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1) Superoxide dismutase (SOD) isoenzymes in soybean.

We are using vertical polyacrylamide gel electrophoresis (Davis, 1964) and a staining system modified after Beauchamp and Fridovich (1971) to study superoxide dismutase polymorphisms in the subgenus *soja*. This staining system generates superoxide radical; hence, it is specific for SOD activity. We resolve up to 9 SOD bands in dry or germinating soybean cotyledons, and in leaves. Three zymogram patterns were observed.

1) All 9 bands present (cv. 'Century');
2) Bands 4 and 5 absent (cv. 'Evans');
3) Bands 8 and 9 with a slower migration rate (cv. 'Polysoy').

Based on cyanide-inhibition studies, bands 4 through 9 are the copper-zinc form of the enzyme, which has been shown to be a dimer in all species studied (Fridovich, 1975; Baum and Scandalios, 1981). The zymogram patterns we observe for bands 4-6 and 7-9 are consistent with the model of two sets of dimeric, Cu-Zn isozymes which form interlocus heterodimers. Bands 1-3 are not inhibited by CN; we believe these to be the manganese enzyme, which has been shown to be a tetramer occurring in the mitochondria of all species studied to date (Fridovich, 1975; Baum and Scandalios, 1981).

The observed zymograms correspond closely to the int-oxidase patterns observed on a similar electrophoretic system (Larsen and Benson, 1970). There are also certain similarities to the tetrazolium oxidase zymograms described by Gorman and Kiang (1977). Based on a survey of over 150 soybean cultivars, we conclude that our SOD pattern 1 corresponds to the type-1 TO zymogram described by Gorman and Kiang; likewise, our SOD patterns 2 and 3 are equivalent to their TO zymogram types 2 and 3. Further, under these staining conditions, the *Ep* locus (for seed coat peroxidase) does not produce an achromatic band (band 4 of Gorman et al.).

Previous reports (Gorman and Kiang, 1978) indicated that the type 1 vs. type 2 TO zymograms were conditioned by a single locus, *To4*, with a recessive null allele, *to4*.

The present study provides evidence that the activity visualized by the nonspecific tetrazolium oxidase stain (actually, an artifact in the electron transfer staining system used to detect dehydrogenases) is actually catalyzed by superoxide dismutase isoenzymes. Since the name tetrazolium oxidase has fallen into disuse in isozyme literature, we conclude that the proteins previously referred to as tetrazolium oxidases should be referred to correctly as superoxide dismutases, EC 1.15.1.1. Further, in accordance with guidelines for assigning gene symbols to isoenzyme loci, we propose that the *To4* locus and alleles be changed from *To4* and *to4* to *SOD* and *sod*. The inheritance of the second SOD variant, affecting the mobility of bands 8 and 9, has not been reported.

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2) Inheritance of a miniature mutant in soybean.

Mutant T251 was found by Dr. R. L. Bernard at the University of Illinois in an F_2 progeny from the cross 'Harosoy'[5] x T139. (T139 is a yellow mutant found in 'Illini' in 1936.) T251 is maintained in the Soybean Genetic Type Collection as the heterozygote T251H because of its low seed set. It is characterized by its short and slender stature. It has fewer nodes, shorter internodes, and smaller leaves than do normal plants, but internode length is greater than that of the dwarf mutants. Therefore, its growth type is reduced, resulting in the phenotype of a miniature plant.

Experiments were conducted from 1978 to 1981 at Iowa State University in order to determine the inheritance of T251. Two different crosses were performed: 'Minsoy' x T251, and 'Clark' T/T x T251. Minsoy carries the fr_1 recessive allele for the absence of root fluorescence and the Pb allele for sharp pubescence tip. Clark T/T is an isoline of 'Clark' carrying a homozygous translocation from G. soja PI 101,404B. Clark T/T also carries the T allele for tawny pubescence. T251 is Fr_1 pb t and carries the normal soybean chromosome complement. Homozygous recessive plants of T251 were used in the crosses.

For the Minsoy x T251 cross, F_2 seed were germinated on paper towels for root fluorescence classification, then transplanted into a sandbench in the greenhouse for evaluation of plant height and pubescence tip.

For the Clark T/T x T251 cross, the F_2 plants were grown in the field and each normal stature plant was classified at maturity as homozygous (fertile) or heterozygous (semi-sterile) for the translocation, and harvested separately. The pubescence color was recorded at the same time. Twenty seed from each plant were then grown in the sandbench in the greenhouse to determine if the F_2 plant was heterozygous or homozygous dominant for the gene controlling plant height. Because of the poor viability of the mutant in the field, it was not possible to determine the segregation ratios at the F_2 generation.

The F_2 population from the Minsoy x T251 cross consisted of 1505 normal and 532 miniature types, which fits a 3:1 ratio (χ^2 = 1.35; P > 0.10). For the Clark T/T x T251 cross, 453 rows segregated for the miniature trait, and 249 were uniformly normal. This fits an expected 2:1 ratio (χ^2 = 1.44; P > 0.10). Those data, therefore, suggest that the miniature trait is controlled by a single recessive gene.

Because of the morphological difference between T251 and the dwarf mutants df_2, df_3, df_4, and df_5, it was not considered necessary to perform an allelism test with those mutants, and we, therefore, propose for the T251 mutation the new gene symbol mn (for "miniature").

Table 1. Linkage tests from soybean crosses Minsoy x T251 and Clark T/T x T251

		Minsoy x T251		Total	χ^2
Fr_1 Mn	Fr_1 mn	fr_1 Mn	fr_1 mn		
813	277	264	86	1440	0.099
Pb Mn	Pb mn	pb Mn	pb mn		
1096	395	406	137	2037	0.406
		Clark T/T x T251			
$F*Mnmn$	F $MnMn$	$SS^\dagger Mnmn$	SS $MnMn$		
219	110	234	139	702	1.121
T $Mnmn$	T $MnMn$	tt $Mnmn$	tt $MnMn$		
333	192	120	57	702	1.103

* F = fertile (homozygous for the translocation)
†SS = semi-sterile (heterozygous for the translocation).

As seen in Table 1, an independence chi-square was performed between the mn gene and all other genes segregating from the crosses. No linkage was detected between mn and any of the genes fr_1, Pb, or T. Also, mn was not found to be linked to the breakpoint of the translocation from PI 101,404B.

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3) Genetic studies with T263.

We reported inheritance studies and linkage tests with T263 (Palmer, 1977), a line carrying a gene for dwarfness. We had not completed allelism tests with the other available dwarfs, df_2, df_3, and df_4, at that time. In this report, we give the allelism test results, as well as results of linkage tests of T263 with y_{13}, y_{12}, G, T, and a chromosome interchange from PI 101,404B (*Glycine soja*). On the basis of allelism test results, the Soybean Genetics Committee has assigned the symbol df_5.

Crosses of T263 with the other dwarfs were made and the F_1 plants grown in the greenhouse. The F_2 seed were planted in the field at Ames at 7 seed per meter of row to allow for less competition between tall plants and dwarf plants. Dwarf plants were tagged at flowering and examined again at maturity. No attempt was made to distinguish between the dwarf phenotypes within an F_2 population. About 80 tall F_2 plants and about 20 dwarf F_2 plants from each allelism test were threshed individually. Twenty-five seed were planted as F_2 plant-progeny rows for evaluation. The relationship of observed and expected ratios were evaluated with the standard chi-square test for goodness of fit.

In linkage tests, a 'Clark' isoline homozygous for a chromosome interchange was used as the female parent and T263 plants as male parent. The F_1 plants were semisterile as expected and the F_2 plants were classified for tall/dwarf and tawny/gray but not for semisterility. It is difficult to determine if a dwarf plant is fertile or semisterile in a population segregating tall plants and dwarf plants. Fertile tall F_2 plants and semisterile tall F_2 plants were threshed individually, seed planted, and evaluated as F_2 plant-progeny rows the next year. The F_3 plants identifed F_2 genotypes; recombination value between df_5 and interchange breakpoint was calculated according to Shands (1964).

