Cytogenetic studies of $N Lc_1 yg_2 R_2$ marker genes and chromosome deficiences in cotton*

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1. INTRODUCTION

Genetic studies in cotton, *Gossypium hirsutum* L., reported by Stephens in 1955 revealed that the mutants $N Lc_1 yg_2 R_2$ formed a linkage group in that linear order (N = naked seed, Lc_1 = brown lint, yg_2 = yellow-green plant, R_2 = petal spot). The data showed significant evidence of linkage of N and Lc_1, with recombination frequency of 44·4 % between the two loci. This linkage group has been placed in the A genome because Harland (1935) has shown that R_2 (Petal Spot) of *G. hirsutum* is an allele of R_2 (Petal Spot) in the diploid A genome species, *G. arboreum* L. (Rhyne, 1955; Stephens, 1955).

Following the establishment of the linkage group, the linked markers have been used in a number of genetic studies. One study in particular, from data accumulated on recombinations over the chromosome region N through R_2, revealed the occurrence of a recombination phenomenon in cotton that was different from that in corn in which comparable data had been reported (Stephens, 1961). This phenomenon, referred to as 'compensatory recombination', has also been reported in cotton by other investigators (Rhyne, 1958, 1960, 1962; Giles, 1961). Its discovery has influenced much of the current thinking of cotton workers concerning the interspecific transference of genetic characters and has stimulated research into methods for inducing and detecting shifts in chiasma position and frequency in other chromosomes of the species.

This paper describes cytogenetic studies involving a monosome, which show that the N locus is on a different chromosome from the one carrying the $Lc_1 yg_2 R_2$ linkage. The identification of this monosome marks a specific chromosome in the tetraploid complement. The discovery that the N locus is not a member of this linkage group requires some re-interpretation of published studies on this group of markers, and also requires a re-evaluation of the data, particularly those involving this linkage group, which supposedly illustrate the compensatory recombination phenomenon. Studies with telocentric chromosomes and the $Lc_1 yg_2 R_2$ loci are also reported here.

2. PLANT MATERIALS

The plant material used is described below:

Acala and Tennessee 92 are a variety and a breeding strain, respectively, of commercial cotton. The present study reveals that these two stocks have the monomeric genotype $yg_1yg_1Yg_2Yg_2$ for green plant body. Other markers carried by these two stocks, which are pertinent to the present study, are: nn, fuzzy seed; lc_1lc_1, white lint; and r_2r_2, spotless flower petals.

TM1 is an inbred line of the cultivated variety Deltapine 14. TM1 is commonly used as the standard type in genetic studies and it has the same genotype as the two above stocks.

Texas 414 is a marker stock genetically similar to the above three except that it has the duplicate recessive genotype $yg_1yg_1yg_2yg_2$ for yellow-green plant body.

Texas 586 carries the genetic markers: $yg_1yg_1Yg_2Yg_2$, green plant body; NN, naked seed; Lc_1Lc_1, brown lint; and R_2R_2, petal spot.

A monosomic plant $(2n-1)$ has one chromosome missing, and chromosome pairing in a plant of this kind in cotton is 25 bivalents and one univalent. The heteromorphic bivalents described herein consist in each case of a normal chromosome and a telocentric chromosome.

3. DUPLICATE LOCI Yg_1 Yg_2

The yg_2 factor in the $Lc_1yg_2R_2$ group is one member of a pair of duplicate recessives which affect chlorophyll formation (Rhyne, 1955). The genotype $yg_1yg_1yg_2yg_2$ gives a yellow-green phenotype, whereas a single dominant allele at either locus gives a normal green phenotype. According to tests conducted by Rhyne (1955), most *G. hirsutum* cottons proved to be monomeric for the duplicate factors (i.e. $Yg_1Yg_1yg_2yg_2$ or $yg_1yg_1Yg_2Yg_2$). Among these cottons were several of the Acala variety, suggesting that the Acalas in general are monomeric. The yg_1 factor is located on a chromosome of the D genome, which is homoeologous to the chromosome carrying the $Lc_1yg_2R_2$ group (Rhyne, 1957; White & Endrizzi, 1965; Endrizzi & Kohel, 1966).

