A THIRD CASE OF COMPENSATORY RECOMBINATION IN INTERSPECIFIC HYBRIDS OF GOSSYPIUM¹

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THERE are now several cases reported in the literature in which the transfer of a chromosomal segment from one species of *Gossypium* to another results in altered recombination frequency in the chromosome to which the "foreign" segment has been transferred (SILOW 1944; RHYNE 1958; PHILLIPS 1961; STEPHENS 1961). Further, it is known that the altered recombination may take the form of either increased or decreased map distance (RHYNE 1958) and that a decrease in the region including the inserted segment may be more or less exactly compensated by an increase proximal to the inserted segment (STEPHENS 1961). This type of compensation is not confined to the chromosomes of species known to be cytologically differentiated, but also occurs between chromosomes which exhibit apparently normal pairing behavior during the meiotic cycle, and whose products of recombination appear to be completely viable (i.e. complete fertility of the F_1 hybrid). The present case is concerned with recombination in the leaf shape-crinkle-green lint linkage group of *Gossypium hirsutum* L. into which has been inserted by backcrossing a segment including the leaf shape locus from the related wild American species, *G. thurberi* Tod.

The linkage group has been described previously by STEPHENS (1955). He found that leaf shape (*L*) and crinkle (*cr*) are 41.2 map units apart, and that the map distance between crinkle (*cr*) and green lint (*Lg*) is 6.6. These map distances were based on recombinations obtained in intervarietal crosses of *hirsutum*. The diploid species, *G. thurberi*, carries a "homologous" chromosome which exhibits preferential pairing with its *hirsutum* counterpart in appropriate synthetic polyploid combinations (GERSTEL and PHILLIPS 1958). The narrow leaf of *thurberi* is known to be an allele of the leaf shape series in *hirsutum* (GREEN 1953), so that one might expect that the *thurberi* and *hirsutum* chromosomes would be homologous in the *L* region. GILES (in press) found that the *thurberi* chromosome does not carry a normal allele (*Cr*) of *hirsutum* crinkle (*cr*) which may indicate that the *thurberi* and *hirsutum* chromosomes are non-homologous in this region. The seeds of *G. thurberi* bear no true lint; seeds of the synthetic amphiploid, *G. arboreum* $\times$ *G. thurberi*, bear a greyish-white fiber if the *arboreum* parent is white-linted. In crosses between *G. hirsutum* types with green lint (*Lg*) and the synthetic amphiploid, *arboreum* $\times$ *thurberi*, with grey-

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The source material for this study was a trispecies hybrid, (*G. arboreum* × *G. thurberi*) × *G. hirsutum*, whose synthesis and constitution have been reported previously (GILES, in press). The *hirsutum* parent, SM2, carried the linked combination, *l*—*Cr*—*Lg*. The trispecies hybrid was backcrossed to a recessive marker stock of *hirsutum*, SM3, which carried the linked combination, *l*—*cr*—*lg*. From this backcross generation four plants with narrow leaf (*Lⁿ* from *thurberi*), noncrinkle and green lint phenotype were selected and backcrossed again to the recessive tester, SM3. The constitution of the selected plants should therefore be:

A contingency test showed that the segregations were not homogeneous, although the individual gene segregations did not differ significantly from Mendelian expectation. The major source of heterogeneity was the recombination

Linkage analysis of three second backcross families of the trispecies hybrid, (arboreum × thurberi) × hirsutum, backcrossed to hirsutum

$\chi^2(12) = 21.35, P = 0.02-0.05$

Family	Percent crossing over	
	L^u-Cr	$Cr-L_g$
G2-21	28.13 $\pm$ 7.9	25.00 $\pm$ 7.7
G2-44	25.00 $\pm$ 7.2	2.78 $\pm$ 2.7
G2-59	35.42 $\pm$ 6.9	16.67 $\pm$ 5.4
Total	30.18 $\pm$ 4.3	14.66

frequency in *Cr—Lg* region. In order to determine the nature of this heterogeneity single plants carrying the appropriate dominant markers were selected from Families G2-21 and G2-44 and backcrossed a third time to the recessive tester, SM3. Their segregations in the *Cr—Lg* interval are analyzed in Table 2. It can be seen that the two families segregated homogeneously in the third backcross generation and that their joint crossover percentage agrees reasonably well with the average crossover percent obtained in the previous generation (Table 1).

In Table 3, the recombination frequencies obtained in the interval, *l—lg*, for the data presented here are compared with the estimates obtained earlier (STEPHENS 1955) from intraspecific crosses. It can be seen that the insertion of a *thurberi* segment in the region of the *l* locus has reduced recombination from 41.2 percent to 30.2 percent in the *l—cr* interval. In the neighboring interval, *cr—lg*, in which no *thurberi* segment is involved, there is a compensatory increase from 6.6 percent to 15.9 percent. The total map length from *l* to *lg* remains essentially unchanged (47.8 in the intraspecific data as compared with 46.1 in the data from the interspecific cross reported here). This suggests that the total chiasma frequency has not been reduced in the interspecific cross, but that the position in which the chiasma most frequently occurs has been shifted as the result of inserting a "foreign" segment. Thus, although the genetic evidence obtained by GREEN (1953) indicates that *thurberi* and *hirsutum* possess a leaf shape locus in common, the cytogenetic evidence presented here suggests that the chromosomal segments in which the common locus occurs are not strictly homologous.

TABLE 2

*Linkage analysis of two third backcross families of the trispecies hybrid,
(arboreum × thurberi) × hirsutum, backcrossed to hirsutum*

Family	<i>Cr Lg</i>	<i>Cr lg</i>	<i>cr Lg</i>	<i>cr lg</i>	Total
G2-21	24	5	10	42	81
G2-44	44	6	9	48	107
Total	68	11	19	90	188
$\chi^2(3) = 3.03, P = 0.30-0.50$					
Combined crossover percent = 15.86 ± 2.7					

TABLE 3

*A comparison of intra- and interspecific recombination in the segment, l—cr—lg.
(Intraspecific data from STEPHENS 1955)*

Interval:—	<i>l—cr</i>	<i>cr—lg</i>	Total
Intraspecific	41.2 ± 3.1	6.6 ± 3.2	47.8
Interspecific	30.2 ± 4.3	15.9 ± 2.7	46.1

SUMMARY

A case of compensatory recombination in the segregating progenies of interspecific hybrids in *Gossypium* is described. The insertion of a chromosomal segment, marked by a leaf shape gene (L^u), from *G. thurberi* into the "homologous" chromosome of *G. hirsutum*, produces a change in recombination pattern. Crossing over in the inserted segment is reduced from 41.2 to 30.2 percent, and increased in the neighboring *cr*—*lg* segment from 6.6 to 15.9 percent. Recombination in the total mapped region from *l* to *lg* remains virtually constant. The insertion of the "foreign" segment apparently results in a shift in chiasma position.

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