F_2 linkage tests from crosses between T263 and various mutants are presented using the general relationship that a = XY, b = Xy, c = xY, and d = xy for the gene pairs listed in the form of Xx and Yy. Percentage recombination was obtained from the ratio of products (Immer and Henderson, 1943).

In the allelism tests, all F_1 plants were tall and the observed F_2 ratio fit the expected 9 tall:7 dwarf ratio in each case (Table 1). Progeny of dwarf F_2 plants bred true for dwarf in the F_3. Progeny of tall F_2 plants could be classified as nonsegregating, segregating 3 tall:1 dwarf, and segregating 9 tall:7 dwarf. The observed ratio fit the expected ratio in each case (Table 1). The F_1, F_2, and F_3 data confirm the conclusion that the dwarf gene in T263 is different from df_2, df_3, and df_4.

In the T263 x homozygous chromosome interchange cross, the F_2 plant-progeny rows identified F_2 genotypes $Df_5 Df_5$ and $Df_5 df_5$. Percentage recombination between df_5 and the interchange breakpoint was about 47.6 ± 2.1

T263 had been crossed to trisomics A, B, and C; and F_2 plants (tall and dwarf) had been tagged for flower color and pubescence color (Palmer, 1977). Trait df_5 was not located on trisomics A, B, or C, nor was it linked to flower color. It was linked to T t, of linkage group 1 with 15.4 percent recombination (Palmer, 1977).

Table 1. Expected and observed F_2 phenotypic and F_2 genotypic ratios from soybean crosses between dwarf plants ($df_5\ df_5$) and dwarf plants $df_2\ df_2$, $df_3\ df_3$, and $df_4\ df_4$, respectively

Cross and phenotypes	No. F_2 plants	χ^2 9:7	P	No. F_2 plant-progeny rows			χ^2 1:4:4	P	No. all dwarfs
				Not seg.	3:1	9:7			
$df_2\ df_2$ x $df_5\ df_5$		0.43	>0.95						
Tall	254			8	32	31	0.02	0.99	
Dwarf	210								20
$df_5\ df_5$ x $df_3\ df_3$		0.33	>0.90						
Tall	98			7	32	35	0.37	>0.75	
Dwarf	83								23
$df_4\ df_4$ x $df_5\ df_5$ and		0.39	0.95						
$df_5\ df_5$ x $df_4\ df_4$									
Tall	231			9	38	33	0.36	>0.75	
Dwarf	191								22

Table 2. Genotypic classification for the df_5 gene among fertile plants and semisterile F_2 soybean plants from crosses between df_5 df_5 plants and a homozygous chromosome interchange

Genotype	Fertile *	Semisterile *
Df_5 Df_5	43	47
Df_5 df_5	87	96

*Within each fertility classification, data represent number of F_2 plant-progeny rows evaluated.

Table 3. F_2 linkage tests from crosses between dwarf plants (df_5 df_5) with various soybean mutants

Genes	General phenotypic classes						Linkage phase*
	a	b	c	d	Sum	% R±	
Y_{13} y_{13} Df_5 df_5	270	89	105	32	496	49±3.4	R
G g Df_5 df_5	252	99	91	34	476	51±3.5	C
Y_{12} y_{12} Df_5 df_5	1144	531	528	0	2203	0±2.13	R
T_1 t_1 Df_5 df_5	1530	142	156	375	2203	14.5±0.81	C

*R = repulsion and C = coupling.

In additional linkage tests, df_5 was crossed to y_{13} and to G. Both of these mutants were independent of df_5 (Table 3). T263 was crossed to y_{12} of Linkage Group 1. In the F_2 no df_5 y_{12} plants were identified. All tall yellow F_2 plants and dwarf green F_2 plants were threshed individually and will be evaluated as F_2 plant-progeny rows. R. I. Buzzell (Agriculture Canada) and I are working with df_5, y_{12} and other mutants of Linkage Group 1 to determine gene order.

The F_2 plants in the chromosome interchange experiment provided us with additional Df_5 df_5 - T_1 t_1 linkage data. The percentage recombination was about 14.5±0.81 which agrees well with our previous value of 15.4 ± 1.0. The results with y_{12} and T_1 confirm the conclusion that df_5 is in linkage group 1.

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4) Linkage Group 12.

Weiss (1970a, b, c, d, e) described linkage groups 1 to 7 in soybean. Buzzell (1974, 1979) and Palmer (1977, 1984) have characterized further linkage group 1. Linkage group 8 was reported by Buzzell et al. (1977) and described further by Palmer and Kaul (1983), Sadanaga (1983) and Sadanaga and Grindeland (1984). Linkage groups 9, 10, and 11 were reported by Hildebrand et al. (1980), Kilen and Barrentine (1983), and Devine et al. (1983), respectively.

Broich et al. (1978) noted linkage between seed coat peroxidase level (*ep*) and nonfluorescent roots (*fr-1*). The purpose of this report is to present additional data on this linkage.

Linkage was calculated by the product method as described by Immer and Henderson (1943), where a = number of individuals carrying dominant alleles at both loci (*A - B -*), b = number of individuals carrying a dominant allele only for the *A* locus, c = number of individuals carrying a dominant allele only for the *B* locus, and d = number of individuals homozygous recessive at both loci (Table 1).

Ep has been found independent of *W-1*, *e-3*, *fg-1*, *fg-2*, and *fg-3* (Buzzell et al., 1974) and *f* (Albertsen et al., 1983). *Fr-1* was independent of *rj-1*, *Rj-2*, and *P* (Devine et al., 1983). We suggest that *ep* and *fr-1* are loosely linked and define linkage group 12.

Table 1. Crosses, alleles, F_2 progeny distributions and calculated recombination relationships for soybean linkage tests

Parents and alleles			Number of F_2 plants					Recombination % and SE
			a	b	c	d	Total	
Minsoy	x	Hark						
ep ep fr-1 fr-1		*Ep Ep Fr-1 Fr-1*	240	62	76	36	414	41.6 ± 3.3
Minsoy	x	T239						
ep ep fr-1 fr-1		*Ep Ep Fr-1 Fr-1*	398	113	127	61	699	42.7 ± 2.6
Minsoy	x	Trisomic C						
ep ep fr-1 fr-1		*Ep Ep Fr-1 Fr-1*	172	50	48	22	292	43.7 ± 4.9
		Total	810	225	251	119	1405	42.6 ± 1.8

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5) <u>Molecular analysis of organelle genomes of a cytoplasmically inherited mutant of soybean.</u>

Very little is known about the physical and molecular organization of the genomes of plant organelles. Unlike the genes of a nuclear genome, which can be recombined by selective matings and mapped by recombinational events, the genes on an organelle genome are usually inherited as a unit, solely through a single parent. Therefore, when a uniparentally inherited mutation is observed, it is usually not possible to determine the location of the gene relative to other genes on the organelle genome, nor is it usually possible to determine genetically the organelle genome responsible for the mutant phenotype.

Provided that normal and mutant plants are sibs, we can assume that any difference between "normal" and "mutant" DNA is probably directly related to the molecular lesion causing the mutant phenotype. Thus, if we can screen normal and mutant organelle DNAs and somehow identify the molecular lesion associated with the mutant, we will have a molecular "tag" by which we can identify the coding sequence responsible for the mutant phenotype.

Palmer and Mascia (1980) reported the existence of a cytoplasmically inherited foliar mutant in soybean. This mutant is assigned Genetic Type Collection Number T275, and gene symbol $cyt-Y_2$. $cyt-Y_2$ arose as a chimeric plant and subsequent selfings produced progeny that were yellow ($cyt-Y_2$), green ($cyt-G_2$), and chimeras. Therefore, $cyt-Y_2$ and $cyt-G_2$ are sibs and any sequence heterogeneity between the two would be indicative of the molecular event causing the mutant phenotype.

