LINKAGE STUDIES IN GOSSYPIUM. II. ALTERED RECOMBINATION VALUES IN A LINKAGE GROUP OF ALLOTETRAPLOID G. HIRSUTUM L. AS A RESULT OF TRANSFERRED DIPLOID SPECIES GENES[1]

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ACCORDING to STEPHENS (1950) speciation in the genus Gossypium occurs both by cryptic structural differentiation of chromosomes and by major gene substitution and mutation. In the first paper of this series RHYNE (1958) reported a sizeable reduction of recombination values within linkage groups following a transfer of intact diploid Gossypium linkage groups into allotetraploid *G. hirsutum*. These results show that chromosomal structural differences are more important in the altering of genetic recombination than is the influence of genotypic background. GERSTEL (1956) and GERSTEL and PHILLIPS (1958) indicate that chromosomal structural differences were in part responsible for decreasing the segregation of marker genes in hexaploid hybrids of *G. hirsutum* × Gossypium diploid species. The segregation ratios were larger in the hexaploid hybrids $2A_hD_hD_x$, in which *G. hirsutum* L. $2A_hD_h$ and wild American D diploids species were involved, than the expected ratio of five dominant to one recessive for duplex genes in the autotetraploid D genome chromosomes. Each of these studies thus conforms to one of the criteria which STEPHENS (1950) proposed for indicating cryptic structural differentiation among chromosomes in Gossypium interspecific hybrids.

The assumption is, therefore, that structural differences exist among chromosomes of diploid and allotetraploid Gossypium species, and that diploid structural arrangements can be incorporated into *G. hirsutum* chromosomes by an insertion of genes and segments of diploid linkage groups into *G. hirsutum* linkage groups. Possibly these inserted diploid structural arrangements could alter recombination values within the *G. hirsutum* linkage groups. One expected alteration should be a reduction of recombination values in certain regions of a linkage group. Such a reduction was reported by RHYNE (1958) for intact, diploid, linkage groups transferred into *G. hirsutum*. A second expected alteration could be an increase of recombination values in regions of a linkage group adjacent to structural arrangements. Such an increase of recombination values in regions adjacent to inversions in maize chromosomes was assembled by SWANSON (1957). The present paper reports on the insertion of genes and associated structural arrangements of diploid

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Gossypium species into a linkage group of *G. hirsutum* and records the concomitant alteration of recombination values within the linkage group. A possible explanation for the observed alteration of recombination values is offered.

METHODS AND MATERIALS

In order to measure the alteration of recombination values caused by the insertion of diploid genes and structural arrangements, a linkage group must have three or more known loci. Three linkage groups in *G. hirsutum* are known to have three or more linked loci, but only one is useful for this study. It carries the loci *Cl1–R1–Yg1–dw*; but *dw* is of limited use because of classification difficulties since no known allele occurs within *G. hirsutum*. The linkage group is in the D_h genome of allotetraploid *G. hirsutum* $2A_hD_h$. Genes and segments of linkage groups were obtained from the wild American diploid *G. raimondii* Ulbr., $2D_5$, and *G. armourianum* Kearney, $2D_2$, by using hexaploid hybrids $2A_hD_hD_5$ and trispecies hybrids $A_hA_2D_hD_5$ or D_2. Allelic genes from the diploids were then substituted at the various loci of the D_h linkage group using the backcross technique with *G. hirsutum* as the recurrent ovule parent. In the study the genes used are given as follows, omitting the subscript "one":

cl—cluster fruiting habit, a *G. hirsutum* recessive allele.

Cl—normal fruiting habit, the *G. hirsutum* dominant allele.

Cl^{rai}—normal fruiting habit, from *G. raimondii* $2D_5$, and dominant to *cl*.

r—"green" plant parts, clear petal margin, no anther or filament coloration; a *G. hirsutum* recessive allele.

R—red plant parts, red petal margin, no anther or filament coloration; an incompletely dominant *G. hirsutum* allele of *r*.

r^{rai}—green plant parts, clear petal margin, red anthers and filaments, red petal spot. The allele is dominant to *r*. It was derived from *G. raimondii* $2D_5$. An R/r^{rai} phenotype is red plant parts, red anthers and filaments, red petal margin and petal spot. This phenotype was most useful in the synthesis of experimental stocks and in the classification of plants of F_2 populations, as is illustrated in the experiment.

r^{arm}—when in an otherwise hirsutum background, can be distinguished from *r* by the presence of red anther cases. When transferred in the intact *Cl-R-Yg* linkage group from *G. armourianum* $2D_2$, the allele imparts red anther and filament coloration and a large red petal spot. It interacts with *R* in a fashion similar to r^{rai}.

yg—yellow-green cotyledons and true leaves in the presence of *yg2*, a *G. hirsutum* mutant gene.

