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Genetic Analysis of Leaf Differentiation Mutants in Upland Cotton[1]

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ABSTRACT

A series of leaf mutants in *Gossypium hirsutum* L. was tested for allelism and linkage, and three closely linked loci were established on chromosome 15. One locus is represented by a single mutant allele, crinkled leaf (*crcr*), and the other two loci are represented by a multiple allelic series. The two loci with the multiple allelic series were designated as strap leaf and veins-fused. Alleles of the strap leaf locus are rugose ($s^r s^r$), Lubbock-1 ($s^l s^l$), strap leaf (*ss*), normal (*SS*), and Heritable Abnormality-3 ($S^h S^h$). Alleles of the veins-fused locus are veins-fused (*vfvf*), normal (*VfVf*), and Heritable Abnormality-1 ($Vf^h Vf^h$). From independent two and three-point linkage data, we generated a calculated four-locus linkage map as follows:

cr-0.20-*s*-1.20-*vf*-4.90-*Lg* [*Lg* = Green lint]

The seven mutants tested all affect leaf development. Each of the three distinct loci appeared to function differently in leaf development and differentiation in cotton.

Additional index words: **Multiple alleles, Linkage.**

NUMEROUS genetic mutants affect leaf development in American upland cotton (*Gossypium hirtusum* L.). Five of these leaf developmental mutants (Okra leaf, strap leaf, veins-fused, crinkled leaf, and rugose) are located on chromosome 15 (Dilday and Waddle, 1968; Kohel, 1967; Stephens, 1955). Okra leaf has been placed in the short arm of chromosome 15, whereas the other four mutants have been identified as residing in the long arm (Dilday and Waddle, 1968; Endrizzi and Kohel, 1966; Kohel, 1967). Genetic analysis of several of these mutants has shown that they either are members of one multiple-allelic series or are closely linked loci (Hutchinson, 1946; Kohel, 1967). However, it is possible to group the four mutants located in the long arm into three distinct phenotypic classes, thus suggesting the action of separate loci.

Crinkled leaf (*crcr*), one of the most throughly studied mutants in cotton, was reported to be a member of a multiple allelic series (Hutchinson, 1946). Harland (1918) first observed this mutant in 1916 in Sea Island cotton (*G. barbadense* L.). He described it, studied in detail its genetic behavior, and determined that it is was a monogenic recessive (Harland, 1918, 1932, 1933, 1935, 1936; Hutchinson, 1946). At the time of its discovery and early investigation, crinkled leaf occurred only in *G. barbadense*, but Harland (1932) transferred it into American upland cotton (*G. hirsutum*).

Hutchinson and Ghose (1937) found an abnormal plant ('Indore 1') in *G. hirsutum* at Indore, central India; they concluded that the gene controlling the mutant expression was an allele at the crinkled leaf locus. Hutchinson (1946) continued the crinkled leaf study by testing Harland's crinkled leaf and contorta alleles with his mutant from Indore (designated rugose). He proposed a crinkled leaf multiple allelic series in *G. hirsutum*.

In the first published report on genetic linkage in *G. hirsutum*, Harland (1939) stated that crinkled leaf and Green lint (*LgLg*) were linked by five crossover units. Stephens (1955) expanded this linkage group when he reported that Okra leaf ($L^o L^o$), the first genetic marker identified in cotton (Shoemaker, 1909), and crinkled leaf were 41 crossover units apart. Stephens (1955) reported the gene order to be: *Lg*-6.6-*cr*-41.2-L^o. The chromosome carrying these three genetic markers was placed in the D subgenome by Green (1953) and later designated as chromosome 15 by Endrizzi and Brown (1964). Endrizzi and Kohel (1966) used a telosome of chromosome 15 to establish the relationship of the genetic markers to the centromere. They concluded that the gene order and map distance were *cr*-6.3-*Lg*-44.5-centromere-3.2-L^o, thereby differing in gene order from that suggested earlier by Stephens (1955). Wilson and Kohel (1970) found the distance between *Lg*-L^o to be even greater than that reported by Endrizzi and Kohel (1966). They used a heterozygous reciprocal translocation involving chromosomes 4 and 15 and determined that the gene order and distance were *Lg*-43.26-breakpoint-32.58-L^o.