4. RESULTS AND DISCUSSION

(i) *Monosomic analysis*

In 1963 a number of morphologically aberrant plants were observed in field stands of *G. hirsutum* var. Acala. In the following year, a single monosomic plant was recovered in the progeny of one of the aberrant plants. The monosomic chromosome at metaphase I was quite large in size, indicating that it was a member of the A genome rather than the D genome of the tetraploid species. Associated with the monosome was a distinct set of plant morphological characters which easily distinguished the monosomic plant from its disomic sibs.

The monosomic plant was crossed to Texas 414 which is homozygous $yg_1yg_1yg_2yg_2$, and $25F_1$ seed were germinated; three seedlings were yellow-green and the remaining 22 were normal green. When the plants produced flower buds, the pollen

mother cells of six of the green plants and two of the yellow-green plants were analysed cytologically. The six green plants had 26 bivalents at metaphase I, whereas the two yellow-green plants had 25 bivalents plus a univalent, thus they were monosomics.

The recovery of the normal green phenotype in the cytologically normal plants (26 bivalents) and the yellow-green phenotype in the plants monosomic for a large (A genome) chromosome permits two interrelated conclusions concerning the monosome and the parental plant carrying it: first, that the parental monosomic plant is monomeric with the $yg_1 yg_1 Yg_2$—genotype; secondly, that the monosomic chromosome, since it was associated with the yg_2 locus, must carry the $N Lc_1 yg_2 R_2$ linkage group. From studies involving translocations, the chromosome with the $N Lc_1 yg_2 R_2$ linkage has been designated as number 7 (unpublished data of Meta S. Brown). The $Lc_1 R_2$ markers were the ones found linked with the interchange. Since the above results establish that the monosome carries the yg_2 locus which is linked with these markers, the monosome therefore can be classified as chromosome 7. The isolation of a monosome for chromosome 7 makes eight chromosomes of the allotetraploid cottons now distinguished by monosomy.

To show conclusively that $N Lc_1 R_2$ markers are also located on this chromosome, a green monosomic plant was crossed to Texas 586 which carries the dominants $N Lc_1 R_2$. Twenty F_1 plants of the $2n - 1 \times T586$ cross were grown. Both morphological and cytological studies showed that three of the F_1's were monosomics and that the remaining 17 were disomics.

The three monosomic F_1's were test-crossed reciprocally to TM1 which has the genotype $n lc_1 r_2$ (fuzzy seed, white lint and spotless flowers) to verify the linkage of these three loci with the monosome. The chromosome structures and genotypes of the progeny recovered in the reciprocal test crosses are shown in Table 1.

Table 1. *Segregation in reciprocal test crosses of the monosomic*
$$F_1(n lc_1 r_2 \times N Lc_1 R_2) \times T M 1 n lc_1 r_2$$

Test cross		$N Lc_1 R_2$	$n Lc_1 R_2$	$N lc_1 r_2$	$n lc_1 r_2$	Total no. plants
$2n - 1$ $F_1 \times$ TM1	$2n$	213	225	0	0	438
	$2n - 1$	0	0	21	42	63
TM1 $\times 2n - 1$ $F1$	$2n$	11	9	0	0	20

The criterion for determining whether a plant in the test cross populations was $2n$ or $2n - 1$ was based on the syndrome of morphological characters that distinguishes the monosomics from the disomics. As compared to the disomics, the monosomic plants characteristically have leaves which are generally larger and cup-shaped, with many of them exhibiting a distorted growth pattern; the calyces are distinctly contorted and the bolls are smaller and misshapen due to ovule abortion.