Yg—green cotyledons and true leaves in the presence of *yg2;* a *G. hirsutum* dominant gene.

Yg^{rai}—green cotyledons and true leaves in the presence of *yg2;* a gene dominant to *yg* and obtained from *G. raimondii*.

dw—white lint and seed fuzz; a *G. hirsutum* gene having no known allele within the species.

dw^{rai}—dirty-white lint and tan seed fuzz; a gene incompletely dominant to *dw* and derived from *G. raimondii.*

The genes *yg1* and *yg2* are found in the D and A genomes of *G. hirsutum*, respectively. Each gene must be in homozygous condition to produce a yellow-green phenotype. The dominant *Yg1* is less common than *Yg2*. Many stocks including some used in these experiments have the *Yg2Yg2 yg1yg1* genotype which is indistinguishable in phenotype from the *yg2yg2 Yg1Yg1* genotype used herein. For presentation purposes the loci of the A_h genomes are omitted unless they are needed in genotypes to describe particular phenotypes.

The D_h chromosome was marked generally with the linkage *cl-R-yg-dw*, the D_5 by *Cl*^{rai}-*r*^{rai}-*Yg*^{rai}-*dw*^{rai}, and the D_2 by *Cl*^{arm}-*r*^{arm}-*Yg*^{arm}-*dw*^{arm}. The diploid linkages were transferred intact by three to 12 backcrosses into the *G. hirsutum* standard stock. The D_5 diploid genes and associated structural arrangements were then inserted into the *G. hirsutum* linkage group and transferred intact to the 12th backcross generation. This procedure reduced the number of diploid genes in other D_h chromosomes. (Subsequently the series of backcrosses proved to be unessential, for D_5 and other diploid genes in other chromosomes had little if any effect on the recombination values of the linkage group undertest. The results of the first backcross were comparable to those of the later backcrosses.) The reported data from the 14th and later backcrosses are representative of the alteration of recombination values within a *G. hirsutum* linkage, caused by genes and structural arrangements of other Gossypium species when inserted into the linkage group.

The following genotypes were provided by appropriate genetic procedure:

Genotype A, $\frac{Cl\text{-}r\text{-}Yg\text{-}dw}{cl\text{-}R\text{-}yg\text{-}dw}$, was a control D_h chromosome in the genotypic background of genotypes B and C below. Recombination was measured at *Cl-r* and *r-Yg* by backcrossing.

Genotypes B and C were most readily obtained by growing a large F_2 from the 12th backcross hybrid $\frac{cl\text{-}R\text{-}yg\text{-}dw}{Cl^{rai}\text{-}r^{rai}\text{-}Yg^{rai}\text{-}dw^{rai}}$ and inserting genes and segments into the D_h linkage by crossing over. Recombination in each of the regions of the D_h linkage is much reduced and double recombination has not been detected. Plants of the genotype $\frac{cl\text{-}R\text{-}Yg^{rai}\text{-}dw^{rai}}{Cl^{rai}\text{-}R\text{-}yg\text{-}dw}$ having a crossover between *R* and *Yg*^{rai} in one gamete and between *Cl*^{rai} and *R* in the other gamete were desired. These plants then were crossed to appropriate lines of the standard *G. hirsutum* stock to obtain

Genotype B, $\frac{cl\text{-}R\text{-}Yg^{rai}\text{-}dw^{rai}}{Cl\text{-}r\text{-}yg \quad\quad -dw}$, which provided the *Yg-dw* segment of D_5 in a *G. hirsutum* linkage group. Recombination was measured at *Cl-R* and *R-yg* in F_2 populations by the method of MURTY (1954). The *yg-dw* linkage was of little use since its recombination value within *G. hirsutum* is not known and *yg-dw*^{rai} recombination fluctuates depending on the "genes" at the adjacent *cl-R-yg* loci.

Genotype C, $\frac{cl\text{-}R\text{-}Yg^{rai}\text{-}dw}{Cl\text{-}r\text{-}yg \quad \text{-}dw}$, provided the *Yg* segment of D_5 in a *G. hirsutum* linkage group. Recombination was measured at *Cl-R* and *R-yg* as in genotype B.

