

THE CYTOGENETICS OF SPECIATION IN GOSSYPIUM. I.
SELECTIVE ELIMINATION OF THE DONOR PARENT
GENOTYPE IN INTERSPECIFIC BACKCROSSES

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THE cultivated amphidiploid species, *G. hirsutum* L. and *G. barbadense* L., cross readily and the F₁ hybrid shows regular bivalent pairing and is apparently fully fertile. F₂ progenies show considerable depression in vigor, and the net effect of inbreeding is the establishment of types practically indistinguishable from the parent species. All intermediate types are at a great selective disadvantage and fail to establish themselves. A similar situation is found in the hybrid progenies of the Asiatic cultivated diploid species, *G. arboreum* L. and *G. herbaceum* L.

HARLAND's interpretation of these phenomena (see HARLAND 1933, 1936, 1939) is that the species differences are mainly attributable to differences in "genetic architecture." Through natural selection an integrated system of modifier complexes is built up which is characteristic of each species. When different species are intercrossed, modifier segregation occurs in F₂ and later generations, with a consequent mutual disruption of the two internally balanced parental systems. Species differences on this basis would be independent of structural differentiation of the chromosomes, and the respective genomes could remain cytologically homologous throughout. The regular bivalent pairing and full fertility of the F₁ hybrid has been usually considered to support HARLAND's hypothesis (SILOW 1941, 1944; DOBZHANSKY 1941; MATHER 1943). For a contrary viewpoint see GOLDSCHMIDT (1940).

In a recent review (STEPHENS 1949b) the writer has suggested an alternative interpretation, and has cited lines of evidence from cytological, genetic and plant breeding sources, which show collectively that something more than multiple gene substitution has been responsible for the differentiation of these species. It has been pointed out that regular bivalent pairing is not a valid criterion of structural homology when the chromosomes are small and the chiasma frequency low. Preferential pairing in synthetic allotetraploids, selective elimination of genes from the donor parent in certain interspecific backcrosses, block transference of linked complexes in others, and the frequency of pseudo-allelic complexes, all suggest that the chromosomes of different species of *Gossypium* have manifold small scale structural differences which are not easily detected by cytological methods. For this type of differentiation, STEBBINS (1945, 1947) has used the convenient term "cryptic structural differentiation."

The evidence for cryptic differentiation is at present only to be found in data

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accumulated for other purposes, and it is important that tests now be set up for the specific purpose of determining its extent and importance in the speciation mechanism. Three possible tests have been briefly indicated (STEPHENS, *loc. cit.*), and it is the purpose of this paper to consider the results of only one of these.

METHODS

If interfertile species have cryptic structural differences it is likely that crossing over between corresponding but only partially homologous chromatids in the F_1 hybrid will lead to the production of gametes containing several small deficiencies and duplications. In *Gossypium* species the typical situation during meiosis is for two chiasmata to be produced (one per chromosome arm)

TABLE 1
Genetic constitution of parents and tester stocks

Parents				Backcross Testers			
<i>hirsutum</i>		<i>barbadense</i>		7 independent loci		5 independent loci	
R_1	Red plant body	r_1	Green plant body	r_1	Green plant body	r_1	Green plant body
R_2^{AF}	Weak spot	R_2^{AS}	Full spot	R_2^{AO}	Spotless	R_2^{AS}	Full spot
p	Cream pollen	P	Yellow pollen	p	Cream pollen	P	Yellow pollen
y	Cream petal	Y	Yellow petal	y	Cream petal	Y	Yellow petal
K	Brown lint	k	White lint	k	White lint	k	White lint
N	Naked seed	n	Not Naked (tufted)	n	Not Naked (fuzzy)	n	Not Naked (tufted)
L^O	Narrow leaf		seed		seed		seed
Cr^H	"Low" Normal	L^B	Intermediate leaf	l	Broad leaf	L^B	Intermediate leaf
		Cr^B	"High" Normal	Cr^H	"Low" Normal	cr^D	Crinkled