Table 1 shows that in the cross of $2n - 1$ $F_1 \times$ TM1, 438 plants were classified as disomics and 63 plants were classified as monosomics, giving approximately 12 %

rate of recovery for the monosome. The results also show that all disomic plants had the $Lc_1 R_2$ phenotype, whereas all the monosomic plants had the $lc_1 r_2$ phenotype, establishing that the $Lc_1 R_2$ loci are located on the monosomic chromosome. The N locus, however, unlike the $Lc_1 R_2$ loci, shows segregation in both the disomic and monosomic classes. The N and n alleles were recovered in essentially a $1:1$ ratio in the disomic class ($\chi^2 = 0.33$; $P = 0.7–0.5$) and in a $1:2$ ratio in the monosomic class ($\chi^2 = 7.0$; $P = <0.01$ for fit of $1:1$ ratio). Other than by chance, there is no explanation that will suitably account for the significant excess of the fuzzy seeded (n) character among the monosomic plants.

In the reciprocal cross, $TM1 \times 2n-1$ F_1, all progeny were disomic, which is expected since $n-1$ male gametes rarely function. All of the 20 progeny had $Lc_1 R_2$ alleles which is to be expected with linkage of the markers and the monosomes and non-functioning of $n-1$ male gametes. In this test cross as in the previous one, the N and n alleles were recovered in essentially a $1:1$ ratio. Both test crosses show that the monosome does carry the $Lc_1 R_2$ factors but that it *does not* carry the N locus. Obviously, the N locus is not on the same chromosome as the $Lc_1 yg_2 R_2$ marker loci as previously concluded. It is emphasized that cytological analysis established that the three F_1's used for producing the test-cross seed were indeed simple monosomics. Furthermore, the test-cross seeds of each of the three F_1 monosomics were planted separately and in each case the monosome showed complete linkage with the Lc_1 and R_2 loci and independence with the N locus.

(ii) *Heteromorphic bivalent of chromosome 7*

Conducted simultaneously with the study described above involving the monosome was a study embodying a heteromorphic bivalent and the $N Lc_1 R_2$ markers, which is described below. For ease in following the origin of the heteromorphic bivalent and the genetic tests conducted with it, a diagram outlining these steps is given in Fig. 1.

Shortly prior to the time of isolating the monosome identified above, ten F_2 seeds of a cross of Tenn. 92 ($n lc_1 r_2$) × T586 ($N Lc_1 R_2$) in which the pollen of the male parent had been exposed to γ-radiation, were received from Dr J. B. Pate. These seeds came from an F_1 that was 'deficient' for the $N Lc_1 R_2$ alleles as a result of the pollen irradiation. It was assumed at that time, of course, that $N Lc_1 R_2$ consisted of a single linkage group in which the N locus was located in the chromosome arm opposite to that in which the R_2 locus was located (Stephens, 1955). Therefore, the absence of the three dominant mutants in the F_1 was ascribed to monosomy for the chromosome carrying these marker genes. This conclusion is now known to be untenable since it was shown in the monosomic analysis that the N locus is on a different chromosome from the one carrying $Lc_1 R_2$. The loss of the N allele and the $Lc_1 R_2$ linkage group from a single gamete was due most likely to separate mutational events involving the two chromosomes carrying these markers. Since the N marker is not on the chromosome that carries the $Lc_1 R_2$ markers it will henceforth be ignored for the most part in further discussion of the genetic analysis of the relationship of $Lc_1 R_2$ and the heteromorphic bivalent.