Genotype D, $\frac{Cl^{rai}\text{-}R\text{-}Yg^{rai}\text{-}dw^{rai}}{cl \quad \text{-}r\text{-}yg \quad \text{-}dw}$, provided the *R* segment of the D_h linkage in a D_5 chromosome. Recombination was measured at *Cl-R* and *R-yg* as in genotype B.

The remaining genotypes were obtained in comparable genetic backgrounds. The *Yg1* allele of the D_h linkage was absent from many genotypes since the appropriate testers having *Yg1* were unavailable at the beginning of the synthesis:

Genotype E_1, $\frac{Cl\text{-}r^{arm}\text{-}Yg\text{-}dw}{cl\text{-}R \quad \text{-}yg\ \text{-}dw} \frac{Yg2}{yg2}$, provided the r^{arm} segment of the D_2 linkage in a D_h chromosome. It was paired with

Genotype E_2, $\frac{Cl\text{-}r\text{-}yg\text{-}dw}{cl\text{-}R\text{-}yg\text{-}dw} \frac{Yg2}{yg2}$, which provided a D_h linkage in the E genotypic background.

Genotype G_1, $\frac{cl\ \text{-}r^{rai}\text{-}yg\text{-}dw}{Cl\text{-}R \quad \text{-}yg\text{-}dw} \frac{Yg2}{yg2}$, provided the r^{rai} segment of D_5 in a D_h chromosome. It was paired with

Genotype G_2, $\frac{cl\ \text{-}r\ \text{-}yg\text{-}dw}{Cl\text{-}R\text{-}yg\text{-}dw} \frac{Yg2}{yg2}$ which provided a D_h linkage in a G genotypic background.

Genotype H, $\frac{Cl\text{-}r\text{-}Yg\text{-}dw}{cl\text{-}R\text{-}yg\text{-}dw}$, provided an independent estimate of the control D_h linkage in the year that genotypes D and E were grown. The D_h chromosome *Cl-r-Yg-dw* was transferred to the common A genotypic background from Hopi Moencopi, a *G. hirsutum* cotton but not of Upland ancestry. Its *r* allele is actually recessive to the *r* Upland allele in genotypes A, E_2 and G_2.

The hybrids of the various genotypes were grown in the winter at Iguala, Mexico, where backcrossing facilities are limited. The use of backcrossing was restricted to the control genotypes A and H in order to increase population size. Coupling phase F_2 linkage was highly efficient for estimating recombination in regions 1 (*Cl-R*) and 2 (*R-Yg*) and large populations were obtained by self-pollinating the hybrid plants. Classification was done in the summer at Clayton, North Carolina. The ease of recognizing three phenotypes for the three genotypes *RR*, *Rr*, and *rr* permitted gene *R* to be classed as either dominant or recessive to *r*. This incomplete dominance of *R* permitted the use of coupling phase for a more accurate estimation of recombination values. Even so the values for *cl-Yg* had to be obtained from repulsion phase in certain genotypes. The *cl-Yg* recombination was obtained by a calculated and an observed method since poor estimation of recombination in repulsion phase and the occurrence of double recombination reduced the accuracy of the observed value. The calculated method estimates were obtained by adding the values of regions 1 and 2, ignoring doubles. The actual frequency of doubles must be higher in the genotypes B, C, D, and E_1 than the reported observed value. The rate of doubles in F_2 was impossible to estimate accurately since all doubles were not detected, even by progeny testing.

TABLE 1

Recombination in the D_h genome linkage group (cl-R-yg-dw) *of* G. hirsutum *before and after substitution of a D_s genome "gene" at the* Yg *locus*

	Genotype tested	Source and population size	Recombination value: Region 1 (*Cl-R*)	Region 2 (*R-Yg*)	*Cl-Yg* Observed	*Cl-Yg* Calculated (region 1+2)	Observed double recombinants: Percent	Observed double recombinants: Number
A	$\frac{(Cl\text{-}r\text{-}Yg\text{-}dw)}{cl\text{-}R\text{-}yg\text{-}dw}$	Backcross 1841	15.0	13.5	28.5	28.5	0.59	11
B	$\frac{(cl\text{-}R\text{-}Yg^{rai}\text{-}dw^{rai})}{Cl\text{-}r\text{-}yg \quad \text{-}dw}$	F_2 427*	28.6	10.2	27.4	38.8	0.67	1†
C	$\frac{(cl\text{-}R\text{-}Yg^{rai}\text{-}dw)}{Cl\text{-}r\text{-}yg \quad \text{-}dw}$	F_2 373*	23.0	7.3	29.6	30.3	0.00	0†

* The phenotypes associated with the genotypes *rr*, *Rr*, and *RR* are readily separable. The data were calculated as coupling phase assuming *r* dominant to *R* in region 1 and *R* dominant to *r* in region 2.