The members of the crinkled leaf multiple-allelic series appeared to increase in number when Kohel (1967) tested five other leaf-development mutants with rugose, which according to Hutchinson (1946) was a crinkled leaf allele. The five mutants [veins-fused, *vfvf* (Kohel and Lewis, 1962); Ragged leaf, *RgRg* (Kohel and Lewis, 1962); and Heritable Abnormalities-1, 2, and 3, HA-1, 2, and 3 (McNamara and Porter, 1950] were chosen because Kohel, Lewis, and Richmond (1965) had previously found that veins-fused, Heritable Abnormality-1, and rugose were linked to Green lint by 13.6, 8.3, and 10.7 crossover units, respectively. Kohel et al. (1965) theorized that veins-fused, Heritable Abnormality-1, and rugose either were alleles at the crinkled leaf locus or represented two closely linked loci. Dilday and Waddle (1968) added a new dimension to the problem when they reported that another leaf mutant, strap leaf (*ss*), was linked to Green lint and veins-fused by 11.1 and 3.7 crossover units, respectively. These results suggest that the long arm of chromosome 15 carries more than one leaf-differentiation gene. Therefore, the main objective of this study was to determine the allelic and linkage relationships of genes affecting leaf development, all of which are located on chromosome 15 of *G. hirsutum*.

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MATERIALS

One Green lint mutant and seven leaf mutants had already been located on chromosome 15 when this study began in 1967. The seven leaf mutants were; crinkled leaf, rugose, veins-fused, strap leaf, Heritable Abnormality-1, Heritable Abnormality-3, and Okra leaf. The first six mutants appeared to be members of one allelic series or closely linked loci. The seventh leaf mutant (Okra leaf) was located in the opposite arm of the chromosome (approx. 76 crossover units from the six leaf-developmental mutants). Besides these marker genes, workers at the Tex. Agric. Exp. Stn., College Station, had collected six more stocks that produced abnormal leaves. Three of these stocks were obtained from H. A. Peacock, Ga. Agric. Exp. Stn., Experiment; two were obtained from B. A. Waddle, Ark. Agric. Exp. Stn., Fayetteville; and one was obtained from L. L. Ray, Tex. Agric. Res. and Ext. Cen., Lubbock.

The six leaf-developmental mutants that are controlled by genes on chromosome 15 can be separated into three types of developmental patterns, as shown by Fig. 1. Crinkled leaf represents the first type (Fig. 1A). The leaves of these mutant plants curl slightly to the dorsal side, the leaf edges have a yellowish appearance, and the midrib and main veins do not differentiate or elongate in synchronization with the leaf lamina. Fig. 1A shows a leaf in which the lack of synchronous development has resulted in transverse folds or a corrugated appearance of the lamina region of the lobe. In the extreme, the leaf margin may be torn by the lack of synchronized growth between vein elongation and lamina differentiation.

Rugose, strap leaf, and Heritable Abnormality-3 characterize the second type of leaf development (Fig. 1B). The main veins of this group originate at the pulvinus and extend to the apex of each leaf lobe. However, they do not grow in a straight line from the pulvinus to the apex, as in a normal leaf. On the contary, the main veins of this group of mutants appear to grow parallel to the midrib for a short distance and then start to diverge at about a 45° angle, as in a normal leaf (Fig. 1D). In this group of mutant plants, the parallel growth of the main veins to the midrib (shown by Fig. 1B) causes the leaf to roll to the dorsal side.