Eight of the $10 F_2$ seeds germinated and all were analysed cytologically for chromosome associations at metaphase I. Six plants had the normal number of 26 bivalents and the other two had 26 bivalents plus a small telocentric chromosome
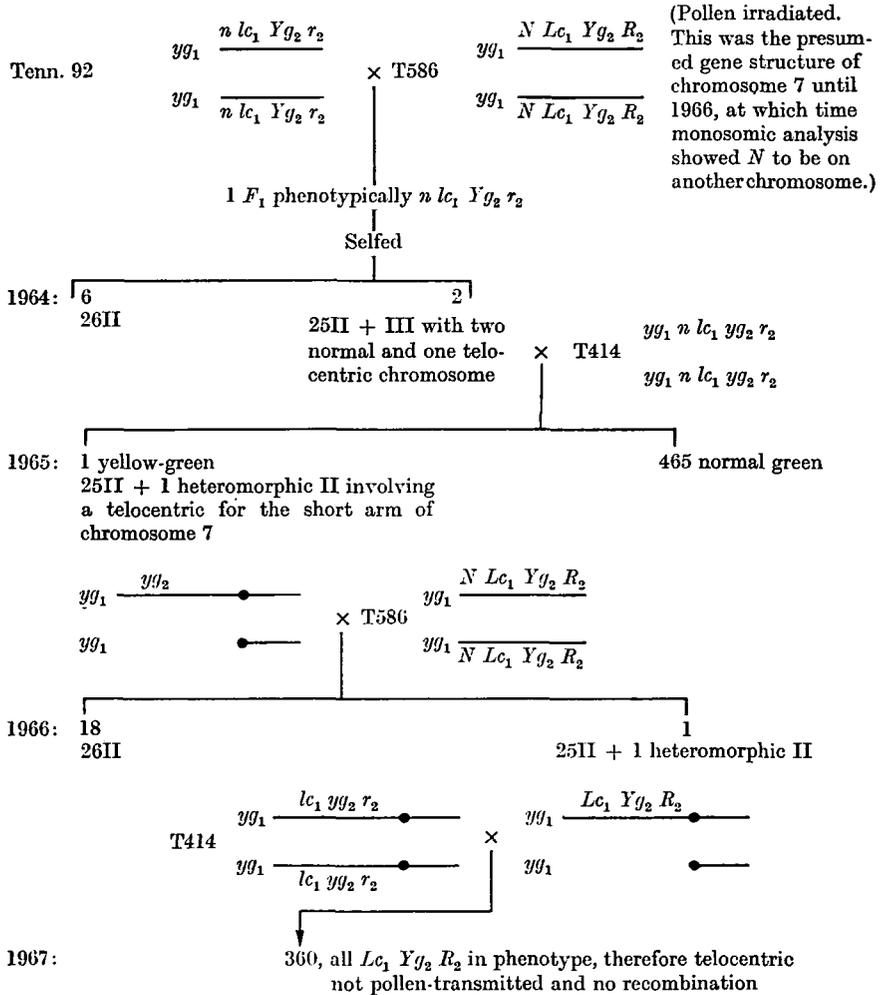

Fig. 1. Diagram of the origin of the heteromorphic bivalent of chromosome 7 and the presumed structure of the chromosomes in successive genetic tests.

which paired frequently with two large chromosomes to make a trivalent, indicating that the telocentric was a member of the A genome. Since the telocentric chromosome was recovered from an F_1 that was 'deficient' for the $R_2 Lc_1$ markers as the result of exposure of the pollen to gamma radiation, it was assumed that the telocentric involved the chromosome carrying these markers.

When the telocentric was found associated in a trivalent with its normal homologues, the configuration at metaphase I was usually a chain consisting of two

normal chromosomes and the telocentric. When the chain-of-three was oriented on the spindle plate, it was noted that the normal chromosome in the middle position of the chain occasionally had failed to become attached to the spindle fibres. The orientation of the trivalent suggested that some gametes might be formed with one telocentric and 25 normal chromosomes. Consequently the two F_2 plants carrying the extra telocentric chromosomes were pollinated with the $yg_1yg_1yg_2yg_2$ marker line Texas 414, to obtain plants with 52 chromosomes one of which was telocentric.

