THE TRANSMISSION OF MARKER GENES IN INTRASPECIFIC BACKCROSSES OF GOSSYPIUM HIRSUTUM L.

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ONE polyploid species, *Gossypium hirsutum* L., commonly called American Upland cotton, accounts for practically all the cotton produced in the United States. RICHMOND (1951) stated that " Reselection within varieties, and even within the progeny of varietal hybrids, over a period of many years inevitably has resulted in severe inbreeding and the elimination of many beneficial as well as deleterious genes which were present in the native stocks. Since American Upland varieties in the United States are all interrelated and probably descended from not more than a dozen original introductions, it is doubtful if future requirements of special fiber properties, disease, insect, and drought resistance, mechanical harvesting, and other specialized uses and properties can be met by the usual selection methods restricted to present cultivated varieties." Because of the need for greater genetic variability plant breeders are attempting to improve American Upland cotton by transferring to it genes from the tetraploid species, *G. barbadense* L., and from induced polyploids which are combinations of diploid species. The success of this program depends on an understanding of the differences in behavior of intraspecific and interspecific hybrid material.

A thorough review of interspecific cotton hybrids was given by STEPHENS (1950), who concluded that in addition to multiple gene substitution it is necessary to assume small structural differences between the chromosomes of the closely related genomes.

STEPHENS (1949) produced an F_1 hybrid between marked lines of *G. hirsutum* and *G. barbadense*. When the F_1 was backcrossed to each parent, there was considerable selective elimination of the donor parent genotype. The conclusion was that these results were peculiar to this interspecific hybrid, and reasons were given for believing that the chromosomes of the two species contained cryptic structural differences. The evidence for this conclusion was not completely critical, since the absence of selective elimination was not demonstrated in intraspecific backcrosses. It is possible that the selective elimination of the donor parent genotype was caused by the particular marker stock used or by the marker genes *per se*. Additional evidence would be furnished by a study of intraspecific backcrosses using similarly marked stocks of the one species, *G. hirsutum*. The purpose of this paper is to describe the transmission of marker genes in intraspecific backcrosses of certain stocks of *G. hirsutum*.

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METHODS

The *G. hirsutum* stocks used in this experiment were (1) SL 7-9, a multiple marker line carrying five dominant genes and one recessive gene, (2) Pubescent, (SIMPSON 1947), carrying contrasting alleles to those of SL 7-9 at the same six loci, and (3) Deltapine 14, a commercial variety carrying recessive genes at all six loci. The genetic constitution of each of these lines is shown in table 1.

A cross was made between SL 7-9 and Pubescent. The F_1 was backcrossed to each parent and crossed to the recessive tester stock, Deltapine 14. Although the cross of the $F_1 \times$ Deltapine 14 is not strictly a backcross, it will be considered as such for simplicity of discussion. The three backcross progenies were grown in the field in 1950 in a simple randomized block design. The randomized design was not necessary for the analysis of qualitative characters, but was used as a precaution against the loss or damage of plants in any particular spot in the experimental area. Each plant was scored for all characters that could be distinguished with certainty; the data from all replications were

TABLE 1

Genetic constitution of G. hirsutum marker lines.

SL 7-9		Pubescent		Deltapine 14	
R_1	Red plant body	r_1	Green plant body	r_1	Green plant body
R_2^{AF}	Weak spot	R_2^{AO}	Spotless	R_2^{AO}	Spotless
K	Brown lint	k	White lint	k	White lint
N	Naked seed	n	Not naked (fuzzy) seed	n	Not naked (fuzzy) seed
L^o	Narrow leaf	l	Broad leaf	l	Broad leaf
pb	Non-pubescent leaf	Pb	Pubescent leaf	pb	Non-pubescent leaf

pooled. Homozygous dominants could not be distinguished accurately from heterozygous individuals for petal spot, brown lint, naked seed, and pubescent leaf. In the backcross to SL 7-9, only the genes for plant body color, leaf shape, and leaf pubescence could be scored. In the backcross to Pubescent, all characters could be scored with ease except leaf pubescence. With the possible exception of petal spot, no difficulty was encountered in classifying any of the six characters in the backcross to Deltapine 14. The cross to Deltapine 14 was also used to test the linkage relationships between the pubescent gene and the five independent marker genes in SL 7-9.