† The F_2 populations did not permit a ready detection of double recombinants although the incompletely dominant *R* gene helped in choosing suspected plants for progeny testing. The observed number in genotypes C and B was shown to be a minimum estimate since a number of suspected plants proved to have originated from double crossover gametes.

RESULTS

Effect of substitution of Yg^{rai} *for* yg: The backcross population from genotype A described in Table 1 had a recombination of 15 percent in region 1 and 13.5 percent in region 2. The expected number of doubles should be 15.0 × 13.5 percent if two chiasmata were to occur randomly between *cl* and *Yg* loci. The observed estimate was 0.59 percent for 11 doubles, five of one type and six of the other. Roughly only one third of the expected doubles were obtained. It appeared thus that one chiasma is the most common occurrence in the *cl-R-yg* portion of the chromosome. No estimate of *dw* recombination was possible.

The substitution of Yg^{rai}-dw^{rai} in genotype B resulted in 28.6 percent recombination, and the substitution of Yg^{rai} in genotype C resulted in 23.0 percent in region 1. These values are not only significantly greater than those found in the control A genotype but are greater than any intra-*hirsutum* value reported in the literature.

The recombination in region 2 for genotype B was intermediate in value between that of genotype A and genotype C. In this experiment the small population size for genotype B permits a good fit to the expectation of either the 13.5 percent of genotype A or 7.3 percent of genotype C. If 10.2 percent for genotype B occurred in a population of 1841 plants as genotype A has, this estimate would be significantly smaller than the observed 13.5 percent for value A. On the other hand, since double recombination is low and since by procedure genotypes B and C should have had the same break between *R* and Yg^{rai}, the populations of genotypes B and C can be pooled. The 8.9 percent estimate is significantly less than the 13.5 percent value of the control genotype.

The observed recombination value for *Cl-yg* was similar in each of the three genotypes; but the calculated value suggests that recombination increased significantly in genotype B and remained the same in the other two genotypes. The rate of doubles must have been higher than in genotype A despite the fact that

double recombinants are not readily detected in F_2 populations. Several of the suspected plants in the F_2 of genotype B prove by appropriate tests to be from double recombination gametes; thus, the rate of double rceombination should be considered to be higher than the reported 0.67 percent value.

Intercalated substitutions of r *alleles at the* R *locus:* The primary interest of Table 2 lies in region 1 of the genotypes since the absence of *Yg1* in genotypes E and G limited the information on recombination in region 2. The recombination values of the three control genotypes (E_2, G_2, and H) were essentially 17.0 percent, whereas the values of three substitution genotypes ranged from 26.2 to 33.5 percent. The value for each of the three substitution genotypes was significantly higher than either that of any of the control genotypes or any value given in the literature for recombination in the *cl-R* region.

At region 2 recombination was estimated for three genotypes only. The H control genotype showed a higher value for this region than usually was obtained for control genotype A in previous years. However, the value of 19.1 percent is not different from a value of 20.0 percent obtained in other *G. hirsutum* genotypes by RHYNE (1957, 1958). Control genotypes A and its hirsutum derivatives ranked consistently lower in recombination at region 2 than the H and other series did under similar conditions. The recombination values for genotypes D and E_1 were similar to that value for genotype B found in Table 1.

TABLE 2

Recombination in the D genome linkage (cl-R-yg-dw) *of* G. hirsutum *before and after substitution of various interspecific alleles at the* R *locus*