resulting in a ring bivalent at Metaphase I. In interspecific hybrids several of the paired chromosomes only form one chiasma and a rod bivalent results. A type of selection may therefore be envisaged in interspecific backcrosses which would tend to eliminate gametes carrying crossover chromatids, and favor gametes containing non-crossover chromatids. It is likely, too, that non-crossover chromatids of the *recurrent* parent type would have a selective advantage over non-crossover chromatids of the *donor* parent type, since KEARNEY and HARRISON (1932) have shown that selective fertilization occurs in favor of *barbadense* pollen when mixed *barbadense* and *hirsutum* pollen is applied to *barbadense* stigmas, and in favor of *hirsutum* pollen when the mixed pollen is applied to *hirsutum* stigmas. The net effect to be expected, therefore, would be a selective elimination of the donor parent genotype. This may be tested by introducing suitable marker genes into the two species under investigation, making an interspecific hybrid heterozygous for several independent gene pairs, and testing their segregations in reciprocal backcrosses. On the basis of random recombination none of the segregations obtained should differ significantly from a 1:1 ratio but if preferential elimination of gametes occurs the ratios should be skewed due to deficiencies in the classes containing genes from the donor parent.

The stocks chosen for experiment were (1) a line of Upland cotton (*G. hirsutum*) carrying six dominant and two recessive independent marker genes which has been maintained in the genetic collection at this station and (2) an inbred line of Seaberry Sea Island (*G. barbadense*) which carries contrasting alleles to those carried by the Upland stock at the same eight loci. The detailed constitutions of these stocks are shown in table 1. The interspecific hybrid obtained by crossing these two stocks was thus heterozygous for eight marker genes. Ideally the gametes of this hybrid should have been tested by crossing to multiple recessive stocks of both *barbadense* and *hirsutum*. Unfortunately such stocks were not available, and the *hirsutum* stock used (Delta-pine 14) only tested seven out of the eight loci. The *barbadense* stock (Sea Island Crinkle) only tested five loci. The detailed constitutions of these tester stocks are also shown in table 1. Backcrosses, *i.e.* crosses to the tester stocks were carried out reciprocally ($F_1 \text{♀} \times \text{tester } \text{♂}$ and $\text{tester } \text{♀} \times F_1 \text{♂}$).

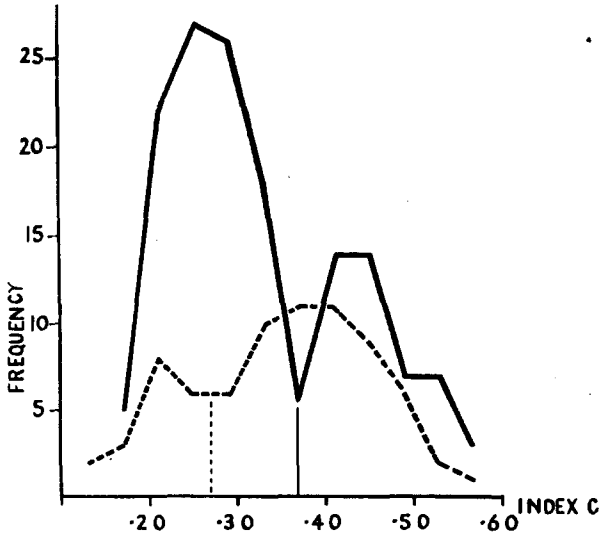


FIGURE 1.—Frequency distributions of leaf shape indices in the backcross, $F_1 \times \textit{hirsutum}$ (solid line), and the backcross, $F_1 \times \textit{barbadense}$ (broken line). For additional information see text.

No difficulty was encountered in scoring the backcrosses, as the alternative classes were sharply distinct and with the exception of the leaf shape segregations could be scored visually. In order to classify the leaf shape segregations a climax leaf from each plant was measured and its Index C value calculated according to SILOW'S (1939) method. Frequency distributions of Index C values for both backcrosses (data from reciprocal backcrosses being pooled) are shown in figure 1. It can be seen that in both cases the frequency distributions are bimodal corresponding to the alternative leaf shape classes expected.