RESULTS

The data from the backcrosses of F_1 SL 7-9 $\times$ Pubescent to SL 7-9, Pubescent, and Deltapine 14 are given in table 2. Chi-square values were calculated for each of the monofactorial segregations and, with one exception, none were significantly different from a 1 : 1 ratio. The segregation of the R_2^{AF}: R_2^{AO} genes in the $F_1 \times$ Deltapine 14 cross showed a deficiency of spot and an excess of spotless petals. The gene R_2^{AF} in the heterozygous condition often expresses itself so weakly that careful examination by a hand lens or a dissecting micro-

scope is necessary to detect a few colored cells in the petals. It is possible that in scoring the segregates of the $F_1 \times$ Deltapine 14 cross some weakly spotted flowers might have been scored as spotless when classified by the unaided eye in the field; however, the same alleles gave a good fit to a 1 : 1 ratio in the cross, $F_1 \times$ Pubescent. Why the R_2^{AF} gene would express itself more clearly in a cross with Pubescent than with Deltapine is not apparent from the data available.

STEPHENS (1949) reported a highly significant deficiency of the *K* type in the segregation of *K* : *k* in the backcross to *hirsutum* and a deficiency that almost reached significance in the backcross to *barbadense*. In the present work the segregation of *K* : *k* gave a good fit to a 1 : 1 ratio in crosses of $F_1 \times$ Pubescent and $F_1 \times$ Deltapine 14. This finding demonstrates again that the white lint gene *per se* has no selective advantage over its brown lint allele.

TABLE 2

Monofactorial segregation in backcrosses of intraspecific G. hirsutum hybrids. F_1 refers to SL 7-9 × Pubescent and alleles from the SL 7-9 stock are shown on left in each case.

	R_1	r_1	R_2^{AF}	R_2^{AO}	K	k	N	n	L^0	l	pb	Pb
$F_1 \times$ Pubescent	251	271	257	260	253	267	252	268	253	269	....	....
χ^2 (1 : 1)	.766		.017		.377		.492		.490		....	
P (1)	.30–.50		.80–.90		.50–.70		.30–.50		.30–.50			
$F_1 \times$ SL 7-9	249	256	....	....	....	....	....	....	241	264	254	251
χ^2 (1 : 1)	.097		....		....		....		1.048		.018	
P (1)	.70–.80								.30–.50		.80–.90	
$F_1 \times$ Deltapine 14	292	293	250	331	314	269	281	302	287	298	302	283
χ^2 (1 : 1)	.001		11.293**		3.473		.756		.207		.617	
P (1)	.98		<.01		.05–.10		.30–.50		.50–.70		.30–.50	

** = significance at .01 level of probability.

The monofactorial segregations of all the genes, except the questionable classification of petal spot, did not deviate significantly from a 1 : 1 ratio; however, the gene from the donor parent was deficient in all five classifications in the cross, $F_1 \times$ Pubescent, and in one of the three classifications of $F_1 \times$ SL 7-9. In the cross, $F_1 \times$ Deltapine 14, the gene from SL 7-9 was deficient in four out of six classes. Although the individual segregations were not significantly different from a 1 : 1 ratio, the cumulative effect of slight deficiencies in several genes might be significant. To investigate this possibility, the frequencies of SL 7-9 genes expected on the basis of random recombination were calculated and compared with the actual numbers observed. This was done by expanding the binomial $(\frac{1}{2} + \frac{1}{2})^n$, where *n* is the number of marker genes that could be scored with certainty in each cross. The gene for petal spot was omitted from the cumulative totals since the classification was not considered completely reliable. In table 3 the actual numbers obtained are compared with the numbers expected. Chi-square values calculated from these data show that in each backcross the deviations from the expected on the basis of random recombinations are not great enough to be significant.