Our objective in this research was to isolate organelle DNA from normal and mutant plants, digest the DNA with a variety of restriction endonucleases, electrophorese the restricted DNA and analyze the restriction-fragment patterns for restriction-fragment size polymorphisms. In this way, we hoped to locate the mutation responsible for the $cyt-Y_2$ phenotype to either the mitochondrial or the chloroplast genome and to gain information concerning the nature of the molecular lesion causing the mutant phenotype.

<u>Materials and methods:</u> Seed for the organelle-DNA comparisons of $cyt-Y_2$ and $cyt-G_2$ was increased in field plots at Ames, Iowa, and Isabela, Puerto Rico.

Isolation of mtDNA was carried out according to the procedure of Sisson et al. (1978) with the exception that dialysis was against low-TE buffer (0.01 M Tris, 0.005 M Na_2 EDTA, pH 8.0) and deproteinization was accomplished with phenol extractions followed by ether washes. ctDNA was isolated according to our rapid isolation procedure (Shoemaker et al., 1984).

mtDNA was digested with restriction endonucleases BamH I, EcoR I, Hind III, Kpn I, Sma I, and Xho I. ctDNA was digested with restriction endonucleases Ava I, Cla I, BamH I, Hind III, Xho I, and EcoR I. DNA was electrophoresed in 0.7% agarose gels made up in 90 mM Tris, 90 mM boric acid, and 2.5 mM Na_2 EDTA. Electrophoresis was carried out at room temperature for 17 hours at 40 V. ctDNA was electrophoresed in 0.8% agarose gels made up in 40 mM Tris-acetate and 2 mM Na_2 EDTA. Electrophoresis was conducted at room temperature for 18 hours at 50 V. Gels were stained in distilled water containing 0.5 µm/ml ethidium bromide and were photographed over short-wave ultra-violet light using an MP-4 camera with UV filter and Type 665 film.

Results and discussion: We observed no restriction-fragment polymorphism between mtDNAs or ctDNAs of $cyt-Y_2$ and $cyt-G_2$ comparisons. Therefore, we did not identify the organelle genome in which the mutation is located. Our results do, however, provide some valuable information concerning the nature of the molecular lesion causing the $cyt-Y_2$ phenotype.

Restriction endonucleases recognize and cleave a 4-8 base pair sequence of double-stranded DNA (Smith, 1979). The absence of restriction-fragment polymorphism tells us that the $cyt-Y_2$ phenotype is not the result of a base change in the recognition sequence of one of the enzymes used in this study. From the absence of restriction fragment polymorphism, we also know that the $cyt-Y_2$ phenotype is not the result of a large addition or deletion, a translocation, or an inversion asymmetrically involving a restriction site. We can conclude that the $cyt-Y_2$ phenotype probably results from a simple point-mutation. The normal chloroplast ultrastructure of $cyt-Y_2$, and its ability to develop near-normal pigment levels, might suggest that the point-mutation is in a regulatory portion of the organelle genome, rather than in a structural gene. This information may provide physiologists valuable insight for the analysis of the biochemistry associated with chloroplast development and chlorophyll biosynthesis in the $cyt-Y_2$ mutant.

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6) Is the ms_4 male-sterile mutant partially fertile?

The ms_4 male-sterile mutant is inherited as a recessive allele. Plants homozygous for ms_4 are male-sterile; heterozygotes are completely male-fertile. Male-sterility in the ms_4 system results from the absence of cytokinesis following telophase II of microsporogenesis (Delannay and Palmer, 1982). A four-nucleate structure (coenocytic microspore) results that forms a pollen-like wall but does not seem capable of effecting fertilization. However, in many anthers, a delayed cytokinesis may occur (i.e., after pollen-wall deposition). This may result in tetrad-like clusters of cells resembling pollen grains. Delannay and Palmer raised the possibility that these structures may lead to infrequent self-pollination in "male-sterile" individuals. They noted that 75% of the seed harvested from ms_4 male-sterile plants gave male-sterile progeny. Field-grown ms_4 male-sterile plants often set up to 100 seed per plant, much higher than normal for other male-sterile plants grown in Iowa. This report summarizes current efforts to determine whether plants homozygous for ms_4 can yield progeny via selfing.

In 1982, seed was harvested at random from five populations of male-sterile plants grown in the field at Ames, Iowa. The ms_1, ms_2, ms_3, $m\bar{s}_4$, and Beeson mutants were used. The latter is nonallelic to ms_1, ms_2, ms_3, and ms_4. We currently are conducting allelism tests with the ms_5 mutant. The maximum frequency of male-sterile progeny one can expect in seed from male-sterile plants is 50%. This would occur only if male parents were always heterozygous for the locus in question. Pollination in the experiment was uncontrolled; any significant increase in the frequency of male-sterile progeny above the 50% level must be due to some mechanism other than outcrossing. Results (Table 1) show that only in the case of ms_4 was a frequency of male-sterile individuals in excess of 50% attained. This led us to suspect that some form of selfing was occurring.

Table 1. Frequency of fertile and male-sterile individuals in progeny of field-grown male-sterile plants

Parental genotype	Progeny		Percent sterile
	Fertile	Sterile	
$ms_1 \, ms_1$	69	18	20.1
$ms_2 \, ms_2$	47	32	40.5
$ms_3 \, ms_3$	51	18	26.1
$ms_4 \, ms_4$	4	105	96.3
Beeson	33	32	49.2

In addition to the field-grown individuals, 65 progeny of field-grown ms_4 male-sterile plants were greenhouse-grown in the summer of 1983. Of the 65, 62 were male sterile. We wanted to determine whether ms_4 ms_4 individuals would set seed in the absence of pollinators. Of the 62 ms_4 male-sterile plants, 23 produced pods in the greenhouse. The number of seed ranged from one to eight per plant. From the 23 ms_4 plants, 60 seed were obtained. Forty of these germinated and grew to maturity; 38 were male-sterile. The over-abundance of male-sterile progeny from these plants supports the hypothesis of self-pollination by ms_4 ms_4 individuals. Six individuals of the genotype ms_2 ms_2 were included in the same house as controls. Two of the ms_2 plants produced a single seed each. Progeny of the ms_2 plants were both male fertile, indicating that pollen vectors must have gained access to the greenhouse.

We have begun growth-chamber experiments in an attempt to determine whether the environment may influence the tendency toward selfing. Plants were grown under 16-hour daylengths for 3 weeks; daylength was then reduced to 14 hours. Both fluorescent and incandescent lights were used. Results of one trial using three temperature regimes are given in Table 2. The medium temperature (29°/23°C) appears to be optimal for seed production. All male-sterile plants set seed under this temperature regime. In the high temperature environment, not a single male-sterile plant produced seed. Seed was produced by male-sterile plants grown in the cool chamber, but the number, expressed both as mean number of seed per plant and as a percentage of fertile seed set, was less than in the medium environment.

Table 2. Seed production by male-sterile (ms_4) and male-fertile plants grown under three temperature regimes

Temperature (°C) (day/night)	No. of sterile plants	Seeds per plant (mean)	No. of fertile plants	Seeds per plant (mean)	Sterile yield / Fertile yield
24°/21°	6	0.67	3	25.7	2.6%
29°/23°	6	6.50	5	167.0	3.9%
35°/32°	10	0.0	2	64.0	0.0

The mechanism of male-sterility in ms_4 is similar to that of ms_1 (Albertsen and Palmer, 1979). The ms_1 locus is known to have a pleiotropic effect on female reproduction. A high frequency of polyploid and polyembryonic seedlings is recovered in the progeny of ms_1 ms_1 plants (Kenworthy et al., 1973; Beversdorf and Bingham, 1977). We have yet to find a similar response in ms_4. Over 300 seedlings were screened for polyembryony, with negative results. Chromosome numbers were established for 40 progeny of male-sterile plants; all had the normal diploid component of 2n=40.