The point of minimum frequency was taken as the point of demarcation between genotypes, and the segregations were classified on this basis as follows:

		<i>Class</i>	<i>Index C</i>
(1)	$F_1 (L^O/L^E) \times hirsutum (l)$	$L^O/l \dots$	0.16-0.36
		$L^E/l \dots$	0.38-0.56
(2)	$F_1 (L^O/L^E) \times barbadense (L^E)$	$L^O/L^E \dots$	0.12-0.26
		$L^E/L^E \dots$	0.28-0.56

A word of explanation is necessary about the Crinkle (*Cr*) locus. The alleles, Cr^B and Cr^H both give a normal phenotype but differ in dominance potency (HUTCHINSON 1946a). The heterozygote, Cr^B/cr^D , is phenotypically normal, while Cr^H/cr^D is weakly Crinkled.

RESULTS

The complete data for the backcrosses ($F_1 \times hirsutum$ tester, $F_1 \times barbadense$ tester and the corresponding reciprocals) are given in table 2. The segregations of the different allelomorphic pairs are listed in double columns, the left hand column in each case representing the gene from the *hirsutum* parent.

TABLE 2

Monofactorial segregations in reciprocal backcrosses of the interspecific hybrid hirsutum × barbadense. Alleles from the hirsutum parent are listed in the left hand column in each case.

	R_1	r_1	R_2^{AF}	R_2^{AS}	p	P	y	Y	K	k	N	n	L^O	L^E	Cr^H	Cr^B
(a) <i>hirsutum</i> ♀ × F_1 ♂	34	23	39	12	31	25	32	24	22	35	24	33	34	23	—	—
F_1 ♀ × <i>hirsutum</i> ♂	54	47	50	38	47	44	48	43	25	63	45	44	69	31	—	—
(a) Combined data	88	70	89	50	78	69	80	67	47	98	69	77	103	54	—	—
Heterogeneity χ^2	0.555		4.988		0.191		0.268		1.436		0.994		1.270		—	—
P (1)	.30-.50		.02-.05		.50-.70		.50-.70		.20-.30		.30-.50		.20-.30		—	—
χ^2 (1:1)	2.051		10.942		0.551		1.150		17.940		0.438		15.293		—	—
P (1)	.10-.20		v. low		.70-.80		.20-.30		v. low		.50-.70		v. low		—	—
(b) <i>barbadense</i> ♀ × F_1 ♂	3	10	—	—	—	—	—	—	6	6	5	7	6	7	4	9
F_1 ♀ × <i>barbadense</i> ♂	37	27	—	—	—	—	—	—	21	36	28	29	13	51	22	42
(b) Combined data	40	37	—	—	—	—	—	—	27	42	33	36	19	58	26	51
Heterogeneity χ^2	5.215		—	—	—	—	—	—	0.686		0.221		2.887		0.056	
P (1)	.02-.05		—	—	—	—	—	—	.30-.50		.50-.70		.05-.10		.80-.90	
χ^2 (1:1)	0.117		—	—	—	—	—	—	3.261		0.130		19.753		8.117	
P (1)	.70-.80		—	—	—	—	—	—	.05-.10		.70-.80		v. low		.001-.01	

Significant differences at 5 percent level shown in bold type. For evidence of allelomorphism of genes listed see HARLAND 1929a ($R_1=R$ and $R_2=S$ in his nomenclature), 1929b (P), 1929c (V), 1935 (K), 1938 (N); STEPHENS 1945 (L); HUTCHINSON 1946a (Cr).

The backcross, hirsutum tester × F₁, and its reciprocal. The results of this backcross are shown in table 2 (a). Of the seven independent monofactorial segregations tested only one ($R_2^{AF}:R_2^{AS}$) shows a significant difference between

reciprocal crosses. In this case χ^2 for heterogeneity is just significant at the 5 percent level of probability. Inspection shows, however, that in both crosses there is a deficiency in the R_2^{AS} class, and since the object of the experiment was to test the direction rather than degree of skewness, it seems permissible to pool the data from the two crosses. Considering, therefore, the combined data it can be seen that in five out of the seven segregations tested, the class containing the gene from the *hirsutum* parent is in excess of that expected on a 1:1 basis and in two of these five cases the deviation is highly significant, viz. in the segregations $R_2^{AF}:R_2^{AS}$ and $L^O:L^E$. In the remaining two segregations, a reverse situation is found—the classes containing genes from the *barbadense* parent are in excess and in one case ($K:k$) the deviation is highly significant.