Genotype tested	Source and population size	Recombination value: Region 1 (*Cl-R*)	Region 2 (*R-Yg*)	For *Cl-Yg*: Observed	For *Cl-Yg*: Calculated (region 1 + 2)	Double recombination percent detected
D $\frac{(Cl^{rai}\text{-}R\text{-}Yg^{rai}\text{-}Dw)}{cl \quad -r\text{-}yg \quad dw}$	Backcross 71	29.6	11.3	40.9	40.9	1.40
	F_2 238	33.5	12.4	40.7	45.9	.78
E_1 $\frac{(Cl\text{-}r^{arm}\text{-}Yg\text{-}dw)}{cl\text{-}R \quad -yg\text{-}dw}$	F_2 373	31.3*	11.2†	43.3	42.5	.54†
E_2 $\frac{(Cl\text{-}r \quad -yg\text{-}dw)}{cl\text{-}R \quad -yg\text{-}dw}$	F_2 341	17.5*	...	...	...	...
G_1 $\frac{(cl\text{-}r^{rai}\text{-}yg\text{-}dw)}{Cl\text{-}R \quad -yg\text{-}dw}$	F_2 1,119	26.2*	...	...	...	...
G_2 $\frac{(cl\text{-}r \quad -yg\text{-}dw)}{Cl\text{-}R \quad -yg\text{-}dw}$	F_2 834	17.5*	...	...	...	...
H $\frac{(Cl\text{-}r \quad -Yg\text{-}dw)}{cl\text{-}R \quad -yg\text{-}dw}$	Backcross 141	17.0*	19.1	36.1	36.1	2.80

* Since *rr*, *rR*, and *RR* have separable phenotypes coupling phase linkage was used assuming *r* to be dominant to *R* in regions 1 and 2.

† Yg^g was present in this genotype requiring duplicate factor estimation of linkage and permitting only one double recombinant to be detected. The rate of doubles could be higher than the value given.

The recombination between the *Cl-Yg* loci for genotypes D and E_1 was not significantly different from the value of the control H genotype. The values 41–43 percent from D and E_1 however were greater than ordinarily expected from any D_h linkage group; a 28–30 percent value was reported for genotypes A and C of Table 1. A trend has been observed for an increase in recombination for the *Cl-Yg* loci for substitution genotypes like those of Tables 1 and 2. Population size, however, has been insufficient to provide statistical proof for an increase. Also, the necessity to measure recombination of F_2 populations in repulsion phase (genotypes B and C) and in duplicate factor segregation where *Yg2* and *Yg1* are present (genotype E_1) made linkage estimation inefficient for *Cl-Yg* loci.

DISCUSSION

A consistent reduction in the amount of recombination was reported by RHYNE (1958) in hybrids having an intact linkage group from cotton species of the A and D diploid genomes, and especially *G. raimondii* $2D_5$, inserted in amphidiploid *G. hirsutum*. In the present experiments by appropriate technique, making use of certain recombinants, the intact donor's chromosomes of the D_5 and D_2 diploid genomes were broken and portions were introduced into a *G. hirsutum* linkage group. These inserted chromosome segments contained genes which showed allelism with genes at specific loci of the *Cl-R-yg-dw* linkage group. A substitution of the D_5 segment with genes Yg^{rai}-dw^{rai} for D_h genes *Yg-dw* (genotype B, Table 1) increased recombination at the distal *cl-R* region. A "smaller" substitution of the D_5 segment with gene Yg^{rai} (genotype C, Table 1) increased recombination at distal *cl-R*, but the amount of increase was significantly smaller than the substitution at *yg-dw*. Substitution of a small D_5 or D_2 segment with its allele at the *R locus* (genotypes G_1 and E_1, respectively, in Table 2) increased recombination in the adjacent *cl-R* region. Similarly, the substitution of the *R* allele of the D_h linkage for r^{rai} in a D_5 linkage (genotype D) increased recombination in the adjacent *cl-r* region. On the other hand, a definite trend exists for a reduction in recombination in the *R-yg* region adjacent to the *cl-R* region, but only genotype B showed a significant decrease in the *R-yg* region. The *yg-dw* recombination was not reported, yet the recombination value fluctuated from genotype to genotype whenever dw^{rai} could be classified. This fluctuation would be expected if substitution in the *R-yg* region altered recombination in the adjacent *yg-dw* region as obviously it did in the *cl-R* region.

The calculated recombination values for the over-all *Cl-Yg* segment, the largest segment measureable, showed a higher estimate of recombination for substitution genotypes than for the *G. hirsutum* controls. An over-all estimate of recombination in the *cl-R-yg-dw* linkage group of *G. hirsutum* is unobtainable in the absence of known loci distal to *cl* and proximal to *dw*. The best evidence, however, suggests that this linkage group is in one arm of a D_h chromosome and that its typical chiasma number is one per arm. Two chiasmata can occur since double recombinants were observed in genotype A. But these doubles were obtained much less frequently than expected. A reduction in recombination at *R-yg* and an increase between *cl-R* would be expected if a single chiasma had shifted its position be-

cause of some unexplained chromosomal difficulty. A slight increase in the *Cl-Yg* recombination would also be expected if a single chiasma occurred within the limits of *Cl-Yg* much of the time; but the total chiasmata frequency in the *cl-R-yg-dw* arm might, but would not necessarily have to, remain constant.

