	104.2 a	—	27.7	29.3 bcd	29.2 b	—
24	26.9	28.5 bc	28.8 c	—	89.4	94.2 e	97.1 b	*	24.1	26.8 fg	28.0 cd	*
31	26.2	27.5 e	27.9 de	—	87.6	94.5 e	93.9 cd	—	23.0	26.0 g	26.2 f	—
32	26.8	28.0 d	27.9 d	—	91.9	92.9 e	93.1 d	—	24.7	26.0 g	26.0 f	—
34	26.2	27.3 e	27.6 de	—	94.7	97.8 cd	97.9 b	—	24.9	26.7 fg	27.0 ef	—
35	27.5	27.4 e	27.4 e	—	102.7 ab	102.4 ab	106.5 a	*	28.2	28.1 e	29.2 b	—
LSD$_{0.05}$	0.7	0.4	0.4		4.3	2.6	2.6		1.4	0.8	0.8	

[a] From a complete F_1 diallel cross system of cotton lines.

[b] Duncan's multiple range test at 0.05 level of probability.

[c] *, Significant at 0.05 level of probability.

TABLE 5

Mean Squares from Hayman's (7) Analysis of Variance for Seed-Oil Percentage (SO), Seed Index (SI) and Seed-Oil Index (SOI)[a]

		SO				
Source	df[b]	Glanded	Glandless	Both	SI	SOI
Genotypes (G)	143	4.83**,[d]	6.75**	6.29**	1.847**	0.235**
Blocks (R)	3	47.49**	49.83**	178.66**	8.358**	4.366*
G*R	429	0.68	0.95	0.84	0.357	0.036
a	11	24.78**	35.44**	61.23**	12.113**	1.721**
b	66	1.93	2.03	1.61**	1.028**	0.104**
b_1	1	8.36**	0.21	7.76**	1.125**	0.271**
b_2	11	1.37	4.75**	3.08**	1.184**	0.172**
b_3	54	1.52	0.73	1.07	0.994**	0.087**
c	11	0.92	2.01	2.73**	0.700	0.177**
d	55	1.17	1.85	1.74**	0.892**	0.106**
R*a	33	0.60	0.94	0.81	0.441	0.037
R*b	198	0.82	1.06	0.89	0.314	0.034
R*b_1	3	0.06	1.37	1.09	0.208	0.004
R*b_2	33	0.71	1.04	0.54	0.322	0.032
R*b_3	162	0.97	1.15	0.96	0.317	0.035
R*c	33	0.44	1.03	0.80	0.603	0.055
R*d	165	0.62	0.75	0.79	0.343	0.033
(Error)[c]	(309)	(0.82)	(1.60)	(1.21)	(0.63)	(0.070)

[a] From an F_1 diallel cross system (F_0, F_1, reciprocals) of 12, 6 glanded and 6 glandless cotton lines.

[b] Applicable to the diallel experiment of 12 parents.

[c] From experiment analysis of variance.

[d] *,**, Significant at 0.05 and 0.01 level of probability, respectively.

TABLE 6

Parameters of Hayman's (10) Genetic Analysis with Standard Deviations[a]

	SO				
Parameters	Glanded	Glandless	Both	SI	SOI
D	2.45 ± 1.09	4.26 ± 1.56*,[b]	3.47 ± 0.92*	0.59 ± 0.53	0.14 ± 0.17
F	0.60 ± 1.40	1.96 ± 1.80	1.24 ± 1.53	0.24 ± 0.88	0.09 ± 0.28
H_1	0.98 ± 3.35	1.28 ± 5.90	0.69 ± 2.77	0.42 ± 1.53	0.06 ± 0.48
H_2	0.84 ± 3.04	0.70 ± 5.48	0.41 ± 2.18	0.27 ± 1.11	0.03 ± 0.34
h^2	0.81 ± 0.87	0.07 ± 1.62	0.58 ± 0.67	−0.02 ± 0.17	0.01 ± 0.05
E	0.68 ± 1.53	0.95 ± 2.75	0.84 ± 1.09	0.36 ± 0.55	0.17 ± 0.17

[a] Estimated from the F_1 full diallel cross system of 6 glanded, 6 glandless and the 12 combined cotton lines, for seed-oil content (SO), seed index (SI) and seed-oil index (SOI).

[b] Significant at 0.05 level of probability.

of epistasis for SI were reported in the literature (17–19). Because SOI was a product of SO by SI, it also could be affected by epistasis in SI. Indeed, the power of the analysis of (Wr − Vr) array variance in detecting failure of assumptions has been questioned (20,21).

Results of the genetic analysis (Table 6) indicated that only the additive component ("D") was significant for SO, and none were significant for SI and SOI. Further partitioning indicated the "D" parameter was significant only for the glandless diallel. This result suggests that additive effects are more evident in crosses involving glandless parents. High heritability was reported in the literature for SO (4,5); thus, a significant additive component was expected. In fact, heritability of 0.53 was found in this experiment, using the combining ability analyses procedure.

The lack of significance of the genetic parameters for SI and SOI indicated that the genetic model was not adequate, or that some of the assumptions were violated and not detected. However, the combining ability and diallel analysis demonstrated that GCA was highly significant for both traits, which indicated that progress can be made through selection procedures. Furthermore, the averages for SO glandless genotypic arrays were higher than for glanded ones. The highest glandless SO parent (line no. 3) could be used as a source of high oil in breeding programs. Because SO and SI were independently correlated (r = 0.15), genetic improvement can be achieved for both traits.

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