The backcross, barbadense tester $\times F_1$, and its reciprocal. The results are shown in table 2 (b). Unfortunately only a small family of the cross *barbadense* tester $\text{♀} \times F_1 \text{♂}$ was available for study, so that no adequate test could be made for possible reciprocal differences. One significant difference between reciprocal crosses was found, in the segregation $R_1:r_1$, where the ratios are skewed in opposite directions. However, the numbers in the first family are so small that they cannot materially affect the ratios obtained in the second family, so that the combined data may be considered as in the case of the *hirsutum* backcrosses in table 2 (a). Of the five segregations recorded, four show an excess in the class containing the gene from the *barbadense* parent and in two of these the deviation from a 1:1 ratio is highly significant, viz. in the segregations $L^O:L^E$ and $Cr^H:Cr^B$.

Comparison between reciprocal crosses in the two backcrosses. Reciprocal differences are only tested adequately in the backcross to *hirsutum*. Nevertheless within the limits of the material studied there seems to be no over-all tendency for selective elimination to be affected by the way in which the cross is made. More precisely there is no consistent tendency for selective elimination to be greater in the F_1 pollen than in the F_1 ovules. This does not imply that gametic selection is unimportant, and in fact there is some evidence that selective elimination in both male and female gametes rather than zygotic selection is mainly responsible for the skewed backcross ratios. It was noticed in making the backcrosses that when the F_1 was used as female about eight to ten percent of the seeds were abortive ("motes"), while when the F_1 was used as male not more than two percent abortive seeds occurred i.e. probably not more than would occur by chance in the self fertilized parental species. It is clear that if elimination occurred in the zygote the same proportion of motes should occur whichever way the cross was made, so the most likely situation is that elimination occurs both in the male and female gametes. Elimination in the former cannot be tested directly since there is no adequate technique available for testing the viability of cotton pollen (IYENGAR 1939; STEPHENS 1942) but the absence of heterogeneity in most of the reciprocal backcross segregations does suggest that elimination may be of the same order in male and female gametes.

Comparison between backcross to hirsutum and backcross to barbadense. In

comparing the segregations obtained in backcrosses to *hirsutum* and backcrosses to *barbadense* it will be convenient to consider each allelic pair separately. The segregation $L^O:L^B$ (tables 1 (a) and (b)) gave highly significant deviations from a 1:1 ratio in both backcrosses, and it can be seen that in both cases there is a selective elimination of the allele carried by the donor parent. Thus in the backcross to *hirsutum* the L^O class is in excess of the L^B class while the reverse situation is found in the backcross to *barbadense*. This reversal shows that the deviations cannot be due to the effects of the alleles themselves, and suggests strongly that there is a selection against the chromosome segment from the donor parent which is marked by the particular locus. In other words it is consistent with the hypothesis that the corresponding leaf shape chromosomes of *hirsutum* and *barbadense* are structurally differentiated. This interpretation is supported by independent evidence (STEPHENS 1949b) that the leaf shape genes are apparently transferred with a block of linked genes in backcrosses of *hirsutum* to *barbadense* and vice versa.

In the case of the $Cr^H:Cr^B$ segregation (table 2 (b)) there is a marked deficiency of the gene from the donor parent in the backcross to *barbadense*. Owing to the absence of a suitable tester stock no comparable data could be obtained in the backcross to *hirsutum*. However, HARLAND'S data (1932) do provide this information. They show that in a first backcross of *barbadense* to *hirsutum* of the constitution $Cr^H/cr^D(F_1) \times Cr^H$ (*hirsutum*) the class containing the gene from the donor parent is markedly deficient. It seems likely that the Crinkled chromosomes of *hirsutum* and *barbadense* may also be structurally differentiated. Again this interpretation is supported by independent evidence, as the Crinkled "locus" and the closely linked Corky "locus" are suspected to constitute a complex of pseudo-alleles (STEPHENS 1949a), and the strength of the linkage between Green lint and Crinkled is altered after transference from *barbadense* to *hirsutum* (STEPHENS 1949b).