There are three possible means by which male-sterile individuals can set seed in the absence of cross-pollination. The pollen-like structures noted by Delannay and Palmer may be capable of pollination and fertilization. In some anthers, however, cytokinesis may occur as in fertile anthers, resulting in normal pollen formation. We cannot rule out this possibility; however, we have never observed normal cytokinesis in the hundreds of anthers examined. A third possibility is that apomixis is occurring. We are presently using the chlorophyll-deficient mutant y_{11} in an attempt to discriminate between apomictic reproduction and self-pollination as the origin of the seed produced by male-sterile plants.

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7) Evaluation of *Glycine soja* from The People's Republic of China and the USSR.

A chromosome interchange was suspected by Williams (1948) in a cross involving *Glycine soja* Sieb. and Zucc. PI 101404B. This interchange was confirmed by Palmer and Heer (n.d.).

The objective of the present study was to search for chromosome interchanges among *G. soja* accessions from The People's Republic of China and the USSR.

Crosses were made between these accessions and cultivars of *G. max*, which had noninterchange chromosomes and were designated N/N for normal chromosome structure. Plants were classified for pollen fertility by using a solution of I_2KI. Fertile pollen grains were plump and stained red-brown; aborted pollen grains were shrunken, collapsed, and unstained or only very lightly stained. This latter condition is termed semisterility since the sterility is about 50%. Percentage of ovule abortion was calculated by dividing the number of ovule abortions by the total number of mature seed, seed abortions, and ovule abortions.

The People's Republic of China: Sixteen accessions of *G. soja* were crossed to *G. max* (Table 1). Only two recent accessions gave fertile F_1 hybrids; the remaining 14 gave F_1 hybrids with about 50% pollen sterility. In the four F_1 hybrids examined, ovule sterility agreed with the pollen sterility. F_2 plants from these same four F_1 hybrids gave both the expected fertile plants and the semisterile plants. These 14 accessions were considered to have homozygous interchange chromosomes (T/T).

These 14 accessions were crossed in various combinations, and pollen sterility and, in some cases, ovule sterility were determined (Table 2). All these accessions have the identical chromosome interchange.

USSR: Twenty-one accessions of *G. soja* were crossed to *G. max* (Table 3). Two accessions were found to be a mixture of chromosome structure genotypes. These accessions are PI 423989B and PI 423990A. The −1 and −2 designations in Tables 3, 4, and 5 are ours, and not part of the official Plant Introduction number. Only two accessions had N/N chromosome structure, while 17 were considered to have T/T chromosome structure.

These 21 accessions, plus others from the USSR, were intercrossed. Based upon pollen sterility and ovule sterility, these accessions were considered to have interchange chromosomes (Table 4), or normal chromosomes (Table 5). We have identified additional PIs 423990B, 423992, 423995, and 423999B as having T/T chromosome structure. The data in Table 5 offer confirmation of the N/N or T/T chromosome structure for many of the USSR *G. soja* accessions. All T/T accessions have the identical chromosome interchange. The only cross of two homozygous normal chromosome accessions (PI 423990A-2 x PI 424001) gave male- and female-fertile F_1 and F_2 plants (data not given).

The People's Republic of China - USSR Intercrosses: We made eight different intercrosses between accessions from these two countries that had T/T chromosome structure (Table 6). All F_1 hybrids were fertile. This indicates that all the accessions from The People's Republic of China and the USSR that have homozygous interchange chromosomes have the identical chromosome structure. In fact, the majority of accessions from these countries have this interchange.

Crossing studies with *G. soja* accessions from Korea and Japan and *G. max* cultivars have been initiated. Preliminary results indicate that these accessions have a low frequency of homozygous interchange chromosomes (Delannay et al., 1982).

Table 1. *Glycine soja* from The People's Republic of China: Pollen and ovule sterility of F1 and F2 plants in crosses with cultivated soybean *G. max* as female parent

Plant Introduction	No. of F1 plants	Sterility (%)		No. of F2 plants	Sterility (%)
		Female	Male		Male
65549	5*	47.2	55.1	16	4.4
				10	52.5
101404A	2*	48.1	53.3	4	3.2
				6	51.9
101404B	2*	50.0	50.4	15	5.1
				18	50.9
135624	4*	49.3	51.0	6	7.1
				4	53.2
391587	2		51.2		
407288	8*		50.5		
407290	1		53.1		
407291	1		51.8		
407292	1		52.3		
407294	4*		53.5		
407296	2		52.3		
407299	2		50.0		
407301	1		47.8		
407302	2		48.5		
468916	2		2.1		
468918	2		1.7		

*Includes reciprocal cross.

Table 2. *Glycine soja* from The People's Republic of China: Pollen and ovule sterility of F1 and F2 plants in crosses between homozygous interchange plants

Plant Introduction	Plant Introduction	Number of F1 plants	Sterility (%) Female	Male	Number of F2 plants	Sterility (%) Male
65549	101404A	4*	3.9	3.2	10	1.6
65549	101404B	2*	6.0	1.9	5	1.0
65549	135624	4*	7.9	2.1	10	3.6
101404A	135624	4*	5.8	2.4	10	3.5
101404B	101404A	2	4.1	1.8	5	2.0
135624	101404B	2	10.3	1.7	5	3.5
101404B**	65549	2	10.5	2.3	5	1.0
"	101404A	2	11.7	2.1	5	2.0
"	101404B	2	11.2	1.4	5	4.2
"	135624	2	5.6	1.5	5	1.6
"	391587	2		3.2		
"	407288	4		2.2		
"	407290	2		4.1		
"	407291	2		1.9		
"	407292	2		3.2		
"	407294	2		2.8		
"	407296	2		2.5		
"	407299	2		3.1		
"	407301	2		1.9		
"	407302	2		2.5		

*Includes reciprocal crosses.

**'Clark' near-isogenic line homozygous for a chromosome interchange from *G. soja* PI 101404B.

Table 3. *Glycine soja* from the USSR:　Pollen and ovule sterility of F1
plants in crosses with cultivated soybean　*G. max* as female parent

Plant Introduction	Number of F1 plants	Sterility (%) Female	Male
81762	4		51.2
326581	6*		6.6
326582A	2		52.9
342618B	2		51.4
342622A	8*		47.2
342622B	2		53.2
423988	2	48.4	53.3
423989A	1	53.1	55.1
423989B-1	5*	49.1	52.2
423989B-2	2	6.9	2.0
423990A-1	3	48.7	53.0
423990A-2	1	5.3	1.2
423991	3	49.7	53.1
423993	1	52.1	52.1
423994	2	48.7	49.0
423996	2	47.3	49.1
423997	1	49.0	45.0
423998	5*	46.9	50.6
423999A	1	49.0	52.3
424000	2	47.3	49.9
424001	5*	9.1	4.2
424002	3	47.4	53.0
424003	1	46.8	51.9

*Includes reciprocal cross.