If the telocentric was derived from the chromosome that carries the Lc_1R_2 loci, as assumed in the discussion above, then a seedling with 25 normal bivalents plus a heteromorphic bivalent, recovered from pollinating the two F_2's with $yg_1yg_1yg_2$ yg_2, should be yellow-green. This, of course, assumes that the Yg_2 locus was located in the arm of the complete chromosome that was deficient from the telocentric and that the genotype of the maternal F_2 plants was $yg_1yg_1 Yg_2 Yg_2$.

From this cross, 492 seed were obtained of which 466 germinated and one seedling was yellow-green in phenotype. Cytological analysis of pollen mother cells of this one yellow-green plant revealed that it had, as expected, 25 normal bivalents plus a heteromorphic bivalent consisting of a normal chromosome and a telocentric chromosome for the short arm. Since the plant is yellow-green and has the large heteromorphic bivalent, this denotes that it is the chromosome with the yg_2 locus rather than that with the yg_1 that is involved in the association. Hence this establishes that the telocentric is homologous with the chromosome carrying the Lc_1 $yg_2 R_2$ linkage group, and that the yg_2 locus is located in the long arm since it is this arm that is deficient. These results also show that the F_2 plants were monomeric with the $yg_1yg_1 Yg_2 Yg_2$ genotype, which is required in order to recover the yellow-green phenotype in the cytologically aberrant plant.

For information on the location of Lc_1R_2 with respect to the chromosome arms, the plant with the heteromorphic bivalent was crossed to T586 which has the yg_1 $N Lc_1 Yg_2 R_2$ genotype. An F_1 with the heteromorphic bivalent would have the Yg_2 allele in the hemizygous state as well as one or both of the $Lc_1 R_2$ alleles depending upon the location of the centromere with respect to these two markers. From this cross, cytological analysis showed that only one plant out of a total of 19 had the heteromorphic bivalent. For determining the arm locations of the $R_2 Lc_1$ loci, this plant with the heteromorphic bivalent was test crossed as male to T414$yg_1yg_2lc_1r_2$. The use of a plant with the yg_1yg_2 genotype allowed the detection of transmission of the telocentric through the pollen, which would be evident by the presence of yellow-green seedlings in the progeny. In this cross, 441 seeds were recovered but only 375 germinated, and none of the seedlings were yellow-green showing that the telocentric was not pollen transmitted. Three hundred and sixty-one of the seedlings were transplanted to the field and scored for segregation of the $Lc_1 R_2$ and N markers. The results are shown in Table 2.

It can be seen in Table 2 that all plants except one (which was determined to be a contaminant as will be discussed later) had the brown lint (Lc_1) and petal spot (R_2) alleles. The most logical explanation for the recovery of only the $Lc_1 R_2$ genotype from the male is that these two loci are in the long arm of chromosome 7, that

is, in the arm not present in the telocentric. Hence, since only the normal chromosome of the heteromorphic bivalent was transmitted by the pollen, all male gametes would necessarily carry the Lc_1 and R_2 alleles. However, it should be pointed out that one of the two loci could be located in the short arm closely associated with the centromere in a region in which crossing over between the locus and centromere is very infrequent.

Table 2. *Segregation of* NLc_1R_2 *in test cross of* $T414nlc_1r_2 \times$
heteromorphic bivalent $F_1(nlc_1r_2 \times NLc_1R_2)$.