In the backcross to *hirsutum* (table 1 (a)) the segregation $R_2^{AF}:R_2^{AS}$ shows selective elimination of the gene R_2^{AS} from the donor parent. This situation is in agreement with HARLAND'S early data (1929a) where a 4th backcross involving the same locus, *viz.* *hirsutum* spotless \times (*hirsutum* spotless \times *barbadense* full spot), segregated 579 spot: 706 spotless—a highly significant deficiency of the donor parent class. Unfortunately no comparable data are available for the backcross to *barbadense*.

The only significant deviation from a 1:1 ratio which cannot be interpreted as the result of selective elimination of a gene from the donor parent, occurs in the segregation $K:k$ in the backcross to *hirsutum* (table 1 (a)). Here there is a highly significant deficiency of K types, *i.e.* in this case the gene from the donor parent has an apparent selective *advantage* over its allele from the recurrent parent. No explanation can at present be offered for this phenomenon. The segregating types were readily classified and there appears to be no suggestion in previous literature (WARE 1932; HARLAND 1935; HUTCHINSON 1946b) that the white lint gene *per se* has any selective advantage over its brown lint alleles. In the corresponding backcross to *barbadense*, there is a

tendency which almost reaches significance for the K class from the donor parent to be deficient.

In none of the other segregations studied were there significant deviations from the expected monofactorial ratios, though in the case of $R_1:r_1$ and $y:Y$ in the backcross to *hirsutum* there is a tendency for the donor parent class to be deficient.

The cumulative effect of selective elimination of the donor parent genotype. Inspection of tables 1 (a) and (b) shows that out of the total of twelve backcross ratios tested nine show a deficiency in the class containing the gene from the donor parent, though in only four of these does the deficiency reach significance. If selective elimination were dependent on structural differentiation, it would seem that only the larger or more extensive structural differences would

TABLE 3

Frequencies of plants carrying various numbers of *hirsutum* "marker" genes in the backcrosses (a) $F_1 \times \textit{hirsutum}$, (b) $F_1 \times \textit{barbadense}$.

NUMBER OF <i>hirsutum</i> MARKERS	7	6	5	4	3	2	1	0	TOTAL
(a) Expected $(\frac{1}{2} + \frac{1}{2})^7$	1.09	7.60	22.80	38.01	38.01	22.80	7.60	1.09	139
Actual	3	9	24	49	32	13	8	1	139
χ^2	3.35	0.26	0.06	3.18	0.95	4.21	0.02	0.01	12.04 (P(6)=0.05-0.10)
N.B. Pooling classes with frequencies less than 5 gives $\chi^2=9.67$, P(4)=0.02-0.05									
(b) Expected $(\frac{1}{2} + \frac{1}{2})^5$	—	—	2.16	10.78	21.56	21.56	10.78	2.16	69
Actual	—	—	1	4	16	25	18	5	69
χ^2	—	—	0.62	4.26	1.43	0.55	4.84	3.73	15.43 (P(4)=0.001-0.01)
N.B. Pooling classes with frequencies less than 5 does not alter the probabilities appreciably.									

lead to a significant disturbance in any particular monofactorial segregation. In other cases one might expect that the structural differences might be so small that their selective effect would be swamped by random fluctuations, so that they would not be detected in any particular single gene segregation. Nevertheless the cumulative effect of many slight structural differences could be of considerable importance. The easiest way to demonstrate a cumulative effect is to compare the proportion of plants in which the parental genotypes *as a whole* are recovered with the proportion expected on the basis of random recombination. The latter is given by the binomial expansion of $(1/2 + 1/2)^n$ where n is the number of genetically marked loci. Thus in the backcross to *hirsutum* in which seven loci are marked the number of plants with 7, 6, . . . 0 independent genes from the *hirsutum* parent should be given by the successive terms in the expansion of the binomial $(1/2 + 1/2)^7$. The corresponding formula for the backcross to *barbadense* is $(1/2 + 1/2)^5$. The actual numbers obtained are compared with those expected on the basis of random recombination in table 3 (a) and (b) and in figure 2. It can be seen that in both backcrosses there are significant deviations from the expected values, and inspection shows that in the backcross to *hirsutum* the genes from the *hirsutum* parent are recovered *more* frequently than expected. In the backcross to *barbadense* the