Table 4. *Glycine soja* from the USSR: Pollen and ovule sterility of F1 and F2 plants in crosses between homozygous interchange plants

Plant Introduction	Plant Introduction	Number of F1 plants	Sterility (%) Female	Sterility (%) Male	Number of F2 plants	Sterility (%) Male
342622A	423998	3		1.2		
423989B-1	423991	1	4.5	8.1	5	5.3
423989B-1	424002	1	8.0	6.7	5	4.8
423990A-1	423991	1	1.3	3.1	5	4.9
423990A-1	423995	1	9.1	4.3	5	3.4
423990A-1	423997	1	10.2	2.7	5	4.4
423990A-1	424000	1	1.8	7.4	5	6.9
423990B	423997	1	8.3	4.0	5	3.5
423991	423999B	2*	10.5	2.9	10	4.8
423991	424003	2*	1.7	3.0	10	3.4
423992	424991	1	9.2	2.7	5	5.7
423992	423994	1	8.4	3.1	5	5.6
423992	424999B	1	4.0	2.9	5	5.5
423992	424000	1	7.3	1.7	5	7.6
423993	423995	1	11.0	1.8	5	4.9
423994	423991	1	3.3	1.6	5	4.4
423994	424003	1	4.6	2.2	5	4.8
423995	423992	1	6.8	3.2	5	3.9
423995	423996	1	6.3	5.5	5	7.8
423997	423991	1	11.3	2.1	5	4.3
423997	423998	1	8.3	2.8	5	6.5
423998	423991	1	11.4	0.7	5	5.7
423999A	423997	1	8.1	3.0	6	6.2
423999B	423994	1	7.3	2.1	5	7.2
423999B	423998	1	6.8	2.1	5	7.4
423999B	423999A	1	8.2	1.7	5	9.5
424000	423991	1	8.0	1.7	5	5.5
424000	423995	1	7.6	2.1	5	2.3
424000	423997	1	11.5	1.4	5	6.2

*Includes reciprocal cross.

Table 5. *Glycine soja* from the USSR: Pollen and ovule sterility of F1 and F2 plants in crosses between homozygous interchange plants and homozygous normal-chromosome plants

Plant Intro.	Plant Intro.	No. of F1 plants	Sterility (%) Female	Sterility (%) Male	No. of F2 plants	Sterility (%) Male
423989B-2	423990A-1	1	48.8	53.1	2	7.8
					3	50.2
423989B-2	423994	1	50.9	53.5	1	7.6
					4	54.2
423989B-2	423998	1	50.3	53.0	3	6.9
					8	49.8
423989B-2	423999A	2*	50.5	56.7	8	6.3
					7	51.9
423990A-1	424001	1	48.1	56.6	2	6.5
					1	54.9
423990A-2	423992	1	52.5	55.4	3	4.1
					2	53.2
423990A-2	423994	2*	49.7	49.9	13	6.1
					2	54.9
423990A-2	423998	2*	49.7	52.0	5	5.6
					5	54.3
423990A-2	423999A	2*	49.4	53.6	14	7.3
					1	50.2
423993	423990A-2	1	49.0	51.8	1	4.3
					4	48.8
423997	423989B-2	1	51.3	50.7	1	8.6
					4	53.4
424001	423991	1	48.8	51.1	4	9.7
					1	53.8
424001	423992	1	48.6	52.7	2	2.5
					3	50.0
424001	423994	1	49.1	52.4	3	2.6
					2	49.2
424001	423997	1	49.7	52.1	5	4.0
					5	50.7
424001	423998	1	48.8	51.7	2	2.5
					3	48.0
424001	423999A	1	48.6	52.5	4	4.5
					1	51.2
424002	424001	1	49.4	52.6	7	5.1
					3	51.3

*Includes reciprocal cross.

Table 6. *Glycine soja* from The People's Republic of China and the USSR: Pollen sterility of F1 plants in crosses between homozygous interchange plants

Plant Introduction	Plant Introduction	Number of F1 plants	Sterility (%) Male
101404B**	81762	2	3.3
101404B**	326581	2	1.9
101404B**	326582A	2	4.1
101404B**	342618B	2	1.9
101404B**	342622A	3	0.6
101404B**	342622B	2	2.6
101404B**	423998	3	4.1
407288	342622A	1	5.3

**A Clark near-isogenic line homozygous for a chromosome interchange from *Glycine soja* PI 101404B.

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8) A possible interaction between $cyt-Y_3$ and $y_{20}-k_2$.

Interactions of organelle genomes are a well-documented fact. Interaction can take the form of metabolite and energy exchange, co-production of enzyme sub-units, and co-production of membrane structural and organizational components (Wallace, 1982). Nucleo-cytoplasmic interaction also has been documented for various traits affecting vegetative and harvest indices (Robertson and Frey, 1984), cytoplasmic male sterility (Levings, 1983), and other agronomic characters (Harvey et al., 1972; Kihara, 1982).

Previous results have indicated that a nucleo-cytoplasmic interaction occurs between the soybean nuclear mutant $y_{20}-k_2$ (chlorophyll-deficient, tan-saddle seed coat; Genetic Type Collection Number T253) and soybean cytoplasmic mutant $cyt-Y_2$ (Palmer and de Cianzio, 1984). The nuclear mutant $y_{20}-k_2$

is unique in that it is inherited as a single gene. Under field conditions, with $y_{20}-k_2$ in the presence of $cyt-Y_2$ cytoplasm, no k_2 (tan-saddle seed coat) seed is found. With special care, $y_{20}-k_2/y_{20}-k_2$ plants can be grown under greenhouse conditions. The combination $cyt-y_2$ $y_{20}-k_2/y_{20}-k_2$ is, therefore, a conditional lethal.

Our objective in this study was to determine if a nucleo-cytoplasmic interaction occurs between the soybean nuclear mutant $y_{20}-k_2$ and the soybean cytoplasmic mutant $cyt-Y_3$ (Genetic Type Collection Number T278). We crossed $y_{20}-k_2$ plants reciprocally with yellow branches of $cyt-Y_3$ chimeras. These crosses were advanced to the F_2 for analysis. All progeny containing the $cyt-Y_3$ cytoplasm were grown in the greenhouse under reduced light conditions. The results of these crosses are shown in Table 1.

Table 1. Phenotypes observed in F_1 and F_2 generations from reciprocal soybean crosses of nuclear mutant $y_{20}-k_2$ and $cyt-Y_3$ chimera

Parents			
Female	Male		
$y_{20}-k_2$	X	Chimera	22 green
			1351 green, nonsaddled seed
			344 yellow, saddled seed
Chimera	X	$y_{20}-k_2$	23 yellow
			87 yellow, nonsaddled seed
			21 yellow, early-lethal
			5 green
			332 green, nonsaddled seed
			85 yellow, saddled seed
			9 chimera

In crosses using $y_{20}-k_2$ as the female parent, we saw normal Mendelian segregation (3:1) of $Y_{20}-K_2:y_{20}-k_2$ in the F_2 generation. In the reciprocal cross, sorting-out and transmission of mutant plastids resulted in F_1 progeny that were yellow, green, or chimera. Among F_2 from the green plants, we again saw a 3:1 segregation of $Y_{20}-K_2:y_{20}-k_2$. These results indicate that the mutant $y_{20}-k_2$ trait behaves normally in "normal" cytoplasm.

Among F_2 of the yellow segregants from the chimera X $y_{20}-k_2$ cross, we observed 87 yellow plants with nonsaddled seed, and 21 yellow plants that died at an early seedling stage. Since the ratio of nonlethal, nonsaddled plants to early-lethal plants was 3:1, we presume that early-lethality is the result of the presence of $y_{20}-k_2/y_{20}-k_2$ in $cyt-Y_3$ cytoplasm. These results are similar to those reported from the interaction between $y_{20}-k_2$ and $cyt-Y_2$ (Palmer and de Cianzio, 1984).

The mutant $cyt-Y_3$ is an extremely weak mutant (Shoemaker et al., 1984) and it is possible that the additive effect of two chlorophyll mutations is simply creating a condition that is so detrimental to the soybean that the plant cannot survive. The question as to whether or not this situation is a true nucleo-cytoplasmic interaction or whether it is only a manifestation of an increased genetic load will only be answered by an in-depth physiological/ biochemical analysis coupled with further detailed genetic studies.