$NnLc_1lc_1R_2r_2$	$nnLc_1lc_1R_2r_2$	$nnlc_1lc_1r_2r_2$	Total
189	171	1	361

However, research in progress involving irradiation experiments supports the conclusion that the Lc_1 and R_2 are both located in the long arm. In these experiments, following pollen irradiation of a line carrying the Lc_1 and R_2 markers and the pollination of plants having the lc_1n genotype, three F_1 plants were observed that were deficient for both Lc_1 and R_2 alleles. Cytological analysis of two of these plants revealed them to have a large heteromorphic bivalent (A genome) in which a long arm was absent. The third plant also had a large heteromorphic bivalent in which a long arm had been deleted from one chromosome, but the plant was also heterozygous for a reciprocal chromosomal interchange. Since the cytological characteristics of the chromosomes making up the interchange indicated that no large deletion accompanied the interchange, it is assumed that the interchanged chromosomes are in no way associated with the deficiency of the Lc_1 and R_2 loci. It was noted that the over-all cytological characteristics of the heteromorphic bivalent in each of the three plants were indeed very similar to those observed in the heteromorphic bivalent associated with the $Lc_1yg_2R_2$ linkage group discussed earlier. Therefore it is concluded that all four heteromorphic bivalents involve the same chromosome, chromosome 7, in which the long arm in each case had been deleted. Furthermore, since all four heteromorphic bivalents are consistent in their cytogenetic behaviour, that is, the absence of the long arm is accompanied by the absence of the brown lint and spot loci, it is concluded that both loci are located in the long arm.

The one plant with the lc_1r_2 genotype, that was pointed out earlier to be an exception, could not have originated by pollen transmission of the telocentric because such a plant would also have been yellow-green. This plant was normal green. Furthermore, cytological analysis showed the plant to have 26 normal bivalents at metaphase I, proving again that the telocentric was not involved. Seedlings of selfed seed from this plant segregated 42 green and 3 yellow-green, indicating that $T414yg_1yg_2$, the maternal parent used in the cross, was one of its parents. The evidence suggests however that the plant carrying the heteromorphic bivalent was not the pollen parent of the odd plant because the Lc_1Yg_2 and R_2 loci were hemizygous in the pollen parent and must have been transmitted with the complete chromosome unless pollen contamination had occurred.

The fact that the N locus is now known not to be linked with $Lc_1 yg_2 R_2$ explains certain discrepancies observed between the genetic behaviour of the N and Lc_1 loci in studies reported by Rhyne (1965).

Stephens (1955) in his linkage study found significant evidence of linkage ($P = 0.02–0.01$) between N and Lc_1 and that the gene order was $N Lc_1 yg_2 R_2$. On the basis of this information and on an hypothesis of one chiasma in each arm, Stephens concluded that the Lc_1 locus would be near the centromere. However, monosomic analysis reported in the present study shows conclusively that the N locus is on a different chromosome from the one carrying the $Lc_1 yg_2 R_2$ linkage group. Therefore, the placement of the Lc_1 locus in the vicinity of the centromere and the R_2 locus distal to it is no longer tenable. It is likely that the reverse relationship may actually exist, and that the R_2 locus may be nearer the centromere and the Lc_1 locus at a distal position. This is the positional relationship reported by Endrizzi & Kohel (1966) for the homoeologous linkage group $R_1 Dw$ (red plant body and brown lint) of the D-genome chromosome 16. However, in that study the $R_1 Dw$ linkage group was located in the short arm of chromosome 16, whereas in the present study of the $Lc_1 yg_2 R_2$ linkage group was found to be located in the long arm of the homoeologous chromosome 7. It is obvious from this that these two homoeologues differ in their chromosome structure.

Numerous cytological studies of hybrids between the tetraploids and the diploids with related genomes show no evidence that either homoeologue has undergone a reciprocal interchange as have several other chromosomes in the tetraploids. Therefore, it is very likely that their structural difference is due simply to a shift in the centromere of one of the homoeologues, which could have occurred in several ways. On the assumption that either homoeologue retains the ancestral structure, one of the simplest structural changes that could produce a centric shift, without changing the size of the chromosome and without breaking up the linkage group, would be pericentric inversion. This would not affect the positional relationships of the loci to the centromere, only their distances from it might be changed. It is emphasized that this interpretation is only conjectural.

(iii) *Compensatory recombination*

The published data in cotton which supposedly illustrate compensatory recombination will now be discussed. In all cases, except the one reported by Menzel (1955), the shifts in recombination were detected following the substitution into the tetraploids of chromosome segments from genomes of related species. In such cases the bivalent consisted of heterospecific and homospecific chromosome segments. In Menzel's case, the paired members consisted wholly of heterospecific associations.