Figure 1C shows the leaf phenotype of veins-fused and Heritable Abnormality-1. These mutants are characterized by leaf development, in which the main veins and midrib originate at the pulvinus and extend to the apex of each leaf lobe. However, the secondary and tertiary veins in the mutant leaves of this group develop into a disorganized mass of veinlets, which reduce the lamina area of the leaf and the angle between the main veins. The disorganized growth of the secondary and tertiary veins could be caused by abnormal differentiation of the veins or to the abnormal growth of cells in the leaf lamina. The reduced angle of the main veins causes the leaf to roll to the dorsal side. Also, the mutant leaf is thicker than the normal leaf.

Several test stocks were used in the genetic analyses, besides the stocks carrying the individual leaf developmental mutants represented in Fig. 1. *Lg* and *cr* were included in the test to obtain three-point linkage information. A Red plant marker stock (R_1R_1 located on chromosome 16) was included to detect possible contaminant plants by providing a dominant marker for outcrossing to F_1 plants. TM-1 (Kohel, Richmond, and Lewis,

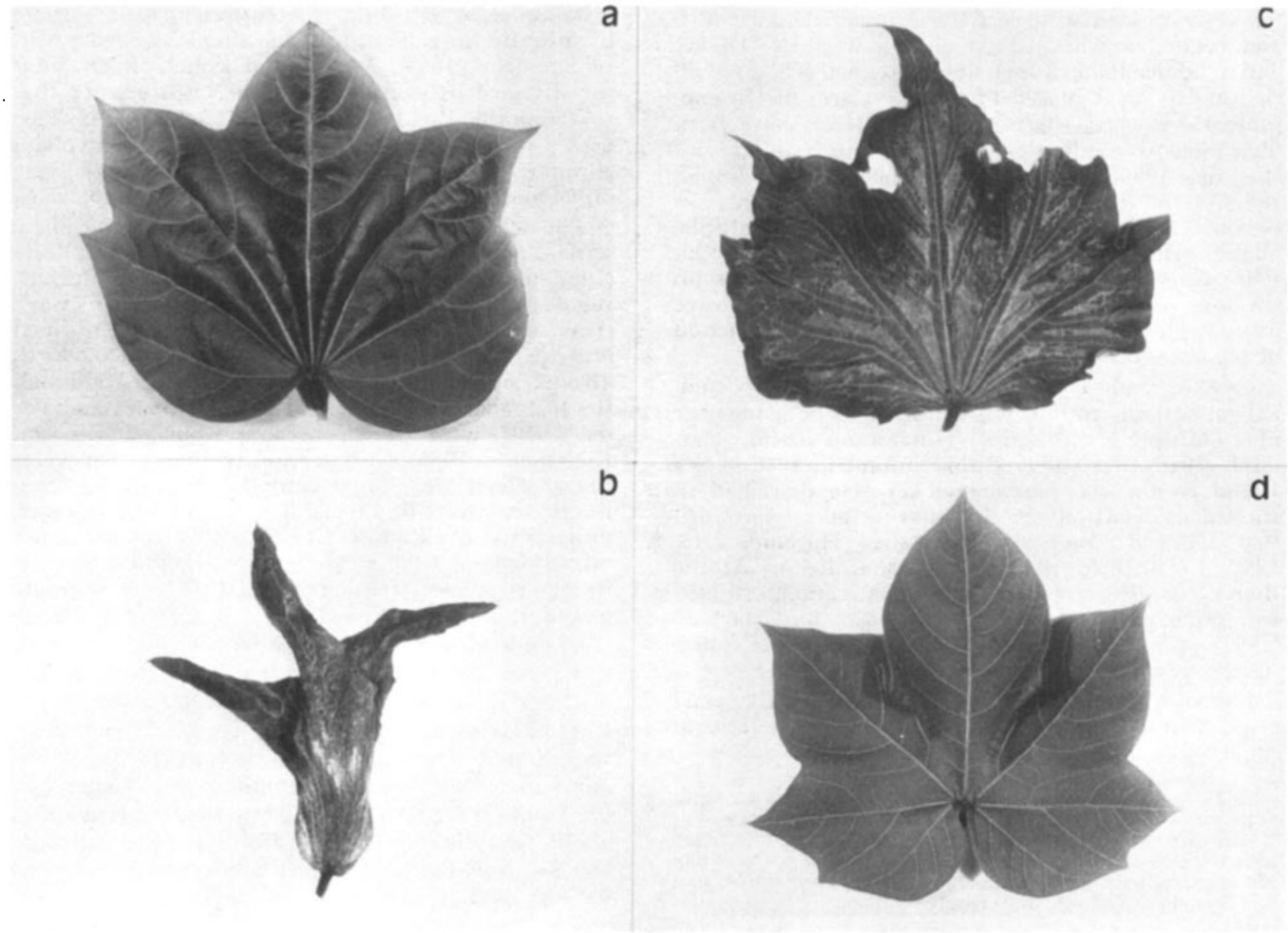

Fig. 1. Crinkled leaf, strip leaf, veins-fused, and normal leaf phenotypes are represented by photographs A to D, respectively.

1970) was included in the test as a standard that would be the "normal" or wild type reference in our determining the inheritance of the newly acquired mutant plants.

METHODS

Seeds and seedlings were propagated by similar methods in each of the 3 years of the study (1967-69). Seeds were planted in 0.18-liter paper cups in a greenhouse at College Station on April 1. Each cup was identified by a numbered wooden stake. Two weeks later the seedlings were transplanted to the genetic nursery. Each plant was spaced 45 cm apart in a 10-m row (20 plants/row).