TABLE 3

Frequency of plants carrying various numbers of SL 7-9 marker genes in crosses of (a) F_1 × Pubescent, (b) F_1 × SL 7-9, and (c) F_1 × Deltapine 14 where the F_1 was SL 7-9 × Pubescent.

No. of SL 7-9 markers	5	4	3	2	1	0	Total	
(a) F_1 × Pubescent								
Expected $(\frac{1}{2} + \frac{1}{2})^4$	....	32.375	129.500	194.250	129.500	32.375	518	
Actual	....	24	138	174	146	36	518	
χ^2	....	2.167	0.558	2.111	2.102	0.406	7.344	(P(4) = .10–.20)
(b) F_1 × SL 7-9								
Expected $(\frac{1}{2} + \frac{1}{2})^3$	....	....	62.5	187.5	187.5	62.5	500	
Actual	....	....	61	178	197	64	500	
χ^2	....	....	0.036	0.481	0.481	0.036	1.034	(P(3) = .50–.95)
(c) F_1 × Deltapine 14								
Expected $(\frac{1}{2} + \frac{1}{2})^5$	18.125	90.625	181.250	181.250	90.625	18.125	580	
Actual	10	100	188	181	82	19	580	
χ^2	3.642	0.970	0.251	0.000	0.821	0.042	5.726	(P(5) = .30–.50)

TABLE 4

Segregation of pubescence in linkage tests with five independent marker genes in SL 7-9 using the cross (SL 7-9 × Pubescent) × Deltapine 14.

Pubescence with:	Frequency of genotypes				Total	χ^2 1:1:1:1	P(3)
Plant body color	R_1 Pb	R_1 pb	r_1 Pb	r_1 pb			
	144	148	139	154	585	0.83	.80–.90
Lint color	K Pb	K pb	k Pb	k pb			
	155	159	127	142	583	4.30	.20–.30
Seed cover	N Pb	N pb	n Pb	n pb			
	142	134	140	159	575	2.39	.30–.50
Leaf shape	L^0 Pb	L^0 pb	l Pb	l pb			
	142	145	141	157	585	1.11	.70–.80
Petal spot	R_2AF Pb	R_2AF pb	R_2AO Pb	R_2AO pb			
	122	128	158	172	580	11.83**	.001–.01
R_2AF *vs.* R_2AO	250		330			11.03**	.01–.02
Pb *vs.* pb	280		300			0.69	.80–.90
Linkage	294		286			0.11	.99–1.00

** = significance at .01 level of probability.

The linkage relationship of the Pubescent gene, *Pb,* had not previously been tested with the marker genes in SL 7-9. As shown in table 4, pubescence was found to be independent of the five other genes. The significant Chi-square for the segregation of petal spot and pubescence was due to the excess of spotless over spotted petals and not to any linkage relationship between the two genes.

DISCUSSION

In intraspecific backcrosses involving certain marked stocks of *G. hirsutum,* the marker genes were recovered as expected on the basis of random recombination. Each allele and combination of alleles proved to be equally viable both in gametes and in zygotes. The deficiency of the petal spot, R_2^{AF}, allele in the backcross to Deltapine 14 was considered to be a matter of reduced expressivity rather than an actual elimination of the gene.

SL 7-9, Pubescent, and Deltapine 14 vary in several quantitative characters and must differ by many genes other than the six qualitative ones with which this study is concerned, but no genic or structural differences interfered with the recovery of the marker genes in the backcross progenies. In view of the regular behavior of the intraspecific hybrids studied in this experiment, it is reasonable to infer that neither the marker genes *per se* nor the particular *G. hirsutum* line used were responsible for the disturbed ratios found in STEPHENS' (1949) material. The selective elimination of the donor parent genotype in interspecific backcrosses must have been caused by genic or structural differences between the " homologous " chromosomes of the two species, *G. barbadense* and *G. hirsutum.*

The Pubescent gene, *Pb,* was independent of five qualitative genes used in the study.

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