genes from the *hirsutum* parent appear much *less* frequently than expected. The distributions are, therefore, skewed in opposite directions instead of being symmetrically distributed around the median class. Since the loci studied which mark only seven out of twenty-six chromosome pairs exhibit such a marked cumulative effect on the recovery of the parental genotypes, it is clear that the total cumulative effect of the differential segments present throughout the chromosome set must be of a very high order indeed, and certainly sufficient to account for the rapid recovery of the recurrent parent genotype in successive backcrosses which is observed in breeding experiments (KNIGHT 1945).

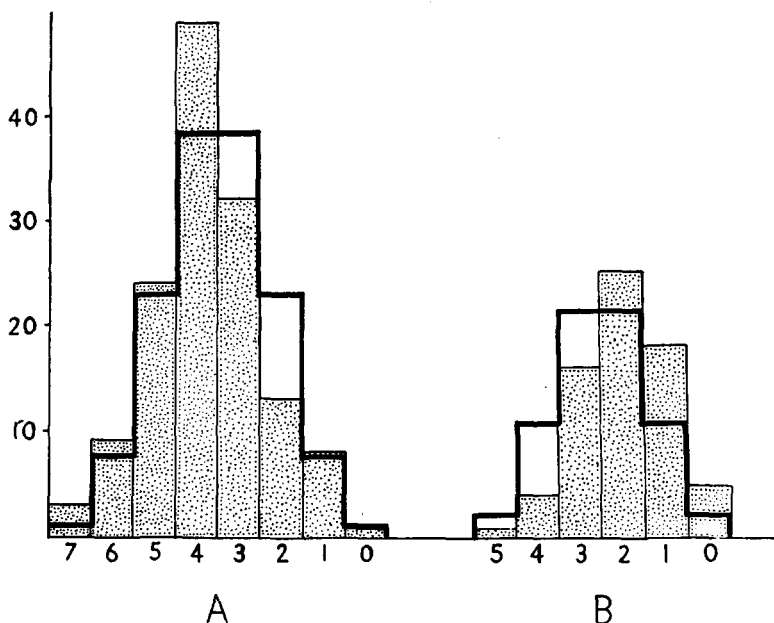


FIGURE 2.—Frequency histograms showing the numbers of plants carrying 0, 1, 2 etc. *hirsutum* marker genes (A) in the backcross to *hirsutum*, (B) in the backcross to *barbadense*. Dotted areas represent the observed frequencies, while the areas enclosed by heavy lines indicate frequencies expected on the basis of random recombination. Data are the same as those shown in table 3.

DISCUSSION

The results of this experiment show that there is a selective elimination of the donor parent genotype in interspecific backcrosses, to whichever parent the backcross is made. The fact that this phenomenon can be demonstrated in small populations in which so few of the chromosomes are marked suggests strongly that the cumulative selective effect on the parental genotypes as a whole must be very great. This agrees with KNIGHT'S (1945) statement that after only two or three backcrosses the progenies closely resemble the recurrent parent. Two obvious questions arise from a consideration of the data. When

is the selection operative—in the gametes or zygotes? What is the mechanism responsible for the elimination?

The fact that very few abortive seeds were found when the F_1 was used as male parent and that practically a complete stand of plants was obtained from the seed collected, shows that zygotic elimination is not an important factor in the first backcross. It might, however, be very important in later backcross generations. About eight percent of all the first backcross plants failed to produce flowers but remained in a vegetative condition. Among the rest of the plants there were considerable differences in time of flowering—some of the plants were harvested before flowering occurred in others. The range of flowering period was much greater than occurs in either parent species. The late flowering types, therefore, in addition to those which did not flower at all, would probably contribute no progeny to the following generation, *i.e.* considerable zygotic elimination would be expected between first and second backcross generations. Returning to the situation in the first backcross, it appears that gametic elimination was of prime importance, and this was confirmed on the female side by the observation that abortive seeds were found when the F_1 was used as female parent, but not when the F_1 was used as male.