When the material reached the flowering stage in the Spring of 1967, diallel crosses were made among plants of the lines carrying marker genes and the aberrant plants. Crosses were made also between TM-1 and each of the abnormal-leaf plants that had been collected at College Station. Self-pollinated and cross-pollinated bolls were harvested, ginned, and identified by individual plant or cross. At appropriate times during the growing season, notes were taken on leaf shape, developmental growth habit, and lint color of each plant.

Selected F_1 combinations, their parents, and the monogenic mutant Red plant (R_1R_1) were planted in cups in the greenhouse and transplanted to the field in the Spring of 1968. The *cr-Lg* parental line was crossed with each mutant to determine gene order. The Red plant marker stock was crossed to each F_1 to produce, for linkage studies, populations that contained another check against contamination.

Progenies were tested to verify previous phenotypic classifications or to identify heterozygous plants that could not be identified in the previous generation. Seeds from the plants that had been self-pollinated in the Summer of 1969 were individually packaged and drill-planted directly in the field in 3.5-m progeny rows.

Standard χ^2 analysis were used to test deviations from expected segregation ratios of individual and combinations of alleles. Mather's (1951) maximum-likelihood method was used for computing recombination values.

RESULTS AND DISCUSSION

Complementation Test

The leaf-developmental mutants were crossed in a diallel mating to determine whether they were controlled by genes at separate loci or whether they were alleles (either structural or functional) of the same gene. Table 1 shows the results of the complementation test. It included all the leaf-developmental marker genes [crinkled leaf (*cr*), rugose (cr^l), strap leaf (*s*), Heritable Abnormality-3 (HA-3), Heritable Abnormality-1 (HA-1), and veins-fused (*vf*] known to reside on chromosome 15. It included also all of the abnormal leaf stocks [Georgia-1 (G-1), Georgia-2 (G-2), Georgia-3 (G-3), Arkansas-1 (A-1), Arkansas-2 (A-2), and Lubbock-1 (L-1)] that had been collected at College Station.

Table 1. Complementation tests among developmental mutants of cottons that have been collected at College Station, Texas.