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SUMMARY OF LOCUS-TO-LOCUS LINKAGE DATA IN SOYBEAN

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
df_5	y_{13}	270	89	105	32	496	49.0 [†]	3.4 [†]	R	25
df_5	g	252	99	91	34	476	51.0	3.5	C	25
df_5	w_1	952	299	336	113	1700	51.0	1.8	R	23
dt_1	ms_2	175	53	39	21	288	57.4	4.0	R	17
dt_1	w_1	179	49	50	10	288	46.7	4.6	R	17
dt_2	ms_2	118	56	70	4	248	77.0	6.0	C	17
dt_2	w_1	120	54	54	20	248	52.0	4.9	C	17
e_1	ms_1	50	16	25	8	99	50.2	7.6	C	17
e_1	w_1	49	17	27	6	99	56.6	8.1	C	17
e_2	ms_1	58	32	44	6	140	32.4	7.5	R	17
e_2	w_1	66	24	42	8	140	40.6	7.0	R	17
e_3	ep	95	20	28	12	155	40.0	5.4	C	3
e_3	ms_1	54	21	45	11	131	43.9	7.0	R	17
e_3	w_1	60	15	44	12	131	48.7	6.7	R	17
e_3	w_1	221	75	71	25	392	49.5	3.7	C	3,4

Continued ...

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
ep	f	739	243	239	80	1301	51.0	2.0	R	1
ep	l_2	146	42	41	11	240	51.0	3.5	C	5
ep	w_1	393	112	141	32	713	46.8	3.0	R	2
ep	w_1	236	62	75	22	395	48.5	3.7	C	3,4
f	ms_1	101	36	38	12	187	48.3	5.6	R	17
f	w_1	855	211	287	86	1439	23.0	2.4	R	2,17
fg_1	dt_1	270	89	82	29	500	49.1	3.3	C	6,10
fg_1	e_3	131	50	44	11	236	>55	5.2	C	3,7
fg_1	ep	96	28	28	4	156	>55	6.4	C	3
fg_1	fg_2	283	95	80	32	190	52.5	5.2	R	3,4
fg_1	fg_3	362	119	114	37	632	49.8	3.0	R	3,3
fg_1	fg_4	200	71	69	17	357	56.0	4.2	C	3
fg_1	i	188	74	58	25	345	51.0	4.0	R	3
fg_1	p_2	208	63	62	24	357	53.0	3.8	R	3
fg_1	r	130	39	39	14	222	52.0	4.9	R	3
fg_1	w_1	248	78	74	29	429	46.8	3.4	C	3,8
fg_1	w_1	76	22	34	9	141	49.0	6.4	R	4

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
fg_2	e_3	84	31	31	9	155	53.0	6.2	C	3
fg_2	ep	212	65	69	25	371	47.5	3.8	C	3,6
fg_2	fg_3	398	125	134	49	706	47.8	2.7	C	3
fg_2	fg_4	121	48	37	15	221	50.3	5.1	R	3
fg_2	i	182	75	64	24	345	49.0	4.1	R	3
fg_2	i^i	126	36	39	14	215	46.8	4.9	C	6
fg_2	p_2	201	65	69	22	357	50.0	4.0	R	3
fg_2	r	125	44	42	11	222	46.0	5.2	R	3
fg_2	t_1	429	133	135	30	727	54.5	2.9	C	3,6,8
fg_2	w_1	245	77	77	29	428	47.5	3.5	C	3,8
fg_3	e_3	90	30	25	10	155	53.0	5.8	R	3
fg_3	ep	91	27	33	5	156	41.0	6.6	R	3
fg_3	fg_4	247	19	20	71	357	12.0	1.8	C	3
fg_3	i	187	71	59	28	345	53.0	3.9	R	3
fg_3	p	205	62	65	25	357	53.0	3.8	R	3
fg_3	r	126	41	43	12	222	48.0	5.1	R	3
fg_3	t	261	129	104	2	261	13.5	2.2	R	6,8
fg_3	w_1	248	75	73	33	429	>55	3.8	R	3,8

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		AB	Ab	aB	ab	Sum	% R	S.E.	Phase	Reference
		Phenotypic classes								
fg_4	i	188	73	58	26	345	52.0	3.9	R	3
fg_4	p_2	208	61	62	26	357	55.0	3.7	R	3
fg_4	r	129	40	40	13	222	50.0	5.0	R	3
fg_4	t	111	47	63	0	221	0	0.0	R	3
fg_4	w_1	206	62	70	17	335	53.0	4.1	C	3
fr_1	ep	810	225	251	119	1405	42.5	1.8	C	28
fr_1	mn	813	277	264	86	1440	50.1	2.0	C	11
fr_1	t_1	846	292	290	111	1539	51.2	1.9	R	2,27
g	dt_1	245	79	89	26	439	51.5	3.8	C	27
i	ms_2	67	43	29	19	158	52.3	5.8	R	17
i	w_1	477	175	130	66	848	54.5	2.4	R	3,17
k_2	ep	398	142	113	46	699	48.1	2.8	C	25
k_2	fr_1	409	131	116	43	699	48.0	2.8	C	25
k_2	l_1	113	48	39	12	212	54.5	5.4	C	25
k_2	pb	411	115	129	44	699	47.2	2.8	C	25
k_2	t_1	374	125	119	39	657	49.8	2.9	R	2
k_2	t_1	3186	1049	1006	356	5597	49.0	1.0	C	25
k_2	y_9	497	147	141	48	833	52.0	2.5	R	25

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
l_1	fg_1	146	48	61	22	277	48.7	4.4	C	8
l_1	fg_2	151	44	59	23	277	45.9	4.3	C	8
l_1	fg_3	146	50	61	22	279	50.6	4.5	R	8
l_1	k_2	113	48	39	12	212	54.5	5.4	C	2
l_1	ms_2	207	71	80	28	386	49.7	3.8	C	8
l_1	t	161	36	61	21	279	44.0	4.2	C	8
l_1	t	165	26	37	8	236	54.5	4.6	R	2
l_1	w_1	356	117	146	44	663	51.2	3.0	C	8,17
lf_1	ms_2	72	30	12	7	121	55.0	6.4	R	19
lf_1	ms_2	124	40	32	22	218	39.7	4.5	C	17
lf_1	w_1	116	48	40	14	218	52.4	5.2	C	17
lf_2	ms_2	121	39	37	14	211	52.5	5.0	R	17
lf_2	w_1	120	40	40	11	211	47.3	5.3	R	17
ln	ms_2	102	33	33	18	163	52.0	5.7	R	19
lo	ms_2	70	16	32	9	127	51.3	6.6	R	17
lo	w_1	74	12	34	7	127	49.8	6.7	R	17

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
lw_1	ms_2	31	16	20	9	76	50.8	8.5	R	17
lw_1	w_1	36	11	23	6	76	45.0	9.1	R	17
ms_3	t_1	743	247	238	82	1310	50.5	2.8	R	27
ms_3	w_1	170	55	61	16	302	47.2	4.4	R	27
n	ms_2	164	66	47	16	303	44.9	4.6	R	17
n	w_1	175	55	52	21	303	53.5	4.1	R	17
p_1	fr_1	291	91	102	32	516	50.0	3.0	C	14
p_1	ln	579	197	212	63	1053	I	2.4	C	15
p_1	ms_2	231	66	96	27	240	50.7	3.7	C	17
p_1	w_1	223	74	100	23	420	55.4	3.9	C	17
p_1	y_9	785	270	291	87	1427	51.8	2.0	C	14,15
p_2	ln	213	53	65	25	356	44.0	3.7	C	4
p_2	ms_2	40	17	14	6	77	50.3	8.5	R	17
p_2	w_1	253	75	79	46	433	>55	3.8	R	3,17
pb	ep	655	204	213	174	1146	>55	2.36	R	2,27
pb	fr_1	1259	428	420	140	2247	49.7	1.5	R	2,27
pb	t_1	660	217	201	76	1154	48	2.2	C	2,27
pb	mn	1096	395	406	137	2037	50.8	1.4	C	11