Alterations of recombination which occur in regions adjacent to, or near, a structurally altered segment, such as an inversion, are discussed by SWANSON (1957, pages 257–260). An increase of recombination occurred in regions adjacent to inversions in maize where such structurally altered segments could be observed cytologically. Cytological observation of small, structurally altered chromosome segments, even if they were present, is unlikely for Gossypium chromosomes, since pachytene preparations have not been favorable for analysis.

STEPHENS (1950) outlined three criteria that would indicate structural differentiation of chromosomes in Gossypium interspecific hybrids. It also follows that the same criteria ought to hold in material obtained as a result of interspecific transference to *G. hirsutum* $2A_hD_h$. One of the more sensitive tests proposed by STEPHENS was an alteration of linkage relationships between marker genes. RHYNE (1958) showed that a reduction in linkage values was maintained in the intact linkage groups of diploid species, even after as many as 6–10 backcross generations of transference to *G. hirsutum*. In the present experiments the intact diploid linkages were broken into smaller segments by crossing over; and the small segments with their diploid alleles were associated with altered recombination within the *cl-R-yg-dw* group, even with increased recombination in the distal region having pure D_h chromosome segments. The reductions and increases of recombination in *Gossypium hirsutum* are consistent with the altered recombination, as SWANSON (1957) described, when known structural alterations occur in chromosomes of various species.

At least two instances of increased recombination may be found in the Gossypium literature on linkage relationships of interspecific gene transfers:

KNIGHT (1944) reported 32 percent recombination in the B2-B3 linkage for the first four backcrosses of *G. hirsutum* to amphidiploid *G. barbadense* L. In the fifth backcross a 48 percent value, followed by values above 40 percent in the sixth and seventh backcross generations, was obtained. STEPHENS (1950) interpreted the low value in the early backcross generations to be a reduction caused by a large segment of *G. hirsutum* chromosome that differs structurally from the chromosome of the *G. barbadense* recurrent parent. Crossing over in the fifth backcross replaced much of the *G. hirsutum* segment with homologous *G. barbadense* chromatin and consequently recombination increased in the later backcross generations.

HUTCHINSON (1946) obtained ten percent recombination in the crinkled dwarf-green lint linkage in later generations, but five percent was obtained in the early generations, of the transfer of the *G. barbadense* gene to *G. hirsutum*. In the early generations crinkle and green lint were in repulsion phase, and in the later generations a crossover placed crinkle and green lint in coupling phase.

In the two above recorded instances a portion of a linkage group from one species was intercalated into the linkage group of another species. An increased

recombination rate was observed. The procedure corresponds with the method used in the present experiments, where a portion of a diploid linkage group was intercalated into a *G. hirsutum* linkage group. The end result, an increase in recombination, therefore may be regarded as a common phenomenon, i.e., a portion of a linkage group of a donor Gossypium species alters recombination values when present in the linkage group of another species. The mechanism for altering the recombination values may be a compensatory shift in chiasma position, which results because of the presence of a structurally altered segment in a chromosome.

SUMMARY

The assumption was made that small structural differences exist among chromosomes of Gossypium species. Structural arrangements and genes of diploid Gossypium species inserted into a *G. hirsutum* linkage group should be expected to alter recombination values within the linkage group. The alteration in recombination could be both a reduction in the region containing the diploid gene and structural arrangement and an increase in the pure *G. hirsutum* regions distal to the inserted diploid gene. The substitution of diploid genes, particularly from *G. raimondii* $2D_5$ to the D_h linkage of *G. hirsutum*, specifically at the *R*, or *Yg* and *dw* loci of the *cl-R-Yg-dw* linkage group, caused genetic recombination between the *cl-R* loci to increase significantly, the *R-Yg* recombination to decrease, and the total *cl-Yg* recombination to remain the same or to show an increase as compared with the D_h control hybrids. The altered recombination, an increase in one region and a decrease in another region, corresponds to the expectation if chiasmata position were being shifted in the presence of small structurally altered segments of chromatin. A question of changed chiasma frequency was not resolved because of the limitation of available genes and loci in the D_h linkage group.

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