	Phenotypic groups†										
	I	II				III					
Leaf mutants*	cr	cr^l	L-1	s	HA-3	HA-1	vf	G-1	G-2	G-3	A-1
A-2	-	-	-	-	-	-	-	-	-	-	-
A-1	-	-	-	-	-	-	-	-	-	-	
G-3	-	-	-	-	-	+	+	+	+		
G-2	-	-	-	-	-	+	+	+			
G-1	-	-	-	-	-	+	+				
vf	-	-	-	-	-	+					
HA-1	-	-	-	-	-						
HA-3	-	+	+	+							
s	-	+	+								
L-1	-	+									
cr^l	-										

* Twenty F_1 plants in each cross combination. † - = F_1 normal, mutant genes are nonallelic and + = F_1 mutant, mutant genes are allelic.

Table 2. *S* and s^l alleles in backcross populations.

	Segregation, no. of plants				
Population	Normal SS	Intermediate Ss^l	Mutant s^ls^l	Total	χ^2 analysis
$(SS \times s^ls^l) \times s^ls^l$		353	363	716	0.1396
$(SS \times s^ls^l) \times SS$	802	783		1,585	0.1286

The phenotypes of the F_1 plants in this complementation test were strong evidence that at least three separate loci controlled abnormal leaf development in 10 of the mutants tested. Specifically, phenotypic data show that i) crinkled leaf is not allelic to any of the other mutants studies; ii) a second group of mutants (rugose, Lubbock-1, strap leaf, and Heritable Abnormality-3) are alleles; iii) a third group of mutants (veins-fused, Georgia-1, 2, and 3, and Heritable Abnormality-1) are alleles and are independent from the second group; and iv) Arkansas-1 and 2 are not allelic to any of the other mutants tested. The allelic series, established by the complementation test, agrees with the classification of phenotypic groups shown in Materials.

The leaves produced by the abnormal plant obtained from L. L. Ray (Lubbock-1) were phenotypically intermediate between rugose and strap leaf. Therefore, a standard genetic analysis of Lubbock-1 was conducted simultaneously with the complementation test. The inheritance test verified that Lubbock-1 was simply inherited (Table 2). These data showed also that the mutant gene behaves as an incomplete recessive, because the heterozygous plant has leaf lobes that are slightly pointed and curled to the dorsal side.

The classifications derived from the complementation test established that Georgia-1, 2, and 3 and veins-fused are alleles. The plants carrying these genes differed only in height and size; these slight differences were attributed to differences in plant background. Therefore, the three abnormal plants obtained from Georgia were assumed to be the same allele as veins-fused and were not continued in this study. The two abnormal plants obtained from Arkansas were eliminated from this study, because the complementation test indicated that they were not allelic to any of the known leaf-marker genes on chromosome 15.

Gene symbols were assigned to each member of the two multiple-allelic series established by the complementation test. Rugose, Lubbock-1, and Heritable Abnormality-3, which proved to be alleles at the strap leaf locus (*s*), are assigned gene and allelic symbols as follows: rugose (s^r), Lubbock-1 (s^l), strap leaf (*s*), Heritable Abnormality-3 (S^h), and Normal (*S*). This order is chosen because rugose (s^rs^r) is completely recessive to the other alleles at the strap leaf locus, whereas S^hS^h is dominant to the other alleles. At the veins-fused locus, veins-fused is designated *vfvf;* Heritable Abnormality-1 is designated Vf^hVf^h; and the normal or wild type is designated *VfVf*.

The rugose marker stock maintained at College Station can be traced to the one identified by Hutchinson and Ghose (1937). Hutchinson (1946) concluded from his F_1, F_2, and backcross data that crinkled-leaf

Table 3. Segregation of crinkled leaf, Green lint × strap leaf.

Segregation			χ^2 analysis			
Classes	Gametes	No. of plants (pooled)	Sources	χ^2	Heterogeneity	Recombination, %
Single crossover-reg. 1	Cr S Lg	1	cr	0.81	0.64	
Double crossover	Cr S lg	0	s	0.66	0.52	
Single crossover-reg. 2	Cr s Lg	17	Lg	0.20	0.01	
Parental	Cr s lg	238	cr s	488.01*	0.01	0.20
Parental	cr S Lg	223	cr Lg	375.81*	0.43	6.30
Single crossover-reg. 2	cr S lg	13	s Lg	379.32*	0.33	6.10
Double crossover	cr s Lg	0	cr s Lg	0.29	0.01	0.00
Single crossover-reg. 1	cr s lg	0				
Total		492				

* A significant departure of that observed from that expected was assumed when χ^2 was greater than that calculated at the 5% probability level.