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
pc	*ms$_2$*	160	56	37	16	269	52.5	4.4	R	17
pc	*w$_1$*	160	56	43	10	269	44.5	4.9	R	17
pd$_1$	*ms$_2$*	215	69	56	33	373	14.8	3.5	C	17
pd$_1$	*w$_1$*	227	57	69	20	373	47.8	3.8	C	17
pd$_2$	*ms$_2$*	46	13	10	4	73	44.8	8.3	C	17
pd$_2$	*w$_1$*	43	16	11	3	73	54.6	9.2	C	17
ps	*ms$_2$*	91	27	30	8	156	51.4	6.1	C	17
ps	*w$_1$*	99	19	25	13	156	36.3	5.1	C	17
r	*ms$_2$*	80	35	36	9	160	42.5	6.4	R	17
r	*w$_1$*	241	55	73	24	383	53.5	5.7	R	3,17
rj$_1$	*f*	756	271	317	54	1398	40.0	2.2	R	15
rj$_1$	*fr$_1$*	292	114	94	32	532	48.2	3.3	R	14,15
rj$_1$	*fr$_2$*	259	67	97	28	451	51.2	3.0	R	15
rj$_1$	*l*	115	31	44	14	204	48.0	5.0	C	15
rj$_1$	*lf*	108	36	30	12	186	52.6	5.0	R	15
rj$_1$	*ln*	107	28	24	14	173	>55	5.0	R	16
rj$_1$	*p*	115	33	34	9	191	51.0	5.0	C	16

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		AB	Ab	aB	ab	Sum	% R	S.E.	Phase	Reference
rj_1	rps	229	45	74	16	364	49.0	4.0	C	15
rj_1	t	110	41	37	10	198	46.0	5.0	R	13
rj_1	w_1	222	80	72	22	396	47.7	3.8	R	13
rj_1	y_3	391	133	128	50	702	51.8	2.8	R	15
rj_2	fr_1	300	115	116	31	670	55.5	3.3	C	15
rj_2	l_1	55	11	20	6	92	56.0	7.0	R	14,15
rj_4	l_1	132	34	27	5	198	45.0	6.0	R	14
rj_4	p	735	251	248	59	1288	44.8	2.2	R	13,15,16
rj_4	y_9	119	37	27	13	196	44.0	5.0	C	13
rmd	fg_1	159	55	46	13	273	47.2	4.7	R	8
rmd	fg_2	163	50	46	14	273	49.2	4.5	R	8
rmd	fg_3	167	51	34	23	275	39.1	3.9	C	8
rmd	l_1	156	60	39	19	274	53.2	4.4	R	8
rmd	t	171	45	48	10	274	46.7	4.7	R	8
rmd	t	68	16	17	6	107	44.4	6.8	C	7
rmd	w_1	163	53	46	12	274	47.0	4.7	R	8

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
rps	fg_1	160	56	44	14	274	48.4	4.6	R	8
rps	fg_2	167	49	41	17	274	54.8	4.3	R	8
rps	fg_3	161	56	44	14	275	51.2	4.6	C	8
rps	l_1	153	64	42	17	276	44.5	4.5	R	8
rps	rmd	164	51	50	7	272	>55	4.8	C	8
rps	rsv_2	54	12	20	7	93	43.7	7.2	C	9
rps	t	168	44	48	16	276	53.2	4.4	R	8
rps	w_1	169	48	40	17	274	>55	4.8	R	8
s	ms_2	147	49	48	10	254	56.4	5.0	C	17
s	w_1	152	44	50	8	254	57.5	5.1	C	17
st_2	f	713	461	229	166	1569	51.7	1.8	R	1,21
t	df_5	1530	142	156	375	2203	14.5	0.81	C	25
t	ep	1230	379	395	121	2125	51.6	1.6	C	2,24
t	ep	399	114	123	50	686	54.8	2.7	R	2,4
t	f	1619	554	514	183	2870	49.5	1.3	C	1,2,27
t	fg_1	157	64	50	7	278	>55	4.8	C	8
t	mn	333	192	120	57	702	52.8	6.0	C	11
t	ms_2	80	35	36	9	160	42.5	6.4	R	17
t	ms_2	246	92	68	34	440	46.2	3.4	C	17
t	y_9	472	147	166	48	833	48.8	2.6	R	27
ti	Le	59	17	15	5	96	52.0	7.4	R	22

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		Phenotypic classes				Sum	% R	S.E.	Phase	Reference
		AB	Ab	aB	ab					
td	ms_2	249	65	65	18	397	51.7	3.7	R	17
td	w_1	226	88	62	21	397	47.6	3.9	R	17
w_1	ms_1	1268	557	583	60	2468	30.4	1.8	R	23
w_1	ms_1	451	91	87	100	729	27.9	2.0	C	23
w_1	ms_2	3574	1163	1034	372	6143	48.6	0.9	C	17
w_1	t	1792	580	587	234	3193	52.8	1.3	R	2,4,17
w_1	t	171	49	36	16	272	45.0	4.3	C	8
w_1	wm	333	6	4	107	450	2.2	0.5	C	5
w_4	t_1	72	21	23	10	126	55.5	6.2	R	3
w_4	wm	71	22	25	8	126	50.0	6.7	R	3
wm	ms_2	133	34	36	9	212	49.6	5.3	R	17,19
wm	t_1	75	21	20	10	126	42.0	6.1	C	3
y_9	fr_2	1953	624	626	200	3403	49.9	1.2	R	12
y_{10}	w_1	3938	1329	1271	441	6977	49.5	0.8	C	27
y_{12}	w_1	106	35	38	14	193	51.8	5.3	R	27

Summary of locus-to-locus linkage data in soybean *(continued)*

Genes		AB	Ab	aB	ab	Sum	% R	S.E.	Phase	Reference
$y_{20}k_2$	ep	458	154	174	62	848	50.8	2.5	R	26
$y_{20}k_2$	fg_1	228	78	68	24	398	50.4	3.8	R	26
$y_{20}k_2$	t_1	852	247	253	96	1448	46.2	2.0	C	26
$y_{20}k_2$	w_1	3124	975	994	334	5427	51.0	1.0	R	26

(Phenotypic classes header spans AB, Ab, aB, ab)

Genes		a	b	c	d	e	f	Sum	Reference
$Ap^b w_1$	$Ap^c W_1$	21	44	28	11	22	8	134	18
$Sp_1{}^a Dt_1$	$Sp_1{}^b dt_1$	42	83	42	32	20	13	232	21
$Sp_1{}^a Ep$	$Sp_1{}^b ep$	40	91	44	24	18	15	232	21
$Sp_1{}^a Le$	$Sp_1{}^b le$	20	49	23	11	9	8	120	21
$Sp_1{}^a W_1$	$Sp_1{}^b w_1$	44	84	49	31	13	11	232	21
$Ti^1 Dt_1$	$Ti^2 dt_1$	34	83	50	24	24	17	272	21
$Ti^1 Ep_1$	$Ti^2 ep_1$	40	80	55	27	19	11	232	21
$Ti^1 W_1$	$Ti^2 w_1$	42	82	53	25	21	9	232	21

[†]Values calculated by the method of Immer and Henderson (1943). Genetics 28:419-440.

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10) <u>Summary of trisomic linkage data in soybean.</u>

Primary trisomics are useful for locating genes and linkage groups on specific chromosomes through the modification of genetic ratios by the extra chromosome. They also are useful in studying the phenotype and biochemical effects of individual chromosomes.