With regard to the mechanism responsible for selective elimination, it is clear that the multiple gene substitution hypothesis in its original form is not sufficient to explain the facts. It does not seem to have been realized that the postulation of unlimited numbers of modifiers in an attempt to explain the blurred segregations and depressed vigor in F_2 , carries with it the responsibility of explaining their rapid elimination following inbreeding or backcrossing. The more modifiers postulated and the more minute their individual effects, the slower should be their rate of elimination on any selective basis. Another difficulty which does not seem to have been realized is the sharp contrast between F_2 and first backcross segregations. Usually it has been supposed that the relatively slight “modifier disturbance” in the backcross is due to the buffering effect of the balanced genome from the recurrent parent. If, however, the individual modifiers were additive and independent, we should expect that the range of expression of any particular gene in the F_2 would be only halved in the corresponding backcross. In order to obtain a greater contrast between F_2 and backcross it would be necessary to postulate multiplicative interaction between the individual modifiers. This in turn would lead to a violent skewing of F_2 segregations for which there appears to be little evidence. Finally it is difficult to understand how numerous freely assorting modifiers could segregate in such a way as to impart a significant skewness to a monofactorial segregation without blurring the segregating classes.

The first step in the elucidation of these difficulties is the recognition that the “modifiers” are not freely assorting but are carried in internally balanced blocks in each chromosome or chromosome segment. That is, we arrive at MATHER'S (1943) important conception of “polygenic balance,” though without being committed to the arbitrary classification of genes into “oligogenes” and “polygenes” which in this connection at least, is not an essential feature

of his theory. It is clear that owing to the low chiasmata frequency in cotton chromosomes these internally balanced complexes could not be broken up effectively in only one generation of backcrossing, and that the chromosomes from the donor parent which carried the complexes (including certain marker genes) might be at a selective disadvantage. Further, any crossing over which did occur in the marked regions would disrupt the balanced complex, and crossover chromatids would also be at a selective disadvantage. Without independent evidence to the contrary, the skewed backcross ratios could therefore be explained by differences based on internally balanced "polygenic complexes" without its being necessary to postulate structural differences. Against this purely genetic interpretation, however, is the independent evidence cited earlier that two of the loci which show the strongest selective elimination are carried on chromosomes which are suspected to be structurally differentiated, and, more generally, the extraordinary rapidity with which the genotype of the donor parent as a whole is eliminated in backcrosses. It is clear that the mechanism of selective elimination would be all the more effective if the "polygenic complexes" were structurally differentiated (*i.e.* were differential segments) since these would have the effect of "locking" the parental gene combinations by reducing crossing over, and any rare crossovers which occurred in their neighborhood would be expected to result in deficiencies and duplications—potentially of far more selective consequence in the gametes than simple genic recombinations. More precise tests for structural differentiation will be considered in later papers in this series.

SUMMARY

(1) Evidence is produced that there is considerable selective elimination of the donor parent genotype in interspecific backcrosses involving *G. hirsutum* L. and *G. barbadense* L. In the first backcross the elimination is primarily gametic and is operative both in pollen and ovules.

(2) The selective elimination can be detected by the significant skewness of specific monofactorial segregations and also by the cumulative tendency for the recurrent parent genotype to be recovered more rapidly than expected as a result of random segregation and recombination.

(3) Out of four loci which showed selective elimination, two are suspected on independent grounds to be carried on structurally differentiated chromosomes.

(4) The results are not explicable by interspecific differentiation based on freely assorting modifier systems, but require some form of internally balanced "polygenic complexes."

(5) Reasons are given for believing that the so-called "polygenic complexes" may actually be structurally differentiated chromosome segments.

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