Table 4. Segregation of crinkled leaf, Green lint × veins-fused.

Segregation			χ^2 analysis			
Classes	Gametes	No. of plants (pooled)	Sources	χ^2	Heterogeneity	Recombination, %
Single crossover-reg. 1	Cr Vf Lg	5	cr	2.59	0.01	
Double crossover	Cr Vf lg	0	vf	1.45	0.09	
Single crossover-reg. 2	Cr vf Lg	10	Lg	1.71	0.18	
Parental	Cr vf lg	199	cr vf	351.34*	21.07	1.52
Parental	cr Vf Lg	170	cr Lg	295.36*	0.48	6.82
Single crossover-reg. 2	cr Vf lg	11	vf Lg	316.45*	5.80	5.30
Double crossover	cr vf Lg	0	cr vf Lg	0.00	0.04	0.00
Single crossover-reg. 1	cr vf lg	1				
Total		396				

* A significant departure of that observed from that expected was assumed when χ^2 was greater than that calculated at the 5% probability level.

and rugose were alleles at a single locus. However, data collected in the present experiment and presented below in Linkage Tests show that these two genetic markers are closely linked, but are not allelic.

Linkage Tests

Strap Leaf, Crinkled-leaf, and Green Lint Loci. The *crcrLgLg* stock was crossed with s^1s^1 and *ss* to map the strap leaf locus in relation to the two known marker loci. Two types of populations were used in testing this linkage. The F_1 plants were backcrossed to the parental lines and also outcrossed to a Red plant (R_1R_1) marker stock that otherwise carried all normal alleles. The latter cross was made to detect possible sources of contamination.

The χ^2 analyses from the backcross and outcross populations of s^1 and *s* show that the individual genes (*cr, s,* and Lg) segregated as expected, but that the gene combinations (*cr* vs. *s, cr* vs. *Lg,* and *s* vs. *Lg*) did not segregate independently of each other (Table 3). The pooled data from the crosses involving s^1 and *s* were used to evaluate linkage relations. Double recombinant genotypes were not observed in any of the populations. The one recombinant plant observed in the (*cr S Lg* r_1/*Cr s lg* r_1) × (*Cr S lg* R_1/*Cr S lg* R_1) population was self-pollinated. Its progeny segregated for Red plant and Green lint colors, which would be expected from a recombinant plant of the genotype (*Cr S Lg* r_1/*Cr S lg* R_1). The results verified that the plant was a recombinant, not a contaminant. These data produced the following gene map:

cr-0.20-*s*-6.10-*Lg*
— 6.30 —

Veins-fused, Crinkled Leaf, and Green Lint Loci. The same method used in testing the *cr, s, Lg* linkage was followed in testing the *cr, vf, Lg* relationship (Table 4). However, when the plants containing *vf* or Vf^h were backcrossed to the digenic (*crcrLgLg*) marker, the homozygous *LgLg* genotype could not be distinguished from the heterozygous *Lglg* genotype. This problem had not been anticipated, and these plants were not self-pollinated. Therefore, because it was not possible to progeny-test this material with confidence, it was not analyzed. Different genetic backgrounds and environmental variability both seem to have an important effect on lint-color expression in cotton. The populations carrying *vf* and Vf^h grew in a low, wet area of the field.