It was pointed out earlier that evidence for the phenomenon of compensatory recombination reported in cotton by Stephens (1961) was based on data showing differences in recombinational patterns in the chromosome region extending supposedly from N to R_2. The data were interpreted to show that a decrease in recom-

bination in the yg_2R_2 region was closely compensated for by increases over the NLc_1 and Lc_1yg_2 regions, thereby leaving the total map length of the chromosome unaffected. The increase in 'recombination (49·1) in the NLc_1 interval' over the supposed linkage value of 44·4 was due to normal independent assortment of N and Lc_1 since the two loci are on separate chromosomes. Therefore, the supposed shift of distribution and increase of frequency of chiasmata in this chromosome in Stephens's data is evident only in the Lc_1yg_2 segment and not in an NLc_1 segment because such a region does not exist. The increase in recombination in the Lc_1yg_2 region was small and did not compensate for the decrease in the yg_2R_2 region. Therefore, the data do not really substantiate the phenomenon of compensatory recombination.

Giles (1961) reported data supposedly demonstrating a third case of compensatory recombination in cotton. He worked with the $crLgL$ linkage group which he assumed to have the gene order of $LgcrL$. However, Endrizzi & Kohel (1966) showed that the true gene order is $crLgL$. Re-evaluation of Giles's data in light of the corrected gene order reveals that his results, like those of Stephens, show a decrease in one region (proximal) and an increase in the nearby region (distal), but that the decrease and increase do not compensate one another.

Menzel (1955) presented chiasma counts in heterospecific associations involving structurally altered chromosomes, which in comparison with the controls showed decrease in one region (proximal) and increase in another (distal). However, the shifts in chiasmata were not compensatory.

The only examples known to the authors which have been interpreted as demonstrating compensatory recombination in cotton are those based on two or three tests among several conducted by Rhyne (1960, 1962) involving the $cl_1R_1yg_1$ dw region of chromosome 16. In one case the insertion of a foreign chromosome segment distal to R_1 but including the yg_1 locus decreased recombination in the R_1yg_1 region and increased recombination by a similar amount in the cl_1R_1 region. In a second case, both the decrease and compensating increase may have occurred in heterospecific regions. The other tests were not as clear-cut; however, several of these could logically be interpreted as demonstrating compensatory recombination when these are compared to one of the two control genotypes. Since the data are not consistent, one might assume that those few cases which apparently demonstrate compensatory recombination could be fortuitous.

Genetic data of heteromorphic bivalents involving telocentrics were analysed for the intrachromosomal compensatory phenomenon in cotton by Endrizzi & Kohel (1966). In such bivalents the deficiency of one arm of one chromosome prevents chiasmata from occurring in that arm; consequently, if compensation for exchange occurs in such chromosomes it ought to be detected in the normal arm. However, they did not observe any major shifts in chiasma frequency in these bivalents.

However, the fact that Rhyne's data for the most part, and that of Stephens, Giles and Menzel, show that a decrease in recombination or chiasma frequency in one region is accompanied by an increase in recombination or chiasma frequency

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elsewhere in the chromosome could be accepted as evidence that some degree of compensatory recombination occurs in cotton.

SUMMARY

A monosome was identified as chromosome 7 of the A genome of the tetraploid cottons by its linkage with the $Lc_1yg_2R_2$ markers. This makes eight chromosomes of the tetraploids now identified by monosomes. For over a decade the N locus has been considered to be linked with the $Lc_1yg_2R_2$ loci. Monosomic analysis, however, reveals that N is on a separate chromosome. Studies with a telocentric of chromosome 7 show that the $Lc_1yg_2R_2$ loci are located in the long arm. It is suggested that the R_2 locus rather than the Lc_1 locus is in the proximal position. These findings are discussed in relation to data, particularly that involving the linkage group, which supposedly illustrate the compensatory recombination phenomenon in cotton.

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