Three primary trisomics (Palmer, 1976) were used in attempts to locate mutants to one of these chromosomes. No distinct morphological differences exist among the three trisomics, or between them and their respective disomic sibs. Therefore, all parent plants of the trisomics and all F_1 plants were checked for mitotic chromosome number (Palmer and Heer, 1973).[1]

Trisomics A, B, and C were crossed to 29 mutants. Disomic and trisomic F_1 plants were threshed individually. The following year, segregation ratios were determined. Many seedling traits were classified on sandbench-grown plants. Adult plant traits were classified on field-grown plants. We used the standard disomic F_2 ratios, rather than theoretical ratios, as standards for comparison with the observed trisomic F_2 ratios.

A total of 29 mutants, representing 9 of the 13 linkage groups in soybean were used; the data are summarized in Tables 1 and 2. In Table 1, the nine linkage groups represented among the 29 mutants tested are listed. Seven of the linkage groups have been tested against all three primary trisomics.

In Table 2, mutants are listed alphabetically, and segregation ratios between trisomic progenies are compared with disomic progenies. Only one mutant, a chimera that segregates as a single-gene recessive, has been assigned to a chromosome on the basis of trisomic inheritance tests. This is trisomic A.

Genetic studies using trisomic chromosomes in soybeans are underway, but it will be many years before all 20 primary trisomics are identified.

Table 1. Linkage groups, mutants tested, and trisomics tested in soybean trisomic inheritance studies

Linkage group	Mutants	Trisomics tested
1	df_5, t, y_1, y_2	A, B, C
3	g	B
4	ln	A, B, C
5	dt_1	A, B, C
6	y_{11}	A, B, C
7	y_{13}	A, B
8	w_1, ms_1	A, B, C
11	rj_1 f	A, B, C
13	fr_1	A, B, C
13	ep	A, B

Table 2. Chi-square tests of F_2 trisomic segregation ratios
compared with observed F_2 disomic segregation ratios
for various soybean mutants

Mutant	Trisomic	A	B	C	D	chi^2	Ref.
chimera	A	3.69	8439	18.39	3160	492.18**	7
Df5 df5	A	2.85	354	3.69	455	5.12	10
Df5 df5	B	2.69	443	3.35	448	3.83	
Df5 df5	C	3.29	146	2.82	443	2.03	
Dt1 dt1	A	3.42	159	3.21	736	0.53	9
Dt1 dt1	B	3.20	189	3.33	740	0.20	
Dt1 dt1	C	2.96	182	3.23	575	0.79	
Ep ep	A	3.28	278	3.23	127	0.00	9
Ep ep	B	2.66	326	3.07	395	1.50	
F f	A	3.28	672	3.23	1095	0.04	1
F f	B	3.19	742	2.94	922	1.16	
F f	C	3.13	409	2.96	995	0.58	
Fg1 fg1	A	3.35	100	2.45	100	2.03	9
Fg1 fg1	B	2.57	100	3.55	100	1.80	
Fr1 fr1	A	2.88	2659	3.09	1467	1.34	2
Fr1 fr1	B	2.90	1343	3.15	1358	1.69	
Fr1 fr1	C	3.07	1480	3.25	1101	0.64	
Fr2 fr2	A	3.45	1741	3.25	999	0.64	2
Fr2 fr2	B	3.16	1656	3.30	331	0.11	
Fr2 fr2	C	2.99	2058	2.94	1191	0.06	
Fs1Fs2 fs1fs2	A	13.40	1945	15.60	1148	1.50	13
Fs1Fs2 fs1fs2	B	13.40	562	16.20	187	0.36	
Fs1Fs2 fs1fs2	C	14.30	768	13.40	722	0.19	
G1 g1	B	2.85	909	3.28	775	2.74	8
Ln ln	A	3.46	125	3.17	429	0.59	8
Ln ln	B	3.02	233	3.22	435	0.32	
Ln ln	C	2.98	382	2.83	134	0.06	
Ms1 ms1	A	2.89	1293	2.72	387	0.28	9
Ms1 ms1	B	2.86	521	2.43	474	2.60	
Ms1 ms1	C	2.48	386	3.02	380	2.76	

A = disomic ratio;   B = number of disomic plants;
C = trisomic ratio;   D = number of trisomic plants

Mutant	Trisomic	A	B	C	B	chi^2	Ref.
Ms2 ms2	A	2.92	501	2.90	555	0.00	5
Ms2 ms2	B	3.03	483	2.88	751	0.36	
Ms2 ms2	C	2.83	340	3.03	801	0.69	
Ms3 ms3	A	2.48	310	2.85	520	1.93	13
Ms3 ms3	B	2.94	627	3.41	785	3.03	
Ms3 ms3	C	2.88	279	3.09	527	0.48	
Ms4 ms4	A	2.90	2707	2.82	2228	0.33	3
Ms4 ms4	B	3.04	3385	2.84	1933	1.72	
Ms4 ms4	C	3.05	1073	2.98	972	0.09	
Pb pb	A	2.92	2659	2.73	1467	1.30	2
Pb pb	B	2.87	1343	3.20	1358	2.92	
Pb pb	C	2.97	1480	3.00	1101	0.02	
Rj1 rj1	A	2.86	320	2.76	809	0.19	9
Rj1 rj1	B	2.98	803	3.13	818	0.36	
Rj1 rj1	C	2.98	789	2.95	1119	0.02	
Rj4 rj4	A	3.17	313	3.25	1100	0.12	4
Rj4 rj4	B	3.15	514	3.26	1128	0.23	
Rxp rxp	A	3.07	1071	2.88	946	0.73	6
Rxp rxp	B	2.92	762	2.82	680	0.16	
T t	A	3.20	290	3.22	489	0.00	9
T t	B	2.96	1102	3.03	826	0.08	
T t	C	3.31	851	3.03	901	1.31	
W1 w1	A	3.00	3808	2.93	2507	0.26	9
W1 w1	B	2.92	2527	3.08	2139	1.12	
W1 w1	C	2.86	1879	3.04	1290	0.89	
Y9 y9	A	2.99	1852	3.02	1257	0.02	2
Y9 y9	B	2.86	2865	2.81	2127	0.12	
Y9 y9	C	3.16	2328	3.01	1813	0.80	
Y10 y10	A	3.32	2301	3.01	1440	2.59	8
Y10 y10	B	3.10	2228	3.14	1588	0.04	
Y10 y10	C	3.06	1278	3.00	776	0.05	
Y11 y11	A	2.91	824	2.75	1283	0.80	8
Y11 y11	B	3.20	1502	3.17	921	0.01	
Y11 y11	C	2.74	1550	3.64	881	12.09*	

A = disomic ratio; B = number of disomic plants;
C = trisomic ratio; D = number of trisomic plants

Mutant	Trisomic	A	B	C	B	chi^2	Ref.
Y12 y12	A	3.39	411	3.46	183	0.01	9
Y12 y12	B	3.01	333	2.74	161	0.28	
Y12 y12	C	3.35	209	2.91	227	0.85	
Y13 y13	A	3.45	365	3.68	604	0.42	8
Y13 y13	B	2.77	279	3.23	1965	8.39*	
Y18 y18	A	3.22	308	3.41	474	0.27	8
Y18 y18	B	3.99	2573	3.67	1490	1.75	
Y19 y19	A	3.86	1243	3.26	711	3.65	9
Y19 y19	C	3.56	1501	3.08	528	2.05	
Y20K2 y20k2	A	3.51	415	3.28	394	0.32	11
Y20K2 y20k2	B	3.11	1102	2.97	826	0.33	
Y20K2 y20k2	C	3.49	763	3.54	618	0.02	

A = disomic ratio;   B = number of disomic plants;
C = trisomic ratio;   D = number of trisomic plants

** = Statistically significant (P = .01)
 * = Statistically significant (P = .05); however, based on the
    observed ratios, these are not believed to be biologically
    significant. These mutants are being tested further.

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