The χ^2 analysis for three-point linkage data was based on those populations that had been backcrossed to material carrying the *lglg* alleles. Table 4 shows the results of the backcross and outcross populations involving pooled *vf* and Vf^h data. Results from these populations suggest that the individual genes (*cr, vf,* and *Lg*) segregated as expected. However, χ^2 analyses of these data also show that the gene combinations *cr* vs. *vf, cr* vs. *Lg,* and *vf* vs. *Lg* did not segregate independently. The pooled data from the three crosses were evaluated for linkage information, because the χ^2 indicated that these three loci, represented by *cr, vf,* and *Lg,* were linked on chromosome 15. Data in Table 4 resulted in the following three-point linkage map:

cr-1.52-*vf*-5.30-*Lg*
— 6.82 —

Veins-fused with Strap Leaf. Cross combinations involving *vf* with s^1, *s,* or S^h, and Vf^h with s^1, *s,* or S^h, were evaluated to test the hypothesis that the veins-fused and strap leaf loci are about 1.0 to 1.5 crossover units apart. This hypothesis was based on the three-point linkage data of *cr*-0.20-*s*-6.30-*Lg* and *cr*-1.52-*vf*-5.30-*Lg*. The data were placed into three groups; i) populations derived from recessive mutants at one locus crossed to recessive mutants at the other locus, ii) populations derived from recessive crossed to dominant mutants, and iii) populations derived from dominant mutants crossed to dominant mutants.

Table 5. Segregation of the two-point linkage of a recessive allele at the veins-fused locus (*vf*) crossed with recessive allele at the strap leaf (s^1 or *s*) locus.

Segregation			χ^2 analysis			
Classes	Gametes	No. of plants	Sources	χ^2	Hetero-geneity	Recombi-nation, %
Single crossover	s vf	3	s	1.37	0.81	
Parental	s Vf	1,223	vf	1.29	0.23	
Parental	S vf	1,281	s vf	2,483.08*	0.00	0.28
Single crossover	S Vf	4				
Total		2,511				

* A significant departure of that observed from that expected was assumed when χ^2 was greater than that calculated at the 5% probability level.

Table 6. Segregation of the two-point linkage of recessive mutants crossed with dominant mutants (s^1 or *s* with Vf^h and *vf* with S^h) and then backcrossed to the corresponding recessive mutant at the veins-fused or strap leaf locus.

Segregation			χ^2 analysis			
Classes	Gametes	No. of plants	Sources	χ^2	Hetero-geneity	Recombi-nation, %
Single crossover	S vf	1	S	2.40	1.45	
Parental	S Vf	625	Vf	2.57	1.61	
Parental	s vf	682	S Vf	1,304.00*	0.01	0.08
Single crossover	s Vf	0				
Total		1,308				

* A significant departure of that observed from that expected was assumed when χ^2 was greater than that calculated at the 5% probability level.

The pooled recombination value derived from populations involving recessive at one locus crossed with recessives at the other locus (*vf* with s^1 and *s*) was *s*-0.28-*vf* (Table 5). The pooled recombination value derived from the populations involving recessives at one locus crossed with dominants at the second locus (s^1 or *s* with Vf^h plus *vf* with S^h) was *s*-0.08-*vf* (Table 6). No recombination was observed among 727 plants from crosses involving dominant S^h with dominant Vf^h mutants.

The results in Table 1 showed that the mutant alleles resided on chromosome 15 at three distinct loci. The precise position of these three loci was determined with respect to each other and with the other chromosome-15 marker, Green lint. Both two and three-point linkage tests were used in this study to determine whether recombination occurs among the three loci. The two-point linkage test involved an allele at the veins-fused locus crossed to one at the strap leaf locus. The three-point linkage test involved the marker genes; crinkled leaf, Green lint, and one member from either the veins-fused or the strap leaf locus.

The information obtained from the two independent three-point linkage test suggests that the order of the four loci is *cr-s-vf-Lg*. When the data from these two populations are expressed on a common basis for which 6.30 is the distance for *cr-Lg*, then the calculated distances between these loci are *cr*-0.20-*s*-6.10-*Lg* and *cr*-1.40-*vf*-4.90-*Lg*. From these results, it is possible to generate a calculated four-locus linkage map as follows:

cr-0.20-*s*-1.20-*vf*-4.90-*Lg*

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